

Keeping Pace with Fast Climate Change: Can Arctic Life Count on Evolution?¹

DOMINIQUE BERTEAUX,^{2,*} DENIS RÉALE,[†] ANDREW G. MCADAM,[‡] AND STAN BOUTIN[‡]

^{*}Canada Research Chair in Conservation of Northern Ecosystems, Université du Québec à Rimouski, 300 allée des Ursulines, Rimouski, Québec G5L 3A1, Canada

[†]Canada Research Chair in Behavioural Ecology, Université du Québec à Montréal, Case postale 8888, Succursale Centre-Ville, Montréal, Québec H3C 3P8, Canada

[‡]Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada

SYNOPSIS. Adaptations to the cold and to short growing seasons characterize arctic life, but climate in the Arctic is warming at an unprecedented rate. Will plant and animal populations of the Arctic be able to cope with these drastic changes in environmental conditions? Here we explore the potential contribution of evolution by natural selection to the current response of populations to climate change. We focus on the spring phenology of populations because it is highly responsive to climate change and easy to document across a wide range of species. We show that evolution can be fast and can occur at the time scale of a few decades. We present an example of reproductive phenological change associated with climate change (North American red squirrels in the Yukon), where a detailed analysis of quantitative genetic parameters demonstrates contemporary evolution. We answer a series of frequently asked questions that should help biologists less familiar with evolutionary theory and quantitative genetic methods to think about the role of evolution in current responses of ecological systems to climate change. Our conclusion is that evolution by natural selection is a pertinent force to consider even at the time scale of contemporary climate changes. However, all species may not be equal in their capacity to benefit from contemporary evolution.

INTRODUCTION

Cold temperatures and short growing seasons are the most obvious characteristics of the physical environment in the Arctic. Biologists have, therefore, spent decades describing and understanding the adaptations of plants and animals to these harsh living conditions (Chernov, 1985; Billings, 1987; Pielou, 1994). Now the arctic climate is quickly warming up (Moritz *et al.*, 2002), which raises numerous questions about the future of arctic life. In this paper we ask a simple question: given that evolution through natural selection is the main source of adaptation on earth, can we expect arctic life to evolve and adapt to rapidly changing climatic conditions? Answering this question is critical to conservation biologists and is a key test for evolutionary biologists seeking practical applications to their discipline.

The question we ask is timely for two reasons. First, several literature reviews have recently documented the many ecological responses to current climate changes (McCarty, 2002; Walther *et al.*, 2002; Parmesan and Yohe, 2003). These reviews show that ecological systems respond to climate change at a time scale compatible with our observation capabilities. Therefore the potential to investigate the role of evolution in current responses of biological systems to climate change does exist. Second, although evolution is often seen as a long term process, acting over much longer time periods than a human lifetime, recent find-

ings demonstrate that evolution can in fact sometimes be very fast, and a pertinent force to consider when studying contemporary biological changes (Hedrick, 2001; Palumbi, 2001; Stockwell *et al.*, 2003; Ashley *et al.*, 2003). A few studies have even started to suggest evolutionary responses to the currently observed directional climate change (de Jong and Brakefield, 1998; Rodriguez-Trellis and Rodriguez, 1998; Bradshaw and Holzapfel, 2001; Réale *et al.*, 2003a).

There are four main difficulties in answering the question “Can we expect arctic life to quickly evolve and adapt to the new climatic conditions?”

1. “Arctic life” is a general term that we must narrow down. Most reviews on the ecological responses to climate change have structured these responses along four major axes: the physiology and behaviour of individuals, the distribution of species, the structure of communities, and the dynamics of ecosystems (Walther *et al.*, 2002). Here we concentrate on physiology and behaviour because this is the level at which natural selection works, and we believe other categories to ultimately depend on physiology and behaviour of organisms. The most dramatic and best documented changes in physiology and behaviour associated with climate change are no doubt changes in phenology, the annual timing of life history events in populations (Ahas *et al.*, 2002; Sparks and Menzel, 2002; van Vliet and Schwartz, 2002). Therefore we deal with phenological changes in this paper. Phenology is a key aspect of the adaptation of arctic populations, and our analysis of the role of evolution in current phenological changes should illuminate more general questions about the links between climate change and adaptation in arctic systems.

¹ From the Symposium *Biology of the Canadian Arctic: A Crucible for Change in the 21st Century* presented at the Annual Meeting of the Society for Integrative and Comparative Biology, 4–8 January 2003, at Toronto, Canada.

² E-mail: Dominique.Berteaux@uqar.qc.ca

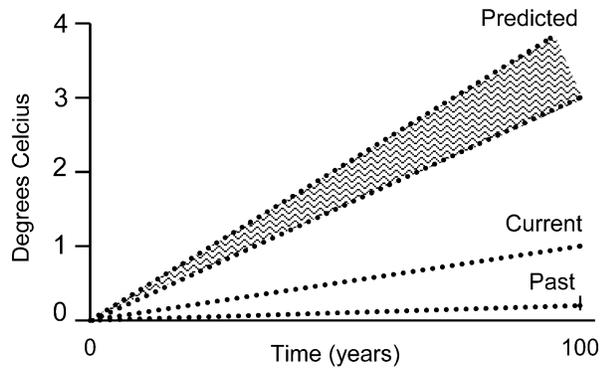


FIG. 1. Past, current, and predicted surface air temperature increases in the Canadian Arctic and Northern Hemisphere, expressed over a period of 100 years. Past increase calculated over the period 800 to 2000 from Mann-Bradley-Hughes multiproxy reconstruction of Northern Hemisphere annual temperatures (data from Fig. 3 in Esper *et al.*, 2002). Current increase calculated over the period 1900 to 2000 from surface air temperatures in the Arctic (data from Fig. 1a in Moritz *et al.*, 2002). Predicted increase calculated over the period 2000–2100 for the Arctic from the general circulation models combining the effects of projected greenhouse gas and sulphate aerosol increases—Canadian model (data from Fig. 6 in Hengeveld, 2000). Shaded area represents uncertainty of model predictions.

2. “Quickly” is a relative concept that must be attached to a time scale. Here we equate quick evolution to “contemporary evolution,” that is an evolutionary change observable over a few decades (Stockwell *et al.*, 2003). We recognize that time is not the best measure of evolutionary rate and that a better approach is to quantify phenotypic change in standard deviations per generation (the haldane is then the unit of measure; Hendry and Kinnison, 1999). However changes through time are intuitively easier to understand and can be more easily compared to the rate of climate change.
3. “New climatic conditions” is a complex concept as climate is changing with regard to several variables (*e.g.*, temperature and precipitation) and several measures (*e.g.*, averages and extremes). Here we simplify this concept in considering only changes in average temperatures, which are the best documented and probably the most influential climate changes occurring in the Arctic. The term “new” also depends on the time scale considered. Here we consider as “new” the rapid increase in average temperature that has occurred in the past decades in the Arctic, and will likely continue to occur in the next decades (Fig. 1).
4. The fourth source of complexity does not deal with the definition of terms but stems from the virtual absence of data on quantitative genetic parameters for most arctic species, due to the difficulties of gathering detailed information on usually very remote populations. Hard data are needed to answer our question. We partly circumvent this problem by using recent data from a northern mammalian (the North American red squirrel, *Tamiasciurus hudsonicus*) population studied in the Yukon. This popu-

lation has been subject to climate change for at least 25 years and we have performed in-depth analyses of its quantitative genetic parameters (McAdam *et al.*, 2002; Réale *et al.*, 2003a, b). In addition, we review existing literature on one important quantitative genetic parameter (heritability) to test whether northern species are different from other species.

In the following we first summarize why phenology is a key aspect of the biology of arctic species. Then we show how the phenology of a population can change through time, and identify the critical conditions for a population to keep pace with drastic and prolonged environmental change. In a third part we present and discuss phenological (breeding date) changes in the Yukon red squirrels, which illustrate the different sources of change in the phenology of a population and show the speed at which evolution can work. We review heritability estimates for a number of northern species in the fourth part. Finally, we have included a frequently asked questions section to present biologists less familiar with evolutionary ecology and quantitative genetics some of the key concepts needed to understand contemporary evolution in the context of climate change.

PHENOLOGY

Defining phenology

There are several definitions to phenology. A detailed one has been adopted by the European Phenology Network, which defines phenology as “the study of the timing of recurring biological phases, the causes of their timing with regard to biotic and abiotic forces, and the interrelation among phases of the same or different species” (<http://www.benp.wageningen-ur.nl/msa/e/pn/>). However, simpler definitions have been used such as “The study of natural events, or of biological events, in relation to climate” (Schnelle, 1955; cited in Sparks and Menzel, 2002), and many biologists restrict their definition to “the study of seasonal plant and animal activity driven by environmental factors” (Menzel and Fabian, 1999). In its minimal form, phenology is defined as a biological variable rather than a scientific discipline, and no causal link is included in the definition, which simply becomes “the seasonal timing of animal and plant activities” (*e.g.*, Beebee, 2002, p. 1454). Here we adopt this last definition. Spring and fall phenology then describe the timing of animal and plant activities for each season. Typical plant and animal activities involved in studies of phenology include flowering, bud burst, and initiation of growth (plants) or migration, egg laying or hatching, and parturition (animals).

The importance of phenology

The phenology of organisms has evolved through natural selection to match the environmental conditions and maximize fitness of individuals (Futuyma, 1998). A good match of the timing of life history events (*e.g.*, migration, reproduction, flowering) with

local variability in environmental conditions is critical and many studies have shown the costs of a mismatch (Quinn and Adams, 1996; Thomas *et al.*, 2001; Stenseth and Mysterud, 2002). Interestingly, changes in environmental conditions can have cascading effects on match–mismatch relations. For example, Visser and Holleman (2001) reported a tight trophic interaction involving strong selection on synchronization that was disrupted because species did not react at the same rate to changes in environmental conditions (*i.e.*, egg hatching of winter moth [*Operophtera brumata*] became mismatched with bud burst of oak [*Quercus robur*]).

A good match between phenology and environmental variables is important in any seasonal environment, but is exacerbated in arctic systems, where the growing season is ephemeral and the transition between seasons extremely rapid. For example, birds arriving too late may fail to reproduce, whereas those arriving too early may face capricious weather conditions and possible food shortages. As a result, birds failing to adjust to the local timing of spring events can suffer drastically reduced reproductive success (Wingfield and Hunt, 2002). Similarly, initiation of growth and flowering of arctic plant species is closely associated with date of snowmelt (Totland and Alatalo, 2002), and changes in length of growing season may have profound effects on the population dynamics of plants.

Under the pressure of climate change and earlier springs, arctic plant and animal populations *must* change their phenology to maintain a fitness compatible with population persistence, and avoid increased risks of extinction. In order to predict whether arctic populations will be able to adapt their phenology to the new climatic conditions currently emerging, we must understand the mechanics of phenological change, and evaluate whether this mechanics is sufficient to allow populations to keep pace with the quick climate changes.

PHENOLOGICAL CHANGE

Here we first explore what governs plant and animal phenology, we then summarize our knowledge regarding how phenology can change through time in a population, and we finally show what ingredients are necessary to generate predictions of phenological responses to climate change.

What governs phenology

Animal phenology is governed to a large extent by hormones. For example, seasonal changes in sex steroid hormones result in a cascade of seasonal changes in steroid-dependent behaviours in mammals (Nelson, 2000). As another example, arctic spring weather can induce hormonal responses to stress that have inhibitory effects on reproduction of birds (Wingfield and Hunt, 2002). The regulation of plant phenology is different and more directly linked to environmental conditions. For example, the phenology of arctic plant species is directly related to the length of the snow-

free period, the number of thaw-degree days, and nutrient availability (Starr *et al.*, 2000 and references herein).

How phenology can change

Whether phenology is mostly driven by direct (plants) or indirect (animals) cues reflecting changes in environmental conditions, the mechanisms responsible for phenological change can potentially be of two kinds. First, phenotypic plasticity (changes within individuals, PP hereafter) allows organisms to cope with short-term changes of the environment. Plant PP is usually called “acclimation” when phenotype alterations are reversible (Huey *et al.*, 2002). Second, evolution (changes in gene frequencies between generations) allows populations to cope with longer-term environmental changes, through permanent modifications of phenotypes.

When faced with long-term directional changes in environmental conditions, evolutionary adaptation is essential for the long-term persistence of natural populations. No population can track environmental changes perfectly, but a number of factors can improve the evolutionary response of a population to directional environmental change, thereby mitigating the negative demographic effects of selection and improving their probability of persistence. Ultimately, populations only persist if the rate of adaptive evolution at least matches the rate of environmental change (Bürger and Lynch, 1995).

A necessary condition for any evolutionary response of a quantitative trait (influenced by multiple genes, each having a small effect) to selection is the presence of heritable variation (Falconer and Mackay, 1996; Roff, 1997; Lynch and Walsh, 1998). Significant levels of genetic variation (heritability; h^2) have been estimated for a large number of traits in many different organisms (Mousseau and Roff, 1987; Roff and Mousseau, 1987; Weigensberg and Roff, 1996; Merilä and Sheldon, 1999; Hoffmann, 2000; Stirling *et al.*, 2002), suggesting that most traits possess at least some potential to respond in an evolutionary way to environmental change. The response of a single trait to selection, however, may be inhibited by antagonistic selection on a genetically correlated trait (Lynch and Walsh, 1998). Genetic correlations are more difficult to quantify precisely than heritabilities (Roff, 1997), but have been found in some cases to be sufficiently large to restrict the potential response to climate change (Etterson and Shaw, 2001; but see Réale *et al.*, 2003a).

What is needed to predict phenological change

The two main ingredients necessary to predict how the phenology of a population might change in response to climate change are the magnitude of PP in the population (which determines the potential of the population to respond over the short term), and the speed at which the population can evolve (which determine the potential of the population to respond over the longer term). For a quantitative trait (influenced by

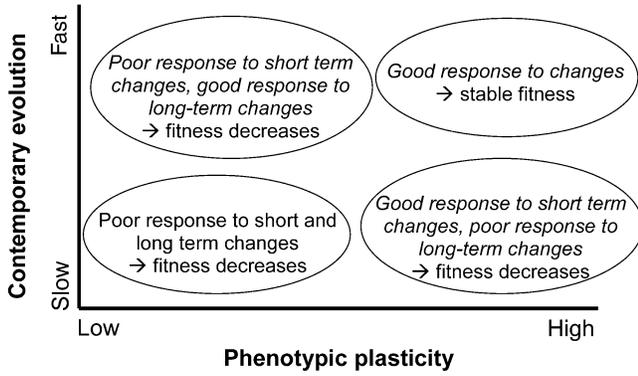


FIG. 2. Qualitative predictions regarding the response of a population to quick environmental change (such as current and predicted climate changes in the Arctic), according to the level of phenotypic plasticity (x axis) and rate of contemporary evolution (y axis) in the population. We assume here that phenotypic plasticity and contemporary evolution have effects going in the same direction (see Merilä *et al.*, 2001 for an example where phenotypic plasticity and contemporary evolution have effects going in opposite directions).

multiple genes, each having a small effect), we can therefore describe several situations depending on the magnitude of PP and the speed of evolution. In one extreme situation, contemporary evolution is slow and there is virtually no PP for the trait considered. Sources of change in the average trait value are weak, and if the selection gradient acting on the trait (the slope of the relationship between the trait and fitness) is steep, the average fitness of the population decreases under the pressure of climate change. In the other extreme situation, on the contrary PP is large and contemporary evolution is fast, so that sources of change in the average trait value are strong, and the average fitness of the population remains stable (Fig. 2). A

particular situation can occur, where antagonistic plastic (*i.e.*, PP) and genetic responses to environmental change will lead to apparent evolutionary stasis (no change or contradictory change in the phenotype with time), despite selection and genetic variation of the trait (Merilä *et al.*, 2001). Depending on the magnitude of PP and the speed of evolution, we can thus generate optimistic or pessimistic scenarios when predicting the phenotypic response of organisms to climate change (Fig. 3).

The following section on the reproductive phenology of North American red squirrels under the pressure of climate change illustrates the two routes for phenological change, and how the importance of PP and speed of evolution allows one to make predictions regarding the ability of species to cope with climate change.

We present a dataset of high interest because there is virtually no other data available to quantify the speed of evolution in the face of climate change, especially in northern environments. This lack of hard data was emphasized by Hedrick (2001), who ended a recent book on evolutionary ecology (Fox *et al.*, 2001, p. 383) by highlighting that “determining the potential for adaptation of a population in a changing environment is a critical unanswered question in most cases.”

CASE STUDY: RED SQUIRRELS AT KLUANE, YUKON

Here we report a gradual advancement of the mean lifetime parturition date in a population of North American red squirrels near Kluane Lake, Yukon, Canada. The study involved the long-term monitoring (1989–2002) of a total of 664 marked females, 325 of which being followed throughout their lifetime. Spring climate has changed in the southwest Yukon such that

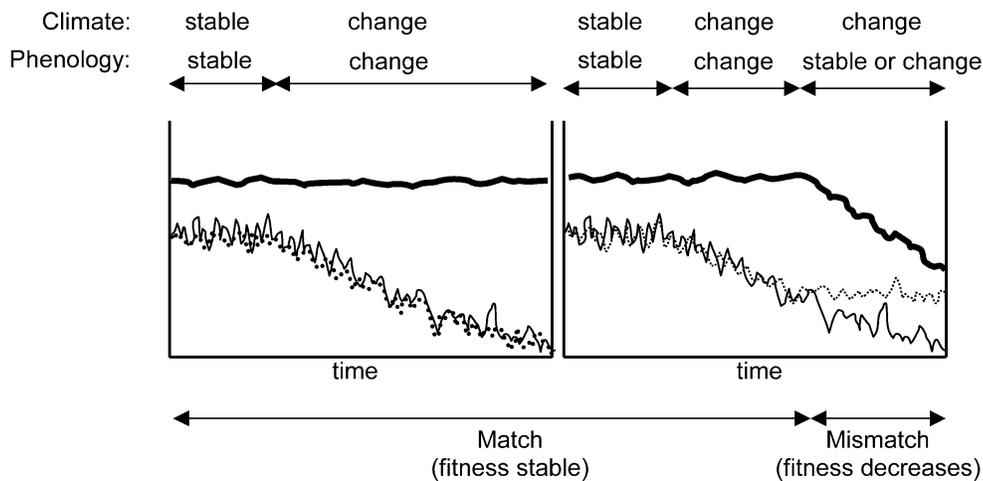


FIG. 3. Optimistic and pessimistic scenarios regarding changes in phenology associated with climate change. In the optimistic scenario (left), phenological changes track climate changes well and a good match is kept between the two variables; there is no decrease in the average fitness of the population. In the pessimistic scenario (right), phenological changes track changes in climate well in the beginning but are unable to cope with a prolonged climate change, the population becomes mismatched with environmental conditions or the temporal distribution of resources, and its average fitness decreases. Full line = temperature, dotted line = phenology, bold line = average fitness of the population. Note that average fitness is not represented as a straight line as it actually jumps around depending on random variation of the optimum from the actual mean value in the population.

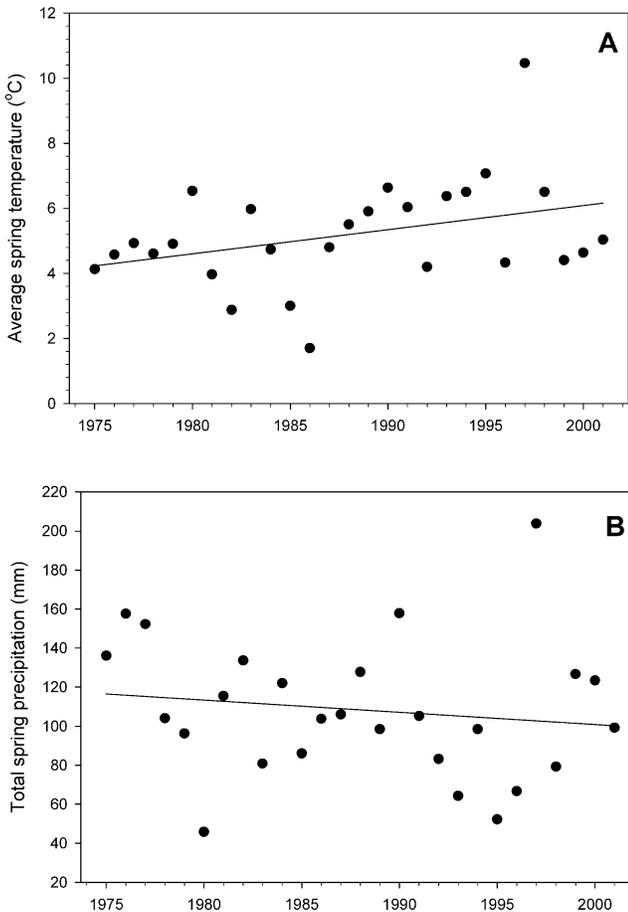


FIG. 4. Changes in spring climatic conditions experienced by a population of North American red squirrels at Kluane, Yukon, Canada, between 1975 and 2001. a) average spring temperature from April to June; b) total spring precipitation from January to June.

the squirrel population has experienced an increase of *ca.* 2°C in spring temperature (Fig. 4a) and a trend toward less precipitation over the last 27 years (Fig. 4b; Réale *et al.*, 2003a). During the last 10 years, white spruce (*Picea glauca*) cones abundance, which is the primary food source of squirrels, has increased dramatically (Fig. 5). Over this same 10-year period, mean lifetime parturition date of female squirrels has advanced by about 18 days (Fig. 5), which represents a change of 6 days per generation (Réale *et al.*, 2003a).

Such advancement could have resulted either from PP, through a direct response of individual females to changes in environmental cues, or from the microevolution of parturition date through natural selection, or from some combination of the two processes.

We first detected the plastic response of females by looking at the timing of breeding by the same females in several years as a function of cone abundance, and using a mixed-model (Przybylo *et al.*, 2000). The general approach of this analysis is to determine the magnitude of the response of individuals to changes in environmental conditions within their lifetime.

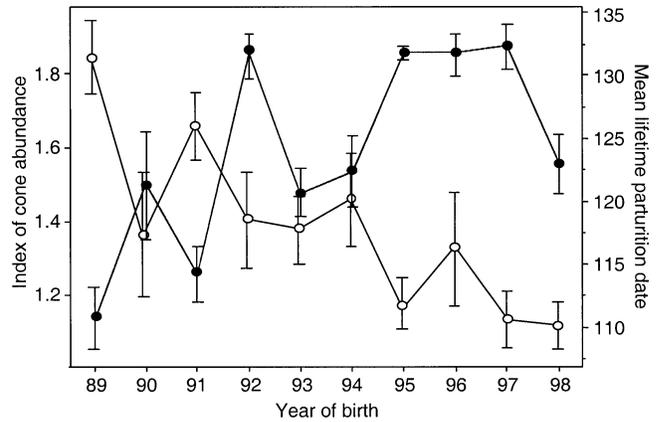


FIG. 5. Changes in cone production and parturition dates for 10 successive cohorts of North American red squirrel females at Kluane, Yukon, Canada. Closed circles: spruce cone abundance (log transformed \pm SE); Open circles: parturition date (Julian date \pm SE). Each data point represents the mean for average cone abundance, or the mean for average lifetime parturition date, for individuals of each given cohort.

We then estimated the combined additive effects of all an individual's genes (*i.e.*, Estimated Breeding Values, EBVs) for parturition date, using Restricted Maximum-Likelihood 'animal models' (Réale *et al.*, 2003a). REML animal models have been developed in the context of artificial selection of domestic breeds, but few attempts have been made to use this approach with a wild population. Comparison of EBVs across four generations of females provided an estimate of the genetic changes influencing parturition date in the population. Most of the advancement in parturition date could be attributed to PP (62% of the total or 3.7 days per generation). A small but significant part of the phenotypic changes in parturition date also resulted from microevolutionary change in this trait (13% or 0.8 days per generation; Fig. 6). Genetic change esti-

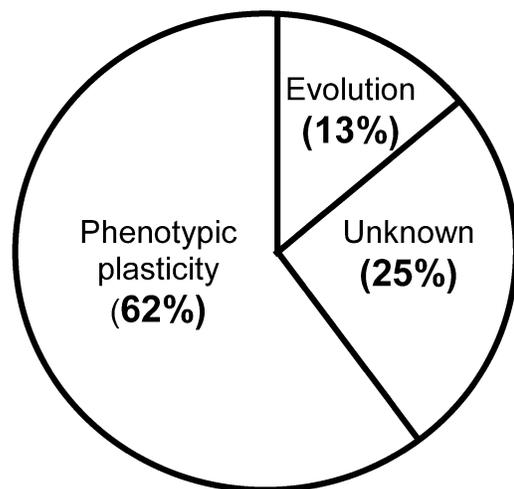


FIG. 6. Sources of variability in observed parturition dates in a population of North American red squirrels studied during ten years in the Yukon, Canada.

mated from EBVs closely matched the response to selection, R (0.6 days per generation), predicted by the breeder's equation $R = h^2S$, where h^2 is the heritability of the trait, and S is the selection differential on the trait (Falconer and Mackay, 1996). The good fit between measured EBVs and R , the predicted response to selection, indicates that evolutionary changes resulted from natural selection.

Our model explained a large part of the change in parturition date over time (Fig. 6). The unexplained 25% of the variability can be due to measurement errors at different steps of the study, for instance during estimation of heritability and selection gradients (reviewed Merilä *et al.*, 2001). Also, we may not have considered in our model some environmental factors that may have covaried with food abundance and may have affected the individual responses of females. In such a case, plastic response would be stronger than we estimated.

The proximal mechanisms responsible for an advanced timing of reproduction in the Kluane red squirrels are currently unknown. Although we suspect that differential fitness of females according to their reproductive phenology is probably related to food availability and quality influencing their weaning success, the ecological factors responsible for the higher fitness of early breeders compared to late breeders have still to be discovered.

As we have seen above, the maintenance of a natural population facing environmental changes depends on its ability to respond (*i.e.*, plastic or genetic responses) to the new selection pressures. We should thus expect that, if efficient, plastic and genetic responses to changing conditions may lead to the maintenance of a constant fitness in the population, or at least to a level above a critical threshold for extinction (see question 3, below). This can be tested by comparing fitness indices (*e.g.*, lifetime reproductive success) across generations.

Despite large environmental changes experienced by this population over a short period of time, we have no evidence that the mean lifetime reproductive success of females in the population has declined. Selection intensities did not change across generations (Réale *et al.*, 2003b) and lifetime reproductive success (measured as the total number of offspring weaned during a female's lifetime) did not decrease with generation (ANOVA; $F_{3,248} = 2.28$, $P = 0.08$, Fig. 7). This suggests that the large combined effects of PP and microevolutionary change have allowed this population of squirrels to keep pace with rapid changes in environmental conditions over the last 10 years.

This case study clearly shows that evolution can be a significant contributor to the maintenance of average fitness in a northern population facing fast climate change. Our study deals with one species, however, and it is useful to investigate whether our findings can be generalized to other species. The following section answers some common questions in this respect.

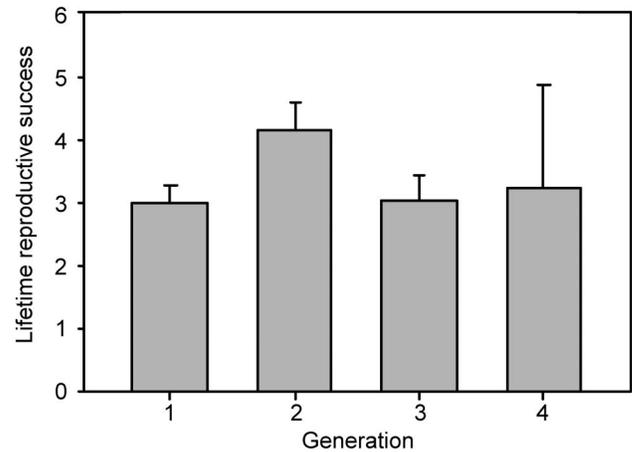


FIG. 7. Mean lifetime reproductive success (+ SE) of female red squirrels by generation. Reproductive success was measured as the total number of offspring weaned by an individual female in her lifetime. The four generations represented here represent females that were alive between 1990 and 2001. Females from the 1997 and 1998 cohorts were excluded from this analysis because many of them were still alive in 2001, when the data analysis was performed. Sample sizes (number of females) are indicated above each bar.

FREQUENTLY ASKED QUESTIONS AND CONSIDERATIONS FOR FUTURE STUDIES

Whether evolutionary processes can be quick enough to allow adaptation of arctic populations facing climate change is a pervading but unanswered question among arctic biologists. Stockwell *et al.* (2003) recently introduced contemporary evolution to conservation biology, but didn't raise the issue of climate change and its impacts on the evolution of populations or species. The fields of evolutionary ecology and quantitative genetics are technical in nature and use jargon with which arctic biologists may not all be familiar. Here we answer a series of frequently asked questions dealing with evolutionary processes as they relate to climate change. Questions 1–4 deal with basic information on which factors enhance genetic variation and the ability of species to evolve, questions 5–7 provide more direct recommendations on how studies should be conducted and which characters should be measured, and finally question 8 deals with the management of small populations.

1) What are the main factors affecting the ability of a species to evolve at a quick rate?

Short answer: Genetic variability for fitness-related or ecologically important traits.

Long answer: As we have seen earlier, the main factor affecting the ability of a species to evolve rapidly in the face of environmental changes, is its genetic variability for fitness-related or ecologically important traits. The reasons why genetic variation of quantitative traits is maintained in wild populations is still a debated question in evolutionary biology (Roff, 1997). To simplify, let us say that it results from the combination of mutation and migration, which tends to increase variation, and selection (or some aspects of ge-

netic drift in small populations), which decreases variation, and the existence of trade-offs (or negative genetic correlations) between traits caused by antagonistic pleiotropy (see above). Climate change affects selection pressures and probably migration patterns, but it is unclear whether they can affect mutation rates. It is impossible to predict how climate change can affect the genetic variability of a population.

There is now evidence that genetic variance for traits measured under unfavourable or stressful conditions could be higher than when measured under favourable conditions, because of differential expression of genes according to environmental conditions (Hoffmann and Merilä, 1999). This suggests that new climatic conditions in the Arctic, by providing new selection pressures and being associated with an increase in the evolutionary potential of the traits, may lead to rapid changes of population characteristics.

Other factors may affect the ability of a species to evolve at a quick rate. We have shown previously that phenotypic plasticity could play an important role in the way populations respond to environmental change. Phenotypic plasticity could be considered adaptive if it allows a population to maintain a constant fitness despite environmental changes, and may thus have evolved as a result of past selection pressures (Schlichting and Pigliucci, 1998). Considering that the arctic climate has fluctuated in the past, most Arctic species probably do have some adaptive phenotypic plasticity in the bank to respond to current climate change.

Adaptive phenotypic plasticity may also dampen or increase the effect of selection on a trait. For instance, phenotypic plasticity allowed the advancement in parturition date in the Kluane squirrel population, which may have weakened the intensity of selection on parturition date, and thus decreased the evolutionary response of parturition date. To our knowledge no research has been done on the role of phenotypic plasticity on the evolutionary response of a trait to selection.

Maternal effects, which could be considered as cross-generation phenotypic plasticity (Mousseau and Fox, 1998), could also play an important role in the maintenance of fitness of arctic populations experiencing climate change. Maternal effects have important consequences on the ecology and the demography of species (Bernardo, 1996) and their ability to adapt to new environmental conditions (Badyaev *et al.*, 2002). The potential impact of maternal effects on the rate and direction of evolution of a trait has been shown (Kirkpatrick and Lande, 1989; Wolf *et al.*, 1998), but empirical evidence of maternal effects on evolutionary dynamics in natural populations is lacking. Maternal inheritance has been proposed as a mechanism by which selection may result in rapid adaptation and the observed population fluctuations in collared lemmings (*Dicrostonyx groenlandicus*; Boonstra and Hochachka, 1997), but the level with which maternal effects will dampen or accelerate the response to climate-induced

selection pressures in arctic populations is currently unknown.

2) *Is there naturally more or less genetic variation in northern populations than in other populations?*

Short answer: Genetic variation does not seem to be different from other populations, but more information is needed.

Long answer: Under certain circumstances, populations experiencing temporal or spatial variation in selection can maintain higher levels of genetic variation (Ellner and Hairston, 1994) and thus a greater potential to respond to selection than populations experiencing consistent selection. As a result, northern populations at the edge of species' distributions might be expected to harbour increased levels of genetic variation if they have historically experienced unpredictable environmental conditions. Alternatively, populations at the margins of distributions may only be able to persist in very specialized and predictable habitats (Thomas *et al.*, 2001) and as a result may experience very little spatial or temporal variation in selection. Furthermore, several reasons such as founder effects, specific population structure or selection regime, may explain why populations located at a species margins may be characterized by a low genetic variation (Hoffmann and Parsons, 1991).

A brief review of the literature revealed few estimates of heritability for arctic or northern populations, especially for phenological traits (Table 1). Most of these studies found significant levels of genetic variation that were typical of levels of genetic variation in similar traits in more temperate populations (see Mousseau and Roff, 1987; Weigensberg and Roff, 1996). A notable exception was the collared lemming (*Dicrostonyx groenlandicus*), which was found to have very low levels of genetic variation (Boonstra and Hochachka, 1997). However, maternal effects were strong for most traits examined in the collared lemming (Boonstra and Hochachka, 1997), which may provide a substantial indirect contribution to the potential for an evolutionary response to selection (Wolf *et al.*, 1998; McAdam *et al.*, 2002). Results from these studies provide some evidence of the potential for evolution in northern populations, but clearly much more work needs to be done before a comprehensive understanding of the capacity for evolution in northern populations emerges. The potential importance of genetic variation to the persistence of northern populations faced with rapid changes in climate certainly warrants more investigations into the heritability of adaptive traits in northern ecosystems.

3) *Is species generation length an important factor in its potential to evolve?*

Short answer: Yes.

Long answer: Given that microevolutionary processes occur across generations, generation time should be an important factor affecting the evolutionary potential of species when environmental change is

TABLE 1. *Published estimates of heritability from northern populations.**

Species	Location	Trait	h^2	Source
Mountain birch, <i>Betula pubescens</i>	Finland	Rust resistance	0.27–0.41	Elamo <i>et al.</i> , 2000
Scots pine, <i>Pinus sylvestris</i>	Sweden	Height growth	0.06–0.11	Andersson and Danell, 1997
		Rust resistance	0.08	Andersson and Danell, 1997
<i>Cyclops scutifer</i>	Norway	Time to metamorphosis	0.32	Twombly, 1993
Lesser snow goose, <i>Anser caerulescens</i>	La Pérouse Bay, Canada	Clutch size	0.20	Findlay and Cooke, 1983, 1987
Arctic skua, <i>Stercorarius parasiticus</i>	Foula, UK	Offspring condition	1.03	Phillips and Furness, 1998
		Relative hatch date	0.27	Phillips and Furness, 1998
		Hatch date	0.02	Phillips and Furness, 1998
	Fair Isle, UK	Hatch date	0.85	O'Donald, 1983
Common gull, <i>Larus canus</i>	Estonia	Head size	0.38–0.70	Larsson <i>et al.</i> , 1997
Tengmalm's owl, <i>Aegolius funereus</i>	Finland	Female wing length	0.60	Hakkarainen <i>et al.</i> , 1996
		Male wing length	0.10	Hakkarainen <i>et al.</i> , 1996
		Clutch size	0.56	Hakkarainen <i>et al.</i> , 1996
Dall sheep, <i>Ovis dalli</i>	Yukon, Canada	Horn length	0.2–0.4	Ludwig and Hoefs, 1995
		Horn circumference	0.5–0.7	Ludwig and Hoefs, 1995
Red squirrel, <i>Tamiasciurus hudsonicus</i>	Yukon, Canada	Parturition date	0.16	Réale <i>et al.</i> , 2003b
		Litter size	0.15	Réale <i>et al.</i> , 2003b
		Growth in body mass	0.36**	McAdam <i>et al.</i> , 2002
		Growth in body size	0.36**	McAdam <i>et al.</i> , 2002
Bank vole, <i>Clethrionomys glareolus</i>	Konnevesi, Finland	Male mating success	0.60	Oksanen <i>et al.</i> , 1999
Collared lemming, <i>Dicrostonyx groenlandicus</i>	Pierce Point, Canada	Growth in body mass	0.00	Boonstra and Hochachka, 1997
		Male age at maturity	0.00	Boonstra and Hochachka, 1997
		Female age at maturity	0.03	Boonstra and Hochachka, 1997

* Some heritability estimates are from breeding experiments in the laboratory, but individuals were from northern natural populations. The literature review is representative rather than exhaustive.

** Includes the contribution of genetic maternal effects.

rapid (Rosenheim and Tabshnik, 1991; Janzen, 1992). Everything else being equal, species with long generation time should have less ability to respond to new selective pressures (Rosenheim and Tabshnik, 1991; Janzen, 1992), and may thus have higher risk of extinction than species with a short generation time (Owens and Bennett, 2000). We, therefore, expect that large, long-lived species, such as polar bear or caribou, will be more fragile than short-lived insects or annual plants. Reality is more complex, however, and the risk of extinction does not always relate to species generation time in comparative studies, as it interacts with other ecological factors (Owens and Bennett, 2000).

A demographic argument also points to the importance of generation time in species' potential to evolve. The evolutionary response to selection is a function of the strength of selection. However, while an increase in the strength of selection results in a greater evolutionary response, it also comes at a demographic cost. Any previously adapted population experiencing a change in the optimum phenotype of a trait will experience the demographic cost of a decrease in fecundity or survival. If the effective population size is too small or the environmental change is too great, the rate

of long-term adaptation may not be sufficient to compensate for these short-term demographic costs and the population may fall below a critical threshold for extinction (Gomulkiewicz and Holt, 1995; Stockwell *et al.*, 2003). The probability of population persistence will then depend on the capacity for population growth. Large bodied species with long generation times are particularly susceptible to extinction as a result of their low capacity for population growth (Gomulkiewicz and Holt, 1995).

4) *What kind of new selective pressures are expected to act on northern populations facing climate warming?*

Short answer: Many, both direct through changing biotic factors and indirect through modified pressures from competition, predation, parasitism, mutualism, etc.

Long answer: New selective pressures occur when changes in environmental conditions affect the relationship between the phenotype and fitness. There is no doubt that selective pressures are changing rapidly under climate change. We expect that climate change will have a direct impact on the biology of northern

populations, by changing abiotic conditions, but it may also affect them indirectly, by changing many biotic variables. For instance, following the increasing migration rate of species up to northern latitudes (Root *et al.*, 2003), new species of predators, preys, parasites, and competitors will be in contact with arctic species. Overall, the general food-web of arctic ecosystems may be modified by climate changes in the future (Hansell *et al.*, 1998). The influence of climate change on migration patterns may have strong influence on the contemporary evolution of Arctic species, because increasing gene flow from southern populations may reduce the fitness of some locally adapted populations through outbreeding depression.

Increased fragmentation of the habitat of arctic species has been observed following climate change in the past, and seems to be at the origin of some population divergence or even speciation (Avisé and Walker, 1998; Fedorov, 1999; Kraaijeveld and Nieboer, 2000). Studies on past events suggest that the impact of climate change on evolution will depend on the species and on its current distribution (Fedorov, 1999; Kraaijeveld and Nieboer, 2000). Given their specific geographic location, arctic populations may experience a shrinkage of their geographical range following climate warming (they cannot move up north). Hoffmann and Parsons (1991) have considered the genetic and ecological characteristics of marginal populations to explain the limitation of a species' range expansion. The study of marginal populations will probably help us understanding how arctic species could maintain their range despite important changes in the environment.

5) *What information do we need to predict/measure evolutionary change?*

Short answer: We need long-term data sets with measurements on phenotypic traits collected over many individuals of known relationship to one another.

Long answer: Microevolutionary changes in wild populations is detected mostly using two general approaches, which can both be experimental or observational (Hendry and Kinnison, 1999; Kinnison and Hendry, 2001). First, traits from populations that have diverged through time from the same ancestral population can be compared (the synchronic approach). This can for example be done by assessing phenotypes in a common garden environment, that is by raising individuals from different years in the same environment, such as a greenhouse. Second, the long-term monitoring of a given population can also show microevolutionary changes (the allochronic approach). This second approach has provided results on the contemporary evolution of natural populations in response to environmental changes (*e.g.*, Grant and Grant, 1995, 2002; Reznick *et al.*, 1997; Réale *et al.*, 2003a).

Given that climate change may be generalized across the Arctic, we think that the allochronic approach is the most appropriate to study the response of Arctic populations to climate change. A longitudinal

study allows to look in parallel at changes in climate and at the rate of evolution of a phenotype. In contrast, the synchronic approach would provide estimation of the rate of divergence between populations (Hendry and Kinnison, 1999). As shown in our case study (this paper; see also Merilä *et al.*, 2001), the examination of phenotypic traits is not sufficient to determine evolutionary change, because part of that change can be caused by phenotypic plasticity and local environmental conditions. Microevolutionary studies need data on phenotypic traits collected from a large number of individuals of known relationship to one another. Obtaining data sets equivalent to the Kluane red squirrel data set, however, is not an easy task and necessitates efforts over the long-term. Moreover, the allochronic approach has its own limits and may not always provide the expected answers (Merilä *et al.*, 2001). For instance, bias in heritability estimates, selection fluctuating in time and space, or antagonistic plastic and genetic responses, can prevent the finding of a correspondence between observed and predicted responses to selection (Merilä *et al.*, 2001).

Some data sets from long-term research programs on animal and plant populations may already exist and studies similar to ours could perhaps be performed. Furthermore, the monitoring of arctic populations at the phenotypic level will provide useful information about the maintenance of populations following climate change. The development of new methods based on molecular tools to create pedigrees or to infer genetic relationships within a population, will facilitate the estimation of quantitative genetic parameters in the wild (Moore and Kukuk, 2002).

6) *We already have molecular indices of genetic diversity for many populations. Are these sufficient to estimate the evolutionary potential of these populations?*

Short answer: No.

Long answer: Some authors have proposed (Merilä and Crnokrak, 2001; Reed and Frankham, 2001) to use molecular genetic markers as an indicator of the evolutionary potential of wild populations. These markers are generally easy to obtain, not invasive and allow rapid decisions in the management of wild populations (McKay and Latta, 2002). Recent studies, however, have questioned the usefulness of molecular indices of genetic variability to detect the evolutionary potential of natural populations (McKay and Latta, 2002). For example, no relationship has been found between molecular measures of genetic diversity and heritability estimates (Reed and Frankham, 2001), and a positive but weak correlation has been found between F_{st} (an index of differentiation between two populations using molecular markers) and Q_{st} (an index of differentiation between two populations using quantitative traits) (McKay and Latta, 2002). This suggests the low relevance of molecular tools for predicting evolutionary changes in the wild (Reed and Frankham, 2001), although a recent study has shown a positive relationship

between indices of genetic diversity and fitness in wild populations (Reed and Frankham, 2003). Therefore we encourage ecologists with long-term data sets on arctic species to report estimates of evolutionary changes, as we have done with our squirrel data set (Réale *et al.*, 2003a, b).

7) *What traits should be monitored to estimate the response of arctic populations to climate change?*

Short answer: Fitness-related traits.

Long answer: The traits that have been mostly studied in relation to climate change are phenological traits (Root *et al.*, 2003). As shown above, phenological traits have been chosen because they represent an important aspect of the biology of arctic species and are directly linked to changes in seasonality. They also are easy to measure. Gathering data on physiological, behavioural, or life-history traits is more labor intensive or more invasive, as capture of individuals, long periods of observation, or monitoring of individuals throughout their lifetime are needed. Given that phenological traits are of high ecological importance, it is tempting to encourage further monitoring efforts on these traits. However, the study of phenological traits in the absence of data on fitness related traits (*e.g.*, survival, longevity or reproductive success), would prevent us from looking at some demographic and evolutionary consequences of climate change on arctic populations. In conclusion, collecting data over the long-term on both phenological traits and fitness-related traits are required to be able to predict the impact of climate change on wild populations and make informed management decisions.

8) *Given that genetic variability is the main factor responsible for evolutionary potential, is it possible to increase genetic variability in small populations?*

Short answer: Yes but this may generate other problems.

Long answer: We have seen above that high genetic variation for fitness-related traits was the main condition for evolutionary potential of populations facing environmental changes. Genetic variation declines with decreasing population size (Lynch, 1996; Frankham, 1999), in conjunction with the effects of inbreeding of fitness-related traits (Frankham, 1999), which makes small isolated populations particularly vulnerable to environmental changes. One solution would be to increase the genetic variation of these populations by transferring individuals from other populations. For instance, given that phenology of northern populations is generally related to latitude, the transfer (natural or artificial) of individuals from southern populations to northern populations could increase the adaptability of the latter to new climatic conditions. This solution, however, should be considered with caution, because of potential outbreeding depression (Frankham, 1999; Edmands and Timmerman, 2003; Stockwell *et al.*, 2003) resulting from local adaptations

of each population to environmental conditions other than climatic. For example, populations at different latitudes may have evolved in the presence of different predators, parasites or competitors, and may not be adapted to the same general conditions as northern populations.

CONCLUSION

Can Arctic life count on evolution to keep pace with fast climate change? We have summarized some of the recent literature and used data on a northern population of squirrels to answer this question. Evolution can certainly help arctic populations, even over short time scales. This should generate optimism.

But predictions as to which species will evolve fast enough to adapt to new climatic and ecological conditions are currently difficult because 1) there is a lack of data on the quantitative genetics of many species; 2) although we know that populations with high genetic variability and short generation time are at an advantage, the diversity of new selective pressures associated with climate change makes species—specific predictions difficult; and 3) contingency will play a large role in future evolution, as it has in past evolution, therefore we necessarily face limits regarding our ability to make predictions about the evolution of species.

ACKNOWLEDGMENTS

We thank David Hik and Rudy Boonstra for organizing the symposium on The Biology of the Canadian Arctic, the generations of field workers who used all the range of their phenotypic plasticity to study red squirrels under highly variable climatic conditions, and Sébastien Descamps and two anonymous reviewers for comments on the manuscript. Field research on the squirrel population was supported by grants from the Natural Sciences and Engineering Research Council of Canada, and the Northern Scientific Training Program of the Department of Indian Affairs and Northern Development (DIAND) with the Canadian Circumpolar Institute at the University of Alberta.

REFERENCES

- Ahas, R., A. Aasa, A. Menzel, V. G. Fedotova, and H. Scheifinger. 2002. Changes in European spring phenology. *Int. J. Clim.* 22: 1727–1738.
- Andersson, B. and Ö. Danell. 1997. Is *Pinus sylvestris* resistance to pine twist rust associated with fitness costs or benefits? *Evolution* 51:1808–1814.
- Ashley, M. V., M. F. Wilson, O. R. W. Pergams, D. J. O'Dowd, S. M. Gende, and J. S. Brown. 2003. Evolutionary enlightened management. *Biol. Conserv.* 111:115–123.
- Avise, J. C. and D. Walker. 1998. Pleistocene phylogeographic effects on avian populations and the speciation process. *Proc. R. Soc. London B* 265:457–463.
- Badyaev, A. V., G. E. Hill, and L. A. Whittingham. 2002. Population consequences of maternal effects: Sex-bias in egg-laying order facilitates divergence in sexual dimorphism between bird populations. *J. Evol. Biol.* 16:997–1003.
- Beebe, T. J. C. 2002. Amphibian phenology and climate change. *Conserv. Biol.* 16:1454–1455.

- Bernardo, J. 1996. Maternal effects in animal ecology. *Amer. Zool.* 36:83–105.
- Billings, W. D. 1987. Constraints to plant growth, reproduction, and establishment in arctic environments. *Arctic and Alpine Res.* 19:357–365.
- Boonstra, R. and W. M. Hochachka. 1997. Maternal effects and additive genetic inheritance in the collared lemming *Dicrostonyx groenlandicus*. *Evol. Ecol.* 11:169–182.
- Bradshaw, W. E. and C. M. Holzapfel. 2001. Genetic shift in photoperiodic response correlated with global warming. *Proc. Natl Acad. Sci. U.S.A.* 98:14509–14511.
- Bürger, R. and M. Lynch. 1995. Evolution and extinction in a changing environment: A quantitative-genetic analysis. *Evolution* 49:151–163.
- Chernov, Yu. I. 1985. *The living tundra*. Cambridge University Press, Cambridge.
- de Jong, P. W. and P. M. Brakefield. 1998. Climate and change in clines for melanism in the two-spot ladybird, *Adalia bipunctata* (Coleoptera: coccinellidae). *Proc. R. Soc. London. B* 265:39–43.
- Edmunds, S. and C. C. Timmerman. 2003. Modeling factors affecting the severity of outbreeding depression. *Cons. Biol.* 17:883–892.
- Elamo, P., I. Saloniemi, M. L. Helander, and S. Neuvonen. 2000. Genetic and environmental variation in rust frequency on mature mountain birch trees. *Scand. J. For. Res.* 15:510–522.
- Ellner, S. and N. G. Hairston, Jr. 1994. Role of overlapping generations in maintaining genetic variation in a fluctuating environment. *Am. Nat.* 143:403–417.
- Esper, J., E. R. Cook, and F. H. Schweingruber. 2002. Low-frequency signals in long tree-ring chronologies for reconstructing past temperature variability. *Science* 295:2250–2253.
- Etterson, J. R. and R. G. Shaw. 2001. Constraint to adaptive evolution in response to global warming. *Science* 294:151–154.
- Falconer, D. S. and T. F. C. Mackay. 1996. *Introduction to quantitative genetics*. Longman, New York.
- Fedorov, V. B. 1999. Contrasting mitochondrial DNA diversity estimates in two sympatric genera of Arctic lemmings (*Dicrostonyx*; *Lemmus*) indicate different responses to Quaternary environmental fluctuations. *Proc. R. Soc. London. B* 266:621–626.
- Findlay, C. S. and F. Cooke. 1983. Genetic and environmental components of clutch size variance in a wild population of lesser snow geese (*Anser caerulescens caerulescens*). *Evolution* 37:724–734.
- Findlay, C. S. and F. Cooke. 1987. Repeatability and heritability of clutch size in lesser snow geese. *Evolution* 41:453.
- Frankham, R. 1999. Quantitative genetics in conservation biology. *Genet. Res. Camb.* 74:237–244.
- Futuyma, D. J. 1998. *Evolutionary biology*. Sinauer, Sunderland, USA.
- Gomulkiewicz, R. and R. D. Holt. 1995. When does evolution by natural selection prevent extinction? *Evolution* 49:201–207.
- Grant, P. R. and B. R. Grant. 1995. Predicting microevolutionary responses to directional selection on heritable variation. *Evolution* 49:241–251.
- Grant, P. R. and B. R. Grant. 2002. Unpredictable evolution in a 30-year study of Darwin's finches. *Science* 296:707–711.
- Hakkarainen, H., E. Korpimäki, J. Ryssy, and S. Vikström. 1996. Low heritability in morphological characters of Tengmalm's owls: The role of cyclic food and laying date? *Evol. Ecol.* 10:207–219.
- Hansell, R. I. C., J. R. Malcolm, H. Welch, and R. L. Scott. 1998. Atmospheric change and biodiversity in the Arctic. *Environ. Monit. Assess.* 49:303–325.
- Hedrick, P. W. 2001. Evolutionary conservation biology. In C. W. Fox, D. A. Roff, and D. J. Fairbairn (eds.), *Evolutionary ecology: Concepts and case studies*, pp. 371–383. Oxford University Press, Oxford, UK.
- Hendry, A. P. and M. T. Kinnison. 1999. The pace of modern life: Measuring rates of contemporary microevolution. *Evolution* 53:1637–1653.
- Hengeveld, H. G. 2000. Projections for Canada's climate future. Minister of public works and government services, Canada. Also available at www.tor.ec.gc.ca/apac/.
- Hoffmann, A. A. 2000. Laboratory and field heritabilities: Some lessons from *Drosophila*. In T. A. Mousseau, B. Sinervo, and J. Endler (eds.), *Adaptive Genetic Variation in the wild*, pp. 200–218. Oxford Univ. Press, New York.
- Hoffmann, A. A. and P. A. Parsons. 1991. *Evolutionary genetics and environmental stress*. Oxford University Press, Oxford.
- Hoffmann, A. A. and J. Merilä. 1999. Heritable variation and evolution under favourable and unfavourable conditions. *Trends Ecol. Evol.* 14:96–101.
- Huey, R. B., M. Carlson, L. Crozier, M. Frazier, H. Hamilton, C. Harley, A. Hoang, and J. G. Kingsolver. 2002. Plants versus animals: do they deal with stress in different ways? *Integ. And Comp. Biol.* 42:415–423.
- Janzen, F. J. 1992. Heritable variation for sex ratio under environmental sex determination in the common snapping turtle (*Chelydra serpentina*). *Genetics* 131:155–191.
- Kinnison, M. T. and A. P. Hendry. 2001. The pace of modern life II: From rates of contemporary microevolution to pattern and process. *Genetica* 112–113:145–164.
- Kirkpatrick, M. and R. Lande. 1989. The evolution of maternal characters. *Evolution* 43:485–503.
- Kraaijeveld, K. and E. N. Nieboer. 2000. Late Quaternary paleogeography and evolution of Arctic waders. *Ardea* 88:193–205.
- Larsson, K., K. Rattiste, and V. Lilleleht. 1997. Heritability of head size in the common gull *Larus canus* in relation to the environmental conditions during offspring growth. *Heredity* 79:201–207.
- Ludwig, J. and M. Hoefs. 1995. A population genetic study of Dall sheep (*Ovis dalli dalli*) in the southwestern Yukon Territory. *Zeitschrift für Jagdwissenschaft* 41:256–266.
- Lynch, M. 1996. A quantitative-genetic perspective on conservation issues. In J. C. Avise and J. L. Hamrick (eds.), *Conservation genetics: Case histories from nature*, pp. 471–501. Chapman & Hall, New York.
- Lynch, M. and B. Walsh. 1998. *Genetics and analysis of quantitative traits*. Sinauer Associates, Sunderland, Massachusetts.
- McAdam, A. G., S. Boutin, D. Réale, and D. Berteaux. 2002. Maternal effects and the potential for evolution in a natural population of animals. *Evolution* 56:846–851.
- McCarty, J. P. 2002. Ecological consequences of recent climate change. *Cons. Biol.* 15:320–331.
- McKay, J. K. and R. G. Latta. 2002. Adaptive population divergence: Markers, QTL and traits. *Trends Ecol. Evol.* 17:285–291.
- Menzel, A. and P. Fabian. 1999. Growing season extended in Europe. *Nature* 397:659.
- Merilä, J. and B. C. Sheldon. 1999. Genetic architecture of fitness and nonfitness traits: Empirical patterns and development of ideas. *Heredity* 83:103–109.
- Merilä, J. and P. Crnokrak. 2001. Comparison of genetic differentiation at marker loci and quantitative traits. *J. Evol. Biol.* 14:892–903.
- Merilä, J., B. C. Sheldon, and L. E. B. Kruuk. 2001. Explaining stasis: Microevolutionary studies in natural populations. *Genetica* 112–113:199–222.
- Moore, A. J. and P. F. Kukuk. 2002. Quantitative genetic analysis of natural populations. *Nature Genetics*. 3:971–978.
- Moritz, R. E., C. M. Bitz, and E. J. Steig. 2002. Dynamics of recent climate change in the Arctic. *Science* 297:1497–1502.
- Mousseau, T. A. and C. W. Fox. 1998. *Maternal effects as adaptation*. Oxford Univ. Press, New York.
- Mousseau, T. A. and D. A. Roff. 1987. Natural selection and the heritability of fitness components. *Heredity* 59:181–197.
- Nelson, R. J. 2000. *An introduction to behavioral endocrinology*. 2nd ed. Sinauer Associates, Inc., Sunderland, Massachusetts.
- O'Donald, P. 1983. *The Arctic Skua: The study of the ecology and evolution of a seabird*. Cambridge University Press, Cambridge.
- Oksanen, T. A., R. V. Alatalo, T. J. Horne, E. Koselka, J. Mappes, and T. Mappes. 1999. Maternal effort and male quality in the bank vole, *Clethrionomys glareolus*. *Proc. Roy. Soc. London. B* 266:1495–1499.
- Owens, I. P. F. and P. M. Bennett. 2000. Ecological basis of extinct-

- risk in birds: habitat loss versus human persecution and introduced predators. *Proc. Natl. Acad. Sci. U.S.A.* 97:12144–12148.
- Palumbi, S. R. 2001. *The evolution explosion: How humans cause rapid evolutionary change*. Norton, New York.
- Parmesan, C. and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42.
- Phillips, R. A. and R. W. Furness. 1998. Measurement of heritability of hatching date and chick condition in parasitic jaegers. *Can. J. Zool.* 76:2290–2294.
- Pielou, E. C. 1994. *A naturalist's guide to the Arctic*. The University of Chicago Press, Chicago, USA.
- Przybylo, R., B. C. Sheldon, and J. Merilä. 2000. Patterns of natural selection on morphology of male and female collared flycatchers (*Ficedula albicollis*). *Biol. J. Linn. Soc.* 69:213–232.
- Quinn, T. P. and D. J. Adams. 1996. Environmental changes affecting the migratory timing of American shad and sockeye salmon. *Ecology* 77:1151–1162.
- Réale, D., A. G. McAdam, S. Boutin, and D. Berteaux. 2003a. Genetic and plastic response of a northern mammal to climate change. *Proc. R. Soc. London B.* 270:591–596.
- Réale, D., D. Berteaux, A. G. McAdam, and S. Boutin. 2003b. Lifetime selection on heritable life history traits in a natural population of red squirrels. *Evolution*. (In press)
- Reed, D. H. and R. Frankham. 2001. How closely correlated are molecular and quantitative measures of genetic variation? A meta-analysis. *Evolution* 55:1095–1103.
- Reed, D. H. and R. Frankham. 2003. Correlation between fitness and genetic diversity. *Conserv. Biol.* 17:230–237.
- Reznick, D. N., F. H. Shaw, F. H. Rodd, and R. G. Shaw. 1997. Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). *Science* 275:1934–1937.
- Rodriguez-Trellis, F. and M. A. Rodriguez. 1998. Rapid micro-evolution and loss of chromosomal diversity in *Drosophila* in response to climate warming. *Evol. Ecol.* 12:829–838.
- Roff, D. A. 1997. *Evolutionary quantitative genetics*. Chapman and Hall, New York.
- Roff, D. A. and T. A. Mousseau. 1987. Quantitative genetics and fitness: Lessons from *Drosophila*. *Heredity* 58:103–118.
- Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421:57–60.
- Rosenheim, J. A. and B. E. Tabashnik. 1991. Influence of generation time on the rate of response to selection. *Am. Nat.* 137:527–541.
- Schlichting, C. D. and M. Pigliucci. 1998. *Phenotypic plasticity: A reaction norm perspective*. Sinauer, Sunderland.
- Schnelle, F. 1955. *Pflanzen-Phänologie*. Akademische Verlagsgesellschaft Geest und Portig: Leipzig.
- Sparks, T. H. and A. Menzel. 2002. Observed changes in seasons: An overview. *Int. J. Clim.* 22:1715–1725.
- Starr, G., S. F. Oberbauer and E. W. Pop. 2000. Effects of lengthened growing season and soil warming on the phenology and physiology of *Polygonum bistorta*. *Global Change Biol.* 6:357–369.
- Stenseth, N. C. and A. Mysterud. 2002. Climate, changing phenology, and other life history traits: Nonlinearity and match-mismatch to the environment. *Proc. Natl. Acad. Sci. U.S.A.* 99:13379–13381.
- Stirling, D. G., D. Réale, and D. A. Roff. 2002. Selection, structure and the heritability of behaviour. *J. Evol. Biol.* 15:277–289.
- Stockwell, C. A., A. P. Hendry, and M. T. Kinnison. 2003. Contemporary evolution meets conservation biology. *Trends Ecol. Evol.* 18:94–101.
- Storfer, A. 1996. Quantitative genetics: A promising approach for the assessment of genetic variation in endangered species. *Trends Ecol. Evol.* 11:343–348.
- Thomas, C. D., E. J. Bodsworth, R. J. Wilson, A. D. Simmons, Z. G. Davies, M. Musche, and L. Conrard. 2001. Ecological and evolutionary processes at expanding range margins. *Nature* 411:577–581.
- Totland, O. and J. M. Alatalo. 2002. Effects of temperature and date of snowmelt on growth, reproduction, and flowering phenology in the arctic/alpine herb, *Ranunculus glacialis*. *Oecologia* 133:168–175.
- Twombly, S. 1993. Inter- and intrapopulation variation in time to metamorphosis in a freshwater copepod. *Freshwater Biol.* 30:105–118.
- van Vliet, A. J. H. and M. D. Schwartz. 2002. Phenology and climate: The timing of life cycle events as indicators of climate variability and change. *Int. J. Clim.* 22:1713–1714.
- Visser, M. E. and L. J. M. Holleman. 2001. Warmer springs disrupt the synchrony of oak and winter moth phenology. *Proc. Roy. Soc. London B* 268:289–294.
- Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. *Nature* 416:389–395.
- Weigensberg, I. and D. A. Roff. 1996. Natural heritabilities: Can they be reliably estimated in the laboratory? *Evolution* 50:2149–2157.
- Wingfield, J. C. and K. E. Hunt. 2002. Arctic spring: Hormone-behavior interactions in a severe environment. *Comp. Biochem. Phys. B* 132:275–286.
- Wolf, J. B., E. D. L. Brodie, J. M. Cheverud, A. J. Moore, and M. J. Wade. 1998. Evolutionary consequences of indirect genetic effects. *Trends Ecol. Evol.* 13:64–69.