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Differential admixture shapes morphological variation among invasive populations of the lizard *Anolis sagrei*

JASON J. KOLBE, ALLAN LARSON and JONATHAN B. LOSOS
Department of Biology, Campus Box 1137, Washington University, St Louis, Missouri 63130–4899, USA

Abstract

The biological invasion of the lizard *Anolis sagrei* provides an opportunity to study evolutionary mechanisms that produce morphological differentiation among non-native populations. Because the *A. sagrei* invasion represents multiple native-range source populations, differential admixture as well as random genetic drift and natural selection, could shape morphological evolution during the invasion. Mitochondrial DNA (mtDNA) analyses reveal seven distinct native-range source populations for 10 introduced *A. sagrei* populations from Florida, Louisiana and Texas (USA), and Grand Cayman, with 2–5 native-range sources contributing to each non-native population. These introduced populations differ significantly in frequencies of haplotypes from different native-range sources and in body size, toepad-lamella number, and body shape. Variation among introduced populations for both lamella number and body shape is explained by differential admixture of various source populations; mean morphological values of introduced populations are correlated with the relative genetic contributions from different native-range source populations. The number of source populations contributing to an introduced population correlates with body size, which appears independent of the relative contributions of particular source populations. Thus, differential admixture of various native-range source populations explains morphological differences among introduced *A. sagrei* populations. Morphological differentiation among populations is compatible with the hypothesis of selective neutrality, although we are unable to test the hypothesis of interdemic selection among introductions from different native-range source populations.

Keywords: admixture, biological invasion, morphological evolution, mtDNA, multiple source populations, random genetic drift

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Introduction

Biological invasions provide an excellent opportunity to test alternative hypotheses of phenotypic evolution (Sakai *et al*. 2001; Lee 2002; Wares *et al*. 2005). Both random genetic drift and natural selection can produce phenotypic evolution in non-native populations (e.g. Baker 1980; Badyaev & Hill 2000; Huey *et al*. 2000; Maron *et al*. 2004; Rasner *et al*. 2004; Kliber & Eckert 2005). If multiple introductions occur from genetically and phenotypically distinct native-range sources, then differential admixture (the varying preportional contributions of two or more sources to introduced populations) also can cause non-native populations to differ from their native-range sources and from each other. Multiple introductions from distinct native-range sources are common in biological invasions (see Bossdorf *et al*. 2005; Wares *et al*. 2005), but few studies, if any, explicitly test differential admixture as an explanation for phenotypic evolution in biological invasions.

The process of invasion likely enhances random genetic drift, predicting a net loss of variation for an introduced population compared to its original source population (e.g. Nei *et al*. 1975; Sakai *et al*. 2001; Novak & Mack 2005; but see Cheverud & Routman 1996). Smaller propagules contain less variation and increase the likelihood that trait means will deviate from those of the original source population. Random genetic drift is most severe if the population size remains small for multiple generations during transport

Correspondence: Department of Biology, 1001 E 3rd Street, Indiana University, Bloomington, Indiana 47405, USA. Fax: 812 855 6705, E-mail: jkolbe@indiana.edu

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and subsequent establishment in a non-native area (Sakai *et al*. 2001; Frankham *et al*. 2002), increasing the probability of phenotypic differences among introduced populations. Random genetic drift is inferred in biological invasions when the pattern of differentiation among introduced populations is haphazard with regard to geography or environmental gradients (e.g. Baker *et al*. 1990) or does not exceed neutral expectations for the time since introduction (i.e. Lande 1976; Lynch 1988).

Natural selection may also produce phenotypic divergence during biological invasions. Non-native populations often encounter predators, competitors, and food types absent from their previous evolutionary histories (Sakai *et al*. 2001). Similarly, differences in abiotic conditions such as temperature, precipitation, or structural habitat between native and non-native ranges could influence adaptive differentiation. Alternatively, differences in environmental conditions could release introduced populations from selective pressures experienced in their native range. Several previous studies of introductions reveal selectively driven phenotypic diversification (e.g. Huey *et al*. 2000; Reznick & Ghalambor 2001; Clegg *et al*. 2002; Maron *et al*. 2004; Phillips *et al*. 2006). For example, Rasner *et al*. (2004) used a common-garden experiment to confirm a major role for natural selection in the evolution of shorter wings and tails in a recently established population of dark-eyed juncos, *Junco hyemalis*, in California.

Two general approaches exist for evaluating morphological evolution: (i) testing hypotheses of adaptive differentiation with trait-environment correlations, and (ii) comparing patterns of within-population and between-population phenotypic trait variances and covariances. A significant relationship between morphological variation and an environmental variable among populations suggests an adaptive hypothesis (Endler 1986). In the context of a biological invasion, well-studied trait-environment relationships in the native range of an introduced species can serve as a priori predictions of adaptive differentiation in the non-native range. Thus, if environmental differences among introduced populations drive morphological differences, then we predict a correlation between morphology and habitat use among introduced populations.

Without relying on specific hypotheses for adaptive differentiation, natural selection as the cause for multivariate morphological divergence among populations can be tested using patterns of trait variation and covariation (Ackermann & Cheverud 2002; Marroig & Cheverud 2004). Under random genetic drift, a correlation is expected between patterns of within-population and between-population phenotypic variation. In an introduction, such a correlation would suggest that morphological differentiation among introduced populations is directed by the pattern of multivariate trait variation and covariation within populations (Ackermann & Cheverud 2002). In other words, populations experiencing phenotypic divergence due to random genetic drift will produce a pattern of mean phenotypic divergence among populations that is proportional to the multivariate pattern of trait variation within populations (Arnold *et al*. 2001). By contrast, selection on a given set of traits will lead to greater differences among populations in those traits than expected from within-population variation. Thus, if patterns of multivariate trait variance and covariance differ within and among populations, random genetic drift alone cannot explain the observed patterns (Ackermann & Cheverud 2002; Marroig & Cheverud 2004).

Introductions can occur from multiple native-range source populations during a biological invasion. This blending of variation can create new genotypes and phenotypes distinct from those of both source populations and other introduced populations (e.g. Rieseberg 1995). Admixture from multiple sources predicts a correlation among introduced populations between morphology and the degree to which they share native-range source populations. Natural selection or random genetic drift within introduced populations subsequent to an admixture event could, however, erase this correlation and obscure the imprint of admixture. We are unaware of any previous study that explicitly evaluates the role of differential admixture in phenotypic differentiation among introduced populations derived from multiple native-range sources.

Here, we focus on the invasive lizard, *Anolis sagrei*, for which we have previously identified at least nine distinct native-range sources and extensive differential admixture in non-native populations (Kolbe *et al*. 2004). The native range of *A. sagrei* comprises the Bahamas, Belize, Cuba, Little Cayman, Cayman Brac, and Mexico (Schwartz & Henderson 1991); introduced populations are well established in the southeastern United States (Florida, Georgia, Louisiana, and Texas), and on the Caribbean (Grand Cayman, Grenada, and Jamaica) and Pacific (Hawaii and Taiwan) islands (Minton & Minton 1984; Campbell 1996; McKeown 1996; Greene *et al*. 2002; Norval *et al*. 2002; Lever 2003; Meshaka *et al*. 2004). Initial introductions in the Florida Keys occurred in the late 19th century, while independent introductions to peninsular Florida occurred in the 1940s. Lizards were first reported in Grand Cayman, Texas, and Louisiana in the 1980s (Lever 2003). Introduced *A. sagrei* populations are derived primarily from Cuba but also the Bahamas and Belize (Kolbe *et al*. 2004). Admixture of introductions from multiple sources has increased within-population genetic variation in most introduced populations relative to native-range populations. Secondary introductions from well-established populations in Florida have occurred in Grand Cayman and Grenada as well as in Hawaii and Taiwan, the latter two populations having maintained high levels of genetic variation (Kolbe *et al*. 2004). Given its independent and secondary introductions to various localities around the world, and contributions

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from multiple native-range source populations, *A. sagrei* provides an excellent opportunity to evaluate how random genetic drift, natural selection, and admixture interact to influence phenotypic differentiation during a biological invasion.

The goal of this study is to determine which evolutionary mechanisms best explain morphological differences among non-native populations during the biological invasion of *A. sagrei*. We first test for differences among non-native *A. sagrei* populations, then evaluate whether adaptive differentiation among non-native populations or differential admixture from various native-range source populations best explains these morphological differences. If morphological differences exist, yet there is no support for adaptive differentiation or admixture, then the null hypothesis of random genetic drift cannot be rejected as the cause of morphological differences among populations. We test for adaptive differentiation in two ways: first, we test a priori hypotheses for trait-environment relationships (Endler 1986; Wainwright & Reilly 1994), and second, we test whether the overall pattern of multivariate morphological divergence is consistent with natural selection (Ackermann & Cheverud 2002). Finally, we assess admixture by determining whether differences in morphological traits are related to differences among introduced populations in their native-range sources.

Materials and methods

Habitat use and morphology

We sampled habitat use, morphology, and genetic variation in 10 introduced populations of the lizard *Anolis sagrei*: six populations from Florida, two from Texas, and one each from Louisiana and Grand Cayman. Two habitat-use variables were collected from undisturbed adult male lizards at each site: perch diameter was measured to the nearest 1.0 mm, and perch height to the nearest 0.5 cm. Using a ruler, we took two morphological measurements on live lizards in the field: snout-vent length (SVL) and hindlimb length (HL). Each measurement was to the nearest 0.5 mm with SVL taken from the tip of the snout to the cloacal opening and HL taken from the insertion of the limb into the body wall to the distal tip of the claw on metatarsal IV. For the six Florida populations, we collected at least 20 adult male lizards from each population. These lizards were preserved and radiographs taken to measure the following skeletal elements: lengths of the humerus, ulna, femur, tibia, 1st phalange on the 3rd toe of the forefoot, 1st and 2nd phalanges on the 4th toe of the hindfoot, and widths of the pelvic and pectoral girdles. We summed the measurements for the humerus, ulna, and 1st phalange on the 3rd toe of the forefoot into a single 'forelimb' variable and the measurements for the femur, tibia, and 1st and 2nd phalanges on the 4th toe of the hindfoot into a single 'hindlimb' variable for some analyses. We also counted the number of lamellae on the 2nd and 3rd phalanges of both the 3rd toe of the forelimb and the 4th toe of the hindlimb with a monocular lens (Glossip & Losos 1997), and took external measurements of head length, head width and head height for each specimen using calipers.

DNA sequences

To identify native-range sources for individuals in introduced populations, we extracted genomic DNA from liver or tail tissue for 164 individuals from 10 introduced populations of *A. sagrei* using Viogene extraction kits (Viogene). Polymerase chain reaction (PCR) amplified gene products with the following protocol: 300 s at 95 C followed by 30 cycles of 95 C for 35 s, 53 C for 35 s, and 72 C for 150 s. PCR volumes varied from 25 to 50 L and included 1–5 L genomic DNA and a mixture of 49.5% H_2O, 10% M190G thermophilic DNA polymerase 10x buffer, 10% 25 mM $MgCl_2$, 10% dNTPs, and 10% 2 pmol of each primer, and 0.5% Promega *Taq* DNA polymerase. We purified PCR products using Viogene Gel-M purification kits (Viogene). We sequenced an approximately 500 base-pair region of mitochondrial DNA (mtDNA) including a portion of the gene encoding ND2 using primers H5730, L4882c, and L4437 (Macey *et al*. 1997). Sequencing reactions were run with BigDye Terminator Ready-Reaction Kits (Perkin-Elmer) on either a BaseStation automated sequencer (MJ Research) or an ABI 3130 capillary sequencer (Applied Biosystems). Mitochondrial DNA sequences were easily aligned manually due to length conservatism in this gene region.

Phylogenetic analyses

MRMODELTEST 1.1B (http://www.ebc.uu.se/syszoo/staff/nylander.html), a modified version of MODELTEST (Posada & Crandall 1998), conducted hierarchical hypothesis testing to choose the appropriate model of evolution for subsequent Bayesian phylogenetic analyses. We implemented Bayesian phylogenetic analyses using MRBAYES 3.1 (Huelsenbeck & Ronquist 2001). This analysis ran four chains for 2 000 000 generations and sampled trees every 10 000 generations. We determined the 'burn-in' trees by plotting the likelihood score of each sampled tree against its generation; trees prior to reaching an asymptotic likelihood score were discarded (the first 20% of trees to be conservative). Using the remaining tree set, we calculated a 50% majority-rule consensus tree in PAUP* 4.0b10 (Swofford 2002). Posterior probabilities indicate the percentage of trees in the posterior distribution that include a given node. These trees were used to identify well-supported, geographically restricted native-range clades that also contained haplotypes from

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introduced populations nested within them (Kolbe *et al*. 2004).

Mitochondrial DNA sequence data collected here were combined with previously published mtDNA haplotype data for 35 individuals from six of these introduced populations (Kolbe *et al*. 2004). Thus, the final mtDNA data set for introduced populations consisted of haplotype data for 20 individuals per population for all 10 introduced *A. sagrei* populations except the Houston, Texas population ($N = 19$). GenBank Accession nos for previously published sequences in this study are AY655164–AY655483.

Statistical analyses

We tested for overall differences in morphology among introduced populations of *A. sagrei* using multivariate analysis of covariance (MANCOVA). Morphological variables analysed were forelimb lamella number, hindlimb lamella number, head width, head height, head length, forelimb length, hindlimb length, pelvis width, and pectoral width with SVL as the covariate. All variables were ln-transformed prior to statistical analyses. Given a significant MANCOVA., we also conducted univariate analyses of covariance (ANCOVA) for each morphological variable independently to determine which variables differed among introduced populations. We also tested for differences among populations in the two habitat variables with MANOVA using ln(x + 1)-transformed perch height and ln-transformed perch diameter. Finally, we tested for a difference among introduced populations in the frequency of mtDNA haplotypes from distinct native-range source populations with a χ^2-contingency test. The significance of this test was determined by randomization due to the high proportion of cells with zero. All statistical analyses were conducted in JMP 5.1 (SAS 2003) except the randomization test, which was conducted in the R statistical package (R Development Core Team 2005).

Adaptive differentiation: a priori hypotheses for morphology-habitat correlations

If differences in morphology among introduced populations are due to adaptive differentiation, then we expect a significant relationship between morphological and habitat-use variables. Previous studies of *A. sagrei* suggest three a priori hypotheses for morphology-habitat use correlations. First, there is a positive relationship between hindlimb length and perch diameter among both natural and experimental populations of *A. sagrei* (Losos *et al*. 1994, 1997). The predicted functional significance of this relationship is that individuals with longer legs can run faster on broader surfaces and those with shorter legs can move more adeptly on narrower perches (Losos & Sinervo 1989; Losos & Irschick 1996). Second, a positive correlation exists between lamella number and perch height among native populations (Collette 1961; Lister 1976). Toepad lamellae are expanded subdigital scales that enhance a lizard's ability to cling to smooth surfaces, with larger toepads having greater clinging ability (Ruibal & Ernst 1965; Irschick *et al*. 1996). Lastly, *A. sagrei* appear to be larger in introduced populations than in their native range (Campbell & Echternacht 2003), suggesting post-introduction divergence in body size.

To evaluate these predictions, we used linear regression to test for a relationship between relative hindlimb length and perch diameter, lamella number and perch height, and a multiple regression to test for a relationship between body size (ln-SVL) and habitat, both perch diameter and perch height, using JMP 5.1 (SAS 2003). Relative hindlimb length was calculated as the residuals from the regression of ln-hindlimb length against ln-SVL using population means. We also tested for a relationship between body shape and habitat by calculating pairwise-difference matrices among introduced populations for body shape and habitat, and tested for matrix correlations with Mantel tests (Manly 1991). For the body-shape difference matrix, we used the Mahalanobis distance among populations of all morphological variables except lamella numbers and SVL using the population centroids obtained from a MANCOVA with SVL as the covariate. The habitat-difference matrix was calculated as the Euclidean distance among population means for perch diameter and perch height. Since variation in habitat might be correlated with geographical distance among populations, we also tested for a correlation between habitat and geographical-difference matrices and controlled for geographical distance in subsequent analyses as necessary. The statistical significance of Mantel tests was evaluated using 9999 random permutations implemented in the software package PASSAGE (Rosenberg 2001).

Adaptive differentiation: multivariate trait variance-covariance comparisons

We compared phenotypic trait variances and covariances (VCV) found within and between introduced *A. sagrei* populations (Ackermann & Cheverud 2002; Marroig & Cheverud 2004). A potential problem with applying this method to introduced *A. sagrei* populations is if admixed native-range source populations were divergent in within-population VCV structure. As an indirect test of this assumption, we compared all pairs of within-population correlation and VCV matrices of introduced populations using Mantel tests and random skewers. If these matrices are correlated, then it is possible that underlying genetic VCV matrices are also correlated. Dissimilar within-population phenotypic VCV matrices, however, suggest that similarity in underlying genetic VCV matrices is

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unlikely. Since all pairwise comparisons of within-population phenotypic correlation and VCV matrices among the six introduced populations were significant (see Results), we generated pooled within-population matrices for subsequent comparisons. While the sample size for the pooled within-population VCV is good ($N = 174$), sample sizes for estimates of within-population VCV for each individual population are somewhat small (mean = 29, range = 20–49).

First, we tested for a correlation between the pooled within-population and between-population phenotypic correlation matrices using a Mantel test (Manly 1991) in PASSAGE (Rosenberg 2001). The pooled within-population correlation matrix was extracted from a MANOVA testing for morphological differences among the six introduced Florida populations using all morphological variables except ln-SVL. The between-population matrix was calculated by determining the correlation between population means for each morphological variable. Second, we tested for a correlation between the pooled within-population and between-population VCV matrices using a random-skewers approach (Cheverud 1996). This method multiplies each VCV matrix by the same random vector, calculates the correlation between the two resulting vectors, and repeats this procedure 10 000 times to generate a distribution of correlation values. Significance is tested by comparing the average vector correlation to a distribution of vector correlations between random vectors (Cheverud 1996). This test was implemented in a C program. Random genetic drift predicts a correlation between these matrices. If the null hypothesis of random genetic drift is rejected, then selection is implicated as producing the observed pattern of trait VCV (Ackermann & Cheverud 2002). Third, in addition to random genetic drift, a significant correlation between within- and between-population VCV matrices could also be due to selection acting along the 'genetic lines of least resistance' (Schluter 1996). To test this, we compared the within-population and between-population variances of principal-component (PC) axes derived from the pooled within-population VCV matrix by regressing the ln-transformed variances against each other (Marroig & Cheverud 2004). Under random genetic drift, the regression of these variances will have a slope of 1, which we tested with a *t* test of regression-slope differences (Sokal & Rohlf 1995). A slope significantly greater than 1 suggests diversifying selection of the first few PC axes or stabilizing selection on the last few PC axes, whereas a slope smaller than 1 suggests the opposite pattern of PC variation and interpretation of selection (Marroig & Cheverud 2004). We also tested for significant correlations among the first five PC axes. A significant correlation between a pair of PC scores suggests coselection of these traits. Multiple comparisons were corrected using the Bonferroni criterion (Marroig & Cheverud 2004).

Admixture

To determine whether differential admixture explains morphological differences among introduced populations, we tested for correlations between three matrices of morphological differences (body size, lamella number, and body shape) and two matrices representing differences in source populations. The body-size matrix was the difference in ln-SVL among introduced populations, the lamella-number matrix was the Euclidean distance among populations using mean values for both forelimb and hindlimb lamellae, and the body-shape matrix was the Mahalanobis distance as calculated for previous comparisons with habitat. The two source-population difference matrices represented the frequency of mtDNA haplotypes detected within an introduced population that were derived from different native source populations and the number of native-range source populations contributing to an introduced population. To generate the first source-population matrix, we calculated the frequency of mtDNA haplotypes from each native-range source population found within each introduced population. From these frequencies, we then calculated the Manhattan distance between each pair of introduced populations; this represents the overall difference in sources among introduced populations. The second source-population matrix represents the number of admixture events contributing to genetic and morphological variation within that introduced population, calculated as the difference between the number of sources for each pair of introduced populations. Since variation in the pattern of introductions from different sources might be correlated with geographical distance among introduced populations, we also tested for a correlation between source-population difference and geographical-distance matrices and controlled for geographical distance in subsequent analyses when appropriate. The statistical significance of Mantel tests was evaluated using 9999 random permutations implemented in the software package PASSAGE (Rosenberg 2001). In the case of body size and number of sources, we also tested this relationship with linear regression using JMP 5.1 (SAS 2003).

Results

Mitochondrial DNA analyses

The aligned mtDNA data set includes 488 sites for 282 unique sequences, 274 sequences for *Anolis sagrei* from introduced and native-range populations and eight sequences for three outgroup *Anolis* species (*A. bremeri*, *A. homolechis*, and *A. quadriocellifer*). Twenty of these sequences are newly reported mtDNA haplotypes (GenBank Accession nos DQ846752–DQ846771) and 262 are previously published sequences from Kolbe *et al.* (2004). Bayesian

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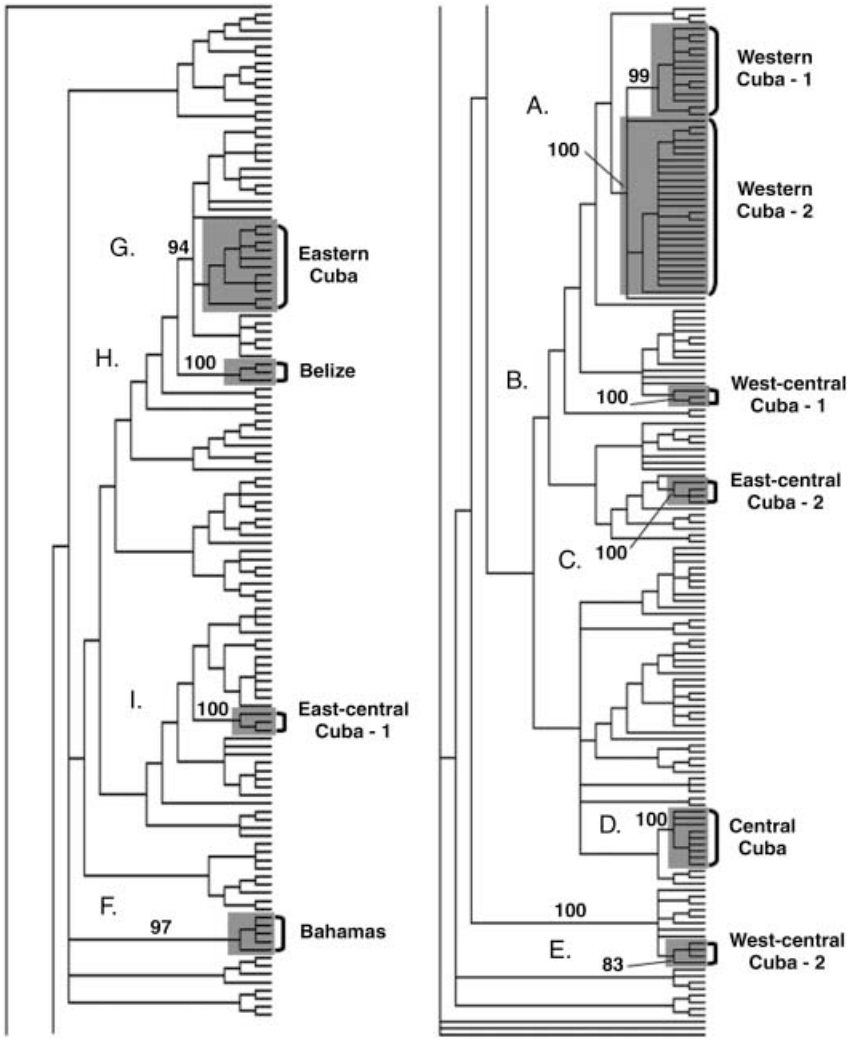

Fig. 1 Phylogenetic tree from the Bayesian analysis of all mtDNA haplotypes sampled from introduced and native populations of *Anolis sagrei*. Shading and letters (A–I) indicate well-supported clades that are geographically distinct in the native range but contain all haplotypes sampled from introduced populations. Bayesian posterior probabilities are shown above the branches leading to these clades. Geographical regions in the native range are shown for each clade. Three native-range clades do not contribute to the 10 focal introduced populations in this study: West-central Cuba-2 (E), the Bahamas (F), and East-central Cuba-1 (I).

phylogenetic analysis using the HKY + I + Γ model of evolution reveals seven native-range sources for mtDNA haplotypes in the 10 introduced *A. sagrei* populations (Figs 1 and 2; Table 1). These are the same native-range sources previously identified for introduced *A. sagrei* populations (Kolbe *et al*. 2004) with the exception of the Bahamas, East-central Cuba-1, and West-central Cuba-2 source populations, which do not contribute to the 10 introduced populations in this study.

Thirty-seven haplotypes are found among the 199 individuals from 10 introduced populations in the phylogenetic analysis. The number of sources varies with 5 sources for St Petersburg and Tampa, 4 sources for Gainesville and Orlando, 3 sources for Coral Gables, George Town, and Lower Matecumbe Key, and 2 sources for Corpus Christi, Houston, and New Orleans (Fig. 2; Table 1). The frequency of native-range source populations is significantly different among the 10 introduced populations ($\chi^2 = 311.069$, $P < 0.0001$). Thus, introduced populations vary in the identity of native-range source populations contributing to them as well as the relative contributions from each source. The pattern of haplotype variation suggests that secondary introductions from south Florida are responsible for introduced populations in Grand Cayman, Louisiana, and Texas (Kolbe *et al*. 2004). All haplotypes in these four populations are either identical or closely related to haplotypes found in Coral Gables (Fig. 2 and Table 1) and south Florida in general (Kolbe *et al*. 2004), and introductions in south Florida occurred much earlier than introductions in Grand Cayman, Louisiana, and Texas (Minton & Minton 1984; Lever 2003).

Morphological and habitat-use analyses

Significant morphological differences occur among introduced populations (MANCOVA.: *Wilks'* $\lambda = 0.338$, $P < 0.0001$; Fig. 3; Tables 2–4). Homogeneity of slopes was rejected for the MANCOVA (*Wilks'* $\lambda = 0.671$, $P = 0.010$), suggesting

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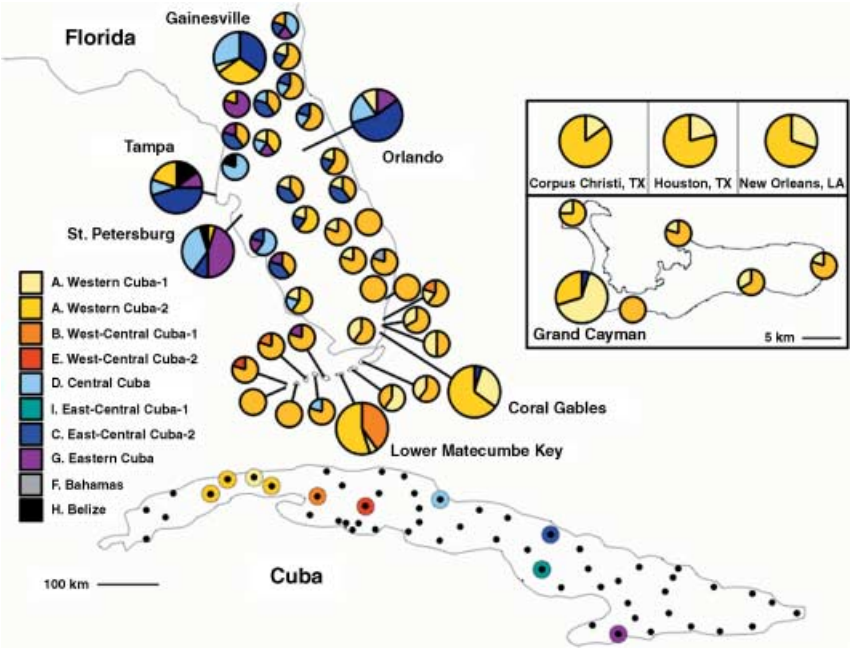

Fig. 2 A map of genetic variation in introduced *Anolis sagrei* populations and the source of this genetic variation from native-range source populations. Black dots indicate native Cuban populations sampled, and colours encircling some black dots denote Cuban populations containing haplotypes to which introduced-population haplotypes are most closely related. Pie charts representing each introduced population indicate the frequency of haplotypes from different native-range sources. Sample sizes are 2–5 individuals for the small pie charts (see Kolbe *et al*. 2004) and 19–20 individuals for the large pie charts (see Table 1). Letters (A–I) in the legend correspond to clades in Fig. 1.

Table 1 Numbers of mtDNA haplotypes from the seven native-range source populations contributing to the 10 introduced *Anolis sagrei* populations in this study. These source populations correspond to those identified in the phylogenetic analysis in this study and Kolbe *et al*. (2004). The Western Cuba clade (A) was divided into two subgroups (1 and 2) to recognize the haplotype divergence within this clade. Three native-range sources identified in Fig. 1 do not contribute to the 10 focal populations in this study: West-central Cuba-2 (E), the Bahamas (F), and East-central Cuba-1 (I)

Introduced populations	*N*	A. Western Cuba-1	A. Western Cuba-2	B. West-central Cuba-1	C. East-central Cuba-2	D. Central Cuba	G. Eastern Cuba	H. Belize
Coral Gables, Florida	20	6	13	0	1	0	0	0
Corpus Christi, Texas	20	3	17	0	0	0	0	0
Gainesville, Florida	20	1	6	0	7	6	0	0
George Town, Grand Cayman	20	13	6	0	1	0	0	0
Houston, Texas	19	4	15	0	0	0	0	0
Lower Matecumbe Key, Florida	20	1	11	8	0	0	0	0
New Orleans, Louisiana	20	6	14	0	0	0	0	0
Orlando, Florida	20	2	0	0	11	4	3	0
St Petersburg, Florida	20	0	1	0	2	7	9	1
Tampa, Florida	20	0	4	0	9	2	2	3
Totals	199	36	87	8	31	19	14	4

variation in the relationship between morphological traits and body size among some populations. Univariate ANCOVAS show differences among introduced populations in all morphological variables except head width and pelvis width with significant slope heterogeneity in three variables (Table 4). Significant differences in habitat (perch height and perch diameter) exist among all 10 introduced populations (MANOVA: $F_{9,352} = 2.204$, $P = 0.021$), but not among the six Florida populations (MANOVA: $F_{5,236} = 0.674$, $P = 0.644$; Table 5).

Adaptive differentiation: a priori hypotheses for morphology-habitat correlations

No relationship exists between relative hindlimb length and perch diameter (linear regression: $R^2 = 0.102$, $P = 0.368$) nor between the number of lamellae and perch height (linear regression: $R^2 = 0.002$, $P = 0.934$) for introduced *A. sagrei* populations. The relationship between body size and habitat use is nearly significant overall (multiple regression: $F = 3.544$, $R^2 = 0.503$, $P = 0.087$), and perch height is significantly

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Table 2 Morphological variation in introduced *Anolis sagrei* populations. Mean ± SE for snout-vent length (SVL), forefoot lamellae (LAM3), and hindfoot lamellae (LAM4), and ratios of the other morphological variables with SVL. SVL and hindlimb length (Hind) were measured in all 10 introduced populations, whereas the other eight morphological variables were measured in only the six non-native Florida populations. Fore, forelimb length; Pec, pectoral width; Pel, pelvis width; HW, head width; HH, head height; and HL, head length. All measurements are in mm

Introduced population	*N*	SVL	Fore/SVL	Hind/SVL	Pec/SVL	Pel/SVL
Coral Gables, Florida	20	55.7 ± 1.5	0.348	0.770	0.133	0.101
Corpus Christi, Texas	12	54.1 ± 1.6	—	0.769	—	—
Gainesville, Florida	37	57.8 ± 0.7	0.334	0.735	0.133	0.100
George Town, Grand Cayman	13	53.6 ± 1.7	—	0.720	—	—
Houston, Texas	19	54.2 ± 1.1	—	0.744	—	—
Lower Matecumbe Key , Florida	23	57.5 ± 0.7	0.351	0.783	0.132	0.101
New Orleans, Louisiana	13	51.4 ± 2.4	—	0.751	—	—
Orlando, Florida	24	55.6 ± 1.1	0.336	0.739	0.131	0.097
St Petersburg, Florida	21	57.6 ± 0.7	0.351	0.750	0.135	0.101
Tampa, Florida	49	58.6 ± 0.6	0.340	0.741	0.137	0.102
Introduced population	*N*	LAM3	LAM4	HW/SVL	HH/SVL	HL/SVL
Coral Gables, Florida	20	10.8 ± 0.1	20.2 ± 0.2	0.165	0.142	0.260
Corpus Christi, Texas	12	—	—	—	—	—
Gainesville, Florida	37	11.3 ± 0.1	20.7 ± 0.2	0.163	0.137	0.258
George Town, Grand Cayman	13	—	—	—	—	—
Houston, Texas	19	—	—	—	—	—
Lower Matecumbe Key, Florida	23	10.6 ± 0.1	20.0 ± 0.2	0.165	0.136	0.257
New Orleans, Louisiana	13	—	—	—	—	—
Orlando, Florida	24	11.2 ± 0.1	20.4 ± 0.2	0.165	0.137	0.254
St Petersburg, Florida	21	11.6 ± 0.1	21.2 ± 0.3	0.167	0.135	0.262
Tampa, Florida	49	11.2 ± 0.1	20.5 ± 0.1	0.166	0.143	0.256

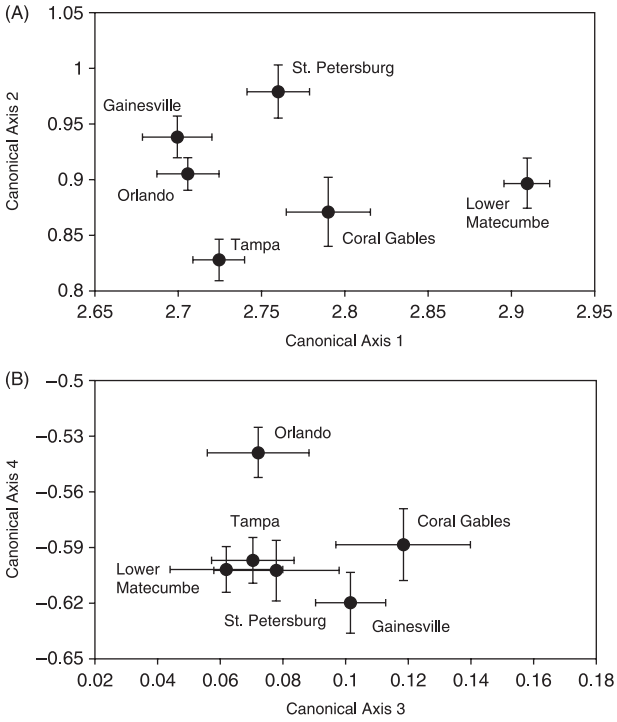

Fig. 3 Morphological differences among six introduced Florida populations of *Anolis sagrei* for canonical axes (A) CA1 and CA2 and (B) CA3 and CA4 from the MANCOVA. Error bars show ± 1 SE.

Table 3 Correlation between the nine morphological variables and the canonical axes (CA) from a MANCOVA with SVL as a covariate testing for differences among six introduced populations of *Anolis sagrei*

Variable	CA1	CA2	CA3	CA4
Lamellae 3F	−0.4403	0.2225	−0.0727	0.2697
Lamellae 4H	−0.2565	0.1223	0.0580	−0.0581
Head width	0.4922	−0.6769	0.2422	0.0100
Head height	0.3977	−0.8933	0.4158	−0.0898
Head length	0.5059	−0.6162	0.4689	−0.2519
Forelimb length	0.6705	−0.6411	0.3707	−0.0954
Hindlimb length	0.7587	−0.6340	0.2778	−0.1775
Pelvis width	0.4260	−0.7350	0.2198	−0.2927
Pectoral width	0.3769	−0.7012	0.1605	−0.3319

related to body size (perch height: $P = 7.087$, $P = 0.032$; perch diameter: $F = 1.820$, $P = 0.219$). This positive relationship (linear regression: $R^2 = 0.374$, $P = 0.060$) between body size and perch height is, however, heavily influenced by one outlier. The New Orleans population is the smallest and lowest perching, and when this point is removed from the analysis, the relationship vanishes (linear regression: $R^2 = 0.007$, $P = 0.828$). Habitat differences are not correlated with geographical distance (Mantel test: $r = -0.050$, $P = 0.537$) or

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Table 4 Results of ANCOVAs with SVL as a covariate (and ANOVA for SVL) testing for differences in 10 morphological variables among introduced populations of *Anolis sagrei*. Lamellae variables are scale counts on the 3rd toe of the forelimb (3F) and 4th toe on the hindlimb (4H). All variables are ln-transformed. Sample size (N) refers to the number of populations. An asterisk indicates that the homogeneity of slopes could not be rejected and that the interaction term therefore was removed in the final ANCOVA

Variable	*N*	R^2	*F*	d.f.	*P*-value
Snout-vent length	10	0.158	4.600	9221	< 0.0001
Lamellae 3F*	6	0.157	6.214	5167	< 0.0001
SVL	—	—	0.194	1167	0.6605
Lamellae 4H*	6	0.088	3.178	5167	0.0091
SVL	—	—	0.007	1167	0.9339
Head width*	6	0.827	1.587	5167	0.1665
SVL	—	—	737.967	1167	< 0.0001
Head height	6	0.814	4.676	5167	0.0005
SVL	—	—	421.306	1167	< 0.0001
Population × SVL	—	—	2.769	5167	0.0198
Head length*	6	0.884	4.069	5167	0.0016
SVL	—	—	1168.511	1167	< 0.0001
Forelimb length	6	0.884	11.912	5167	< 0.0001
SVL	—	—	727.759	1167	< 0.0001
Population × SVL	—	—	2.559	5167	0.0294
Hindlimb length*	10	0.905	12.255	9220	< 0.0001
SVL	—	—	1670.564	1220	< 0.0001
Pelvis width	6	0.769	1.734	5167	0.1296
SVL	—	—	362.995	1167	< 0.0001
Population × SVL	—	—	2.272	5167	0.0499
Pectoral width*	6	0.781	2.922	5167	0.0148
SVL	—	—	515.318	1167	< 0.0001

Table 5 Mean ± 1 SE for habitat variables, perch diameter and perch height, from 10 introduced populations of *Anolis sagrei*. Sample size (*N*) refers to the number of observations per population. Measurements are in mm

Introduced population	*N*	Perch diameter (mean ± SE)	Perch height (mean ± SE)
Coral Gables, Florida	50	215.8 ± 25.1	800.4 ± 72.1
Corpus Christi, Texas	29	173.1 ± 33.2	818.6 ± 94.6
Gainesville, Florida	37	174.5 ± 28.7	627.9 ± 83.8
George Town, Grand Cayman	18	241.5 ± 39.4	579.0 ± 120.1
Houston, Texas	68	150.1 ± 21.4	612.5 ± 61.8
Lower Matecumbe Key, Florida	52	104.4 ± 24.0	601.2 ± 70.7
New Orleans, Louisiana	22	102.1 ± 35.5	318.4 ± 108.7
Orlando, Florida	43	117.4 ± 24.8	662.8 ± 77.7
St Petersburg, Florida	41	106.1 ± 28.7	628.4 ± 79.6
Tampa, Florida	48	179.5 ± 23.7	811.4 ± 73.6

body shape (Mantel test: $r = 0.248$, $P = 0.153$) among introduced populations. Thus, no support exists for our a priori adaptive explanations for the current morphological differences among introduced *A. sagrei* populations.

Adaptive differentiation: multivariate trait variance-covariance comparisons

All pairs of within-population correlation (Mantel tests: mean $r = 0.593$, all $P < 0.05$) and VCV matrices (random skewers: mean $r = 0.822$, all $P < 0.05$) were significantly correlated (Table 6). The pooled within-population trait-correlation matrix is significantly correlated with the between-population trait correlation matrix (Mantel test: $r = 0.403$, $P = 0.016$) and the pooled within-population trait VCV matrix is significantly correlated with the between-population trait VCV matrix (random skewers: $r = 0.603$, $P = 0.032$). Thus, the pattern of within-population trait VCV is similar to the pattern among populations as predicted if differentiation has resulted from random genetic drift. Furthermore, the regression slope of ln-transformed within and between population PC variances is not significantly different from one (slope ± SE: 0.822 ± 0.311; p[slope ≠ 1] = 0.585), and no PC axes were significantly correlated after Bonferroni correction ($P > 0.005$); neither result provides evidence for natural selection. Thus, the hypothesis that random genetic drift explains the divergence of morphological traits among introduced populations of *A. sagrei* cannot be rejected.

Table 6 Correlation coefficients (*r*) for all pairwise comparisons of within-population correlation and VCV matrices for six introduced Florida populations of *Anolis sagrei*. *r* values above the diagonal are Mantel correlations and those below the diagonal are random skewers correlations. $P < 0.05$ for all correlations

Introduced Populations	Coral Gables	Gainesville	Lower Matecumbe Key	Orlando	St Petersburg	Tampa
Coral Gables	—	0.582	0.741	0.601	0.530	0.816
Gainesville	**0.754**	—	0.465	0.667	0.536	0.647
Lower Matecumbe Key	**0.783**	**0.776**	—	0.576	0.329	0.631
Orlando	**0.801**	**0.894**	**0.841**	—	0.516	0.652
St Petersburg	**0.739**	**0.866**	**0.780**	**0.841**	—	0.609
Tampa	**0.840**	**0.837**	**0.830**	**0.892**	**0.862**	—

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Table 7 Results of Mantel tests for correlations between morphological variables (body size, lamella number, and body shape) and native-range source frequency and source number. We also tested for spatial autocorrelation of source frequency and source number; *r* is the Mantel correlation coefficient. Significant correlations are in bold

Matrix 1	Matrix 2	*r*	*P* value
Body size	Source frequency	0.153	0.226
Body sze	Source number	**0.458**	**0.013**
Lamella number	Source frequency	**0.839**	**0.006**
Lamella number	Source number	0.597	0.071
Body shape	Source frequency	**0.512**	**0.036**
Body shape	Source number	0.230	0.244
Source frequency	Geographical distance	0.626	0.063
Source number	Geographical distance	0.589	0.089

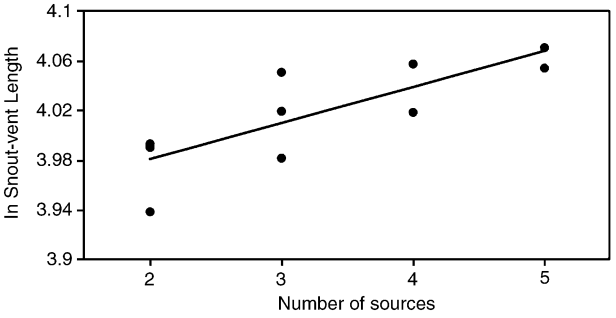

Fig. 4 Plot showing the positive relationship between body size (ln-SVL) and the number of native-range source populations contributing to an introduced population

Admixture

Among-population similarities in both lamella number and body shape are correlated with source-population similarities among introduced *A. sagrei* populations (Table 7). In contrast, body size is not associated with similarity in source populations, although body size is correlated with the number of sources contributing to an introduced population (linear regression: $R^2 = 0.647$, $P = 0.005$; Fig. 4; Table 7). Lamella number and body shape are not significantly correlated with the number of sources (Table 7), although lamella number is nearly significant ($P = 0.070$). Thus, admixture affects all morphological characters in this study, but it does so in different ways. Lamella number and body shape are affected by source-population similarity, whereas body size is related to number of source populations.

Discussion

This study reveals a strong effect of differential admixture on phenotypic variation among introduced populations, while no evidence was found for divergence by natural selection. This result contrasts with most previous studies of phenotypic evolution in biological invasions, which have found evidence for random genetic drift and natural selection (e.g. Baker *et al*. 1990; Clegg *et al*. 2002; Rasner *et al*. 2004). Thus, differential admixture is an important evolutionary force in morphological differentiation among introduced *Anolis sagrei* populations, resulting in a genetic and phenotypic mosaic across its non-native range (Figs 1–3; Tables 1, 2 and 4). Because many recent studies have detected multiple native-range source populations in biological invasions (e.g. Facon *et al*. 2003; Voisin *et al*. 2005), differential admixture should be considered a potentially important cause of phenotypic divergence in biological invasions.

Admixture

Mean values for lamella number and body shape within introduced *A. sagrei* populations reflect the values of 2–5 distinct native-range populations weighted by their respective genetic contributions to the introduced population (Table 7). These results are compatible with previous findings on morphometric variation in introduced *A. sagrei* populations. In a multivariate analysis of trait variation, Lee (1992) found non-native Florida *A. sagrei* populations mostly intermediate relative to native populations (i.e. the Bahamas, Cuba, and Mexico/Central America), but closer to Cuban populations. This result is consistent with most native-range sources being from Cuba (Fig. 1; Table 1). The finding of intermediate morphological values for non-native Florida populations also suggests that native-range sources are differentiated in lamella number and body shape, either through local adaptation or random genetic drift, a finding consistent with previous studies of native *A. sagrei* populations (Lister 1976; Lee 1992).

Given the correlation between mean morphology and source-population similarity among introduced *A. sagrei* populations, progeny in these populations most likely have morphological values intermediate between the admixed native-range source populations. In a review of empirical evidence, Rieseberg (1995) showed that hybrids are usually morphologically similar to a parental type or intermediate between the two parents (e.g. Grant & Grant 1994), but a significant percentage also show extreme characters. A direct comparison of phenotypic distributions in introduced and native-range source populations is needed to evaluate shared patterns of phenotypic variation and to test for occurrence of transgressive phenotypes.

Natural selection

Our tests for adaptive morphological differentiation among introduced populations fail to reject the hypothesis of selective neutrality, suggesting that random genetic drift alone can explain the observed morphological

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diversification. Thus, it would be difficult to reconcile the presence of post-introduction selection on lamella number or body shape with the strong imprint of admixture detected for these traits. Directional selection should obscure the effect of admixture by moving a population's mean trait value away from that produced by initial mixing of individuals from different native-range sources. However, we can think of at least one scenario in which natural selection could be important in introduced *A. sagrei* populations. Because we do not have information on the representation of source populations among the founders of introduced populations, we cannot test the hypothesis that differential survival and reproduction among lizards from different sources explains morphological differences among introduced populations. Interdemic selection among propagules from native-range sources after introduction could alter the initial frequencies of individuals from the different sources (Lewontin 1965), thereby influencing the current frequencies of mtDNA haplotypes and pattern of morphological differentiation among introduced populations.

Habitat differences between the native and introduced ranges of *A. sagrei* may explain the inference that variation in perch diameter is an important source of selection in the former but not the latter range. Mean perch diameters for introduced populations range from 100 to 240 mm (Table 5), whereas mean perch diameters for native Bahamian populations, where the positive relationship between hindlimb length and perch diameter was originally detected, are all less than 100 mm (Losos *et al*. 1994). Regardless of whether the pattern of adaptive differentiation in hindlimb length among native *A. sagrei* populations (Losos *et al*. 1994, 1997) is explained by natural selection (Losos *et al*. 2004) acting on genetic variation for hindlimb length, mediated through the environment by phenotypic plasticity (Losos *et al*. 2000), or a combination of both, the perches used by *A. sagrei* in non-native populations may exceed an upper threshold where performance is no longer enhanced by increasing perch diameter (Losos & Sinervo 1989; Losos & Irschick 1996) or developmental constraint restricts further lengthening or plasticity of hindlimbs to accommodate perch diameters. Thus, while studies from the native range are invaluable for providing hypotheses to test in introduced populations, such relationships may not always be directly relevant for populations in the non-native range. In this case, the environmental conditions (i.e. perch diameter) differ substantially in the non-native range compared to where the adaptive relationship was studied in the native range (i.e. the Bahamas).

A previous comparison of body size in native and introduced populations of *A. sagrei* suggested an increase in body size in non-native populations (Campbell & Echternacht 2003). Our study likewise reveals that non-native populations in Florida have larger body sizes than native Cuban populations (60–63 mm vs. 56–58 mm SVL); however, non-native populations outside Florida have smaller bodies than native populations (51–54 mm vs. 56–58 mm SVL). The difference in body size among introduced populations corresponds to a difference in the number of source populations (Fig. 4; Tables 1 and 2). Non-native Florida populations have 3–5 native sources, whereas most non-native populations outside Florida have only 2 native sources. More native sources contributing to an introduced population will likely increase genetic variation underlying morphological traits (e.g. Maron *et al*. 2004). Thus, the correlation between body size and number of sources suggests one possible explanation for body size differences; if directional selection favours increased body size in non-native populations, then those populations with the most additive genetic variance (i.e. most native-range source populations) would respond faster. Other possible explanations include phenotypic plasticity induced by environmental differences among populations or hybrid vigour (Facon *et al*. 2005). On a cautionary note, if geographical variation exists within the native range of an invader, as it does for body size in *A. sagrei* (Campbell & Echternacht 2003), it is imperative that comparisons be made as closely as possible to the exact native-range source population(s).

Our major finding is that differential admixture explains morphological differences among introduced populations in the biological invasion of *A. sagrei*. Because numerous recent studies reveal multiple sources in biological invasions (see Bossdorf *et al*. 2005; Wares *et al*. 2005), differential admixture is an important general hypothesis for explaining phenotypic differentiation among introduced populations. Unfortunately, multiple sources may go undetected in many instances if not explicitly evaluated. Testing for multiple source populations and admixture within non-native populations is important, not only because of its potential role in phenotypic differentiation among introduced populations, but also because multiple sources can produce increased genetic variation within non-native populations (Kolbe *et al*. 2004; Voisin *et al*. 2005), and admixture may stimulate invasiveness (Ellstrand & Schierenbeck 2000).

We suggest two kinds of studies to aid predictions of morphological evolution during biological invasions. First, studies identifying geographical variation and phenotype-environment relationships in the native ranges of biological invaders will provide specific predictions for morphological variation in non-native populations. Second, detailed analyses of invasion histories using both documented introductions and molecular markers are essential for understanding the complex nature of biological invasions involving differential admixture of source populations (Estoup *et al*. 2001; Wares *et al*. 2005). Such analyses are also essential for identifying appropriate comparisons between introduced and native-range source populations when evaluating genetic and phenotypic evolution during biological invasions.

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References

Ackermann RR, Cheverud JM (2002) Discerning evolutionary processes in patterns of tamarin (genus *Saguinus*) craniofacial variation. *American Journal of Physical Anthropology*, **117**, 260–271.

Arnold SJ, Pfrender ME, Jones AG (2001) The adaptive landscape as a conceptual bridge between micro- and macroevolution. *Genetica*, **112–113**, 9–32.

Badyaev AV, Hill GE (2000) The evolution of sexual dimorphism in the house finch. I. Population divergence in morphological covariance structure. *Evolution*, **54**, 1784–1794.

Baker AJ (1980) Morphometric differentiation in New Zealand populations of the house sparrow (*Passer domesticus*). *Evolution*, **34**, 638–653.

Baker AJ, Peck MK, Goldsmith MA (1990) Genetic and morphometric differentiation in introduced populations of common chaffinches (*Fringilla coelebs*) in New Zealand. *Condor*, **92**, 76–88.

Bossdorf O, Auge H, Lafuma L, Rogers WE, Siemann E, Prati D (2005) Phenotypic and genetic differentiation between native and introduced plant populations. *Oecologia*, **144**, 1–11.

Campbell TS (1996) Northern range expansion of the brown anole (*Anolis sagrei*) in Florida and Georgia. *Herpetological Review*, **27**, 155–157.

Campbell TS, Echternacht AC (2003) Introduced species as moving targets: changes in body sizes of introduced lizards following experimental introductions and historical invasions. *Biological Invasions*, **5**, 193–212.

Cheverud JM (1996) Quantitative genetic analysis of cranial morphology in the cotton-top (*Saguinus oedipus*) and saddleback (*S. fuscicollis*) tamarins. *Journal of Evolutionary Biology*, **9**, 5–42.

Cheverud JM, Routman EJ (1996) Epistasis as a source of increased additive genetic variance at population bottlenecks. *Evolution*, **50**, 1042–1051.

Clegg SM, Degnan SM, Moritz C, Estoup A, Kikkawa J, Owens IPF (2002) Microevolution in island forms: the roles of drift and directional selection in morphological divergence of a passerine bird. *Evolution*, **56**, 2090–2099.

Collette BB (1961) Correlations between ecology and morphology in anoline lizards from Havana, Cuba and southern Florida. *Bulletin of the Museum Comparative Zoology*, **125**, 137–162.

Ellstrand NC, Schierenbeck KA (2000) Hybridization as a stimulus for the evolution of invasiveness in plants? *Proceedings of the National Academy of Sciences, USA*, **97**, 7043–7050.

Endler JA (1986) *Natural Selection in the Wild*. Princeton University Press, Princeton, New Jersey.

Estoup A, Wilson IJ, Sullivan C, Cornuet J-M, Moritz C (2001) Inferring population history from microsatellite and enzyme data in serially introduced cane toads, *Bufo marinus*. *Genetics*, **159**, 1671–1687.

Facon B, Pointier J-P, Glaubrecht M, Poux C, Jarne P, David P (2003) A molecular phylogeography approach to biological invasions of the New World by parthenogenetic Thiarid snails. *Molecular Ecology*, **12**, 3027–3039.

Facon B, Jarne P, Pointier P, David P (2005) Hybridization and invasiveness in the freshwater snail *Melanoides tuberculata*: hybrid vigour is more important than increase in genetic variance. *Journal of Evolutionary Biology*, **18**, 524–535.

Frankham R, Ballou JD, Briscoe DA (2002) *Introduction to Conservation Genetics*. Cambridge University Press, Cambridge, UK.

Glossip D, Losos JB (1997) Ecological correlates of number of subdigital lamellae in anoles. *Herpetologica*, **53**, 192–199.

Grant PR, Grant BR (1994) Phenotypic and genetic effects of hybridization in Darwinís finches. *Evolution*, **48**, 297–316.

Greene BT, Yorks DT, Parmerlee JS, Powell R, Henderson RW (2002) Discovery of *Anolis sagrei* in Grenada with comments on its potential impact on native anoles. *Caribbean Journal of Science*, **38**, 270–272.

Huelsenbeck JP, Ronquist F (2001) MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics*, **17**, 754–755.

Huey RB, Gilchrist GW, Carlson ML, Berrigan D, Serra L (2000) Rapid evolution of a geographic cline in size in an introduced fly. *Science*, **287**, 308–309.

Irschick DJ, Austin CC, Petren K, Fisher RN, Losos JB, Ellers O (1996) A comparative analysis of clinging ability among pad-bearing lizards. *Biological Journal of the Linnean Society*, **59**, 21–35.

Kliber A, Eckert CG (2005) Interaction between founder effects and selection during biological invasion in an aquatic plant. *Evolution*, **59**, 1900–1913.

Kolbe JJ, Glor RE, RodrÌguez Schettino L, Chamizo Lara A, Larson A, Losos JB (2004) Genetic variation increases during biological invasion by a Cuban lizard. *Nature*, **431**, 177–181.

Lande R (1976) Natural selection and random drift in phenotypic evolution. *Evolution*, **30**, 314–334.

Lee JC (1992) *Anolis sagrei*. Florida: phenetics of a colonizing species III. West Indian and Middle American comparisons. *Copeia*, **1992**, 942–954.

Lee CE (2002) Evolutionary genetics of invasive species. *Trends in Ecology & Evolution*, **17**, 386–391.

Lever C (2003) *Naturalized Reptiles and Amphibians of the World*. Oxford University Press, Oxford.

Lewontin RC (1965) Selection for colonizing ability. In: *The Genetics of Colonizing Species* (eds Baker HG, Stebbins GL), pp. 77–91. Academic Press, New York.

Lister BC (1976) The nature of niche expansion in West Indian *Anolis* lizards I: ecological consequences of reduced competition. *Evolution*, **30**, 659–676.

Losos JB, Irschick DJ (1996) The effect of perch diameter on escape behaviour of *Anolis* lizards: laboratory-based predictions and field tests. *Animal Behaviour*, **51**, 593–602.

Losos JB, Sinervo B (1989) The effect of morphology and perch diameter on sprint performance of *Anolis* lizards. *Journal of Experimental Biology*, **145**, 23–30.

Losos JB, Irschick DJ, Schoener TW (1994) Adaptation and constraint in the evolution of specialization of Bahamian *Anolis* lizards. *Evolution*, **48**, 1786–1798.

Losos JB, Warheit KI, Schoener TW (1997) Adaptive differentiation following experimental island colonization in *Anolis* lizards. *Nature*, **387**, 70–73.

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Losos JB, Creer DA, Glossip D *et al.* (2000) Evolutionary implications of phenotypic plasticity in the hindlimb of the lizard *Anolis sagrei*. *Evolution*, **54**, 301–305.

Losos JB, Schoener TW, Spiller DA (2004) Predator-induced behaviour shifts and natural selection in field-experimental lizard populations. *Nature*, **432**, 505–508.

Lynch M (1988) The divergence of neutral quantitative characters among partially isolated populations. *Evolution*, **42**, 455–466.

Macey JR, Larson A, Ananjeva NB, Papenfuss TJ (1997) Evolutionary shifts in three major structural features of the mitochondrial genome among iguanian lizards. *Journal of Molecular Evolution*, **44**, 660–674.

Manly BFJ (1991) *Randomization and Monte Carlo Methods in Biology*. Chapman & Hall, New York.

Maron JL, Vil M, Bommarco R, Elmendorf S, Beardsley P (2004) Rapid evolution of an invasive plant. *Ecological Monographs*, **74**, 261–280.

Marroig G, Cheverud JM (2004) Did natural selection or genetic drift produce the cranial diversification of Neotropical monkeys? *American Naturalist*, **163**, 417–428.

McKeown S (1996) *A Field Guide to Reptiles and Amphibians in the Hawaiian Islands*. Diamond Head Publishing, Los Osos, California.

Meshaka WE, Butterfield BP, Hauge JB (2004) *The Exotic Amphibians and Reptiles of Florida*. Krieger Publishing Company, Malabar, Florida.

Minton SA, Minton MR (1984) Geographic distribution, *Anolis sagrei*, Grand Caymans. *Herpetological Review*, **15**, 77.

Nei M, Maruyama T, Chakraborty R (1975) The bottleneck effect and genetic variability in populations. *Evolution*, **29**, 1–10.

Norval G, Mao JJ, Chu HP, Chen LC (2002) A new record of an introduced species, the brown anole (*Anolis sagrei*) in Taiwan. *Zoological Studies*, **41**, 332–336.

Novak SJ, Mack RN (2005) Genetic bottlenecks in alien plant species: influence of mating systems and introduction dynamics. In: *Species Invasions: Insights Into Ecology, Evolution, and Biogeography* (eds Sax DF, Stachowicz JJ, Gaines SD), pp. 201–228. Sinauer Associates, Sunderland, Massachusetts.

Phillips BL, Brown GP, Webb JK, Shine R (2006) Invasion and the evolution of speed in toads. *Nature*, **439**, 803.

Posada D, Crandall KA (1998) MODELTEST: testing the model of DNA substitution. *Bioinfomatics*, **14**, 817–818.

R Development Core Team (2005) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Rasner CA, Yeh P, Eggert LS, Hunt KE, Woodruff DS, Price TD (2004) Genetic and morphological evolution following a founder event in the dark-eyed junco, *Junco hyemalis thurberi*. *Molecular Ecology*, **13**, 671–681.

Reznick DN, Ghalambor C (2001) The population ecology of contemporary adaptation: what empirical studies reveal about the conditions that promote adaptive evolution. *Genetica*, **112–113**, 183–198.

Rieseberg LH (1995) The role of hybridization in evolution: old wine in new skins. *American Journal of Botany*, **82**, 944–953.

Rosenberg MS (2001) PASSAGE: *Pattern Analysis, Spatial Statistics and Geographic Exegesis*, Version 1.0. Department of Biology, Arizona State University, Tempe, Arizona.

Ruibal R, Ernst V (1965) The structure of the digital setae of lizards. *Journal of Morphology*, **117**, 271–294.

Sakai AK, Allendorf FW, Holt JSet al. (2001) The population biology of invasive species. *Annual Review of Ecology and Systematics*, **32**, 305–332.

SAS Institute Inc (2003) JMP *in Version 5.1*. SAS Institute, Cary, North Carolina.

Schluter D (1996) Adaptive radiation along genetic lines of least resistance. *Evolution*, **50**, 1766–1774.

Schwartz A, Henderson RW (1991) *Amphibians and Reptiles of the West Indies: Descriptions, Distributions, and Natural History*. University of Florida Press, Gainesville, Florida.

Sokal RR, Rohlf FJ (1995) *Biometry*, 3rd edn. W.H. Freeman, San Francisco, California.

Swofford D (2002) PAUP*. *Phylogenetic Analysis Using Parsimony (*and Other Methods)*. Sinauer Associates, Sunderland, Massachusetts.

Voisin M, Engel CR, Viard F (2005) Differential shuffling of native genetic diversity across introduced regions in a brown alga: aquaculture vs. maritime traffic effects. *Proceedings of the National Academy of Sciences, USA*, **102**, 5432–5437.

Wainwright PC, Reilly SM (1994) *Ecological Morphology: Integrative Organismal Biology*. University of Chicago Press, Chicago, Illinois.

Wares JP, Hughes AR, Grosberg RK (2005) Mechanisms that drive evolutionary change: insights from species introductions and invasions. In: *Species Invasions: Insights into Ecology, Evolution, and Biogeography* (eds Sax DF, Stachowicz JJ, Gaines SD), pp. 229–257. Sinauer Associates, Sunderland, Massachusetts.

Dr. Jason Kolbe is a postdoctoral fellow in the Department of Biology at Indiana University. His research focuses on the ecology and evolution of biological invasions, particularly lizards. Dr. Allan Larson is Professor of Biology at Washington University. His research specialty is molecular evolution of vertebrates, particularly lizards and salamanders. Dr. Jonathan Losos is Curator of Herpetology at the Museum of Comparative Zoology and a Professor in Department of Organismic and Evolutionary Biology at Harvard University. He is interested in evolutionary ecology and adaptive radiation, with a special emphasis on reptiles.

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