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

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Abstract

31

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 are freed from 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

radiations remain at least partially unresolved (Herrmann et al. 2020). 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

81   which niche shifts occur depend on availability of novel and exploitable microhabitats? Do

82   the relatively simple environments of islands result in ecological release such that colonisers

83   expand their niche breadths or shift to a new realised niche once they are freed from

84   predation and competition? To answer these questions, we require direct observations of

85   adaptive dynamics in the first few generations after colonisation (Reznick et al. 2018).

86   When individuals first colonise an island, it is likely that they are exposed to a

87   relatively novel set of environmental conditions. Relative to mainland environments, islands

88   are often depauperate, having fewer competitors, predators, and parasites with which the

89   colonisers will contend (Cooper et al. 2014; Cox et al. 2020), and they may also have

90   different structural and climatic environments (Giles Leigh Jr et al. 1993; Salazar et al. 2019).

91   The first response of colonising populations to this sudden exposure to a new environment is

92   likely to be behavioural (Gross et al. 2010; Fey et al. 2019), and behavioral responses can

93   occur in one of two ways. First, individuals may track their ancestral niche (Logan et al.

94   2019). For example, an ectothermic species that colonises an island which is warmer (on

95   average) than the mainland environment from which it came may seek out cooler, shaded

96   microclimates, avoiding stressful body temperatures and "hiding" from selection. The process

97   of behaviour resulting in niche tracking and weak or nonexistent selection in the new

98   environment is called *behavioural inertia* (Huey et al. 2003; Muñoz and Bodensteiner 2019).

99   Behavioral inertia would reduce the rate of genetic adaptation to island environments and is

100   therefore likely to slow divergence between the ancestral (mainland) and derived (island)

101   populations. By contrast, it is possible that behavioral responses to island environments result

102   in the use of new microhabitats, exposing populations to selection for increased performance

103   in those new microhabitats. The process of behavior facilitating niche shifts is called

104   *behavioral drive* (Huey et al. 2003; Lapiedra et al. 2013; Muñoz et al. 2014) and is likely to

105   accelerate phenotypic divergence between the mainland ancestor and the island colonisers.

106 Few studies have explored the ways in which behavioral shifts either facilitate or constrain

107 trait divergence during the early stages of island colonisation (but see; Losos et al. 1997,

108 2006).

109   A classic example of adaptive radiation on islands is the genus *Anolis* in the

110 Caribbean. Lizards in this genus have independently colonised the islands of the Greater

111 Antilles (Cuba, Hispaniola, Jamaica, and Puerto Rico). On each of these islands, the same set

112 of "ecomorphs" has evolved to occupy distinct structural niches that are common to all of the

113 islands (reviewed in Losos, 2009). For example, on each of the greater Antillean islands,

114 there are semi-arboreal "trunk-ground" anoles that live in the lower reaches of tree trunks,

115 about a meter or so above the ground (Losos, 2009). Compared to the other ecomorphs,

116 trunk-ground anoles have long legs and small toe pads which optimize performance in their

117 preferred microhabitat. Similarly, each island has one or more "crown-giant" anoles, which

118 live high in the canopy (Losos, 2009). Crown giants have large toe pads which aid their

119 highly arboreal lifestyle, allowing them to cling effectively to branches and leaves. Despite

120 the existence of this remarkable adaptive radiation of Caribbean anoles, we still know

121 relatively little about the importance of early processes favoring their divergence from

122 mainland ancestors. Nevertheless, recent studies on anoles both accidentally and intentionally

123 introduced to novel environments have shown that behavioral responses are important

124 mediators of selection (Losos et al. 2004, 2006; Stuart et al. 2014; Lapiedra et al. 2018).

125 Stuart *et al.* (2014) observed evolutionary shifts in toe pad morphology in native green anoles

126 (*Anolis carolinensis)* that had altered their perching behaviour to escape competition with

127 invasive brown anoles (*Anolis sagrei*). Additionally, behaviour itself may be under selection

128 on islands. Lapiedra *et al.* (2018) transplanted brown anoles to small islands that were either

129 predator-free or had curly-tailed lizards, a ground-dwelling predator of brown anoles. These

130 researchers observed strong selection favouring bold lizards (individuals that were more

131 exploratory), but only on islands without the predator. Thus, previous work bolsters the idea

132 that behaviour can function as a gateway to evolutionary change in novel or rapidly changing

133 environments.

134   The relationships between habitat structure, morphology, and animal biomechanics

135 are well established, particularly for lizards (Losos et al. 2000; Vanhooydonck et al. 2006;

136 Calsbeek and Irschick 2007; Ord and Klomp 2014; Hagey et al. 2017*b*, 2017*a*). In anoles

137 specifically, researchers have shown that individuals with longer hindlimbs are faster on

138 broader surfaces but lack agility on narrow surfaces (Losos & Sinervo, 1989; Vanhooydonck

139 et al., 2006). Thus, lizards with longer limbs tend to be favoured by selection on broad

140 surfaces where they are faster, whereas shorter limbed individuals are favoured in more

141 arboreal habitats where stability on narrow branches is critical. Arboreal species of anoles

142 also tend to have larger toe pads with greater numbers of lamellae, and these generate friction

143 and adhesion on small branches and smoother surfaces such as leaves (Hagey et al. 2017*b*).

144 Larger toe pads might decrease the probability that lizards fall and have to expend the energy

145 to climb back into the canopy or be eaten by terrestrial predators. These associations between

146 habitat use, morphology, and performance suggest that behavioral shifts on islands that lead

147 to the use of new structural habitats may generate strong selection on (or plasticity in)

148 morphological traits.

149   We investigated behavioral and morphological responses of Panamanian slender

150 anole lizards (*Anolis apletophallus*, henceforth, "slender anoles") that we experimentally

151 introduced to a set of islands in the Panama Canal. Slender anoles are small (<3 g) arboreal

152 lizards found primarily in the forest understory (Andrews 1991). They are ambush predators

153 and consume a wide range of invertebrates, including isopods, insects, and arachnids (Sexton

154 et al. 1972). They are essentially an annual species, reaching sexual maturity at about 4-6

155 months with greater than 95% annual mortality (Andrews 1979, 1991). This rapid population

156 turnover renders them an excellent system by which to study the early stages of island

157 colonisation because it is possible to track behavioural and phenotypic change over multiple

158 generations (Cox et al. 2020). To this end, we transplanted 210 Panamanian slender anoles

159 from a single source site on mainland Panama to three islands that have fewer competitors,

160 and likely have fewer predators and parasites, compared to the mainland. We tracked changes

161 in habitat use and behaviour in the colonising lizards and then examined shifts in morphology

162 in their adult offspring in the next generation to explore the early processes of differentiation

163 on islands.

164

165 **Materials and Methods**

166 We studied the initial response of populations to colonisation of islands using an

167 experimental island system in Panama's Lake Gatún. Lake Gatún is a 425 km^2 artificial lake

168 created by the damming of the Chagres River during the construction of the Panama Canal in

169 1913 (Giles Leigh Jr et al. 1993). We used three small (<7,000 m^2) islands that were formerly

170 hilltops before the valley was flooded. We thoroughly surveyed each of these islands prior to

171 transplantation for the presence of resident populations of anoles of any species. Although

172 none of the islands had pre-existing slender anoles, one of the islands (Island D) had a

173 different resident species of anole (*Anolis gaigei*; hereafter, "Gaige's anole") that is similar

174 enough in ecology (perch use) and body size to slender anoles that it likely competes with our

175 focal species (Cox et al. 2020). Nevertheless, all three experimental islands had fewer

176 competitor species compared to the mainland, and due to their small size and isolation almost

177 certainly had lower parasite and predator diversity as well. These islands have come to vary

178 in habitat structure through stochastic colonisation and extinction of local plant species (Giles

179 Leigh Jr et al. 1993). We also transplanted lizards to an additional island which had a native

180 population of Gaige's anole, but this population went functionally extinct by the second

181 generation and was therefore not included in this study.

182   The founder generation of slender anoles (n=210, even sex ratio) was collected

183 between July and September 2017 from Soberanía National Park on mainland Panama near

184 the town of Gamboa (9°08'00.1" N, 79°43'11.0" W). We caught adult lizards (>38 mm

185 snout-vent-length, or "SVL"; mean SVL = 42.34 ± 0.043 mm) either by hand or with a lizard

186 catch-pole (fishing rod and line with a slipknot) and measured the diameter and height of the

187 perch they were initially observed on using digital calipers and a tape measure, respectively.

188 Lizards were transported to the Smithsonian facility in Gamboa, where they were housed in

189 small plastic terraria for a maximum of 48 hours. We included a balled-up piece of paper

190 towel saturated with water as a source of humidity within each terrarium. Due to the short

191 processing time, we did not feed captive individuals.

192   Before transplantation, we used digital calipers (precision = 1/100 mm) to measure

193 SVL, humerus and radius/ulna length (added together = forelimb length), femur and

194 tibia/fibia length (added together = hindlimb length), and head depth. For each of these

195 measurements, lizards were gently immobilised in a clear plastic bag prior to using the

196 calipers. We used a digital balance (precision = 0.01 g) to measure mass. To measure toe pad

197 size, we imaged each individual using a flatbed scanner (Canon LiDE 220, 1200 dpi

198 resolution) and traced the outline of the largest hindlimb toe pad and one of the two largest

199 toe pads (on the 3rd or 4th toe) on the forelimb using ImageJ v.1.52a (Schneider et al. 2012).

200 On the forelimb, we only used the 4th toe when the 3rd toe was not visible on the scan for a

201 particular individual, and we were able to do this because the third and fourth toes on the

202 forelimbs of slender anoles are extremely similar in size. Regardless, 94% of our estimates

203 were on the 3rd toe and results did not differ substantially irrespective of whether 4th toes

204 were included. We gave lizards regular 90-minute breaks from handling and processing to

205   reduce stress (Langkilde 2006). We then implanted visual elastomers (VIE codes; Northwest

206   Marine Technology Inc.) to give each lizard a unique identifier (Nicholson et al. 2015) and

207   released a total of 35 male and 35 female lizards to each experimental island in batches. Each

208   batch was composed of 20 – 40 lizards that were assigned randomly to an island and released

209   between July and August 2017.

210   We conducted mark-recapture surveys on the founder (F_0) populations between

211   October and December 2017 and on their adult offspring (F_1 generation) between June and

212   November 2018, searching each island twice per week during the study period. Due to the

213   short generation time of slender anoles, there was little overlap between the F_0 and F_1

214   generations, with 8.5% of F_0 individuals surviving to the next year. In 2017, when F_0 lizards

215   were recaptured on islands, we recorded their perch height and diameter, then immediately

216   released them at the spot of capture. In 2018, when adult F_1 individuals were first caught on

217   the islands, we recorded their perch height and diameter and then transported them back to

218   the Smithsonian facility in Gamboa and measured the same morphological traits as for the

219   founders. The same researcher (DJN) took all morphological measurements (aside from toe

220   pad scans) from both survey years to reduce observer bias. While different researchers

221   estimated toe pad size from scans, the researcher that analyzed each image was noted so that

222   'observer' could be accounted for in models of toe pad size (see below). F_1 lizards were

223   returned to their point of capture on the islands no more than 48 hours after collection. If F_1

224   lizards were recaptured during subsequent surveys, we recorded their perch heights and perch

225   diameters but released them immediately at the spot of capture. We also surveyed our

226   mainland site (the source site for the F_0 generation) again in 2018 to see if habitat use or

227   morphology had changed in the source population after one generation.

228   Our initial sample sizes (70 lizards per island) and subsequent recapture rates were

229   insufficient to accurately estimate selection gradients following traditional regression-based

230   protocols which require very large sample sizes (Lande and Arnold 1983). Instead, we used

231   Huggins robust design model, implemented in the *RMark* package (Laake 2013), to quantify

232   the relationship between survival and trait variation in our study populations. This approach

233   allowed us to bin individuals into low (bottom third) and high (top third) trait values and then

234   to determine whether these categories of individuals differed in their survival probabilities.

235   While this approach does not provide standardized selection gradients that can be included in

236   population genetic or evolutionary models, it nevertheless provides information about if and

237   how selection may have operated. For selection analyses, we focused on the three traits (hind

238   limb length, hindlimb toe pad size, and head depth) that changed in consistent directions

239   across islands.

240   In 2018, we quantified habitat structure at all sites (mainland and island) using

241   randomised quadrat sampling of vegetation composition and the diameters of potential lizard

242   perches (detailed methods in Online Supplementary Information; Figure S1).

243   In 2019, we quantified flight initiation distance (FID) at several sites (mainland site

244   plus three islands), including a new island (Island H1) to which we had just transplanted

245   lizards that year. To measure FID on the mainland, we followed a trail (Pipeline Road) that

246   bisects the national park (at least one researcher on each side of the trail). Once a lizard was

247   spotted, the same observer (EF) approached it (from whatever distance she was at when the

248   lizard was first seen) at a consistent pace until the lizard displayed an evasive behaviour of

249   some kind (diving into leaf litter, moving around to the other side of the tree, etc.). The

250   observer also wore similarly colored clothing each day to avoid variable effects on lizard

251   fleeing behavior in response to different colored "predators." Once the lizard fled, we then

252   recorded the distance between the observer and the location of the lizard before it fled. We

253   followed a similar procedure on the islands, except that instead of a linear transect, two or

254   more researchers occupied distinct "lanes" (separated from the nearest observer by a

255 minimum of 3 meters on the left and right) and walked around the island one time in a circle.

256 This careful sampling strategy whereby the same area of habitat was never searched twice, in

257 combination with the small territory size of slender anoles, ensured that we did not

258 accidentally sample the same individual more than once on a given sampling day. On the

259 islands, if possible, any lizard we observed was subsequently captured and either identified or

260 given a unique VIE code if the individual was new to our data set.

261 Note that we do not have FID data from all islands included in our initial transplant

262 because Panama experienced a record drought during the 2019 dry season (January – May),

263 and this resulted in large population die-offs on several of our experimental islands. Thus, our

264 sample sizes for the F_2 generation on several islands are too small to be confident in

265 phenotypic parameter estimates, and we therefore focus on islands that were seeded in 2017

266 for understanding changes in habitat use and morphology that occurred in the first two

267 generations after colonisation, while we include FID data from 2019 to gain additional

268 understanding of behavioural differences between island and mainland lizards. Our sample

269 sizes of FID estimates among sites ranged from 13 – 39 (including resampling of a small

270 percentage of individuals at some sites on separate days).

271 We compared differences in available perch diameters among the mainland and three

272 islands in our initial transplant using a linear mixed effects model with $\log_{10}$-transformed

273 'available perch diameter' as the dependent variable, 'site' (island identity or mainland) as a

274 fixed factor, and 'quadrat' as a random factor. To calculate differences in the density of

275 different vegetation types (large trees, small branches, palms, and spiny understory plants)

276 among sites we used ANOVA with the density of each vegetation type $\log_{10}$-transformed. We

277 also assessed variation in total vegetation density by pooling each plant category. We

278 analysed lizard habitat use by fitting linear mixed-effect models with 'lizard ID' as a random

279 effect to account for repeated measures. We ran separate models for used perch diameter and

280   perch height, both of which were $\log_{10}$-transformed to meet the model assumption for

281   normality and homoscedasticity of residuals. In these models, the habitat use variable (used

282   perch diameter or perch height) was the dependent variable with 'site' as the independent

283   variable. 'Sex' and the 'sex by site' interaction were also included as factors in the model for

284   perch height because male and female slender anoles (as with other species in this genus) are

285   known to differ in perch height (Logan et al. 2021). For this same reason, 'sex' was included

286   as a covariate in models for shifts in mean values of morphological traits across generations

287   (see below). We did not include 'sex' or 'sex by site' interactions in other statistical models

288   (e.g., those for flight initiation distance) because of a lack of a priori evidence that these

289   variables differ between the sexes in slender anoles and the fact that these terms were

290   insignificant and did not substantially affect estimates of the main parameters in earlier

291   iterations of our statistical models.

292   To assess the difference between available and used perch diameters among the

293   mainland and our initial transplant sites, we performed a two-factor ANOVA with 'site' and

294   'used versus available' (binary variable) as the independent variables and 'perch diameter' as

295   the dependent variable (the latter of which we $\log_{10}$-transformed to meet the assumptions of

296   the model).

297   To visualize phenotypic divergence between the mainland and island populations, we

298   used a principal component analysis (PCA) with all morphological traits included. To

299   statistically compare the multivariate position of populations in morphological space, we

300   conducted a PERMANOVA, using all morphological traits as the dependent variables and

301   'site', 'generation', and 'sex' as independent variables. For the F_0 generation, we compared

302   the morphology of all lizards moved to islands from the mainland to a control group on the

303   mainland that was not transplanted. For the F_1 generation, we compared the island

304   populations to individuals caught on the mainland in the same year. To test for changes in

305 individual trait means between generations, we used separate linear models for each trait and

306 site. Each of these models included the relevant trait as the dependent variable and

307 'generation' as a categorical independent variable. 'SVL' (to account for body size) and 'sex'

308 were included as covariates in all models that included morphological traits. For all

309 morphological analyses, only adults (SVL > 38 mm) were included. To compare the

310 magnitude of total phenotypic change among sites, we calculated the average percent trait

311 change, summed across all traits, between the F_0 and F_1 generations.

312   We compared differences in flight initiation distance among sites using a linear

313 mixed-effects model with 'flight initiation distance' as the dependent variable, 'site' as a

314 fixed factor, and 'lizard ID' as a random factor to account for repeated measures. All analyses

315 were conducted in R version 3.5.3 (R Core Team 2019) and mixed-effects models were

316 implemented in the *lme4* package (Bates et al. 2015). Diagnostic plots were checked for

317 appropriate residual distributions for all fitted models.

318

319 **Results**

320 *Differences in habitat structure and use among sites*

321 On average, available perch diameters were larger on most islands compared to the mainland

322 (mean perch diameters; Mainland = 31.65 mm ± 1.92 S.E.M., Island C = 67.02 mm ± 7.58

323 S.E.M., Island P = 46.47 mm ± 9.88 S.E.M.; significance confirmed by the coefficient

324 estimates and standard errors in a mixed-effects model), although available perch diameters

325 on Island D (mean perch diameter = 47.08 mm ± 8.02 S.E.M.) were not statistically

326 distinguishable from the mainland, and only Island P differed from the other islands (Table

327 S1). Additionally, vegetation density (when summed across vegetation types) was higher on

328 all islands relative to the mainland ($F_{3,125} = 6.45$, $P < 0.001$). Island C and Island P had

329 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

($F_{3,125} = 0.55$, $P = 0.645$). 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 S1),

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 S1). Confidence limits and effect sizes for this

model revealed that there were no differences in

lizard perch height among islands, although males

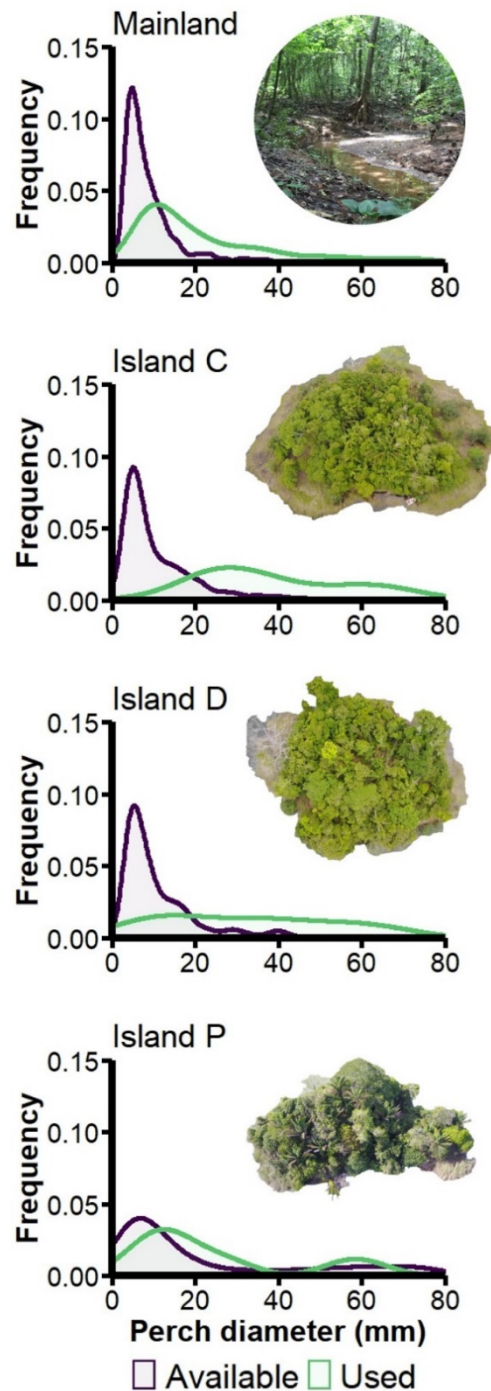perched higher than females at all sites. Additionally,

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.

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 S2, 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 S5). 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 S1). 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

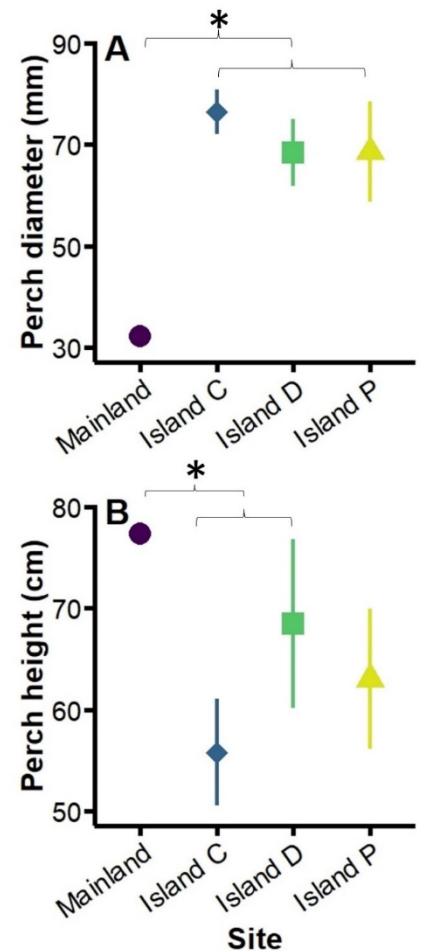forelimb toepad size showed few differences in morphology

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).

380   between the founders that were transplanted to islands and a separate control group on the

381   mainland (Figure 3a). Thus, all island populations started in approximately the same location

382   in morphospace. By the F_1 generation, however, island populations had already diverged

383   from the mainland population in morphospace (Figure 3b). A detailed description of PCA

384   component loadings and the PERMANOVA output are presented in Table S3.
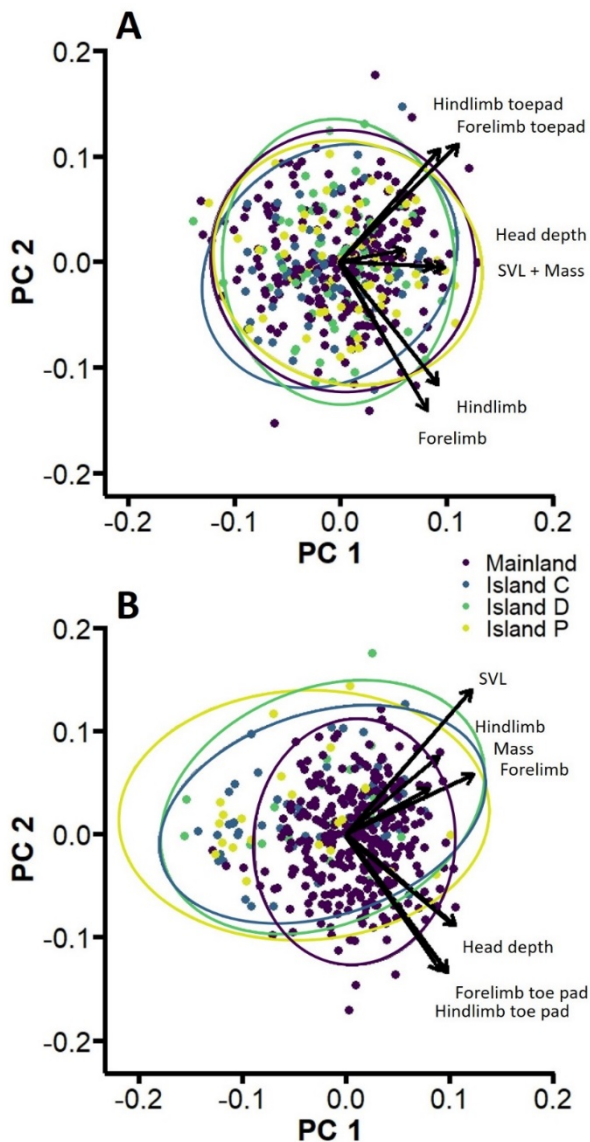

Figure 3. Changes in multivariate trait space for mainland and island populations after one generation. A) The F_0 (founder) populations overlap broadly in trait space across all sites (data from 2017). B) F_1 island lizards diverged from the mainland population after only a single generation (one year;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

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 S4). 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 only significant on Island D. There were, however, much larger effect sizes on the islands compared to the mainland (Table S4), 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
S4). 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 S4).
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
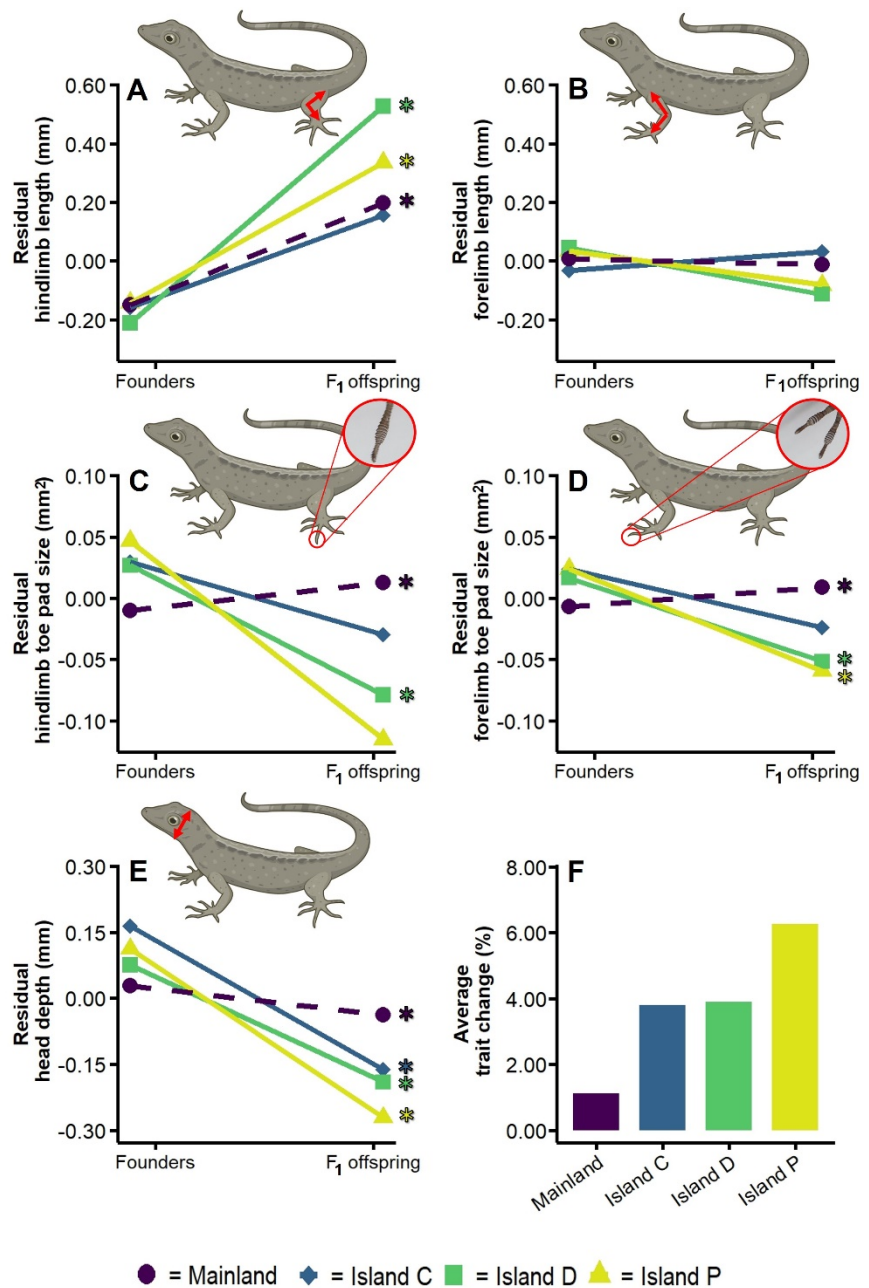change in trait means after
one generation (averaged

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).

430 across all traits) was three to six-fold higher on the islands relative to the mainland (Figure

431 4f). We summarize the extent to which parameter estimates of survival, and the magnitude

432 and direction of trait shifts matched predictions based on lizard habitat use ecological

433 variation among sites in Table S6.

434

435 **Discussion**

436 Lizards that were experimentally introduced to several islands shifted their habitat use and

437 behaviour almost immediately after "colonisation". While we found only weak evidence that

438 after this behavioural shift, lizards with longer hindlimbs, smaller toe pads, and smaller heads

439 were more likely to survive, these same traits shifted in the predicted direction in the next

440 generation on most islands. The mainland (source) population also displayed changes in some

441 traits during this period, yet these changes were typically of smaller magnitude and often in

442 the opposite direction than those exhibited by island populations. We provide experimental

443 support that behavioural drive can operate over a single generation to cause divergence

444 between mainland and island populations. Nevertheless, it is important to note that we

445 studied only three island populations, and changes in trait means were not always consistent

446 across sites (with insufficient samples sizes to confirm that selection drove the changes we

447 did see). As such, we urge caution in interpreting our results as conclusive evidence for

448 adaptation to island environments.

449 We found, almost immediately after colonisation, that island lizards started using

450 perches with a mean diameter roughly double that of the mainland, they began perching

451 lower in the vegetation, and they let an observer approach more closely before fleeing (but

452 again, only some of these patterns were statistically significant). Additionally, lizards

453 changed their perch usage beyond what we would expect from differences in perch

454 availability on two of three islands and in a consistent direction across islands, suggesting

455   that this change represents a behavioural shift towards using preferred perches rather than

456   lizards simply conforming to variation among island habitats. These results suggest the

457   possibility that once introduced to islands, lizards experienced ecological release and began

458   occupying their preferred microhabitat after being freed from the intense interspecific

459   competition and predation that is typical of mainland environments in the lowland tropics

460   (Losos and Queiroz 1997; Des Roches et al. 2011, 2015; Herrmann et al. 2020). While

461   slender anoles perch higher in the vegetation on the mainland, they primarily feed on leaf

462   litter arthropods (Sexton et al. 1972). Individuals of this species are frequently observed in

463   "foraging posture", whereby they perch head down towards the ground as they scan for prey

464   movement (Sexton et al. 1972; Jenssen and Hover 1974; Hover and Jenssen 1976). When

465   they spot a potential prey item, they drop onto the ground and consume it. It is possible that

466   lizards are more efficient at catching and consuming prey if they perch closer to the ground.

467   However, on the mainland, there are several other species of lizards (including other anoles)

468   that are more-or-less strictly terrestrial (e.g., *Anolis capito*, *Anolis elcopeensis*, *Ameiva*

469   *festiva*, *Ameiva leptophrys,* and *Lepidoblepharis sanctaemartae*) and these may compete with

470   slender anoles, driving them further up in the vegetation. A similar dynamic has been

471   observed in populations of green anoles (*Anolis carolinensis*) in the southeastern United

472   States that perch higher in areas of overlap with the invasive and more terrestrial brown anole

473   (Stuart et al. 2014). Interestingly, Gaige's anole, the potential competitor species that

474   occurred on Island D prior to the start of our transplant experiment, did not substantially alter

475   the behavioural changes we observed in slender anoles after island colonisation. Indeed,

476   slender anoles on Island D perched on lower, broader surfaces (relative to perch availability)

477   and had lower FIDs than mainland lizards—the same patterns we observed on the other

478   islands. Gaige's anole is not a terrestrial species, and thus, slender anoles may have been able

479   to move lower in the vegetation on Island D without incurring a competition cost.

480   Predation pressure likely differed between the mainland and islands, as well. There

481 are a slew of terrestrial snake and mammal predators on the mainland that (to our knowledge)

482 do not occur on the islands, such as the Colubrid snakes *Chironius carinatus*, *Dendrophidion*

483 *nuchale*, and *Mastigodryas alternatus*, and the ground-dwelling mammal *Nasua narica*. Our

484 mainland field site even has ground-dwelling bird predators that do not occur on the islands,

485 including the ground cuckoo (*Neomorphis geoffroyi*) and the tinamou (*Tinamus major*). This

486 broad suite of terrestrial predators might make lower perches particularly hazardous for

487 slender anoles on the mainland. Indeed, in field experiments conducted in The Bahamas, the

488 experimental introduction of a terrestrial predator caused brown anoles to perch higher in the

489 vegetation (Losos et al., 2004; 2006). In the absence of terrestrial predators on the

490 experimental islands, slender anoles may prefer to perch lower in the vegetation to maximize

491 prey capture efficiency.

492   Island lizards had shorter flight initiation distances compared to mainland lizards and

493 we interpret this as a line of evidence that predation pressure was lower on our study islands.

494 Cooper, Pyron, and Garland (2014) compared flight initiation distance across a broad suite of

495 mainland and island-dwelling lizard species in a phylogenetic context. They found that island

496 lizards had consistently lower FIDs (even after accounting for phylogenetic relationships),

497 and they similarly interpreted this as a response to lower predation pressure on islands.

498 Interestingly, we observed this shift towards decreased FID even in the founders of Island

499 H1, which we transplanted from the mainland in 2019 and measured on the island in the same

500 year, suggesting that this trait is highly plastic and responds quickly to changes in predation

501 pressure. We cannot, however, rule out the possibility that decreased competition on islands

502 also played a role in decreasing FIDs, or that the lizards which were least likely to flee had

503 higher detection probabilities on islands compared to the mainland.

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 certain 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.

528   Our findings are congruent with the "behavioural drive" hypothesis, which suggests

529   that behaviour underpins adaptive change in non-behavioural traits (Huey et al. 2003; Marais

530   and Chown 2008). The morphological shifts we observed were unlikely to have been driven

531   by genetic drift as the direction of trait change was broadly consistent across islands, often in

532   the opposite direction of trait change on the mainland, was loosely associated with survival,

533   and followed biomechanical predictions (Vanhooydonck et al. 2006; Losos 2009; Hagey et

534   al. 2017*a*). Moreover, our PCA and PERMANOVA analyses revealed that in a single

535   generation, island populations diverged in multivariate morphological space from the

536   mainland, and again these changes were consistent across islands. Finally, compared to

537   mainland lizards, island lizards experienced a much greater rate of phenotypic change over

538   the same period. Taken together, these results suggest the possibility that many of the

539   phenotypic changes we observed in island populations were the result of adaptation over the

540   first two generations after colonisation.

541   We also found that head depth decreased across all islands to a much greater extent

542   than on the mainland. Head sizes of lizards on one island (Island P) decreased by 10% in one

543   generation, which is much faster than similar changes that have been reported in other

544   systems. For example, a species of gecko (*Gymnodactylus amarali)* experienced a change in

545   head size associated with shifts in prey availability after 15 years (approximately 15

546   generations) on islands in the Serra da Mesa Reservoir in Brazil (Eloy de Amorim et al.

547   2017). Changes in prey availability might have favoured a change in head size on our

548   experimental islands as well, as anoles are gape-limited predators (Schoener and Spiller

549   1992), and small islands could have invertebrates with smaller body size distributions

550   compared to the mainland. Furthermore, larger heads can be costly (as they are heavy),

551   requiring greater energetic investment (Wittorski et al. 2016; De Meyer et al. 2019). Head

552   size is often related to bite force in lizards (Huyghe et al. 2008; Broeckhoven and Mouton

553 2014; Herrel et al. 2014; Sagonas et al. 2014; Wittorski et al. 2016). As such, head size can

554 be related to intra- and interspecific competition, as well as predation pressure. The diversity

555 of competitor species was lower on the islands, and this may have resulted in reduced

556 encounter rates between individuals and less need for strong jaw musculature that is critical

557 for winning competitive bouts (Lailvaux and Irschick 2007; Wegener et al. 2019). Further

558 research is needed to evaluate the role of intraspecific competition and prey size distributions

559 to ultimately determine the forces resulting in rapidly shrinking lizard heads on our

560 experimental islands.

561   We have shown that behavioural and morphological divergence can occur rapidly in

562 wild lizard populations that "colonised" several islands. We observed similar behavioural and

563 morphological changes across islands, suggesting that a feature (or features) of island

564 environments caused these shifts. We argue that a lack of predators and competitors resulted

565 in ecological release, whereby lizard populations shifted to use a different structural niche,

566 and this led to rapid morphological divergence between the islands and mainland (Des

567 Roches et al. 2015; Herrmann et al. 2020). The well-established relationships between

568 habitat, morphology, and biomechanics of anoles indicate that some of these morphological

569 changes may have been adaptive. Finally, our results suggest that behavioural drive may be

570 an important process operating in populations that colonise islands and may represent one of

571 the first steps of adaptive radiation.

572

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597

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