

LETTER

Game theory sheds new light on ecological responses to current climate change when phenology is historically mismatched

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Abstract

Phenological changes are well documented biological effects of current climate change but their adaptive value and demographic consequences are poorly known. Game theoretical models have shown that deviating from the fitness-maximising phenology can be evolutionary stable under frequency-dependent selection. We study eco-evolutionary responses to climate change when the historical phenology is mismatched in this way. For illustration we model adaptation of arrival dates in migratory birds that compete for territories at their breeding grounds. We simulate climate change by shifting the timing and the length of the favourable season for breeding. We show that initial trends in changes of population densities can be either reinforced or counteracted during the ensuing evolutionary adaptation. We find in total seven qualitatively different population trajectories during the transition to a new evolutionary equilibrium. This surprising diversity of eco-evolutionary responses provides adaptive explanations to the observed variation in phenological responses to recent climate change.

Keywords

Climate change, evolutionary game theory, life history, migration, phenology, timing.

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“...to the extent that species’ interactions might have had an evolved asynchrony or mismatch as their starting point, assumptions of baseline synchrony would risk mis-detection, mis-estimation and mis-attribution of climate change impacts.” Singer & Parmesan (2010)

INTRODUCTION

Phenological changes are among the most well documented biological effects of current climate change (Parmesan 2006). In temperate areas in the Northern Hemisphere many biological events now occur earlier in the year, presumably in response to warmer temperatures and other abiotic changes (Menzel *et al.* 2006). Although the general pattern is that as phenology advances, there is also a large variation in species’ responses. This variation is often suggested to mirror variation in either genetic variance affecting the rate of adaptation through microevolution, and/or constraints on phenotypic plasticity (e.g. Gienapp *et al.* 2007). Warming may also have differential effects on development rate and hence ontogeny of different organisms, and on cues that affect the appearance of a species (Yang & Rudolf 2010 and references therein; McNamara *et al.* 2011).

Much research is dedicated to better understand the short- and long-term consequences of these unequal shifts. One often-discussed possibility is that species that do not sufficiently adjust their phenologies may become mistimed in relation to food resources or important abiotic factors in their environment (Stenseth & Mysterud 2002; Visser & Both 2005). Another question of concern among biologists is to what extent species will be able to adapt evolutionarily to future climate by adjusting their phenologies and thereby ‘restore synchrony’ of species interactions (Visser 2008).

These questions make sense when assuming that consumer phenologies, due to evolution, matched maximal resource abundance

before current climate change. Studies that show a connection between differential phenological responses across trophic levels and decreased population sizes for consumer species (Both *et al.* 2006; Post & Forchhammer 2008) lend support to such hypotheses. In general, however, we know very little about demographic responses to shifting phenology (Miller-Rushing *et al.* 2010). Critically, we cannot always expect the historical baseline phenology to match maximal resource abundance or optimal environmental conditions. For instance, Singer & Parmesan (2010) put forward empirical evidence that trophic synchrony was not the historical state in two plant-insect interactions. They argue that when trade-offs between fecundity and mortality are taken into account, the phenologies of the insects are nevertheless adaptive. The authors denote the historical phenologies of the butterflies ‘superficially maladaptive’, emphasising that trophic asynchrony can be part of a strategy that increases overall fitness. However, even if the whole life history is taken into account, evolution can still not always be expected to result in phenological strategies that maximise fitness of consumers. Coevolution may for example lead to trophic asynchrony and reduced consumer fitness since prey species are likely to evolve so as to avoid predation (Law *et al.* 2001; Singer & Parmesan 2010). As shown by a recent model backed up with experiments (Forrest & Thomson 2009), interactions among mutualistic species may also lead to mismatch, suggesting that interactions with pollinators may impede adaptation of flowering time. Several studies also show that frequency-dependent selection within a single trophic level may favour phenological strategies that are not maximising group fitness. In birds, early reproduction relative to the rest of the population may for example give an advantage in social competition for territories among offspring (Nilsson & Smith 1988). Competition for territories among migratory birds may also favour early arrival compared to fitness maxima as suggested by game theoretical models (Kokko 1999; Jonzén *et al.* 2007; Johansson & Jonzén 2012).

Similarly, it has been shown that competition for matings among insects favour relatively early emergence (Wiklund & Fagerström 1977; Iwasa *et al.* 1983).

As pointed out by Singer & Parmesan (2010) the possibility that mismatch can be the historical baseline affects the interpretation of phenological responses to on-going climate change in fundamental ways. Consider for example a situation where fitness is maximised by temporally matching the maximum resource requirements with the peak food availability (cf. Durant *et al.* 2005; Miller-Rushing *et al.* 2010). Furthermore, assume that climate change affects the timing of one or both of these peaks. If the historical phenology is perfect matching, any differential change will have negative fitness consequence for the focal species. The evolutionary responses are also predictable: Initially, selection among consumers is expected to decrease the mismatch and in the long run evolution is expected to restore the perfect match or perfect synchrony, at least provided that the environment eventually stabilises and that evolution is not impeded by genetic constraints. If the starting point is mismatch, however, the biological responses to phenological shifts are harder to anticipate. The mismatch may increase but could also decrease and give positive effects on fitness. Since the same mechanisms that once caused the mismatch are likely to influence the selective responses, the evolutionary outcome is also less predictable.

To better understand species' responses when the historical state involves mismatch we need theoretical guidance. In this article we explore how populations will respond to environmental changes, presumably driven by climate change, when the historical phenology deviates from the fitness-maximising phenology due to frequency-dependent selection. We will apply the concept of the Evolutionarily Stable Strategy (ESS) from evolutionary game theory. An ESS is the expected outcome of gradual evolution as well as a likely end-point of ecological succession in the form of a series of invasion attempts (Maynard Smith 1976; Brown & Vincent 1987) and thus provides an appropriate definition of a historical baseline phenology.

We develop and study a model of an organism which experience (1) a reproductive cost of too early or too late arrival to the breeding grounds, and (2) an individual benefit of arrival before the other individuals, e.g. increased access to limiting resources. This general setting may apply to many systems, e.g. lekking species such as bullfrogs where older and larger males arrive early at the breeding pond and defend a territory within the central areas of a chorus (Emlen 1976), or hibernating species, e.g., small territorial mammals, in which hibernation emergence is hypothesised to have evolved so that subsequent reproduction coincides with the upcoming resource peak (e.g., Lane *et al.* 2011). To facilitate reading, however, we focus on one example and let migratory birds competing for territories at their breeding grounds (cf. Johansson & Jonzén 2012) exemplify and motivate the model assumptions.

Assuming that the mean arrival date adopted by the population constitutes an ESS prior to the environmental change, we study two scenarios of environmental change: (1) advancement of the benign season for reproduction and (2) changes leading to a broader or narrower benign period. We show that initial increases in population density following climate change can be counteracted during the ensuing evolutionary adaptation, resulting in declining population density in the long term. Our study also highlights several qualitatively different population trajectories during the transition to a new evolutionary equilibrium. Compared to the expected responses when

the historical baseline is perfect match, the study thereby significantly broadens the range of possible adaptive eco-evolutionary responses involving phenological shifts to recent climate change.

MODEL AND METHODS

We model phenological adaptation in migratory birds under territory competition using a similar approach as Jonzén *et al.* (2007) and Johansson & Jonzén (2012). In comparison to these previous studies the present model includes population dynamics and gradual evolutionary change but assumes a simplified ecological scenario. We let x denote mean time of arrival of a population of migratory birds to the breeding grounds. Reproductive output is modelled as a Gaussian function (Fig. 1a and b);

$$E(x) = E_0 \exp(-(x - x_{opt})^2 / 2\sigma^2), \quad (1)$$

where E_0 represents maximal reproductive output, x_{opt} represents optimal day for reproduction and σ represents the length of the benign season. Low reproductive success in early arriving individuals can for example represent that adults are in poor condition due to challenging abiotic conditions (Nilsson 1994). Reduced fecundity in later arriving individuals, on the other hand, may represent effects of low resource levels, e.g. due to a temporal mismatch between resource requirements and availability (e.g. Both 2010).

We let n_t denote the density of individuals that compete for territories (e.g. adult males) in year t and assume it is proportional to the total population density. We let K denote the density of territories. We assume individuals occupy their territories only during the

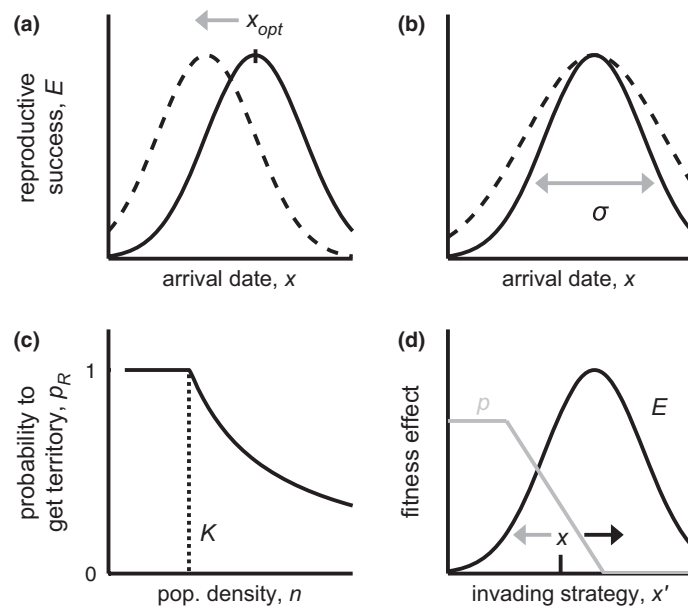


Figure 1 Model assumptions and key variables. (a and b) The reproductive success before environmental change (solid lines). Environmental change is simulated as changes in the arrival date x_{opt} that maximises reproduction (a, dashed line) or in the length σ of the breeding season (b, dashed line). (c) The probability of obtaining a territory for individuals in a monomorphic population. When $n < K$ (dotted line in c) all individuals obtain a territory ($p_R = 1$). (d) Factors affecting fitness of an invading trait x' . The probability of obtaining a territory (shaded line) increases with early arrival relative to the dominating trait x , while reproductive success E (solid line) is independent of x . Shaded (solid) arrow indicates selection pressures to increase p (E).

breeding season, such that competition starts anew every year. We assume that if $n_t < K$ all individuals obtain a territory. If $n_t > K$ we assume that the probability of obtaining a territory drops below one. The positive difference $n_t - K$ can be interpreted as floaters (e.g. Kokko & Lundberg 2001). We let p_R denote the probability of obtaining a territory in a population consisting of individuals with the same mean arrival date. For simplicity we assume that $p_R(K/n_t) = K/n_t$ for $n_t > K$ and $p_R(K/n_t) = 1$ for $n_t < K$ (Fig. 1c). We assume that only individuals that occupy territories reproduce, thus the expected number of offspring per capita will be

$$w(x) = E(x)p_R(K/n). \quad (2)$$

Population dynamics are assumed to follow

$$n_{t+1} = n_t w(x) + sn_t, \quad (3)$$

where s is a density- and timing independent survival. We identify fitness W as the per capita growth rate of the population, which can be extracted from equation 3 as $W = w(x) + s$. The equilibrium population density n^* is obtained by setting $W = 1$, such that $n_{t+1} = n_t$ in equation 3, which results in

$$n^* = KE(x)/(1 - s). \quad (4)$$

To find the evolutionarily stable arrival time we use adaptive dynamics (Geritz *et al.* 1998) and assume an evolutionary scenario by which resident strategies are gradually replaced by more successful, invading mutant strategies until a strategy is adopted that cannot be invaded. We let x denote the arrival time of the resident strategy and x' denote the arrival time of an invading strategy.

We assume that early arrival compared to the resident strategy population confers an increased probability of obtaining a territory (Fig. 1d, cf. Jonzén *et al.* 2007). This assumption is meant to mirror empirical findings showing that early arriving individuals tend to get the upper hand in competition for territories (von Haartman 1968; Dale & Slagsvold 1995; Kokko *et al.* 2006). The probability of obtaining a territory for invading individuals with arrival date x' is denoted $p(x', x)$. This probability is assumed to increase linearly with the difference between resident and invading arrival date by a factor a ($a \geq 0$) that represents the competitive advantage of early arrival:

$$p(x', x) = p_R(K/n)(1 + a(x - x')). \quad (5)$$

We assume that $p(x', x)$ is truncated to take values only between 0 and 1. Note that

$$p(x', x) = p_R \text{ when } x = x'.$$

An alternative interpretation of the assumed density and frequency dependence is that the reproductive costs of crowding are shared equally among the individuals when $n_t > K$, e.g. in the form of smaller territories. In that case p_R can be seen as a discount factor and early arriving individuals obtain an advantage in the form of larger territories. With this interpretation the model does not contain floaters. With a more abstract interpretation of model relations $p(x', x)$ could also represent other types of benefits of arriving relatively early, such as higher territory quality (e.g. Bensch & Hasselquist 1991) or higher probability of mating (e.g. Møller 1994).

We start by calculating the ESS arrival time, denoted x^* , and the corresponding population density. We then study how fitness and population densities are affected by environmental changes. Finally,

we study the evolution of arrival time to a new ESS, and how population densities are affected during this transition. We use the term mismatch to denote the difference between the resident mean arrival time x of a population and x_{opt} and the term historical mismatch, denoted x_{HM} , for the difference between the x^* and x_{opt} . The environment is assumed to undergo a single change, either in the form of a shift of the environmental peak x_{opt} (Fig. 1a) or a change in the season length σ (Fig. 1b). The evolutionary rate of change is assumed to be equal to the selection gradient multiplied by a constant in line with several approaches to model gradual evolution (Lande 1982; Abrams *et al.* 1993). In all cases the resident strategy is assumed to be at ecological and evolutionary equilibrium ($x = x^*$, $W = 1$ and $n_t = n^*$) before the environmental change. We also set parameters such that $n^* > K$, which is necessary for stable equilibrium. Details of the calculations are presented in Appendix S1. The cost of too early arrival can be manifested as reduced reproductive success, as assumed herein, or as a survival cost paid by the adults (Jonzén *et al.* 2007). In reality both costs may occur (Murphy *et al.* 2000) but less is known about pre-breeding survival due to the difficulty of measuring pre-breeding survival in the wild. As a robustness check, we compare the results presented below with simulations where survival is an increasing, sigmoid, function of arrival time such that fitness approaches the above model only for late-arriving strategies (Appendix S1).

RESULTS

Historical mismatch

Evolution in this model is governed by selection for improving (1) reproductive output and (2) the success in territory competition (Fig. 1d). At ESS there is a balance between these two forces, which hence occurs when

$$x^* = x_{opt} - \sigma^2 a. \quad (6)$$

where the historical mismatch, as defined above, is

$$x_{HM} = \sigma^2 a. \quad (7)$$

Logically, x_{HM} increases with the competitive advantage of being early, a . It also increases when the benign season is long since the selection pressure for improving reproductive output then becomes less important.

The equilibrium population density at ESS is

$$n^* = KE_0 \exp(-(x_{HM}/2\sigma)^2)/(1 - s), \quad (8)$$

which hence decreases with historical mismatch (Fig. 2a).

Effects of environmental change on fitness and equilibrium population density

The immediate effects of a shift of the reproductive optimum on a population with a given degree of historical mismatch can be deduced graphically, by comparing the population densities before and after the shift (Fig. 2b). When there is no historical mismatch, the peak shift results in decreasing population density. With a small historical mismatch the population may end up at the same distance from x_{opt} as before the shift and the population density may stay the same. When there is a large historical mismatch, the peak shift instead increases the population density.

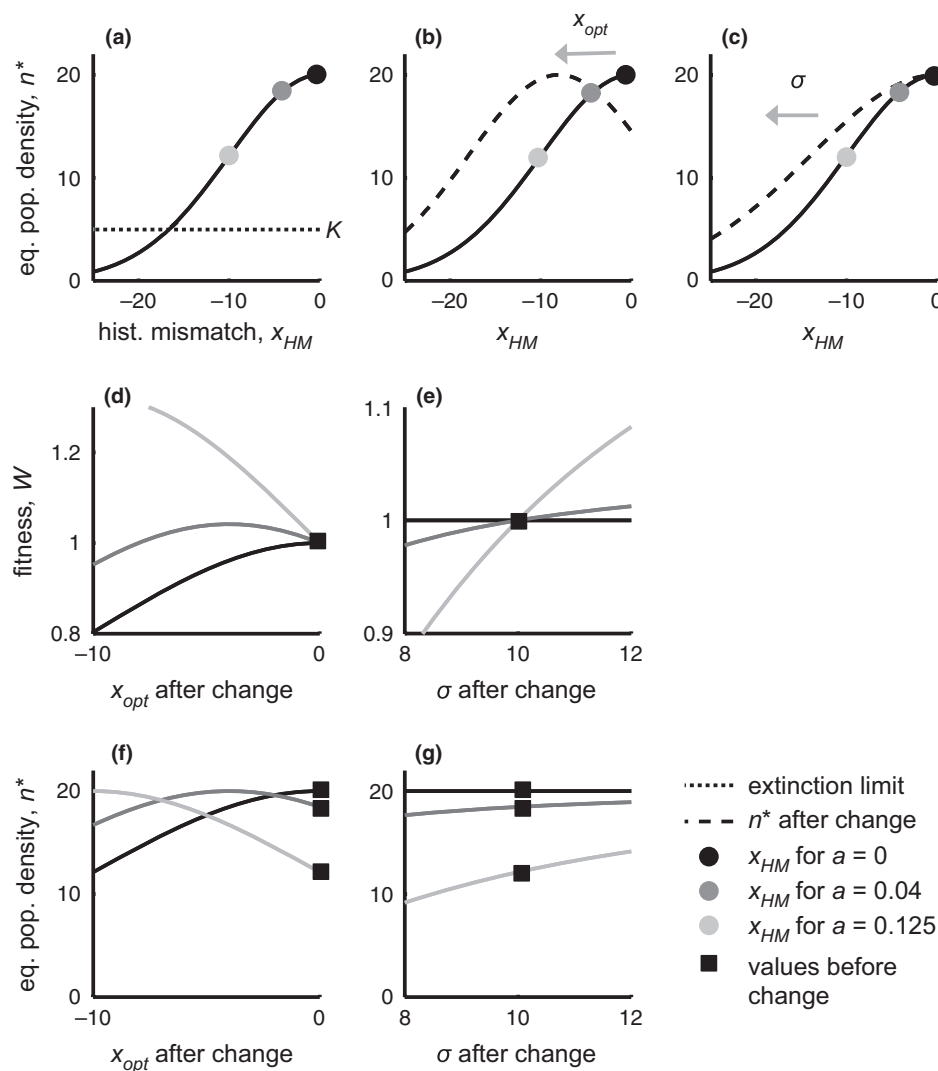


Figure 2 Effects of historical mismatch and environmental change on fitness and population density. The figure compares three different scenarios with differently strong competitive advantage of arriving early (different values of a) and thereby different historical baselines (represented by circles). (a) Effect of historical mismatch on equilibrium population density. When $n^* < K$ the population density will decline to zero. (b and c) Effects of environmental change on equilibrium population densities. (d–g) Fitness and equilibrium population densities after a shift in an environmental variable in the different scenarios. Grey scale of lines in d–g corresponds to different values of a and to the grey scale of filled circles. Parameters: $K = 5$, $x_{opt} = 0$ (before change) and $\sigma = 10$ (before change).

The effects of changes in the length of the benign season σ on fitness and population densities can be deduced graphically in a similar way (Fig. 2c). If σ is increased the reproductive success increases for a mismatched population, and thereby the fitness and the population density increase as well.

Fitness and population densities can be calculated as functions of the shift, the new season length, and the competitive advantage (Fig. 2d–g, see Appendix S1 for details). These curves confirm the intuitive, graphical results above, and show in addition that fitness is more sensitive to changes when a , and thus the historical mismatch, is large (Fig. 2d and e).

Effects of environmental change on population densities at the new ESS

We now turn to study how population densities are affected by environmental changes in the long run i.e. after evolution to a new

ESS. A shift in x_{opt} does not affect the population density at the new ESS, since it does not affect x_{HM} (eqn 8). In contrast, a change of the season length σ affects both the population density (eqn 8) and the degree of mismatch at ESS (eqn 7). These two changes go in different directions. Increasing σ increases the population density for any given degree of mismatch, but increases the mismatch at ESS as well, which may have a negative effect on population densities. To investigate the combined effect on the population density at the new ESS we insert eqn 7 into eqn 8 and simplify to obtain

$$n^* = KE_0 \exp(-\sigma^2 a^2 / 2) / (1 - s). \quad (9)$$

We see that increasing σ decreases the equilibrium population density at ESS when $a > 0$ and conclude that the increased mismatch has a stronger effect on the population density at the ESS than the overall improvement in reproductive output. When there is no competitive advantage ($a = 0$) the equilibrium density is not affected, however, (cf. Fig. 2c).

Transition to a new ESS after an environmental change

We will now study the combined changes in phenological traits (Fig. 3a–d) and in population densities (Fig. 3e–h) that follow upon an environmental change. To start with, we study how responses to shifts in x_{opt} depend on competitive advantage a (Fig. 3a and e). When $a = 0$, i.e. there is no historical mismatch (I), the population density first decreases and then increases as a consequence of evolution decreasing the mismatch. When a is large (III) we get the opposite pattern. Since the shift of x_{opt} increases the match with the environment, the population size increases initially, but as evolution proceeds the mismatch increases again, until the new ESS with a low population size again is reached. The population density of a species with small, intermediate historical mismatch (II) may initially not be affected at all (cf. Fig. 2b). During the evolutionary transition, the population density increases somewhat, as the evolving phenology passes the environmental maximum, however (Fig. 3a).

When a is such that the historical mismatch is smaller than the peak shift, population densities may increase or decrease (Fig. 3b and f) depending on whether the historical phenology is closer to or further away from the optimum after the change (cf. Fig. 2d). As evolution towards earlier arrival proceeds and the strategies pass the reproductive maximum, population densities may increase temporarily, before the new ESS is reached. It follows that the population densities can describe more complicated curves over time in these cases (Fig. 3f).

Finally, we study how responses to changes in σ depend on the competitive advantage a (Fig. 3c, d, g, and h). When $a = 0$ there is no historical mismatch and traits and population densities are unaffected (cf. Fig. 2e and g). When the season length is increased, den-

sities of historically mismatched ($a > 0$) population densities increase initially (Fig. 3g). Later, however, they decrease due to evolution, to finally reach a lower level than in the original environment (cf. eqn 9). When the season length is decreased, we get the opposite pattern (Fig. 3h).

Effects of timing-dependent survival on the results

Assuming that survival depends on timing of arrival as described above affects the predictions of the model in a number of ways (Appendix S1). The ESS arrival date occurs later and population densities are generally lower. The magnitude of immediate and long-term changes in densities may change too and thereby affect the eco-evolutionary trajectories in different ways. The diversity of response types predicted by the model (cf. Fig. 3) does not decrease, however, and is still much larger in the presence of frequency-dependent selection ($a > 0$).

DISCUSSION

To assume that phenologies matched the environment such that fitness was maximised prior to recent climate change seems natural, and is in line with evolutionary optimisation principles. It follows from this assumption that differential phenological shifts lead to mismatch, declining fitness and population densities and selection to decrease mismatch and increase fitness. These general ideas permeate the way ecologists think about phenology and adaptive phenological responses to climate change (e.g. Both 2010). Our results show, however, that bringing in just a single element of an evolutionary game, an advantage of being earlier than the competitors, completely changes this picture. To start with, the evolutionary

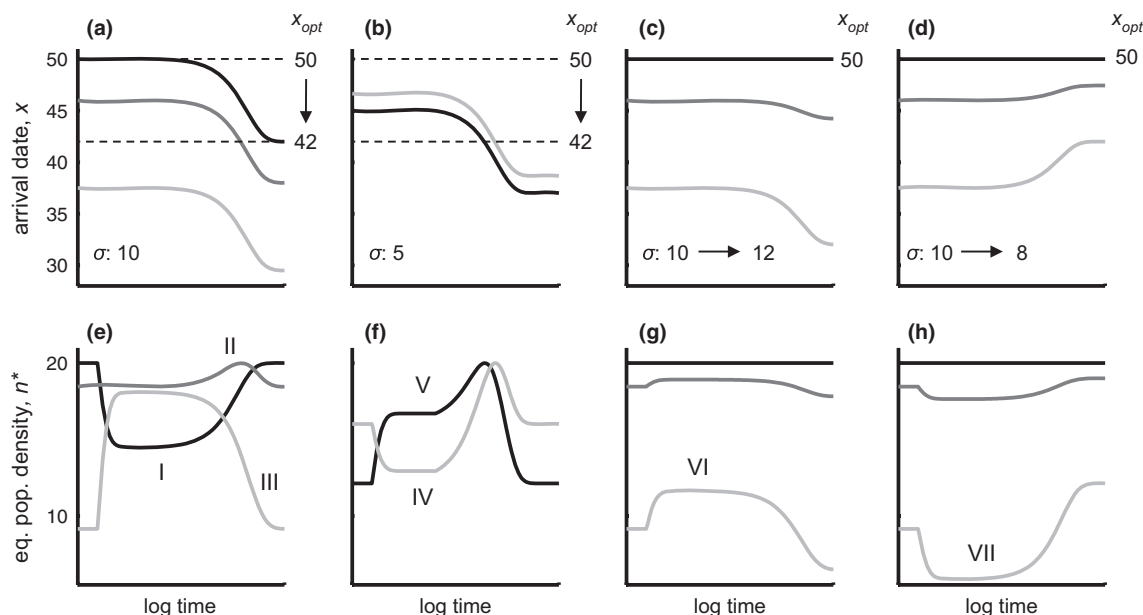


Figure 3 Evolutionary changes in arrival dates (a–d) and in equilibrium population densities (e–h) during the transition to a new ESS after environmental change. Lines with similar shades of grey in upper and lower panels represent populations with a certain competitive advantage of early arrival. The numbers I–VII represent qualitatively different population dynamic trajectories (e–h). Parameter changes representing environmental changes are indicated in a–d. In b and f σ is set to a lower value compared to other examples to enhance visibility and $a = 0.13$ and 0.2 for the shaded and solid line respectively. Non-changing parameters and values of the parameter a for the differently shaded lines are otherwise as in Fig. 2.

game results in an ESS that is mismatched to the environment (cf. Kokko 1999). From this starting point, environmental changes may reduce the mismatch and lead to a temporary boost of fitness and population densities before the advantage of being early anew starts an evolutionary down-hill race (III in Fig. 3e). Interestingly, a historically early phenology does not guarantee that an advancement of the reproductive peak improves fitness. If the historical mismatch is relatively small compared to changes in the reproductive peak, the population density may initially increase, decrease or remain constant (II, IV and V in Fig. 3e and f).

It is noteworthy too, that changing the season length in our model provides yet another case where a phenological response should be expected from evolution, even though the fitness-maximising strategy (x_{opt}) is unaffected. The trajectories with evolutionary overcompensation to ecological responses (VI and VII in Fig. 3g and h) add to the number of response patterns that are possible when taking evolutionary games into account. It has previously been highlighted that specialist species that are dependent on a resource or abiotic conditions with narrow extension in time are more sensitive to environmental changes than generalist species for which this period is longer (Durant *et al.* 2005; Miller-Rushing *et al.* 2010). It has also been shown that changing the resource distribution could affect the ESS arrival date in a game theoretical model of bird migration (Jonzén *et al.* 2007). Our model complements these findings by showing that the short-term response of the population density to changes in σ can be qualitatively different compared to the long-term response.

The wide array of potential eco-evolutionary responses to climate change that we find has implications for the interpretation of studies relating population trends to changes in phenology. Jones & Cresswell (2010) analysed population trends from 193 Nearctic and Palaearctic bird populations and how they were related to an index of phenology mismatch, calculated as the difference between wintering and breeding temperature trends. Most notably, the interspecific variation is striking and, in the light of our study, it is not surprising that there is no clear and unequivocal relationship between phenology mismatch and population trend. The species analysed may very well differ in the degree of historical mismatch, the exact penalties for too early and/or late arrival, which would generate variation in observed phenology and population patterns even if they experienced exactly the same environment.

Another related example is given by a study of European breeding birds that have, in general, advanced their spring arrival time (e.g., Rubolini *et al.* 2005). Interestingly, species showing no or only weak phenological change, expressed either as change in mean/median arrival date (Møller *et al.* 2008) or degree-days (Saino *et al.* 2011), tend to decrease in population size. The interpretation is that species that have not responded phenologically to climate change are in decline due to increased mismatch with food resources needed for successful breeding. Our study shows, however, that adaptive responses to e.g. an advanced food peak, also may result in a lower equilibrium population size (Fig. 3e). It should be noted that to be able to interpret our model in terms of reproductive mismatch we need to assume that timing of arrival and timing of breeding are strongly correlated. Although not applicable to all species (e.g., Lourenço *et al.* 2011) this is still a reasonable assumption, especially for late arriving birds such as tropical migrants. The existence of the different possibilities illustrated in Fig. 3 makes it hard

to make long-term predictions from short-term observations even in situations where the environmental change itself is not particularly complex. In fact, our results show that short-term and long-term responses need not be correlated at all.

Our predictions are based on the assumption that phenologies are mismatched to environmental conditions due to evolutionary games. In general, and as mentioned in the introduction, apparent mismatches in phenology may also be caused by life history trade-offs, coevolution and other mechanisms. Historical mismatch could also be non-adaptive, e.g. due to genetic constraints, as discussed by Singer & Parmesan (2010). Including such mechanisms in similar models for comparisons provide interesting avenues for future research. Another interesting extension could be to include individual differences in the model and structure the population by e.g. sex to include different selection pressures in males and females (e.g. Spottiswoode & Saino 2010). Extensions into that direction would also enable closer connections to stage-structured model approaches to study demographic effects of climate change. Such models have been applied to study effects of changes in seasonal environment e.g. for birds (Jenouvrier *et al.* 2009), mammals (Ozgul *et al.* 2010) and plants (Marrero-Gómez *et al.* 2007). However, due to the assumption of density-independence often made in these models, they typically predict either growth or decline of a population. Our results suggest, however, that short- and long-term effects of population densities may differ substantially. Therefore, continuing to build in density dependence and evolution into structured projection models (e.g. Coulson & Tuljapourkar 2008; Caswell 2009) may prove critical to fully understand phenological responses to climate change.

Finally, our study meshes well with a recent call for a more explicit consideration of variation in the strength of selection and of the eco-evolutionary landscape (MacColl 2011). Several studies have shown that evolutionary games may favour phenologies that do not maximise fitness (Iwasa *et al.* 1983; Kokko 1999; Law *et al.* 2001). It has also been shown that responses of the ESS phenologies to environmental changes differ quantitatively and qualitatively from responses of fitness-maximising strategies (Johansson & Jonzén 2012). Herein we add to the picture that mismatches owing to evolutionary games modify population dynamics during adaptation as well. Taken together, these different developments beg the question of whether game theory is indeed the missing link for explaining the often poorly understood biological responses involving phenological shifts in data (Knudsen *et al.* 2011). To move forward on this point, this article offers plenty of scope for continued research to improve predictions of ecological responses to climate change.

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AUTHORSHIP

JJ conceived and analysed the model. The authors jointly interpreted the biological implications of assumptions and results. JJ designed

and wrote the first draft of the ms and both authors contributed substantially to revisions.

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