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Source: Breviora, 574(1) : 1-15

Published By: Museum of Comparative Zoology, Harvard University

URL: https://doi.org/10.3099/0006-9698-574.1.1

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BREVIORA

Museum of Comparative Zoology



US ISSN 0006-9698

CAMBRIDGE, MASS. 22 FEBRUARY 2022 NUMBER 574

ECOLOGICAL RELEASE ANALYZED AMONG INDIVIDUALS, ACROSS TWO GENERATIONS, AND ALONG MULTIPLE NICHE AXES IN *ANOLIS CAROLINENSIS*

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ABSTRACT. A population freed from a constraining interspecific interaction (e.g., competition or predation) may experience niche shifts and expansions. This phenomenon, termed ecological release, is an eco-evolutionary process driven by individual behaviors and interindividual interactions. However, empirical studies of these interactions seldom observe them directly, instead inferring process from pattern. Here, we set up experimental conditions for ecological release of the lizard *Anolis carolinensis* (green anole) from constraining interactions with its congener, *Anolis sagrei* (brown anole), by constituting populations of lizards on small islands. We monitored individual and population habitat use along three niche axes (perch height, perch diameter, and lateral movement between perches) on one experimental (one-species) and one control (two-species) island, for three time periods: 1) preremoval, when both islands had both species; 2) postremoval, shortly after *A. sagrei* were cleared from the experimental island; and 3) delayed postremoval, 7 months later, when long-lived lizards were joined by a second generation born in the intervening months. We found that green anole perch height decreased on the one-species island and increased on the two-species island. These shifts did not occur during postremoval but were evident by delayed postremoval, when both generations on the one-species island were perching nearly 130 cm lower than their counterparts on the two-species island. We also documented correlated changes in perch diameter at both the individual and population level but no changes in the extent of individuals' lateral movement. Lastly, changes in population-level niche width (i.e.,

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perch height and diameter variances) occurred without detectable changes in niche overlap among individuals. Our results demonstrate that that the dynamics of ecological release in nature need not be inferred, because experiments can observe them directly in individuals, across generations, and along multiple niche axes.

KEY WORDS: ecological release; interspecific competition; behavioral plasticity; individual specialization; ecological character displacement; *Anolis*

INTRODUCTION

A central challenge of eco-evolutionary dynamics is understanding how patterns of trait variation and species diversity emerge from processes that involve individual behaviors and interindividual interactions (Pelletier et al., 2009; Hendry, 2017; Romero-Mujalli et al., 2019). Indeed, a suite of phenomena that link patterns and processes across levels of biological organization—including character displacement, reinforcement, and other mechanisms of diversification—have made up the core of evolutionary ecology for decades (reviewed in Schluter, 2000; Pfennig and Pfennig, 2012). Ecological release, defined as niche expansions and shifts when a constraining interspecific interaction (i.e., competition, predation, parasitism, pathogenicity) is reduced or removed, is one such phenomenon (Herrmann et al., 2021).

The process of ecological release and the patterns it is thought to generate have been studied empirically at the population level for over half a century (Connell, 1961; Wilson, 1961; Crowell, 1962; Paine, 1966). More recently, changes in individual behavior that may drive ecological release have been inferred by observational studies comparing individual-level niche variation across populations that differ in, for example, number of purported competitors (Costa et al., 2008; Cloyed and Eason, 2016; Costa-Pereira et al., 2019; Rainville et al., 2021). However, we have almost no direct field observations of individual responses during the initial stages of ecological release. Partly, the challenge is due to the difficulty of observing the process in action—in natural populations, by the time one notices evidence of ecological release, it is either well underway or thought to have occurred in the distant past.

Experimentally generating the conditions that cause ecological release in natural settings can address this challenge. For example, Bolnick et al. (2010) experimentally induced ecological release in stickleback, deployed for 15 days in mesh enclosures in natural lakes, by comparing control populations in the presence of two interspecific competitors to experimental populations where one or both competing species were removed. Crucially, such a setup allowed the authors to demonstrate that ecological release alters stickleback diets on behavioral timescales (within the lifetimes of individual fish); that individuals can change their diets in response to competitor removal, even while the population-level niche remains stable; and that release from different competing species can have different effects. Still, numerous questions about the eco-evolutionary dynamics of ecological release remain largely untested by field experiments. For example, how does ecological release affect individuals across multiple niche axes instead of a single axis (MacArthur and Wilson, 1967)? Also, how do niche changes during ecological release compare across subsequent generations, and what does this suggest about the roles of plasticity versus evolution during the initial stages of ecological release?

Lizards in the genus *Anolis* (anoles) are a compelling system for studying the process of ecological release. Individuals within a population have been shown to differ along three niche axes that define their largely

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arboreal habitat use: perch height, perch diameter, and the lateral extent of their movement among perches (Kamath and Losos, 2017a, 2018). Furthermore, interspecific competition appears to drive habitat partitioning among co-occurring species (reviewed in Losos, 2009), and field experiments that manipulate competitor presence or density consistently demonstrate population-level niche changes (Pacala and Roughgarden, 1985; Rummel and Roughgarden, 1985; Leal et al., 1998). However, such experimentally induced niche changes are yet to be dissected at the level of individuals, across generations, or along more than two niche axes.

Here, we describe a field-based, experimental test for ecological release in *Anolis carolinensis* (green anole). In southern Florida, green anoles perch higher where they overlap with introduced *Anolis sagrei* (brown anole; Stuart et al., 2014). This interspecific interaction that constrains habitat use appears to have several underlying mechanisms, including resource competition for arthropod prey (Campbell, 2000), direct aggression (Culbertson and Herrmann, 2019), and intraguild predation (Gerber and Echternacht, 2000). We hypothesized that the experimental removal of brown anoles would lead to a decrease in green anole mean perch height (niche shift), an increase in perch height variance (niche expansion), or both. We tested for these changes across two generations and compared them with those experienced by green anoles in continued sympatry with brown anoles. To capture the potential multidimensionality of niche changes, we also tracked individuals along two other axes that describe habitat use in anoles: perch diameter, which often distinguishes species that occupy distinct microhabitats but is relatively understudied at level of individuals within populations (Losos, 2009; Kamath and Losos, 2017a), and the lateral extent of individuals' movements among perches, which can affect access to food and potential mates (Stamps and Tanaka, 1981; Schoener and Schoener, 1982; Jenssen and Nunez, 1998; Kamath and Losos 2018) and may be modulated by the avoidance of interspecific interactions (Jenssen et al., 1984). Finally, we explored each niche axis at both the individual and population levels, with the goal of understanding the individual behavioral processes that underlie population patterns of ecological release.

METHODS

Study sites and populations

The experiment was conducted on two islands—SL1B (0.04 ha; 27°29′36.5″N, 80°19′42.0″W) and SL13C (0.03 ha; 27°32′45.5″N, 80°20′34.0″W; Fig. 1)—which belong to a chain of low-lying islands in Florida's Indian River Lagoon. The islands were created about 60 years ago from dredge spoil, a byproduct of the U.S. Army Corps of Engineers deepening the channel that runs through the lagoon (Campbell, 2000). Despite their small size, both study islands have vegetation similar to that of larger islands nearby; they contain a mix of open areas and closed-canopy stands with several trees exceeding 4 m in height, most commonly red mangroves (*Rhizophora mangle*), black mangroves (*Avicennia germinans*), and Brazilian pepper (*Schinus terebinthifolia*).

Green and brown anoles have established themselves on most dredge spoil islands in the lagoon, including several islands smaller than 0.05 ha. However, neither were initially present on our study islands despite the islands having tall and varied vegetation, along with visually abundant arthropod prey, to accommodate both species. We transplanted lizards of both species to

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Figure 1. The two islands used for this experiment, SL1B (left) and SL13C (right). Photographed on 13 August 2018 by NCH.

establish sympatric populations on each island. These lizards came from larger, nearby islands where both species were relatively abundant (SL12: 27°29′55″N, 80°19′46″W; SL3: 27°32′07″N, 80°20′20″W; IR11: 27°48′01″N, 80°27′12″W), with each experimental island receiving a mix of individuals from each source island. Green anoles from our source populations have lived in sympatry with brown anoles for at least 25 generations (Campbell, 2000).

Experiment establishment and timeline

We established study populations on SL1B and SL13C in May 2018. Individuals were captured from source islands by lasso or by hand, transported to field housing for processing, and released at a randomly selected location on either SL1B or SL13C within 48 hours. Green anoles received a unique bead tag sewn into the tail (Fisher and Muth, 1989). To help identify individuals that lost their bead tag, we also inserted a UV-fluorescent alphanumeric tag (Northwest Marine Technology, Inc.) subcutaneously in each hindlimb. Because bead tags may increase the visibility of a lizard to potential predators, brown anoles also received bead tags, even though they were not the focus of this study. We transplanted a total of 69 anoles (24 green and 45 brown) to SL1B and 92 anoles (32 green and 60 brown) to SL13C. Then, the populations were given 4 weeks to acclimate to the experimental islands before field observations. Following the acclimation period, all transplanted populations had a roughly a 1:1 sex ratio and were at naturally occurring densities (~500 individuals/ha for green anoles and ~1000 individuals/ha for brown anoles; Campbell, 2000).

Subsequent observations of green anole habitat use occurred in three stages, each of which lasted approximately 3 weeks: preremoval, when both islands had both species (July 2018); postremoval, shortly after *A. sagrei* were cleared from one island (August 2018); and delayed postremoval, 7 months later (March 2019). During the preremoval stage (July 2018), both islands contained both species. Then, we flipped a coin to determine which island would have its brown anoles removed. It took 2 days to remove all the brown anoles from SL13C (hereafter, "one-species island"), which were caught by lasso or by hand. We spent an equal number of hours those days walking around SL1B (hereafter, "two-species island") as a procedural control but did not remove any brown

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anoles. The postremoval observation stage (August 2018) began 2 days later.

Study populations were observed again during the delayed postremoval stage (March 2019). At this time, the one-species island still had only green anoles (we encountered no new brown anoles), and the two-species island still had both species. However, populations on both islands were a mix of old individuals, measured and tagged in 2018, and a generation of new, yet untagged individuals born on the study islands (young of year). We captured new green anoles on both islands and processed them identically to individuals from the previous year.

Measuring the niche

We used the same protocol to quantify green anole habitat use on both islands during the preremoval, postremoval, and delayed postremoval stages. Upon arriving at an island, a team of two or three people would scan the site for green anoles with binoculars, first by wading in the shallow water surrounding the island and then by traversing the interior. When a green anole was spotted and undisturbed by our presence, we recorded the individual's unique bead tag ID and its habitat use along three axes—perch height, perch diameter, and lateral location—in a manner described below. Only the first observation of each individual was recorded during a visit.

Visits occurred during daylight hours when lizards were active (0730-1800 hours). Total time per visit varied by the number of observations and was seldom longer than an hour. Visits usually occurred in pairs between islands (one-species island followed by two-species island or vice versa), and all same-day visits to a site were separated by at least 1 hour. We typically alternated which island we visited first to ensure that the sites received similar representation across times of day. We also approximately equalized the total number of person-hours per island (search time × number of people) during each stage (preremoval: ~68 person-hours per island, postremoval: ~68 person-hours, delayed postremoval: ~49 person-hours).

Green anole perch height and perch diameter were recorded to the nearest centimeter. Perch heights above 150 cm were measured with a digital measuring pole (Sokkia, Inc.) that can extend up to 8 m. Lizards observed on the ground were noted as such and were not assigned a perch diameter at the time (although they were assigned one later—see below).

To track the extent of individuals' lateral movement, we laid out a grid of 2 × 2-m squares on each island with small flags (one-species island: 78 squares; two-species island: 62 squares) and recorded the grid location of each green anole observation (Supplemental Fig. S1). Outer grid squares extended at least to the water's edge. In areas where tree limbs protruded over the water, we marked grid vertices by tying small pieces of flagging tape to branches.

Statistical analyses

Perch height. To compare population perch height means across islands and experimental stages, we ran a linear mixed effects model (the *lme* function in the R package *nlme*) with perch height as the response variable, island–stage combination (e.g., two-species island during preremoval, one-species island during delayed postremoval) as a fixed effect with six levels, and individual lizard ID as a random effect. To visualize how individuals contributed to population-level perch height means, we calculated the mean perch height for each individual in each session and generated three plots: 1) means for all individuals

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across all stages, 2) individual mean shifts from preremoval to postremoval (although not to delayed postremoval, because approximately half of the founding individuals on each island did not survive to this stage), 3) delayed postremoval means separated by old (long-lived) and new (young of year) individuals. We also conducted three Wilcoxon rank-sum tests on individual perch height means, one for each stage, to test for rank order differences between the two islands.

To compare population perch height variances across islands and experimental stages, we first calculated perch height residuals (deviations) from the mean, separately for each island–stage combination, by subtracting the population's perch height mean from each observed value. We then ran an analysis of variance comparing the absolute value of these residuals. This operation is functionally equivalent to the Levene test for homogeneity of group variances, but it allows for post hoc pairwise comparisons between groups (for which a standard Levene test does not). We used a Tukey's honest significance test to make post hoc comparisons between island–stage combinations, with *P* values adjusted for multiple comparisons with a family-wise error rate.

To compare the degree to which the distribution of individual perch height use differed from the population distribution (i.e., individual niche specialization) across islands and experimental stages, we used the *WTcMC* function in the R package *RInSp* (Zaccarelli et al., 2013) to calculate the total niche width (TNW), the within-individual component of perch height variation (WIC), and the proportion of total variation nested within individuals (WIC/TNW) separately for each island–stage combination. High WIC/TNW suggests that individual niche widths are similar to population-level niche widths, whereas low WIC/TNW suggests niche differentiation among individual habitat use specialists. The package *RInSp* interprets zeros as missing values, so we added 1 to all recorded perch heights before this analysis. To help interpret differences in WIC/TNW across islands and stages, we ran simulations to determine whether these differences could be explained by sampling error (see Supplemental Methods).

Perch diameter. We conducted analyses of population- and individual-level changes in perch diameter identical to those described above for perch height. Of 829 total observations, 24 green anoles were perched on the ground. To a small lizard, this flat surface is functionally very similar to the widest perches it may use above the ground, such as a broad tree trunk (Spezzano and Jayne, 2004).To incorporate these observations into our analyses without overinflating their influence, we assigned all ground observations a diameter equal to the largest diameter in the rest of the data set (24 cm).

Lateral movement. We manually assigned each individual a measure of lateral movement for each session by counting the minimum number of grid squares it must have occupied at some point during that session, on the basis of all locations in which it was observed. We conducted three Wilcoxon rank sum tests, one for each stage, to compare the extent of individuals' lateral movement across islands. Unlike individual mean perch height or perch diameter, this metric scales positively with number of observations per individual (see Supplemental Methods), a confounding factor that we account for in our interpretation of the results.

All analyses were conducted in R version 4.0.2. Data and an annotated R script are available on GitHub (Herrmann, 2021).

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TABLE 1. SUMMARY OF POPULATIONS AND SAMPLING EFFORT ON EXPERIMENTAL ISLANDS.[a]

	Two-Species Island (SL1B)									One-species Island (SL13C)								
	Green Anoles							Brown Anoles		Green Anoles							Brown Anoles	
	Male		Female		Total					Male		Female		Total				
	Ind.	Obs.	Ind.	Obs.	Ind.	Obs.	Ind./ha	Ind.	Ind./ha	Ind.	Obs.	Ind.	Obs.	Ind.	Obs.	Ind./ha	Ind.	Ind./ha
Preremoval (July 2018)	9	93	7	29	16	122	533	30	1,000	10	83	11	37	21	120	525	40	1,000
Postremoval (August 2018)	8	125	6	37	14	162	467	27	900	8	107	11	59	19	166	475	0	0
Delayed postremoval (March 2019)	5	37	7	35	12	72	400	40	1,333	14	108	15	79	29	187	725	0	0

[a]Ind., individuals; Obs., observations; Ind./ha, individuals/hectare.

RESULTS

Sampling summary

In total, we made 356 observations of 24 unique green anoles on the two-species island, and 473 observations of 40 unique green anoles on the one-species island. Table 1 breaks down this sampling effort by sex and experimental stage. Of the adult green anoles observed during postremoval, 35% (5 of 14) survived until delayed postremoval on the two-species island, whereas 53% (10 of 19) survived on the one-species island. During the final stage, we observed seven new (young of year) green anoles on the two-species island and 19 new green anoles on the one-species island.

Perch height

Population mean perch height was statistically indistinguishable across islands during the pre- and postremoval stages (Fig. 2A, Table 2). However, in the delayed postremoval stage, perch height decreased on the one-species island and increased substantially on the two-species island. During this stage, one-species island green anoles were perching nearly 130 cm lower than two-species island green anoles on average.

Individual lizards varied in how they changed their perch height across experimental stages (Fig. 2B). Some individuals underwent large perch height shifts from preremoval to postremoval (Supplemental Fig. S2), although because these extreme individual shifts occurred on both islands and in both directions, population-level distributions remained relatively stable. In contrast, the delayed postremoval divergence in population-level perch height was driven by consistent, directional shifts at the individual level. During this final stage, mean perch heights for old (long-lived) individuals mostly decreased on the one-species island (7 of 9 individuals) and ubiquitously increased on the two-species island (compare the slopes of lines connecting individuals observed across stages in Fig. 2B). Perch height means for new (young of year) individuals were similarly distinct between islands (Fig. 2C). Overall, old lizards and new lizards on the same island had extremely similar individual perch height means during the final stage (two-species island: 281 cm versus 274 cm; one-species island: 151 cm versus 146 cm). Wilcoxon rank sum tests comparing individual perch height means between islands showed no distinction during preremoval ($W = 179$, $P > 0.7$) or postremoval (W

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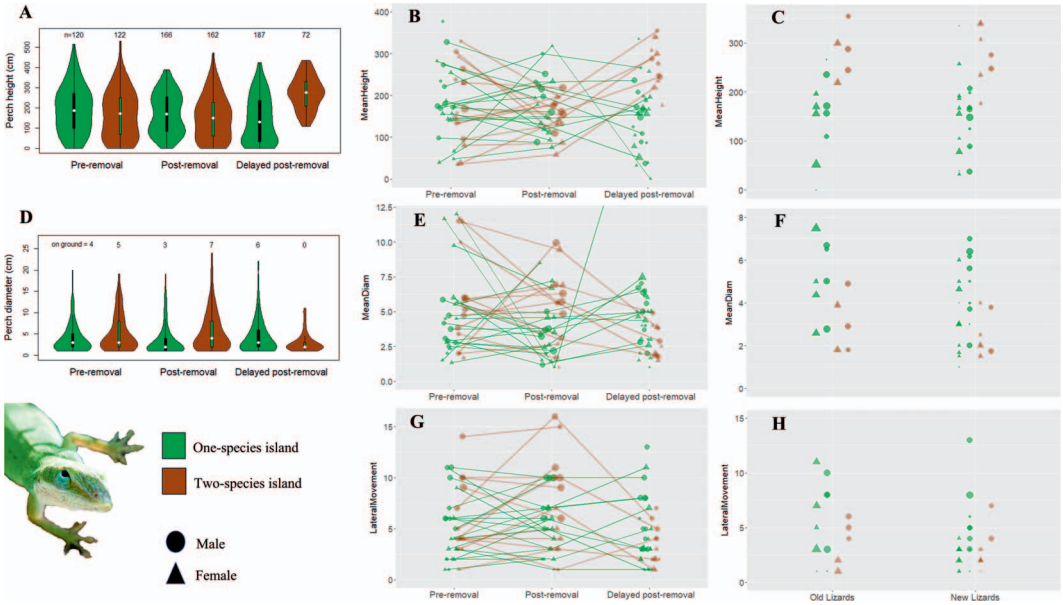


Figure 2. Green anole population and individual-level niche changes along three axes: perch height (top row), perch diameter (middle row), and the extent of lateral movement (bottom row). A, Violin plot depicting all perch heights measured during the experiment, broken down by island and experimental stage. The width corresponds to the density of observations at a given height. The box and whisker plot nested within each violin depicts the median (hollow circle) and interquartile range (vertical rectangle). Populations diverged during the delayed postremoval stage. B, Individual mean perch height for all green anoles across all stages. Each point within a stage represents a unique individual and carries information about the individual's island (color), sex (shape), and number of observations (size). Horizontal lines connect the same individual observed across stages. C, Individual mean perch heights for old (long-lived) versus new (young of year) green anoles observed during delayed postremoval. D, Same as in panel A, but for perch diameter. Sample sizes are equivalent to those depicted in panel A. Here, the number above each violin represents the number of ground observations in each group, which are not incorporated into the violin distributions. As in panel A, populations diverged during delayed postremoval. E, Same as in panel B, but for individual mean perch diameter. The line that continues above the field of view connects to a point at 24 cm. This female from the one-species island was observed once, on the ground (and was therefore assigned a perch diameter of 24 cm), during delayed postremoval. F, Same as in panel C, but for individual mean perch diameter. (Not pictured: the individual whose mean perch diameter landed it above the field of view in panel E) G, Same as in panels B and E, but for the extent of individuals' lateral movement, measured as the minimum number of unique grid squares a lizard must have traversed on the basis of all the locations it was observed during a particular stage. H, Same as in panels C and F, but for the extent of individuals' lateral movement.

$= 168$, $P > 0.2$), but during delayed postremoval, individuals on the one-species island perched lower than individuals on the two-species island ($W = 27$, $P < 0.001$).

Like mean perch height, population perch height variances ultimately differed between islands. Specifically, population perch height variance decreased sharply on the two-species island during delayed postremoval, because this population ceased perching near the ground (Fig. 2A, Table 3). However, this population-level change was not driven by individuals on the two-species island becoming more specialized (as indicated by the within-individual contribution to perch height variation [WIC] divided by the total niche width [TNW]; final row of Table 4). In other words, even though total niche width

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TABLE 2. MIXED EFFECTS MODEL TESTING FOR POPULATION-LEVEL PERCH HEIGHT SHIFTS. PREREMOVAL-STAGE LIZARDS ON THE ONE-SPECIES ISLAND ARE THE BASELINE (INTERCEPT) OF THIS MODEL.[a] THE ESTIMATED WITHIN-ISLAND CHANGE FROM PREVIOUS STAGE AND ESTIMATED DIFFERENCE BETWEEN ISLAND COLUMNS ARE CALCULATED BY COMPARING THE RELEVANT COEFFICIENTS ESTIMATED BY THE MODEL.

		Value	SE	*t* Value	*P* Value[b]	Estimated Within-Island Change from Previous Stage	Estimated Difference between Islands (One-Species Minus Two-Species)
Preremoval	(Intercept) One-species island	180	12.9	13.9	**<0.001**	NA	11.4
	Two-species island	−11.4	19.5	−0.6	0.56	NA	
Postremoval	One-species island	−10.3	12.3	−0.8	0.4	−10.3	18.9
	Two-species island	−29.2	19.2	−1.5	0.13	−17.8	
Delayed postremoval	One-species island	−31.2	13.4	−2.3	**0.02**	−20.9	−129.9
	Two-species island	98.7	20.9	4.7	**<0.001**	127.9	

[a]Individual ID (random effect) standard deviation: intercept = 45.5, residual = 99.5.
[b]*P* values <0.05 are bolded.

on the one-species island was twice that on the control island, the proportion of perch height variation nested within individuals, compared with the variation between individuals, was similar between islands during this final stage (0.74 versus 0.69, a difference easily explained by sampling error; see Supplemental Methods). In general, individual perch height specialization exhibited no obvious relationship to total perch height niche width throughout the experiment (Table 4).

Testing for correlated changes along other niche axes

Perch diameter. The substantial perch height changes that occurred during delayed postremoval were accompanied by changes in perch diameter; population perch diameter mean and variance were both higher on the one-species island than on the two-species island during this final stage (Fig. 2D, Supplemental Tables S1, S2). This between-island divergence during delayed postremoval was driven mostly by changes that occurred over time on the two-species

TABLE 3. COMPARISON OF POPULATION PERCH HEIGHT VARIANCES AMONG ALL ISLAND–STAGE COMBINATIONS. CELL VALUES REPRESENT THE DIFFERENCE IN VARIANCE (TOP MINUS LEFT) ESTIMATED FROM A TUKEY POST HOC TEST, FOR WHICH THE ANALYSIS OF VARIANCE WAS CONDUCTED ON PERCH HEIGHT RESIDUALS RATHER THAN RAW PERCH HEIGHT. BOLD VALUES REPRESENT DIFFERENCES THAT ARE SIGNIFICANT AFTER ACCOUNTING FOR THE FAMILY-WISE ERROR RATE (I.E., *P* VALUES ARE ADJUSTED FOR MULTIPLE COMPARISONS).

		Preremoval		Postremoval		Delayed postremoval	
		One-Species Island	Two-Species Island	One-Species Island	Two-Species Island	One-Species Island	Two-Species Island
Preremoval	One-species island	—	1.6	−9.7	−8.0	0.8	**−33.1****
	Two-species island	—	—	−11.3	−9.7	−0.8	**−34.7*****
Postremoval	One-species island	—	—	—	1.6	10.5	**−23.4***
	Two-species island	—	—	—	—	8.8	**−25.0***
Delayed postremoval	One-species island	—	—	—	—	—	**−33.9*****
	Two-species island	—	—	—	—	—	—

*Adjusted $P < 0.05$.
**Adjusted $P < 0.01$.
***Adjusted $P < 0.001$.

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Table 4. Individual perch height specialization across islands and stages, as measured by within-individual contribution to perch height variation (WIC) divided by the total niche width (TNW). These values were calculated by the *RInSp* package (Zaccarelli et al., 2013) in R, with the contribution of each individual lizard weighted by its number of observations.

	Two-Species Island			One-Species Island		
	WIC	TNW	WIC/TNW	WIC	TNW	WIC/TNW
Preremoval	7,570	13,625	0.56	8,174	13,602	0.60
Postremoval	9,978	11,602	0.86	6,409	9,851	0.65
Delayed postremoval	4,489	6,485	0.69	9,510	12,784	0.74

island (Fig. 2D). Although mean perch diameter fluctuated dramatically for some long-lived individuals on the one-species island, the population-level distribution of perch diameters on this island was relatively stable over time (Fig. 2E). In contrast, during delayed postremoval, two-species island lizards occupied a narrower range of narrower perches than they had occupied during either the preremoval or postremoval stages. There are also hints of an inverse relationship between individual mean perch height shift and individual mean perch diameter shift from preremoval to postremoval, although the strength of this relationship is marginal at best (Supplemental Fig. S2).

Wilcoxon rank sum tests comparing individual perch diameter means between islands showed no distinction during preremoval ($W = 134$, $P > 0.3$) or postremoval ($W = 86$, $P > 0.09$), but during delayed postremoval, individuals on the one-species island occupied wider perches than individuals on the two-species island ($W = 265$, $P < 0.01$). As was true for perch height, between-island divergence in delayed postremoval perch diameter occurred among both old and new individuals (Fig. 2F). Differences in individual perch diameter specialization between islands and across stages were negligible and could all be explained by sampling error (see Supplemental Methods; Supplemental Table S3).

Lateral movement. There is no evidence that perch height changes were accompanied by changes in the extent of individuals' lateral movement. Coincident with their increase in perch height, individuals on the two-species island appear to have shrunk their lateral movement during delayed postremoval, whereas lateral movement on the one-species island remained relatively stable throughout the experiment (Fig. 2G). However, because the lateral movement metric scales positively with number of observations (see Supplemental Methods), and individuals on the two-species island were observed far less frequently than removal island individuals during the final stage (77 observations versus 187 observations), this visual pattern may be a result of sampling differences. Moreover, Wilcoxon rank sum tests comparing the extent of individuals' lateral movement between islands showed no distinction during preremoval ($W = 144$, $P > 0.4$, postremoval ($W = 95$, $P > 0.17$), or delayed postremoval ($W = 223$, $P > 0.16$). When comparing individuals from preremoval to postremoval, shifts in their extent of lateral movement were uncorrelated with shifts in their mean perch height (Supplemental Fig. 2).

DISCUSSION

In this study, we set up experimental conditions for ecological release of the lizard *A. carolinensis* from constraining interac-

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tions with its congener *A. sagrei* by constituting populations of lizards on small dredge-spoil islands that served as experimental units. We monitored individual and population habitat use along three niche axes (perch height, perch diameter, and lateral movement) on one experimental (one-species) island and one control (two-species) island, for three time periods: preremoval, postremoval, and delayed postremoval.

The foremost takeaway of this study is that, in this system of green and brown anoles, population-level niche changes can occur within individual lifetimes, but they are not instantaneous. We saw no shifts in mean perch height during the postremoval period. This differs from other experimental assessments of ecological release (e.g., Bolnick et al., 2010), where both population- and individual-level niche shifts were seen within 2 weeks. In our experiment, niche shifts occurred sometime between the postremoval stage (which ended about 1 month after brown anole removal) and the delayed postremoval stage (7 months later). Myriad factors—the type of organism, the types of constraining interactions, and the specific niche axes under examination—may affect the progression of ecological release, and so, to the extent possible, experiments should persist and be monitored as long as possible to reveal longer term temporal dynamics.

Changes in perch height with time were apparent on both one- and two-species islands, indicating that despite a long history of sympatry between green and brown anoles on the source islands from which the lizards were collected (at least 25 generations; Campbell, 2000), their introduction to our experimental islands was akin to reassembling the community. By the time of delayed postremoval sampling, green anoles on the one-species island had moved downward, consistent with ecological release, whereas green anoles on the two-species island had moved upward, consistent with character displacement (Stuart et al., 2014). Although ecological release and character displacement need not have strictly inverse effects on a species' niche (Herrmann et al., 2021), in this system, the processes may be like two sides of the same coin.

Nonetheless, we were surprised by the magnitude of increase in perch height with time on the two-species island; it was comparable to the increases experienced by allopatric green anoles responding to the introduction of brown anoles (Stuart et al., 2014; Kamath et al., 2020). Seasonal variation in perching behavior may have contributed to this height increase, but the limited available data suggest that seasonal shifts in green anole perch height pale in comparison to what we observed (Jenssen et al. 1995). More likely, this perch height increase was caused by brown anoles. Despite our attempt to begin the experiment with a high density of brown anoles to ensure a strong interspecific interaction, the abundance of brown anoles on the two-species island increased by nearly 50% between the postremoval and delayed postremoval stages as a result of reproduction (Table 1). A recent comparison of anole communities on other Floridian islands found that green anole perch height is positively correlated with brown anole density (Kamath et al., 2020), suggesting that the green anole niche shift on our two-species island was driven by pressure from a growing population of brown anoles. In future work, setting up replicate islands in both the one-species and two-species categories will reveal if such density increases are the exception or the norm.

We are confident the perch height shifts we observed in green anoles are attributable to changes in brown anole abundance, and not some other factor. Vegetation structure was extremely similar between the islands and essentially unchanged throughout the exper-

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iment (no trees fell or lost major limbs), so green anole niche shifts through time were not the result of changes in habitat availability. Furthermore, the proximity of the islands suggests they experience comparable predation pressure from wading birds, and we observed no terrestrial predators (e.g., snakes, carnivorous mammals) on either island. Additionally, we used operative temperature models to confirm that the islands had nearly identical thermal environments during each stage of the experiment (see Supplemental Methods). Nonetheless, we recognize that our study lacks replication in island-wide treatments (one-species versus two-species). Although this shortcoming prevents us from drawing generalizable conclusions about how ecological release unfolds, our results nonetheless offer insights into the early stages of the process, specifically temporal dynamics extending into a second generation, interplay between individual- and population-level variation, and interactions among niche axes.

In the delayed postremoval stage, both long-lived individuals and the young of year perched lower on the one-species island and higher on the two-species island. Long-lived individuals' habitat use constitutes evidence against this behavior being genetically determined and demonstrates the importance of behavioral flexibility in eco-evolutionary interactions. In this system, the morphological traits associated with perch height (toepad area and number of adhesive toepad scales) are known to evolve after changes in interspecific interactions and include a heritable component (Stuart et al., 2014), a potential example of behavioral flexibility in habitat use acting as a "motor" for evolutionary change in morphology (Muñoz and Losos, 2018). Similar habitat use behavior by the young of year may arise from comparable individual responses to interspecific interactions, but may also be due to social learning (i.e., copying the habitat use behavior of conspecifics; Whiting et al., 2018), which is known to be more common in young individuals in some species of lizard (Noble et al., 2014). Whatever the mechanism driving similar perching behavior between long-lived individuals and the young of year, it was sufficiently strong to suppress intraspecific behavioral differences correlated with body size; young of year had, on average, a snout–vent length 6 mm shorter than long-lived individuals, but their distribution of perch heights was nearly identical to that of long-lived individuals on both islands.

Despite a large population niche width contraction (i.e., decrease in perch height and diameter variances) on the two-species island at the delayed postremoval stage, we detected no change in individual niche specialization (WIC/TNW). Moreover, there were no between-island differences in niche specialization during delayed postremoval, even though the one-species island had a substantially larger population niche width. If WIC/TNW remains stable as the population-level niche expands or contracts, then such population-level changes are driven jointly by niche changes within individuals and between individuals. These results run counter to the niche variation hypothesis (NVH; Van Valen, 1965), which posits that populations with wider niches because of ecological release are more likely to be made up of individual specialists (i.e., niche expansion occurs between individuals) than of generalists (i.e., niche expansion occurs within individuals). Empirical evidence thus far has revealed mixed support for the NVH (Bolnick et al., 2007; Cloyed and Eason, 2016; Sjödin et al., 2018), suggesting a need for further empirical evaluations in a diversity of systems and on a variety of resource use traits.

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Finally, although our results are consistent with perch height being the primary niche axis affected by interactions between green and brown anoles (Collette 1961; Stuart et al. 2014), other niche axes varied in their responses; correlated changes occurred in perch diameter, but not in the extent of individuals' lateral movement. However, the effects of ecological release we observed on niche axes other than perch height may differ across environmental contexts. For example, a correlation between perch height and perch diameter depends on the structure of available habitat (here, vegetation). In areas dominated by trees where trunk and branch diameter narrow as height increases, which was true for our study sites, correlated changes between perch height and perch diameter are more likely. Also, because researchers' ability to detect changes in animal movement depends on both the spatial and temporal extent of sampling (Kamath and Losos 2017b), we cannot rule out that ecological release would alter the lateral movement of green anoles on larger islands over longer time periods. Because there is no single eco-evolutionary pathway for ecological release (Herrmann et al. 2021), biologists should continue to study this process both across systems and across environmental conditions within systems.

ACKNOWLEDGMENTS

This work would not have been possible without the logistical and intellectual support provided by Irene Arpayoglou and staff at the Florida Department of Environmental Protection's Aquatic Preserve Program. We thank Alexandra Bachorik. Chelsea DeCambre, Jeremy Herrmann, Ron Herrmann, Frank Kahoun, Aaron Hochberg, and Kim Vasquez for help in the field. We also thank Debbie and Kenny Langley for logistical support. This work was funded by a Putnam Expedition Grant from the Harvard Museum of Comparative Zoology. AK was supported by the Miller Institute for Basic Research in Science.

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