Evolutionary and demographic consequences of phenological mismatches

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Abstract

Climate change has often led to unequal shifts in the seasonal timing (phenology) of interacting species, such as consumers and their resource, leading to phenological 'mismatches'. Mismatches occur when the time where resource demands of the consumer species are high does not match with the period when this resource is abundant. Here, we review the evolutionary and population consequences of such mismatches and how these depend on other ecological factors, as, for example, additional drivers of selection or density-dependent recruitment. This review puts the research on phenological mismatches into a conceptual framework, applies this framework beyond consumer-resource interactions, and illustrates this framework using examples drawn from the vast body of literature on mismatches. Finally, we point out priority questions for research on this key impact of climate change.

Introduction

Phenology, the seasonal timing of life-cycle events, is generally important for individual fitness because for each of these events a period exists during which environmental conditions are most advantageous, i.e. an 'optimal time window'. For many species and phenological events this 'optimal time window' is set by the phenology of other species. Many species have shifted their phenology in response to global climate change, but species often do not shift at the same rate[1–4]. For example, terrestrial invertebrates shifted faster (4.1 days per decade) than terrestrial vertebrates (2.6 days per decade)[5]. When the phenologies of interacting species, such as consumers and their resource, shift at different rates[3], this may lead to a mismatch in phenology[4].

Mismatches between the phenology of resource and consumer should affect demographic rates of the consumer due to reduced reproductive success or survival. They can also lead to

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selection on seasonal timing of the consumer because individuals that are better matched to the phenology of the resource will have a higher fitness than individuals that are less well matched. To address the consequences of mismatches from both a population and evolutionary perspective, we will discuss a conceptual framework of mismatch that goes beyond the often studied consumer-resource interactions, and that clearly outlines evolutionary and population consequences of mismatches. We will illustrate this framework with examples from the vast literature on consume-resource mismatches and end by presenting priority questions for further research.

Conceptual framework

Mismatched phenology

The mismatch concept was introduced as a 'critical period' by Hjort[6] and extended by Cushing[7], who termed it the 'match-mismatch hypothesis' in his study on the annual variation in recruitment in fish populations in marine ecosystems. In this usage of the term, mismatches are said to occur when the time in the annual cycle when resource demands of the consumer species (*i.e.* predators, herbivores) are highest does not match with the period when its resource (i.e. prey, plants) is most abundant[8–12] (Fig. 1A). Instead of using mismatch, other authors have used the terms "synchrony" and "asynchrony"[13–16].

Much of the research on the match-mismatch hypothesis focused on the timing of the consumer peak resource demands, which has to match the timing of the peak resource availability. A more precise measurement of mismatches than this difference in peak phenology would be to measure the temporal overlap between the distributions of demands and availability[11,13], but see[17]. The height of the resource peak will also be of relevance: in years or areas where resources are plentiful it is likely that a (mild) mismatch will not have any negative effects on the consumer.

More recently, the match-mismatch framework has also been applied to species interactions other than consumer and resource, for example, pollinators and plants (e.g. [18]) or host and parasites (e.g. [19]) but also competing species (e.g. [20]). In the following, we will, however, focus on mismatches between consumers and their resource because this kind of mismatch has been most frequently studied. We will discuss these other kind of mismatches in the Outlook.

Why mismatches occur

A key issue of seasonal timing is that in many biological systems the optimal time for phenological events varies from year to year depending on environmental conditions. To track this inter-annual variation, seasonal timing is often phenotypically plastic[21,22]. Individuals are either directly constrained by environmental variables, for example, due to their ectothermic physiology or use environmental variables (termed 'cues') that are predictive of the 'optimal time window' to adjust their phenology[23]. The two cues most relevant for phenology are photoperiod and temperature[24] but also rainfall[25] and development of vegetation[26] have been shown to play a role.

Species differ in the relative importance of the different variables that affect their phenology, and in the ways they respond to them. Mismatches between trophic levels can thus occur because the cue used by one trophic level has changed at a different rate than the cue used by the other trophic level e.g. 5,27,28,29. Even if two species both rely on temperature, these cues are often temperatures during different periods in the year. Climate change has not led to a uniform increase in temperatures over the entire year (e.g. 30) and these unequal increases in temperature can thus easily lead to differential phenological shifts, and thereby to mismatches31–33.

Another reason why mismatches may occur due to climate change is that the predictability of the phenology of the interacting species is limited. The cues used by consumers are predictive for the annual timing of their resource peak, but this predictability is not perfect as in almost all cases the environment that affects the decision-making on the phenology of a life-cycle stage is not the same as the environment that determines resource phenology, i.e. the environment of the selective drivers on this stage32. This imperfect cue reliability leads to the selection on consumers to being less sensitive to the cue than their resource. Thus, the phenotypic plasticity of phenology relative to temperature is predicted to be weaker in consumers than in their resource and hence climate change will lead to a weaker phenological advancement of predators than the advancement of their prey, leading to mismatches8,31,34–38.

Evolutionary consequences of mismatches at the individual level

Mismatches can lead to selection on phenology if better-matched individuals have a higher fitness than less well-matched individuals. If consumer phenology is heritable, this selection should lead to an evolutionary response. In the following we will discuss the difference between mismatch and 'mistiming' and whether mismatch will necessarily lead to mistiming39.

For most traits there is an optimal phenotype and an individual's fitness will decline the more their phenology deviates from the optimal phenotype. Mistiming (rather than mismatch) is then defined as the deviation between the actual (either of the individual or the population) and the optimal phenotype (Fig. 1B). Depending on the phenological event, different fitness components can be affected, for example, reproductive success in case of breeding or survival in case of migration phenology. When the fitness of the consumers depends solely or very strongly on the consumer mismatch with resource phenology, as for example in many bird species reproductive success depends on food phenology8,34–38, mismatches lead to selection on phenology37 and thus mismatch equals mistiming.

However, if fitness depends (additionally) on other ecological variables, there may be no relationship between mismatches and mistiming. For example, pre-breeding survival of long-distance migrants may be affected by temperatures upon arrival40 and this additional fitness component may alter the optimal breeding time to a later date as inferred from mismatch only. Since selection on a trait depends on whether total fitness, i.e. the net effect of all fitness components, co-varies with the trait, true mistiming may also depend on environmental variables other than only mismatch, as, for example, the cost of egg-production under potentially still adverse conditions in early spring39,41. In that case,

animals may be optimally mismatched, *i.e.* fitness of the consumer is maximized at some degree of mismatch with the peak in resource availability (Fig. 2a)[39].

Optimal mismatches can also be caused by a non-symmetrical fitness curve for consumer phenology relative to the timing of peak abundance of its resource because the consumers' phenology will have evolved to be away from the 'fitness cliff'[41–43]. Such asymmetric 'fitness landscapes' can arise through the combination of different fitness components (Fig. 2b). In the Edith's checkerspot butterfly (*Euphydryas editha*) there may be life-history trade-offs between fecundity and mortality that can lead to optimal mismatches[14]. In migratory birds, frequency-dependent competition for breeding territories can result in asymmetric relationships between reproductive success and arrival date to the breeding grounds, even though the fitness landscape determined by breeding resources might have a symmetrical distribution[44,45]. A similar argument can be made when the costs of egg production are dependent on timing[46,47] and thus a better match between offspring needs and resource availability will reduce fitness due to the fitness costs of producing eggs early in the season when conditions are still harsh[39] (see also Johansson[48] for an overview about such complex evolutionary consequences of mistiming).

While many studies reported potential mismatches between trophic levels (e.g. 1,15), the number of studies showing that these mismatches lead to selection, i.e. that individuals were truly mistimed, is more limited[8,34–38]. These studies generally reported increasing selection with increasing mismatch but some studies lack data on resource phenology and only used temperature as a proxy for mismatch[34,35,38]. This limited evidence for mismatch driving selection on phenology can be explained by the logistical challenges of obtaining individual-level data on mismatch and fitness in wild populations, which also limited such studies to mainly birds and mammals.

Evolutionary consequences of mismatches at the population level

At the population level, mismatches can lead to directional selection on phenology. If the optimal time window for consumer phenology is narrow (compared to population-level variation in phenology), fitness will increase and decrease sharply with increasing and decreasing synchrony between individual phenotypes and the optimal phenotype leading to (strong) stabilising selection. If the optimal time window is shifted relative to the consumer phenology and the majority of individual phenotypes occur earlier (or later) than the optimal phenotype, there is directional selection for earlier (or later) phenology.

When a population is mistimed, the resulting directional selection on timing may lead to genetic changes, i.e. to micro-evolution, but due to the difficulties of detecting genetic change in wild populations the number of studies on this is even more limited[49]. One well documented example comes from egg hatching in winter moths where climate change has led to a too early hatch date relative to the timing of bud burst of the host plants[16]. Over a decade selection has now led to genetic adaptation and hatching date has shifted to later dates[50].

Population consequences of mismatches

To analyse the effects of mismatch on demography, the demographic rate of interest is often regressed against 'population mismatch': the difference between the mean population phenology and the resource phenology (i.e. the overall mean of individual mismatches)[37] (Fig. 3a,b). When individual mismatch is an important driver of selection, i.e. when mismatch has a strong effect on fitness, population mismatch will affect demographic rates, such as population offspring production or mean adult survival. This link between population mismatch and demographic rates can, however, be complicated by the fact that the 'height' of fitness landscape may differ among years (Fig. 3b). Theoretically, variation in resource height could correlate with (population) mismatch, which would lead to complex relationships between mismatch and demographic rates.

Even when population mismatch affects demographic rates, there may not be a clear effect on population numbers. Density dependence can buffer these effects when for instance recruitment rates of offspring decrease with the number of offspring produced. This has been shown in great tits where population mismatch led to lower number of fledged offspring, but where recruitment of these offspring was higher in years with low offspring production (because density-dependent winter survival increased juvenile recruitment) and hence there was no detectable effect of population mismatch on population growth rate[51]. This shows that inferring negative effects of mismatch on population dynamics without demonstrating this link in the data (e.g. 35,52,53–55) may be problematic.

A number of studies found negative effects of mismatched phenology on demographic rates, mostly reproductive success, in terrestrial[34,56–58], freshwater[28] or marine systems[59,60]. For example, in caribou (*Rangifer tarandus*), roe deer (*Capreolus capreolus*) and arctic breeding geese increased temperatures led to a phenological mismatch between timing of reproduction and plant growth phenology, which reduced reproductive success[56–58]. Similarly, increasing mismatch between breeding time in common murres (*Uria aalge*) and the timing of inshore migration of their main prey, the capelin (*Mallotus villosus*), reduced reproductive success despite increased adult foraging effort[60].

Unfortunately, the number of studies that analysed the effect of mismatch on both demographic rates and natural selection on the trait is even more limited (e.g. 34,36,51), which limits our ability to reliably predict eco-evolutionary consequences of mismatch and hence the likelihood of successful adaptation to climate change. Interestingly, none of these studies found demographic consequences of selection for various reasons. In one case, mismatch increased selection on breeding time in great tits and expectedly reduced reproductive success but population growth was unaffected due to density-dependent winter survival [51]. In another case, demographic rates of wheatears (*Oenanthe oenanthe*) declined markedly simultaneously with a reduction in 'thermal matching', which is a proxy for phenological match between the consumer and its resource[34]. Selection, however, did not increase and even changed from directional to more or less absent. This counterintuitive finding could be explained by relaxed selection on arrival time, mediated by reduced competition for high-quality territories, due to low population sizes[61].

Priority questions for the field

Below, we outline four priority research questions in the field of phenological mismatches.

1 Eco-evolutionary interactions of mismatches

As highlighted above, mismatches can have evolutionary (through selection) and ecological effects (through demography). These effects can even interact if, for example, reduced population density relaxes selection[34,61], which would reduce the need for evolutionary responses. Such eco-evolutionary interactions may be more common than previously thought because it is now increasingly realised that evolutionary and ecological processes can happen at similar time-scales (e.g. [62]). The evidence for such eco-evolutionary interactions is, however, likely limited by the need for individual level fitness data to quantify selection, which requires linking parent and offspring. Furthermore, it would also be desirable to explore the (quantitative) genetics of phenological traits to assess whether they could respond fast enough to selection. Studies quantifying selection and (quantitative) genetics have been mostly limited to mammal and bird species for logistical reasons but the increasing availability of genomic tools for 'non model' species could potentially overcome these hurdles[63,64].

2 Experimental approach to fitness consequences of mismatches

Key to the match-mismatch hypothesis is that there are negative fitness effects of being mismatched. To asses fitness consequences of mismatch most often correlative data are used (e.g. [8,34–37]). However, there is a large body of literature from life-history theory that shows that to establish the true, causal link between a trait, here phenology, and fitness, experimental work is needed where individuals are shifted on the timing (mismatch) axis and their fitness is measured (see [65] for a review). Such experimental work that assessed whether mismatches are indeed mistiming is extremely rare. One example is where flowering time of plants was experimentally manipulated in the green house and then visitation rates, as a proxy for pollination, measured[66]. To determine how often mismatches indeed lead to selection as opposed to reflecting pre-existing adaptive mismatches, or adaptive responses to environmental change (i.e. individuals maximize their fitness even when they are mismatched with the phenology of their resource), more experimental work is needed.

3 Mismatches in interactions other than consumer-resource

Most of the reported instances of mismatches concern mismatches between consumers and their resource but obviously other types of species interactions, such as predation risk, competition and mutualism, can also become mismatched. Another potential area where mistiming can occur is between life-cycle stages 'within' a species (see Box 1).

Studies on mismatches between consumers and resource typically studied demographic or evolutionary consequences for the consumer but ignored consequences of altered phenological match for the resource[67]. For example, in the UK, newts (*Triturus spp.*) now enter ponds earlier, whereas frogs (*Rana temporaria*) did not advance their breeding phenology. As a consequence, the larvae of the frogs are exposed to higher levels of newt

predation68. Increasing temperatures increased the overlap in autumn migration times of long-distance migratory birds and one of their avian predators, the sparrowhawk (*Accipiter nisus*), while they decreased the overlap between short-distance migrants and sparrowhawks, but population consequences remained unclear69. However, the consequences of mismatches do not need to be of similar importance for the different trophic levels70. For instance, while for the predator it may be important to be matched with the phenology of its prey, predation may not be an important selection pressure on the phenology of the prey, as in the case of the great tit and their caterpillar prey. As these temporal distributions of predation risks are much harder to measure, more studies on predation risk phenology are needed.

Mismatches may also play a role in competition. For example, increasing temperatures altered the competitive interactions between bird species or plankton species and thereby equilibrium population densities or community structures20,71. In the case of mutualisms, for example between plants and pollinators, species are also likely to become mismatched with each other since climate change affects different trophic levels at different rates18. However, whether such mismatches will have consequences depends on the degree of specialisation and the asymmetry of the mutualism. For example, certain plant species can only be fertilised by a single insect species, such as the early spider orchid (*Ophrys sphegodes*) that depends almost exclusively on a solitary bee species (*Andrena nigroaenea*) for pollination. Differential shifts in the phenology of these species would have negative effects for the plant but not for the bee72. More generalist plant species are, however, less likely to entirely miss out on being pollinated66 but generally mismatches between plants and pollinators and potential demographic effects are not well studied18.

Parasites obviously depend on their hosts being present or vulnerable, which generally varies seasonally73. Differential shifts in parasite and host phenology can hence also lead to mismatches. For example, migration time of common cuckoos (*Cuculus canorus*) and some of their host species have advanced at different rates55, while (experimental) temperature increases led to a strong mismatch between the phenologies of a trematode (*Ribeiroia ondatrae*) and its amphibian hosts19. Such mismatches could have strong consequences for parasite or host population dynamics, potentially leading to local extinction of the parasite74.

Increasing temperatures do not only affect biological processes but also agricultural practices. For example, in Finland sowing or mowing dates have shifted, which can lead to mismatches between these practices and breeding time of farmland or meadow birds, possibly negatively affecting their reproductive success and population numbers75. Mismatches may also have consequences for biochemical processes but these are hardly explored. For instance, a mismatch between the geese grazing and plant growing season in arctic coastal wetlands affected the greenhouse gas fluxes76.

4   Community ecological effects and ecosystem consequences

Most research on the match-mismatch hypothesis focuses on pairwise predator–prey, plant–herbivore or plant– pollinator interactions. However, the selection on phenology of a focal species depends on the (mis)matched phenology with the many species it interacts with. For

example, a plant that is pollinated by many different insect species will not suffer from mismatch with a single species (e.g. 66). The challenge is to scale up from pairwise interactions to more complex food webs. Only via a better understanding of entire food web phenology we can understand community77 and possibly ecosystem-level consequences of climate change induced shifts in phenology78. Some pionering work has been done in this area, in food web models that involve phenological shifts79,80 and in plant – pollinator communities 81–84. The way forward is to assess the strength of the connections between the different species in the food web, and then determine how these change due to the differential shifts in phenology of the different species. Then using network theory, the properties of the networks prior to the shifts in phenology and after the shifts in phenology can be assessed, to evaluate for instance whether the network has become less stable. For this, detailed experimental work is needed for instance in simplified food webs where the phenology of the species can be manipulated. This is, however, not a trivial challenge.

Concluding remarks

Phenological mismatches are one of the clearest consequences of climate change and over the past two decades an impressive body of literature has been build up. We have outlined a conceptual frame-work and illustrated this with key-examples from this body of literature. Challenges for the next decade are to further study the population and evolutionary consequences of mismatches, for which long-term studies are essential, and from there move on to community ecological effects and ecosystem consequences. Ultimately, what is needed is to link climate change predictions to the predicted degree of mismatch in species interactions and networks, taking evolutionary changes into account, and from there assess the consequences for biodiversity and ecosystem functioning. Such information is essential to link climate predictions to consequences for nature, which is needed for such consequences to play a role in the debate on the acceptable rate of global climate change85.

Acknowledgements

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Box 1

Mistiming in annual life-cycles

Differential shifts in phenological events may not only happen between species but also between different life-cycle stages within an individual as these life-cycles stages may respond differently to a cue[48,86]. Some life cycle events will be more sensitive to photoperiod (as, for example, moult in birds[87]) while others are more sensitive to temperature (such as reproduction[5]). Such different sensitivities can lead to differential shifts in the phenology of these life-stages due to climate change[12,88,89] provided that there are no strong effects of one life-cycle stage on the phenology of the next stage. Examples of differential shifts in the phenologies of coupled life-history traits are arrival date and breeding date in migratory birds, where a lack of the shift in arrival date could potentially constrain shifts in breeding phenology[90,91]. However, changes in temperature can also lead to differential shifts in reproduction and moult. For example, in pied flycatchers (*Ficedula hypoleuca*) moult is comparatively less sensitive than reproduction[86]. In red deer (*Cervus elaphus*) the phenologies of six traits were measured over a 28-year period[92], and in female deer, parturition dates advanced almost twice as fast as date of first oestrus. In males, antler casting and cleaning advanced at a similar rate but the end of the rut shifted twice as fast as its start dates. Clearly, mistiming within the annual life-cycle could be very common.
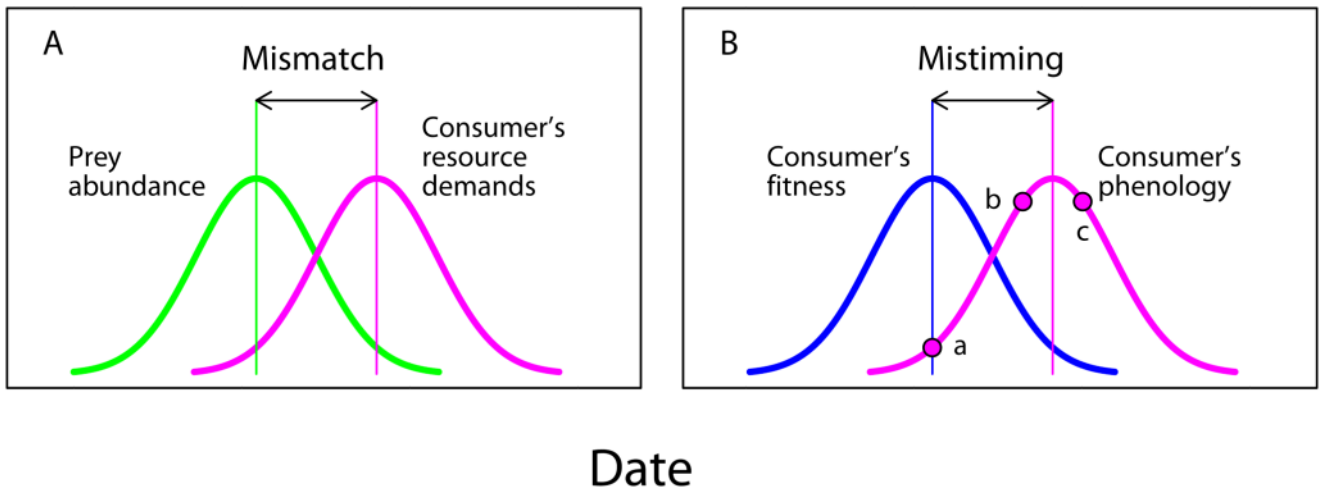
Fig. 1.

Definitions of mismatch and mistiming. (A) Mismatch occurs when the time in the annual cycle where resource demands of the consumer species are highest does not match with the period where this resource is most abundant. (B) Mistiming occurs when the phenology (of either the individual (dots) or the population (vertical line)) deviates from the date at which fitness peaks, which will then lead to directional selection for either earlier (as depicted here) or later consumer phenology. Individual (a) is well-timed with the fitness optimum, while individuals (b) and (c) are too late and hence mistimed.
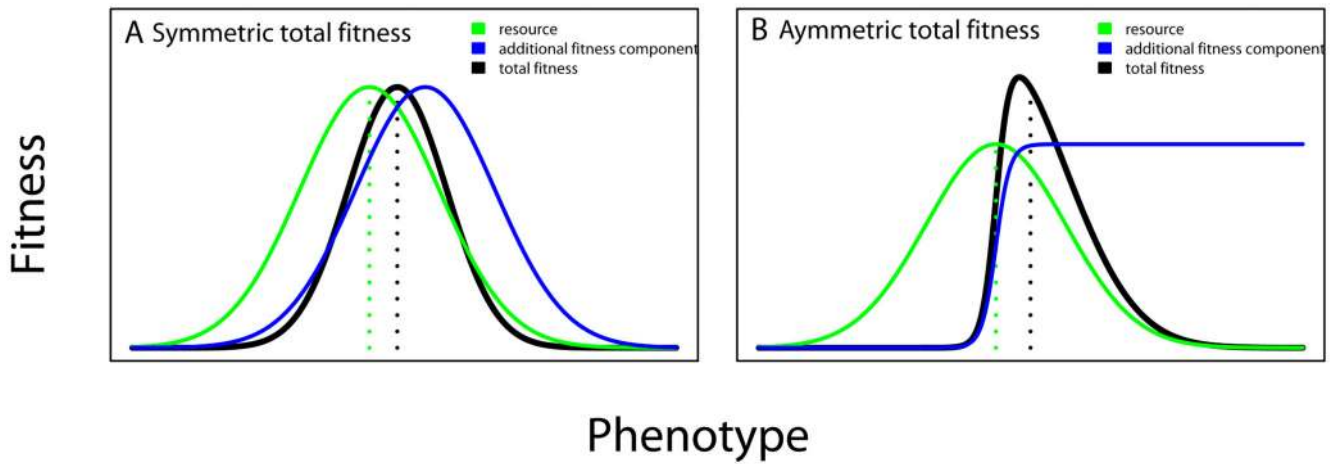
Fig. 2.
Optimal mismatches caused by multiple fitness components of phenology. Total fitness (black solid line) is the product of fitness determined by resource phenology (green solid line) and another fitness component (blue solid line). In (A) the later fitness optima of the blue fitness component, e.g. fledgling survival probability due to predation, leads to a later optimal fitness and hence an optimal mismatch (difference between green and black dashed vertical lines). In (B) also the shape of the blue fitness component, e.g. adult pre-breeding survival, leads not only to a later peak of total fitness but also to an asymmetric total fitness curve, which will shift the optimal phenotype to an even later date when the environment varies through time (black dotted line). The overall outcome is an optimal mismatch (difference between green and black dashed vertical lines).
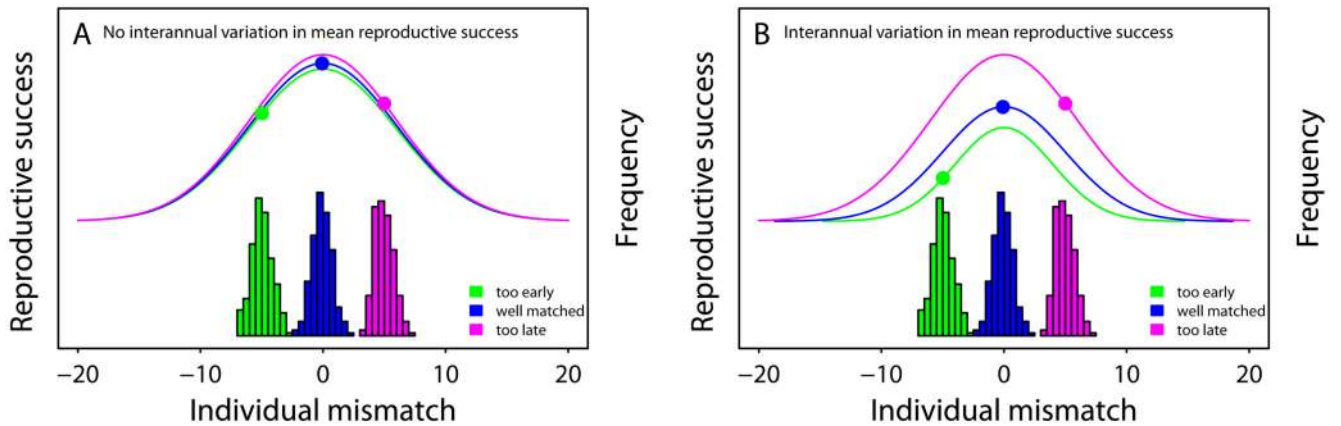
Fig. 3.

Relationships between mismatch and reproductive success at the individual and population level. The coloured lines depict fitness curves in relation to individual mismatch for three different scenarios of mismatch (green: too early, blue: well matched, red: too late) indicated by the three frequency distributions of individual mismatch. The dots on the fitness functions indicate population mean fitness for each scenario. In (A) the height of the fitness curves of three scenarios is similar. This means that population mean reproductive success is only a function of population mean mismatch: If the population is on average too early (frequency distribution of phenology in green) or too late (red) it has a reduced population mean reproductive success (cf. dots on fitness curves). In (B) the height of the fitness curves differ: It is lowest when the population is too early (green curve and green frequency distribution) and highest when the population is too late (red curve and red frequency distribution). This leads to an increase of population mean reproductive success with mismatch (cf. dots on fitness curves), because mean mismatch covaries positively with the height of the resource peak. Note that the units of mismatch and the relationship between population mean mismatch and the height of the fitness curve have been chosen arbitrarily (this works the other way around too, i.e. a negative covariance between mean mismatch and the height of the resource peak).

Fig. 4.
Examples for mismatch affecting reproductive success: In common murres (*Uria aalge*, top left), great tits (*Parus major*, top right), caribou (*Rangifer tarandus*, bottom left) and roe deer (*Capreolus capreolus*, bottom right) mean breeding success is reduced in years with an increased population-level mismatch between breeding phenology and the phenology of the main food resource. Picture credits and licenses: Melissa McMasters CC-BY, Luc Viatour CC-BY-SA, Andreas Eichler CC-BY-SA, Alexandre Buisse CC-BY-SA (clockwise from top left).