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Evolutionary insights from behavioural geography: plasticity, evolution, and responses to rapid environmental change

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ABSTRACT

Background: Species with complex phylogeographies often exhibit patterns of behavioural variation that appear to mirror variation in selective pressures, whereas in other cases population differences are not clearly adaptive. The genetic and environmental causes of this variation are diverse, and are likely to vary geographically even when phenotypes are similar.

Questions: How can geographic variation provide insight into fundamental evolutionary processes? In what ways can geographic variation in behaviour provide novel insights into the responses of populations and species to rapid environmental change?

Methods: The threespine stickleback fish (*Gasterosteus aculeatus*) comprises, in part, a post-glacial adaptive radiation in which ocean fish have given rise to a diversity of independently derived freshwater populations. Our understanding of the causes of variation in, and the underpinnings of behavioural variation in this radiation is used to provide insights into evolutionary processes and to provide direction for research on the likely evolution of populations in response to rapid environmental change as mediated by behaviour. Behaviour is considered to be of special importance because it exhibits remarkable plasticity that is likely to influence the evolutionary process.

Behaviour and the evolutionary process: The plasticity of behaviour can facilitate or constrain evolution and can enhance population persistence. Patterns of plasticity can evolve, but equally, unexpressed behavioural traits also can persist for long periods, re-emerging as environments change. Re-emergent traits can appear to be novelties, rather than ancient, recently unexpressed traits.

Behaviour and responses to rapid environmental change: Remarkable regional variation in behaviour can exist in widespread, phylogeographically complex populations. Similar phenotypes in different regions can have different genetic and plastic underpinnings, with the outcome that populations in different regions are likely to have different responses to environmental change. Behavioural mediation of evolutionary responses is likely to be difficult to detect but is critical to evaluate.

Keywords: anthropogenic environmental change, behavioural phenotype,
contemporary evolution, evolutionary mismatch, geographic variation, phenotypic plasticity.

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INTRODUCTION

Geographic variation in behaviour within species is undoubtedly common, especially in species that have wide geographic ranges or are extensively subdivided. Individuals in geographically disparate parts of the range, and those in populations that are geographically isolated, are likely to exhibit differences in behaviour as a consequence of differing selective regimes, mutations, genetic drift, or varying patterns of gene flow (Endler, 1977; Arnold, 1981a, 1981b; Foster, 1999; Foster and Endler, 1999; Nosil, 2012). This is true of all aspects of the phenotype (e.g. Endler, 1977; Piersma and Drent, 2003; Piersma and van Gils, 2011), but few phenotypes are likely to be more immediately responsive to environmental conditions than are behavioural traits (e.g. Baldwin, 1902; Wcislo, 1989; West-Eberhard, 2003; Duckworth, 2009; Ghalambor *et al.*, 2010; Foster, 2013; Snell-Rood, 2013).

This responsiveness to environmental conditions, termed 'phenotypic plasticity' (e.g. Schlichting and Pigliucci, 1998; West-Eberhardt, 2003), can produce phenotypes that differ across populations in an apparently adaptive manner without underlying genetic differentiation. Thus, if we are to understand evolutionary responses to changing environments, whether natural or anthropogenic, we must consider the influences of phenotypic plasticity on evolutionary processes. The underlying causes of geographic variation in phenotype can provide unusual insights into this process – insights that are important as, in appropriately chosen cases, geographic comparisons can offer insights into both historical changes in phenotype within lineages or radiations, or they can offer insights into likely future responses to environmental change.

Enhancing the complexity of the process, the pattern of phenotypic responsiveness of behavioural traits to environmental variation can itself evolve in response to novel or diverging selective regimes, resulting in adaptive differentiation of phenotypic plasticity over the range of environments to which the population is typically exposed (e.g. Schlichting and Pigliucci, 1998; Carroll and Corneli, 1999; West-Eberhardt, 2003; Ghalambor *et al.*, 2010; Foster, 2013). Thus, geographic differences in behaviour can reflect (1) genetically fixed differences among populations, (2) plasticity of behavioural responses to differing conditions among regions or locations without underlying genetic differentiation, or (3) geographic variation in norms of reaction (patterns of plastic response to environmental differences) in combination with the influence of differing local conditions. Consequently, similar, apparently adaptive behavioural phenotypes expressed by populations in disparate locations can be the products of quite different combinations of these alternatives (Wake, 1991; Stern and Orgogozo, 2009; Chevin *et al.*, 2010; Christin *et al.*, 2010; Feldman *et al.*, 2012; Foster, 2013). Thus, geographically varying populations can comprise mosaics, the study of which can offer insight into the evolutionary process, and into likely responses of populations in different regions to environmental change.

Although the field of behavioural ecology has provided many examples of apparently adaptive behavioural phenotypes, there also exist cases in which theoretical predictions are not met, or populations fail to vary across environments in the patterns anticipated on the basis of variation in selective regimes (for a review, see Westneat and Fox, 2010). Often, population divergence from the predicted optimum phenotype can be ascribed to counteracting effects of gene flow from nearby populations in which different phenotypes are favoured (Endler, 1977, 1986; Slatkin, 1987; Riechert 1993, 1999; Lenormand, 2002; Bridle and Vines, 2006; Garant *et al.*, 2007; Räsänen and Hendry, 2008). Alternatively, departures from expectation can be imposed by constraints on evolutionary responses to novel environments due to inadequate standing genetic variation, trait correlations due to pleiotropy, epistatic interactions or linkage disequilibrium, or to functional constraints and physiological limits (for reviews, see Futuyma, 2010; Barrett and Hendry, 2012).

Both gene flow and constraint can lead to a mismatch between the environment and population phenotypes (e.g. Riechert, 1993, 1999; Diaz and Blondel, 1996; Lenormand, 2002; Price *et al.*, 2003; Spitzer, 2006; Hanifin *et al.*, 2008; Nosil, 2012), as can environmental induction of non-adaptive plastic phenotypes (West-Eberhard, 2003; Ghalambor *et al.*, 2007, 2010; Foster, 2013).

Species that exhibit extensive geographic variation in behaviour, including recent adaptive radiations, thus offer potentially powerful opportunities to examine the processes that contribute to micro-evolutionary change (Arnold, 1981a, 1981b; Grant, 1986; Bell and Foster, 1994; Foster, 1999; Foster and Endler, 1999; Schluter, 2000; Nosil, 2012). This is clearly evident when the processes in question, such as the role of gene flow in evolution, are explicitly geographic in nature, or when comparative studies between ancestral and derivative populations offer insights into the directionality of evolutionary change. However, the study of geographic variation in behaviour, and in other aspects of phenotype, can also provide critical insights into responses to changing environments that play out over time frames longer than those that can be monitored in studies of contemporary evolution (Hendry and Kinnison, 1999), but shorter than those over which speciation typically occurs, offering an unusual window into the evolutionary process. Here I illustrate the kind of insights that can be obtained, primarily using research on the adaptive radiation of the threespine stickleback fish, *Gasterosteus aculeatus*, in which geographic variation in behaviour has arguably been more thoroughly explored for a diversity of phenotypes than is the case in any other taxon. I will conclude with a discussion of what studies of geographic variation in behaviour offer for understanding population responses to rapid, anthropogenic, environmental change.

PHENOTYPIC PLASTICITY: A BRIEF BACKGROUND

Although the potential importance of behavioural plasticity as an influence upon evolutionary change was recognized a century ago (e.g. Morgan, 1896; Baldwin, 1902), there are few studies of behavioural phenotypes in this context (Carroll and Corneli, 1999; Foster, 1999, 2013; Ghalambor *et al.*, 2010). This suggests that many who study behaviour are unfamiliar with the terminology used in the evolutionary study of phenotypic plasticity and so I provide a brief overview here.

Phenotypic plasticity is the ability of a single genotype to produce different phenotypes in response to differing environmental conditions. To evaluate phenotypic plasticity in a population, randomly selected offspring are reared in two environments thought likely to influence the traits of interest. If there is no consistent difference in phenotype under the two conditions, the phenotype is considered not to exhibit phenotypic plasticity in response to the particular environmental parameter. If instead, in the simplest case, phenotypes differ consistently in expression between two environments, the population response to the environmental conditions is considered to be phenotypically plastic. The pattern of shift (or lack thereof) is termed a phenotypic norm of reaction. These norms of reaction, in the simplest case depicted as a straight line between phenotypes in the two environments, are likely to be far more complex (e.g. Sultan and Stearns, 2005; Rocha and Klaczko, 2012). Given the time required to evaluate behavioural norms of reaction, the most common approach is likely to involve evaluation of phenotypic responses to the two environmental conditions thought most likely to explain differences in behaviour in two current habitats, or in a current environment and one anticipated in the future. Although these approaches will fail to detect the complexity of environmental influences on phenotype, they can address specific questions effectively.

Norms of reaction can evolve, as can other aspects of phenotype. Thus, geographically disparate populations, or populations in the same region experiencing different selective regimes, can evolve different patterns of plasticity (e.g. Schlichting and Pigliucci, 1998; West-Eberhard, 2003). An ancestral population that exhibits plasticity can evolve to become overall more or less responsive to the environmental signal (change in the elevation of the linear reaction norm), to exhibit a difference in the pattern of response to different environmental conditions (the slope of the reaction norm can evolve), or genetic assimilation, the loss of plasticity, can occur (no influence of the environment). Traits that exhibit little plasticity (constitutive traits) can also evolve to become increasingly responsive to environmental conditions (i.e. more plastic)

A general term for the evolution of phenotypic norms of reaction is genetic accommodation (*sensu* West-Eberhardt 2003). Given that phenotypic norms of reaction can undergo genetic accommodation, differences in the expression of phenotypically plastic traits in different regions can reflect differential genetically based responses to environmental conditions, as well as genetically fixed responses, or plastic responses by populations without underlying genetic differentiation (Foster, 1999; Foster and Endler, 1999). Thus, if we are to understand evolutionary responses to changing environments, whether natural or anthropogenic, we must consider the influences of plasticity on the evolutionary process.

THE ADAPTIVE RADIATION OF THE THREESPINE STICKLEBACK

The threespine stickleback is a small teleost with a Holarctic distribution. It is found in both oceanic and freshwater habitats. Oceanic fish, comprising those with both anadromous and marine life histories, have colonized coastal freshwater habitats repeatedly, giving rise to a remarkable freshwater adaptive radiation (Bell and Foster, 1994). As the last glaciers began to withdraw 12,000 years ago (Mathews *et al.*, 1970; Clague *et al.*, 1982; Reger and Pinney, 1996), the most recent flush of colonization was initiated, producing a new wave of adaptive differentiation in deglaciated freshwater habitats (Bell and Foster, 1994; McPhail, 1994; Hohenlohe *et al.*, 2010, 2012).

Oceanic stickleback are remarkably uniform in morphology relative to their freshwater derivatives (Walker and Bell, 2000), and the large size of oceanic populations, combined with the relative stability of the ocean habitat makes it unlikely that these populations have changed much in the last 12,000 years (Taylor and McPhail, 1999, 2000; Cresko, 2000; Hohenlohe *et al.*, 2010). Thus, oceanic fish can be used as surrogates for the ancestral type that gave rise to the post-glacial freshwater derivatives. However, this generalization may hold only within regions (i.e. oceanic populations can only be used to infer the ancestral condition for post-glacial freshwater derivatives in the same region) as there exists significant phylogenetic complexity within the Pacific Basin (e.g. Ortí *et al.*, 1994; Johnson and Taylor, 2004) and Atlantic populations differ significantly from those in the Pacific (Jones *et al.*, 2012a). In addition, stickleback populations, particularly oceanic populations, may in fact be complex metapopulations, the genomic architecture of which may be strongly influenced by gene flow from rapidly adapting freshwater populations (Schluter and Conte, 2009; Hohenlohe *et al.*, 2012). Thus, regional oceanic populations are likely to be reasonable surrogates for the ancestor that gave rise to post-glacial populations within regions, but the long-term dynamics may have produced regional structure in oceanic populations that make between-region generalization problematic.

The genetic structure of freshwater populations also offers substantial complexity of value in the study of geographic variation. Many lacustrine populations are entirely isolated one from the other, and thus show strong differentiation of behaviour, life history, and morphology (Lavin and McPhail, 1986; Baker, 1994; Bell and Foster, 1994; Bell and Ortí, 1994; Foster, 1995; Walker, 1997; Foster *et al.*, 1998; Vamosi, 2003; Baker *et al.*, 2008), whereas others, interconnected by streams, can be affected by gene flow, particularly between lacustrine and stream populations, and have offered significant insights into the influence of gene flow upon adaptive divergence (Moore and Hendry, 2005, 2009; Moore *et al.*, 2007; Aguirre, 2009; Berner *et al.*, 2009; Baker *et al.*, 2013).

The stickleback adaptive radiation is also notable for high levels of parallelism, such that populations resident in similar freshwater habitats typically are similar in phenotype, even when clearly independently derived from oceanic ancestors. The association between phenotype and environment in multiple independent cases permits inference of adaptive value of particular traits (Bell and Foster, 1994; Foster *et al.*, 1998; Schluter, 2000, Foster and Baker, 2004; Hendry *et al.*, 2013) and, with the advent of sophisticated genomic tools, is facilitating our understanding of the degree to which parallel adaptive divergence reflects parallelism in the underlying genetic architecture of the traits (Hohenlohe *et al.*, 2010, 2012; Jones *et al.*, 2012a, 2012b).

Geographic variation in the behaviour of stickleback has been examined in the greatest detail along two environmental axes: predation intensity and habitat-influenced foraging mode (the benthic–limnetic continuum). The influence of predation needs little background development, whereas an understanding of the cascading effects of population differences in adult foraging by stickleback does, and so I provide it here. Juvenile threespine stickleback are largely planktivorous, a foraging mode retained by adults in some deep, steep-sided lakes (limnetic ecotypes). In shallower lakes with a more extensive littoral zone, reproductive individuals often reach larger sizes and shift to foraging on benthic invertebrates (benthic ecotypes) (Lavin and McPhail, 1985; McPhail, 1994). This shift is also observed in oceanic fish on the breeding grounds. Benthic foragers, whether lacustrine or oceanic, forage in large groups and attack young in nests guarded by male stickleback if the nests are detected (Foster, 1994). In some populations they may destroy more than half of the nests with young (Foster, 1988). In benthic populations, the conspicuous zig-zag courtship dance of limnetic males is rarely observed, and courtship is instead initiated by females, after which a behaviour called ‘dorsal pricking’ ensues (Foster, 1995; Foster *et al.*, 1998, 2008). This behaviour is less conspicuous than the zig-zag and apparently allows the males to survey their surroundings for risk (Sargent, 1982). In benthic populations, a complex diversionary display is often elicited by the approach of groups of conspecifics, which, if effective, diverts the group from approaching the nest (Foster, 1988, 1994). In contrast, in behaviourally limnetic populations, males typically court females in approaching groups and the diversionary display is not seen (Foster, 1994, 1995; Foster *et al.*, 2008).

The focus here is on allopatric lacustrine ecotypes, rather than on the benthic–limnetic species pairs so intensively studied as models for the process of ecological speciation (McPhail, 1994; Schluter, 2000; McKinnon and Rundle, 2002). Research on the species pairs has been reviewed repeatedly, most recently by Nosil (2012), and will be considered here only in the context of geographic variation and the evolutionary process, not in the context of speciation.

EVOLUTIONARY INSIGHTS FROM GEOGRAPHIC VARIATION IN BEHAVIOUR

Here I illustrate the complexity of the possible genetic and environmental influences upon geographic variation in behaviour of threespine stickleback, although in a number of cases the relative contributions of genetic and environmental influences are uncertain due to the substantial difficulty of evaluating these influences upon behavioural phenotypes in multiple populations exposed to two or more environments.

When behaviour varies in parallel with environmental variation

In 1982, Felicity Huntingford published a remarkable comparative study of 13 freshwater stickleback populations in Scotland exposed to high and low levels of predation threat, in which she demonstrated an association between predation risk and anti-predator behaviour. Together with Steve Arnold's work on geographic variation in garter snake foraging behaviour (Arnold, 1981a, 1981b), these seminal studies provided the context for empirical research on the interface between geographic variation and behaviour, the origins of this variation, and its influence on the evolution of behavioural and other phenotypes. I therefore begin with insights from studies of geographic variation in anti-predator behaviour related to differences in predation regime in threespine stickleback, and then consider geographic variation in reproductive behaviour.

Predation regime and anti-predator behaviour

Huntingford and co-workers' early research demonstrated that stickleback from populations in Scotland exposed to relatively high predation threat tended to be less bold, and exhibited greater anti-predator responses, than did those experiencing little or no threat from predatory fish (Fig. 1) (Huntingford, 1982; Giles and Huntingford, 1984; Huntingford *et al.*, 1994). This work has subsequently been extended to include an evaluation of behavioural syndromes that also are associated with the presence or absence of piscine predators. In large man-made ponds in Wales where piscivorous fish were present, stickleback tended either

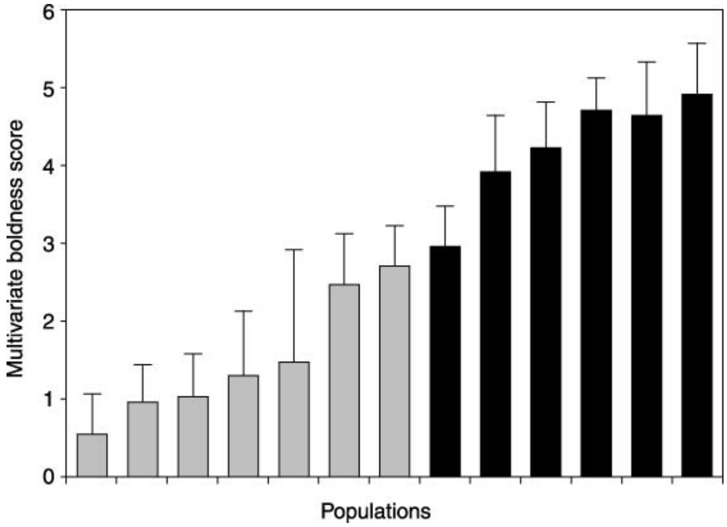

Fig. 1. Anti-predator responses of non-breeding adult stickleback from seven populations exposed to high predation risk (light bars), and six exposed to low predation risk (dark bars) in Scotland, UK. Population mean values (± 1 standard error) of a multivariate boldness score for low-risk populations fell above the overall mean more often than did those for high-risk sites [$P < 0.001$, Fisher's exact test (after Huntingford, 1982)]. Redrawn from Huntingford *et al.* (1994).

to be aggressive, active and exploratory, or, if less aggressive, they also tended to be less active and to explore less. Thus, differences in predation threat among populations can have complex effects upon behaviour (Dingemanse *et al.*, 2007).

In all of these studies, the fish were wild caught, so discrimination of the relative contributions of genetic differentiation and plasticity (experience) was not possible across this array of populations. The differences between one high-risk population and one low-risk population did persist following laboratory rearing (Tulley and Huntingford, 1987), suggesting a genetic contribution to population differences in responses to predators. Subsequent rearing studies with two of the populations demonstrated a learning difference between them: fry from the low predation population reared by their fathers exhibited elevated anti-predator responses, relative to those reared without the father, whereas rearing conditions had no influence on fry behaviour in the low predation population (Huntingford *et al.*, 1994). This fascinating insight suggests that interactions with the father, who retrieves fry when they stray from the nest, may enhance the ability of fry to avoid predators. Whether the difference in outcome between the two populations lies in differences in the behaviour of the father or in the ability of fry to learn from interactions with the father is unknown. This is an excellent example of the unexpected ways in which genetically based population differences in behaviour can be modified to produce population or geographic differences in behaviour.

There appear also to be large regional differences in the degree to which populations express behavioural divergence reflective of predation regime. Recent research in Alaska suggests that differences in predation regime do not result in clear differences in behaviour in the expected direction among populations likely to have experienced variation in risk of predation. In an initial comparison of three populations, among which the oceanic population (Resurrection Bay) might have been expected to have experienced the greatest predation risk, and the Jean Lake population, a freshwater population devoid of predatory fish, the least, there are no clear differences in responses to any of three types of predator threat found in the ancestral oceanic population (Fig. 2) (Messler *et al.*, 2007). Intriguingly, the population in Kalmbach Lake exhibited the greatest anti-predator response (longest duration of freezing following attack) even though, like the Jean population, it was historically devoid of predatory fish. Rainbow trout, *Oncorynchus mykiss*, have, however, been stocked in this lake, suggesting the possibility that ancestral anti-predator responses have been elevated in response to the high-density stocking of trout. Subsequent research on a larger suite of populations has failed to detect consistent differences between Alaskan freshwater populations exposed to high and low levels of predation, whether the fish were wild-caught or laboratory-reared, although there remains an indication that ancestral responses to elevated predation risk may enhance anti-predator responses to novel piscine predators where they have been introduced to lakes historically devoid of trout (M.A. Wund *et al.*, unpublished).

There can be little question that differences exist in the degree to which behavioural phenotypes in the populations in Wales and Scotland, versus those in Alaska, reflect local predation regimes. Whereas the relationship is quite weak in Alaskan freshwater populations, it is far more prominent in the Scottish populations, and is reflected not only in anti-predator behaviour but also in boldness in other contexts (Huntingford *et al.*, 1994; Walling *et al.*, 2004; Bell *et al.*, 2013). Thus, freshwater stickleback in Scotland exhibit geographic variation in anti-predator and related behaviour on a fine, apparently ecotypic scale, while a similar pattern does not exist, or is weaker, in Alaska.

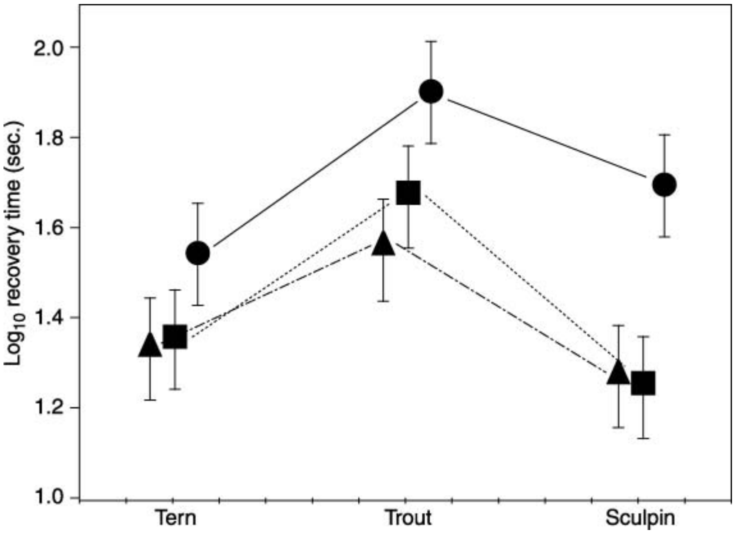

Fig. 2. Results of a two-way mixed-model ANOVA of log-transformed recovery times of fish from three populations of threespine stickleback responding to three model predators. Mean values of log-transformed recovery times and 95% confidence intervals are plotted. ANOVA results were: predator, $F_{2,4.02} = 22.52$, $P = 0.007$; population, $F_{2,4.01} = 17.44$, $P = 0.011$; interaction, $F_{4,272} = 0.76$, $P = 0.55$. Degrees of freedom are fractional because a synthetic denominator was calculated for each main effect test. Predator is a fixed effect; population is a random effect. Redrawn from Messler *et al.* (2007).

This regional difference in response to predation regime could be explained in two ways. One possibility involves differences in predation intensity. A major native predator on stickleback in Scotland is the pike, *Esox lucius*, a species only recently introduced to south-central Alaska. This voracious predator can have dramatic impacts on stickleback populations to which it is introduced, including extinction, and can cause very rapid evolutionary change in anti-predator behaviour in stickleback populations as well (von Hippel, 2008; Bruckner, 2012). Thus, one possibility is that pike presence/absence is driving much of the behavioural differentiation in Scotland, and that the difference in predation intensity among Alaskan populations is less because piscine predators native to Alaskan populations impose less selection on behavioural phenotypes. A second, more intriguing possibility is that differences in the genomic architecture of the oceanic populations from which freshwater populations in these two regions were derived, influenced the evolutionary responses to novel environments, including novel predation regimes, differentially producing regionally divergent evolutionary outcomes (Hohenlohe *et al.*, 2012) (see above). This is a possibility that will be discussed further below.

The benthic–limnetic continuum and reproductive behaviour

Our first indication of geographic differences in the courtship behaviour of threespine stickleback is found in a largely overlooked paper by Wilz (1973), in which he demonstrated quantitative differences in courtship behaviour of wild-caught stickleback from an Old World and a New World population. The differences between the populations paralleled differences in courtship more recently observed between extreme benthic and limnetic populations from northwestern North America (see Fig. 3 and above) (Foster, 1995; Foster *et al.*,

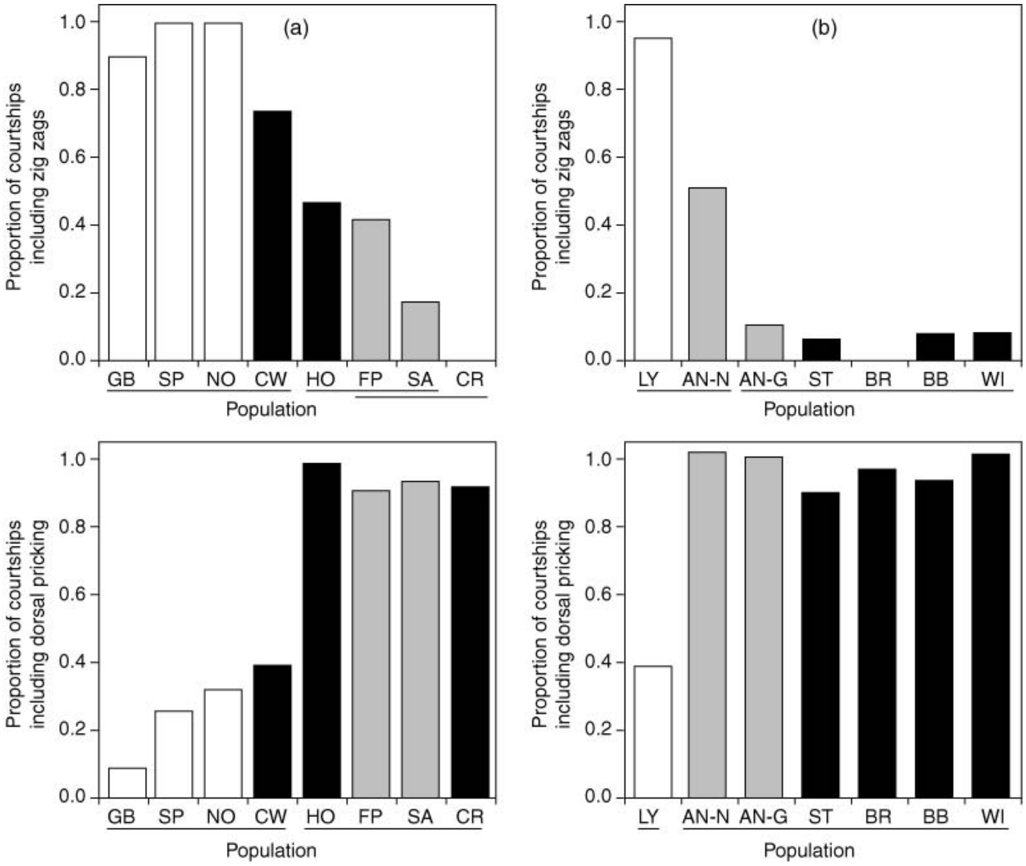

Fig. 3. Proportions of courtship interactions incorporating the zig-zag dance and dorsal pricking in 14 populations of threespine stickleback from (a) southern British Columbia and (b) Alaska. Open bars designate limnetic, non-cannibalistic populations. Grey bars are oceanic and solid bars benthic populations, both of which exhibit group cannibalism of young in nests guarded by males. Within histograms, bars connected by horizontal lines are not different [$P > 0.05$; STP contrast procedure of Sokal and Rohlf (1995)]. Data include at least 16 courtships at each site. Details of populations can be found in Foster (1995) and Foster *et al.* (1998). Redrawn from Foster *et al.* (1998).

1998, 2008). These data demonstrate that the zig-zag dance is a more prominent component of foraging behaviour in limnetic than in benthic ecotypes, and that dorsal pricking is more prevalent in both benthic and oceanic stickleback than in limnetics. The data in Fig. 3 also offer our first evidence of natural plasticity and its cause in a wild population. In a year in which females, and associated cannibalistic groups, were abundant in tide pools at Anchor River, Alaska, the zig-zag dance was rare and dorsal pricking common (Fig. 3b; AN-G). In a year in which females were rare, however, the zig-zag dance was more often a component of courtship, although dorsal pricking remained a constant in courtship (Fig. 3b; AN-N). These observations suggested that there existed plasticity for courtship in an ancestral population, and that there were likely to be differences in norms of reaction among populations, as the Anchor River population exhibited courtship behaviour intermediate between the most extreme benthic and limnetic populations in both contexts,

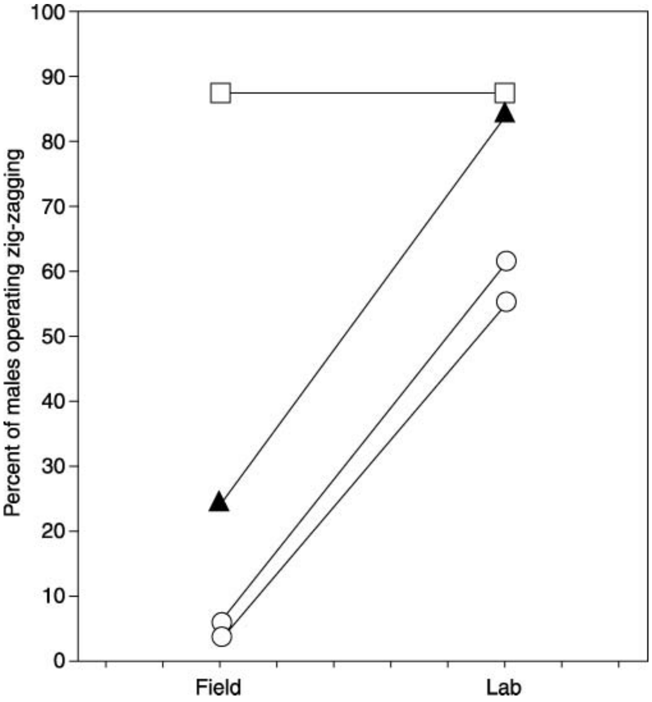

Fig. 4. The proportion of males from four Alaskan threespine stickleback populations that incorporated or failed to incorporate zig-zags into courtship in field and laboratory environments. Cannibalistic groups are present in the field in benthic (open circles) and oceanic populations (solid triangles). Although historically absent in the limnetic Lynne Lake population (open squares), cannibalistic groups are now common there as well. Recent data support the hypothesis that the zig-zag dance has undergone genetic assimilation in this population. Figure adapted from Shaw *et al.* (2007).

but differed in expression in parallel with the differences between the freshwater ecotypes (Fig. 3).

Subsequent comparisons of behaviour between males in the field where foraging groups are typically common, and males captured just prior to breeding, but evaluated in the laboratory (no cannibalistic groups), offer evidence of differentiation not just of mean population phenotypes, but also of differentiation of the patterns of plasticity among ecotypes (Fig. 4) (Shaw *et al.*, 2007). Males from the ancestral, oceanic population exhibited different plastic responses to field versus laboratory conditions, as did those from the two benthic populations tested, although the latter zig-zagged less in both contexts than did males from the oceanic population. This may reflect the greater intensity and consistency of cannibalism in benthic populations. The limnetic population from Lynne Lake has, on the other hand, lost responsiveness to foraging groups, as indicated in Fig. 4. Although the original field observations in this historically limnetic population could not have confirmed the absence of plasticity because, at the time these data were collected, there were no foraging groups in the lake, increases in productivity in this lake have led to increased growth rates, larger adult body size, and a transition to benthic foraging and cannibalism. Data collected in the field after the appearance of group cannibalism in the population indicated that a similar proportion of males (the percentage was virtually identical) include zig-zag dances in their courtship as did males prior to the appearance of cannibalism (Chock, 2008). Apparently, then, the changing environment has led to a mismatch between courtship behaviour and risk of cannibalism, as the Lynne Lake males no longer respond to the presence of foraging groups by plastic inhibition of the zig-zag dance (Shaw *et al.*, 2007; Chock, 2008). This, then, reflects genetic assimilation in which ancestral plasticity has been lost over the 11,000 or so years during which cannibalism was unexpressed. The likely explanation for the loss of plasticity is that although groups still existed in the lakes, they simply did not pose a threat. Males that responded with diversionary displays failed to court females in passing groups, and thus lost mating opportunities.

An intriguing insight from these and related observations is that unused behavioural phenotypes can re-emerge after thousands of years of disuse. In the Crystal Lake population in British Columbia, male stickleback were shown capable of performing the zig-zag dance in the laboratory although the dance was not seen in 700 hours of field observation focused upon reproductive behaviour (Fig. 3; CR) (Foster, 1995; Foster *et al.*, 2008). Even more striking, the diversionary display, used by parental males to deflect cannibalistic groups from approaching nests, has re-emerged in Lynne Lake in association with the return to ancestral patterns of benthic foraging and cannibalism (Chock, 2008). This behaviour can also be elicited from males in two additional populations of behavioural limnetics (Garden Bay and North lakes in British Columbia) under laboratory conditions when groups attack nests, even though the behaviour has never been seen in the field in either population (O'Neil, 2012). Without the ancestral type for comparison, this would appear to be a novel, adaptive, and complex phenotype emerging *de novo* in a rapidly changing environment – when in fact it is the re-emergence of an ancestral phenotype (Foster, 1994).

A final potential contributor to geographic variation in reproductive behaviour that has been well studied in stickleback is learning of mating preferences, possibly via imprinting. Imprinting is learning that occurs at a particular time in an animal's life, usually early in life, is restricted with respect to what can be learned, and often involves species-specific characters that have the potential to influence mate choice (for reviews, see Immelman, 1975; Dukas, 2013), and hence, potentially, speciation. This possibility, initially suggested by J.D. McPhail (1994), has recently been examined experimentally, and both learning from conspecifics (Kozak and Boughman, 2009) and sexual imprinting (Kozak *et al.*, 2011) have been shown to contribute to sexual isolation between the Paxton Lake benthic–limnetic species pair. Although imprinting has not been examined in the context of geographic variation in mating preferences, it could certainly contribute to population differences in mating preferences (e.g. Vines and Schluter, 2006; Hughes *et al.*, 2013). As the differences upon which females imprinted were subtle [odour, and slight variation in colour (Kozak *et al.*, 2011)], this contribution to geographic variation could easily be overlooked.

Taken together, the research presented above suggests that behaviour can vary substantially among populations, either as a reflection of local patterns of environmental variation in strongly subdivided populations, or on a regional basis. The differences can reflect genetic differences among populations, including differentiated patterns of plastic responses to environmental conditions, or purely plastic differences in response to environmental variation. Even when geographic variation is apparently adaptive, its underlying causes can vary dramatically, at least in the case of behavioural phenotypes, and this can have implications for understanding population responses to changing environments, as I will discuss below.

When behaviour does not vary in parallel with environmental variation

There are two general reasons that populations fail to display adaptive responses to geographic variation in selection. The first is gene flow, or the movement of alleles or gene complexes among populations. If gene flow is sufficient, it can counteract the ability of natural selection to produce local adaptation (e.g. Endler, 1973, 1977; Slatkin, 1987; Lenormand, 2002; Garant *et al.*, 2007; Räsänen and Hendry, 2008). Equally, evolutionary responses to selection can be constrained by genomic architecture or inadequate genetic variation, precluding the evolution of favoured phenotypes. Thus, geographically disparate populations, harbouring different alleles and differently structured genomes, can influence the responses to selection in different ways (e.g. Kawecki and Ebert, 2004; Stern and Orgogozo, 2009; Hohenlohe *et al.*, 2012). Few relevant studies involve behaviour in stickleback, or any other taxon (Foster, 1999; Riechert, 1999; Thompson, 1999), but I will provide a brief overview of what is known and what we might expect to learn.

The influence of gene flow

Although there exist few cases in which gene flow has been shown to reduce behavioural adaptation to local environments, a now-classic example is that in which Susan Riechert demonstrated that gene flow from arid habitats limits behavioural adaptation of a riparian population of the funnel-web spider, *Agelenopsis aperta* (Riechert, 1993, 1999). Remarkably, through game theoretical modelling and careful empirical assessment of the necessary parameters, Riechert and co-workers were able to demonstrate that gene flow both prevented the riparian population from reaching adaptive optima for diet choice, agonistic behaviour, territory size and anti-predator behaviour, and maintained higher levels of standing variation than expected. This is without question the most thorough exploration of the role of gene flow as a constraining force on evolution outside of studies of behavioural components of reproductive isolation (for a review, see Nosil, 2012).

The geography of the stickleback adaptive radiation also offers significant opportunity to examine the role of gene flow in mitigating local adaptation, as oceanic (typically anadromous) populations often overlap on breeding grounds with varying degrees of gene flow, and lake–stream population pairs are common (Bell and Foster, 1994; McKinnon and Rundle, 2002; Hendry and Taylor, 2004). Despite significant opportunities for gene flow among populations of stickleback occupying differing habitats within drainages, substantial, apparently adaptive morphological and life-history divergence between stream and lake stickleback can evolve, although gene flow does often have a constraining, directional influence upon local adaptation (Hendry and Taylor, 2004; Moore *et al.*, 2007; Aguirre, 2009; Moore and Hendry, 2009; Baker *et al.*, 2013).

Relatively little is known about the extent to which behavioural diversification is impacted by gene flow in stickleback. Only in the well-studied Misty Lake system has behaviour been evaluated and here results are equivocal. Differences in aggressiveness of courtship have been detected between the inlet stream population and the lake population, but not between the lake and outlet populations as predicted by patterns of gene flow and population sizes (Delcourt *et al.*, 2008), but the differences in behaviour between the inlet and lake populations do not translate into positive assortative mating in laboratory-reared fish tested under two-choice paradigms (Raeymaekers *et al.*, 2010). Thus, it is possible that gene flow has, in this case, precluded the evolution of assortative mating, although the complexity introduced by the plasticity of behaviour leaves open the possibility that assortative mating simply could not be detected given the design of the experiments (Räsänen *et al.*, 2012). That assortative mating does restrict gene flow is, however, known in many other cases where populations of stickleback co-occur (McKinnon and Rundle, 2002), and behaviour is known to contribute to reproductive incompatibility in some cases, often in complex ways (Kozak and Boughman, 2009; Kozak *et al.*, 2011; Conte and Schluter, 2013).

Gene flow also has the potential to maintain genetic diversity in populations that can enable evolutionary responses to rapidly changing environments (for reviews, see Lenormand, 2002; Nosil, 2012). Stickleback populations can be used to explore this possibility through comparative study of the responses of populations historically influenced by differing levels of gene flow as they respond to current, environmental change. Alternatively, mesocosm experiments can be used to examine the ways in which such populations respond to environmental manipulation, although here caution in interpretation is recommended (e.g. Winkler and Van Buskirk, 2012), particularly when behaviour is a prominent attribute of the species. The possibility that elevated levels of standing variation maintained by gene flow could enhance population responses to changing environments has not been explored for behavioural or other phenotypes.

The influence of constraint

Population responses to local selective regimes can be constrained by standing genetic variation inadequate to permit evolution of the optimal local phenotype, by genetic correlations among traits that limit evolutionary responses to selection on an individual trait, or by absolute constraints including functional or physiological limits and trade-offs for which there is no genetic or plastic solution (for reviews, see Hallgrimsson and Hall, 2005; Futuyma, 2010; Barrett and Hendry, 2012). Although constraint is expected to influence the evolution of behaviour as it does other aspects of the phenotype (Brooks and McLennan, 1991; Martins, 1996; Barrett and Hendry, 2012), there exist few compelling examples (Barrett and Hendry, 2012). As there is a particular paucity of information with respect to the latter two causes of constraint relative to behaviour, I will address these first.

Absolute constraints include limits to physiological capacities, trade-offs between growth and physiological or developmental requirements, or trade-offs between body shape and performance. A classic example that has been studied in the stickleback is the trade-off between body shape and stiffness and the performance of the fast start response in fish. The fast start is a rapid movement away from a threatening stimulus, the performance of which enables prey fish to escape predators (Walker *et al.*, 2005). It is thought to be a major contributing factor in the evolution of shape in fish (Webb, 1978, 1984). Stickleback in oceanic habitats possess armour plates extending from the operculum to the caudal peduncle. These, and the dorsal and pelvic spines the anterior set of plates support, are consistent elements of ancestral armouring that can be lost upon invasion of freshwater habitats (e.g. Bell *et al.*, 1993). This full armouring of oceanic stickleback comes at the cost of reduced fast start performance relative to stickleback with only anterior plates, probably due to body stiffening and drag (Law and Blake, 1996; Bergstrom, 2002), and is likely an unavoidable cost of the armour.

The second category of constraint, that caused by genetic correlations among traits can, in theory, prevent evolution of the optimal phenotype in an environment when selection on one trait forces disadvantageous alterations in another. Alternatively, correlations can potentially force evolutionary responses to changing selection pressures to follow particular trajectories of ‘least resistance’ (Schluter, 1996; Otto, 2004; Weinreich *et al.*, 2005; Grant and Grant, 2006; Futuyma, 2010). The stickleback radiation does provide an unusual opportunity to determine whether genetic correlations influence the pattern of evolutionary change, in that patterns of genetic covariation in the oceanic ancestor can be evaluated to determine whether they would have facilitated or constrained the evolution of freshwater ecotypes. Genetic correlations underlying body shape and trophic morphology have been examined in this context, but the work has offered little support for either form of constraint (Schluter, 1996; Berner *et al.*, 2010; McGuigan *et al.*, 2010). These possibilities have not been evaluated for behaviour in any species to my knowledge, although it is possible that the failure of the stickleback diversionary display to decay despite lack of expression (above) could be a consequence of genetic correlation. Like avian diversionary displays (Armstrong, 1949), stickleback displays appear to incorporate motor patterns involved in nest building and courtship (Foster, 1994). A possibility is that the same neural circuitry is used in both contexts, and that disruption of the diversionary display would also disrupt critical elements of reproductive behaviour.

Finally, genetic variation can be inadequate to permit the evolution of optimal behaviour – a possibility that appears to be likely in the stickleback radiation. Although considerable quantitative genetic variation may be harboured in populations for a diversity of traits (Roff, 2007; Hansen and Houle, 2008), an observation that holds for ancestral stickleback populations (e.g. Withler and McPhail, 1985; Hohenlohe *et al.*, 2010), rarely are there estimates of genetic variation associated with particular behavioural phenotypes. However, the regional differences in the degree to which predation regimes are associated with apparently adaptive differences in behaviour (see above) could reflect differences in the genomic architecture of the oceanic populations that gave rise to the Old World and New World freshwater populations respectively. It is very hard to explain why ecotypic variation should occur in one region but not in another, and we are now finding an additional set of regional differences that are proving very difficult to explain from an adaptive perspective, suggesting the possibility of either different underlying genetic architecture or insufficient genetic variation to permit local adaptation in some regions.

Male sneaking behaviour offers another example. In 1992, Goldschmidt and co-workers described possible regional differences in male sneaking behaviour between a Dutch population and several in south-central Alaska. Because only a single population was observed in the Netherlands, the possibility that the difference was regional was not initially recognized. In sneaking populations, some males establish nests, but then assume a mottled drab coloration, leave their nest, and range widely over the breeding area. If a courting male is detected leading a female to his nest, the sneaking male drops to the bottom and moves over the substratum to the entry of the courting male's nest. If successful, the sneaking male enters the nest, releases sperm over the eggs, and then returns to the nest entry to collect eggs, returning them to his own nest. After this, he repairs his own nest, develops bright nuptial coloration, and courts females. Subsequent research in Alaska demonstrated sneaking in all study populations, yet it has never been observed in any freshwater population in southern British Columbia and only recently has appeared in one oceanic population (K.A. Shaw and S.A. Foster, unpublished). We have not detected any environmental or social differences among regions that should consistently alter the value of sneaking, suggesting the possibility of differential genetic propensities for sneaking among regions. Similarly, there exist consistent differences in the responsiveness of stickleback to olfactory cues released by predators between Alaskan stickleback populations and those from southern British Columbia (Kennedy, 2011; J.L. Golub and S.A. Foster, unpublished). These intriguing observations beg exploration of the genomic bases of the behaviours in both the ancestral oceanic populations and in the freshwater populations to which they gave rise.

Only recently, with the advent of new molecular technologies, has it become possible to begin to explore the role of genetic variation (and indeed genomic architecture) upon initial responses to environmental change, the evolution of parallel phenotypes in similar environments, speciation or adaptive radiation (e.g. Stern and Orgogozo, 2009; Hohenlohe *et al.*, 2012; Jones *et al.*, 2012a, 2012b; Hendry *et al.*, 2013). As widespread species can have complex genetic geographies, responses to environmental change are likely to differ locally and regionally – and therefore could lead to geographic differences in derivative phenotypes, or to similar phenotypes being underlain by different genetic architectures. We are just beginning to understand the influence of ancestral genetic variation on the evolution of the stickleback radiation.

GEOGRAPHIC INSIGHT AND ENVIRONMENTAL CHANGE

Geographic variation in behaviour, or in any other phenotype, is likely to comprise a mosaic of plastic and relatively strongly genetically determined phenotypes, in combination with similar phenotypes underlain by either similar or different genetic architectures in different populations. Such variation reflects a complicated interplay between the genetic composition of ancestral populations, environmental variation influencing both plastic trait expression and selection over both short and long time frames, modern patterns of gene flow, and genomic and functional constraint. Complex phylogeographies, particularly those in which ancestral and derivative populations can be identified for comparison (Foster, 1999; Foster and Endler, 1999; Lee and Bell, 1999; Zuk *et al.*, 2006; Hanifin *et al.*, 2008; Helms and Helms Cahan, 2012; Rajakumar *et al.*, 2012), provide an unusual opportunity to study the processes that influence the early stages of diversification in response to environmental change. This is nowhere more apparent than in the remarkable insights into the causes and patterns of evolution in the adaptive radiation of the threespine stickleback that has developed over the last half century.

Although the most dramatic recent insights into the evolutionary process arguably derive from research on relatively easily scored morphological characters (e.g. Hohenlohe *et al.*, 2012; Jones *et al.*, 2012b), we have also garnered unusual insights into the patterns of geographic variation in behaviour in the stickleback radiation, the degree to which populations exhibit adaptive differentiation of behaviour, and the potential contributions of behaviour to population diversification. An intriguing emerging insight into stickleback behavioural geography is the extent of regional differentiation of behaviour. Differences in the influence of predation regime upon the anti-predator responses of stickleback between Alaskan and Old World populations can perhaps be explained by differences in methodology, learning opportunities, or predator species, but regional differences in responses to olfactory cues from predators between populations of stickleback from Alaska and southern Canada (Kennedy, 2011; J.L. Golub and S.A. Foster, unpublished), and differences in sneaking behaviour between the same regions (K.A. Shaw and S.A. Foster, unpublished), cannot be similarly explained as all fish were laboratory-reared.

These regional differences could, in part, reflect the phylogeography of oceanic and derivative stickleback (Buth and Haglund, 1994; Ortí *et al.*, 1994). Both allozyme and mitochondrial data document two major clades, one that is widespread in Japan and that has been detected in oceanic fish as far south as northern Vancouver Island (Johnson and Taylor, 2004) and a second that is widespread in Europe and along both coasts of North America. Differences in behavioural expression between Alaskan populations and those from southern British Columbia could thus reflect differences in genetic composition of oceanic populations that colonized Alaskan freshwater habitats and those that colonized the freshwater habitats of southern British Columbia. A puzzle remains, however, with respect to the high frequency of sneaking in Dutch populations and its absence in British Columbia populations (Goldschmidt *et al.*, 1992), as oceanic and derivative freshwater populations are members of the clade that spans both oceans (Ortí *et al.*, 1994). This is clearly an area of research that requires additional attention, and that also highlights the singular importance of understanding the genetic composition of ancestral populations if we are to predict evolutionary outcomes of exposure to novel environments.

Although the geographic variation described above offers evidence of high levels of ecotypic behavioural parallelism, at least within regions, the genetic bases of adaptive differentiation of behaviour in this radiation have not been explored. With respect to other aspects of phenotype that are more readily measured, the pattern that is emerging for stickleback is one in which oceanic populations possess high levels of standing variation from which parallel phenotypes (ecotypes) can be assembled, with the result that there also exists a high level of parallelism in the genetic architecture underlying the evolution of ecotypic differentiation. Parallel reassembly is particularly prominent at regional levels but is also apparent globally (Hohenlohe *et al.*, 2012; Jones *et al.*, 2012b). Although behavioural phenotypes have not been studied in this context, presumably because of the difficulty of characterization, the same mechanisms are likely to have contributed to the parallel adaptive differentiation discussed here. However, independent mutations have been shown to be responsible for loss of pelvic armour in this radiation (Chan *et al.*, 2010), reminding us that not all parallelism of phenotype is likely to reflect this underlying mechanism. Equally important in the case of behaviour is the possibility that apparently adaptive, evolutionary changes in behaviour are the products of evolutionary modification of gene expression (Aubin-Horth and Renn, 2009; Renn and Schumer, 2013).

The remarkable plasticity of many behavioural phenotypes is both the characteristic of behaviour that makes it so unusual, and also the characteristic that makes it so difficult to study. Adaptive behavioural plasticity offers the potential for population persistence either without additional evolutionary change if plasticity is great enough, or likely more often, until selection can improve population fit to the environment (for reviews, see Ghalambor *et al.*, 2010; Foster, 2013). Discovering the way in which a behavioural phenotype will respond to environmental change can be exceptionally difficult given that complex behavioural phenotypes can apparently remain unexpressed, and unchanged for surprisingly long periods of time (for reviews, see Lahti *et al.*, 2009; Foster, 2013). Thus, complex phenotypes can reappear, apparently *de novo*, if the environment reverts to ancestral conditions, facilitating population persistence. Learning, including imprinting, can also be very difficult to detect but could strongly influence population responses to novel environments, possibly, for example, allowing mate choice patterns to shift with changing population phenotypes that are the products of evolutionary or plastic responses to changing environments.

Although not always the case (Endler, 1977, 1986; Foster, 1999; Foster and Endler, 1999), geographic variation is very likely to reflect responses, whether plastic or genetic, to environmental variation. Consequently, careful exploration of the range of environmental conditions over which species persist, and dissection of the relative contributions of plasticity and genetic variation to phenotypic variation, can enable us to evaluate likely responses to rapid, anthropogenically induced environmental change. This approach can also offer insight into the relative vulnerabilities of differently adapted populations and species to various aspects of rapid environmental change. That geographic variation in phenotype can provide insight into likely population and species level responses to climate change has recently been suggested by others (e.g. Magnani, 2009; Pelini *et al.*, 2011, 2012; Ibáñez *et al.*, 2012), but behavioural modulation of these responses has not been considered. For organisms capable of behaviour, inclusion of this aspect of phenotype in any effort to understand population responses to rapid, human-induced environmental change is essential (Sih *et al.*, 2011; Sih, 2013).

Given current concern that human-induced environmental change is occurring at rates exceeding the abilities of populations/species to respond adaptively (Parmesan, 2006; Schwartz *et al.*, 2006), research is now focused upon mechanisms by which populations can persist until evolutionary rescue can occur. Evolutionary rescue (*sensu* Gonzalez *et al.*, 2012) occurs when environmental change threatens the persistence of populations, but genetic adaptation permits recovery from population decline initiated by the environmental change. Evolutionary rescue is necessary when populations harbour insufficient plasticity to permit population persistence in the new environment (Chevin *et al.*, 2010; Barrett and Hendry, 2012; Gonzalez *et al.*, 2012). Because plastic modification of phenotypes may often precede evolutionary rescue in nature (Hendry *et al.*, 2008; Westley, 2011), understanding the influence of phenotypic plasticity, including behavioural plasticity in evolutionary rescue, has emerged as a core goal in efforts to predict how populations will respond to rapid environmental change (Sih *et al.*, 2011; Barrett and Hendry, 2012; Kovach-Orr and Fussman, 2012; Sih, 2013).

Approaches to understanding the relative roles of plasticity and genetic change in response to environmental modification include laboratory experiments using model laboratory organisms, common-garden experiments, observations following introductions to mesocosms or novel natural environments (including habitat manipulation in such environments), and observations of natural populations exposed to changing environments (Kawecki and Ebert, 2004; Williams *et al.*, 2008; Kawecki *et al.*, 2012; Winkler and Van Buskirk, 2012). Such studies are usually intended to evaluate first responses to environmental modification, and hence to determine the relative contributions of genetic change (contemporary evolution) and plasticity to population persistence and to evolution at the onset of rapid environmental modification. There can be little question that a carefully designed research programme initiated at the onset of phenotypic transitions in response to environmental change can be used to examine the nature of plastic and genetic changes in populations exposed to novel environmental conditions, elucidating the mechanisms facilitating genetic rescue (e.g. Sih *et al.*, 2011; Foster, 2013; Sih, 2013). The difficulty with this approach is that many ubiquitous environmental challenges to populations, although extreme from a historical perspective, may in fact be relatively gradual from fitness and demographic perspectives, making evolutionary rescue and its causes difficult to detect under natural conditions (Gonzalez *et al.*, 2012; Vander Wal *et al.*, 2012).

A corollary of this observation is that environmental change can have outcomes for population or species viability, and for evolution, that play out long into the future – in some cases because cascading shifts in species interactions are initiated or in others because costs are imposed upon populations that are ultimately unsustainable (e.g. Haldane, 1939; Chapleau *et al.*, 1997; Gonzalez *et al.*, 2012; Ibáñez *et al.*, 2012). For example, extinctions of small prey fish may occur many generations after the introduction of predators (Chapleau *et al.*, 1997), ranges of widespread species can become restricted over time (Schiffers *et al.*, 2012), populations may remain vulnerable until fortuitous novel mutations allow evolution towards an adaptive peak, enhancing the probability of population persistence (Price *et al.*, 2003; Zuk *et al.*, 2006), or genetically based clines may disappear many years after establishment as a consequence of shifts in behavioural thermoregulation (Castañeda *et al.*, 2013). Thus, although studies of contemporary responses to rapid environmental change can yield both practical and theoretical insights into initial population responses, they may initiate longer-term processes into which they can provide little insight.

It is here that studies of geographic variation can prove especially valuable, as comparative studies of differentiated populations offer a window into changes that occur over periods intermediate between those evaluated through studies of contemporary evolution and those involving phylogenetic analyses of species relationships. Populations of widespread species can be distributed across a range of environments, offering the opportunity to evaluate the extent to which the species is capable of adapting to novel conditions, in some cases, including those likely to be experienced in the future by populations of particular concern. There are three ways in which geographic comparisons can provide especially valuable insight. The first involves the ability to compare ancestral populations with the daughter populations to which they have given rise (Foster and Bell, 1994; Lee and Bell, 1999; Pfennig *et al.*, 2010; Moczek *et al.*, 2011). Invasive species offer the most common opportunities for ancestral-derived population comparison, but invasive species typically are considered invasive because of very recent range extensions, and thus offer insight only into the earliest stages of evolutionary responses to changing environments (for a review, see Westley, 2011). Adaptive radiations like that of the stickleback, offer unusual opportunities to evaluate evolution over intermediate time frames, as regional oceanic populations are likely to have changed little since giving rise to post-glacial populations, and new freshwater populations have been established throughout this period (Foster and Bell, 1994; Shaw *et al.*, 2007; Wund *et al.*, 2008; Hohenlohe *et al.*, 2010). Thus, within regions the stages of adaptive evolution can be evaluated over a range of time frames, offering rarely available temporal insights into the evolutionary process.

Second, these temporal insights can be expanded by comparisons among regions, because differentiation of oceanic populations is the product of long periods of isolation and resultant historical contingency (Hohenlohe *et al.*, 2010, 2012; Jones *et al.*, 2012b). In combination with local ecological conditions, regional differences among oceanic populations appear to have influenced the evolution of behavioural and other phenotypes in derivative populations. Both local environmental conditions and population of origin are equally likely to influence responses of widespread populations to changing environmental conditions in other species as well, and research on species responses to environmental change is increasingly taking into consideration the possibility that widespread species are not uniform entities, but instead can comprise a complex of variably genetically differentiated populations that can respond differently to environmental challenges (Colautti *et al.*, 2009; Magnani, 2009; Pelini *et al.*, 2011, 2012; Ibáñez *et al.*, 2012). Clearly, then, when evaluating likely responses to rapidly changing environments, it is essential to directly examine the populations of immediate concern, as they may be genetically differentiated from other populations, and thus respond differently to environmental change. The methods for assessment of population responses to differing environments are well established (Kawecki and Ebert, 2004), although recent evidence suggests that the method of assessment can have significant influences upon outcomes, so caution is required in interpretation (Williams *et al.*, 2008; Winkler and Van Buskirk, 2012).

A third means of gaining insight into the likely responses of populations to rapid environmental change is to examine the causes of current species boundaries. One general reason for range limitation is dispersal opportunity; in some cases, propagules may simply not have had the time to reach all suitable regions. In this instance, range expansion is certainly a possibility. On the other hand, limits to geographic distributions may be a consequence of insufficient plasticity or genetic variation within populations to permit expansion into regions in which biotic or abiotic factors impose trade-offs that are excessive, or challenges that are too great to permit population persistence following dispersal (for reviews, see Sexton *et al.*, 2009; Holt and Barfield, 2011). Only recently has geographic variation in population characteristics been suggested as a source of insight into factors influencing range limits – factors that can clearly be instrumental in determining responses to environmental change (Ibáñez *et al.*, 2012). Evaluation of the genetic, physiological, and behavioural causes of range limits along clines can elucidate the mechanisms that impose those limits and offer insight into the evolutionary potential of regionally adapted populations for range expansion, and possibly into the evolutionary potential of populations of the same species in other geographic regions.

There can be little question that adding a geographic perspective to the exploration of evolutionary processes, whether to inform particular theoretical issues in evolution, or to better understand likely population responses to rapid environmental change, will add a significant level of complexity in interpretation and experimental design. However, many processes that influence evolutionary outcomes are geographically explicit in nature (e.g. range limits, gene flow, phylogeographic population histories, contingency), requiring a geographic perspective in evolutionary studies of these phenomena. Behaviour evolves just as do all aspects of the phenotype, although the lability of behaviour is likely to require description as a phenotypic norm of reaction – an approach that can effectively capture the evolution of strongly plastic phenotypes. Although it may be simpler to examine gene expression or physiological responses to geographically varying environments, or to rapid environmental change, behaviour can play such an important role in immediate and longer term adaptation that ignoring it is likely to come at a cost – a cost that can be particularly great when the goal is to understand the influence of environmental change on population viabililty. After all, behaviour often determines foraging success, mate choice, reproductive isolation, survival when under attack by a predator, and niche characteristics (niche constructions), and it is often the first response to a changing environment. Research on geographic variation in behaviour can thus offer significant insights into both evolutionary processes and the ability of threatened species to persist. It is an unusual – and important – window into issues that are of critical importance from both theoretical and applied perspectives, and can no longer be ignored.

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