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NEWS AND VIEWS

PERSPECTIVE

Modelling contemporary evolution in stickleback

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During the past decade, two lines of research have advanced our understanding of micro-evolution. On the one hand, a number of studies have generated evidence for strong selection on phenotypes (Kingsolver *et al.* 2001) and the contemporary (sometimes deemed 'rapid') evolution of phenotypic traits (Hendry & Kinnison 1999). On the other hand, other studies have sought to identify the genes that underlie ecologically important traits (Ungerer *et al.* 2008). Over the next decade, micro-evolutionists might expect considerable progress from the study of contemporary evolution at both the phenotypic and genetic level *simultaneously*. In this issue of *Molecular Ecology*, Le Rouzic *et al.* (2011) present a teaser for this approach. They examined contemporary evolution of an adaptive trait with a well-studied genetic basis, the number of lateral plates, in threespine stickleback (*Gasterosteus aculeatus* L.). A time series of 20 years of change for this trait after introduction into a pond in Norway was compared with a similar time series of 12 years following the invasion of a lake in Alaska. Using a modelling approach, the authors then teased apart selection acting upon the phenotype and selection acting on a major effect gene. In both time series, selection was strong and consistent. The models suggested that selection could act directly on the phenotype, or through the gene's pleiotropic effects.

Identification of the target of natural selection is important, but difficult. One of the reasons is that we often do not know the genetic architecture of adaptive traits. Selection acts on phenotypes regardless of their genetic basis, but the evolutionary *response* to selection depends on the underlying genes (Dalziel *et al.* 2009). Including genetic information alongside phenotypic information makes it fea-

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sible to assess the contribution to adaptive divergence by selection favouring one allele over another—hence making links between genetic variation, phenotypic variation, and fitness.
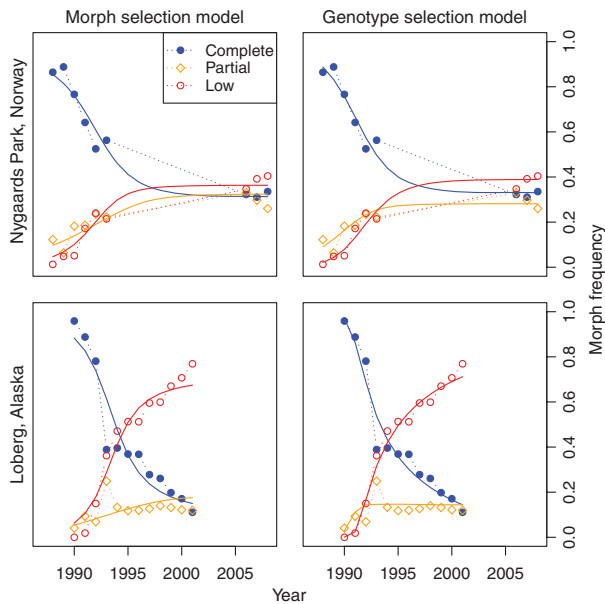
Considerable progress in this regard has been made for the remarkable variation in the number of lateral armour plates in threespine stickleback. This variation is continuous, but is often divided into three plate morph categories (Fig. 1): the completely-plated morph (>20 plates), the low-plated morph (<11 plates), and the partially plated morph (11–20 plates). Populations from marine and coastal habitats are characterized by a high number of lateral plates, whereas this number is strongly reduced in freshwater populations (Bell 2001). Starting with Heuts (1947), multiple generations of researchers have tried to identify the selective agents causing evolution towards low-platedness, which has occurred independently in multiple instances where marine stickleback have colonized freshwater. The recent discovery that plate number is strongly influenced by the Ectodysplasin (*Eda*) gene (Colosimo *et al.* 2005) has motivated a number of researchers to repeat these studies — this time at the genetic level. Examples include the detection of signatures of selection at the *Eda* locus in the field (e.g. Raeymaekers *et al.* 2007) and in short-term experiments (e.g. Barrett *et al.* 2009).

Measuring the *rate* of evolution, however, can occur only in real time (Hendry & Kinnison 1999). This works for plate number in stickleback because some studies have shown that when completely-plated marine stickleback populations colonize freshwater, they evolve low plate number over only a few decades (reviewed in Bell (2001)). The most accurate time series is that of a marine stickleback population that colonized Loberg Lake in Alaska (Bell *et al.* 2004), where the proportion of the completely-plated morph decreased from 96% in 1990 to 11% in 2001 (Fig. 2). In this issue, Le Rouzic *et al.* (2011) present an analogous time series based on the experimental introduction in 1987 of 250 completely-plated and 250 low-plated stickleback into a freshwater pond in Nygaards Park (Bergen, Norway). Low-plated fish were not very successful in the first year and, as a result, 86% of the individuals in 1988 were completely-plated. From 1988 onwards, the Nygaards Park population showed the expected increase in low-platedness, albeit at a slower pace than the Loberg Lake population (Fig. 2).

The novelty of the study by Le Rouzic *et al.* (2011) is that they tied the phenotypic data from the Nygaards Park pond and Loberg Lake directly to the evolution at the *Eda* locus. The authors first screened *Eda* genotypes in the Nygaards Park sample from 2008 and investigated how these genotypes match the plate phenotype. Their next step was to use a modelling approach to compare a scenario of

Fig. 1 Le Rouzic *et al.* (2011) quantified the strength of selection when populations of threespine stickleback evolve rapidly from completely-platedness (top) towards low-platedness (bottom) (Photo: Anna Mazzarella).

Fig. 2 Frequencies of completely-plated, partially plated and low-plated threespine stickleback changed much more drastically following the invasion of Loberg Lake (Alaska; data from 1990 to 2001) than after experimental introduction into a pond in Nygaards Park (Bergen, Norway; data from 1988 to 2008). Le Rouzic *et al.* (2011) predicted these frequencies assuming that selection acts on the plate morph (morph selection model; left) or assuming that selection acts on the Ectodysplasin genotype (genotype selection model; right).

phenotypic evolution driven by selection on plate morphology (the 'morph-selection model') with a scenario of phenotypic evolution driven by selection on the *Eda* genotype (the 'genotype-selection model'). This is a crucial comparison, because although lateral plates themselves are probably a target of selection (for instance by predators), *Eda* may have pleiotropic effects on other traits that are also under selection. For instance, it has been suggested that *Eda* also influences growth rate, which obviously has fitness consequences (Barrett *et al.* 2009). In both time series the genotype-selection model appeared to fit the plate morph time series more convincingly than the morph-selection model. This seems impossible, as all selection must work through the phenotype. However, the genotype-selection model might be more sensitive to pleiotropic effects, putting less constraint on the various ways selection might affect phenotypes. Furthermore, the authors evaluated models assuming constant or frequency-dependent selection after freshwater colonization. Frequency-dependent selection implies that the strength of selection depends on the frequency of the morphs or genotypes at each moment in time. Here, the models showed that individuals with a low number of plates have a strong fitness advantage as long as their frequency is low, such as at the onset of freshwater invasion.

As in all models, those considered by Le Rouzic *et al.* (2011) rely on a number of simplifications. In particular, they ignore the fact that the genetic architecture of plate number involves a number of other genes of more modest effect than *Eda*. Furthermore, modelling plate morph categories rather than plate number itself is somewhat arbitrary, and implies that only plate morph and not the detailed features of lateral plates matter for selection. The consequences of these simplifications are hard to assess, but the models nevertheless provide an indication that changes in plate number are driven by strong directional selection in both empirical systems.

A question that remains is why selection was stronger in Loberg Lake than in Nygaards Park, and Le Rouzic *et al.* (2011) cannot provide a definitive answer. Neither Le Rouzic *et al.* (2011) nor Bell *et al.* (2004) make strong claims about the type and strength of the responsible selection pressures in their respective studies. But even when the selective agents are very similar, the rate of evolution in both systems does not have to be the same. First, we know that selection is tempered by genetic drift and acts more efficiently in systems with high effective population size (N_e) (low drift) than in systems with low N_e (high drift). Loberg Lake is about 90 times bigger than the pond in Nygaards Park, and so one could speculate that adaptive evolution in the latter has been more strongly constrained by drift. Estimates of N_e, which of course also depend on the number of founders, would be required to test this hypothesis. Second, the completely-plated and low-plated founders of the Nygaards Park population came from different source populations, whereas the sticklebacks invading Loberg Lake belonged to a single population. This heterogeneous background of the Nygaards Park population might have promoted the evolution of reproductive barriers, slowing

down the introgression of the two introduced source populations. Third, the completely-plated and low-plated founders of the Nygaards Park population were both already adapted to freshwater, whereas the invaders of Loberg Lake belonged to a marine or anadromous population. Selection against the *Eda* allele for completely-platedness in Nygaards Park might have been weaker, because selection on other loci in the past might already have compensated for some of its disadvantages in freshwater. Fourth, the details of the genetic architecture of plate morphology might differ between Alaska and Norway, including the loci linked to *Eda* that might also drive the evolution of lateral plates. Each of these possibilities highlights the need to further investigate the factors shaping contemporary evolution.

Finally, and putting aside the difficulties inherent in predicting the future, the model of Le Rouzic *et al.* (2011) predicts that the population of the pond in Nygaards Park might remain polymorphic, as the system seems to have achieved an equilibrium (Fig. 2). In contrast, the model predicts that the frequency of the completely-plated allele in the Loberg Lake population — which is still being monitored every year — will drop below 1% in 2015. After that, allele frequencies might or might not stabilize. However, as Michael Bell has decided to retire only after the fixation of the low-plated allele in the Loberg Lake population, the model of Le Rouzic *et al.* (2011) might encourage him to optimize his sample size detection limits.

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