A Multigenerational Field Experiment on Eco-evolutionary Dynamics of the Influential Lizard *Anolis sagrei*: A Mid-term Report

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Only a handful of multi-generational experiments in natural systems of eco-evolutionary dynamics currently exist, despite Fussmann et al.'s call for more such studies nearly a decade ago. To perform such a study, in 2008 we introduced the lizard *Leiocephalus carinatus*, a predator (and possible food competitor) of the lizard *Anolis sagrei*, to seven islands having *A. sagrei*, with seven unmanipulated islands having *A. sagrei* as controls. Almost immediately, *L. carinatus*, which is larger and more terrestrial than *A. sagrei*, caused a major habitat shift in *A. sagrei* away from the ground and toward higher and thinner perches; focal behavioral surveys showed that on islands where its predator was introduced, *A. sagrei* had less conspicuous visual displays. The expected pattern for density of *A. sagrei* is that it would decrease markedly at first via predation from the larger lizard, but then it would increase as the habitat shift selected for individuals better able to live in higher vegetation. Data through 2015 show this pattern, but a return to previous densities (time-by-treatment interaction) was not yet significant. A previous within-generation selection study and comparative data suggest that short legs should evolve as the lizards adapt to better maneuver on the thin perches of higher vegetation. However, no indication of the expected morphological change in limb length was present through 2015. Previous studies showed *A. sagrei* producing many effects on lower levels of the food web, some quite large. In this study through 2012, we found significant differences only in spiders (web and ground). A possible complication is that the study site was hit by two major hurricanes in the last five years, decreasing population sizes of both lizard species and reducing the experimental perturbations. A benefit of the hurricanes, however, is that they eliminated lizards from some islands, providing the opportunity to monitor natural recolonization, the frequency of which has eco-evolutionary implications. Surveys of the 44 islands that lost lizards showed that recolonization is rather slow. To explore long-term patterns of morphological variation, we monitored morphology of 31 island populations for up to 19 years. Mean limb length oscillated across the 19-year period, both increasing and decreasing substantially, yet the net effect over that period is almost no change. In years following hurricanes, limb length increases significantly more than expected by chance.

THE effect of ecological change on evolution has been a common theme for many years, but the reverse—how evolutionary dynamics affect ecological traits such as population growth rate—has only recently begun to take hold with the increasing realization that evolution can occur over ecological time scales (Schoener, 2011, 2013; DeLong et al., 2016). In 2007, Fussmann et al. surveyed the literature for examples that provided empirical support for eco-evolutionary dynamics using four criteria: (1) Does the study document population change over several generations? (2) Is there a record of genetic frequencies and their changes over time? (3) Is the mechanistic link between ecological and evolutionary dynamics plausible? (4) Is there a control? Only eight studies were found that partially supported their criteria, and none were experimental studies in the field. There have been numerous relevant studies since this survey, some of which supported one or both of the evo-to-eco and eco-to-evo links (see especially Turcotte et al., 2011 and Agrawal et al., 2013; Hendry and Kinnison, 1999; Reznick and Ghalambor, 2001; Hariston et al., 2005; Saccheri and Hanski, 2006; Ezard et al., 2009; Coulson et al., 2011; various papers this volume, including Kindsvater and Palkovacs [this volume, 2017], Tuckett et al. [this volume, 2017], Urban et al. [this volume, 2017]; recent partial reviews in Ellner [2013], Hiltunen et al. [2015], Schoener [2013], Schoener et al.

[2014]). However, moderately long-term, substantially multi-generational experiments in natural systems of eco-evolutionary dynamics—particularly how evolution affects ecology—remain elusive.

Beginning in 2008, we initiated a study in an entirely natural system, a set of small islands in the Bahamas. The current study was preceded by several other field-experimental manipulations as well as substantial observational work, providing in some cases continuous data going back to 1997. In the present study, we selected 14 islands with natural populations of the lizard *Anolis sagrei* and introduced the larger, mostly terrestrial lizard *Leiocephalus carinatus* (a known predator of smaller lizards [Schoener et al., 1982]) onto seven randomly chosen islands, leaving the other seven islands as controls. Each year, we measured properties of lizard populations—abundance, structural habitat use (perch height and diameter), morphological traits, and various components of the lizard-topped food web. In addition to the experimental islands, we monitored food-web components on three islands with no lizards to assess the effects of lizards.

This experiment has yielded major abundance change (great decrease), habitat-use change (upward shift to narrower perches), and other behavioral change (e.g., in signaling behavior [Steinberg et al., 2014]) in *A. sagrei,* as well as some

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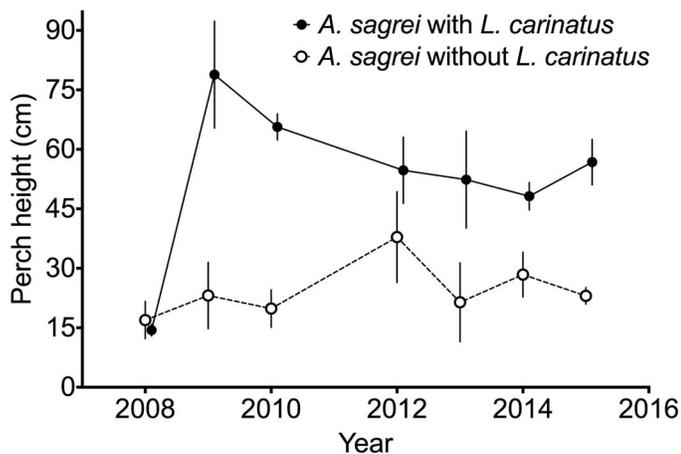[3] Division of Biological Sciences, University of Missouri, Columbia, Missouri 65211; Email: lealm@missouri.edu.
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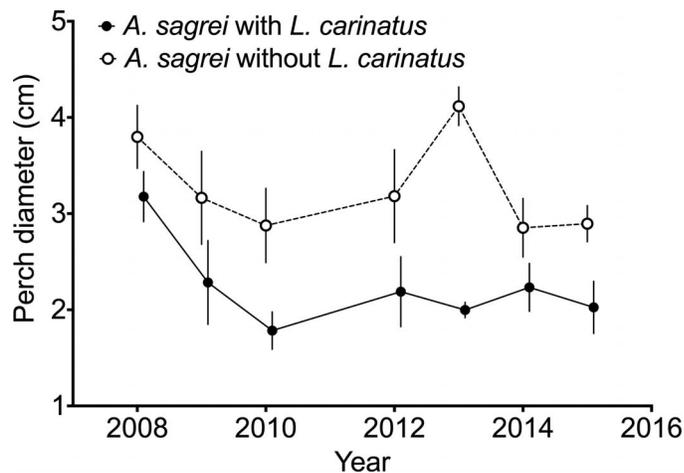
Fig. 1. Mean (±SE) perch heights of *A. sagrei* shift higher ($F_{1,7} = 17.2$, $P = 0.004$ repeated measures MANOVA; Effect size [log ratio] = 0.79) on islands after the experimental introduction of the predatory lizard *L. carinatus*. Islands on which lizards were extirpated during the course of the experiment (see text) were not included in this or subsequent analyses.

Fig. 2. Mean (±SE) perch diameters of *A. sagrei* decrease ($F_{1,7} = 5.3$, $P = 0.05$ repeated measures MANOVA; Effect size [log ratio] = 1.27) on islands after the experimental introduction of the predatory lizard *L. carinatus*.

food-web effects. However, it has produced no significant morphological change in lizard limb length and only a suggestive change in abundance of *A. sagrei* in the direction predicted by adaptive ecological change. A possible explanation for these so-far negative results is the severe effects of two hurricanes—Irene (2011) and Sandy (2012)—which exterminated *A. sagrei* on some islands while on others greatly lowered their abundance as well as that of their predator *L. carinatus*. We have taken advantage of these hurricanes to monitor the natural recolonization by lizards of islands from which they were exterminated. Such disturbance must have greatly affected the strength and even possibly the direction of selection, plausibly forestalling the expected morphological changes.

What follows is a progress report of ongoing efforts to understand the multifaceted nature of the eco-evolutionary feedbacks in *A. sagrei* in response to biotic (predator additions) and abiotic (hurricanes) perturbations and the cascading impacts on the rest of our island food webs. We begin by describing the temporal progression of habitat use, density, and morphology found for *A. sagrei* after introduction of the larger predator. We then discuss effects of the manipulation on other levels of the food web: various kinds of arthropods and plants. We summarize the data on natural colonization by *A. sagrei* in the wake of extinctions caused by the two hurricanes, and we explore long-term data on morphological change in the aftermath of hurricanes.

EFFECT OF THE LARGER LIZARD ON HABITAT USE OF THE SUBJECT LIZARD

We predicted that the introduction of the ground-dwelling predatory lizard *L. carinatus* would force *A. sagrei* to shift its habitat use up into the vegetation, decreasing the percentage of the time it was found on the ground, increasing its average perch height, and decreasing its average perch diameter. We visited each island multiple times during annual fieldwork in May and recorded structural habitat use (i.e., perch height and diameter in cm) for every undisturbed lizard encountered. For perch height and all other response variables, we used repeated-measures MANOVA, an alternative designation for "multivariate repeated measures," with treatment (*A. sagrei*

with *L. carinatus* introduced, *A. sagrei* alone) as the main between-subjects factor, time (2009–2015) as the repeated within-subjects factor, and the treatment-by-time interaction. Sphericity was significant ($P < 0.03$) for this and all other analyses except morphology ($P = 0.064$); therefore, the multivariate approach was used in all analyses for consistency. The predicted shifts occurred soon after the introduction of the predatory lizard and have been maintained over the six-year period (Figs. 1, 2). Moreover, focal behavioral surveys indicate that *A. sagrei* has altered its behavior: on islands on which the predator was introduced, *A. sagrei* produces less conspicuous visual displays (Steinberg et al., 2014).

EFFECT OF THE LARGER LIZARD ON DENSITIES OF THE SUBJECT LIZARD

Strauss et al. (2008) have argued that evolutionary change in the focal species may often influence effect size of treatments in ecological field experiments, given that ecological and evolutionary time can be commensurate. For a negative interaction such as predation, Strauss et al. (2008) hypothesized that the effect size should first increase as the prey is diminished by the predator, then decrease as the prey adapt, evolving morphologies and other kinds of traits more appropriate to their new situation and thereby eventually increasing the prey density. Indeed, lack of apparent change of ecological traits such as population size may reflect much ongoing evolution (Kinnison et al., 2015). Although there are various relevant field studies (e.g., Harmon et al., 2009; Palkovacs et al., 2009; Bassar et al., 2012; Ingram et al., 2012; Simon et al., this volume, 2017, and others cited above), as well as numerous lab studies (reviewed in Schoener, 2013; Hiltunen et al., 2015; Schoener et al., 2014), to our knowledge the specific predation effect suggested in Strauss et al. (2008) is not yet demonstrated in the field.

To estimate population size of *A. sagrei* on entire islands (which are closed systems), we used log-linear capture-recapture methods (Fienberg et al., 1999), which are promoted by an international working group including Fienberg, Buckland, Seber, and Cormack (Fienberg, pers. comm.). These methods have been described as particularly useful for modeling the capture dependencies between censuses that weather imposes on our system (Schwarz and Seber, 1999).
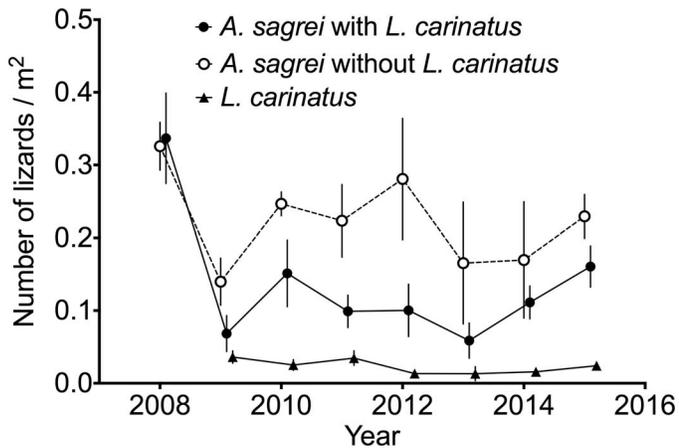
Fig. 3. Mean (±SE) densities of *A. sagrei* on islands with and without the introduced predatory lizard *L. carinatus*. Also included are mean (±SE) densities of *L. carinatus* after introduction. See text for statistical analysis.

Introduction of the larger lizard resulted in a marked decrease in the density of *A. sagrei* (Fig. 3). Densities first diverge and then converge: before Hurricane Sandy (which occurred in 2012) the effect of *L. carinatus* on density of *A. sagrei* was significant (2009–2012, $F_{1,7} = 6.9$, $P = 0.034$), but not after Sandy (2013–2015, $F_{1,7} = 1.7$, $P = 0.236$). The time-by-treatment interaction (the test for whether a return to pre-experimental densities occurs, run for the entire time series) is not significant, however (2009–2015, $F_{6,2} = 5.4$, $P = 0.165$, repeated-measures MANOVA). In view of our results on leg length, this is perhaps not surprising, as there is no significant difference in leg length through the same period of time (see below). Given the results in a previous experiment (Losos et al., 2006) in which survival selection did shift over time toward favoring shorter limbs (Fig. 4), we predict that without further severe disturbance we will eventually find a significant decrease in effect size as the lizards adapt to living in the arboreal matrix. Indeed, in a different experiment undisturbed by hurricanes (Schoener and Spiller, 1999), we found a similar reversal in effect size over the course of seven years: upon introduction of *A. sagrei*, plant damage first increased, then decreased back to the pre-introduction value, perhaps due to in part to adaptation by the herbivore prey.

EFFECT OF THE LARGER LIZARD ON LIMB LENGTH OF THE SUBJECT LIZARD

Both comparative and biomechanical studies make clear predictions about how *A. sagrei* will adapt to its use of narrower perches in the presence of *L. carinatus*: species that use broad surfaces, such as tree trunks or the ground, evolve long hindlegs and tails, whereas species specialized to use narrow surfaces have shorter limbs and tails. In addition, more arboreal species tend to have narrow heads and well-developed toepads. These trends have evolved independently on four Greater Antillean islands and among populations of *A. sagrei* on islands in the Bahamas and elsewhere (Lister, 1976; Williams, 1983; Losos et al., 1994, 1998; Calsbeek et al., 2006); however, whether population-level changes are the result of adaptive phenotypic plasticity or genetic change is always an issue. Although anoles do exhibit phenotypic plasticity in limb length (Losos et al., 2000; Kolbe and Losos, 2005), in at least some of these cases genetic change seems the more likely explanation (Kolbe et al., 2012). Biomechanical models predict
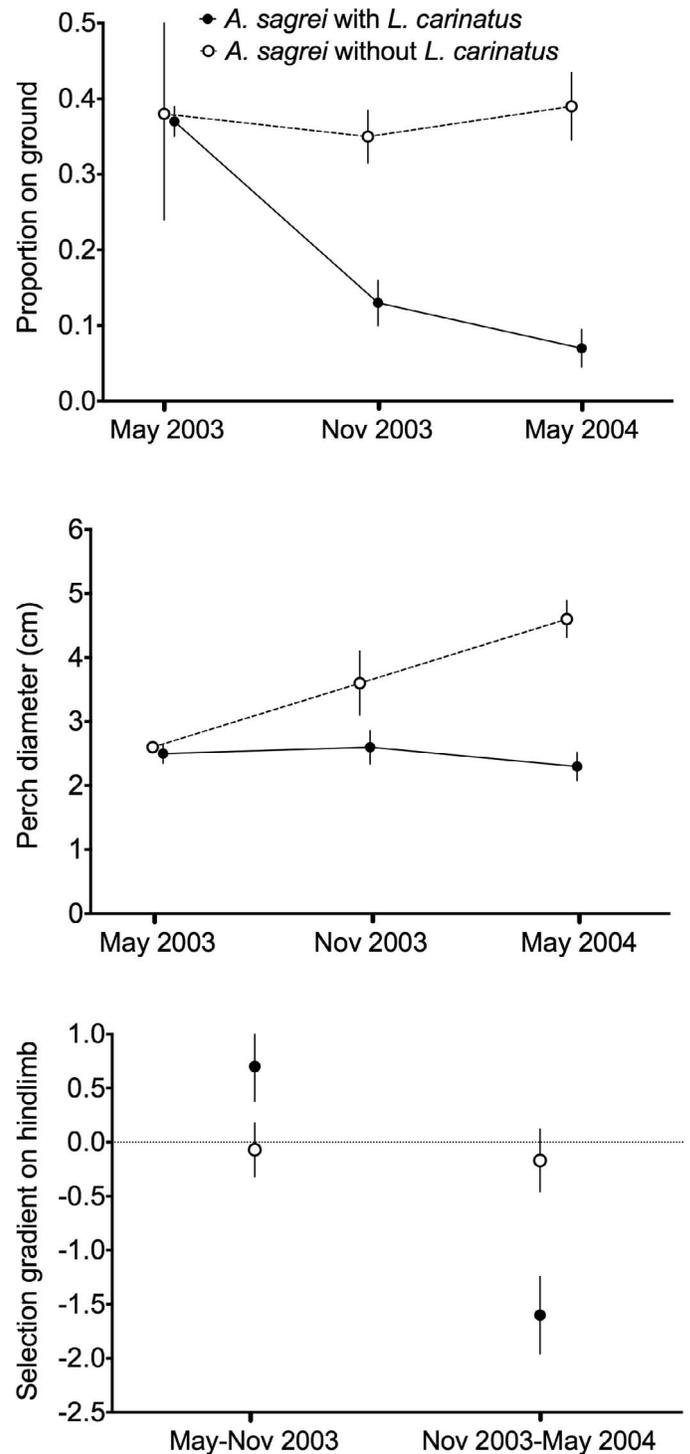
Fig. 4. Changes in habitat use and pattern of natural selection from Losos et al. (2006). For use of the ground (top) and perch diameter (middle), data from May 2003 represent habitat use before the initiation of the experiment. All data are for individuals initially measured and marked in May 2003. Lizards grew throughout the experiment, probably explaining the increase in perch diameter on control islands (an intraspecific relationship between body size and perch diameter is well established in *Anolis* lizards). (Bottom) Selection gradients were calculated for two time periods, May 2003 to November 2003 and November 2003 to May 2004. Selection gradients in the figure were adjusted for log-transformed island area (included in the repeated-measures analysis as a covariate) by using least squares means from the ANCOVA. Open symbols indicate control islands; filled symbols, introduction islands. Error bars ± SE.
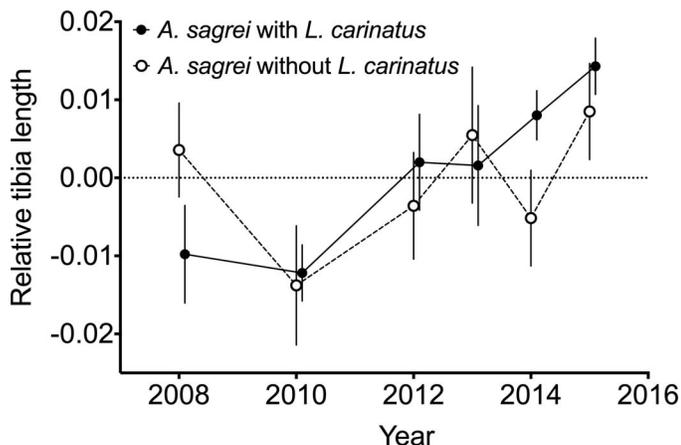
Fig. 5. Mean (±SE) tibia length for treatment islands with introduced *L. carinatus* and control islands with only *A. sagrei* (*P* = 0.53 repeated measures MANOVA). Note that this measure was taken with x-rays, and Figure 3's measure was done by hand, as well as being hindlimb not tibia. The correlations between the hindlimb measures taken by hand and the tibia by x-ray are very high: males r = 0.98 (*n* = 15), females r = 0.92 (*n* = 12) using data from mainland Great Abaco.

that lizards using narrower surfaces should evolve shorter legs, narrower heads, and larger toepads (reviewed in Losos, 2009). In accordance with these trends, our previous selection experiments revealed that once *A. sagrei* occupied higher and narrower vegetation on islands that had the predator introduced, selection favored shorter limb length (Fig. 4 taken from Losos et al., 2006).

To characterize trait change, we collected, measured, and returned lizards to their point of capture within 24 hours. We analyzed skeletal morphology from images collected with a field-portable, custom-built, digital x-ray system (minimum image dimensions 1500 × 1900; X-ray Associates East), which we used to measure snout–vent length (SVL) and tibia length using ObjectJ (https://sils.fnwi.uva.nl/bcb/objectj/), a plug-in for ImageJ (Schneider et al., 2012). We calculated mean relative tibia length as the residuals of the regression of log-tibia on log-SVL, separately for each sex, and then calculated a mean for islands in each year (2008–2015) with the sexes combined. Despite the strong effects of the predatory lizard on habitat use and density of *A. sagrei* (see above), to date there is no evidence of any difference in hindlimb morphology between populations on experimental and control islands (Fig. 5). We hypothesize that the lack of an effect may be the result of Hurricanes Irene and Sandy. Not only did populations of *A. sagrei* greatly decrease on many islands, but the populations of the predatory lizard were reduced as well; consequently, for several years, the selective effect of the experimental treatment may have been minimized. Indeed, there is a 0.83 ordinary Pearson correlation between perch-height effect size (log treatment/control) and mean number of *L. carinatus* per island in a given year. We plan to continue to monitor the islands on a yearly basis: now that the islands and their populations have recovered from the hurricanes, we expect that the treatments will begin to diverge in morphology.

EFFECT OF ECO-EVOLUTIONARY CHANGE ON COMPONENTS OF THE FOOD WEB

To attempt to experimentally document evolutionary trait-mediated indirect effects (Ohgushi et al., 2012; El-Sabaawi, this volume, 2017; Hendry, 2017), we measured a number of

food web attributes: (1) Web spiders were censused by searching the entirety of each island and recording the species identity and web height of each spider individual or fresh web observed. (2) Relative abundance of aerial arthropods was measured on 2–3 focal buttonwood shrubs (see below) on each island using sticky traps (22 × 14 cm sheets of clear plastic coated with Tangletrap® adhesive and tied to the vegetation). On each shrub, one trap was tied in the upper vegetation (1–2 m above ground) and one was tied lower (0.2–0.5 m). After 24 hr, body length and taxon (to order or lower when possible) of each arthropod caught in each trap was recorded in the field. (3) Ground arthropods were sampled with plastic bowls filled with 500 ml of water and a trace amount of detergent. Two bowls were placed on the ground under each focal shrub, and specimens caught after 24 hr were preserved. (4) We measured leaf damage and foliage growth on 2–3 buttonwood (*Conocarpus erectus*) shrubs on each island from May to December as follows. In May, on each shrub, three randomly chosen branches were tagged in the upper (1–2 m above ground) and in the lower (0.2–0.5 m) vegetation layers. On each branch, the most distal leaves present were marked with ink. In December, only leaves that emerged after May (those more distal than the marked ones) were collected. Sampled leaves were immediately pressed and then photographed. Total leaf and damaged areas were measured digitally from photographs using SigmaScan Pro Image Analysis System. Percent of the leaf area damaged on each shrub was computed by summing the total and damaged areas of all the leaves sampled. We categorized three different types of damage: holes, scars, and lines. Growth rate per branch was the sum of the total leaf areas that emerge from May to December.

Through 2012 only a few food-web elements showed significant changes, even though many responded in previous experiments (Schoener et al., 2002, and references therein). Web-spider density immediately increased on introduction islands and tended to remain higher than on islands with only *A. sagrei* present (repeated measures ANOVA: $F_{1,13} = 6.33$, $P = 0.026$; Effect size [log ratio] = 0.24). We suggest that the positive effect of *L. carinatus* on web spiders was indirect: large lizards reduced the density of the small lizard (the major web-spider predator), which increased web spiders. We found no significant difference between treatments in the height of webs above the ground (repeated measures ANOVA: $F_{2,12} = 1.71$, $P = 0.22$). Numbers of cursorial spiders (mostly lycosids and salticids) were higher on islands with lizards absent than on islands with only *A. sagrei* (repeated measures ANOVA: $F_{1,14} = 45.21$, $P = 0.0001$; Effect size = 1.26) and were higher on islands with introduced *L. carinatus* than on islands with only *A. sagrei* ($F_{1,13} = 6.85$, $P = 0.021$; Effect size = 0.46). As for the web spiders, we suggest that the negative effect of small lizards on cursorial spiders was direct, whereas the positive effect of large lizards was indirect. Although there was no significant overall difference among treatments in the number of springtails caught in bowls (repeated measures ANOVA: $F_{2,13} = 1.30$, $P = 0.31$), in 2011 they were noticeably lower on introduction islands than on islands with only small lizards (ANOVA: $F_{1,14} = 4.90$, $P = 0.044$; Effect size = 0.35) and on no-lizard islands than on islands with only small lizards ($F_{1,14} = 5.55$, $P = 0.034$; Effect size = 0.61). We suggest that this pattern might be caused by a 4-level trophic cascade in which large lizards reduce small lizards, leading to an increase in cursorial spiders, which decreases springtails. We expected the more arboreal arthropods to decline with the increasingly arboreal adaptation of

A. sagrei and plant damage from arthropod herbivory to decrease disproportionately in the higher vegetation, but neither happened. Nor was there an effect on foliage growth. Nothing has substantially changed through 2015. Because the morphological changes are not yet in the predicted direction, it is unsurprising that most food-web expectations are unfulfilled. Hence as above, we can attribute the lack of response to effects of hurricanes: recall (see above) that populations of *Anolis sagrei* were not only greatly decreased on many islands, but the populations of the predatory lizard were greatly reduced; consequently, for several years, the selective effect of the experimental treatment may have been minimized.

EFFECT OF HURRICANES ON THE EXPERIMENTAL SYSTEM

We have been monitoring 44 islands that have had *A. sagrei* in the past, some for decades. Of those, 26 islands had their populations exterminated by Hurricane Sandy (as determined in 2013 censuses) Only three of those 26 were recolonized in 2014 (although one of the no-lizard control islands was colonized for the first time), and one was recolonized in 2015. Hurricanes have had devastating effects on some islands in our experiments, but here is one benefit: by clearing all lizards from relatively large islands, for the first time we are able to measure lizard recolonization of islands of this size. Our genetic studies have allowed us to estimate rates of immigration onto already occupied islands (Kolbe et al., 2012), and from those we might have expected relatively high recolonization rates. However, the results to date do not support this expectation; recolonization rates have been very low, even for islands much larger than the local threshold area for *A. sagrei* (see also Schoener and Schoener, 1983a, 1983b).

Our current study is embedded in a much longer-term study. Over the past two decades, we have been tracking morphology of *A. sagrei* in 31 populations in the same region. Some islands were part of previous experiments; some have never been included in any of our previous studies. Over this 19-year period, mean limb length has barely changed. However, this stasis is more apparent than real, as limb length has varied markedly over this period (Fig. 6). Research on Darwin's finches has illustrated how long periods of little net evolutionary change can result from oscillating selection (Grant and Grant, 2014)—i.e., directional selection that alternates in direction (Gibbs and Grant, 1987). The prevalence of oscillating selection is currently debated (Siepielski et al., 2009, 2013; Morrissey and Hadfield, 2012), and the extent to which long-term stasis is the result of alternating selection is unclear. Our time series suggests such a pattern: in years following hurricanes, limb length tends to increase, followed by a decline (Fig. 6): all four years after a hurricane show an increase, and three of those four are the largest increase in the time series. A Monte Carlo simulation was performed, in which we computed 1000 random arrangements of the four hurricanes over the time series and computed as the test statistic the signed change in limb length the year before a given year. The increase in limb length after a hurricane year is unusually large: the two-tailed $P = 0.005$, that is, only 0.5 percent of 1000 random arrangements of the four hurricanes over the time series give a more extreme difference in either direction than the observed. We will continue to measure morphology for lizards on these islands, as well as measure the morphology of any newly established populations resulting from natural
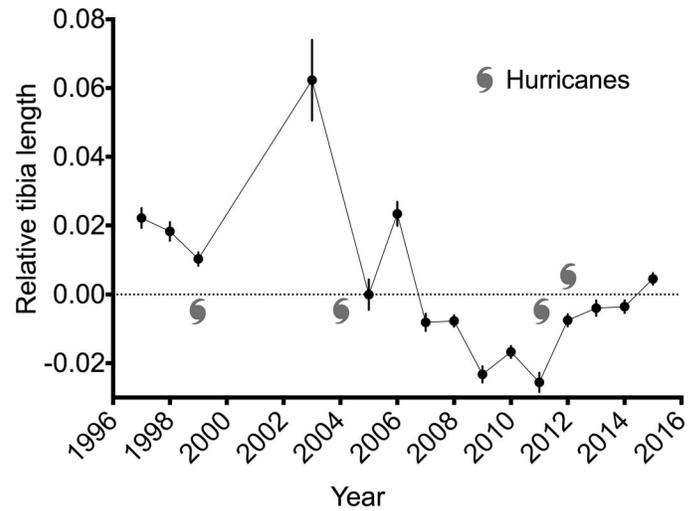
Fig. 6. Mean (±SE) relative limb length (residuals from the tibia length vs. snout–vent length regression, separate by sex) across all islands has fluctuated over the 19-year study period with little net change (year-to-year change results from within-island evolution, population extinction, and the inclusion of different islands at different points in the study; trends are similar when only the nine islands sampled across the 19-year period are considered [results not shown]). Limb values increase after hurricanes ($P = 0.005$, see text).

colonization (including the three recent populations we have detected in the last three years). Our prediction is that limb length will decline across all populations in the absence of further hurricanes but will increase if the islands are hit by another hurricane.

CONCLUSION

We caution that the results herein represent an interim report. As described, certain results (habitat shifts in *A. sagrei*) are exceptionally strong, certain results (changes in density of *A. sagrei*, a few food-web effects) are moderate, and certain results (morphological changes in *A. sagrei*) show no trend so far. Hurricanes have impacted the study site greatly during the course of the experiment, and these may have slowed down some of the expected eco-evolutionary changes and food-web effects, a possibility we will hopefully be able to assess in a few years. Indeed, extreme climatic events may often reset the pathway that eco-evolutionary dynamics is following, a possibility explored further in a recent Gordon conference keynote address (T. W. Schoener, unpubl.), and which is an example of context-dependence as conceptualized by Tuckett et al. (this volume, 2017). Hurricanes have not been an unmitigated negative, however: they have allowed us to gather unique data on natural recolonization rates as well as study their possible effects on morphological and other traits. Our exploratory finding that hindlimb length of *A. sagrei* increases after the four hurricanes over the past 19 years generates the testable hypothesis that hurricanes select for longer legs, a phenomenon that we are actively investigating both empirically and theoretically. Ultimately, our goal is to tie together the effects of major disturbances, in our case hurricanes, to chronic eco-evolutionary dynamics in metacommunities.

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