

that contact with the invading migrants spurred on any of these changes; rather, fluctuations in environmental conditions possibly drove their continued evolution⁹. The discovery of new fossil localities dating to the Oligocene/Miocene boundary will be required to test the remaining possibility that competitive exclusion between the Afro-Arabian endemics and the invading immigrants was responsible for the extinction of the former. It seems likely that the phyletic conservatism and perhaps generalized habits of many of the endemic taxa greatly limited their ability to compete with the invaders; other endemics such as the proboscideans, which underwent greater diversification and specialization in the Afro-Arabian Oligocene, ended up on the winning side of the equation. □

Methods

Chronology

The Chilga section has more than 90 m of volcanics at its base that are overlain by at least 130 m of fluvial sediments. The basalt at the base of the section is dated at 32.4 ± 1.6 Myr (see Supplementary Information) and provides a maximum age for the section. Studies of the isothermal remanent magnetism⁷ for a suite of siltstones show a dominance of low-coercivity grains indicating magnetite or maghaematite, an expected result given that basalts form the dominant parent material. All sediments show some evidence of intermediate-coercivity grains indicating specular haematite as well as small amounts of high-coercivity grains suggesting pigmentary haematite and goethite, but these are both minor constituents relative to the low-coercivity fraction. Stepwise alternating-field demagnetization was carried out on 118 samples with generally three samples per stratigraphic level. Palaeomagnetic reversal stratigraphy demonstrates a dominance of normal polarity. Duplicate ⁴⁰Ar–³⁹Ar age spectra analyses of K-feldspar each separated from a tuff at 165 m produced a weighted average of 27.36 ± 0.11 Myr (see Supplementary Information) that provides an absolute tie point to Chron C9n ($27.004\text{--}27.946$ Myr). Small arrows to the far right of the geomagnetic polarity timescale (GPTS)⁸ in Fig. 2 represent “tiny wiggles” and the two brief reversals within Chron C9n may be present at Chilga, thereby providing additional but more indirect support for this correlation. Together these data suggest that this section is probably limited to the duration of Chron C9n (<1 Myr). Vertebrate localities occur primarily through the middle part of the section.

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Ocean currents mediate evolution in island lizards

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Islands are considered to be natural laboratories in which to examine evolution because of the implicit assumption that limited gene flow allows tests of evolutionary processes in isolated replicates¹. Here we show that this well-accepted idea requires re-examination. Island inundation during hurricanes can have devastating effects on lizard populations in the Bahamas^{2,3}. After severe storms, islands may be recolonized by over-water dispersal of lizards from neighbouring islands³. High levels of gene flow may homogenize genes responsible for divergence, and are widely viewed as a constraining force on evolution^{4,5}. Ultimately, the magnitude of gene flow determines the extent to which populations diverge from one another, and whether or not they eventually form new species^{6,7}. We show that patterns of gene flow among island populations of *Anolis* lizards are best explained by prevailing ocean currents, and that over-water dispersal has evolutionary consequences. Across islands, divergence in fitness-related morphology decreases with increasing gene flow⁵. Results suggest that over-water dispersal after hurricanes constrains adaptive diversification in *Anolis* lizards, and that it may have an important but previously undocumented role in this classical example of adaptive radiation.

Anolis lizards in the Caribbean represent one of the best examples of a vertebrate adaptive radiation^{8–10}. Over 140 species of Caribbean anoles have radiated into six morphological classes (termed ‘ecomorphs’)⁸ that are specialized for different habitat types^{11,12}. Ecomorphs that perch on broad-diameter substrates (for example, tree trunks) tend to have longer limbs compared with ecomorphs that perch on narrow-diameter substrates (for example, twigs; see below), and based on locomotor performance, these differences are adaptive¹¹. Phylogenetic evidence has shown that morphological classes evolved independently on different islands in the Greater Antilles¹³ and that islands were colonized by a common ancestor from Cuba, which subsequently radiated into the diversity of species found today.

Recent work indicates that hurricanes have important effects on *Anolis* demography^{2,3}. During September 1999 the category IV hurricane Floyd devastated island lizard populations in the Bahamas with winds exceeding 250 km h⁻¹ and associated tidal surges of over 6 m; populations on 66 study islands were either killed or washed off the islands by the storm³. Schoener *et al.*³ suggested that the initial recovery of these island lizard populations (approximately 2 months after hurricane Floyd) was by progeny hatching from eggs laid before the storm. Although no islands were reported to have received immigrants as a result of hurricane transport, subsequent recolonization of islands over the next 17 months was rapid and indicated over-water dispersal of adult lizards from neighbouring islands³. Here we use microsatellite markers to show that weather-related abiotic factors, including prevailing winds and ocean currents, probably determine the direction of gene flow between islands and consequently the magnitude of

morphological divergence by natural selection. Our study provides genetic evidence that supports the mechanism of island recolonization after hurricanes that was proposed by Schoener *et al.*³, and thus indicates that the joint action of hurricanes and ocean currents may have an important influence on the adaptive radiation of this group.

Variation in microsatellite allele frequencies was used to test the hypothesis that gene flow between insular populations of *Anolis sagrei* occurs by over-water dispersal on ocean currents in the Bahamas. We tested whether differences in the magnitude of gene flow between islands could affect microevolutionary patterns of morphological diversification in this group. The adaptive radiation of Caribbean anoles is believed to be driven by ecologically based natural selection arising from variation in habitat use^{9,10,14}. Selection is thought to operate on traits such as limb length through locomotor performance associated with differences in perch diameter and perch height¹¹. Longer limbs are favoured on broad perching surfaces because long limbs increase maximum sprint speed, allowing lizards to catch prey or escape predators more efficiently. However, shorter limbs are favoured on narrow perches because they enhance agility relative to longer limbs^{11,15}. Numbers of toe-pad lamellae are also correlated with perching height, owing to the importance of clinging ability¹⁶. Interspecific variation in these three characters features prominently in divergence of ecomorphs and consequently in the adaptive radiation of this group^{9,10}. Moreover, intraspecific variation in *A. sagrei* mirrors that of the adaptive radiation of anoles, suggesting that ecologically based natural selection acts similarly at the population and species levels¹⁷.

Prevailing winds and surface ocean currents in the Bahamas have a net westerly flow among islands^{18,19}, except where the Florida

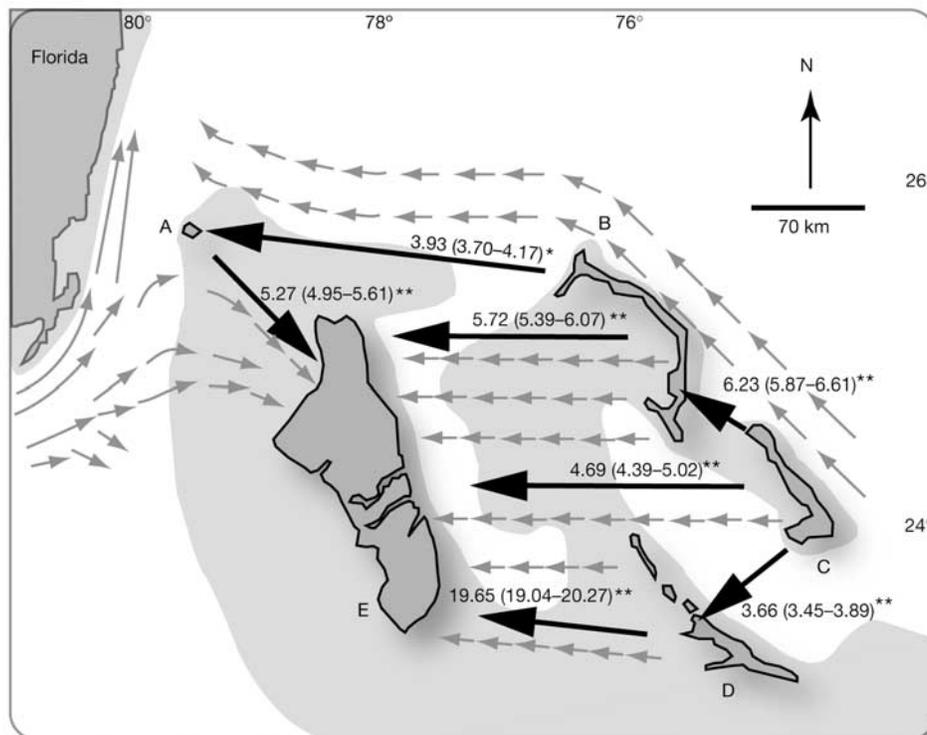


Figure 1 Map of the study islands showing the polarity and magnitude of ocean currents (thin arrows) and gene flow (thick arrows) between adjacent islands. The lightly shaded areas indicate shallow banks surrounding the study islands and Florida. Numbers of migrants per generation (N_m) and 5% and 95% confidence intervals are reported for each pair of adjacent islands in the dominant direction of gene flow as computed in MIGRATE. Confidence intervals indicate N_m values that are significantly greater in the direction shown than in the reverse direction based on maximum likelihood estimates from

MIGRATE. Note that the direction of gene flow is congruent everywhere with the flow of ocean currents. In the case of islands C and D, the juxtaposition of islands relative to ocean currents may account for comparatively small N_m values. Islands are labelled as follows: A, South Bimini; B, Eleuthera; C, Cat Island; D, Great Exuma; E, Andros. Asterisk, non-overlapping 0.5% and 99.5% confidence intervals; double asterisk, non-overlapping 5% and 95% confidence intervals.

current meets the western boundary of the Caribbean current (Fig. 1). Here, the current has a northerly flow around the eastern side of Florida, and an intermittent southward flow from Bimini to Andros islands in the Bahamas²⁰. The deep Florida current cannot flow over the shallow banks of the Bahamas, but flows northward to the Gulf Stream. By contrast, the southward flow from Bimini to Andros islands (Fig. 1) might be driven by northwesterly trade winds associated with the passage of cold fronts during winter months, which could force southeastward surface currents over the shallow banks of the Bahamas. This suggests that propagules (including *Anolis* lizards) introduced to the Atlantic Ocean around the Bahamas should also drift from east to west among most islands, and south from Bimini to Andros.

During June and July of 2002 we visited five islands on the Great Bahama bank and captured approximately 50 *A. sagrei* lizards from each island. We assessed variation at eight microsatellite loci in the laboratory. Maximum likelihood estimates of gene flow direction based on Markov chain Monte-Carlo simulations²¹ indicated that the direction of gene flow among islands is best explained by patterns of ocean currents in the Caribbean, and has occurred predominantly from east to west in the Bahamas (Rayleigh test of directionality $r = 0.76$, $P < 0.008$, Fig. 1; see ref. 22). The average distance among islands in our study is 124 km (Fig. 1). Assuming an average ocean-surface flow velocity of 20 cm s^{-1} (ref. 19), floating or rafting between islands would require approximately 1 week (range 2–15 days). This is a conservative estimate because wind and wave velocities increase substantially during periods of intense storm activity. Moreover, lizard migration could proceed in a stepping-stone fashion, where intermediate islands would reduce exposure time in the open ocean. Laboratory experiments indicate that *A. sagrei* are capable of surviving long-term exposure to sea water (for example, $>24 \text{ h}$ unaided by rafts)²³, and field observations indicate that under some conditions *A. sagrei* willfully enter the ocean and swim away from small, inhospitable islands²⁴. Thus, these results support the assertion of Schoener *et al.*³ that over-water dispersal may be a significant factor in the ecology and evolution of

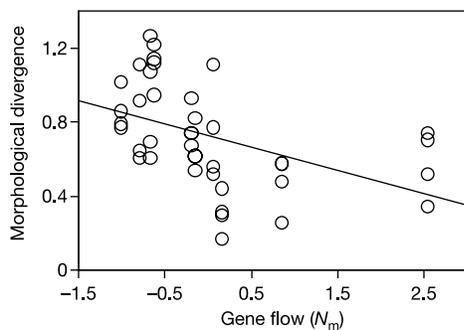


Figure 2 Standardized morphological divergence (mean = 0, unit variance) in four morphological characters, as a function of the standardized number of migrants (N_m) between islands. Morphological divergence decreased with increasing gene flow, showing that migration between islands slows the rate of adaptive divergence due to natural selection. The significant negative slope indicates that the difference in trait divergence has a genetic basis and is not simply due to environmental factors²⁵. We calculated trait divergence as the absolute value of the difference in euclidean distance between the following standardized characters: hindlimb length, forelimb length, toe-pad lamella width and snout-vent length. We calculated morphological divergence within and between habitat types (broad- and narrow-perch diameters) and among island populations. Each pair of islands generated four morphological comparisons, two each within and between habitat types. Thus, each population was used in multiple morphological comparisons and we used pairwise matrix correlations (Mantel's test) to account for non-independence among population comparisons. We present the least-squares regression line for illustrative purposes only.

lizard populations in the Caribbean.

A multivariate estimate of shape (see Methods) based on four morphological characters, including those considered most likely affected by natural selection, revealed that levels of gene flow between islands were significantly correlated with population-level divergence in morphology (Mantel's $r = 1.23$, $P < 0.02$; Fig. 2). One explanation for this correlation is that gene flow has homogenizing effects on morphology and adaptive divergence by natural selection. An alternative explanation, that gene flow and morphological divergence are both correlated with geographical distance between islands, is not supported by our data. There was no relationship between morphological distance and geographical distance between our study populations ($r^2 = 0.019$, $P = 0.40$). Gene flow between islands could therefore have important implications for the adaptive radiation of this group by constraining the ability of natural selection to drive morphological divergence. Moreover, although some of the variation in fitness-related characters may arise by plastic changes in response to the environment (for example, differences in perch diameter)²⁵, plasticity alone cannot explain the significantly negative relationship between divergence and gene flow. Gene flow would not be expected to have homogenizing effects on divergence among populations in a trait that was completely plastic²⁶. The homogenizing effects of gene flow on morphological divergence reported here indicate that some of the phenotypic variation probably arises owing to differences among individuals at genetic loci controlling limb length.

Alternative explanations for the directional patterns of gene flow reported in this study include human transportation of lizards among islands, and historical contingencies such as land bridges that connected islands of the Great Bahama bank during the Last Glacial Maximum (approximately 8,000–10,000 yr before present)²⁷ or island colonization from Cuban ancestors. These are unlikely explanations. First, neither human-mediated dispersal of anoles nor historical connections among islands would be expected to produce dominantly unidirectional patterns of gene flow. In contrast, we find directionality of gene flow that is congruent in all cases with the prevailing direction of ocean currents, including the exceptional case in which currents adjacent to Florida drive gene flow south from Bimini to Andros islands (Fig. 1). Second, *Anolis* populations in the Bahamas are derived from Cuban anoles located to the southwest of the Bahamas. Thus colonization from Cuba should have produced a directionality of gene flow exactly opposite to that reported here (that is, west to east rather than east to west). We therefore conclude that transport on ocean currents remains the most parsimonious explanation for the highly directional patterns of gene flow among islands.

Studies on islands have revealed many of the fundamental mechanisms of evolution, particularly the paramount influence of geographical isolation to diversification¹. Here, we add an important caveat to these studies, showing that prevailing ocean currents may influence gene flow and adaptive divergence in a terrestrial vertebrate. The adaptive radiation of anoles in the Caribbean is thought to have arisen by ecologically based natural selection related to habitat use²⁸. However, the level of gene flow between populations will impose an upper limit on the ability of natural selection to drive adaptive divergence⁵. We have provided evidence that weather-related abiotic phenomena might have important effects on the evolution and adaptive radiation of lizard populations. □

Methods

Field

We captured 45–52 lizards from each island (mean of 51) by hand or using a silk noose. Lizards were captured at three to five locations along linear transects on each island (end points separated by 20 km except on South Bimini where small island size constrained transect length to 6 km). Animals were sexed, weighed and measured. Hindlimb and forelimb lengths were measured (to nearest millimetre) from the point of insertion at the abdomen to the distal tip of the femoral-tibial and humero-radio-ulnar joints. Toe-pad lamella width was measured with dial calipers (average of three measurements) at the

widest point of the distal toe pad on the fourth toe of the hind foot. We collected a 2-mm piece of tissue from the distal tip of the tail for molecular analyses. All lizards were marked with a small spot of white paint to prevent re-capture and were immediately released to their original point of capture.

Morphology

We regressed natural-log-transformed limb lengths and toe-pad width on snout-vent length (following procedure of ref. 29) and considered the residuals about the regression line to represent size-independent morphology. Lizards captured on broad-diameter (>15 cm) perches had significantly longer hind- and forelimbs (mean ± standard error) relative to body size compared with lizards captured on narrow-diameter (<15 cm) perches (residual hindlimb_{broad} = 0.028 ± 0.10 versus residual hindlimb_{narrow} = -0.009 ± 0.007, P < 0.002; residual forelimb_{broad} = 0.029 ± 0.11 versus residual forelimb_{narrow} = -0.015 ± 0.10, P < 0.006). This difference was also significant when we controlled for snout-vent length in an analysis of covariance¹⁷.

To reduce the dimensionality of our data, we combined the three fitness-related morphological characters and snout-vent length (that is, body size) into a unique, multivariate estimate of shape by calculating the euclidean distance between the four traits using SYSTAT version 5.2.1. Morphological divergence between islands was calculated using mean values for morphological traits from each island population. Before calculating means, data for all variables were standardized to mean zero with unit variance. The significance of the correlation between morphological divergence and gene flow was calculated using pairwise matrix correlations (Mantel's test) in the statistical package 'R' version 4.0. We computed the test statistic using two 10 × 10 matrices representing populations from two habitat types on each of five islands. Significance level was computed with 9,999 permutations (as recommended by ref. 30).

Genetics

Genomic DNA was extracted from tail tissue by overnight incubation at 55 °C in 500 µl 5% Chelex (Biourad) and 2 µl proteinase K solution (at 20 mg ml⁻¹) followed by centrifugation and 1:10 dilution of the extract. We amplified eight loci from the genomic template via polymerase chain reaction, and length polymorphism among individuals (40–44 lizards per island) was assessed with fluorescent labelling of one of the primers on an automated DNA sequencer (ABI 3700).

We estimated the magnitude and polarity of gene flow using the maximum likelihood approach implemented by MIGRATE-1.6.9. MIGRATE extends a coalescence approach to include migration rates among populations, assuming a per-locus mutation rate µ, and constant population sizes. This approach has been used in numerous studies and is considered to estimate gene flow more accurately than other Fst methods²¹. Results reported here use 50 short-chain searches and three long-chain searches over eight microsatellite loci using a brownian motion approximation to the ladder model of evolution. This search strategy resulted in the best likelihood scores, although other runs using fewer short-chain searches produce qualitatively similar results (N_m values from all runs were highly correlated and we report mean values with confidence intervals). N_m values represent the per-generation migration rate between the study islands depicted in Fig. 1 and are reported for the direction of greater magnitude between each pair of adjacent islands.

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Delta-promoted filopodia mediate long-range lateral inhibition in *Drosophila*

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Drosophila thoracic mechanosensory bristles originate from cells that are singled out from 'proneural' groups of competent epithelial cells. Neural competence is restricted to individual sensory organ precursors (SOPs) by Delta/Notch-mediated 'lateral inhibition', whereas other cells in the proneural field adopt an epidermal fate. The precursors of the large macrochaetes differentiate separately from individual proneural clusters that comprise about 20–30 cells or as heterochronic pairs from groups of more than 100 cells¹, whereas the precursors of the small regularly spaced microchaetes emerge from even larger proneural fields². This indicates that lateral inhibition might act over several cell diameters; it was difficult to reconcile with the fact that the inhibitory ligand Delta is membrane-bound until the observation that SOPs frequently extend thin processes^{3,4} offered an attractive hypothesis. Here we show that the extension of these planar filopodia—a common attribute of wing imaginal disc cells—is promoted by Delta and that their experimental suppression reduces Notch signalling in distant cells and