INVITED REVIEW

Population structure attributable to reproductive time: isolation by time and adaptation by time

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Abstract

Many populations are composed of a mixture of individuals that reproduce at different times, and these times are often heritable. Under these conditions, gene flow should be limited between early and late reproducers, even within populations having a unimodal temporal distribution of reproductive activity. This temporal restriction on gene flow might be called 'isolation by time' (IBT) to acknowledge its analogy with isolation by distance (IBD). IBD and IBT are not exactly equivalent, however, owing to differences between dispersal in space and dispersal in time. We review empirical studies of natural populations that provide evidence for IBT based on heritabilities of reproductive time and on molecular genetic differences associated with reproductive time. When IBT is present, variation in selection through the reproductive season may lead to adaptive temporal variation in phenotypic traits [adaptation by time (ABT)]. We introduce a novel theoretical model that shows how ABT increases as (i) selection on the trait increases; (ii) environmental influences on reproductive time decrease; (iii) the heritability of reproductive time increases; and (iv) the temporal distribution of reproductive activity becomes increasingly uniform. We then review empirical studies of natural populations that provide evidence for ABT by documenting adaptive temporal clines in phenotypic traits. The best evidence for IBT and ABT currently comes from salmonid fishes and flowering plants, but we expect that future work will show these processes are more widespread.

Keywords: assortative mating, breeding time, gene flow, migration, phenology, temporal isolation

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Introduction

Many populations are composed of a mixture of individuals that reproduce at different times within a particular season and location. Within such populations, phenotypic traits often covary with reproductive time: for example, clutch size with egg laying date in birds (e.g. Meijer *et al.* 1990; Rowe *et al.* 1994; Winkler *et al.* 2002), body size with metamorphosis date in insects (e.g. Vannote & Sweeney 1980; Forrest 1987; Rowe & Ludwig 1991), reproductive lifespan with breeding date in salmonid fishes (e.g. McPhee & Quinn 1998; Morbey & Ydenberg 2003; Hendry *et al.* 2004), and flower number with flowering date in

plants (e.g. Dieringer 1991; Lyons & Mully 1992; Andersson 1996). Several explanations have been advanced for these temporal phenotypic clines, and our goal is to provide theoretical and empirical support for one of them.

One class of explanations assumes that reproductive times are individually flexible, rather than strongly heritable. Temporal phenotypic clines might then arise if reproductive time is influenced by phenotypic traits, such as body size or energy stores. These influences might reflect constraints (individuals can only reproduce when they surpass a particular threshold) or adaptive tactics (individuals reproduce at times for which their traits are best suited). Temporal phenotypic clines might also arise when cause and effect are reversed, such that trait expression is influenced by the conditions experienced at the chosen reproductive time. This might occur if traits are directly influenced by the environment or by the condition of

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individuals at a particular reproductive time, or if individuals alter their trait expression to suit their chosen time (i.e. adaptive tactics).

A second class of explanations assumes that reproductive times are strongly heritable, rather than individually flexible. Temporal phenotypic clines might then arise for several reasons. First, trait expression might be directly influenced by the environment or by the condition of individuals that reproduce at a particular time (as previously noted). Second, trait expression might reflect adaptive tactics by individuals reproducing at a particular time (also as previously noted). In either of these scenarios, an individual with a heritable tendency to reproduce early that instead reproduced late might express traits typical of late reproducers. Third, limited gene flow through the reproductive season (owing to heritable reproductive times) might allow adaptation to environmental conditions typically experienced at particular reproductive times. In this scenario, an individual with a heritable tendency to reproduce early that instead reproduced late might express traits typical of early reproducers. This adaptation to heritable reproductive times is the mechanism we here explore in detail.

The previous explanations are not mutually exclusive. That is, reproductive times may be influenced by a combination of heritable variation, random environmental effects, and individual choice. Moreover, phenotypic traits may both influence and be influenced by reproductive time owing to a combination of constraints, direct environmental influences, adaptive tactics, and adaptation to particular times. Disentangling this complexity, must await the demonstration that each mechanism can work on its own. To advance this initial goal, we first outline theoretical considerations and empirical evidence for temporal restrictions on gene flow that result from heritable reproductive times (i.e. 'isolation by time'). We then outline theoretical considerations and empirical evidence for adaptive temporal clines in phenotypic traits (i.e. 'adaptation by time'). Our empirical examples focus mainly on the taxa in which these ideas have been developed in greatest detail: salmonid fishes and flowering plants.

Isolation by time

Consider a seasonally reproducing population composed of individuals with different reproductive times, some reproducing early in the season, some late, and some at intermediate times. In such a population, individuals reproducing at similar times will be more likely to mate with each other than will those reproducing at different times (i.e. temporal assortative mating). If some of this timing variation is heritable, the probability that two individuals will mate should be inversely related to the difference in the heritable component of their reproductive times (Fox

2003; Weis & Kossler 2004). If this heritable component has an additive genetic basis, which often seems to be the case (Table 1), the probability that two individuals will mate should be inversely related to the difference in their breeding values for reproductive time. [Breeding values are the phenotypic trait value of an individual, expressed as the expected phenotypic trait value of its offspring (Roff 1997; p. 27)]. As a result, individuals with a heritable tendency to reproduce at a particular time will generate offspring of a similar proclivity. The net result will be genetic mixing within the population that decreases with increasing differences in reproductive time. We call this phenomenon isolation by time (Hendry *et al.* 1998, 1999, 2001, 2004).

Theoretical considerations

The term isolation by time (IBT) acknowledges a conceptual analogy with 'isolation by distance' (IBD), wherein limited dispersal in space leads to increasing genetic differences with increasing spatial distances (Wright 1943, 1946; Kimura & Weiss 1964; Slatkin 1993; Rousset 1997, 2000). IBD predictions may apply in a qualitative fashion to IBT, but they certainly differ quantitatively owing to fundamental differences between dispersal in space and 'dispersal' in time. In IBD, organisms reproducing at a particular location (e.g. points on the horizontal lines in Fig. 1) generate offspring that disperse according to a symmetrical probability distribution centred at that location (e.g. *a* in Fig. 1A). Offspring that disperse to new locations will then generate their own offspring that disperse according to a similar probability distribution centred at the new locations (e.g. *b* and *c* in Fig. 1A).

In IBT for *asexual* organisms, an individual having a breeding value for a particular reproductive time (*a* in Fig. 1B) will produce offspring that may 'disperse' because of environmental effects to reproduce at other times (e.g. *b* and *c* in Fig. 1B). We suggest that this temporal dispersal might follow a probability distribution with a width inversely related to the heritability of reproductive time. Now we come to the critical difference between IBT and IBD: an individual whose actual reproductive time differs from that specified by its breeding value will nevertheless produce offspring whose expected reproductive time is the same as the original breeding value (*d* in Fig. 1B). In short, dispersers in time produce offspring that return to disperse from the expected reproductive time of their ancestors.

In IBT for *sexual* organisms, parents reproducing at a particular time will generate offspring that carry a mixture of breeding values and therefore disperse to other reproductive times owing to both genetic and environmental effects. To understand how this might work, consider two groups of individuals having different breeding values for reproductive time (*a* and *b* in Fig. 2A). Owing to environmental effects, some of these individuals will disperse to

Table 1 Narrow-sense heritabilities for reproductive timing traits in a variety of taxa. Timing traits include breeding site arrival (arrival), maturation (maturation), egg laying (laying), egg hatching (hatching), parturition (parturition), eclosion (eclosion), and flowering (flowering). Multiple values are reported when studies provided separate estimates for sexes, populations, years, or estimation methods. Estimation methods include sibling relationships (sibs), the sire component based on sibling relationships (sibs–sire), restricted maximum likelihood (REML), responses to selection (realized), and parent–offspring regressions (parent–offspring). See original studies for full scientific names and significance levels

Species	Trait	Treatment	Heritability	Estimation method
Fish				
O. tshawytscha[1]	Maturation	Wild/Hatchery	0.82, 1.06, 1.28	Sibs–sire
O. gorbuscha[2]	Arrival	Wild	0.18, 0.39	Sibs–sire
O. mykiss[3]	Maturation	Hatchery	0.50, 0.84, 0.87	REML
O. mykiss[4]	Maturation	Hatchery	0.53, 0.55	Realized
O. mykiss[5]	Maturation	Hatchery	0.50, 0.50	REML
O. kisutch[6]	Maturation	Farm	0.24	REML
Birds				
T. bicolor[7]	Laying	Wild	1.44	Parent–offspring
H. rustica[8]	Arrival	Wild	0.54	Parent–offspring
F. albicollis[9]	Laying	Wild	0.41	Parent–offspring
F. albicollis[10]	Laying	Wild	0.19	REML
F. hypoleuca[11]	Arrival	Wild	0.34	Parent–offspring
P. caeruleus[12]	Laying	Wild	0.44	Parent–offspring
P. major[13]	Laying	Wild	−0.18, 0.04, 0.13, 0.16	Parent-offspring
P. major[13]	Laying	Wild	−0.14, 0.00, 0.13, 0.16	Parent–offspring
P. major[14]	Laying	Wild	0.21, 0.24	Parent–offspring
A. caerulescens[15]	Laying	Wild	0.02	Parent–offspring
F. atra[16]	Hatching	Wild	0.44	Parent–offspring
Mammals				
T. hudsonicus[17]	Parturition	Wild	0.16	REML
Lizards				
U. stansburiana[18]	Laying	Wild	0.10	Parent–offspring
Insects				
E. autumnata[19]	Eclosion	Laboratory	0.61	Sibs–sire
Plants				
P. congesta[20]	Flowering	Greenhouse	0.60, 0.72, 0.75, 0.77	Parent–offspring/Realized
P. brachystemon[20]	Flowering	Greenhouse	0.42, 0.49	Parent–offspring/Realized
R. raphanistrum[21]	Flowering	Greenhouse	0.06, 0.12, 0.97, 1.41	Sibs
R. raphanistrum[22]	Flowering	Greenhouse	0.63	Sibs–sire
B. campestris[23]	Flowering	Greenhouse	0.68	Parent–offspring
R. sativus[24]	Flowering	Garden	0.35, 0.50, 0.10	Sibs
C. fasciculata[25]	Flowering	Greenhouse	0.04, 0.32	Sibs
P. centranthifolius[26]	Flowering	Greenhouse	0.26	Sibs
G. hybrida[27]	Flowering	Greenhouse	0.54	REML
S. integrifolius[28]	Flowering	Greenhouse	0.44, 0.47, 0.93, 1.26	Sibs–sire
M. guttatus[29]	Flowering	Greenhouse	0.37, 0.63	Parent–offspring
S. granulata[30]	Flowering	Garden	0.24, 0.41	Sibs–sire
L. salicaria[31]	Flowering	Garden	0.09, 0.09, 0.10	Parent–offspring
B. rapa[32]	Flowering	Greenhouse	0.71	Parent–offspring

Notes:

[1]Quinn *et al*. (2000): females in two populations, one with two estimates (hatchery and wild). [2]Smoker *et al*. (1998): females and males. [3]Su *et al*. (1997, 1999): females. [4]Siitonen & Gall (1989): two year classes of females. [5]Wilson *et al*. (2003): females at two ages. [6]Gall & Neira (2004): females. [7]Wiggins (1991): females. [8]Møller (2001): males. [9]Merilä & Sheldon (2000): females. [10]Sheldon *et al*. (2003): females. [11]Potti (1998): males. [12]Svensson (1997): females. [13]Van Noordwijk *et al*. (1981): first row gives mother–daughter regressions for four populations and the second row gives father–son regressions for four populations. [14]Van der Jeugd & McCleery (2002): males and females, correction for spatial autocorrelation yielded an estimate of 0.16. [15]Perdeck & Cavé (1992): females corrected for season and age. [16]Findlay & Cooke (1982): females. [17]Réale *et al*. (2003): females. [18]Sinervo & Doughty (1996): females. [19]Tammaru *et al*. (1999): length of the pupal period. [20]Carey (1983): the four values for *Phyllostachys congesta* are based on realized heritabilities and parent–offspring regressions for outcrossed and selfed plants. The two values for *Plectritis brachystemon* are based on realized heritabilities and parent–offspring regressions for selfed plants. [21]Mazer (1987): sire and dam components in two crosses. [22]Conner & Via (1993). [23]Dorn & Mitchell-Olds (1991). [24]Mazer & Schick (1991): low, medium, and high densities. [25]Kelly (1993): sire and dam components. [26]Mitchell & Shaw (1993): heritability based on clones was 0.06. [27]Yu *et al*. (1993). [28]Widén & Andersson (1993): two populations in two years. [29]Carr & Fenster (1994): two populations. [30]Andersson (1996): two years. [31]O'Neil (1997): dam, sire, and mid-parent regressions. [32]Weis & Kossler (2004).
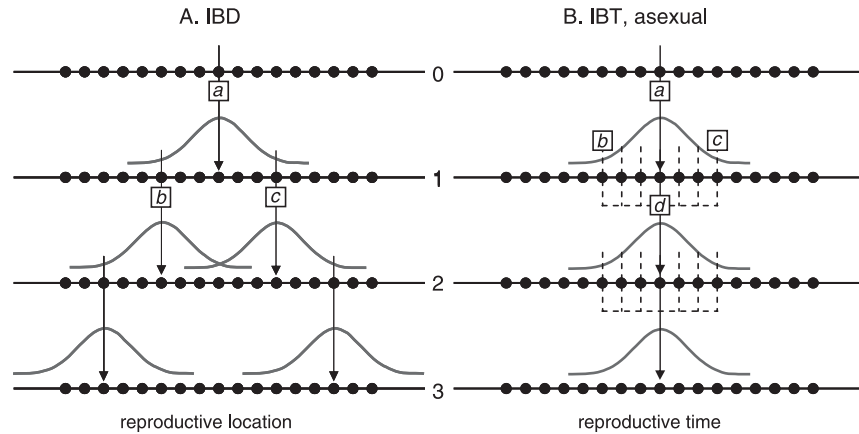
Fig. 1 Illustrations of dispersal under isolation by distance (IBD) (panel A) and isolation by time (IBT) in the case of asexual reproduction (panel B). The different horizontal lines represent reproduction in successive generations and the points on each line represent locations in space (panel A) or time (panel B). In panel A, the solid vertical lines represent the relationship between an individual's reproductive location and the average reproductive location of its offspring. In panel (B), the solid vertical lines represent the relationship between an individual's breeding value for reproductive time and the average reproductive time of its offspring. The curves represent probability distributions for the dispersal of offspring from their parent's reproductive location (panel A) or their parent's breeding value for reproductive time (Panel B). In panel B, the broken lines indicate that individuals of a common breeding value that reproduce at different times, owing to environmental effects, still produce offspring having the original parental breeding value. These offspring therefore disperse anew from the original time. Parent/offspring relationships are only shown for a few representative locations or times, but similar relationships are assumed for the other locations and times. The lower case letters refer to specific events discussed in the text.

reproduce at other times, perhaps encountering each other. Mating between individuals from these two groups will then produce offspring having an average breeding value that is intermediate between the two parental breeding values (*c* in Fig. 2A). The offspring from this mating will then disperse from this new time, both as a result of environmental effects and because the offspring in a brood generated by sexual reproduction have a range of breeding values.

Temporal variation in the intensity of reproductive activity further complicates dispersal in time. Consider first a uniform temporal distribution of reproductive activity with identical dispersal distributions at each time (Fig. 2B). In this case, a group of individuals reproducing at a particular time (e.g. *a* in Fig. 2B) will carry a mixture of breeding values. This mixture might follow a symmetrical density distribution centred at the parental reproductive time (*a* in Fig. 2B). As a result, parents reproducing at a particular time will generate offspring that have a similar *average* reproductive time (*b* in Fig. 2B). Now, consider a situation where reproductive activity or dispersal is not uniform through time. In this case, a group of individuals reproducing at a particular time will carry an uneven mixture of breeding values that is skewed toward times of higher activity or higher dispersal. As a result, they will produce offspring that have an *average* reproductive time that is biased toward earlier or later times. This scenario is qualitatively illustrated in Fig. 2(C) for the simple case of breeding values for only two times.

In summary, dispersal in time acts differently than dispersal in space. Although IBT theory has yet to be developed, consideration of the above properties allows at least qualitative predictions. In particular, we expect that decreasing heritabilities of reproductive time will increase temporal dispersal, which will increase temporal gene flow, which will lead to a weaker relationship between genetic differences and time differences (Fig. 3). We further suggest that IBD relationships may ultimately allow the estimation of temporal gene flow and the heritability of reproductive time. This would be analogous to the use of IBD relationships to infer spatial gene flow (Slatkin 1993) and dispersal (Rousset 1997, 2000).

Empirical evidence

How might IBT be detected and quantified in natural populations? A number of individual-based methods seem possible. One is to determine the reproductive times of parents and their offspring, with a positive correlation implying IBT. This method parallels the use of parent/offspring regressions to infer the heritability of reproductive time (Table 1; Weis & Kossler 2004). Although heritable reproductive times should indeed cause IBT, they do not actually demonstrate its presence. Another approach might be to use genetic 'assignment methods' (Hansen *et al.* 2001; Berry *et al.* 2004) to identify individuals that disperse from their parents' reproductive time, as well as any offspring they generate. A third possible approach is to plot relatedness between individuals against their difference in reproductive time, analogous to suggested approaches for IBD (Rousset 2000). As none of these individual-based methods
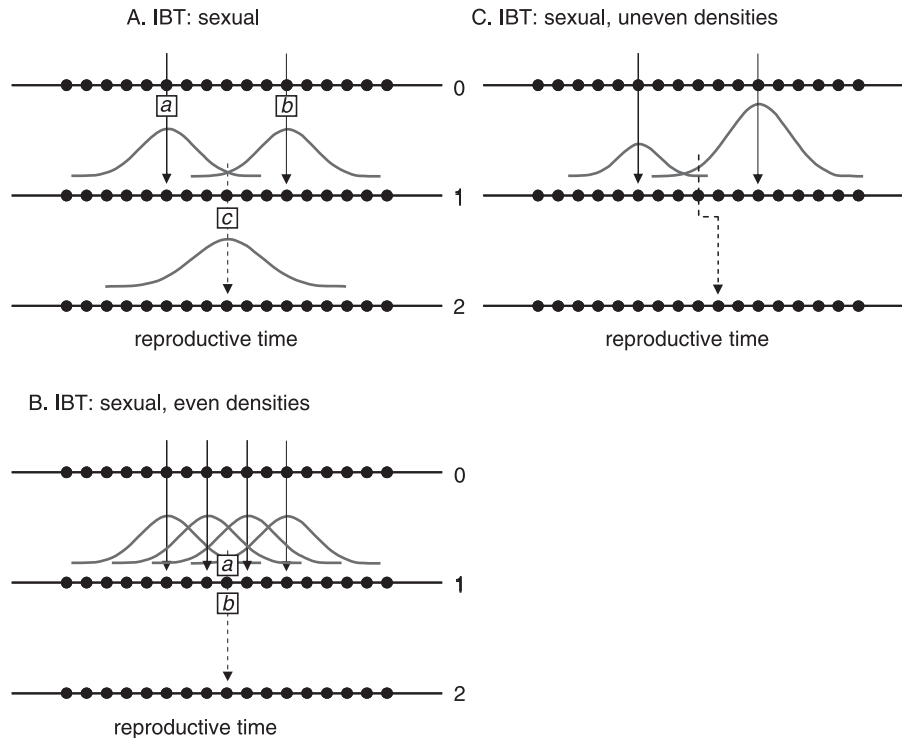
A. IBT: sexual

C. IBT: sexual, uneven densities

reproductive time

B. IBT: sexual, even densities

reproductive time

reproductive time

Fig. 2 Illustrations of dispersal under IBT in the case of sexual reproduction. All symbols and conventions follow those in Fig. 1 except for the following. In panel A, the solid vertical lines represent the relationship between a particular breeding value for reproductive time and the average reproductive time of individuals carrying that breeding value. The corresponding curves represent dispersal of offspring from that time owing to environmental effects. The broken line then represents the relationship between the average breeding value of a mating pair and of their offspring. The corresponding curve represents dispersal of these offspring owing to both environmental effects and the variation in breeding values that result from sexual reproduction. In panels B and C, the solid lines represent the average breeding value of all individuals reproducing at a particular time and of their offspring. The curves represent the dispersal of all offspring produced by matings at a particular time in the population, with the different heights in panel C indicating different numbers of offspring produced. The broken lines then show the average reproductive time of all the offspring produced by all the matings at a particular time.
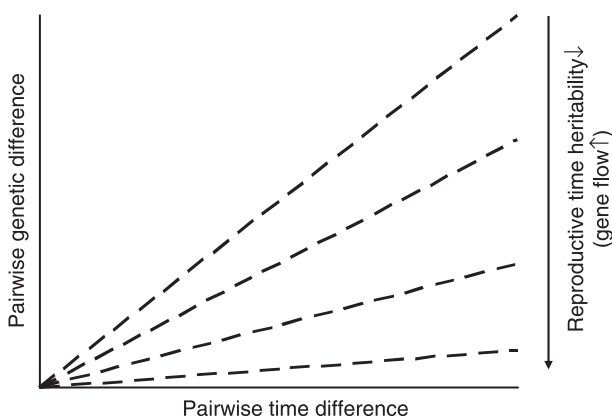
Fig. 3 Qualitative predictions for isolation by time, shown as expected relationships between pairwise genetic differences [$F_{ST}/(1 - F_{ST})$] and pairwise time differences. A decrease in the heritability of reproductive time should lead to an increase in temporal gene flow and a weaker IBT relationship. These predictions are meant to parallel those generated by Rousset's (1997) IBD model.

has yet been applied to IBT, the following treatment focuses on the more common approach of estimating historical gene flow between groups that reproduce at different times.

If two samples are collected from a single, randomly mating (panmictic) group, they should not genetically differ apart from sampling error. If, however, the samples are from groups between which mating is not random, they may differ genetically owing to mutation, drift, or selection. Heritable reproductive times cause nonrandom mating (Fox 2003; Weis & Kossler 2004) and should therefore lead to genetic differences associated with reproductive time. Such differences should be stable across generations, such that samples from multiple reproductive times in multiple years cluster genetically by time rather than by year. Although consistent genetic differences at any locus or trait might reflect IBT, we focus on presumed neutral loci because these are more useful for inferring gene flow.

Two-sample approaches (e.g. early vs. late) are most common, and they can be used to confirm genetic differences

Table 2 Molecular genetic differentiation associated with reproductive timing in salmonid fishes of the genus *Oncorhynchus*

Species	Population(s)	Genetic differentiation
O. nerka[1]	Tustumena Lake, AK	Statistically significant microsatellite differences (F_{ST} = 0.006) between salmon entering Nikolai Creek 21–25 d apart. Smaller, nonsignificant differences (F_{ST} = 0.003) between salmon entering a Glacier Flats Creek 13–15 d apart.
O. nerka[2]	Klukshu River, Yukon	Statistically significant and consistent (across years) microsatellite differences (F_{ST} = 0.018–0.041) between salmon entering the river about 2 months apart.
O. nerka[3]	Bear Lake, AK	Statistically significant and consistent (across years) microsatellite differences (F_{ST} = 0.017) between salmon entering the lake about 1 month apart.
O. nerka[4]	Pick Creek, AK	Limited gene flow at microsatellites (N_em = 2.59, m = 0.00023) between salmon breeding 29 d apart at the same location in a small creek.
O. gorbuscha[5]	Auke Creek, AK	Statistically significant allozyme differences (F_{ST} = 0.004) between salmon entering the creek about 1 month apart.
O. gorbuscha[6]	Sakhalin Island, Russia	Statistically significant mtDNA differences (Φ_{ST} = 0.020–0.025) among four samples collected at two-week intervals in each of two creeks. No differences were found in a second year.
O. gorbuscha[7]	Dungeness River, WA	Statistically significant microsatellite and allozyme differences (F_{ST} = 0.020) between salmon breeding about 1 month apart. The two groups also breed at different locations in the river.
O. keta[8]	Bush Creek, BC	Low gene flow (m = 0.004) into the lower reaches of Bush Creek from fish breeding about 1 month later in the upper reaches of Bush Creek and in nearby Walker Creek.
O. mykiss[9]	Eagle and Arlee, MT	Statistically significant allozyme differences among trout maturing at different times within a hatchery population. Temporal clines were evident in the frequencies of some alleles.
O. mykiss[10]	Nine hatcheries, ON	Statistically significant mtDNA and allozyme differences among trout maturing in different seasons within hatchery populations.
O. mykiss[11]	Two hatcheries, ON	Statistically significant mtDNA differences among trout maturing in different seasons within a population where maturation time is under selection (Goosen) but not within a population where maturation time is not under selection (Ganaraska).
O. mykiss[12]	Rainbow Springs Hatchery, ON	Statistically significant microsatellite differences among trout artificially selected to mature in different seasons.

Notes:
[1]Woody *et al.* (2000). [2]Fillatre *et al.* (2003). [3]Ramstad *et al.* (2003). [4]Hendry *et al.* (2004). [5]McGregor *et al.* (1998). [6]Brykov *et al.* (1999). [7]Olsen *et al.* (2000). [8]Tallman & Healey (1994). [9]Leary *et al.* (1989). [10]Ferguson *et al.* (1993). [11]Danzmann *et al.* (1994). [12]Fishback *et al.* (2000).

associated with reproductive time. Other possible approaches include tests for heterozygote deficits (Wahlund effect) and linkage disequilibrium when temporal samples are pooled. None of these two-sample approaches, however, is ideal for demonstrating IBT as a continuous process. For this, one might sample individuals from multiple reproductive times and test for temporal clines in allele frequencies, or for correlations between pairwise genetic differences and pairwise time differences. The latter approach is analogous to IBD methods (e.g. Slatkin 1993; Rousset 1997), but may have lower statistical power in the temporal context because breeding usually varies more in space than in time. In the following sections, we review studies using these and other approaches to infer IBT in salmonid fishes and flowering plants.

Salmonid fishes. Salmonids would seem particularly likely to manifest IBT owing to their highly heritable breeding times (Table 1). Accordingly, many studies have shown that populations with different breeding times are

significantly, and sometimes substantially, differentiated at presumed neutral loci (Table 2). Moreover, studies sampling early and late breeders from multiple years typically reveal clustering by reproductive time rather than by year (e.g. Fillatre *et al.* 2003; Ramstad *et al.* 2003). Unfortunately, temporal and spatial separation may be partially confounded in these studies, making it difficult to evaluate the relative importance of each isolating barrier.

Two studies minimized confounding spatial effects by comparing early with late breeders from a single location. First, Woody *et al.* (2000) sampled mature sockeye salmon (*Oncorhynchus nerka*) 13–15 d apart in each of two Alaskan streams (Nikolai and Glacier Flats). Genetic differences at microsatellites were small between times within both streams, but highly significant for Nikolai Creek (Table 2). Furthermore, genetic differences *between* the streams (20 km apart) were nonexistent for samples taken at the same time but highly significant for samples taken at different times. Second, Hendry *et al.* (2004) sampled sockeye salmon

breeding 29 days apart at the same location in a very small (< 2 km long) Alaskan stream (Pick Creek). Genetic differences at microsatellites were small between times, but nevertheless indicative of limited gene flow (Table 2). Although slight spatial separation might confound temporal isolation in Nikolai Creek (Woody *et al.* 2000), it does not in Pick Creek.

Temporal clines in allele frequencies have not been examined in natural populations but they appear prevalent in hatchery populations, as revealed by allozymes (Leary *et al.* 1989), mitochondrial DNA (mtDNA) (Ferguson *et al.* 1993; Danzmann *et al.* 1994), and microsatellites (Fishback *et al.* 2000). These clines might reflect genetic drift under limited gene flow or physical linkage between neutral marker loci and loci under selection. The latter explanation seems plausible for these hatchery populations because they have been under artificial selection to increase the range of breeding times. Moreover, some of the microsatellite loci are linked to quantitative trait loci (QTL) that influence breeding time (Sakamoto *et al.* 1999; O'Malley *et al.* 2002). Temporal clines caused by physical linkage with selected loci reveal genetic variation associated with breeding time, but they should not be used to infer the *strength* of IBT.

No studies of IBT have yet employed the pairwise approach so often used for IBD, although some studies had the opportunity to do so. For example, Brykov *et al.* (1999) collected pink salmon (*Oncorhynchus gorbuscha*) at four different times in each of two rivers. They found significant mtDNA differences associated with breeding time, but did not analyse their data in a pairwise fashion. Lacking a precedent, we sampled mature sockeye salmon at two-week intervals in the Cedar River, Washington: 6 October, 20 October, 3 November, 20 November, and 3 December (A. Hendry, P. Bentzen, I. Spies and K. Fresh, unpublished). We genotyped 45–53 fish from each sample at six microsatellite loci: *One1*, *One2*, *One8*, *One11*, *One14*, and *Ots103* (Scribner *et al.* 1996; Nelson & Beacham 1999). We then calculated $F_{ST}/(1-F_{ST})$ between all pairs of samples (as suggested for IBD by Rousset 1997), plotted these genetic differences against the corresponding time differences, and evaluated statistical significance with Mantel (1967) tests.

When males and females were pooled, we found a nonsignificant ($P = 0.435$) association between genetic differences and time differences (Fig. 4A). However, the temporal dispersal of adults *within* a breeding season should be greater for males than for females (Fleming & Reynolds 2004). Because we are more interested in long-term gene flow than in contemporary dispersal, we repeated our analysis for females only. Finding a much stronger correlation (Fig. 4B; $P = 0.051$), we conclude that IBT is likely present and may be detectable using the pairwise approach. As in other studies, temporal and spatial separation might
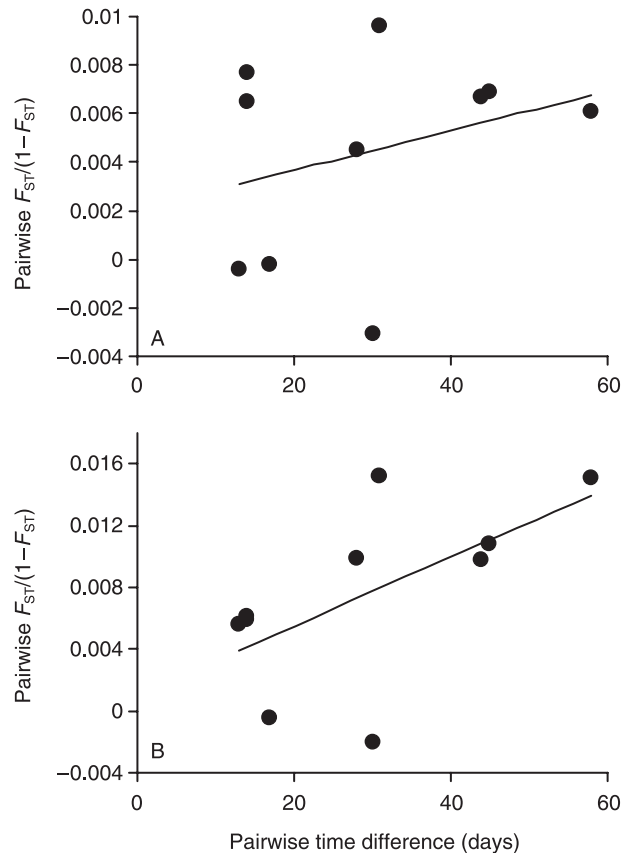

Fig. 4 IBT based on breeding Cedar River sockeye salmon collected at two-week intervals ($N = 5$ collections). Points represent genetic differences vs. time differences for all possible pairs of collections. Panel A was obtained by pooling males and females in each collection, whereas panel B was obtained by excluding males.

be partly confounded in the Cedar River. One option for future work would be to quantify differences in both time and space between paired genetic samples. Partial Mantel tests (Smouse *et al.* 1986; Castellano & Balletto 2002; but see Rousset 2002) might then be used to estimate the effects of time while controlling for space (for an analogous approach see Stanton *et al.* 1997).

Flowering plants. Flowering plants are another group likely to manifest IBT because of their highly heritable flowering times (Table 1): mean $h^2 = 0.40$ based on 139 estimates compiled by Geber & Griffen (2003). Moreover, a number of genome regions and candidate genes have been identified that strongly influence flowering time (reviews for *Arabidopsis*: Koornneef *et al.* 1998; McKay *et al.* 2003). These properties should promote IBT, and indeed a number of studies have found substantial genetic differences between distinct early- and late-flowering morphs (e.g. Soliva & Widmer 1999; Gustafsson & Lönn 2003). Few studies,

however, have tested for genetic differences between early- and late-flowering plants within a single population. In perhaps the only example, Stanton *et al.* (1997) used allozymes to examine gene flow along a steep (< 200 m) gradient in snow melt times. Flowering times were determined by snow melt times, but gene flow was not limited between early- and late-melting sites. At face value, this result argues *against* IBT, but then, IBT would not be expected in this system because the variation in flowering time does not have a genetic basis (Stanton *et al.* 1997).

We are not aware of any studies of adult plants in natural populations that have tested for temporal clines in allele frequencies, or used the pairwise approach. A number of studies have, however, documented temporal shifts in allele frequencies *in the pollen pool* (e.g. Fripp *et al.* 1987; Sampson *et al.* 1990). These shifts imply genetic differences among plants flowering at different times, but they do not confirm IBT because individual plants can contribute disproportionately to the pollen pool. We encourage more studies of neutral genetic variation in relation to flowering time, particularly for single populations where temporal differences are not confounded by spatial differences.

Several additional methods provide indirect evidence of IBT in flowering plants. First, detailed information on flowering schedules can be used to predict the strength of temporal assortative mating. Studies adopting this approach have concluded that IBT should be very common and strong (Fox 2003; Weis & Kossler 2004). Second, comparisons can be made between mid-parent/offspring and single-parent/offspring regressions for flowering time, with the former (but not the latter) biased by temporal assortative mating. Weis & Kossler (2004) used this method to infer IBT in an artificial population. Third, experimental populations can be created wherein flowering times are linked to specific genetic markers. After open pollination, the seeds can be screened to determine paternal genotype. Studies adopting this approach have found that flowering times cause major departures from random mating (Gutierrez & Sprague 1959; Ennos & Dodson 1987). All of these indirect approaches suggest that IBT should be common in flowering plants, but they cannot reveal the strength of IBT in natural populations.

In summary, IBT receives diverse support from studies of salmonid fishes and flowering plants. Nevertheless, conclusions regarding the strength and consistency of IBT in nature require more studies specifically designed to test for temporal restrictions on gene flow. Such studies would benefit greatly from the development of theoretical models of IBT, as was the case for IBD (e.g. Slatkin 1993; Rousset 1997, 2000).

Adaptation by time

Adaptive divergence occurs when gene flow is limited between groups exposed to different selective environments (Schluter 2000). Studies of this process usually focus on selection that varies in space, but selection can also vary through the reproductive season. When it does, we logically expect adaptive divergence between groups that reproduce at different times. Adaptive divergence in space can occur between discrete populations in different environments or within a population that is distributed across an ecological gradient (reviews: Endler 1977; Lenormand 2002). By extension, we expect adaptive temporal clines in heritable phenotypic traits when selection varies through the reproductive season and gene flow is limited. We call this phenomenon 'adaptation by time' (ABT) (Hendry *et al.* 1998, 1999, 2001, 2004).

Theoretical considerations

Several theoretical models have examined the evolution of a quantitative trait along an ecological gradient (e.g. Slatkin 1978; Pease *et al.* 1989; García-Ramos & Kirkpatrick 1997; Kirkpatrick & Barton 1997; Day 2000). The predictions of these spatial models probably apply in a *qualitative* sense to ABT (Fig. 5). Specifically, heritable phenotypic traits should show temporal clines when selection varies in time and IBT is present. Observed trait clines should become steeper as the optimal trait cline becomes steeper and as stabilizing selection around the optimum becomes stronger. The degree of mismatch between the observed trait cline and the optimal trait cline should increase as (i) the heritability of reproductive time decreases (because IBT is weaker); (ii) the heritability of the trait decreases (because the response to selection is weaker); and (iii) reproductive activity becomes less uniform through time (because maladaptive gene flow becomes directionally biased).

Quantitative predictions for ABT, however, are unlikely to match those from spatial models. One reason is the aforementioned difference between dispersal in space and dispersal in time. A second reason is that ABT will depend on the evolution of genetic covariance between the selected trait and reproductive time. To explore these complexities we here develop a novel theoretical model that examines adaptation across temporal clines. Our model represents a first step toward ABT theory and is intended primarily to derive simple analytical results for comparison with spatial theory. The model, detailed in the online supplementary materials, tracks the evolution of the joint breeding value distribution for two quantitative traits: the date when an individual reproduces (x, 'reproductive date') and a trait (z) subject to a temporal cline in selection. For ease of presentation, we refer to this selected trait as 'body size', but the model is general to any trait.

The model assumes a population with discrete, non-overlapping generations that has the following life cycle. First, reproduction is initiated by distributing individuals to different reproductive dates according to their breeding
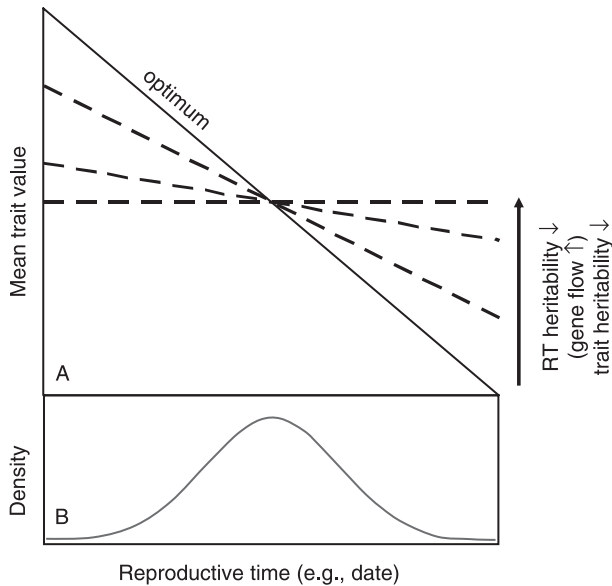
Fig. 5 Qualitative predictions for ABT (panel A) when reproductive activity follows a normal density distribution in time (panel B). In panel A, the solid diagonal line represents optimal trait values and the broken lines represent observed mean trait values. The observed mean trait value is expected to match the optimal trait value at the temporal peak of reproductive activity, regardless of the amount of gene flow. Mean trait values should then increasing deviate from the optimum (i) for times farther from the peak of activity; (ii) as dispersal increases (heritability of reproductive time decreases); and (iv) as the trait heritability decreases. These predictions are meant to parallel those generated by García-Ramos & Kirkpatrick's (1997) spatial model.

value for reproductive date as well as any environmental effects. Second, selection acts on body size according to a linear temporal cline in the optimal trait value, with stabilizing selection around the optimum at each time. Third, actual reproduction takes place, which we assume to be asexual (e.g. Figure 1B). Finally, offspring are mixed back into the population during the nonreproductive period. Here, we assume that the contribution of offspring from a given reproductive date is described by a Gaussian (normal) distribution with respect to time. Our temporal model is thus directly equivalent to the spatial model of García-Ramos & Kirkpatrick (1997), with the important exception of breeding values for reproductive time.

Detailed results for the general model are presented in the online supplementary materials. Here, we provide an intuitive solution by further assuming that stabilizing selection is weak and that body size is perfectly heritable, with an optimum of zero on the date of maximum reproductive activity (also set at zero). With these simplifications (for details see the online supplementary materials), the following equilibrium equation gives the mean body size as a function of reproductive date:
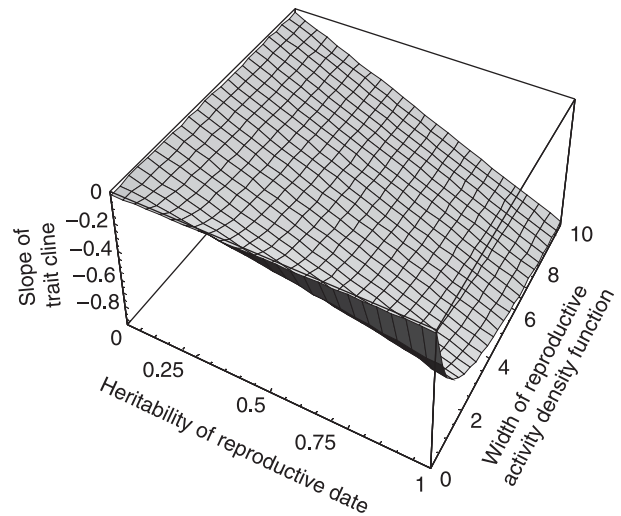

Fig. 6 Effects of the heritability of reproductive date (h^2) and the width of the reproductive activity density function (ω_x) on the degree of adaptation by time. The optimal trait cline is set at $\beta = -1$ and the environmental component of variance in reproductive date is $v_\phi^2 = 0.5$. The observed trait cline matches the optimal trait cline only when the heritability of the reproductive date is high and reproductive activity is uniform (wide density function). Trait clines do not develop if reproductive date is not heritable or if reproductive activity decreases very rapidly from a central maximum (narrow density function).

$$\bar{z}(y) = h^2 \frac{\beta y}{\dfrac{v_\phi^2}{\omega_x} + 1} \qquad \text{(eqn 1)}$$

where $\bar{z}(y)$ is the mean body size on date y, h^2 is the heritability of reproductive date (i.e. $h^2 = v_x^2/(v_x^2 + v_\phi^2)$), v_x^2 is the additive genetic variance for reproductive date, v_ϕ^2 is the environmental variance for reproductive date, β is the slope of the temporal cline in optimal body size, and ω_x is the variance in reproductive activity with respect to date (i.e. width of the temporal density function).

This equation (see also Fig. 6) reveals that precise adaptation is facilitated by small environmental effects (small v_ϕ^2) and uniform reproductive activity (large ω_x). These results are equivalent to the spatial context, where adaptation is more precise with low dispersal and uniform densities. The difference is that temporal clines show an additional decrease in adaptation with a decrease in the heritability of reproductive date (Fig. 6). This heritability determines the consistency of selection across generations owing to the sorting of individuals among dates within generations. As this heritability decreases, groups having specific breeding values for reproductive date will reproduce on increasingly different dates across generations and therefore experience inconsistent selection.

Our simple model reveals some aspects of ABT, but a more complete treatment would include several additional

effects. First, a lower heritability for the selected trait should decrease adaptation. Second, *sexual* reproduction would add additional complexities owing to the mixing of breeding values from different reproductive dates (Fig. 2). A sexual model will likely yield similar qualitative results, but quantitative results may differ. Third, allowing the temporal distribution of reproductive activity to evolve might indicate whether temporal clines in selection can limit the range of a species' reproductive times, just as spatial clines in selection can limit species' geographical ranges (Kirkpatrick & Barton 1997). Fourth, it remains to be determined whether ABT might be a special case of the joint evolution of 'habitat preference' (here, heritability of reproductive date) and a trait determining adaptation to habitat type (here habitat type is the selective environment on a given date). One difference may lie in the continuous nature of reproductive date as opposed to the discrete nature of alternative habitats in existing models of habitat preference (e.g. Kisdi 2002; Ravigne *et al.* 2004).

Empirical evidence

We suggest that a robust demonstration of ABT in natural populations would satisfy the following criteria. First, gene flow should be temporally restricted through the reproductive season (i.e. IBT). Second, a phenotypic trait should vary through the reproductive season, although the lack of such variation does not in itself refute ABT. Third, temporal variation in the phenotypic trait should have a genetic basis. Fourth, temporal variation in the phenotypic trait should be adaptive, although it need not be perfectly so. In the following sections, we review how salmonid fishes and flowering plants provide evidence of ABT by satisfying at least some of these criteria. We also ask whether ABT might contribute to temporal phenotypic clines in insects and birds, systems where other explanations are usually invoked.

Salmonid fishes. Salmonid fishes exhibit IBT (see previous discussions), and should therefore exhibit ABT when selection varies with time. Indeed, populations breeding at a single location often show temporal trends in phenotypic traits thought to be under selection, particularly adult body size, energy allocation, reproductive lifespan, and embryo development rate (Table 3). We consider the last two of these in detail as they have been examined most closely with respect to ABT.

Reproductive lifespan in semelparous Pacific salmon is the length of time from the start of breeding by an individual until its death. The length of this period varies widely but is consistently longer for early breeders than for late breeders (Fig. 7). The adaptive significance of this temporal variation has been elucidated through field observations, experimental manipulations, estimates of selection, and game theory models (Hendry *et al.* 1999; Morbey &
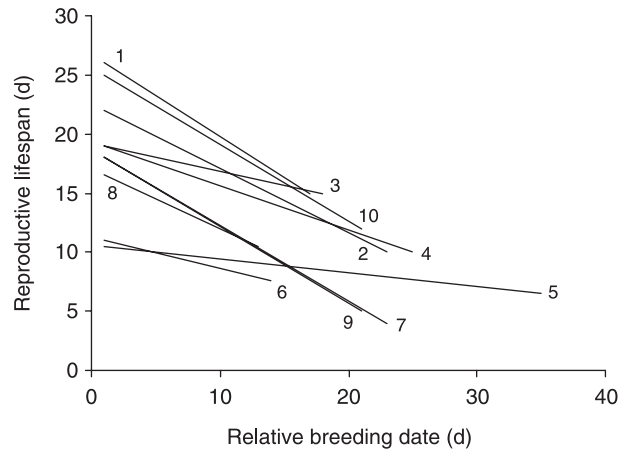

Fig. 7 Empirical data illustrating a possible example of ABT. Each line is the predicted ordinary-least-squares relationship from a study examining the correlation between relative breeding date (the date an individual starts breeding, relative to the first individual) and reproductive lifespan (the length of time from the start of breeding by an individual until its death). Data are for female (lines 1 and 2) and male (lines 3 and 4) sockeye salmon in Pick Creek in each of 2 years (Hendry *et al.* 1999), female pink salmon in Himmel Ceek (line 5; Dickerson *et al.* 2002), sockeye salmon in Hansen Creek (line 6; McPhee & Quinn 1998), chinook salmon in the Morice River (line 7, Neilson & Geen 1981), chinook salmon in the Nechako River (line 8, Neilson & Banford 1983), and female kokanee in Meadow Creek in each of two years (lines 9 and 10; Morbey & Ydenberg 2003).

Ydenberg 2003; Hendry *et al.* 2004; Morbey & Abrams 2004). For females, selection favours long life in early breeders to defend their nests against disturbance by late breeders, which would cause severe mortality of the incubating eggs. For males, selection favours long life in early breeders to allow them access to both early- and late-breeding females. These same selective pressures do not, however, favour long life in late females (because few females will arrive later to threaten their nests) or in late males (because nearly all females have already finished breeding). Late breeders thus evolve shorter reproductive lifespans because they need not reserve as much energy for prolonging life and can instead invest more into other components of fitness, such as egg production (females) or secondary sexual traits (males). What remains unknown is the genetic basis for reproductive lifespan in salmon.

Genetically based differences in 'intrinsic' development rate can be revealed by raising embryos at common laboratory temperatures. When this is done, the embryos of late breeders typically develop faster than the embryos of early breeders. This pattern has been documented for Bush Creek chum salmon, *Oncorhynchus keta* (Tallman 1986), Cultus Lake sockeye salmon (Brannon 1987), Cedar River sockeye salmon (Hendry *et al.* 1998), and Auke Creek pink salmon (Hebert *et al.* 1998). [Note that these systems

Table 3 Examples of phenotypic correlations between reproductive time and phenotypic traits. Multiple table entries are made when studies obtained conflicting results in different populations, years, or treatments

Trait	Correlation with reproductive time	Examples
Animals		
Reproductive lifespan	Negative	Fish: *O. nerka*[1,2,3,4,5], *O. gorbuscha*[6], *O. tshawytscha*[7,8], *O. kisutch*[9]
Adult size	Negative	Fish: *O. nerka*[2], *D. petenense*[10], *N. baileyi*[11], *M. salmoides*[12], *M. dolomieui*[13], *M. minimus*[14], *C. h. membras*[15] Birds: *A. phoeniceus*[16]. Insects: *E. dorothea*[17], *S. acletus*[18], *S. viscinus*[18], *C. s. xanthostoma*[19]
	None	Fish: *O. nerka*[2], *C. h. membras*[15]. Insects: *C. virgo*[20]
Age	Negative	Fish: *D. petenense*[10], *M. dolomieui*[21], *G. minutus*[22] Birds: 16 of 20 species[23]
	None	Birds: 4 of 20 species[23]
Energy/lipid/condition	Negative	Fish: *O. nerka*[2], *M. minimus*[14]
Ovary mass	Negative	Fish: *C. h. membras*[15]
	None (or variable)	Fish: *C. h. membras*[15]
Egg size	Negative	Birds: 20 of 75 studies[24]
	None	Fish: *C. h. membras*[25] Birds: 49 of 75 studies[24]
	Positive	Fish: *O. nerka*[2] Birds: 6 of 75 studies[24]
Fecundity/clutch size	Negative	Birds: *M. melodia*[26], 10 species[27], *T. bicolor*[28]
	None	Fish: *C. h. membras*[25]
	Positive	Fish: *G. minutus*[22]
Development rate	Positive	Fish: *O. nerka*[29,30,31]
Plants		
Plant size	Negative	*R. raphanistrum*[32], *A. strictifolia*[33], *N. alata*[34], *S. granulata*[35]
	None	*L. androsaceus*[36]
	Positive	*B. campestris*[37]
Flowering duration	Negative	*A. strictifolia*[33], *N. alata*[34], *L. salicaria*[38]
	None	*D. toumatou*[39], *L. scoparium*[39], *S. canadensis*[40]
Flower number	Negative	*R. raphanistrum*[32], *A. strictifolia*[33], *N. alata*[34], *S. granulata*[35], *L. salicaria*[38], *C. virginica*[41], *C. fasciculata*[42], *P. centranthifolius*[43], *S. alba*[44], *S. latifolia*[45]
	None	*L. androsaceus*[36], *D. toumatou*[39], *L. scoparium*[39]
Fruit number	Negative	*R. raphanistrum*[32], *A. strictifolia*[33]
Fruiting time	Positive	*C. fasciculata*[42]
Leaf size	Negative	*S. granulata*[35], *R. raphanistrum*[46]

Notes:
[1]McPhee & Quinn (1998). [2]Hendry *et al.* (1999).[3]Hendry *et al.* (2001). [4]Morbey & Ydenberg (2003). [5]Hendry *et al.* (2004). [6]Dickerson *et al.* (2002). [7]Neilson & Geen (1981). [8]Neilson & Banford (1983). [9]Willis (1954). [10]Johnson (1971). [11]Mathur & Ramsey (1974). [12]Miranda & Muncy (1987). [13]Ridgway *et al.* (1991). [14]Schultz *et al.* (1991). [15]Rajasilta *et al.* (2001). [16]Langston *et al.* (1990). [17]Vannote & Sweeney (1980). [18]Forrest (1987). [19]Plaistow & Siva-Jothy (1999). [20]Rantala *et al.* (2001). [21]Wiegmann *et al.* (1997). [22]Healey (1971). [23]Perdeck & Cavé (1992). [24]Christians (2002). [25]Laine & Rajasilta (1998). [26]Hochachka (1990). [27]Meijer *et al.* (1990). [28]Winkler *et al.* (2002). [29]Tallman (1986). [30]Brannon (1987). [31]Hendry *et al.* (1998). [32]Mazer (1987). [33]Dieringer (1991). [34]Lyons & Mully (1992). [35]Andersson (1996). [36]Schmitt (1983). [37]Dorn & Mitchell-Olds (1991). [38]O'Neil (1997). [39]Primack (1980). [40]Pors & Werner (1989). [41]Schemske (1977). [42](Kelly 1993). [43]Mitchell & Shaw (1993). [44]Biere & Antonovics (1996). [45]Purrington & Schmitt (1998). [46]Conner & Via (1993).

include those with genetic evidence for IBT: Bush Creek (Tallman & Healey 1994), Cedar River (Fig. 4), and Auke Creek (McGregor *et al.* 1998).] The faster intrinsic development rate of late embryos appears adaptive because it advances their otherwise late emergence from the gravel. Late emergence would be disadvantageous because juveniles will be smaller at any given time and they will have less time to grow before winter (Brannon 1987). Indeed, several experiments have found evidence of selection against late emerging embryos (Taylor 1980; Einum & Fleming 2000).

Flowering plants. Flowering plants appear to show IBT (see previous discussions) and should therefore show ABT when selection varies through the flowering season (Fox 2003). Several complementary lines of evidence can be advanced in support of this prediction. First, a number of phenotypic traits covary with flowering time (Table 3). Perhaps the most repeatable of these correlations is the decrease in flower number at later flowering dates (Table 3). Second, flower number can be significantly heritable (e.g. $h^2 = 0.30$, Mitchell & Shaw 1993; $h^2 = 0.11$, Andersson 1996). Third, several studies have tested for

genetic correlations between flower number and flowering time, which should be negative if the phenotypic trend has a genetic basis. Here the results are mixed: 0 (paternal) and 0.35 (maternal) in *Chamaecrista fasciculata* (Kelly 1993), −0.35 in *Saxifraga granulata* (Andersson 1996), and −0.52 in *Penstemon centranthifolius* (Mitchell & Shaw 1993). More work is obviously needed, but the results are encouraging in that the nonmaternal correlations tend to be negative.

Is the temporal trend in flower number adaptive? All else being equal, more flowers should improve fitness, so why do later plants have fewer flowers? The answer may lie in a trade-off between flower number and some other component of fitness, with time-specific selection favouring different positions on this trade-off. As an example, late-emerging *Silene latifolia* have fewer flowers and flower late, but have higher survival as seedlings (Purrington & Schmitt 1998). As another example, late flowering and fewer flowers in *Silene alba* reduce infection by *Ustilago violacea*, a fungal disease florally transmitted by insect vectors (Thrall & Jarosz 1994; Biere & Antonovics 1996). In either case, selection might favour a different balance between these fitness components for early vs. late reproducers. We encourage explicit work on the possible adaptive significance of temporal variation in flower number.

Several other phenotypic traits are genetically correlated with flowering time (Conner & Via 1993; Mitchell & Shaw 1993; Carr & Fenster 1994; Andersson 1996; O'Neil 1997), suggesting that these too might be candidates for ABT. For example, water use efficiency is higher for late-flowering than for early-flowering plants (Geber & Dawson 1990; McKay *et al.* 2003). Early flowering and high water use efficiency are both drought adaptations, a redundancy that implies selection for water use efficiency should be weaker in early-flowering plants. If water use efficiency trades-off with some other aspect of fitness, the temporal trend might well reflect ABT. A possible alternative to adaptation is constraint. For example, McKay *et al.* (2003) have shown that the genetic correlation between flowering time and water use efficiency is influenced by pleiotropy: mutations at the same gene influence both traits. Conclusively determining whether or not the temporal trend in water use efficiency is adaptive requires further work.

Insects and birds

The decline in body size with metamorphosis date in insects and in clutch size with breeding date in birds (Table 3) are usually interpreted not as ABT but as condition-dependent optimization in a seasonal environment. This latter theory has been mathematically formalized for insect metamorphosis by Rowe & Ludwig (1991) and for avian clutch size by Rowe *et al.* (1994). The clutch size

model, for example, assumes a trade-off between the benefits of breeding early (offspring have higher survival) and the benefits of breeding late (more energy can be acquired by adults). The optimal breeding time for an individual is then determined by its condition and by proximity to the end of the season. The model predicts that high-condition individuals should reproduce early and have large clutches, whereas low-condition individuals should reproduce late and have small clutches (Rowe *et al.* 1994; Bêty *et al.* 2003).

Both ABT and condition-dependent optimization invoke adaptive explanations for temporal trends, but they differ in that the former emphasizes heritable reproductive times, whereas the later emphasizes flexible reproductive times. As both mechanisms might act in any given population, it seems worthwhile to ask whether ABT might be important for birds and insects. ABT does seem less likely for birds than for salmonids or plants, simply because birds have lower heritabilities for reproductive time (Table 1), and yet reproductive time in at least some bird populations is heritable (Table 1). Moreover, clutch sizes are often heritable (e.g. $h^2 = 0.34$, van der Jeugd & McCleery 2002; $h^2 = 0.29$, Sheldon *et al.* 2003), can show negative genetic correlations with breeding time (−0.41, Sheldon *et al.* 2003), and could reasonably be under selection that varies through the breeding season. Less work has been done on insects, but the length of the pupal period (closely related to eclosion time) can be highly heritable ($h^2 = 0.61$, Tammaru *et al.* 1999). We suggest that ABT is a viable alternative hypothesis warranting explicit testing in these and other systems.

Conclusions

Heritable reproductive times should lead to temporal limitations on gene flow even within a single population. This 'isolation by time' (IBT) appears present in both salmonid fishes and flowering plants. IBT should allow the evolution of adaptive temporal clines in phenotypic traits when selection varies through the reproductive season ['adaptation by time' (ABT)]. Our theoretical model confirms this logic, but more advanced models will be necessary to fully explore the nuances. The demonstration of ABT in nature would ideally include evidence that (i) gene flow is restricted in time; (ii) phenotypic traits vary through the reproductive season; (iii) the temporal variation has a genetic basis; and (iv) the temporal variation is adaptive. Few studies have explicitly considered ABT, and none has yet tested all of these criteria. Nevertheless, ABT receives diverse support from several natural systems, most notably salmonid fishes and flowering plants. We suspect that IBT and ABT are relatively common in nature, simply because reproductive times are often heritable and selection often varies through the reproductive season. We also suggest the interesting possibility that IBT and ABT within popu-

lations could initiate sympatric speciation by temporal isolation (e.g. Monteiro & Furness 1998; Després & Cherif 2004).

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Supplementary material

The supplementary material is available from
http://www.blackwellpublishing.com/products/journals/
suppmat/MEC/MEC2480/MEC2480sm.htm

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