Island colonisation leads to rapid behavioural and morphological divergence in *Anolis* lizards

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Abstract

1) Islands are hotspots of endemism and often function as engines of adaptive radiation. Nevertheless, we lack a deep understanding of the processes that generate phenotypic divergence when populations first colonise islands.

2) Important questions include: 1) Do populations experience shifts in habitat use and behaviour when they experience reduced competition and predation, and how fast do these changes occur? 2) Do shifts in niche occupancy result in morphological divergence from mainland populations?

3) To investigate these questions, we transplanted 210 slender anole lizards (*Anolis apletophallus*) from mainland Panama to three islands in the Panama Canal that are likely species-poor compared to the mainland. We compared habitat use, flight initiation distance, and morphology among populations across two generations of divergence.

4) We found that island lizards changed their behaviour immediately after colonisation, perching on lower and broader surfaces and allowing observers to approach more closely before fleeing. Although we found only weak evidence for an association between survival and morphological trait variation, trait means in the second generation often shifted in the direction expected if selection had acted on the founders.

5) Our results indicate that colonising individuals can change their behaviour rapidly to exploit new structural niches, and that substantial shifts in morphology can occur after

only a single generation. These changes, which are probably facilitated by ecological release, may represent the first steps in adaptive radiation of island lineages.

Keywords: *Anolis*, Behavioural drive, Bogert effect, Ecological release, Experimental evolution, Island biogeography

Introduction

By area, islands tend to have much higher endemism than nearby mainland environments (Kier et al. 2009) and some of the most famous examples of adaptive radiation come from islands. These include Darwin's finches and tortoises in the Galapagos (Petren et al. 2005; Tebbich et al. 2010; Román-Palacios and Wiens 2018), and honeycreepers, fruit flies, and silversword plants in the Hawaiian archipelago (Witter and Carr 1988; Kambysellis et al. 1995; Lerner et al. 2011). Because islands represent simplified environments where evolution seems to occur in hyperdrive, they have been a major focus of biologists in efforts to understand the processes of local adaptation, speciation, and community assembly (Grant and Grant 2003; Gillespie 2004; Whittaker 2007; Losos and Ricklefs 2009).

Nevertheless, most studies of evolution and adaptation to islands have compared species that initially diverged from a common ancestor hundreds of thousands, or even millions, of years ago (but see; Losos et al. 1997; Ozgul et al. 2009; Kolbe et al. 2012; Hu et al. 2019; Pringle et al. 2019). Because colonisation in these systems occurred so long ago, the original processes that drove divergence in the first few generations after colonisation are almost entirely obscured by the passage of time (Schluter 2000; Logan et al. 2012). A number of questions about the processes that are important during the earliest stages of adaptive radiation on islands remain at least partially unresolved (Herrmann et al. 2021). For example, do colonising individuals initially track their ancestral niche and only diverge from their mainland ancestor after many generations of selection and evolution? If so, do the rates at which niche shifts occur depend on availability of novel and exploitable microhabitats? Do the relatively simple environments of islands result in ecological release such that colonisers expand their niche breadths or shift to a new realised niche once they are freed from predation and competition? To answer these questions, we require direct observations of adaptive dynamics in the first few generations after colonisation (Reznick et al. 2018).

When individuals first colonise an island, it is likely that they are exposed to a relatively novel set of environmental conditions. Relative to mainland environments, islands are often depauperate, having fewer competitors, predators, and parasites with which the colonisers will contend (Cooper et al. 2014; Cox et al. 2020), and they may also have different structural and climatic environments (Giles Leigh Jr et al. 1993; Salazar et al. 2019). The first response of colonising populations to this sudden exposure to a new environment is likely to be behavioural (Gross et al. 2010; Fey et al. 2019), and behavioral responses can occur in one of two ways. First, individuals may track their ancestral niche (Logan et al. 2019). For example, an ectothermic species that colonises an island which is warmer (on average) than the mainland environment from which it came may seek out cooler, shaded microclimates, avoiding stressful body temperatures and "hiding" from selection. The process of behaviour resulting in niche tracking and weak or nonexistent selection in the new environment is called *behavioural inertia*, or the "Bogert effect" (Huey et al. 2003; Muñoz and Bodensteiner 2019). Behavioral inertia would reduce the rate of genetic adaptation to island environments and is therefore likely to slow divergence between the ancestral (mainland) and derived (island) populations. By contrast, it is possible that behavioral responses to island environments result in the use of new microhabitats, exposing populations to selection for increased performance in those new microhabitats. The process of behavior facilitating niche shifts is called *behavioral drive* (Huey et al. 2003; Lapiedra et al. 2013; Muñoz et al. 2014) and is likely to accelerate phenotypic divergence between the mainland ancestor and the island colonisers. Few studies have explored the ways in which behavioral shifts either facilitate or constrain trait divergence during the early stages of island colonisation (but see; Losos et al. 1997, 2006).

Behavioural shifts may drive evolutionary change on islands if individuals begin using different parts of the structural habitat relative to ancestors. The relationships between habitat structure, morphology, and animal biomechanics are well established, particularly for lizards (Losos et al. 2000; Vanhooydonck et al. 2006; Calsbeek and Irschick 2007; Ord and Klomp 2014; Hagey et al. 2017*b*, 2017*a*). In anoles specifically, researchers have shown that individuals with longer hindlimbs are faster on broader surfaces but lack agility on narrow surfaces (Losos & Sinervo, 1989; Vanhooydonck et al., 2006). Thus, lizards with longer limbs tend to be favoured by selection on broad surfaces where they are faster, whereas shorter limbed individuals are favoured in more arboreal habitats where stability on narrow branches is critical. Arboreal species of anoles also tend to have larger toe pads with greater numbers of lamellae, and these generate friction and adhesion on small branches and smoother surfaces such as leaves (Hagey et al. 2017*b*). Larger toe pads might decrease the probability that lizards fall and have to expend the energy to climb back into the canopy or be eaten by terrestrial predators. These associations between habitat use, morphology, and performance suggest that behavioral shifts on islands that lead to the use of new structural habitats may generate strong selection on (or plasticity in) morphological traits.

We investigated behavioral and morphological responses of Panamanian slender anole lizards (*Anolis apletophallus*, henceforth, “slender anoles”) that we experimentally introduced to a set of forested islands in the Panama Canal. Slender anoles are small (<3 g) arboreal lizards found primarily in the forest understory (Andrews 1991). They are ambush predators and consume a wide range of invertebrates, including isopods, insects, and arachnids (Sexton et al. 1972). They are essentially an annual species, reaching sexual maturity at about 4-6 months with greater than 95% annual mortality (Andrews 1979, 1991; Andrews and Nichols 1990). This rapid population turnover renders them an excellent system by which to study the early stages of island colonisation because it is possible to track behavioural and phenotypic change over multiple generations (Cox et al. 2020). To this end, we transplanted 210 Panamanian slender anoles from a single source site on mainland Panama to three islands that have fewer competitor species, and likely have fewer predator and parasite species, compared to the mainland. We tracked changes in habitat use and behaviour in the colonising lizards and then examined shifts in morphology in their adult offspring in the next generation to explore the early processes of differentiation on islands.

Materials and Methods

We studied the initial response of populations to colonisation of islands using an experimental island system in Panama's Lake Gatún. Lake Gatún is a 425 km^2 artificial lake created by the damming of the Chagres River during the construction of the Panama Canal in 1913 (Giles Leigh Jr et al. 1993). We used three small (<7,000 m^2) islands that were formerly hilltops before the valley was flooded. Although these islands were small and depauperate, they nevertheless varied in total area, distance to the nearest point on the mainland, and general physiography (Table S1). We thoroughly surveyed each of these islands prior to transplantation for the presence of resident populations of anoles of any species. Although none of the islands had pre-existing slender anoles (subsequently confirmed with extensive field surveys), one of the islands (Island D) had a different resident species of anole (*Anolis gaigei*; hereafter, "Gaige's anole") that is similar in ecology (perch use) and body size to slender anoles and likely competes with our focal species (Cox et al. 2020; Nicholson et al. 2022). We never found any other anoles species other than the two mentioned above on any of the experimental islands. Due to their small size and isolation all three experimental islands had fewer competitor species compared to the mainland, and almost certainly had lower parasite and predator diversity as well. These islands have come to vary in habitat structure through stochastic colonisation and extinction of local plant species (Giles Leigh Jr et al. 1993). We also transplanted lizards to an additional island which had a native population of Gaige's anole, but this population went functionally extinct by the second generation and was therefore not included in this study.

The founder generation of slender anoles (n=210, even sex ratio) was collected between July and September 2017 from Soberanía National Park on mainland Panama near the town of Gamboa (9°08'00.1" N, 79°43'11.0" W). We caught adult lizards (>38 mm snout-vent-length, or "SVL"; mean SVL = 42.34 ± 0.043 mm) either by hand or with a lizard catch-pole (fishing rod and line with a slipknot) and measured the diameter and height of the perch they were initially observed on using digital calipers and a tape measure, respectively. Lizards were transported to the Smithsonian facility in Gamboa, where they were housed in small plastic terraria for a maximum of 48 hours. We included a balled-up piece of paper towel saturated with water as a source of humidity within each terrarium. Due to the short processing time, we did not feed captive individuals.

Before transplantation, we used digital calipers (precision = 1/100 mm) to measure SVL, humerus and radius/ulna length (added together = forelimb length), femur and tibia/fibia length (added together = hindlimb length), and head depth. For each of these measurements, lizards were gently immobilised in a clear plastic bag prior to using the calipers. We used a digital balance (precision = 0.01 g) to measure mass. To measure toe pad size, we imaged each individual using a flatbed scanner (Canon LiDE 220, 1200 dpi resolution) and traced the outline of the largest hindlimb toe pad and one of the two largest toe pads (on the 3rd or 4th toe) on the forelimb using ImageJ v.1.52a (Schneider et al. 2012). On the forelimb, we only used the 4th toe when the 3rd toe was not visible on the scan for a particular individual, and we were able to do this because the third and fourth toes on the forelimbs of slender anoles are extremely similar in size. Regardless, 94% of our estimates were on the 3rd toe and results did not differ substantially irrespective of whether 4th toes were included. We gave lizards regular 90-minute breaks from handling and processing to reduce stress (Langkilde 2006). We then implanted visual elastomers (VIE codes; Northwest Marine Technology Inc.) to give each lizard a unique identifier (Nicholson et al. 2015) and released a total of 35 male and 35 female lizards to each experimental island in batches. Each batch was composed of 20 – 40 lizards that were assigned randomly to an island and released between July and August 2017.

We conducted mark-recapture surveys on the founder (F_0) populations between October and December 2017 and on their adult offspring (F_1 generation) between June and November 2018, searching each island twice per week during the study period. Due to the short generation time of slender anoles, there was little overlap between the F_0 and F_1 generations, with 8.5% of F_0 individuals surviving to the next year. In 2017, when F_0 lizards were recaptured on islands, we recorded their perch height and diameter, then immediately released them at the spot of capture. In 2018, when adult F_1 individuals were first caught on the islands, we recorded their perch height and diameter and then transported them back to the Smithsonian facility in Gamboa and measured the same morphological traits as for the founders. The same researcher (DJN) took all morphological measurements (aside from toe pad scans) from both survey years to reduce observer bias. While different researchers estimated toe pad size from scans, the researcher that analyzed each image was noted so that ‘observer’ could be accounted for in models of toe pad size (see below). F_1 lizards were returned to their point of capture on the islands no more than 48 hours after collection. If F_1 lizards were recaptured during subsequent surveys, we recorded their perch heights and perch diameters but released them immediately at the spot of capture. We also surveyed our mainland site (the source site for the F_0 generation) again in 2018 to see if habitat use or morphology had changed in the source population after one generation.

Our initial sample sizes (70 lizards per island) and subsequent recapture rates were insufficient to accurately estimate selection gradients following traditional regression-based protocols which require very large sample sizes (Lande and Arnold 1983). Instead, we used Huggins robust design model, implemented in the *RMark* package (Laake 2013), to quantify the relationship between survival and trait variation in our study populations. This approach allowed us to bin individuals into low (bottom third) and high (top third) trait values and then to determine whether these categories of individuals differed in their survival probabilities. While this approach does not provide standardized selection gradients that can be included in population genetic or evolutionary models, it nevertheless provides information about if and how selection may have operated. For selection analyses, we focused on the three traits (hind limb length, hindlimb toe pad size, and head depth) that changed in consistent directions across islands.

In 2018, we quantified habitat structure at all sites (mainland and island) using randomised quadrat sampling of vegetation composition and the diameters of potential lizard perches (including tree trunks; detailed methods in Online Supplementary Information; Figure S1). We considered a given perch to be “available” if the surface could support the weight of an adult slender anole and was found within the typical range of perch heights that this species is documented to occupy. Therefore, available perches included all branches, twigs, trunks, large palm or succulent leaves, and vines that were greater than 2 mm in diameter and below 3 m in height (which is towards the upper perch height limit of this species).

In 2019, we quantified flight initiation distance (FID) at several sites (mainland site plus three islands), including a new island (Island H1) to which we had just transplanted lizards that year. To measure FID on the mainland, we followed a trail (Pipeline Road) that bisects the national park (at least one researcher on each side of the trail). Once a lizard was spotted, the same observer (EF) approached it (from whatever distance she was at when the lizard was first seen) at a consistent pace until the lizard displayed an evasive behaviour of some kind (diving into leaf litter, moving around to the other side of the tree, etc.). The observer also wore similarly colored clothing each day to avoid variable effects on lizard fleeing behavior in response to different colored "predators." Once the lizard fled, we then recorded the distance between the observer and the location of the lizard before it fled. We followed a similar procedure on the islands, except that instead of a linear transect, two or more researchers occupied distinct "lanes" (separated from the nearest observer by a minimum of 3 meters on the left and right) and walked around the island one time in a circle. This careful sampling strategy whereby the same area of habitat was never searched twice, in combination with the small territory size of slender anoles, ensured that we did not accidentally sample the same individual more than once on a given sampling day. On the islands, if possible, any lizard we observed was subsequently captured and either identified or given a unique VIE code if the individual was new to our data set.

Note that we do not have FID data from all islands included in our initial transplant because Panama experienced a record drought during the 2019 dry season (January – May), and this resulted in large population die-offs on several of our experimental islands. Thus, our sample sizes for the F_2 generation on several islands are too small to be confident in phenotypic parameter estimates, and we therefore focus on islands that were seeded in 2017 for understanding changes in habitat use and morphology that occurred in the first two generations after colonisation, while we include FID data from 2019 to gain additional understanding of behavioural differences between island and mainland lizards. Our sample sizes of FID estimates among sites ranged from 13 – 39 (including resampling of a small percentage of individuals at some sites on separate days).

We compared differences in available perch diameters among the mainland and three islands in our initial transplant using a linear mixed effects model with $\log_{10}$-transformed 'available perch diameter' as the dependent variable, 'site' (island identity or mainland) as a fixed factor, and 'quadrat' as a random factor. To calculate differences in the density of different vegetation types (large trees, small branches, palms, and spiny understory plants) among sites we used ANOVA with the density of each vegetation type $\log_{10}$-transformed. We also assessed variation in total vegetation density by pooling each plant category. We analysed lizard habitat use by fitting linear mixed-effect models with 'lizard ID' as a random effect to account for repeated measures. We ran separate models for used perch diameter and perch height, both of which were $\log_{10}$-transformed to meet the model assumption for normality and homoscedasticity of residuals. In these models, the habitat use variable (used perch diameter or perch height) was the dependent variable with 'site' as the independent variable. 'Sex' and the 'sex by site' interaction were also included as factors in the model for perch height because male and female slender anoles (as with other species in this genus) are known to differ in perch height (Logan et al. 2021). For this same reason, 'sex' was included as a covariate in models for shifts in mean values of morphological traits across generations (see below). We did not include 'sex' or 'sex by site' interactions in other statistical models (e.g., those for flight initiation distance) because of a lack of a priori evidence that these variables differ between the sexes in slender anoles and the fact that these terms were insignificant and did not substantially affect estimates of the main parameters in earlier iterations of our statistical models.

To assess the difference between available and used perch diameters among the mainland and our initial transplant sites, we performed a two-factor ANOVA with 'site' and ‘used versus available’ (binary variable) as the independent variables and ‘perch diameter’ as the dependent variable (the latter of which we $\log_{10}$-transformed to meet the assumptions of the model).

To visualize phenotypic divergence between the mainland and island populations, we used a principal component analysis (PCA) with all morphological traits included. To statistically compare the multivariate position of populations in morphological space, we conducted a PERMANOVA, using all morphological traits as the dependent variables and ‘site’, ‘generation’, and ‘sex’ as independent variables. For the F_0 generation, we compared the morphology of all lizards moved to islands from the mainland to a control group on the mainland that was not transplanted. For the F_1 generation, we compared the island populations to individuals caught on the mainland in the same year. To test for changes in individual trait means between generations, we used separate linear models for each trait and site. Each of these models included the relevant trait as the dependent variable and ‘generation’ as a categorical independent variable. ‘SVL’ (to account for body size) and ‘sex’ were included as covariates in all models that included morphological traits. For all morphological analyses, only adults (SVL > 38 mm) were included. To compare the magnitude of total phenotypic change among sites, we calculated the average percent trait change, summed across all traits, between the F_0 and F_1 generations.

We compared differences in flight initiation distance among sites using a linear mixed-effects model with ‘flight initiation distance’ as the dependent variable, ‘site’ as a fixed factor, and ‘lizard ID’ as a random factor to account for repeated measures. All analyses were conducted in R version 3.5.3 (R Core Team 2019) and mixed-effects models were implemented in the *lme4* package (Bates et al. 2015). Diagnostic plots were checked for appropriate residual distributions for all fitted models.

Results

Differences in habitat structure and use among sites

On average, available perch diameters were larger on most islands compared to the mainland (mean perch diameters; Mainland = 31.65 mm ± 1.92 S.E.M., Island C = 67.02 mm ± 7.58 S.E.M., Island P = 46.47 mm ± 9.88 S.E.M.; significance confirmed by the coefficient estimates and standard errors in a mixed-effects model), although available perch diameters on Island D (mean perch diameter = 47.08 mm ± 8.02 S.E.M.) were not statistically distinguishable from the mainland, and only Island P differed from the other islands (Table S2). Additionally, vegetation density (when summed across vegetation types) was higher on all islands relative to the mainland ($F_{3,125} = 6.45$, $P < 0.001$). Island C and Island P had greater branch density (C: $F_{3,125} = 4.83$, $P = 0.003$; P: $F_{3,125} = 4.83$, $P = 0.002$) and lower palm density (C: $F_{3,125} = 10.39$, $P = 0.029$; P: $F_{3,125} = 10.39$, $P < 0.001$) than the mainland. Island D ($F_{3,125} = 10.39$, $P = 0.023$) had greater palm density than the mainland. Island P also had a high density ($F_{3,125}$= 22.47, P = <0.001) of the spiny aloe-like plant *Aechmea magdilinii*, whereas no other site had this vegetation type. Woody tree density did not differ among sites ($F_{3,125}$-

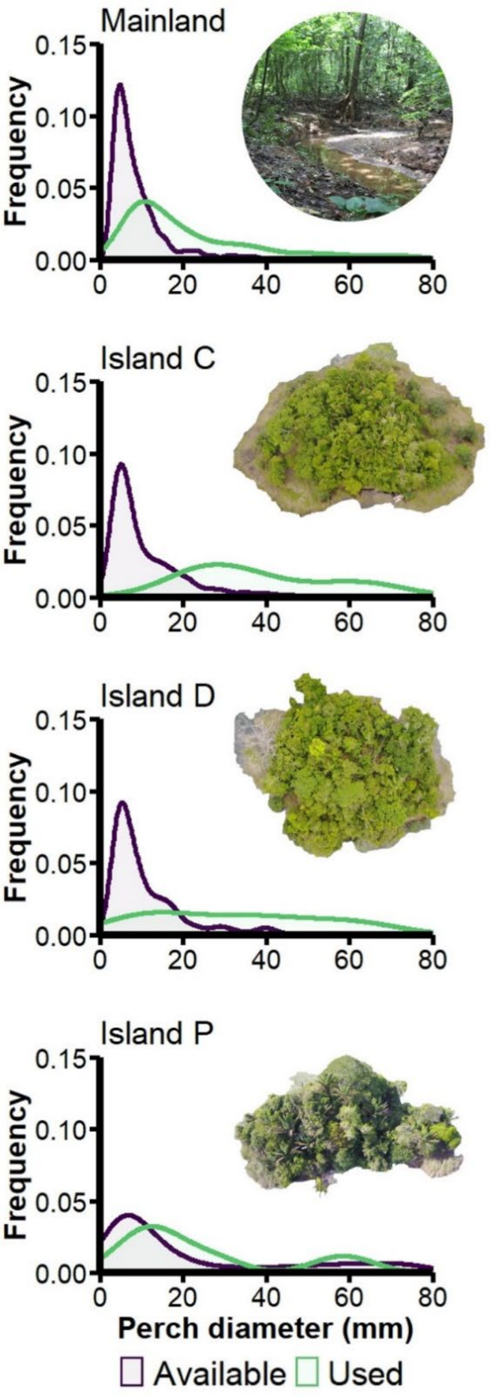

Figure 1. Available versus used perch diameters at each site. Available perch diameters were measured using randomized quadrat sampling. Used perch diameters were recorded at the site of each lizard capture. Curves were created with Gaussian kernel smoothing.

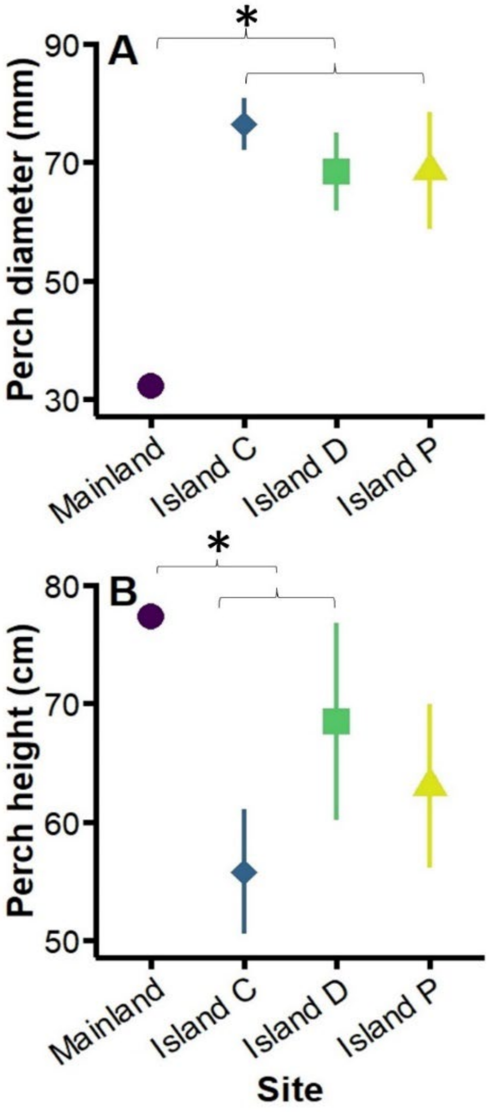

Figure 2. A) Mean used perch diameter and B) mean perch height on the islands (coloured symbols) and the mainland (black circle) in 2017. Island data is from first generation (F_0) individuals in the same year they were transplanted to islands. Mainland data are from lizards that were not transplanted. Significant differences between sites are indicated with brackets and asterisks. Symbols represent mean ± S.E.M (mainland error bars are not visible because of large sample sizes relative to the islands).

= 0.55, $P = 0.645$). Mean differences in the density of vegetation types among sites are presented in Figure S2.

After transplantation, island founders shifted rapidly to using wider perches than their mainland counterparts (confirmed by the coefficient estimates and standard errors for a mixed-effects model; Figures 1 and 2a; Table S2), although the perch diameters used by lizards did not differ among islands. Most island lizards perched lower in the vegetation than mainland lizards (Figure 2b), but the confidence intervals on the coefficients for Island P overlapped zero (Table S2). Confidence limits and effect sizes for this model revealed that there were no differences in lizard perch height among islands, although males perched higher than females at all sites. Additionally, lizards used broader perches than the mean diameters available at all sites, although the differences between available and used perch diameters was more pronounced on two out of three islands relative to the mainland (Table S3, Figure 1).

Natural selection on morphological traits

There was a statistically insignificant trend that lizards with longer hind limbs, smaller toe pad sizes, and smaller head depths were more likely to survive on the islands (Figure S3 and Table S6). However, this pattern did not hold for hind limb length on Island P, and the 95% confidence intervals between estimates for all traits overlapped.

Flight initiation distance

Island lizards had shorter flight initiation distances compared to mainland lizards, irrespective of how many generations each population had been established on an island (Figure S4), but the confidence intervals on the estimated coefficients for Island C overlapped zero (Table S2). On average, relative to mainland lizards, island lizards initiated a flight response when the observer was 30% closer.

Shifts in morphological traits

A principal components analysis including SVL, mass, hindlimb length, forelimb length, head depth, hindlimb toepad size and forelimb toepad size showed few differences in morphology between the founders that were transplanted to islands and a separate comparison group on the mainland who were not transplanted (Figure 3a). Thus, all island populations started in approximately the same location in morphospace. By

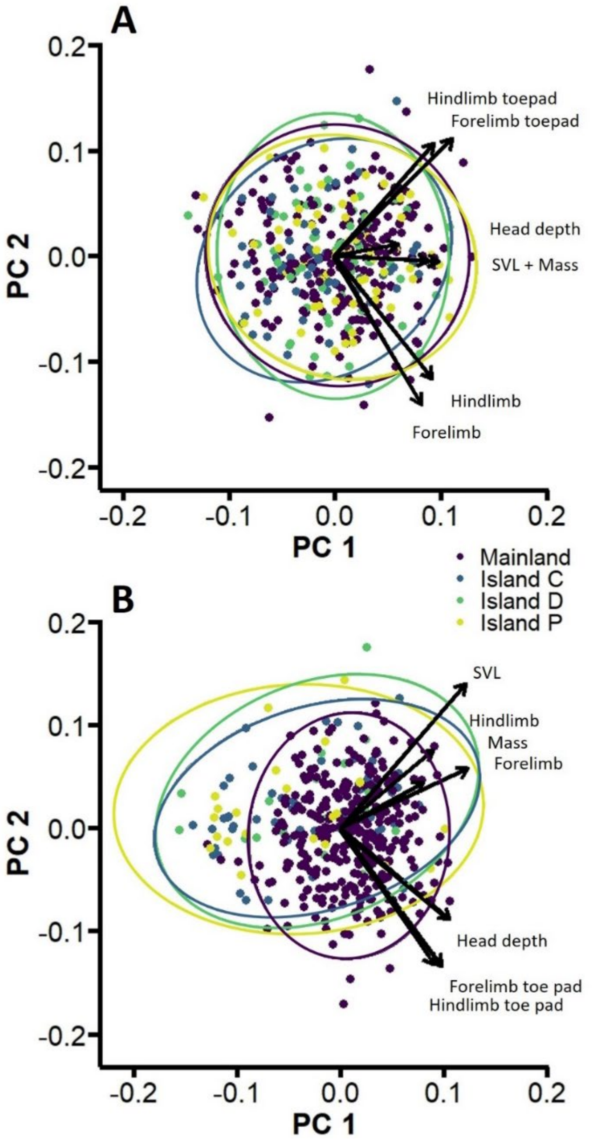

Figure 3. Changes in multivariate trait space for mainland and island populations after one generation. A) The F_0 (founder) populations overlap broadly in trait space across all sites (data from 2017). B) F_1 island lizards diverged from the mainland population after only a single generation (one year; data from 2018). Ellipses represent 95% confidence limits.

the F_1 generation, however, island populations had already diverged from the mainland population in morphospace (Figure 3b). A detailed description of PCA component loadings and the PERMANOVA output are presented in Table S4.

When examining shifts in individual trait means between the founding generation and the F_1 generation, hindlimb length significantly increased in the F_1 generation at all sites except Island C. This shift was more pronounced on two of three islands relative to the mainland (Figure 4a). There was also a stronger effect size on all islands compared to the mainland (Table S5). By contrast, there were no significant changes in forelimb length at any site (Figure 4b). Mean hindlimb toe pad size was smaller on all islands after one generation, but this change was

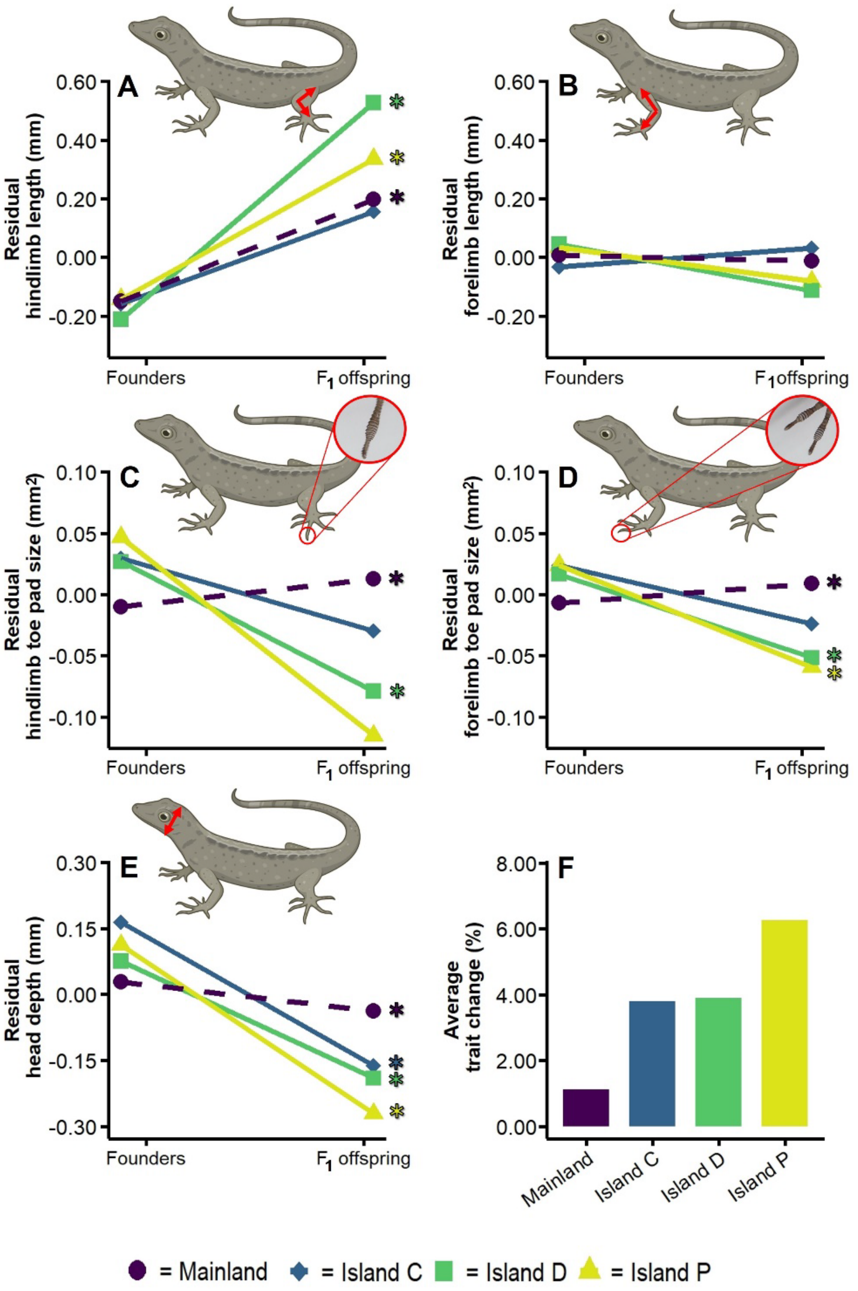

Figure 4. Changes in mean trait values that occurred over one generation (one year) on experimental islands (coloured lines) and the mainland (purple, dashed lines) for A) hindlimb length, B) forelimb length, C) hindlimb toe pad size, D) forelimb toe pad size, and E) head depth (significant changes are indicated with asterisks). F) The percentage trait change (averaged across all traits) was four to six-fold higher on the islands compared to the mainland. The data displayed here are residuals from a regression of each trait on SVL which accounts for the effects of body size. Figure illustrated using BioRender© (biorender.com).

only significant on Island D. There were, however, much larger effect sizes on the islands compared to the mainland (Table S5), and the directionality of change was opposite to that of the mainland (Figure 4c). Forelimb toe pad size also significantly decreased on Island D while significantly increasing on the mainland (Figure 4d), and again there were larger effect sizes on the islands compared to the mainland (Table S5). At all sites, there was a significant reduction in head depth in the F_1 generation, but this reduction was an order of magnitude greater on the islands than on the mainland (Figure 4e; Table S5). There was a significant decrease in SVL after one generation on island P, whereas SVL increased on the mainland (no change at the other sites). Finally, we found that the percentage change in trait means after one generation (averaged across all traits) was three to six-fold higher on the islands relative to the mainland (Figure 4f). We summarize the extent to which parameter estimates of survival, and the magnitude and direction of trait shifts matched predictions based on lizard habitat use ecological variation among sites in Table S7.

Discussion

Lizards that were experimentally introduced to several islands shifted their habitat use and behaviour almost immediately after “colonisation”. While we found only weak evidence that after this behavioural shift, lizards with longer hindlimbs, smaller toe pads, and smaller heads were more likely to survive, these same traits shifted in the next generation (on most islands) in directions that were consistent with optimization of biomechanical performance. The mainland (source) population also displayed changes in some traits during this period, yet these changes were typically of smaller magnitude and often in the opposite direction than those exhibited by island populations. We provide experimental support that behavioural drive can operate over a single generation to cause divergence between mainland and island populations. Nevertheless, it is important to note that we studied only three island populations, and changes in trait means were not always consistent across sites (with insufficient samples sizes to confirm that selection drove the changes we did see). As such, we urge caution in interpreting our results as conclusive evidence for adaptation to island environments.

We found, almost immediately after colonisation, that island lizards started using perches with a mean diameter roughly double that of the mainland, they began perching lower in the vegetation, and they let an observer approach more closely before fleeing (but again, only some of these patterns were statistically significant). Additionally, lizards changed their perch usage beyond what we would expect from differences in perch availability on two of three islands (mean used perch diameter was greater than mean available perch diameter on these islands) and in a consistent direction across islands, suggesting that this change represents a behavioural shift towards using preferred perches rather than lizards simply conforming to variation among island habitats. These results suggest the possibility that once introduced to islands, lizards experienced ecological release (as defined by Herrmann et al. (2021) to include niche shifts in addition to niche expansion) and began occupying their preferred microhabitat after experiencing reduced levels of interspecific competition and predation compared to what might be typical of their ancestral environment (Losos and Queiroz 1997; Des Roches et al. 2011, 2015; Herrmann et al. 2021). While slender anoles perch higher in the vegetation on the mainland, they primarily feed on leaf litter arthropods (Sexton et al. 1972). Individuals of this species are frequently observed in "foraging posture", whereby they perch head down towards the ground as they scan for prey movement (Sexton et al. 1972; Jenssen and Hover 1974; Hover and Jenssen 1976). When they spot a potential prey item, they drop onto the ground and consume it. It is possible that lizards are more efficient at catching and consuming prey if they perch closer to the ground. However, on the mainland, there are several other species of lizards (including other anoles) that are either strictly terrestrial or tend to perch near the ground in understory vegetation (e.g., *Anolis capito*, *Anolis elcopeensis*, *Ameiva festiva*, *Ameiva leptophrys,* and *Lepidoblepharis sanctaemartae*) and these may compete with slender anoles, driving them further up in the vegetation. A similar dynamic has been observed in populations of green anoles (*Anolis carolinensis*) in the southeastern United States that perch higher in areas of overlap with the invasive and more terrestrial brown anole (Stuart et al. 2014). Interestingly, Gaige's anole, the potential competitor species that occurred on Island D prior to the start of our transplant experiment, did not substantially alter the behavioural changes we observed in slender anoles after island colonisation. Indeed, slender anoles on Island D perched on lower, broader surfaces (relative to perch availability) and had lower FIDs than mainland lizards—the same patterns we observed on the other islands. Gaige's anole is not a terrestrial species and prefers higher perches than slender anoles (Nicholson et al. 2022), and thus, slender anoles may have been able to move lower in the vegetation on Island D without incurring a competition cost.

Predator diversity likely differed between the mainland and islands, as well. There are a slew of terrestrial snake and mammal predators on the mainland that (to our knowledge) do not occur on the islands, such as the Colubrid snakes *Chironius carinatus*, *Dendrophidion nuchale*, and *Mastigodryas alternatus*, and the ground-dwelling mammal *Nasua narica*. Our mainland field site even has ground-dwelling bird predators that do not occur on the islands, including the ground cuckoo (*Neomorphis geoffroyi*) and the tinamou (*Tinamus major*). This broad suite of terrestrial predators might make lower perches particularly hazardous for slender anoles on the mainland. Indeed, in field experiments conducted in The Bahamas, the experimental introduction of a terrestrial predator caused brown anoles to perch higher in the vegetation (Losos et al., 2004; 2006). In the absence of terrestrial predators on the experimental islands, slender anoles may prefer to perch lower in the vegetation to maximize prey capture efficiency.

While we acknowledge that lower predator diversity does not necessarily translate to lower predation pressure, island lizards had shorter flight initiation distances compared to mainland lizards and we interpret this as a line of evidence that predation pressure was lower on our study islands. Cooper, Pyron, and Garland (2014) compared flight initiation distance across a broad suite of mainland and island-dwelling lizard species in a phylogenetic context. They found that island lizards had consistently lower FIDs (even after accounting for phylogenetic relationships), and they similarly interpreted this as a response to lower predation pressure on islands. Interestingly, we observed this shift towards decreased FID even in the founders of Island H1, which we transplanted from the mainland in 2019 and measured on the island in the same year, suggesting that this trait is highly plastic and might respond quickly to changes in predation regimes. We cannot, however, rule out the possibility that decreased competition on islands also played a role in decreasing FIDs, that the lizards which were least likely to flee had higher detection probabilities on islands compared to the mainland, or that line-of-site was shorter on islands as a result of higher vegetation densities.

We found only weak evidence that changes in behaviour in island populations resulted in natural selection on morphological traits. For example, while individuals with longer hind limbs had higher mean survival probabilities on two of three islands, and individuals with smaller toe pads and head depths had higher mean survival probabilities on all islands, these differences were not statistically significant. Nonetheless, the mean values of several morphological traits in the second-generation offspring changed in the same direction as mean survival probabilities in the founders. Namely, F_1 offspring had longer hindlimbs, smaller toe pads, and smaller heads on most islands (but again, not all changes in trait means were statistically significant and, in a few cases, similar changes occurred on the mainland). Morphological phenotypes have been linked to habitat use in many taxa, including sticklebacks (Schluter 1993), birds (Zeffer et al. 2003), and chameleons (Bickel and Losos 2002). In anoles, this association is particularly well established. It has been shown that both limb and toe pad morphology directly affect performance on different substrate types and these traits are correlated with perch use across species and populations (Calsbeek & Irschick, 2007; Crandell, Herrel, Sasa, Losos, & Autumn, 2014; Hagey et al., 2017; Losos, 2009; Losos et al., 2000). Thus, selection and adaptive plasticity should lead to smaller toe pads and longer limbs when individuals use lower and broader perches, respectively. We observed these changes on most of our study islands, and they were consistent for both males and females even though male slender anoles perch higher than females, on average. While it is a possibility that the phenotypic changes we observed were driven entirely by plasticity, previous experimental studies (Kolbe & Losos, 2005; Losos et al., 2000) that raised anoles on extremely narrow or broad perches found substantially smaller amounts of limb plasticity than the changes we observed here. At least in the case of limb length, these previous experiments indicate that genetic change may have played a large role in our system.

Our findings are congruent with the "behavioural drive" hypothesis, which suggests that behaviour underpins adaptive change in non-behavioural traits (Huey et al. 2003; Marais and Chown 2008). The morphological shifts we observed were unlikely to have been driven by genetic drift as the direction of trait change was broadly consistent across islands, often in the opposite direction of trait change on the mainland, was loosely associated with survival, and followed biomechanical predictions (Vanhooydonck et al. 2006; Losos 2009; Hagey et al. 2017*a*). Moreover, our PCA and PERMANOVA analyses revealed that in a single generation, island populations diverged in multivariate morphological space from the mainland, and again these changes were consistent across islands. Finally, compared to mainland lizards, island lizards experienced a much greater rate of phenotypic change over the same period. Taken together, these results suggest the possibility that many of the phenotypic changes we observed in island populations were the result of adaptation over the first two generations after colonisation.

We also found that head depth decreased across all islands to a much greater extent than on the mainland. Head sizes of lizards on one island (Island P) decreased by 10% in one generation, which is much faster than similar changes that have been reported in other systems. For example, a species of gecko (*Gymnodactylus amarali)* experienced a change in head size associated with shifts in prey availability after 15 years (approximately 15 generations) on islands in the Serra da Mesa Reservoir in Brazil (Eloy de Amorim et al. 2017). Changes in prey availability might have favoured a change in head size on our experimental islands as well, as anoles are gape-limited predators (Schoener and Spiller 1992), and small islands could have invertebrates with smaller body size distributions compared to the mainland. Furthermore, larger heads can be costly (as they are heavy), requiring greater energetic investment (Wittorski et al. 2016; De Meyer et al. 2019). Head size is often related to bite force in lizards (Huyghe et al. 2008; Broeckhoven and Mouton 2014; Herrel et al. 2014; Sagonas et al. 2014; Wittorski et al. 2016). As such, head size can be related to intra- and interspecific competition, as well as predation pressure. The diversity of competitor species was lower on the islands, and this may have resulted in reduced encounter rates between individuals and less need for strong jaw musculature that is critical for winning competitive bouts (Lailvaux and Irschick 2007; Wegener et al. 2019). Further research is needed to evaluate the role of intraspecific competition and prey size distributions to ultimately determine the forces resulting in rapidly shrinking lizard heads on our experimental islands.

We have shown that behavioural and morphological divergence can occur rapidly in wild lizard populations that “colonised” several islands. We observed similar behavioural and morphological changes across islands, suggesting that a feature (or features) of island environments caused these shifts. We argue that a lack of predator and competitor diversity resulted in ecological release, whereby lizard populations shifted to use a different structural niche, and this led to rapid morphological divergence between the islands and mainland (Des Roches et al. 2015; Herrmann et al. 2021). The well-established relationships between habitat, morphology, and biomechanics of anoles indicate that some of these morphological changes may have been adaptive. Finally, our results suggest that behavioural drive may be an important process operating in populations that colonise islands and may represent one of the first steps of adaptive radiation.

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