Predation can select for later and more synchronous arrival times in migrating species

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For migratory species, the timing of arrival at breeding grounds is an important determinant of fitness. Too early arrival at the breeding ground is associated with various costs, and we focus on one understudied cost: that migrants can experience a higher risk of predation if arriving earlier than the bulk of the breeding population. We show, using both a semi-analytic and simulation model, that predation can select for later arrival. This is because of safety in numbers: predation risk becomes diluted if many other individuals, either con- or heterospecific, are already residing in the area. Predation risk dilution can also select for more synchronous arrival because deviating from the current population-wide norm to earlier or later dates leads to higher predation risk or to failures in territory acquisition, respectively. The fact that selection for high arrival synchrony can in some cases be more important than selection for a specific date (early or late) within the season is an example of an 'evolutionary priority effect': whichever strategy – in this case a particular arrival time – becomes established in a population can remain stable over long periods of time; there are many possible equilibria (multiple stable states) which the population can remain at. Mixed arrival strategies are also possible under some circumstances.

In migratory species, the date of arrival to the breeding grounds is a key biological event that has received increasing interest in the recent literature, both as a case-study of life-history evolution (Alerstam et al. 2003) and due to its response to climate change and its role as an indicator of warming (Pulido 2007). Arrival date is known to be the result of a tradeoff between multiple selection pressures. Early arrival is often beneficial in terms of male competition for territories and females (Kokko 1999, Morbey and Ydenberg 2001, Smith and Moore 2005), female competition for breeding locations (Kokko et al. 2006), reproductive success (Bensch and Hasselquist 1991, Hasselquist 1998, Teder 2014), egg-resource gathering (Nager 2006, Descamps et al. 2011, Kristensen et al. 2015), and to guarantee temporal synchrony between nestling needs and resource phenology (Both et al. 2006, Jonzén et al. 2007). However, early arrival also incurs costs if it exposes arriving individuals to harsh early-season conditions; escaping such conditions is the primary reason why migration occurs at all, thus part-time exposure to these costs can be detrimental (Newton 2008, McKinnon et al. 2010).

Predation at the breeding grounds is a significant factor affecting migratory birds (Martin 1995, Newton 1998, Fontaine and Martin 2006, Krams et al. 2014), yet the effect of predation upon adults on arrival timing has not received much attention in the migration literature (Fontaine and Martin 2006, Low et al. 2010, Chapman et al. 2011). The significance of predation for migratory populations is highlighted by findings that migrating to breed further north can lower the risk of nest predation (McKinnon et al. 2010), and that phenology can be affected by both the predation of adults at stop-over sites (Jonker et al. 2010, Hope et al. 2014), and nest-predation of juveniles (Borgmann et al. 2013, Du et al. 2014). However, given that predation in general is hard to measure, relatively little is known about the effects of predation on adults upon arrival at breeding grounds as a cost of early arrival (Sillett and Holmes 2002, Abrams and Ginzburg 2000, Newton 1998). The question of the effect of predation upon adults at the breeding grounds upon phenology remains therefore largely open.

Migratory species are exposed to predation risk in non-breeding areas, during migration, and in breeding areas (Sillett and Holmes 2002, Lank et al. 2003), but these risk are likely to differ for the following reason. In non-breeding areas, migrants are likely to form a smaller fraction of all potential prey than in breeding areas, at least early in the migration season. This is true as long as we assume that the wintering grounds have a higher total abundance of individuals than breeding grounds at the end of winter; as

a consequence, moving one individual from the former to the latter means that it now forms a larger proportion of the local prey community. Resident predators in breeding areas, that have been sustained by those prey resources that are available throughout the year, can (partially) switch to exploiting migratory species soon after they appear. This creates an interesting dynamic for arrival times within a population of migrants, when their arrival adds a significant number of individuals to the prey community at the breeding grounds early in the spring. This creates the potential for the focal species to experience frequency-dependent predation analogous to the Darling Effect for predation upon juveniles which can select for synchronous breeding (Gochfeld 1982, Ims 1990, Langerhans 2007).

Consider (as a simplification which we will relax below) that a local bird predator takes one bird per day, and that there is an overwintering species with 50 local individuals having survived the winter. The first-arriving individual of the migratory species has mortality risk of 1/51 (assuming it is as easy for the predator to catch as the resident species) if no conspecifics arrive on the same day. If it arrived one day later when three more conspecific individuals also arrive, its risk on that day is now 1/(49 + 4) = 1/53 (note that the local community was diminished by 1 individual in the meantime). This example shows that 'safety in numbers', i.e. the predator dilution effect (Bednekoff and Lima 1998, Connell 2000, Jones 2003), can select for later arrival and potentially also for more synchronous arrival (Ims 1990). Obviously, we must also take into account that there will also be some daily mortality elsewhere than on the breeding grounds; our model below integrates across site-dependent mortality on all days of the potential arrival time period. For now, it is sufficient to note that the frequency-dependent nature of mortality risk, as described above, is probably less strong in milder conditions (the overwintering grounds) where the prey community is likely to be more diverse and abundant throughout the year.

In this study we aim to quantify the likely effects of predation upon arrival phenology by varying the likelihood of being predated in two types of models: a simulation approach where we allow for a population containing individuals with many different arrival time strategies, and a semi-analytical approach where we quantify the success of a mutant in an otherwise monomorphic population. Both models are based on a hypothetical migratory species in which intraspecific competition for territories yields benefits for early arriving individuals. We build our models using the biological example of migratory birds, however the results are general to any system in which the benefits of early arrival is traded against frequency-dependent selection (e.g. emergence time distribution in insects; Williams et al. 1993, Pompanon et al. 1995). In both of our models, we replace the above simplistic calculation of daily risk (above) with predation risk that is based on a type II functional response of the predator (Murdoch 1973) when faced with two types of prey: the resident community of prey which the predator has been diminishing over the winter, and the newly arriving migrants.

Models

Simulation model

The simulation model denotes the migrating species as S1 and the resident species as S2. Note that the resident 'species' may comprise an entire community of resident animals; its precise composition does not matter for our present purpose, which is to examine the effects of predation and the availability of alternative prey on migration timing within the focal species S1.

Each S1 individual has a haploid locus δ that determines arrival time at the breeding ground within the range of options which we denote as days $T = 1 \ldots T_{max}$. The range of locus (δ), $0 \leq \delta \leq 1$, is interpreted such that the lowest values correspond to arriving at the earliest possible arrival day $T = 1$, and the highest value corresponds to $T = T_{max}$. To be precise, an individual arrives at time T whenever its locus (δ) is within the interval $\left[\dfrac{T-1}{T_{max}}, \dfrac{T}{T_{max}}\right]$. For example, if $T_{max} = 5$, those individuals whose locus (δ) falls between 0.4 and 0.6 arrive at the breeding ground on day 3.

Selection for early arrival operates via territory quality: we assume that early arrival gives priority access to better territories. There are V territories of which a proportion α are of good quality, yielding higher reproductive success for their owners. The remaining territories are of lower quality.

We denote total predatory effort by X, and assume that predation is the only force potentially selecting against early arrival. In reality, of course, costs of too early arrival can manifest themselves in many ways, not only through predation. We justify our choice with the conceptual clarity it produces: in the absence of predators (X = 0), we should see individuals arriving as early as possible, and deviations from this must be due to the effects of predation.

Each generation starts with arrival of the focal species S1, and we track the dynamics of arrived individuals for each of the T_{max} time steps (Fig. 1a). At the start of each time step those individuals arrive whose locus (δ) matches the current time, as explained above. Territory acquisition proceeds as follows for each time step T. If there are more good quality territories than individuals arriving, all individuals are assigned to a good quality territory. If there are more individuals arriving than there are good quality territories, the good quality territories will be randomly divided among the arriving individuals and the remaining individuals acquire a poor quality territory (if available). When there are more individuals arriving than there are territories, both the good and poor quality territories are randomly divided among the arrivees and the remaining individuals become floaters, i.e. they are at the breeding ground but have no territory. A floater can become a territory owner in a subsequent time step as territories become available due to predation, in which case floaters compete with arriving individuals for available territories. They acquire territories with equal probability to newly-arrived individuals. When day $T = T_{max}$, territories that have become available due to predation will be filled by randomly chosen floaters. Some territories remain without an owner if there are fewer floaters than available territories at day $T = T_{max}$.

(a) Dynamics over 1 year, full simulation

(b) Dynamics over 1 year, semi-analytic simplification
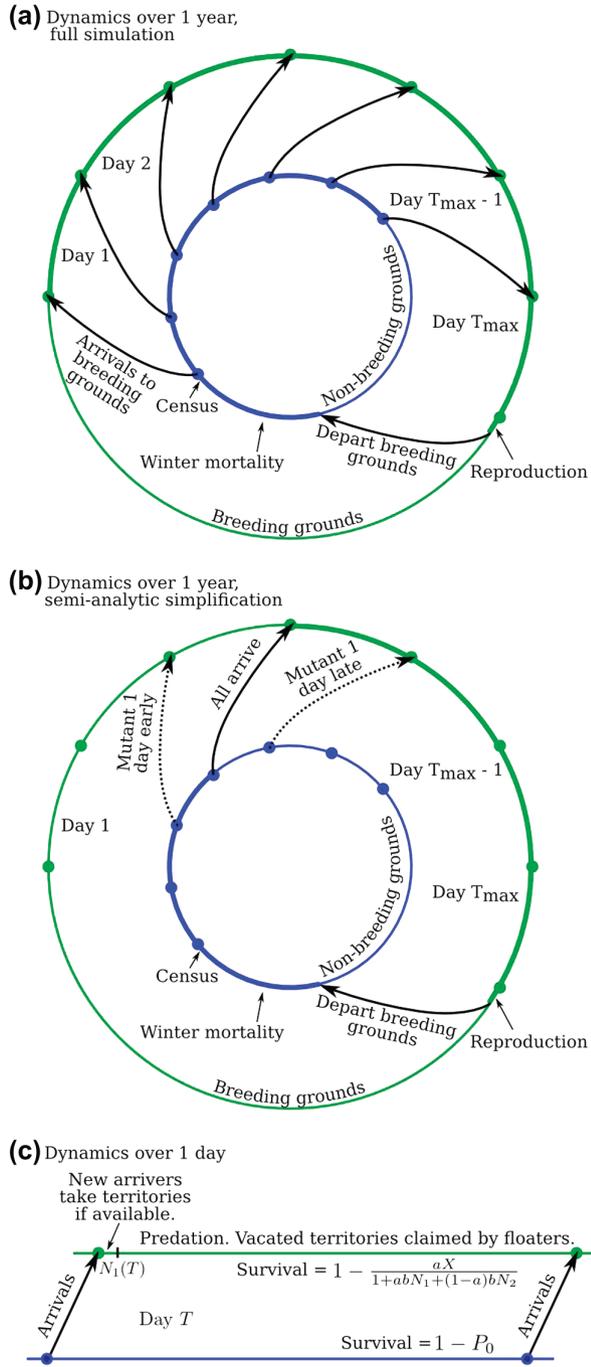
(c) Dynamics over 1 day

Figure 1. Diagram representing (a) the simulation model and (b) the semi-analytic simplification, (c) shows the daily arrival dynamics at the breeding ground for the focal species (S1). Starting after the census, individuals in the simulation model depart from the overwintering grounds (in blue) and migrate to the breeding ground (in green) on the day determined by their arrival time allele (δ). In the semi-analytical model the vast majority of the population arrives on day T except mutants who arrive a day earlier or later (where possible). Both models incorporate a daily mortality throughout the arrival time period, with survival probabilities shown in (c) both for individuals that have not arrived yet (above the blue line) and for individuals that have (below the green line). After arrival of all individuals, reproduction occurs in both (a) and (b), after which all individuals of species S1 migrate back to the overwintering ground where they face winter mortality before they repeat the cycle.

Each time step T exposes individuals that have arrived on the breeding grounds to predation (Fig. 1c). Predation occurs according to a type II functional response with two different types of prey items (Murdoch 1973). This means that at each time step T, the number of the focal species (S1) and resident species (S2) that are taken by predators depend on the number of individuals alive at the breeding grounds, denoted $N_1(T)$ and $N_2(T)$ respectively. Daily predation on the focal species (S1) is assumed to affect floaters and territory owners equally. The number of individuals of the resident species (S2) at the beginning of the season, day $T = 1$, is assumed to be constant, denoted N_2^* (i.e. $N_2(1) = N_2^*$). Individuals of our focal species (S1) that are not yet on the breeding grounds also experience a daily mortality risk (p_0).

A type II functional response specifies the number of individuals predated on a given day: for the focal species (S1) this is $P_1(T) = \dfrac{aN_1(T)X}{1 + abN_1(T) + (1-a)bN_2(T)}$ and for the resident species (S2), $P_2(T) = \dfrac{(1-a)N_1(T)X}{1 + abN_1(T) + (1-a)bN_2(T)}$ (Murdoch 1973). Here a ($0 \leq a \leq 1$) is the predator preference for the focal species (S1) over the resident species (S2) (e.g. one species might be easier to catch than the other), such that $a = 0.5$ indicates no preference, and $a > 0.5$ indicates a preference for the focal species (S1). X reflects total predatory effort, and it is proportional to predator abundance and the time they spend foraging. The handling time b includes both time spent finding and handling prey.

The interpretation of number of individuals predated on a given day of the focal species ($P_1(T)$) and the resident species ($P_2(T)$) is problematic for non-integer values: if we always rounded to the nearest integer to determine the number of individuals taken, then low daily predation pressures would lead to consistent rounding down to zero and the predator never eats. Therefore the fractional portion of P is treated probabilistically, e.g. $P_1 = 0.3$ means that no focal species (S1) prey are taken in 70% of cases and one prey in 30% of cases, and $P_1 = 2.9$ means that two prey are taken in 10% of cases and three prey in 90% of cases. The individuals of the focal species (S1) that are predated are randomly selected from all individuals, i.e. territory owners as well as floaters, that have arrived on the breeding ground. For the resident species (S2), the number of individuals that are predated are simply deducted from the current numbers (using the same rounding rules as for the focal species (S1)): $N_2(T+1) = N_2(T) - P_2(T)$. Not yet arrived individuals of the focal species (S1) are assumed to have a daily mortality risk p_0 that is applied independently for each such individual (Fig. 1c).

We repeat the above procedure for each day $T = 1$ to T_{max}, and then the breeding season commences. Reproductive success on a given territory is Poisson-distributed with mean R_G for good territories and R_P in poor territories ($R_G > R_P$). Offspring inherit the arrival time locus δ from their parent (i.e. asexual reproduction), but this allele may mutate in offspring with probability μ. When mutation occurs, offspring arrival time locus (δ) is changed by a value taken from an uniform distribution with range $[-\sigma, \sigma]$ (if the new value is below 0 or above 1, the new value is set to 0 or 1, respectively). The reproduction of the resident species (S2) is not

tracked explicitly, each generation starts with N_2* individuals of the resident species (S2), as we assume no significant interactions with the focal species (S1) outside the period of interest (the shared predator's effects during the spring migration).

After reproduction all focal individuals (S1) migrate, vacating all territories. Before the start of the new spring migration season each individual dies with probability γ, irrespective of the value of locus (δ). Individuals that survive, i.e. parents and their offspring, form the $N_1(1)$ of the next spring migration season, leading to overlapping generations.

Note that the same individual can go through three types of mortality risk: 1) γ, the mortality outside the season that we consider here (outside $T = [1, T_{max}]$), which is not impacted by migration timing, 2) a daily mortality risk p_0 for individuals who have not yet arrived on the breeding ground (during $T = [1, T_{max}]$), and 3) frequency dependent mortality for individuals that have arrived at the breeding ground. The same individual can experience all these risks over a year, but only one type of risk on a given day.

Each simulation is initiated with a specified $N_1(1) = N_1$* individuals of the focal species (S1) at the start of the first generation (and N_2 individuals of the resident species (S2) as in the beginning of every spring season). The arrival time locus δ is initially normally distributed with mean ε and interval $[\varepsilon - \theta, \varepsilon + \theta]$. The simulations were run for 5000 generations. The results are shown as the average of 10 randomly chosen replicates. Parameter values used (unless varied) are given in Table 1.

Semi-analytic model

The semi-analytic model simplifies the individual-based simulation model by assuming a monomorphic population (Fig. 1b), i.e. one in which all individuals arrive to the breeding grounds on the same day $\widehat{T}$. We are interested in finding out which days (between day T and T_{max}) are evolutionarily stable, depending on variation in predation pressure.

As we are interested in exploring the microevolutionary dynamics of the system, we use three simplifying assumptions commonly invoked in eco-evolutionary models (Geritz et al. 1998). First, we assume that the microevolutionary

timescale is longer than the population dynamic timescale, such that the population can be assumed to be at population-dynamic equilibrium. Second, we assume that the initial number of mutant individuals is small enough that their effect on the dynamics and fitness of individuals in the population using the prevailing arrival strategy can be ignored. Third, we assume that the mutations themselves are small, such that we need only consider the fitness of mutant arrival day strategies that are either one day earlier or one day later than the prevailing strategy.

As in the simulation model, the daily population dynamics for the alternative-prey species during the predation and territory-allocation period is described by

$$N_2(T,\widehat{T}) = \begin{cases} N_2^*, & \text{if } T=1 \\ N_2(T-1,\widehat{T})\left(1 - \dfrac{(1-a)X}{1+abN_1(T-1,\widehat{T})+(1-a)bN_2(T-1,\widehat{T})}\right) & \text{otherwise} \end{cases} \quad (1)$$

For the focal species, the dynamics are described by

$$N_1(T,\widehat{T}) = \begin{cases} 0, & \text{if } T<\widehat{T}. \\ (1-p_0)^{\widehat{T}-1}N_1^*(\widehat{T}), & \text{if } T=\widehat{T}. \\ N_1(T-1,\widehat{T})\left(1 - \dfrac{aX}{1+abN_1(T-1,\widehat{T})+(1-a)bN_2(T-1,\widehat{T})}\right) & \text{otherwise} \end{cases} \quad (2)$$

where $N_1^*(\widehat{T})$ is the species' population size evaluated at steady-state (which depends upon the prevailing arrival-day strategy), in accordance with our first assumption. At the end of the predation and territory-allocation period, the number of individuals remaining to reproduce is

$$M_1^*(\widehat{T}) = N_1(T_{max},\widehat{T})\left(1 - \dfrac{aX}{1+abN_1(T_{max},\widehat{T})+(1-a)bN_2(T_{max},\widehat{T})}\right) \quad (3)$$

The yearly population dynamics can then be described by

$$N_1^*(\widehat{T}) = (1-\gamma)(M_1^*(\widehat{T}) + M_G R_G + M_P R_P) \quad (4)$$

where M_G (M_P) is the number of individuals holding a good (poor) territory at the end of the predation and territory-allocation period. N_1*$(\widehat{T})$ and M_1*$(\widehat{T})$ can be obtained by numerically solving Eq. 4 for different prevailing arrival-day strategies ($\widehat{T}$) (see data accessibility). We are interested in the scenario in which territory competition is a strong selective force and the population contains floaters, and so for the parameter range explored the population is only viable when there is complete occupancy of both types of territories,

Table 1. Parameter values used in the simulation model (unless varied).

Parameter	Description	Standard value (unless varied)
a	predator preference	0.5
X	total predatory effort	850
b	handling time of prey by the predator	5
N_1*	number of individuals of the focal species (S1) at the start of the first generation	1000
N_2*	number of individuals of the resident species (S2) at the start of each generation	1000
T_{max}	number of arrival days	5
p_0	daily mortality for individuals of focal species (S1) that have not yet arrived (during days $T - T_{max}$)	0.05
γ	mortality outside of breeding season	0.1
V	number of territories	500
α	proportion good quality territories	0.5
R_G	reproductive success in good quality territory	2
R_P	reproductive success in poor quality territory	1
ε	mean of arrival time locus (δ) during the first generation	0.5
θ	maximum deviation from mean for arrival time locus (δ) during the first generation	0.5
μ	mutation probability for arrival time locus (δ)	0.1
σ	distribution of change to arrival time locus due to mutation	0.01

therefore M_G equals the number of good territories V_G, and likewise $M_P = V_P$.

The invasion fitness of the mutant with arrival-day strategy T' entering a population with prevailing arrival-day strategy $\widehat{T}$ is

$$W(T', \widehat{T}) = (1 - \gamma)p_s(T', \widehat{T})(1 + p_G(T', \widehat{T})R_G + p_P(T', \widehat{T})R_P) \quad (5)$$

where $p_s(T', \widehat{T})$ is the mutant's probability of survival, and $p_G(T', \widehat{T})$ $(p_P(T', \widehat{T}))$ is the probability that the mutant will obtain a good (poor) territory. In accordance with the second assumption, the mutant at invasion has no influence upon the fitness of individuals in the population using the prevailing strategy, and so their fitness is $W(\widehat{T}, \widehat{T}) = 1$, and the mutant can successfully invade if its invasion fitness is $W(T', \widehat{T}) > 1$.

The probability of an individual surviving a given day T is

$$S(T, \widehat{T}) = \begin{cases} 1 - p_0, & \text{if not yet arrived at breeding grounds.} \\ \max\left(0, 1 - \dfrac{aX}{1 + abN_1(T, \widehat{T}) + (1-a)bN_2(T, \widehat{T})}\right), & \text{if at breeding grounds} \end{cases} \quad (6)$$

In accordance with the third assumption, we need only consider mutants with arrival-day strategies one day earlier or one day later than the prevailing strategy.

The mutant's survival probability is the same as the prevailing strategy modified by the one more and one fewer days spent at or away from the breeding grounds. Therefore, for the mutant arriving one day earlier than the prevailing strategy

$$p_s(\widehat{T} - 1, \widehat{T}) = \frac{M_1^*(\widehat{T})}{N_1^*(\widehat{T})} \frac{\max\left(0.1 - \dfrac{aX}{1 + (1-a)bN_2(\widehat{T} - 1, \widehat{T})}\right)}{1 - p_0} \quad (7)$$

and for the mutant arriving one day later than the prevailing strategy

$$p_s(\widehat{T} + 1, \widehat{T}) = \frac{M_1^*(\widehat{T})}{N_1^*(\widehat{T})} \frac{1 - p_0}{1 - \dfrac{aX}{1 + abN_1(\widehat{T}, \widehat{T}) + (1-a)bN_2(\widehat{T}, \widehat{T})}} \quad (8)$$

The mutant's probability of acquiring a good territory, a poor territory, or no territory at all, depends upon whether it arrives earlier or later. Mutants arriving one day earlier than the prevailing strategy can easily take a good territory, therefore

$$p_G(\widehat{T} - 1, \widehat{T}) = 1 \quad (9a)$$

$$p_P(\widehat{T} - 1, \widehat{T}) = 0 \quad (9b)$$

For mutants arriving one day later than the prevailing strategy, their probability of acquiring a good territory is equivalent to that of the prevailing strategy minus the probability of acquiring a good territory by the end of the first day

$$p_G(\widehat{T} + 1, \widehat{T}) = \frac{V_G}{M_1^*(\widehat{T})} - \frac{V_G}{N_1(\widehat{T} + 1, \widehat{T})} = \frac{V_G(N_1(\widehat{T} + 1, \widehat{T}) - M_1^*(\widehat{T}))}{M_1^*(\widehat{T})N_1(\widehat{T} + 1, \widehat{T})} \quad (10)$$

Similarly the probability of acquiring a poor territory is

$$p_B(\widehat{T} + 1, \widehat{T}) = \frac{V_B(N_1(\widehat{T} + 1, \widehat{T}) - M_1^*(\widehat{T}))}{M_1^*(\widehat{T})N_1(\widehat{T} + 1, \widehat{T})} \quad (11)$$

The invasibility of each prevailing strategy $(\widehat{T})$ can now be classified according to its invasibility to mutants arriving one day earlier and one day later than the prevailing strategy

(Eq. 5). For example, if $W(\widehat{T} + 1, \widehat{T}) > 1$ then the population is invasible by mutants arriving one day later. The evolutionary singular strategy (ESS) T^* is the prevailing strategy which is invasible by neither strategy

$$W(T^* - 1, T^*), W(T^* + 1, T^*) < 1 \quad (12)$$

Data deposition

Results

Our results confirm the intuitive expectation that the arrival time strategy evolves to be as early as possible in the absence of predation pressure (as we included no other costs of early arrival). In the simulation model, 10 replicate simulations without predation (i.e. $X = 0$) produced the result that 6773.3 (29.7 SE) individuals arrive on day $T = 1$, while 3.4 (0.4 SE) individuals arrive on day $T = 2$, and none on days $T = 3 - 5$ (other parameter values as given in Table 1). The small number of individuals arriving on day two are due to mutations in the arrival allele rather than later arrival being favored by selection. In the semi-analytic model, in the absence of predation pressure we obtain a similar result. No strategy is invasible by a later arrival-day strategy $W(\widehat{T} + 1, \widehat{T}) = (1 - \gamma)(1 - p_0)^{\widehat{T}} < 1$ for all $0 < p_0 \leq 1$ and $0 < \gamma \leq 1$. For the default parameter values, $W(\widehat{T} - 1, \widehat{T}) = (1 - \gamma)(1 - p_0)^{\widehat{T} - 2}(1 + B_G) > 1$ for all $1 < \widehat{T} \leq T_{max}$), therefore all arrival-day strategies after the first day are invasible by a strategy of arrival one day earlier.

Figure 2a–c summarises the effect of increasing predation pressure in the individual based simulation model. Predation pressure can be increased in various ways: by increasing predator preference for the focal species a, by increasing the total predation effort X, and by decreasing the number of alternative prey N_2. In each case, we chose a baseline parameter value which leads to arriving as early as possible being favoured, and then examined the effect of stronger predation. Mild increases in the predation pressure from the baseline do not lead to a deviation from the earliest possible arrival, and the only effect is a population size decline (Fig. 2a–c). Increasing the predation pressure further results in later arrival times and larger population sizes (provided the populations survive).

In some simulations, when predation pressure was high ($a > 0.75$, $X > 1175$, $N_2 < 550$), some populations go extinct. This occurs when the simulations are seeded with an initial arrival strategy distribution that is unviable (initial arrival strategy: $\varepsilon = 0.5$, $\theta = 0.5$, $\delta = [0 , 1]$). It can be interpreted as a failure to undergo evolutionary rescue, where the speed of evolution was too slow compared to the loss of individuals caused by the high predation pressure. This corresponds to a scenario in which a new predator invades or an existing predator has a sudden density increase.

In all parameter value explorations, we found parameter regions where different runs of simulations did not converge to the same arrival day strategies; they retained their differences regardless of how long the simulation is run (Fig. 2a–c;
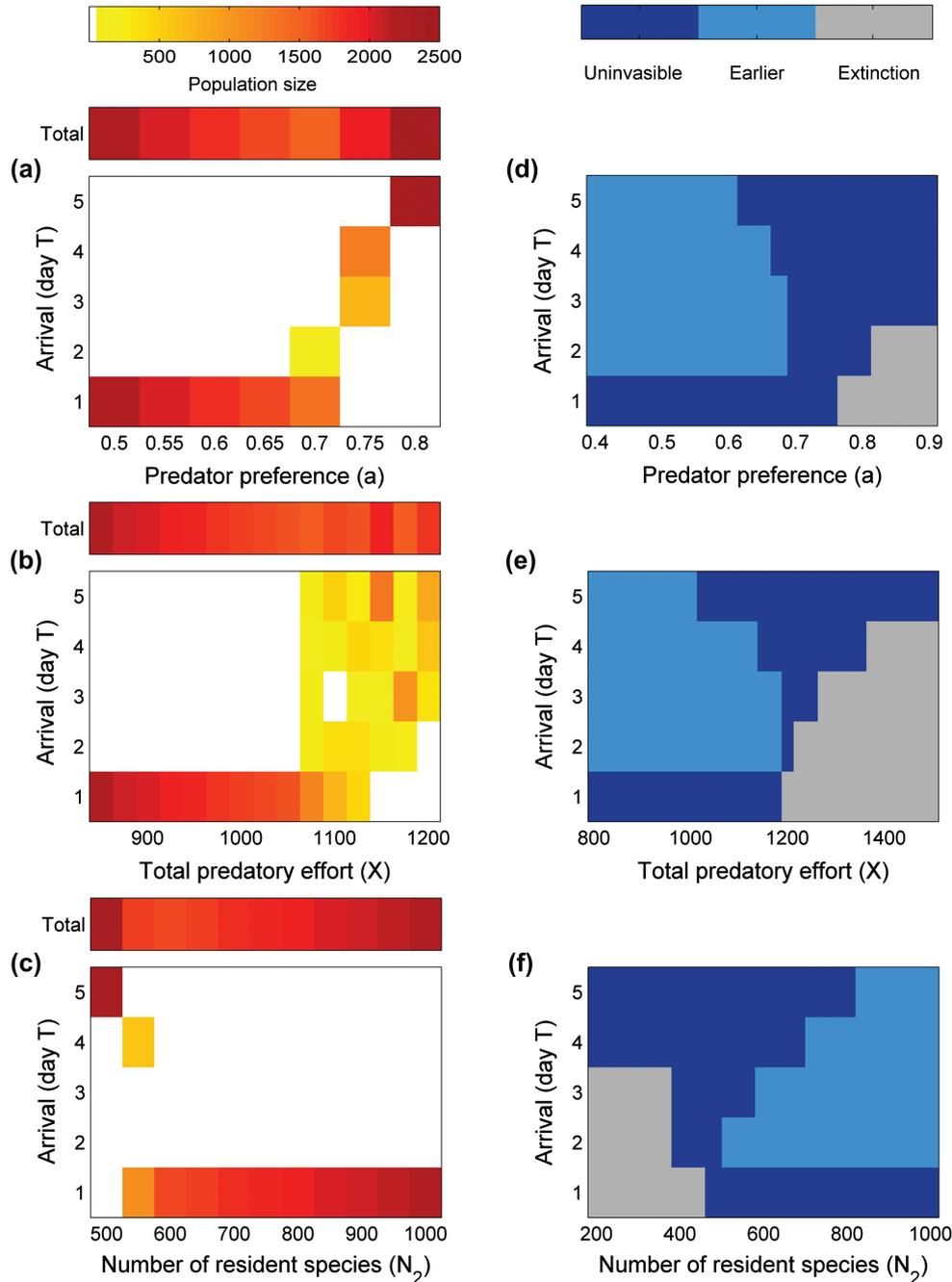
Figure 2. Evolutionary stable arrival day for two different models, the simulation model (a–c) and the semi-analytical model (d–f). Different values for predator preference (a) are shown in (a, d), for total predatory effort (X) (b, e), for number of individuals of resident species (N_2) (c, g). In (a–c), colored (non-white) areas indicate that individuals arrive on this arrival day, white areas indicate no individuals arrive, the color (also see legend) indicates the number of individuals arriving (averaged over 10 simulations unless extinctions occurred), and 'total' refers to the sum of individuals alive when the census (Fig. 1) is taken. In (d–f), the dark blue color indicates an ESS, light blue indicates that individuals arriving earlier have higher fitness and grey shows that extinctions occur. Note that the x-axis may span a different range for the semi-analytical model than for the simulation model. Where not specifically varied (on the respective x-axis), we used parameter values as given in Table 1.

a = 0.7–0.8, X = 1000–1200, N_2 = 500–550). The semi-analytic model (Fig. 2d–f) reveals why this occurs. When predation pressure is low, the earliest arrival-day strategy is the only ESS, and it is also an evolutionary attractor: all later arrival-day strategies can be invaded by the strategy of arriving one day earlier (light blue region, Fig. 2d–f). However as predation pressure is increased, late arrival-day strategies

emerge as alternative ESSs (dark blue region, Fig. 2d–f), emerging first on the last day and then at progressively earlier days. The first late-arrival ESS to emerge is on the last day because this is where the alternative-prey (S2) populations are lowest and consequently daily predation pressure is highest. As predation pressure is increased, earlier late-arrival ESSs emerge. These late-arrival day ESSs are not evolutionary
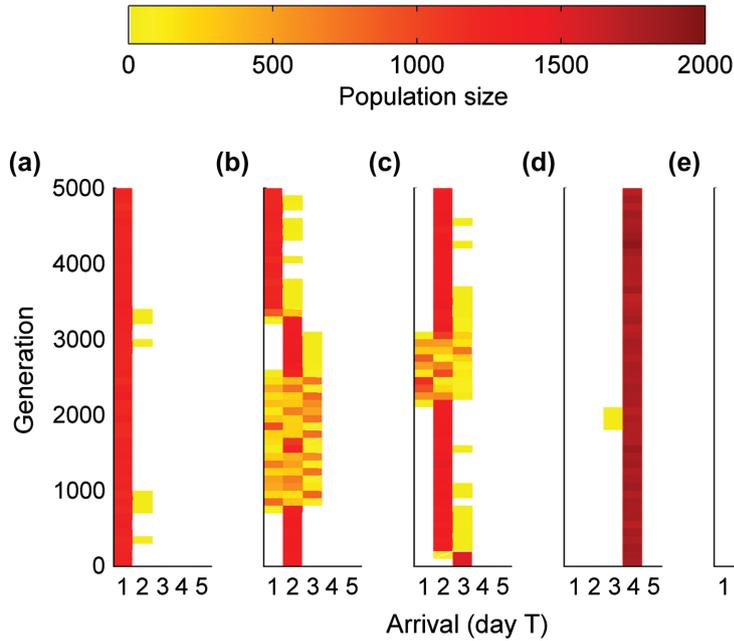
Figure 3. The evolution of the arrival time allele over 5000 generations for five individual simulations (a–e) with predator preference (a) = 0.7 and different initial intervals (i.e. θ = 0.1) for the arrival allele (δ), (a) initial arrival on day 1, δ = [0 , 0.2], ε = 0.1, (b) initial arrival on day 2, δ = [0.2 , 0.4] , ε = 0.3, (c) initial arrival on day 3, δ = [0.4 , 0.6] , ε = 0.5, (d) initial arrival on day 4, δ = [0.6 , 0.8] , ε = 0.7 and (b) initial arrival on day 5, δ = [0.8 , 1.0] , ε = 0.9. All other parameter values as in Table 1. Color indicates the number of individuals arriving (see legend).

attractors, a population strategy near a late-arrival ESS will either move away from it and towards earliest arrival if it is in the light blue region of Fig. 2d–f, or remain where it is if it itself is a late-arrival ESS (dark blue region). Consequently any population initiated with a strategy within the dark blue region will remain at that strategy (an 'evolutionary priority effect' sensu Gourbière and Menu 2009). Finally, when predation pressure is very strong (strong preference for focal species (high a), high total predatory effort (high X), and few individuals of the alternative species (low N_2)), the earliest arrival-day strategies are no longer viable, and a population adopting such a strategy will go extinct (grey regions, Fig. 2d–f).

Which ESS the simulation model reaches depends upon the initial conditions and stochastic events during the evolutionary process. When simulations in the parameter range of multiple ESSs were seeded with different initial arrival day strategies, the evolutionary simulations led to different arrival day strategies. Provided that the evolutionary parameters were set such that the genetic variability was low (i.e. θ = 0.1), these evolutionary endpoints were similar to that with which they were initialised (Fig. 3). This shows that alternative stable states are also possible in the simulation model, with significant inertia that constrains arrival dates to largely stay where they were initiated.

In the region for which the semi-analytic model predicted multiple ESSs, the simulation model additionally predicted that, for a given simulation, persistent mixed arrival-day strategies may occur. For example, when 10 simulations of 10 000 generations were run with total predatory effort (X) = 1125, more than half of the simulations showed the persistence of populations with a mixture of

strategies although, after 10 000 generations, first or last day arrival was more common than arrival on intermediate days (Fig. 4). In simulations where mixed strategies persist for a long period of time (i.e. > 1000 generations), a bimodal pattern (e.g. arrival on day T = 2 and day T = 4) is common, suggesting that one part of the population specialises in a strategy favouring higher reproduction at the cost of higher mortality due to predation, whereas the other specialises in lower mortality at the cost of reproduction.

Discussion

We have explored models of arrival time evolution under two competing objectives: arriving early to obtain a high quality territory versus arriving late to reduce predation risk. Our models were designed to test the idea that frequency-dependent predation can select against early arrival, but they revealed a richer set of outcomes than a simple shift towards later arrival with increased predation. Due to the frequency-dependence and the interplay of the selective forces, high predation pressure is predicted to select for synchronous arrival with conspecifics, however stochastic effects and large arrival strategy mutations can lead to persistence of populations with mixed arrival-day strategies. We discuss these below.

The importance of arriving synchronously is seen most clearly in the semi-analytic model (Fig. 2d–f), where the scenario modelled is a monomorphic population, with a separation between the population-dynamic and evolutionary time-scales, and where mutations in arrival strategy are small (no greater than one day). Selection for synchronous
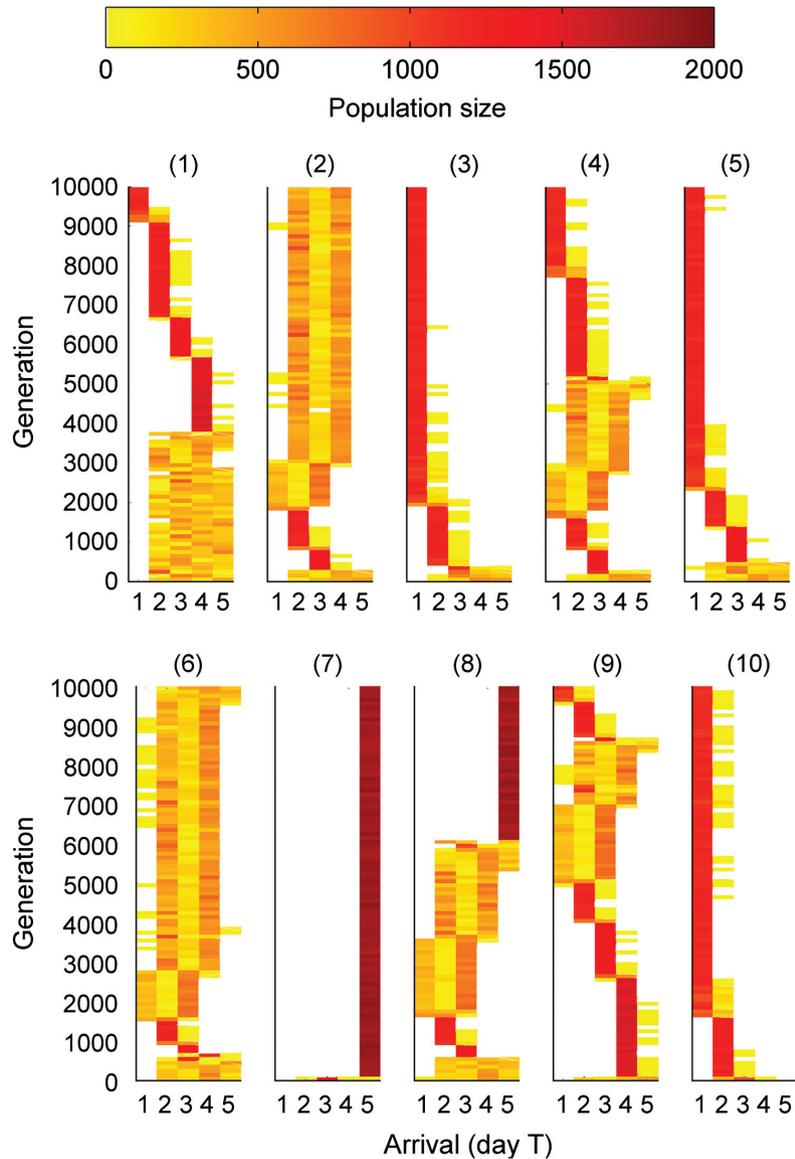
Figure 4. The evolution of the arrival time allele over 5000 generations for ten individual simulations (1–10) with total predatory effort (X) = 1125, all other variables have the standard values as given in Table 1.

arrival is also responsible for the finding of the individual-based simulation model that initial arrival dates can be largely retained for a very large number of generations (Fig. 3). This type of 'evolutionary priority effect', where the strategy that establishes itself first can persist on an evolutionary timescale, has been discussed before in a different context of dormancy evolution (Gourbière and Menu 2009). To understand these effects in the current context, it is important to consider both 1) selection against arriving earlier than the prevailing arrival strategy and 2) selection against arriving later than the prevailing arrival strategy. We consider these in turn.

First, selection against earlier arrival can be understood as a result of predator satiation (Ims 1990) or the predator dilution effect (Bednekoff and Lima 1998, Connell 2000, Jones 2003). Predation risk, from the perspective of the prey, is frequency-dependent: individuals can reduce their predation risk by only being present at the breeding grounds when

many other individuals are also present. In this way they avoid being temporarily one of only few prey items available for resident predators. When predation pressure is high, the predator dilution/ satiation effect is the dominant effect on predation risk, therefore there is strong selection against arriving earlier than the prevailing arrival strategy.

Second, selection against later arrival can be understood as the result of competition for territories. Assuming that territory acquisition is a quick process (Beletsky and Orians 1987, Smith and Moore 2003) with strict priority effects (Newton 2008) and a limiting number of territories, the probability of acquiring a (high-quality) territory is much lower for individuals arriving even one day after the prevailing arrival-day strategy. To understand why, consider the extreme case where most individuals arrive synchronously on the same day. On this day all territories are vacant and available to the competing individuals. In contrast, after this day the only territories that are available to competing floaters

and late-arrivers are those that have been vacated due to a territory-holder being predated. Compared to this cost of much lower territory acquisition, the benefits of arriving one day later than the prevailing strategy are meagre: they consist of a small reduction of predation risk compared to individuals using the prevailing strategy, i.e. a difference of one day exposure to predation.

The net effect of selection against both earlier arrival and later arrival above is that the population cannot be invaded by either strategy, and hence synchronous arrival remains evolutionarily stable. It is noteworthy that the models predict that many adjacent days can all be alternative ESSs. Selection for synchrony means that, to avoid predation, it is best to arrive when the majority does so, regardless of other timing issues. Earlier would be dangerous, while later would mean losing out in the competition for territories. This implies, in accordance with the evolutionary priority effect, that there may be a certain degree of 'inertia' in arrival times: it is costly to deviate from the norm if the norm brings about advantages in terms of predator dilution effect. This result has implications for climate change scenarios, where phenological adaptation to a shift in nestling food resource phenology may be hindered by the stabilising selection for phenological synchrony caused by predation pressure.

Our prediction of synchronous arrival date for migratory birds in response to frequency-dependent adult predation is analogous to breeding synchrony in other systems. For example, the evolution of emergence time of juvenile salmon is a tradeoff between predation risk and territory acquisition; early emergers miss out on dilution effects resulting in heavy mortality from predation, but late emergers suffer from habitat saturation and have difficulty finding high quality feeding habitats (Cutts et al. 1999). As other examples, the mast fruiting of plants, the synchronous emergence of 13-year periodical cicadas, and synchronous metamorphosis in toads may have all evolved to take advantage of predator satiation (Gochfeld 1982, Williams et al. 1993, Devito et al. 1998). Finally, both spatial clustering and temporal breeding synchrony have been observed in many bird taxa (Danchin 1988, Ims 1990, Rolland et al. 1998, Varela et al. 2007). Known as the Fraser Darling effect, it is a strategy of using nest-predator satiation to reduce individual predation risk (Nisbet 1975, Ims 1990, Langerhans 2007). To our knowledge, ours is the first study to suggest that a similar effect may also affect adult migratory phenology.

When the individual-based simulation model is run with genetic parameters set such that genetic variability is high, the model predicts the persistence of populations of mixed arrival day strategies. This difference in results between the simulation and semi-analytic model is due to the different scenarios that are implied by their assumptions. In the simulation model the population has (at least initially) variation for the arrival allele while the semi-analytic model assumes a monomorphic population for the arrival time allele. The invasion approach of the semi-analytic model assumes that there are few individuals that arrive earlier or later than the general population, and only one day earlier or later than the general population, and tests whether these 'invaders' have higher fitness than the general population. In contrast, the simulation model permits many invaders to arrive at once,

and potentially invaders whose arrival strategy is more than one day different to the prevailing strategy.

Which model is most suitable depends upon the particulars of the system of interest. Typically eco-evolutionary phenology models use analytic techniques that make similar assumptions to the semi-analytic model here (Jonzén et al. 2007, Kristensen et al. 2015), however full individual-based simulations are able to reveal much more complex dynamics than can be deduced from analytic techniques alone.

The effects of predation upon arrival for migratory species appear understudied, as research has largely focussed on predation during migration or during nesting (Lindström 1990, Sillett and Holmes 2002, Fontaine and Martin 2006, Chapman et al. 2011, Sofaer et al. 2013). This is largely due to the difficulty of distinguishing between predation and movement to other breeding locations before egg laying (Sillett and Holmes 2002, Alerstam et al. 2003). One reason why predation upon pre-breeding adults may have received less attention is that it has a limited effect upon population persistence. In populations with many floaters, any territory holder that dies can be rapidly replaced, and so predation of adults at the pre-breeding stage will not usually reduce the number of offspring produced (Newton 1998); this is also true in our model. However, we have shown that predation at this crucial time of the life cycle can influence arrival time phenology very significantly despite the small number of individuals affected: precisely because the local population remains small early in the season, the per capita risk can remain significant. The consequent evolutionary response may in turn influence synchrony between peak nestling resource demand and resource phenology. In such cases, predation will influence offspring numbers indirectly, and the predicted inertia could have a stronger impact still if climate change shifts the nestling-resource's phenology.

We note a number of simplifications in both models. Firstly, we assumed that the predator's relative preference for the migrant species is constant across all migrant densities (i.e. we assume type II rather than more complicated functional responses). Perhaps more importantly, our models ignore interyearly fluctuations in weather, food availability, and predator and alternative prey abundances. These have been shown to impact traits such as breeding success (Sofaer et al. 2013) and selection could consequently fluctuate more in time than in our model. Weather may also make it likely that migrant species find it in practice difficult to reach as high synchrony as predicted by our model (unless they travel physically together, as many migrants do; our model together with flocking advantages during travel might give a good set of reasons why individuals strive to keep together during the journey).

We have considered a simple model in order to isolate the effects of interest, however violations of certain of its assumptions may add complexities to the phenomenon of arrival synchrony; we consider a few examples here. First, predation efficiency may increase when the density of the migratory species is high, as predators become aware of the migrating species' arrival (Robertson 1973), and by causing predators to switch to strategies suited to the species (e.g. the search image effect Tinbergen 1960, Wilson et al. 2007). This would decrease the relative predation cost of

early arrival, potentially destabilising the synchronous later-arrival ESSs leading to a single earliest-arrival ESS. Alternatively, predation efficiency may decrease over the season (e.g. due to increasing vegetation cover, Sullivan and Dinsmore 1990), which may encourage the emergence and persistence of mixed strategies, similar to the bimodal pattern predicted by the simulation model.

Second, our model does not consider predation during migration. Variability in arrival times connects with variability in migration phenology en route (Bauer et al. 2015), and predators along the way can have their own functional responses and/or presence patterns. Consider as an extreme example intensive hunting by humans during a fixed temporal window (Mooij et al. 1999), in which case individuals passing through the area either before or after the hunting season can do so more safely. Finally, note that alternative prey may have their own seasonal variation in activity, presence and availability to the predator (Wilson et al. 2007).

In conclusion, our models suggest that the combination of competition for limited breeding territories and strong frequency-dependent predation will select for not only later arrival times but also for more synchronous arrival times, with stochasticity in arrival strategy also potentially leading to the persistence of populations of mixed arrival-day strategies. This dual prediction was made possible by the fact that we explored both a full individual-based simulation as well as a more traditional semi-analytic model that uses the adaptive dynamics framework. This result is made possible by taking a game-theoretic approach to the role that synchronicity with conspecifics plays in predator evasion via the predator satiation effect.

References

Abrams, P. A. and Ginzburg, L. R. 2000. The nature of predation: prey dependent, ratio dependent or neither? – Trends Ecol. Evol. 15: 337–341.

Alerstam, T. et al. 2003. Long-distance migration: evolution and determinants. – Oikos 103: 247–260.

Bauer, S. et al. 2015. Timing is crucial for consequences of migratory connectivity. – Oikos in press. DOI: 10.1111/oik.02706.

Bednekoff, P. A. and Lima, S. L. 1998. Re-examining safety in numbers: interactions between risk dilution and collective detection depend upon predator targeting behaviour. – Proc. R. Soc. B 265: 2021–2026.

Beletsky, L. D. and Orians, G. H. 1987. Territoriality among male red-winged blackbirds. I. Site fidelity and movement patterns. – Behav. Ecol. Sociobiol. 20: 21–34.

Bensch, S. and Hasselquist, D. 1991. Territory infidelity in the polygynous great reed warbler *Acrocephalus arundinaceus*: the effect of variation in territory attractiveness. – J. Anim. Ecol. 60: 857–871.

Borgmann, K. L. et al. 2013. Breeding phenology of birds: mechanisms underlying seasonal declines in the risk of nest predation. – PloS ONE 8: e65909.

Both, C. S. et al. 2006. Climate change and population declines in a long-distance migratory bird. – Nature 441: 81–83.

Chapman, B. B. et al. 2011. The ecology and evolution of partial migration. – Oikos 120: 1764–1775.

Connell, S. D. 2000. Is there safety-in-numbers for prey? – Oikos 88: 527–532.

Cutts, C. J. et al. 1999. Competitive asymmetries in territorial juvenile Atlantic salmon, *Salmo salar*. – Oikos 86: 479–486.

Danchin, É. 1988. Social interactions in kittiwake colonies: social facilitation and/or favourable social environment. – Anim. Behav. 36: 443–451.

Descamps, S. et al. 2011. Individual optimization of reproduction in a long-lived migratory bird: a test of the condition-dependent model of laying date and clutch size. – Funct. Ecol. 25: 671–681.

Devito, J. et al. 1998. The effects of snake predation on metamorphosis of western toads, *Bufo boreas* (Amphibia, Bufonidae). – Ethology 104: 185–193.

Du, B. et al. 2014. Horned larks on the Tibetan Plateau adjust the breeding strategy according to the seasonal changes in the risk of nest predation and food availability. – J. Avian Biol. 45: 466–474.

Fontaine, J. J. and Martin, T. E. 2006. Parent bird assess nest predation risk and adjust their reproductive strategies. – Ecol. Lett. 9: 428–434.

Geritz, S. et al. 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. – Evol. Ecol. 12: 35–57.

Gochfeld, M. 1982. Reproductive synchrony and predator satiation: an analogy between the Darling effect in birds and mast fruiting in plants. – Auk 99: 586–587.

Gourbière, S. and Menu, F. 2009. Adaptive dynamics of dormancy duration variability: evolutionary tradeoff and priority effect lead to suboptimal adaptation. – Evolution 63: 1879–1892.

Harts, A. M. F. et al. 2016. Data from: Predation can select for later and more synchronous arrival times in migrating species. Simulation data – Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.32np3>. Semi-analytic data – Zenodo: <http://dx.doi.org/10.5281/zenodo.45179>.

Hasselquist, D. 1998. Polygyny in great reed warblers: a long-term study of factors contributing to male fitness. – Ecology 79: 2376–2390.

Hope, D. D. et al. 2014. Mortality-minimizing sandpipers vary stopover behavior dependent on age and geographic proximity to migrating predators. – Behav. Ecol. Sociobiol. 68: 827–838.

Ims, R. A. 1990. On the adaptive value of reproductive synchrony as a predator-swamping strategy. – Am. Nat. 136: 485–498.

Jones, C. 2003. Safety in numbers for secondary prey populations: an experimental test using egg predation by small mammals in New Zealand. – Oikos 102: 57–66.

Jonker, R. M. et al. 2010. Predation danger can explain changes in timing of migration: the case of the barnacle goose. – PLoS ONE 5: e11369.

Jonzén, N. et al. 2007. Climate change and the optimal arrival of migratory birds. – Proc. R. Soc. B 274: 269–274.

Kokko, H. 1999. Competition for early arrival in migratory birds. – J. Anim. Ecol. 68: 940–950.

Kokko, H. et al. 2006. Why do female migratory birds arrive later than males? – J. Anim. Ecol. 75: 1293–1303.

Krams, I. et al. 2014. Hissing calls improve survival in incubating female great tits (*Parus major*). – Acta Ethol. 17: 83–88.

Kristensen, N. P. et al. 2015. Phenology of two interdependent traits in migratory birds in response to climate change. – Proc. R. Soc. B 282: 20150288.

Langerhans, R. B. 2007. Evolutionary consequences of predation: avoidance, escape, reproduction, and diversification. – In Elewa, A. M. T. (ed.), Predation in organisms, Springer, pp. 177–220.

Lank, D. B. et al. 2003. Effects of predation danger on migration strategies of sandpipers. – Oikos 103: 303–319.

Lindström, Å. 1990. The role of predation risk in stopover habitat selection in migrating bramblings, *Fringilla montifringilla*. – Behav. Ecol. 1: 102–106.

Low, M. et al. 2010. Habitat-specific differences in adult survival rates and its links to parental workload and on-nest predation. – J. Anim. Ecol. 79: 214–224.

Martin, T. E. 1995. Avian life history in relation to nest sites, nest predation and food. – Ecol. Monograph. 65: 101–127.

McKinnon, L. et al. 2010. Lower predation risk for migratory birds at high latitudes. – Science 327: 326–327.

Mooij, J. H. et al. 1999. White-fronted Goose *Anser albifrons albifrons*. – In: Madsen, J. et al. (eds), Goose populations of the Western Palearctic. A review of status and distribution. Wetlands Int. and Natl Environ. Res. Inst., pp. 94–128.

Morbey, Y. E. and Ydenberg, R. C. 2001. Protandrous arrival timing to breeding areas: a review. – Ecol. Lett. 4: 663–673.

Murdoch, W. W. 1973. The functional response of predators. – J. Appl. Ecol. 10: 335–342.

Nager, R. G. 2006. The challenges of making eggs. – Ardea 94: 323–346.

Newton, I. 1998. Population limitation in birds. – Academic Press.

Newton, I. 2008. The migration ecology of birds. – Academic press.

Nisbet, I. C. T. 1975. Selective effects of predation in a tern colony. – Condor 77: 221–226.

Pompanon, F. et al. 1995. Emergence rhythms and protandry in relation to daily patterns of locomotor activity in *Trichogramma* species. – Evol. Ecol. 9: 467–477.

Pulido, F. 2007. Phenotypic changes in spring arrival: evolution, phenotypic plasticity, effects of weather and condition. – Clim. Res. 35: 5–23.

Robertson, R. J. 1973. Optimal niche space of the redwinged blackbird: spatial and temporal patterns of nesting activity and success. – Ecology 54: 1085–1093.

Rolland, C. et al. 1998. The evolution of coloniality in birds in relation to food, habitat, predation, and life-history traits: a comparative analysis. – Am. Nat. 151: 514–529.

Sillett, T. S. and Holmes, R. T. 2002. Variation in survivorship of migratory songbird throughout its annual cycle. – J. Anim. Ecol. 71: 296–308.

Smith, R. J. and Moore, F. R. 2003. Arrival fat and reproductive performance in a long-distance passerine migrant. – Oecologia 134: 325–331.

Smith, R. J. and Moore, F. R. 2005. Arrival timing and seasonal reproductive performance in a long-distance migratory land-bird. – Behav. Ecol. Sociobiol. 57: 231–239.

Sofaer, H. R. et al. 2013. Differential effects of food availability and nest predation risk on avian reproductive strategies. – Behav. Ecol. 24: 698–707.

Sullivan, B. D. and Dinsmore, J. J. 1990. Factors affecting egg predation by American crows. – J. Wildl. Manage. 54: 433–437.

Teder, T. 2014. Sexual size dimorphism requires a corresponding sex difference in development time: a meta-analysis in insects. – Funct. Ecol. 28: 479–486.

Tinbergen, L. 1960. The natural control of insects in pinewoods. Factors influencing the intensity of predation by songbirds. – Arch. Neerl. Zool. 13: 265–343

Varela, S. A. M. et al. 2007. Does predation select for or against avian coloniality? A comparative analysis. – J. Evol. Biol. 20: 1490–1503.

Williams, K. S. et al. 1993. Emergence of 13-year periodical cicadas (Cicadidae: Magicicada): phenology, mortality, and predators satiation. – Ecology 74: 1143–1152.

Wilson, S. et al. 2007. Nest survival patterns in willow ptarmigan: influence of time, nesting stage, and female characteristics. – Condor 109: 377–388.