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Cast adrift on an island: introduced populations experience an altered balance between selection and drift

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A long-standing question in evolutionary biology is what becomes of adaptive traits when a species expands its range into novel environments. Here, we report the results of a study on an adaptive colour pattern polymorphism (stripes) of the coqui frog, *Eleutherodactylus coqui*, following its introduction to Hawaii from Puerto Rico. We compared population differentiation (ϕ'_{ST} and F_{ST}) for the *stripes* locus—which underlies this colour pattern polymorphism—with neutral microsatellite loci to test for a signature of selection among native and introduced populations. Among native populations, ϕ'_{ST} and F_{ST} for *stripes* were lower than expected under the neutral model, suggesting uniform balancing selection. Alternatively, among introduced populations, ϕ'_{ST} and F_{ST} for *stripes* did not differ from the neutral model. These results suggest that the evolutionary dynamics of this previously adaptive trait have become dominated by random genetic drift following the range expansion.

Keywords: balancing selection; colour patterns; genetic drift; introduced species; polymorphism

1. INTRODUCTION

Many phenotypic traits are under some form of selection in natural populations [1,2]. However, what becomes of these adaptive traits when a species expands its range into novel environments is not well understood [3]. In colonizing populations, previously adaptive traits may be exposed to novel selection and genetic drift via founder effects and bottlenecks [3,4]. Drift can be especially strong during the early stages of colonization because of low propagule pressure and is likely to become the dominant force acting on genetic variation [5]. Changes in the balance between selection and genetic drift may facilitate shifts to novel adaptive peaks [6], changes in genetic architecture [7] and even speciation [3,7,8]. Here, we address whether the evolutionary dynamics of a previously adaptive trait remains dominated by selection after range expansions, or if random genetic

drift becomes the prevailing force contributing to phenotypic trait evolution.

The recent introduction of the coqui frog, *Eleutherodactylus coqui*, from Puerto Rico to Hawaii [9] provides a unique opportunity to examine the fate of an adaptive trait in introduced populations. In its native range, *E. coqui* exhibits a dorsal colour pattern polymorphism comprising four unique dorsal stripe patterns and an unstriped morph [10] (figure 1a–e). These patterns are inherited in a simple Mendelian fashion at a single locus, *stripes*, with four codominant alleles coding for the four stripe patterns and a universally recessive allele coding for the unstriped morph [11]. Long-term field studies in Puerto Rico suggest that this polymorphism is maintained in part by local habitat matching and selection pressure from visual predators [10]. A recent study of populations in Hawaii found reduced allelic variation in the *stripes* locus compared with native populations, suggesting significant founder effects during colonization [12]. However, it remains unclear how selection and drift have acted on the remaining variation in colour patterns in Hawaii. To assess the relative roles of genetic drift and natural selection in both native and introduced populations, we compared among population genetic differentiation in the *stripes* locus, which underlies these colour patterns [11], with microsatellite loci, which provide an estimate of the neutral effects of drift.

2. MATERIAL AND METHODS

(a) Data collection

We visually scored colour patterns from 11 populations in Puerto Rico ($n = 509$) and 15 populations in Hawaii ($n = 1643$). Sample sizes within each population ranged from 29 to 372, with more than 50 individuals sampled from the majority of populations. A single population from Maui exhibited a unique colour pattern combination, the interocular bar and the unstriped morph [12]. Previous studies indicate that this population is the result of an independent introduction and is genetically isolated from other Hawaiian populations, possibly because this introduction was very recent or because of unknown barriers to gene flow [12]; therefore we excluded it from our analyses, which rely on estimates of historical gene flow between populations. We estimated the most likely genotype of the locus *stripes* for each individual using the phenotypes, the published model of inheritance [11], and the expectation-maximization algorithm [13]. Microsatellite data were obtained from a previous study [12] of population genetics of *E. coqui* in Hawaii and Puerto Rico. The microsatellite data represent a subset of the individuals scored for colour patterns (HI: $n = 343$; PR: $n = 283$). All data are available from DRYAD (<http://dx.doi.org/10.5061/dryad.j079s>).

(b) Testing for phenotypic variation among populations

We tested for differences in colour pattern frequencies among populations in both ranges using Fisher's exact tests (FET). For Puerto Rico, we conducted both a global test across all populations and two local tests using clusters of populations previously defined by a STRUCTURE analysis [12]. For Hawaii, we used a single global test because previous analyses indicate extensive gene flow [12], which may largely reflect recent range expansion from the original introduction site(s) to each local population.

(c) Testing for signatures of selection on the *stripes* locus

We estimated ϕ'_{ST} an unbiased analogue of F_{ST} [14,15], from six microsatellite loci and the *stripes* locus for all pairwise comparisons and globally under an AMOVA framework using GENODIVE [16]. We used global ϕ'_{ST} ($\pm 99\%$ CI) across all microsatellite loci for the null distribution and compared this with the point estimates for the *stripes* locus. We also used the distribution of F_{ST} versus heterozygosity to test for a signature of selection on the *stripes* locus [17]. We estimated the null distribution for microsatellites (R_{ST}) under a finite island model with 100 islands, a stepwise mutation model using 20 000 simulations using ARLEQUIN v. 3.5 [18]. We used point estimates of F_{ST} for the *stripes* locus. For the Puerto Rico dataset, we structured populations using a

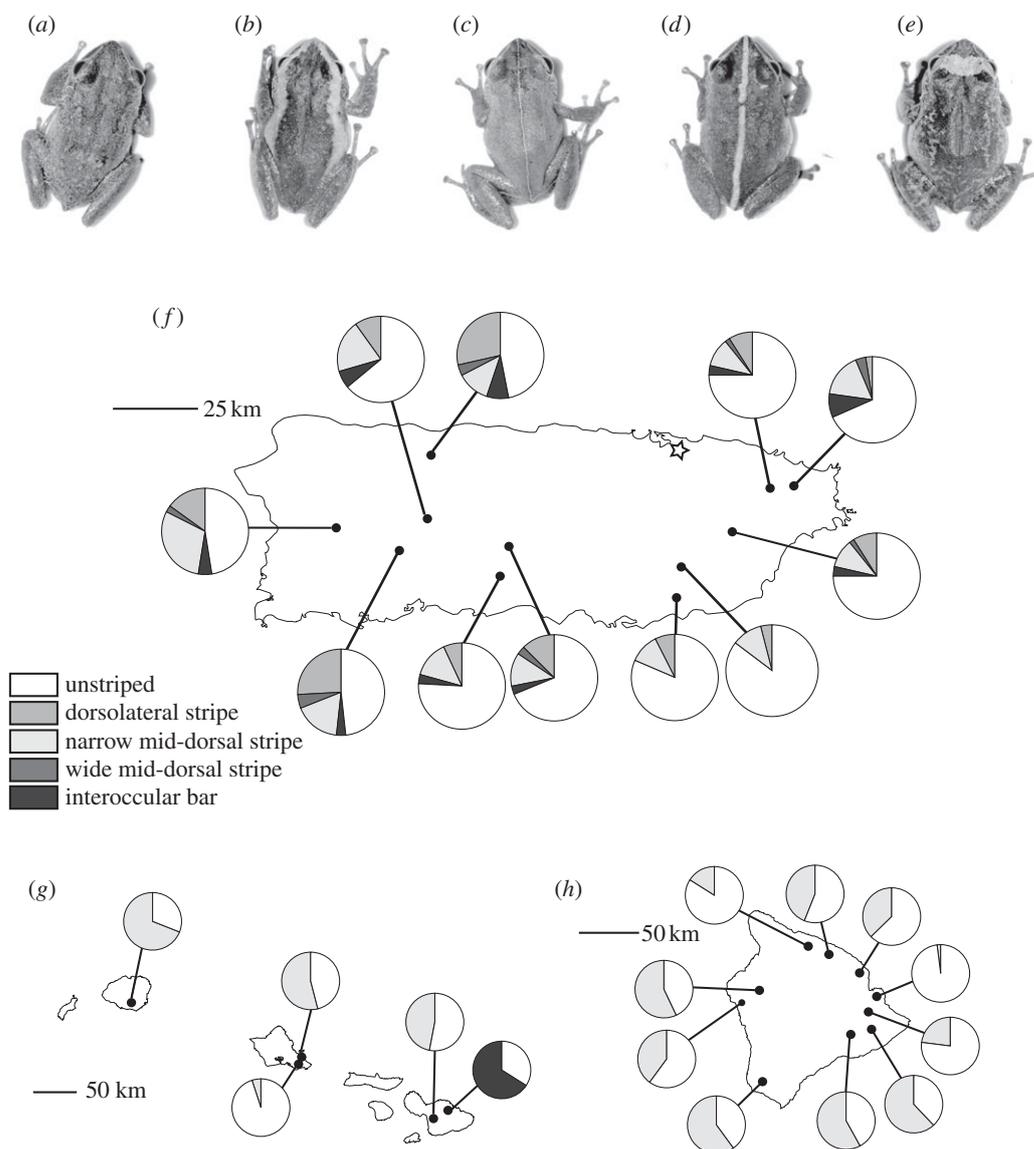


Figure 1. Examples of dorsal stripe patterns and maps of their frequencies. Examples of (a) unstriped, (b) dorsolateral stripes, (c) narrow mid-dorsal stripe, (d) wide mid-dorsal stripe and (e) interocular bar. The maps show (f) the distribution of colour patterns in Puerto Rico and (g,h) Hawaii. Pie charts indicate the frequency of each colour pattern in each population sampled. The star on the Puerto Rico map indicates the city of San Juan in the northeastern Puerto Rican lowlands, which is the most probable source of all Hawaii populations.

hierarchical island model and assigned populations to two groups (eastern and western) based on previous STRUCTURE analyses [12]. For the Hawaii dataset, we used the non-hierarchical island model because there was no evidence of genetic structure among these populations [12]. While this F_{ST} -based test assumes drift migration equilibrium, the null distribution is highly robust to a wide range of models including a colonization model in which multiple populations are founded from a single ancestral population and then grow exponentially in size [17]. This colonization model is consistent with the currently accepted view of how *E. coqui* spread in Hawaii [9,12].

3. RESULTS

In Puerto Rico, the unstriped morph was the most common phenotype, while the four striped phenotypes were less common (figure 1f). In Hawaii, only two colour patterns, unstriped and narrow mid-dorsal stripe, were observed within any population (figure 1g,h). Presumably, the reduction of alleles in Hawaii was the result of founder effects because

these alleles were rare in all populations in Puerto Rico. Colour pattern frequencies were not heterogeneous among all populations in Puerto Rico (FET: $p = 0.06$) or among populations within groups (FET eastern group: $p = 0.62$; western group: $p = 0.34$), but were highly heterogeneous in Hawaii (FET among all populations: $p < 0.0001$). Pairwise comparisons of ϕ_{ST} for stripes clustered below the 1:1 line (the neutral expectation) for Puerto Rico, but were widely scattered around the 1:1 line for Hawaii (figure 2a).

As predicted by the selection hypothesis, genetic differentiation for stripes ($\phi'_{ST} = 0.02$, $F_{ST} = 0.02$) among Puerto Rican populations was lower than the estimate for microsatellites ($\phi'_{ST} = 0.35$, 99% CI = 0.30–0.40; F_{ST} $p < 0.05$; figure 2b,c). As predicted by the drift hypothesis, genetic differentiation for stripes ($\phi_{ST} = 0.22$, $F_{ST} = 0.15$) among Hawaiian populations was not different from the estimate for

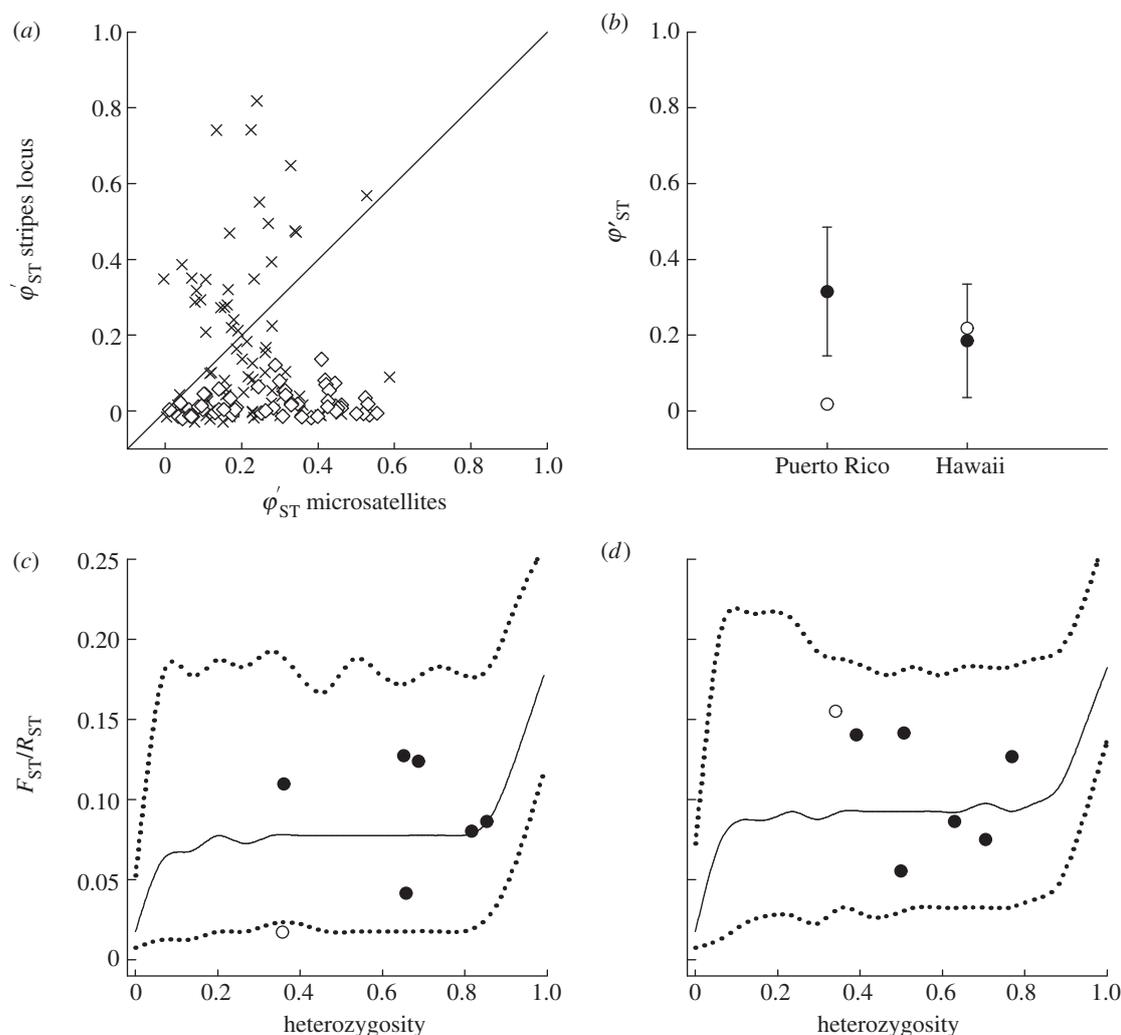


Figure 2. Genetic differentiation among populations of coqui frogs. (a) Pairwise ϕ'_{ST} between populations of *E. coqui* in Puerto Rico (diamonds) and Hawaii (x's) for both microsatellites and the *stripes* locus. The diagonal line represents the 1 : 1 neutral expectation. (b) Global ϕ'_{ST} for the *stripes* locus (open circles) and microsatellites (closed circles, shown as mean \pm 99% CIs) for Puerto Rico and Hawaii. Estimated F_{ST} (*stripes* locus: open circles) and R_{ST} (microsatellites: closed circles) values plotted against heterozygosity for (c) Puerto Rico and (d) Hawaii. The dotted lines represent the estimated upper and lower 5% quantiles for the microsatellite loci.

microsatellites ($\phi'_{ST} = 0.18$, 99% CI = 0.04–0.33; F_{ST} $p > 0.05$; figure 2*b,d*).

4. DISCUSSION

Similar allele frequencies in the *stripes* locus among populations in Puerto Rico suggest either balancing selection or high levels of gene flow among populations. Alternatively, large differences among populations in Hawaii suggest either divergent selection among populations or genetic drift. Both ϕ'_{ST} - and F_{ST} -based analyses support the hypothesis of uniform balancing selection in Puerto Rico, especially within eastern and western regions. Alternatively, these analyses support the hypothesis of genetic drift in Hawaii. Together, these results strongly suggest that the evolutionary dynamics of this previously adaptive trait have become dominated by random genetic drift following the range expansion to Hawaii.

The precise mechanism for selection on colour patterns in Puerto Rico is not known; however, predation is a likely candidate [10]. While multiple predators of

E. coqui are known in Puerto Rico [19], none of these has been introduced to Hawaii [20]. Additionally, few native or introduced species are known to predate *E. coqui* in Hawaii [20]. The intensity of predation may actually be lower in Hawaii than in Puerto Rico because densities of *E. coqui* in Hawaii can greatly exceed those seen in Puerto Rico [21,22]. Therefore, the increased role of drift in Hawaii may be the result of relaxed selection [23] in addition to multiple founder effects and drift as this species expanded its range in Hawaii.

This research conforms to the guidelines for use of animals in research and was approved by Utah State University Institutional Animal Care and Use Committee (nos 1145 and 1251).

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