Seminar Module 5

Phenological Mismatches: Causes and Consequences

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Goals For Student Learning

This seminar module was created to help students:

- Understand the biological significance of phenological mismatches
- Understand how phenological mismatches are identified and studied
- Familiarize themselves with phenological research focusing on marine ecosystems

Phenological mismatches

In ecological communities, interspecific relationships are often mediated through interactions between different **trophic levels**. For example, photosynthetic plants are primary producers that are eaten by primary consumers, such as herbivores, which may in turn be eaten by carnivorous (predatory) secondary consumers. Such interspecific trophic interactions are quite intimate, and in many cases, highly specialized. Moreover, these interactions often help regulate population growth, preventing populations of primary producers, consumers, *and* predators from either increasing out of control or becoming extinct. A large and growing body of research suggests, however, that species' phenological schedules respond differently to climate change. The potential for **phenological mismatches** to disrupt community trophic interactions has thus been a long-standing source of concern for the scientific community.

In a now classic study based on 23 years of monitoring, Visser et al. (1998) reported a climate-mediated phenological mismatch between food abundance and the timing of egg laying in a Dutch population of the European bird species *Parus major*. One key result of their study was that despite strong selection favoring early egg-laying, the phenology of egg-laying at their study site did not shift in tandem with changes in the peak availability of their food source.

More recent studies in other systems show that phenological mismatches may profoundly affect both marine and terrestrial communities. Edwards and Richardson (2004) evaluated long-term interactions among 66 taxa representing five trophic levels in a marine ecosystem. The study presented in this module reported that numerous **functional** groups are responding to climate change and that the magnitude of phenological responses to climate change differs among **trophic levels**. For six years between 1993 and 2006, Post and Forschhammer (2008) monitored the phenology of a single caribou population in West Greenland, as well as the phenology of plant species upon which caribou graze. The researchers detected a phenological mismatch between the caribou and their food source, and found that an index of trophic mismatch was correlated with observed declines in caribou calf production and survivorship.

Articles To Read

Edwards, M., and A. J. Richardson. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. Nature 430:881-884.

Post, E., and M. C. Forchhammer. 2008. Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. Philosophical Transactions of the Royal Society B-Biological Sciences 363:2369-2375.

Visser, M. E., A. J. van Noordwijk, J. M. Tinbergen, and C. M. Lessells. 1998. Warmer springs lead to mistimed reproduction in great tits (*Parus major*). Proceedings of the Royal Society of London Series B-Biological Sciences 265:1867-1870.

Suggested Discussion Questions

1. Why did Edwards and Richardson (2004) use changes in **sea surface temperature (SST)** as an index of climate change?

2. What do Figures 1 and 2 in this article suggest about phenological shifts in different trophic levels in the open ocean? (Edwards and Richardson 2004)

3. What is a major difference between pelagic and terrestrial ecosystems with respect to the timing of peak productivity? (Edwards and Richardson 2004)

4. Phenological monitoring efforts in terrestrial systems often focus on measuring discrete traits, such as the timing of flowering and animal migration/emergence, to quantify phenological changes over time. How did Edwards and Richardson (2004) measure phenology in a pelagic setting?

5. Describe the general study design used in Visser et al. (1998). How (if at all) do Figures 1 and 2 support the general conclusions drawn by the study's authors?

6. What do **selection differentials** estimated across time suggest about the evolution of egg-laying phenology in *Parus major?*

7. Visser et al. (1998) studied one population in the Netherlands, yet *Parus major* occurs throughout much of Europe. Would you expect to see similar results to this study elsewhere? Why or why not?

8. What are some implications with respect to population persistence of Visser et al.'s (1998) findings? Look up some peer-reviewed articles on *Web of Science* or *Google Scholar* to see what ongoing phenological monitoring of *P. major* has shown.

9. Describe the index of trophic mismatch used by Post and Forschhammer (2008) to quantify the phenotypic mismatch between caribou calving and food availability. What

was their justification for using this index? Do you think that it would be appropriate to use a similar index to quantify mismatches in the population of *Parus major* studied by Visser et al. (1998)? Why or why not?

10. After reading these articles, what do you think is necessary for researchers to confirm that a climate-mediated phenological mismatch is negatively affecting an ecological community?

Glossary

- **Copepod:** a small crustacean that often comprises much of the zooplankton in the open ocean. Copepods are a key food source for many fish, birds, and marine mammals.

- **Functional group:** an assemblage of species that have similar features and/or occupy similar trophic levels. For example, the term "plankton" broadly refers to a functional group comprised of species that drift in the open ocean and seas.

- **Holozooplankton**: planktonic organisms that spend their entire lives as plankton.

- **Merozooplankton:** species of planktonic larvae that drift in the open ocean and eventually develop into non-planktonic juveniles and adults. The group merozooplankton includes organisms such as (but not limited to) mollusks, enchinoderms, and fish.

- **Phenological mismatch:** refers to a phenomenon in which the phenophases of two or more interacting species change in such a way that the interaction can no longer occur. For example, a phenological mismatch may occur when the timing of the demand for a given resource does not change (e.g., a bird population may consistently seek and depend on a particular insect species as its food source at a particular time of year), but the timing of that resource's availability *does* change in such a way that it is no longer available to its consumer (e.g., the insect may emerge earlier due to climate change).

- **Trophic level**: the position in a food chain occupied by a given organism or functional group of organisms. For example, the primary producers in most marine ecosystems are photosynthetic algae (e.g., dinoflagellates and diatoms).

- **Pelagic**: a term that refers to areas of oceans and seas that are not in close proximity to land. Sometimes called the open ocean.

- **Selection differential:** an estimate of total (direct and indirect) phenotypic selection on a given trait.

- **Sea surface temperature (SST)**: the temperature of the ocean's surface

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Impact of climate change on marine pelagic phenology and trophic mismatch

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Phenology, the study of annually recurring life cycle events such as the timing of migrations and flowering, can provide particularly sensitive indicators of climate change[1]. Changes in phenology may be important to ecosystem function because the level of response to climate change may vary across functional groups and multiple trophic levels. The decoupling of phenological relationships will have important ramifications for trophic interactions, altering food-web structures and leading to eventual ecosystem-level changes. Temperate marine environments may be particularly vulnerable to these changes because the recruitment success of higher trophic levels is highly dependent on synchronization with pulsed planktonic production[2,3]. Using long-term data of 66 plankton taxa during the period from 1958 to 2002, we investigated whether climate warming signals[4] are emergent across all trophic levels and functional groups within an ecological community. Here we show that not only is the marine pelagic community responding to climate changes, but also that the level of response differs throughout the community and the seasonal cycle, leading to a mismatch between trophic levels and functional groups.

The vast majority of documented phenology studies relating seasonal shifts in biology to climate have come from terrestrial and limnological sources (see refs 5, 6). Furthermore, most studies have solely reported phenological changes for a single species and have not explored trophic and ecological interactions[7]. In this study we investigated changes in marine pelagic phenology in the North Sea across three trophic levels using five functional groups. The major functional groups included diatoms and dinoflagellates separately (primary producers); copepods (secondary producers); non-copepod holozooplankton (secondary and tertiary producers) and meroplankton including fish larvae (secondary and tertiary producers). Inter-annual changes in a measure of the timing of the seasonal peak throughout the whole pelagic production season

(the central tendency; see Methods and Fig. 1a, b) were calculated using data from the Continuous Plankton Recorder (CPR)[8], one of the longest and most spatially extensive marine biological data sets in the world.

The *x* axis of Fig. 1c shows the timing of the seasonal peaks in 1958 of all 66 plankton taxa used in the analysis; this represents the classical view of succession in the temperate marine pelagic ecosystem. Using the linear slope of the time series of the timing of the seasonal peak, we calculated the change in timing of the seasonal cycle (in months) from 1958 to 2002 for each taxon (Fig. 1c; *y* axis). Substantial temporal modifications in seasonal successional peaks have occurred over the past few decades. In particular, seasonal peaks of meroplankton have moved significantly ($P < 0.0001$) forward (for example, the phylum Echinodermata has moved by 47 days (d)). By contrast, diatom peaks in spring and autumn have collectively remained relatively static, albeit with considerable
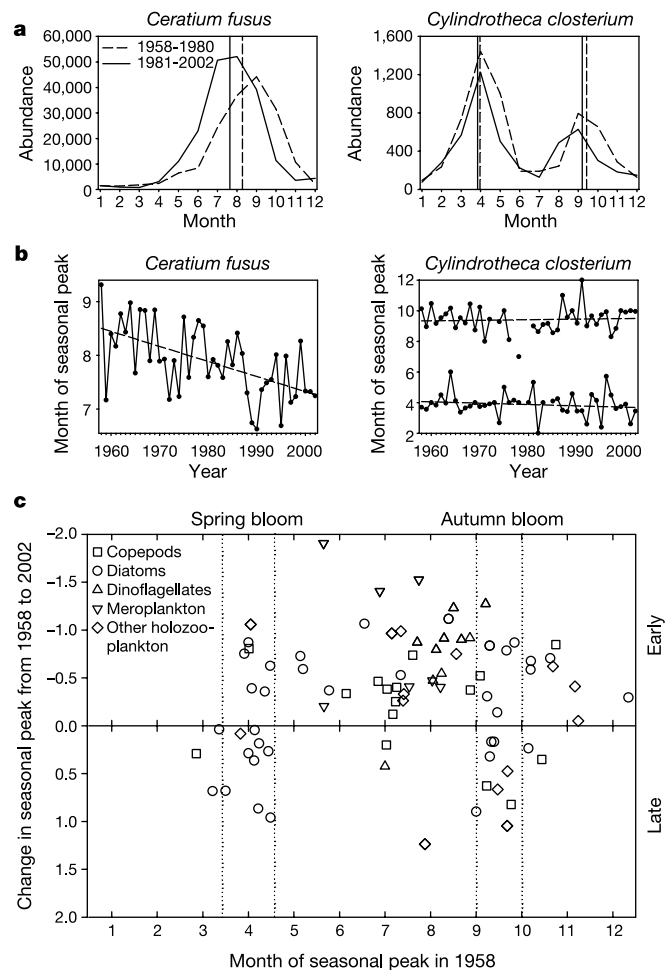
Figure 1 Changes in phenology throughout the pelagic season. **a**, Examples of seasonal cycles for two of the 66 taxa—the dinoflagellate *Ceratium fusus* and the diatom *Cylindrotheca closterium*—used in the analysis for the periods 1958–1980 and 1981–2002. The timing of the seasonal peaks, using the indicator of central tendency, is also shown. **b**, Inter-annual variability of the seasonal peak for the above two species from 1958 to 2002. **c**, The change in the timing of the seasonal peaks (in months) for the 66 taxa over the 45-yr period from 1958 to 2002 plotted against the timing of their seasonal peak in 1958. For each taxon, the linear regression in **b** was used to estimate the difference between the seasonal peak in 1958 and 2002. A negative difference between 1958 and 2002 indicates seasonal cycles are becoming earlier. Standard linear regression was considered appropriate because there was minimal autocorrelation (determined by the Durbin–Watson statistic) in the phenology time series.

inter-taxon variation. Other holozooplankton taxa (mainly of the class Malacostraca) show a wide variety of responses, although the seasonal cycles of the classes Branchiopoda (genus *Evadne*, 30 d) and Appendicularia (30 d), as well as hyperiids (order Amphipoda, class Malacostraca, 32 d) occur substantially earlier. Cycles of the majority of dinoflagellates are also earlier (principally the genera *Ceratium*, 27 d, *Protoperidinium*, 26 d and *Dinophysis*, 24 d), having

important implications for the monitoring and study of harmful algal blooms.

The general pattern observed for taxa that peak when the water column is mixed or in a transitional state is to show considerable variability in phenology, whereas taxa associated with low turbulent conditions have virtually all advanced in their seasonality (34 out of 37 taxa between May–August). The benthic larval component of the zooplankton (meroplankton) has also shown larger shifts forward in seasonality compared with the holozooplankton. During summer, meroplankton have moved forward collectively by 27 d, dino-flagellates by 23 d, copepods by 10 d and non-copepod holozooplankton by 10 d over the 45-yr study period. Diatoms as a group showed the largest variations in phenology, with particular taxa occurring both earlier and later during the spring and autumn blooms. Diatoms show a wide variety of life strategies, and, follow-ing the Sverdrup model[9], delays in the spring bloom for some species could be associated with recent increases in wind forcing in the North Sea and trends in the North Atlantic Oscillation index[10]. Collectively, however, the mean movement in the spring bloom was 0 d and the mean movement in the autumn bloom was to 5 d earlier. Many long-term phytoplankton studies have noted that the timing of the spring bloom is in fact fairly constant, occurring approxi-mately the same time each year under highly variable environmental conditions[11,12]. Other studies have also shown that the development of the pycnocline (which shows considerable geographical/temporal variability in European shelf seas) is not an essential prerequisite for the development of the spring bloom[13,14]. Recent research has implicated photoperiod in the control of diatom spore growth and germination[11,12,15]. Thus the temporal stasis in the spring bloom could be a consequence of the diatom community in this study being dominated by taxa that form resting spores.

To explore the relationship between the timing of the seasonal peak and hydro-climatic change we correlated the annual centre of gravity index for the period 1958–2002 for the five functional groups (expressed as principal components) with spring sea surface temperature (SST) (data supplied by Hadley Centre for Climate Research). We adjusted significance levels to account for temporal autocorrelation, and found highly significant correlations between the first principal component (PC1) of the peak in the seasonal cycle of summer plankton and SST (Fig. 2), particularly for dinoflagel-lates ($r = 0.69$, $P < 0.0001$; PC1 45.5% of the total variability) and meroplankton ($r = 0.70$, $P < 0.0001$; PC1 37.2%). Also during summer, diatoms ($r = 0.31$, $P > 0.05$; PC1 22%), copepods ($r = 0.55$, $P < 0.001$; PC1 33%) and other holozooplankton ($r = 0.34$, $P < 0.05$; PC1 24%) showed positive correlations between phenology and SST. By contrast, diatoms, copepods and other holozooplankton that had peaks in spring and autumn (that is, taxa with bimodal seasonal cycles; data not shown) showed no relationship between phenology and SST. For additional infor-mation on a species-by-species basis, individual correlations and their confidence limits are given in the Supplementary Information.

The relationship between SST and the seasonal development of some plankton taxa, particularly the meroplankton and holozoo-plankton, can be explained by the species-specific effects of tem-perature on many aspects of plankton physiology, such as adult mortality, reproduction, respiration, embryonic and gonad devel-opment[16–20]. Dinoflagellates may not only be responding physio-logically to temperature, but may also respond to temperature indirectly if climate warming enhances stratified conditions and/or if these conditions appeared earlier in the season. Stratified conditions are predicted to intensify with patterns of climate change in the North Sea[21]. The magnitude of changes in phenology reported in this study are greater than those from previous studies on terrestrial communities[4] and indicate that marine pelagic com-munities are particularly sensitive to climate change. These large phenological shifts have occurred with an increase in SST of 0.90 °C (estimated from regression) during the study period (1958–2002).
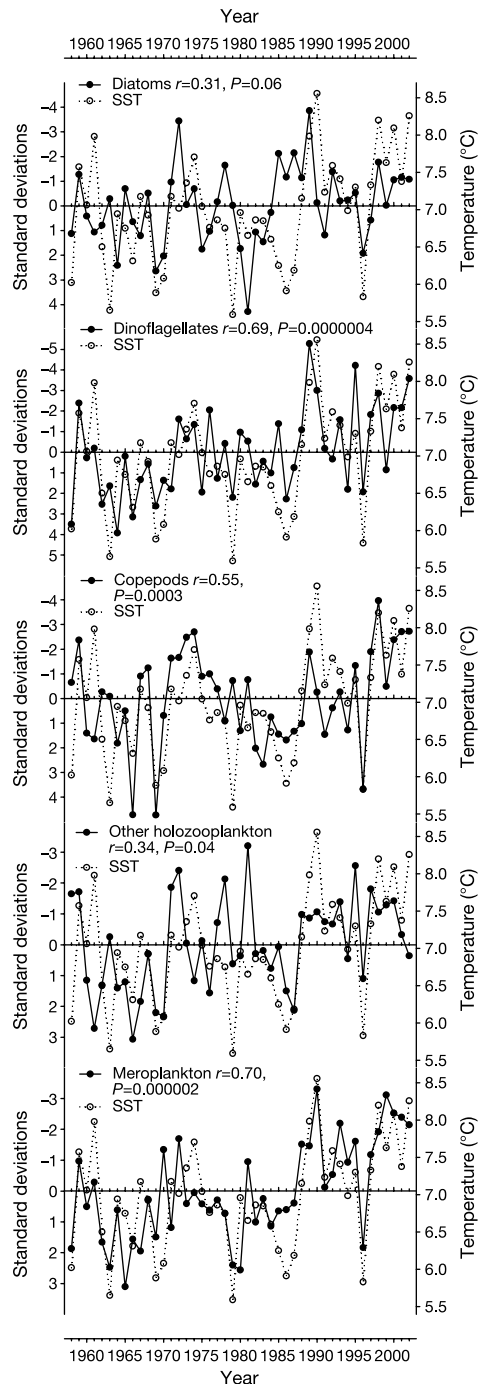
Figure 2 The relationship between the interannual variation in the timing of the seasonal cycle for various functional groups during the summer stratified period and SST. Note the high correlations for dinoflagellates and meroplankton. The time series of the timing of the seasonal cycle for each functional group was represented by principal component analysis of all constituent taxa. Negative standard deviations represent earlier seasonal cycles.

Although we have observed considerable inter-annual variability in plankton phenology, significant underlying patterns over the past few decades have emerged. Diatom blooms in spring, and hence the beginning of the pelagic seasonal cycle, have remained relatively fixed in time, and are presumably dependent on day length or light intensity[11,15] rather than on temperature-mediated physiological responses in their life strategies. Conversely, organisms that are dependent on temperature to stimulate physiological developments and larval release have significantly moved forward in their seasonal cycle in response to temperature, a trend that has continued over the last decade (with the exception of 1996, a negative North Atlantic Oscillation index year). Although many pelagic organisms are responding to climate warming, it is the intensity of the response that varies considerably amongst the pelagic assemblage. The different extent to which functional groups are moving forward in time in response to warming has led to mismatch between successive trophic levels and a change in the synchrony of timing between primary, secondary and tertiary production. Because efficient transfer of marine pelagic production to higher trophic levels, such as commercially important fish species, is largely dependent on the temporal synchrony between successive trophic production peaks[2,3], our study suggests that marine trophodynamics may have already been radically altered (notwithstanding some species adaptations), and will continue to do so in the coming decades if the climate continues to warm at its present rate. In addition to the effects of overfishing, the decline in abundance of key planktonic prey, and shifts in their seasonality, have recently been implicated in exacerbating the decline in North Sea cod stocks[22]. Planktonic phenological shifts of the magnitude reported in this study, coupled with large-scale shifts in plankton biogeography[23], will undoubtedly have a considerable effect on ecosystem function in the North Sea and may help to explain the recently reported dramatic ecological changes observed in the North Sea[24]. □

Methods

Plankton data

The CPR survey is the longest running, large-scale marine biological survey in the world. The CPR is a near-surface (10 m) plankton sampler voluntarily towed each month behind merchant ships on their normal routes of passage. Methods of analysis for ~400 phyto- and zooplankton taxa have remained almost unchanged since 1958[8]. In this study we use data from the most consistently sampled region in the entire survey, the central North Sea (55–58° N). From 1958 to 2002 all months have been sampled in this region. Species found in more than 1% of the samples were included in the analysis, as variations each year in the seasonal cycle of rarer species are not adequately estimated. To aid interpretation, species were assigned to functional groups, namely diatoms, dinoflagellates, copepods, non-copepod holozooplankton and meroplankton.

Sea surface temperature

SST was used as an indicator of climate change in the ocean because organisms respond physiologically to temperature and it has been found to be important in many terrestrial phenological studies[1]. Monthly mean gridded (1° × 1°) SSTs from a blend of satellite AVHRR (advanced very high resolution radiometer) and *in situ* observations were obtained from the Hadley Centre of the UK Met Office (HadISST). We calculated mean spring SST in the central North Sea, because this time of year is important for the seasonal cycles of many pelagic organisms. Similar results, however, were obtained for mean annual SST (data not shown).

Data analysis

Most terrestrial phenological studies have used the first arrival (for example, of migratory species such as swallows) or leaf emergence date (for example, oaks) of a particular species to describe phenological changes[25]. In the present study, we estimated the timing of the seasonal peak throughout the entire growing season (the central tendency, T) using the month co-ordinate of the centre of gravity of the area below graphs of monthly means[26,27]:

$$T = \frac{\sum_{i=1}^{12} M.x_m}{\sum_{i=1}^{12} x_m}$$

where x_m is the mean abundance in month M (January = 1, …, December = 12).

This index is sensitive to changes in the timing of the seasonal cycle (Fig. 1; see also refs 26, 27). The average seasonal cycle over the 45-yr period for each taxon was used to determine whether taxa were unimodal or bimodal (spring and autumn). A fundamental difference between terrestrial and many pelagic ecosystems is that there is just one seasonal primary production peak in terrestrial ecosystems but usually two in temperate marine

environments: one in spring and the other in autumn. During autumn, the pelagic environment reverts back to spring-like conditions, accompanied by another burst in phytoplankton production, albeit not as intensive as the spring bloom. As a result, many pelagic organisms, in particular the floral community (predominantly the class Bacillariophyceae, the diatoms, that are nutrient limited during the summer period), display bimodal seasonality. For unimodal taxa the timing of the seasonal peak was calculated throughout the entire year, whereas for bimodal taxa the timing of the seasonal peak was calculated separately for the first six months and the last six months of the year.

To summarize phenology time series of the different species within each functional group, standardized principal components analysis (PCA) based on a correlation matrix was used[28]. These PCAs based on phenology were correlated with mean spring SST and were adjusted for temporal autocorrelation using the modified Chelton method[29].

Potential biases

A possible source of bias with the central tendency index is associated with changes in the time each month that sampling takes place. Six routes are generally towed within the central North Sea, which helps to minimize bias, although mean sampling time each month has still moved forward by an average of 2.4 d over the entire period from 1958 to 2002. This is relatively small compared with the large shifts earlier of dinoflagellates (23 d) and meroplankton (27 d) over the 45-yr study (Fig. 1). In addition, the slightly earlier sampling each month, over more recent times, would actually tend to delay and not bring forward the timing of peak abundance as calculated by T, because the seasonal cycle when calculated on a monthly basis would shift to the right. To minimize the likelihood of committing type I errors when identifying changes in the timing of the seasonal cycle for each taxon over the 45-yr study period, we used a conservative significance level of 1%. For some taxa that are not speciated (for example, fish larvae) it is difficult to separate observed trends in phenology from changes in community composition caused by climate-induced biogeographical shifts. However, on the basis of the strong and consistent relationships observed between these taxa and SST, coupled with similar patterns in the majority of speciated taxa, we conclude that many components of the pelagic assemblage are responding rapidly to temperature change through changes in the timing of their seasonal cycles.

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Context-dependent autonomous self-fertilization yields reproductive assurance and mixed mating

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The evolution of self-fertilization in hermaphrodites is opposed by costs that decrease the value of self progeny relative to that of outcross progeny[1–3]. However, self-fertilization is common in plants[4]; 20% are highly selfing and 33% are intermediate between selfing and outcrossing[5]. Darwin[6] proposed an adaptive benefit of self-pollination in providing reproductive assurance when outcrossing is impossible[6–9]. Moreover, if outcross pollen receipt is inconsistent within or between years, these conditions likewise favour self-pollination[10], and this can result in a mixture of self and outcross seed production (mixed mating). Despite wide acceptance, the reproductive assurance hypothesis has lacked the support of complete empirical evidence to show that variable pollination can create both the ecological and genetic conditions favouring self-pollination. We recently showed in *Collinsia verna* that during periods of infrequent pollinator visits, autonomous self-pollination boosted seed output per flower[11], the key ecological condition. Here we show low inbreeding depression and marker-based estimates of selfing, demonstrating that when the pollination environment in wild populations necessitates reproductive assurance, selfing rates increase. We provide a complete demonstration of reproductive assurance under variable pollination environments and mechanistically link reproductive assurance to intermediate selfing rates through mixed mating.

Populations of flowering plants that lack mates or pollinators, such as those at the edge of a species' range or colonizing species, rapidly evolve autonomous self-fertilization[12,13] (within-flowers selfing without a pollen vector)[8], and this is thought to occur because selfing provides reproductive assurance[6–9]. Other ecological factors, such as unpredictable outcross pollen receipt within or

among years[8,10,12,14] may also, in theory, produce conditions that favour autonomous selfing through reproductive assurance[10,15,16]. For autonomous selfing to evolve, its benefits must be balanced against the potential costs. Alleles promoting self-fertilization ability increase in frequency because plants that carry them can serve as pollen parents in two ways: both by fertilizing ovules on other plants (that is, outcrossing) and by fertilizing their own ovules (that is, selfing)[17]. Thus, individuals with alleles that cause more selfing have an advantage in transmission over individuals with alleles for outcrossing[18]. In contrast, selfing is disfavoured when there is inbreeding depression (δ, low vigour of self progeny)[1,2] and/or when the production of selfed progeny pre-empts the production of outcrossed progeny (pollen or seed discounting)[8,16]. Previous investigations have failed to show that when outcross pollen receipt is inconsistent, selfing is favoured and outweighs these costs[19]. We are currently unable to predict when autonomous self-fertilization will provide reproductive assurance. An unequivocal demonstration of reproductive assurance under unreliable pollinators requires several types of data[4,14,19]. Plants must fail to receive outcross pollen, but this failure need not occur every season. During periods of low or no outcross pollen receipt, autonomous selfing must boost seed production. Finally, the combined costs (seed discounting, pollen discounting and inbreeding depression) must not completely negate the fitness gain of selfing.

Costs incurred by autonomous selfing vary depending both upon the timing of self-pollination relative to outcross pollen receipt[8] and the availability of pollinators. When pollinators are present, autonomous self-pollination that occurs after all opportunities for outcross pollen receipt have passed (delayed selfing) incurs no pollen or seed discounting costs[8,10]. Additionally, even if inbreeding depression (δ) is high, the survival of any progeny produced by delayed selfing always provides reproductive assurance[10]. In contrast, if autonomous self-pollination coincides with outcross pollen receipt (competing selfing), then pollen discounting, seed discounting and inbreeding depression can disfavour selfing[8]. In theory, if the fitness of self progeny produced by competing selfing is less than or equal to roughly half the fitness of outcrossed progeny (that is $\delta > 0.5$), then the fitness gain due to the transmission advantage is lost[1,2]. Finally, when pollinators are absent, there are no seed and pollen discounting costs of autonomous selfing[3,8,10,20]. In a field experiment, we previously investigated autonomous self-pollination in the winter annual wildflower, *C. verna* (Plantaginaceae). We showed that this species autonomously self-pollinates[21] in a field experiment that compared fruit set of emasculated versus control flowers (Tables 1 and 2 in ref. 11). Further, we quantified the timing of autonomous selfing by comparing both the timing of pollen deposition and the number of pollen grains on the stigmas of flowers in open-pollinated conditions relative to flowers in pollinator-excluded treatments. Selfing in *C. verna* is autonomous and predominantly delayed, with the potential for some competing selfing (Fig. 2 in ref. 11).

Because competing selfing can occur in *C. verna*, it is important to estimate the magnitude of inbreeding depression. Here we report results from three wild populations (BT, EF and TMC; see Methods) located in southwestern Pennsylvania, USA. We produced both selfed and outcrossed progeny on plants from each population and compared their lifetime performance. Mean trait values of self versus outcross progeny for each population were compared, and indicate that only one of the 15 comparisons was statistically significant (seed weight; BT population, $P < 0.001$). All three populations show markedly low average levels of inbreeding depression (Fig. 1; $\delta < 0.15$ for all traits measured, in all populations), lower than the ~0.5 value that opposes competing selfing. Additionally, previous field estimates of early inbreeding depression in the three study populations revealed no significant difference (for all six comparisons $P > 0.2$) in the fruiting success of selfed versus

Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch

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In highly seasonal environments, offspring production by vertebrates is timed to coincide with the annual peak of resource availability. For herbivores, this resource peak is represented by the annual onset and progression of the plant growth season. As plant phenology advances in response to climatic warming, there is potential for development of a mismatch between the peak of resource demands by reproducing herbivores and the peak of resource availability. For migratory herbivores, such as caribou, development of a trophic mismatch is particularly likely because the timing of their seasonal migration to summer ranges, where calves are born, is cued by changes in day length, while onset of the plant-growing season on the same ranges is cued by local temperatures. Using data collected since 1993 on timing of calving by caribou and timing of plant growth in West Greenland, we document the consequences for reproductive success of a developing trophic mismatch between caribou and their forage plants. As mean spring temperatures at our study site have risen by more than 4°C, caribou have not kept pace with advancement of the plant-growing season on their calving range. As a consequence, offspring mortality has risen and offspring production has dropped fourfold.

Keywords: caribou; climate change; global warming; plant phenology

1. INTRODUCTION

Recent studies of the effects of climate change on timing of breeding and reproductive success in migratory birds have focused attention on the phenomenon of trophic mismatch between the timing of nesting and the timing of food availability (Visser *et al.* 1998), which may reduce breeding success (Stevenson & Bryant 2000). Such a mismatch occurs because increases in springtime temperatures lead to advances in the timing of spring events such as plant growth and insect emergence on breeding grounds (Visser & Holleman 2001), while timing of migration from winter areas, which may be cued by seasonal changes in length of daylight, remains constant (Visser *et al.* 1998). Alternatively, trophic mismatch may increase if organisms on different trophic levels display differential plasticity in their responses to similar changes in climate (Høye *et al.* 2007). The ultimate consequence of trophic mismatch is population decline, due to reproductive failure or reduced recruitment, as has been documented in some European populations of the pied flycatcher (*Ficedula hypoleuca*; Both *et al.* 2006). Such mechanistic insights into indirect consequences of climate change for population dynamics are possible only through simultaneous studies at multiple trophic levels (Gunn & Skogland 1997).

As in other seasonal environments, herbivores in the Arctic display seasonal reproduction which is timed to coincide with a highly pulsed peak in resource availability (Post 2003*a*). Caribou and wild reindeer (both *Rangifer tarandus*), for instance, exhibit highly synchronous parturition that coincides with the onset of the plant-growing season (Skogland 1989; Post & Klein 1999; Post *et al.* 2003). However, both the timing and duration of the plant-growing season are expected to respond to climate change in the Arctic (Molau 1997), with the onset beginning earlier and the duration possibly shortening as abiotic constraints on phenological progression are alleviated (Post *et al.* 2001, in press). Indeed, numerous studies have already documented shifts in the timing of plant growth at high latitudes associated with recent climate change (Walther *et al.* 2002; Post 2003*b*; Forchhammer *et al.* 2005). There is, therefore, potential for development of a trophic mismatch between the timing of caribou arrival on their calving ranges and the timing of peak resource availability on-site. Such a trophic mismatch could have negative consequences for offspring production and survival in mammalian herbivores such as caribou because the energetic demands of lactation, which would otherwise be met by intake of newly emergent plant tissue at peak nutritional value, are the highest resource demands of the annual reproductive cycle (Robbins 1983; Clutton-Brock 1991).

Numerous recent studies have focused on adverse effects of recent climate change on caribou populations throughout the Arctic. In the High Arctic of Canada, a population of the endangered Peary caribou (*Rangifer tarandus pearyi*) recently experienced a catastrophic and near-total population crash associated with increasing winter snow and ice crust formation consistent with climate change projections (Miller & Gunn 2003).

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One contribution of 12 to a Theme Issue 'The boreal forest and global change'.

As well, the dynamics of multiple populations of caribou in West Greenland have become synchronized towards the end of the twentieth century in response to rising winter temperatures (Post & Forchhammer 2004). Furthermore, dynamics of caribou and reindeer populations throughout the Northern Hemisphere respond to fluctuations in the North Atlantic Oscillation/Arctic Oscillation (Forchhammer *et al.* 2002; Post 2005), and in some cases are entrained to the point of highly synchronous dynamics across distances of thousands of kilometres (Post & Forchhammer 2006). Such climate-induced synchrony represents a potentially adverse consequence of climate change because synchronously fluctuating populations face a greater risk of global extinction than do independently fluctuating populations (Palmquist & Lundberg 1998).

While these examples suggest direct adverse effects of climate change on caribou populations, it is also possible that increasing temperatures and associated changes in precipitation may influence caribou populations indirectly through changes in the timing of plant growth (Gunn & Skogland 1997). Caribou migrate between seasonal ranges and time their migration to calving ranges to coincide with the timing of emergence of nutritious, highly digestible forage plants, which is crucial to the successful provisioning of newborn calves by female caribou (Gunn & Skogland 1997). To our knowledge, however, no study has yet demonstrated the consequences of trophic mismatch for offspring production and survival in caribou or wild reindeer. In fact, the only study to date that has explicitly addressed trophic mismatch in a mammalian herbivore focused on Soay sheep (*Ovis aries*) on the Scottish island of Hirta (Durant *et al.* 2005). That study found no evidence for an effect of trophic mismatch on offspring survival in Soay sheep, however, presumably because resource dynamics on Hirta are only weakly seasonal (Durant *et al.* 2005). Our focus was therefore to investigate the interaction between trophic mismatch and reproductive success in a system where the potential for its development was high: an Arctic plant–herbivore system.

2. STUDY SITE AND METHODS

(a) *Caribou calving*

Since 1993, we have collected data during six summers (1993, 2002–2006) on the annual timing and progression of the calving season in the Kangerlussuaq population of caribou in West Greenland. Each year, we have visited our field site beginning in mid- to late May and recorded numbers of adult female caribou and calves on a daily to near-daily basis.

This population occupies low Arctic coastal and inland ranges in West Greenland, in the area bounded by the Davis Strait to the west, the Inland Ice to the east, Nordre Isortoq River to the north and Sukkertoppen Icecap to the south (66–67° N, 50–52° W; Bøving & Post 1997). During and following the calving season, the Kangerlussuaq population occupies the furthest eastern inland portion of its range, at the western edge of the Inland Ice (Thing 1984; Bøving & Post 1997). This area is characterized by a dry, continental climate with mean daily minimum and maximum temperatures during the calving and post-calving seasons (late May–late June) of 1.6 and 12.5°C, respectively (Thing 1984).

Annually, we have quantified the seasonal progression of births in this population according to Caughley's 'Indirect

Method A' (Caughley 1977) and its modification for wild populations, for which capture is not necessary (Caughley & Caughley 1974). According to this method, we observe groups of pre-parturient and parturient female caribou on a daily or near-daily basis. Our efforts have focused on observing congregations of females in areas where they occur predictably. A minimum of 50 and an average of 100–200 adult females are observed each day. On each day of observation, using spotting scopes and binoculars from elevated vantage points, we record the numbers of adult females and calves observed. Animals under observation are not aware of our presence.

The onset and progression of the calving season is recorded as the daily proportions of calves (calves/(adult females + calves)) observed (Post *et al.* 2003). These observations display a clear sigmoidal pattern when plotted against 'day of year', indicating a gradual start to, rapid increase in, and levelling off of, numbers of calves produced per day. The proportion of calves observed invariably declines from the maximum observed at peak calving as early mortality occurs (Post *et al.* 2003). Our observations continue each year as long as caribou are present in the core calving area and extend several days after caribou have migrated out of the calving area. The last count of calves observed in late June to early July each year is considered the final proportion of calves produced for the season. It has been estimated that 85% of caribou calf mortality occurs within 8 days of birth (Adams *et al.* 1995), with up to 75% of calf mortality occurring within 48 hours of birth (Whitten *et al.* 1992).

Daily estimates of proportion calves are converted to daily estimates of per cent births in the population according to Caughley & Caughley (1974) and Caughley (1977). The date on which we observe the maximum proportion calves is considered to be the date of 100% births, i.e. the date on which all females that will give birth in a given year have given birth. The proportion of the annual total of the number of births observed on any given day is then quantified as

$$B_i = p_i/p_{max}, \tag{2.1}$$

in which p_i is proportion calves on date i and p_{max} is maximum proportion calves observed that year. This method does not require that sampling periods are contiguous or that observations are spaced evenly throughout the birth season, nor does it require that numbers (of adult females) per sample be equal (Caughley 1977). Moreover, the estimated per cent births to date are statistically independent of each other, and neither the beginning nor the ending of the birth season requires sampling for statistically accurate estimates of the tails of the birth season (Caughley & Caughley 1974; Caughley 1977).

(b) *Plant phenology*

In 2002, we established twelve (0.5 m²) permanently marked phenology plots in the study site, adjacent to the core caribou calving area. These plots replaced those originally established and monitored by us in 1993 (Post *et al.* 2003). Each year, we have monitored them with the same regularity and frequency that caribou are observed. Plots are distributed randomly among three meadows of comparable species composition, aspect and elevation within the study site; these meadows were chosen to be representative of, and adjacent to, the areas where parturient caribou are observed. Information on species composition has been published (Post *et al.* 2003). All species monitored on our plots occur in the diets of caribou in the Kangerlussuaq population during the calving season (Thing 1984; Post *et al.* 2003).

On each visit to the phenology plots, we record the names and numbers of plant species emergent in each plot. For analytical purposes, owing to differences in numbers of species present among plots, daily numbers of species emergent are transformed to daily proportions of the final number of species emergent in each plot. Using the final number of species emergent in each plot at the end of monitoring, we can back-calculate the percentage of this final number in an emergent state on each day of observation prior to the last day of monitoring. This is comparable to the method used for estimating daily per cent births for caribou (equation (2.1)).

(c) Quantifying trophic mismatch

Our index of the degree of trophic mismatch each year is based on the percentage of forage species emergent on the date at which 50% of caribou births have occurred. This index quantifies the temporal state of the forage resource midway through the season of caribou births. We considered using an index of trophic mismatch defined as the percentage of forage species emergent on the date at which 5% of births have occurred, which would quantify the temporal state of the forage resource at the onset of the season of caribou births. However, in some years, our observations of plant phenology were sparse at the beginning of the growing season, and we were concerned about the bias inherent to nonlinear-based estimation of values at the tails of a distribution of observed values (Rachlow & Bowyer 1991). Nonetheless, the index of trophic mismatch we used, that was based on the state of plant phenology on the date of 50% caribou births, correlated closely with the index of trophic mismatch we did not use, that was based on the state of plant phenology on the date of 5% caribou births ($r = 0.93$).

In a simple sense, the more species that have already emerged by the midpoint of the birth season, the greater is the extent to which caribou calving has lagged behind plant phenology, and the greater the trophic mismatch. Conversely, the fewer species that have emerged by the midpoint of the caribou birth season, the more closely caribou calving 'matches' plant phenology, and the lower the trophic mismatch. This index is also closely and inversely related to the correlation between per cent caribou births and per cent of forage species emergent ($r = -0.74$). The correlation between daily per cent births and daily per cent of forage species emergent could also have been used as an index of how closely caribou calving tracks plant phenology each year, but it presents the disadvantage of not allowing us to determine whether a poor correlation indicates that caribou calving precedes emergence of most forage species or lags behind their emergence. Therefore, we used the index that quantifies the temporal state of forage resources midway through the season of births.

To use this approach, we first quantified the relationship between per cent births and per cent of forage species emergent for each year. Because this relationship is approximately sigmoidal, we used the following nonlinear regression model:

$$Y = 1/(1 + e^{-(a+bX)}), \tag{2.2}$$

in which Y and X are per cent births and per cent species emergent, respectively (Thing 1984; Post & Klein 1999; Post et al. 2003). Percent births were estimated from proportions of calves observed each day (figure 1b) on the basis of Caughley's Indirect Method as described above (Caughley 1977). Coefficients (a and b) from equation (2.2) were then used to estimate the degree of trophic mismatch each year as per cent of births at the date of 50% emergence of forage species.
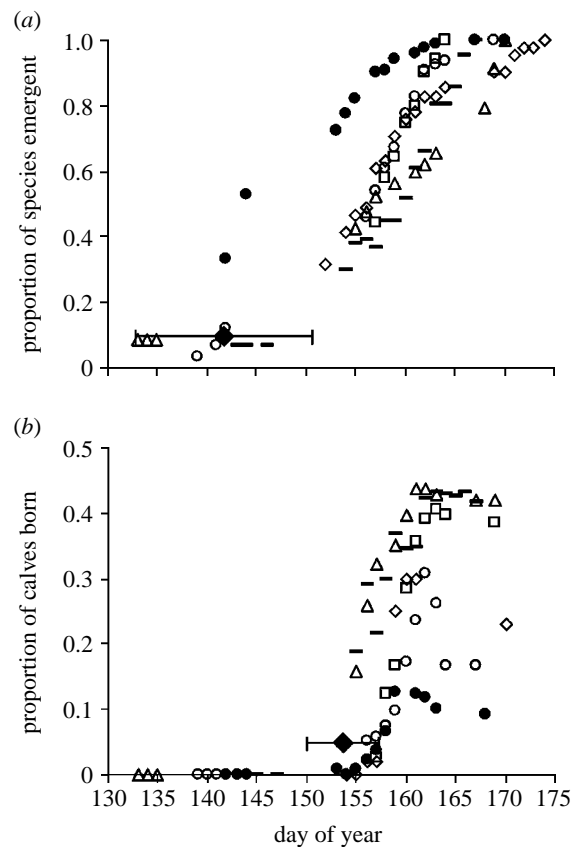
Figure 1. Onset and progression of the annual seasons of (a) plant growth and (b) calving by caribou in the Kangerlussuaq population, West Greenland, 1993 and 2002–2006. In (a), the data are expressed as the mean daily proportion of the final number of species observed on each plot versus day of observation. In (b), the data are expressed as the proportion of calves (calves/(adult females + calves)) observed each day. See §2 for further details. In each panel, the filled diamond represents the mean (± 1 s.d.) among years. In both panels, symbols are unique to each year of observation. Between panels, identical symbols represent observations of plant phenology (a) or calving (b) in the same year.

(d) Relating caribou calf production and survival to trophic mismatch

Offspring production by caribou was quantified in two ways: as the maximum proportion calves observed each year (PC_{max}); and as the final proportion calves observed each year (PC_{final}), presumably after most early calf mortality has occurred (Adams et al. 1995). Annual early calf mortality (i.e. mortality occurring during the season of parturition) was then quantified as the difference between PC_{max} and PC_{final}. In our analysis of the influence of trophic mismatch on caribou calf survival, however, we used an index of calf mortality scaled to calf production each year termed 'relative calf mortality', M_r, estimated as

$$M_r = \frac{PC_{max} - PC_{final}}{PC_{max}}. \tag{2.3}$$

(e) Relating trophic mismatch to abiotic conditions

To determine what abiotic conditions contribute to or ameliorate trophic mismatch between caribou calving and plant phenology, we used our nonlinear regression estimates of the onset and progression of the season of plant growth. We tested for relations between monthly mean temperatures and monthly total precipitation, as well as average spring

temperature (the mean of temperature for the period March–May) and total spring precipitation (the total of precipitation for the period March–May). Weather data were obtained from the station maintained in Kangerlussuaq by the Danish Meteorological Institute. Although we recognize that temperature and precipitation probably interact to influence plant phenology and thereby trophic mismatch, the low number of years of data we have did not lend themselves to multiple regression analyses. Therefore, we report our results as simple linear correlations.

3. RESULTS AND DISCUSSION

Over the course of the study, the mean (± 1 s.d.) date of onset of the plant-growing season (the date of emergence of 5% of species) was 22 May (Julian day 142; ± 8.9 days), whereas the mean date of onset of the caribou calving season (the date of 5% births) was 3 June (Julian day 154; ± 3.6 days; figure 1). Between 1993 and 2006, the timing of onset of the plant-growing season (estimated as the date of emergence of 5% of plant species) advanced by 4.59 days; for the subset of those years for which data are continuous (2002–2006), onset of the plant-growing season advanced by 14.8 days (figure 2: open circles). By contrast, between 1993 and 2006, timing of onset of calving (date of 5% births) advanced by 3.82 days; whereas from 2002 to 2006, when advancement of the plant-growing season was most pronounced, onset of calving advanced by only 1.28 days (figure 2: solid circles). Moreover, interannual variability in onset of plant growth (CV=6.28) was approximately twice as great as that of caribou calving (CV=2.34), though this difference was not significant ($F_{5,5}=2.69$, $p>0.50$). Taken together, these results suggest that caribou display less interannual variability in the timing of their reproductive cycle than do the forage plants upon which they depend for offspring provisioning at the period of peak resource demand. They furthermore indicate a rapidly developing mismatch between caribou reproduction and the timing of availability of their forage (figure 2).

Among years, the timing of onset of the plant-growing season was most closely related to mean April temperature ($r=-0.57$; $p=0.20$). Timing of onset of caribou calving displayed its strongest correlation to mean spring (March–May) temperature ($r=-0.71$; $p=0.12$). Onset of calving was not, however, closely correlated with that of the plant-growing season ($r=0.04$; $p>0.50$), presumably because, as noted above, the onset of plant growth was considerably more variable among years than was the onset of calving (figure 1). Mean spring temperature, over the course of the study, increased by 4.63°C, though the correlation with 'year' is only marginally significant ($r=0.52$, $p=0.058$). We assume that the poor correlation of onset of the growing season with any of our abiotic predictors may be explained by either or both of the following factors. First, because our sampling did not begin early enough to record observations of 0 species emergent (figure 1a), our nonlinear regression estimates of the beginning of the growing season each year are less precise than those of the onset of calving (figure 1b). Second, as in other parts of the Arctic, onset of the plant-growing season may be determined
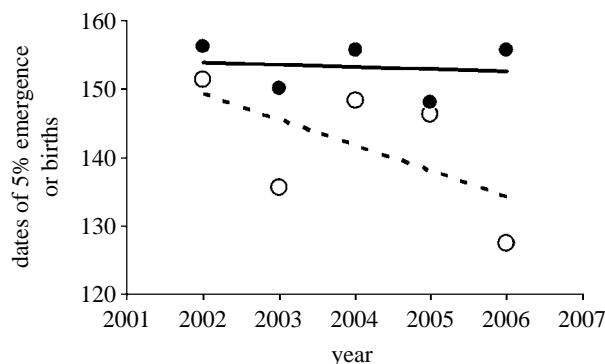

Figure 2. Dates (in day of year) of emergence of 5% of forage species (open circles, dashed line) and of 5% of caribou births (filled circles, solid line) at the study site in Kangerlussuaq, West Greenland, during the period of continuous annual data collection from 2002 to 2006. Fitted lines are linear regressions.

by the combined influences of temperature and snow cover (Høye *et al.* 2007), and our sample was too small to justify multiple regression analysis.

The progression of the plant-growing season was closely related to its onset, as the date of emergence of 50% of forage species was highly positively correlated with the date of emergence of 5% of species ($r=0.84$, $p<0.05$). Hence, warm springs were followed by early onset and rapid progression of the plant-growing season. In turn, a more rapid progression of the plant-growing season led to greater trophic mismatch between caribou calving and plant phenology ($r=-0.77$, $p=0.07$): the per cent of forage species emergent at the date of 50% births was nearly twice as great in the earliest and most rapid spring than in the latest and most gradual spring (figure 3a).

Early caribou calf mortality was closely related to the degree of trophic mismatch around the time of calving ($r=0.70$, $p=0.12$). Calf mortality varied sevenfold between the lowest and highest degrees of trophic mismatch observed (figure 3b). Accordingly, calf production declined with increasing trophic mismatch ($r=-0.89$, $p<0.02$), varying fourfold between the lowest and highest levels of trophic mismatch observed (figure 3c).

For animals inhabiting seasonal environments, successful reproduction depends on synchronizing offspring production with the time of year when resources are most abundant or of highest quality. In the far north, nutritional content and digestibility of plants reach a peak soon after emergence and decline rapidly thereafter (Klein 1990; Albon & Langvatn 1992). Hence, timing of parturition by caribou and wild reindeer (also *R. tarandus*) is closely linked to the start of the plant-growing season (Post & Klein 1999; Post *et al.* 2003). The extent to which onset of parturition in caribou—or in any northern herbivore—can track shifts in plant phenology induced by climatic warming is therefore a key question. While gestation length is fixed at approximately 240 days for this species (Leader-Williams 1988) and the annual reproductive cycle is entrained by seasonal changes in day length (Lincoln & Short 1980), there is some indication that caribou might be able to adjust the timing of their annual reproductive cycle to match, to some extent, changes in plant phenology. For instance,
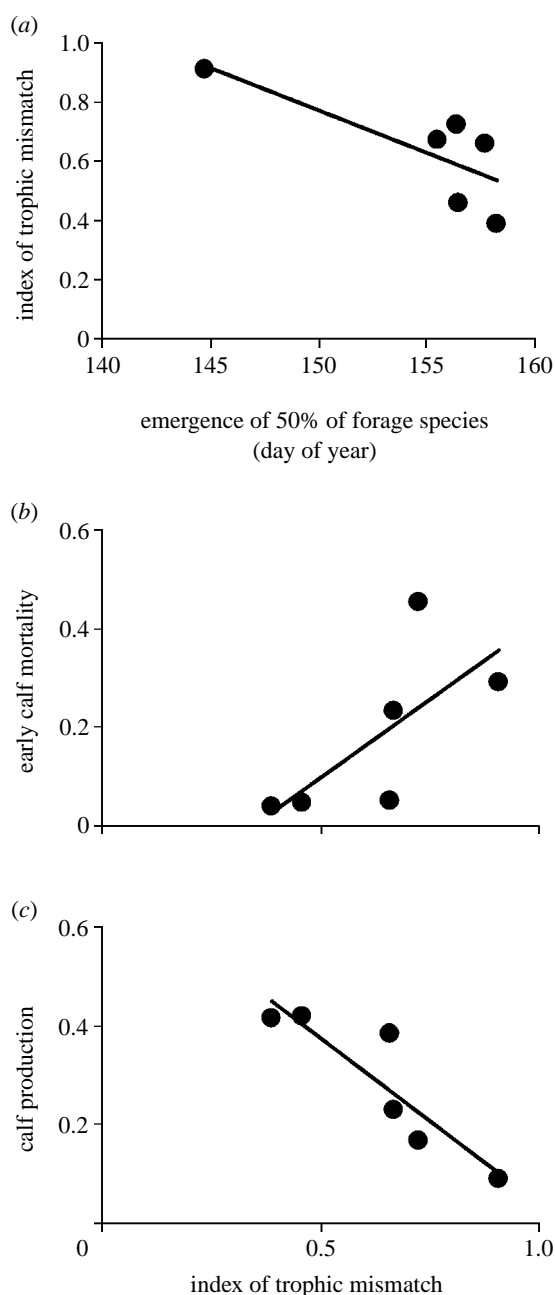
Figure 3. (*a*) Relation between the midpoint of the plant-growing season and the index of trophic mismatch between caribou calving and plant phenology each year; an earlier occurrence of the midpoint of the plant-growing season leads to greater trophic mismatch. (*b*) Relation between the magnitude of trophic mismatch between caribou calving and plant phenology and early calf mortality. Calf mortality is calculated according to equation (2.3) in §2. (*c*) Relation between the magnitude of trophic mismatch between caribou calving and plant phenology and calf production. Calf production is estimated as the final proportion of calves observed each year according to the approach described in §2.

geographical variation in onset and peak of calving among populations of caribou and wild reindeer correlates closely with geographical variation in the timing of the plant-growing season among the areas inhabited by those populations (Skogland 1989). As well, Norwegian reindeer introduced to the sub-Antarctic island of South Georgia completely reversed their annual reproductive cycle by six months within 2 years of introduction, although it would seem this

reversal was ultimately driven by the seasonal reversal of day length variation from the Northern to Southern Hemisphere (Leader-Williams 1988).

Of key importance to caribou in this population, however, is the rate at which plant phenology will advance with further changes in spring temperature. Our results indicate that, whereas onset of plant growth is highly variable among years, onset of parturition by caribou is not (figures 1 and 2). This would suggest a 'bet-hedging' strategy in caribou of timing parturition to coincide with a long-term average onset of favourable conditions. Over the course of our study, an advance in the onset and progression of the plant-growing season by approximately two weeks precipitated an increase in calf mortality and fourfold decline in calf production (figure 3). This two-week advance in plant phenology corresponded to an increase in average spring (March–May) temperature of 4.63°C in our study site over the same period (figure 2). With a further 3–5°C increase in warming expected throughout the Arctic (Maxwell 1997), the extent to which plant phenology will further advance is critically important to the future reproductive success of caribou in this population. The results of a warming experiment we conducted at the same study site indicated that an increase of 4°C advanced phenology of key species, used by caribou at the time of calving, by up to 10 days (Post *et al.* in press, submitted).

To our knowledge, our results are the first such documentation of a developing trophic mismatch in an Arctic mammal and its consequences for offspring production. While the patterns are clear, our analyses are, in some cases, hampered by low sample sizes. Therefore, our results cannot be considered conclusive. Nonetheless, they corroborate results from better-studied systems with longer-term data documenting the implications of climate change for trophic mismatch in aquatic and marine systems (Edwards & Richardson 2004; Winder & Schindler 2004), and of consequences of trophic mismatch for reproductive success and population dynamics in migratory birds. By far, the best studied of such systems is that of insectivorous birds including great tits (*Parus major*) and pied flycatchers (*F. hypoleuca*) in The Netherlands. Insectivorous birds should be especially susceptible to trophic mismatch due to climate change because emergence of their forage species in spring habitats is cued by local temperatures, whereas spring migration by passerines is cued by changes in day length. Great tits, for example, have been shown to suffer mistimed reproduction as climatic warming has advanced the appearance of invertebrate prey but not the timing of their own offspring production (Visser *et al.* 1998). In pied flycatchers nesting in The Netherlands, the timing of spring arrival on nesting grounds has not advanced in association with warming over the past two decades, whereas timing of egg laying has advanced due to selection pressure on offspring provisioning (Both & Visser 2001). Nonetheless, the advance in laying date has not kept pace with the advance of emergence of key forage species of invertebrates, and the magnitude of decline in several Dutch populations matches the extent of the temporal mismatch between caterpillar emergence and nestling production (Both *et al.* 2006).

The example of population declines in pied flycatchers illustrates the consequences of mistimed reproduction in migratory species that are unable to fully compensate through adjustments in their reproductive phenology for climate-driven changes in the timing of availability of resources. We might expect intense selection for earlier reproduction in caribou and other Arctic herbivores if further climatic warming and greater trophic mismatch reduce reproductive success. Some of the female reindeer introduced to the island of South Georgia, for instance, were pregnant and produced offspring in their first May on the island; their calves, however, died because their birth coincided with the onset of winter on the island (Leader-Williams 1988). Nonetheless, those same females eventually adjusted their reproductive cycles to coincide with the sub-Antarctic seasons, and reindeer persist there today (Leader-Williams 1988). We suggest, however, that the role of trophic mismatch in reproductive success and population dynamics of this and other Arctic species warrants urgent attention.

Procedures for observation of animals in this study were approved by the Institutional Animal Care and Use Committee of The Pennsylvania State University

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Warmer springs lead to mistimed reproduction in great tits (*Parus major*)

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In seasonal environments, the main selection pressure on the timing of reproduction (the ultimate factor) is synchrony between offspring requirements and food availability. However, reproduction is initiated much earlier than the time of maximum food requirement of the offspring. Individuals should therefore start reproduction in response to cues (the proximate factors), available in the environment of reproductive decision making, which predict the later environment of selection. With increasing spring temperatures over the past decades, vegetation phenology has advanced, with a concomitant advancement in the reproduction of some species at higher trophic levels. However, a mismatch between food abundance and offspring needs may occur if changes in the environment of decision making do not match those in the environment of selection. Date of egg laying in a great tit (*Parus major*) population has not advanced over a 23-year period, but selection for early laying has intensified. We believe that this is the first documented case of an adaptive response being hampered because a changing abiotic factor affects the environment in which a reproductive decision is made differently from the environment in which selection occurs.

Keywords: timing of reproduction; laying date; *Parus major*; phenotypic plasticity; climate change; selection

1. INTRODUCTION

Over the past decade, the phenology of the vegetation has advanced owing to higher spring temperatures (Myneni *et al.* 1997). This will affect the time at which arthropod populations start to increase in spring (Ellis *et al.* 1997). For insectivorous species, the abundance of arthropods at the time of maximum food requirement of their young is a crucial determinant of reproductive success (Lack 1968). We would therefore expect the timing of reproduction of these species to advance as well. Recently, it has been shown that many bird species in the UK have advanced their date of egg laying over the past 25 years (Crick *et al.* 1997). This pattern is confirmed by long-term studies of a few bird populations (Winkel & Hudde 1997; McCleery & Perrins 1998). It is tempting to conclude that increases in spring temperature will therefore not result in a mismatch between the time of reproduction of birds and the time of food abundance. It has, however, not been shown that the date of egg laying and the food peak advance to the same degree. Moreover, it is not expected that this will generally be the case. Often, individuals make decisions about the timing of reproduction well before their offspring's need for food is at its maximum and will have to rely on cues that act as predictors of this food peak. Photoperiod is an important cue (Rowan 1926), but other cues are needed for 'fine tuning' (Wingfield 1980). As photoperiod is independent of spring temperatures, it cannot account for short-term variation in laying date, and therefore we concentrate

on the 'fine-tuning' cues. With increasing spring temperatures, these cues might change to a different extent compared with the food peak. Furthermore, production of eggs requires nutrients and energy. The source for these might advance to a lesser extent than the peak in the food for the offspring, thereby constraining the advancement of the timing of reproduction. This potential problem of a differential change in the environment of selection and the environment of the initiation of reproduction is exemplified using a long-term study on a Dutch population of the great tit (*Parus major*). We will first show that there has been no advancement of date of egg laying, but that the main ultimate factor, caterpillar abundance, has advanced. Next, we show, by calculating the selection differentials for laying date, that selection for early laying has intensified. Finally, we explore whether this is due to a lack in shifts of the main cues (the proximate factors) or to more severe resource constraints at the time of egg formation.

2. MATERIALS AND METHODS

(a) Study area and methodology

We used 23 years of data (1973 to 1995) from a long-term study of a population of great tits on the Hoge Veluwe (The Netherlands). The study area covers a mixed pine–deciduous wood of 171 ha (1 ha = 10^4 m^2) in which there are about 400 nest-boxes. Nest-boxes are checked weekly to determine laying date and clutch size, and daily during the days immediately before hatching to determine hatching date of the young. When the young are 7 days old, they are ringed and their parents identified. From these measurements, the laying date of the first clutch and the number of

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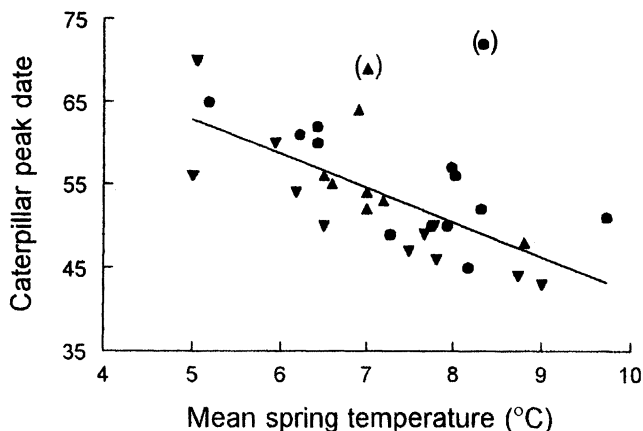
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Figure 1. Caterpillar peak dates (1 = 1 April) against spring temperatures (mean daily temperature from 21 February to 10 May) for 30 years of data on caterpillar peaks from our study populations on the Hoge Veluwe (1985–1997, filled circles), Vlieland (1988–1995, filled upright triangles) and Oosterhout (1958–1968, filled inverted triangles). Biomass peak is well predicted by spring temperature (peak date = $83.5 - 4.1 \times$ temp, $r = 0.73$, excluding 1991 (the points between brackets) when a late frost damaged all oak leaves).

fledglings recruited into the breeding population the following year (our measure of fitness) are known for each breeding pair.

(b) Laying dates

For the analysis of annual mean laying date, only first clutches with a known laying date were used (this excludes 1.7% of the clutches). To assess whether laying has advanced over the 23-year study period, the annual mean laying date was regressed against year.

(c) Annual peak dates of caterpillar biomass

Annual peak dates of caterpillar biomass are calculated from a regression model based on caterpillar peaks determined from frass-fall samples on the Hoge Veluwe (1985–1997), Vlieland (1988–1995) and Oosterhout (1958–1968) (van Balen 1973; Verboven *et al.* 1998; M. E. Visser, unpublished data). The caterpillar peak is well predicted by the mean daily temperature from 21 February to 10 May ($F_{1,26} = 52.3$, $p < 0.0001$; figure 1; see also van Balen 1973). The regression model allows us to predict the date of peak caterpillar biomass each year over the period 1973–1995 using temperature data supplied by the KNMI (Royal Dutch Meteorological Institute) in De Bilt.

(d) Selection differentials

Selection differentials estimate the amount of directional selection on a trait (Falconer 1981; Endler 1986; Schluter & Smith 1986; van Noordwijk *et al.* 1995). We calculated the selection differential for laying date as the difference between the mean date of laying of first clutches, weighted for the number of recruits produced per female over the entire season, and the unweighted mean laying date of first clutches. By including all recruits produced in a season, the fact that early-laying pairs are more likely to produce a second clutch is taken into account. Negative selection differentials indicate that early-laying birds produce on average more recruits than those birds laying later.

The total number of recruits produced per year varied greatly between years. Because selection differentials for years
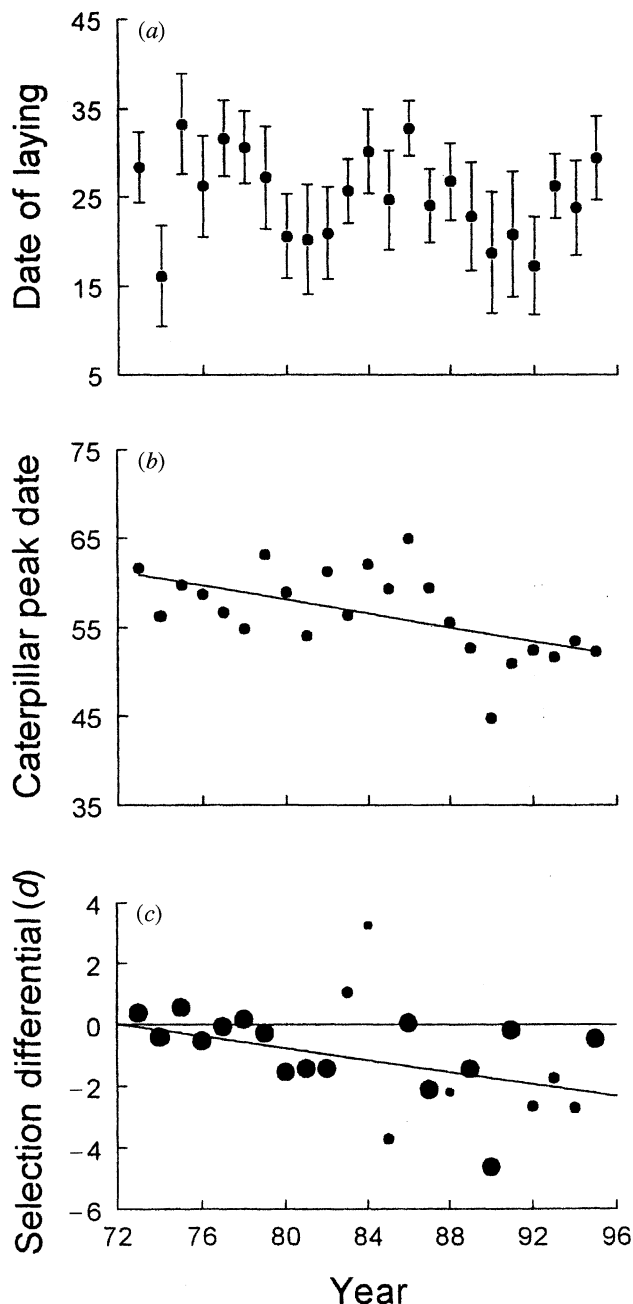
Figure 2. Timing of reproduction and food availability in great tits (*Parus major*) breeding on the Hoge Veluwe for the period 1973–1995. (*a*) Mean (±s.d.) laying date (1 = 1 April) of first clutches. (*b*) The estimated date of peak caterpillar biomass in oak (*Quercus robur*). (*c*) Selection differential for laying date, calculated as the difference between the mean laying date of first clutches, weighted for the number of recruits produced per female over the entire season, and the unweighted mean laying date of first clutches (large symbols, ⩾20 recruits; medium symbols, <20 and ⩾10 recruits; small symbols, <10 recruits produced from all broods in that year).

with only a few recruits are less reliable than those for years with many recruits, we weighted the selection differentials for the annual production of recruits against year.

3. RESULTS

Laying date has not advanced over the years 1973–1995 ($F_{1,21} = 1.00$, $p = 0.33$; figure 2*a*). However, the mean daily

temperature from 21 February to 10 May has increased over the 23 years ($F_{1,21}$=9.50, p=0.006), and hence the predicted date at which caterpillar biomass peaks has advanced by about nine days over this period ($F_{1,20}$=7.86, p=0.01; figure 2b), with perhaps the most rapid change occurring in 1988–1989.

Synchrony between the timing of reproduction and the availability of caterpillar food is the main selection pressure on laying date (van Noordwijk *et al.* 1995). The advance in the timing of the caterpillar peak without a concomitant advance in the timing of reproduction of the great tits is therefore expected to lead to increasingly negative selection differentials over the 23-year period. Selection for earlier laying has indeed become more intense over the 23-year period (regression weighted for the annual number of recruits, $F_{1,21}$=6.54, p=0.018; figure 2c).

Spring temperatures determine the date of peak caterpillar biomass. The effect of temperature is mediated both by the date of bud-burst of oak (*Quercus robur*) trees, before which the main caterpillar prey-species cannot grow (Holliday 1985), and by subsequent temperature-dependent caterpillar development (Topp & Kirsten 1991). Great tits are also phenotypically plastic in their timing of reproduction, laying earlier in warm springs (van Balen 1973). Why then has the date of egg laying not advanced in step with the peak caterpillar biomass over the years? One reason is that the environments of decision making and selection may have changed at different rates.

First, constraints on the timing of egg laying may not have changed in the same way as food availability for the young. The energetic demands of egg production may constrain timing of breeding (Perrins 1970). Great tits forage predominantly in different tree species during egg laying (larch (*Larix decidua*) and birch (*Betula pubescens*)) and chick rearing (oak). The bud-burst of the former species is much less temperature-dependent than that of oak. Based on dates of bud-burst predicted from observed spring temperatures (Kramer 1994), oak bud-burst has advanced over the 23-year period ($F_{1,21}$=9.59, p=0.005), but that of larch ($F_{1,21}$=1.20, p=0.29) and birch ($F_{1,21}$=3.58, p=0.07) has not. Thus the availability of resources needed to produce eggs advances only marginally compared with that needed for chick rearing.

Second, the predictors on which the decision to start breeding are based may not have changed over the years in the same way as the food availability for the young. Great tits lay at about the time that their caterpillar prey starts developing. If subsequent temperatures are high, the young hatch late relative to the caterpillar peak (van Noordwijk *et al.* 1995). The date of egg laying by great tits correlates well with the mean temperature between 1 March and 15 April (van Balen 1973), but this temperature mean has not increased significantly over the study period ($F_{1,21}$=3.17, p=0.09). In contrast, the mean temperature in the subsequent 30-day period, when caterpillars are growing, has increased ($F_{1,21}$=6.98, p=0.015). As these two periods start roughly at the same date, this difference must be due to a stronger increase in temperatures after the 15 April, that is, after and partly during the egg-laying period. Thus the relationship between the timing of peak caterpillar availability and the cues used to initiate laying may have changed over the study period. This interpretation is strengthened by
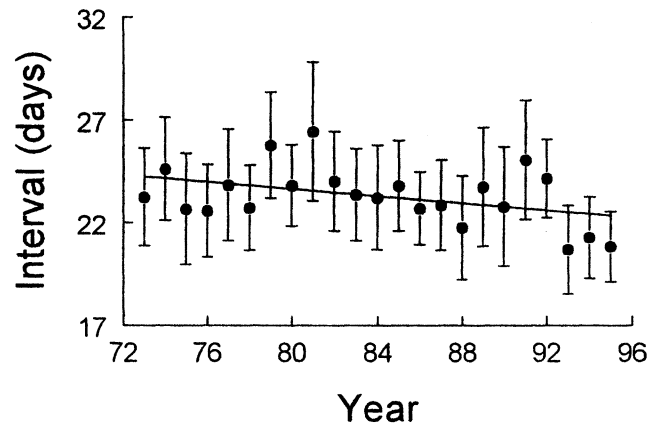

Figure 3. Mean (s.d.) interval between the laying date of the first egg and hatching date against year, for a great tit (*Parus major*) population on the Hoge Veluwe, 1973–1995.

the fact that in the early 1970s there was no correlation between annual mean laying date and selection differential, whereas in recent years a negative relationship exists (as indicated by a near-significant interaction between laying date and year (as a continuous variable) on the selection differential for laying date; $F_{1,19}$=3.79, p=0.067).

Laying date is not the sole determinant of hatching date, and thereby of the timing difference between offspring requirement and food availability. By laying smaller clutches, shortening the gap between the last egg and the onset of incubation (van Balen 1973), or reducing the duration of the incubation period, birds can reduce the interval between laying and hatching. The interval between the first egg and hatching (about 23 days) has indeed become two days shorter over the 23 years of this study ($F_{1,21}$=4.32, p=0.05, figure 3). This decrease is not due to changes in mean clutch size ($F_{1,21}$=0.12, p=0.74), and is thus most likely due to a reduction of the gap between clutch completion and incubation (of which we have no direct measurements). This observation can be explained in terms of both explanations outlined above. If the cues used for the start of egg production have not shifted as much as the peak in caterpillar biomass, the birds may detect that they are late from cues available closer to the nestling phase, and hence attempt to advance their hatching date. If constraints during egg laying have become more severe, the birds might trade-off the costs of producing eggs early against initiating incubation before clutch completion, with asynchronous hatching of the chicks as possible costs.

4. DISCUSSION

In great tits, the timing of reproduction has not advanced in step with early peak availability of food for the young over a 23-year period, leading to increased selection for early laying. We suggest that this results from greater changes in spring temperatures during the period of maximal food demands of the young than in the period of decision making over laying date, either because of constraints on egg laying or cues to initiate egg laying. These two factors have different long-term implications. If egg laying is constrained by energetic demands, the selection differentials displayed in figure 2c should be

modified to include detrimental effects on females attempting to lay earlier. There may then be no net selection on laying date, but climatic change will have caused an overall reduction in fitness by weakening the synchrony between the timing of peak food demands and availability. If, on the other hand, the relationship between food availability and a cue used for timing of breeding has changed, there will be selection on the reaction norm relating these two variables. However, the response to such selection may be slow (van Tienderen & Koelewijn 1994). Up until now, there has been no response to this selection in great tits (no significant interaction between spring temperature sum (1 March–15 April) and year on laying date; $F_{1,19} = 0.69$, $p = 0.42$).

Our findings differ from those of McCleery & Perrins (1998) for a UK great tit population. They find a clear advancement of laying date for the period 1970–1997 and conclude that this is solely due to increasing temperatures in spring. At present, it is unclear why the two great tit populations respond differently to increased spring temperatures. On the basis of the results of McCleery & Perrins (1998), and of the broader data set of Crick et al. (1997), it is tempting to conclude that climatic change may not have substantial adverse effects on reproductive success. Our results caution that climatic change may not always act uniformly on all parts of the breeding season, so that constraints and cues do not alter in step with selection pressures acting later in the breeding season. As a result, there may be a mismatch between timing of reproduction and food abundance, with shorter- or longer-term consequences for population viability.

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