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Spatial variation in climate mediates gene flow across an island archipelago

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High levels of gene flow among partially isolated populations can overwhelm selection and limit local adaptation. This process, known as "gene swamping," can homogenize genetic diversity among populations and reduce the capacity of a species to withstand rapid environmental change. We studied brown anole lizards (*Anolis sagrei*) distributed across seven islands in The Bahamas. We used microsatellite markers to estimate gene flow among islands and then examined the correlation between thermal performance and island temperature. The thermal optimum for sprint performance was correlated with both mean and maximum island temperature, whereas performance breadth was not correlated with any measure of temperature variation. Gene flow between islands decreased as the difference between mean island temperatures increased, even when those islands were adjacent to one another. These data suggest that phenotypic variation is the result of either (1) local genetic adaptation with selection against immigrants maintaining variation in the thermal optimum, (2) irreversible forms of adaptive plasticity such that immigrants have reduced fitness, or (3) an interaction between fixed genetic differences and plasticity. In general, the patterns of gene flow we observed suggest that local thermal environments represent important ecological filters that can mediate gene flow on relatively fine geographic scales.

KEY WORDS: **Bahamas, climate change, metapopulation, natural selection, thermal performance curve, thermoregulation.**

Nearly all species are composed of subpopulations linked by networks of dispersal and gene flow (Hanski 1998). Geographic structure is important because climatic conditions are likely to vary across space, especially for species with broad distributions. This spatial variation in climate may be especially likely to generate and maintain phenotypic and genetic diversity (Latimer et al. 2011; Cox and Rabosky 2013; Gosden et al. 2015), and species with higher levels of phenotypic and genetic diversity are predicted to be more resilient in the face of rapid environmental change (Angilletta 2009; Hoffmann and Sgro 2011).

When local populations are exposed to differing climatic environments, their phenotypes may diverge through two adaptive processes: genetic adaptation and plasticity (Angilletta 2009; Kingsolver et al. 2013). In cases where genetic adaptation and plasticity both generate fixed differences in phenotypes, they can give rise to large-scale patterns of gene flow whereby immigrants have reduced fitness in novel climates (Gosden et al. 2015).

Gene flow between partially isolated populations can have several general effects on species-level phenotypic variation. For example, if the environment is spatially heterogeneous and dispersal is relatively low, selection and plasticity may drive local adaptation (Gilchrist et al. 2004). Conversely, a scenario known as "gene swamping" can occur whereby local adaptation (and therefore species-level phenotypic variation) is constrained by high levels of dispersal and gene flow among subpopulations (Antonovics 1968; Bossart and Scriber 1995; Storfer 1999; Storfer et al. 1999;

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Lenormand 2002). Similarly, if the traits that impact fitness are highly plastic, acclimation to local environments may mask underlying genetic variation and slow genetic adaptation (while simultaneously maintaining population fitness at high levels; Paenke et al. 2007; Buckley et al. 2015). In cases where phenotypic variation is determined by additive genetic variation or by plasticity in traits that then become fixed over development, selection (natural or sexual) against immigrants may ensure that dispersal does not result in gene flow, even when dispersal among populations is high (McNeilly and Antonovics 1968; Rockwell and Cooke 1977; Jimenez-Ambriz et al. 2007; Cheviron and Brumfield 2009; Sexton et al. 2014). Lastly, under certain conditions, higher levels of gene flow may actually enhance local adaptation through the introduction of novel alleles (Slatkin 1987; Caprio and Tabashnik 1992), the erosion of genetic correlations (Guillaume 2011), and the reduction of deleterious mutations (Cooper et al. 2015).

Here, we examine patterns of gene flow and phenotypic diversity in a broadly distributed lizard, the brown anole (*Anolis sagrei*). First, we used microsatellite markers to estimate gene flow among brown anole populations distributed across seven adjacent islands in the Bahamas. The thermal environments of these islands differed substantially from one another, providing opportunities for local adaptation and phenotypic divergence. We then measured the thermal sensitivity of sprint speed for each population in the laboratory to test whether phenotypes match local environments in ways predicted by thermal adaptation theory. We discuss the implications of our results for models of extinction risk under climate change, which typically do not consider the effects of metapopulation structure.

Material and Methods

STUDY SITES

We studied seven adjacent island populations of the brown anole in the Bahamas, including the large island of Great Exuma (area = 150 km^2) and six smaller cays arrayed along the southwestern axis of Great Exuma (Fig. 1). The areas and distances of each cay from Great Exuma are as follows: Hog (area = 1.23 km^2, 5.3 km), Davy (1.14 km^2, 8.5 km), Culmer's (0.79 km^2, 11.6 km), Bowe (0.99 km^2, 16.7 km), Coakely (1.18 km^2, 21.3 km), and Duck (0.34 km^2, 24.7 km). Great Exuma was too large to sample comprehensively. We therefore sampled lizards from a site on Great Exuma that was nearest to Hog Cay (given its proximity, we assumed that this site is where most dispersal from Great Exuma to the cays originated.) Our sampling location on Great Exuma contained typical brown anole habitat (forest edge alongside an abandoned gravel road) and was located near the settlement of George Town (23°29′N, 75°45′W). We captured lizards by hand or by slip noose from 23 May until 3 June, 2013.

THERMAL VARIATION AMONG ISLANDS

To measure the thermal environments experienced by lizards on each island, we deployed between 30 and 32 operative temperature models (OTMs) per island from 23 May to 3 June 2013. Although this sampling period was not long enough to bound annual temperature variation on each island, it permitted us to capture relative variation in temperature among islands that was sufficient to infer local adaptation (Logan et al. 2013, 2014). We were not able to retrieve all OTMs from each island such that final sample sizes varied among islands (range = 27–30 OTMs per island).

OTMs were built with Type-M (thin-walled) copper piping and painted to approximate the photo spectrum absorbance of an average adult brown anole (Bakken 1992; Logan et al. 2013, 2014). iButtons, Embedded Data Systems, Lawrenceburg, KY, USA, set to record temperatures every 10 min were placed inside each OTM (suspended within nonconductive acrylic mesh so that they did not come into direct contact with the inside surface of the copper pipe). These same OTMs had been used in a previous study to reliably estimate operative temperatures in brown anoles (Logan et al. 2014). Models were placed at a random distance (0–5 m, at 1 m intervals), and direction (N, S, E, or W) from haphazardly chosen points that covered a large portion of each island (except on the largest island of Great Exuma, where we focused on a single site). Each model was also placed at a random height in the vegetation (0–2 m, at 0.5 m intervals, which corresponds to the range of perch heights typically used by *A. sagrei*, a trunk-ground anole; Losos et al. 2004, 2006; Losos 2009). To evaluate differences in the operative thermal environments among islands, we averaged temperatures across all OTMs for each hour of the daily activity cycle of the brown anole (0600–1800) and compared the mean, maximum, and diel range of these average temperature distributions using analysis of variance (ANOVA) in the statistical program SYSTAT (Systat Software, Inc., San Jose, CA).

THERMAL PERFORMANCE CURVES

We transported several (range = 7–15) male brown anoles from each island back to our laboratory at Dartmouth College to measure the thermal sensitivity of locomotor performance (sprint speed) of each population. We focused on males because brown anoles are highly sexually dimorphic such that the shapes of their thermal performance curves (TPCs) may be sex-specific. Thus, by measuring only males we were able to maximize our statistical power. We chose sprint speed as our measure of physiological performance because it is an ecologically relevant trait related to fitness in brown anoles (Logan et al. 2014) and other lizard species (Vanberkum 1986; Miles 2004; Husak and Fox 2006; Husak et al. 2006, 2008; Calsbeek and Irschick 2007; Logan et al. 2015). To minimize any acute, residual acclimatory

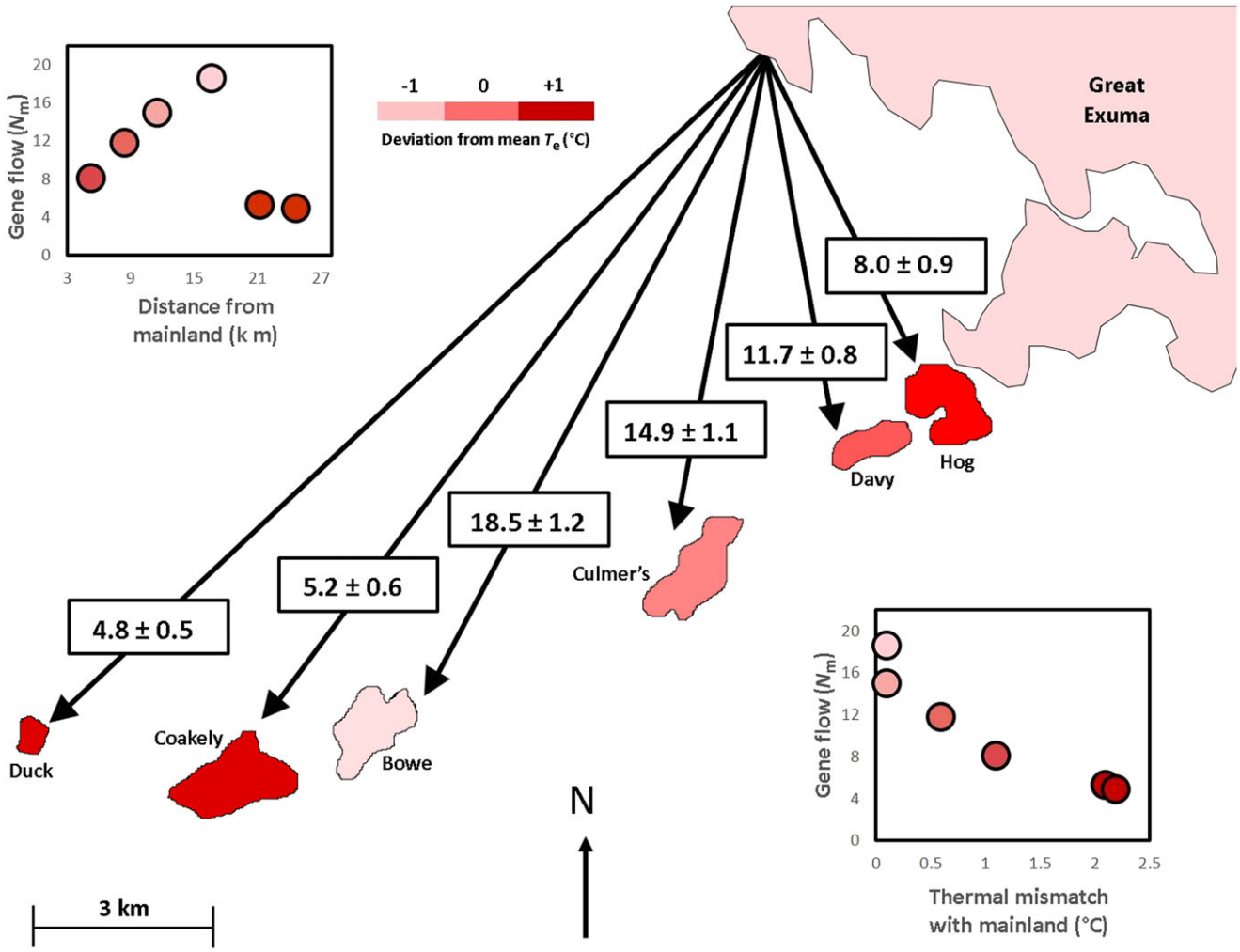

Figure 1. **Maximum likelihood estimates of gene flow (N_m ± 95% CI) from the large island of Great Exuma (mainland) to each offshore cay. Gene flow to the cays was not correlated with their geographic isolation from Great Exuma (upper left inset), but was instead correlated with the degree to which their thermal environments deviated from that of Great Exuma's (lower right inset). Islands are color coded (shaded) by their mean operative temperature (online version in color). The point at which the arrows radiate from Great Exuma was chosen for illustrative purposes only and does not reflect our sampling locality on that island, which was at a site adjacent to Hog Cay. Pairwise estimates of gene flow between all islands are presented in Table S3.**

effects of differing island thermal environments on TPCs, all lizards were allowed to acclimate to a common laboratory environment for 40 days prior to the start of sprint trials (Leal and Gunderson 2012). We note that this procedure was likely insufficient to eliminate all forms of plasticity (we elaborate on this point below). Lizards were maintained in 10 gallon terraria in the laboratory with ultra violet B (UVB) lighting and a 60 W heat lamp on one side of the terrarium to provide a thermal gradient. Each terrarium contained a potted plant. The temperature in the room where all terraria were located cycled between 28°C during the day and 22°C at night (12-h day/12-h night cycle).

We measured performance for a total of 59 individuals, but samples sizes varied among populations and temperatures due to mortality in captivity (some mortality occurred during transport or during their first week in captivity) and failed sprint trials (range: 3–11; mean: 8.0; Table S1). Lizards were motivated to run three times at each of six temperatures: 15, 20, 25, 30, 36, and 42°C in an EnvironAir precision-controlled temperature room (Holman Engineering, Inc., Springfield, MA). The order of the five lowest temperatures were chosen randomly (all individuals were run in batches at each trial temperature). All individuals were sprinted at 42°C last because of potentially lasting stress-related effects from this temperature (Kingsolver et al. 2004). Lizards were given 1 h to equilibrate to the five lowest target temperatures, and we verified that they achieved the target body temperature using a cloacal thermometer just prior to the beginning of each trial. Each individual was then encouraged to run along a wooden dowel

(1 m long, 3 cm in diameter), which was demarcated every 10 cm and positioned at a 20° angle to discourage hopping (Logan et al. 2013). At the warmest temperature (42°C), individuals were heated one at a time in an incubator and sprinted as soon as they reached the target temperature. Each individual was given a minimum of four days' rest between trials at different temperatures. Over the course of the study, lizards were given water and food ad libitum, but were never fed less than 24 h before a sprint trial.

For a given individual measured at a particular temperature, we recorded the fastest sprint speed over any 10 cm section of track for each trial, and then averaged all three trials. We fit a set of asymmetrical parabolic functions to the mean performance values from each population using the statistical package TableCurve 2D (Systat Software, Inc.) (Angilletta 2006). We chose our model set based on the established shape of TPCs, which are left-skewed non-linear functions presumably structured by the thermodynamics of enzyme function (i.e., performance increases with body temperature slowly to an optimum and then drops off rapidly when body temperature exceeds that optimum) (Angilletta 2009). We chose the best fit model for each population using Akaike's information criterion (AIC). If AIC could not be used to distinguish between two competing models, we chose the model with the fewest parameters. If AIC could not distinguish between two models with the same number of parameters, we chose the model with the highest r^2 value (Angilletta 2006; Logan et al. 2014).

We extracted two physiological traits from the best fit curve for each population: the thermal optimum (T_{opt}; the body temperature at which performance is maximized), and the performance breadth (T_{br}; the range of body temperatures at which a population can perform at 80% of maximal performance). We chose these two traits for further analysis because clear theoretical predictions exist for how these traits should be coadapted with environmental temperature distributions (Angilletta et al. 2003; Angilletta 2009; Knies et al. 2009; Somero 2010). Pearson correlations were used to examine the extent to which thermal performance traits corresponded with variation in the operative thermal environments among islands.

GENE FLOW

We collected tissue samples (tail tips) from all individuals captured in the field (including females) and preserved them in 95% ethanol solution (mean sample size = 22 individuals per island, range = 14–27). We extracted DNA using a standard Chelex-100 extraction technique (Walsh et al. 1991). We then amplified and genotyped 11 microsatellite loci that had been previously optimized for either *Anolis sagrei* or *A. carolinensis*: AAAG 61, AAAG 68, AAAG 70, AAAG 76, AAAG 77, AAAG 91, AAAG 94, AAGG 38, Acar 8, Acar 11, and Acar 23 (Bardeleben et al. 2004; Wordley et al. 2011). We confirmed that the three microsatellite loci that were previously optimized for *A. carolinensis* were polymorphic and amplified reliably for *A. sagrei*.

We amplified and genotyped microsatellite loci in two multiplex groups (with 5 and 6 markers in each, respectively). Forward primers were given individual fluorescent tags (Life Technologies, Carlsbad, CA) that were unique by fragment size to each pool. Loci were amplified in multiplex polymerase chain reaction (PCR) using Type-It Kits (Qiagen, Venlo, Limburg, The Netherlands). We conducted each multiplex PCR in a 10 μL volume using 1 μL DNA template, 5 μL Master Mix (Qiagen), 1 μL primer mix, and 3 μL molecular grade water. Primer concentrations were optimized to marker-specific amplification rates based on preliminary genotyping runs. We diluted PCR products for genotyping in 18.85 μL Hi-Di Formamide (Life Technologies, Carlsbad, CA, USA) and 0.15 μL LIZ sizing standard (Life Technologies). Diluted products were genotyped on an ABI3730 Genetic Analyzer (Life Technologies). We removed erroneous allele calls by manual examination of chromatograms using GeneMapper software (Life Technologies). For each sampled population and at each locus, we tested for an excess of heterozygosity using the program GENEPOP (Raymond and Rousset 1995) with default parameter settings, and the presence of null alleles using the programs CERVUS (www.fieldgenetics.com). (Marshall et al. 1998) and MICROCHECKER (norwichresearchpark.com). (Van Oosterhout et al. 2004). We used all 11 microsatellite markers in our final analyses because none of the markers were consistently out of Hardy–Weinberg equilibrium across all islands, nor did they show consistent evidence of null alleles beyond what would be expected for smaller, island populations with reduced genetic diversity.

We estimated rates of gene flow between all pairs of islands. Pairwise maximum likelihood-based gene flow estimates were generated using a Brownian evolution microsatellite model in the statistical package MIGRATE-n (http://popgen.sc.fsu.edu/). (Beerli and Palczewski 2010). This method uses a coalescent approach to generate genealogies from all populations and then estimates immigration and emigration probabilities between each population pair (Beerli and Felsenstein 2001). The maximum-likelihood method in MIGRATE corrects for mutation rates among loci but assumes a constant mutation rate among populations (Beerli and Felsenstein 1999). We verified that all microsatellite loci fit the stepwise model of mutation assumed by MIGRATE by manually examining fragment sizes in GeneMapper. We used a variable theta model (uniform prior distributions) with 10 short chains (500 recorded genealogies in each short chain) and one long chain (5000 recorded genealogies in the long chain), no burn-in, and default heating conditions. We had a sampling increment of 100 for both short and long chains.

Table 1. Summary of thermal trait variation among populations and operative temperature (T_e) variation among islands.

Island	T_{opt}	T_{br}	Mean T_e ± SEM	Max T_e ± SEM	Diel T_e range ± SEM	Spatial heterogeneity in T_e
Great Exuma	35	30.1– 37.7	28.8 ± 0.16	31.8 ± 0.29	8.1 ± 0.30	0.78
Hog	35.6	28.9– 40.4	29.9 ± 0.17	33.7 ± 0.32	10.0 ± 0.34	0.91
Davy	35.8	26.0– 41.1	29.4 ± 0.20	32.7 ± 0.36	8.6 ± 0.38	1.09
Culmer's	34.3	26.8– 39.4	28.9 ± 0.17	32.2 ± 0.33	7.9 ± 0.30	0.88
Bowe	34.3	27.5– 38.7	28.7 ± 0.19	31.9 ± 0.34	7.9 ± 0.33	1.03
Coakely	36.3	29.0– 39.7	30.9 ± 0.26	34.8 ± 0.41	10.4 ± 0.43	1.89
Duck	36.2	28.3– 39.8	31.0 ± 0.26	35.1 ± 0.50	10.2 ± 0.51	2.16

T_{br} is the 80% performance breadth (the range of body temperatures over which the population can sprint at least 80% of its maximal sprint speed). We only analyzed Te measurements taken during the activity period of Anolis sagrei (0600–1800 h). "Mean Te" is the average of all OTM means. "Diel T_e range" is the average difference between the highest and lowest mean hourly temperatures recorded by each OTM. "Spatial heterogeneity in T_e" is the variance among OTM means. Values reported are means ± SE.

Similar run conditions were used by Andrews et al. (2012) to estimate gene flow among sunflower populations.

We report gene flow as N_m averaged across all loci:

$$N_m = (\theta m_{a\to b})/\mu, \quad (1)$$

where N_m is the mutation-scaled migration rate corrected for effective population size, θ is the mutation-scaled effective population size, $m_{a\to b}$ is the proportion of population b that is composed of individuals from population a in the current generation, and μ is the mutation rate. N_m approximates the total number of individuals that migrate from population a to population b per generation, corrected for effective population size (Beerli and Palczewski 2010).

To determine whether gene flow between each pair of islands was affected by island isolation, differences in the thermal environment among islands, or both, we performed two Partial Mantel Tests with the average N_m between each pair of islands as the dependent variable in both, and either the difference in mean operative temperature between those islands or their relative distance from one another (isolation) as the independent variable. The alternative independent variable (temperature differences or isolation) was included as a covariate in each analysis. Partial Mantel Tests were conducted in R. (www.r-project.org). Opinions differ as to the suitability of Partial Mantel Tests in cases where spatial autocorrelation is present in the data (Raufaste and Rousset 2001; Legendre and Fortin 2010), so we verified that island isolation and environmental temperature were not significantly correlated (Mantel Test for spatial autocorrelation in temperature; 500 bootstrap replicates, $r = 0.42$, $P = 0.07$). As a separate examination of the relative effects of island isolation and island temperature on gene flow, we visualized the relationships between these variables and gene flow by treating the large island of Great Exuma as the "mainland," and examining the extent to which gene flow from Great Exuma to the cays depended on (1) the isolation of each cay, and (2) the thermal environment of each cay relative to that of Great Exuma.

Results

ENVIRONMENTAL VARIATION AMONG ISLANDS

Our study islands varied significantly in mean (ANOVA with Tukey post hoc comparisons: $F_{6,204} = 23.43$, $P < 0.001$), maximum (ANOVA with Tukey post hoc comparisons: $F_{6,204} = 13.77$, $P < 0.001$), and diel range (ANOVA with Tukey post hoc comparisons: $F_{6,204} = 9.58$, $P < 0.001$) of operative temperature (T_e; Tables 1 and S2, Figs. S1 and S2). The main island of Great Exuma, as well as Bowe and Culmer's cays, were cooler and less thermally variable than Hog, Davy, Coakely, and Duck cays (Tables 1 and S2, Figs. S1 and S2).

PHENOTYPIC VARIATION AMONG ISLANDS

Thermal optima for sprint speed (T_{opt}) differed among populations (Table 1) and was positively correlated with both mean (Pearson correlation coefficient = 0.891, $P = 0.007$; Fig. 2A) and maximum (Pearson correlation coefficient = 0.860, $P = 0.01$; Fig. 2B) operative temperature. By contrast, performance breadth (T_{br}) was not correlated with any measure of operative temperature variation among islands (Fig. 2C and D). Results were similar when island area was included as a covariate.

GENE FLOW

Our study islands comprised part of a brown anole metapopulation. Rates of gene flow were high across the archipelago (N_m: mean = 11.05 migrants/generation, SD = 5.62, range = 3.8–23.3) (Table S3). The "genetic distance" (the inverse of the magnitude of gene flow; $1/N_m$) between pairs of islands was positively correlated with the difference in their mean operative

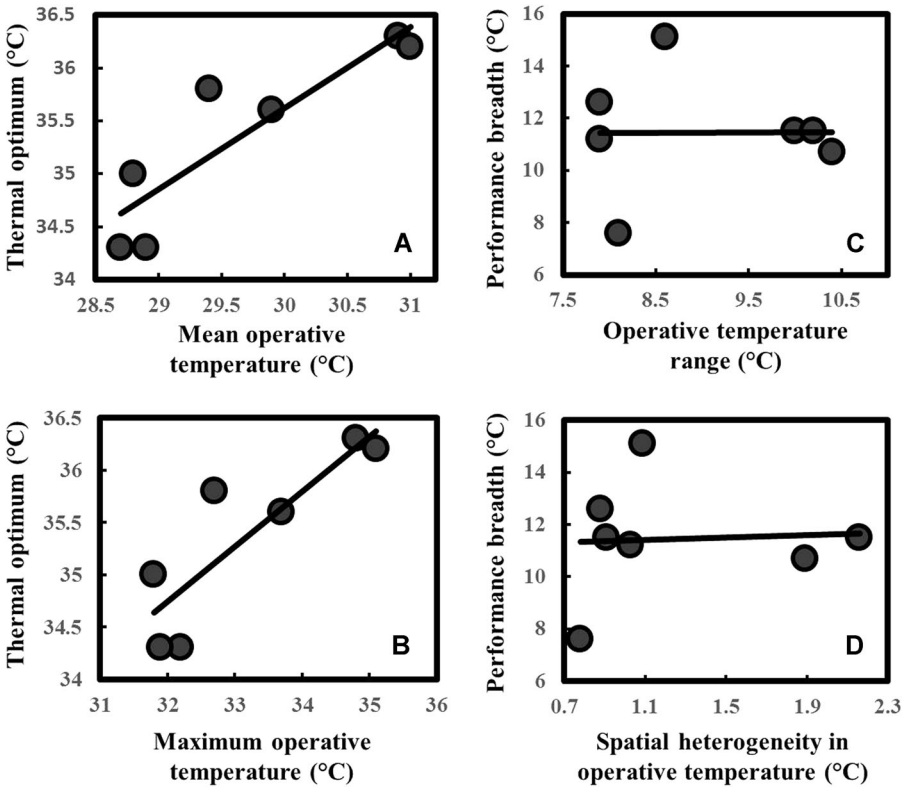

Figure 2. **Local adaptation in thermal performance. The thermal optimum was strongly correlated with both (A) mean operative temperature, and (B) maximum operative temperature. By contrast, performance breadth was not correlated with either (C) the average daily operative temperature range, or (D) the spatial heterogeneity of operative temperature. Each datapoint represents a population. "Spatial heterogeneity of operative temperature" was indexed as the variance in daily OTM means. "Maximum operative temperature" is the mean of the average maximum hourly temperature logged by each OTM.**

temperatures (Partial Mantel Test controlling for geographic isolation; 500 bootstrap replicates, $r = 0.64$, $P = 0.007$) but not with their geographic isolation from one another (Partial Mantel Test controlling for differences in mean operative temperature; 500 bootstrap replicates, $r = 0.14$, $P = 0.52$) (Figs. 1 and 3). Similarly, gene flow from Great Exuma to the smaller cays actually increased with distance until the furthest two cays (Coakely and Duck), but was strongly negatively correlated with the mismatch between island thermal environments (Fig. 1, insets).

Discussion

Offshore cays in the Bahamas differed from one another in their spatial and temporal operative temperature distributions, and changes in operative temperature have been shown elsewhere to generate natural selection on thermal performance in the brown anole (Logan et al. 2014). Although thermal environments differed among islands, lizard populations were not completely isolated from one another—gene flow between islands was high (an average of 11.05 migrants per generation, congruent with previous estimates of gene flow among larger islands in the Bahamas; Calsbeek and Smith 2003). Theory suggests that this magnitude of gene flow between populations may overwhelm local selection and homogenize genetic variation at the species level (Emelianov et al. 2004). Lesser magnitudes of gene flow than those reported here have reduced local adaptation in other systems (Coulleri 2010; Logan et al. 2012; Raeymaekers et al. 2014). Nevertheless, we found that the thermal optimum of each population was correlated with both the mean and maximum operative temperature of each island. Thus, at least one physiological trait in brown anoles appears to be locally adapted despite high levels of migration. This result is consistent with the influence of local genetic adaptation in thermal performance (Sexton et al. 2014) or the capacity for populations to acclimate to local conditions. Gene flow was lowest between islands with dissimilar thermal environments, even when those islands were adjacent to one another (Figs. 1 and 3), implying that immigrants whose thermal optima did not match local conditions had reduced fitness. Thus, spatial variation in climate appears to be an important mediator of gene flow in brown anoles.

Theory (Angilletta 2009) and experimental data (Logan et al. 2014) indicate that performance breadth should be positively

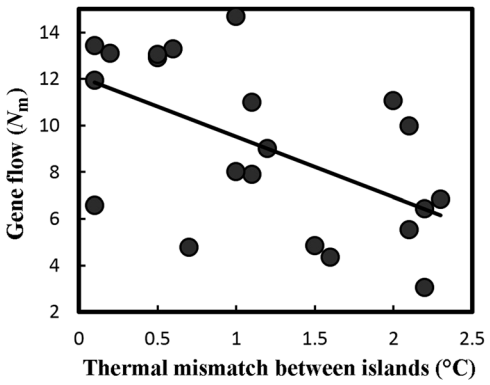

Figure 3. **The magnitude of gene flow between each pair of islands was negatively correlated with the thermal mismatch between those islands. "Thermal mismatch" was computed as the absolute value of the difference between the mean operative temperatures of each island. This scatter plot is intended only as a visual approximation of the general relationship between the variables and should not be viewed as representing a valid statistical test; the actual correlation coefficient between these variables ($r = 0.64$; see "Results") was taken from a Partial Mantel Test where we corrected for the effects of island isolation. The Partial Mantel Test correlation was greater in magnitude and was positive because raw gene flow values were converted to genetic distances.**

correlated with temporal variation in operative temperature and negatively correlated with spatial variation in operative temperature. However, we found no correlation between the 80% performance breadth and any measure of operative temperature variation. This lack of local adaptation in performance breadth is somewhat surprising because a previous field experiment showed that selection can act on this trait in brown anoles (Logan et al. 2014). However, temporal and spatial variation in operative temperature were positively correlated among islands, which may have led to contrasting selection pressures on T_{br}. Additionally, performance breadth may not be heritable, or genetic correlations may prevent populations from simultaneously evolving along multiple axes of variation in thermal performance (Angilletta et al. 2003).

We maintained all lizards from each island in a common laboratory environment for 40 days prior to measuring their thermal sensitivity. This should have reduced or eliminated any acute (short-term) acclimation effects left over from each island (Leal and Gunderson 2012). However, differences in TPCs among populations may arise from forms of irreversible plasticity that fix the phenotypes of individuals over the course of their development. For example, variation in the nest environment (e.g., warmer soil conditions on warmer islands) might generate differences in phenotypes (e.g., higher average T_{opt} on warmer islands) that persist despite exposure to a common garden (Warner 2014). Similarly, cross-generational sources of plasticity such as maternal effects (McGlothlin and Galloway 2014) may lead to divergent phenotypes in differing environments. It is also possible that the thermal optimum is correlated with another, more important trait that varies in the same way among populations but that we did not measure.

In any event, once divergent phenotypes are established on different islands, viability selection against immigrants can mediate gene flow across the archipelago irrespective of whether phenotypic divergence is driven by genetic differences, plasticity, or a combination of both. Indeed, we observed reduced gene flow between islands with alternative thermal regimes, which may reflect the action of selection against immigrants. In a previous field experiment, Logan et al. (2014) showed that brown anoles transplanted to a warmer and more thermally variable environment underwent strong selection favoring those individuals whose thermal physiology matched local conditions. The differences in thermal environments analyzed in that previous experiment were similar to the difference between the warmest and coolest islands in the present study. Thus, results presented here may represent a biogeographic extension of the same process of local selection against maladapted immigrants.

Whether differences in the TPCs of populations are based on fixed genetic differences or adaptive plasticity, the patterns presented here have important implications for the response of species to climate change. If *A. sagrei* can compensate for differences in local thermal environments through acclimation, it suggests that within-generation physiological adaptation may be an important source of resilience for this species (but see Gunderson and Stillman 2015). Alternatively, if differences in TPCs among populations result (at least partially) from genetic differences, then gene flow from warmer to cooler islands may introduce alleles that enhance the fitness of cool-adapted populations as mean temperatures on those islands rise. Similarly, cold snaps (from the projected increase in extreme weather events) may periodically favor cold-adapted alleles when they arrive on warmer islands. As we discuss above, only one of the two thermal performance traits we examined showed evidence of local adaptation, and the implications of this in the context of climate change require further investigation.

Conclusions

Although it is rarely considered in models of extinction risk from climate change, migration-selection balance mediated by climate may be a widespread phenomenon. Indeed, a recent field experiment showed that gene flow and local adaptation in damselfly populations are driven by climatic variation over short distances (Gosden et al. 2015). Moreover, studies dating back several decades have suggested that selection can overwhelm gene flow in diverse taxa and that concern over "gene swamping'" may prove unwarranted (McNeilly and Antonovics 1968; Ehrlich and Raven

1969; Endler 1973; Sexton et al. 2014). In line with these perspectives, our results suggest that spatial variation in climate is an important mediator of gene flow in the brown anole, and that local adaptation (genetic or plastic) may occur in the face of frequent dispersal between islands. The general patterns of gene flow we observed suggest that immigrants are maladapted, either because of genetic differences among populations, plastic responses to divergent environments, or a combination of both. We suggest that future efforts to model the impact of climate change on ectotherms consider the role of migration-selection balance in generating and maintaining phenotypic diversity.

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DATA ARCHIVING

The doi for our data is doi:http://dx.doi.org/10.5061/dryad.68mp3.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Figure S1. Temporal operative temperature distributions among islands.

Figure S2. Frequency distributions of operative temperatures for the main island of Great Exuma and each of the smaller cays.

Table S1. The number of individuals per island whose sprint speeds were successfully measured at each temperature.

Table S2. *P* values from pairwise Tukey's post hoc comparisons of mean (first number), maximum (second number), and diel range (third number) of operative temperature among islands.

Table S3. Gene flow (maximum likelihood estimates of *N*m) between islands.