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

Thomas W. Schoener

Jason J. Kolbe
University of Rhode Island, jjkolbe@uri.edu

Manuel Leal

Jonathan B. Losos

David A. Spiller

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6   # evolutionary Dynamics of the Influential Lizard *Anolis*
7   # *sagrei*: A Mid-term Report

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9   Thomas W. Schoener[1], Jason J. Kolbe[2], Manuel Leal[3], Jonathan B. Losos[4],

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11   David A. Spiller [1]

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23   [1] Department of Evolution and Ecology, University of California, Davis CA 95616
24   (twschoener@ucdavis.edu, daspiller@ucdavis.edu)

25

26   [2] Department of Biological Sciences, University of Rhode Island, Kingston, RI
27   02881 (jjkolbe@uri.edu)

28

29   [3] Division of Biological Sciences, University of Missouri, Columbia, MO 65211
30   (lealm@missouri.edu)

31

32   [4] Museum of Comparative Zoology and Department of Organismic and
33   Evolutionary Biology, Harvard University, Cambridge, MA 02138
34   (jlosos@oeb.harvard.edu)

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(ABSTRACT)

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39   Only a handful of multi-generational experiments in natural systems of eco-evolutionary

40 dynamics currently exist, despite Fussmann et al.'s call for more such studies nearly a decade ago. To

41 perform such a study, in 2008 we introduced the lizard *Leiocephalus carinatus*, a predator (and possible

42 food competitor) of the lizard *Anolis sagrei*, to seven islands having *A. sagrei*, with seven unmanipulated

43 islands having *A. sagrei* as controls. Almost immediately, *L. carinatus*, which is larger and more

44 terrestrial than *A. sagrei*, caused a major habitat shift in *A. sagrei* away from the ground and toward

45 higher and thinner perches; focal behavioral surveys showed that on islands where its predator was

46 introduced, *A. sagrei* had less conspicuous visual displays. The expected pattern for density of *A. sagrei* is

47 that it would decrease markedly at first via predation from the larger lizard, but then it would increase as

48 the habitat shift selected for individuals better able to live in higher vegetation. Data through 2015 show

49 this pattern, but a return to previous densities (time-by-treatment interaction) was not yet significant. A

50 previous within-generation selection study and comparative data suggest that short legs should evolve as

51 the lizards adapt to better maneuver on the thin perches of higher vegetation. However, no indication of

52 the expected morphological change in limb length was present through 2015. Previous studies showed *A.*

53 *sagrei* producing many effects on lower levels of the food web, some quite large. In this study through

54 2012, we found significant differences only in spiders (web and ground). A possible complication is that

55 the study site was hit by two major hurricanes in the last five years, decreasing population sizes of both

56 lizard species and reducing the experimental perturbations. A benefit of the hurricanes, however, is that

57 they eliminated lizards from some islands, providing the opportunity to monitor natural recolonization,

58 the frequency of which has eco-evolutionary implications. Annual surveys of the 46 islands that lost

59 lizards showed that recolonization is rather slow. To explore long-term patterns of morphological

60 variation, we monitored morphology of 31 island populations for up to 19 years. Mean limb length

61 oscillated across the 19-year period, both increasing and decreasing substantially, yet the net effect over

62   that period is almost no change. In years following hurricanes, limb length increases significantly more

63   than expected by chance.

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65 **(BODY OF TEXT)**

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68   The effect of ecological change on evolution has been a common theme for many years, but the

69 reverse—how evolutionary dynamics affect ecological traits such as population growth rate—has only

70 recently begun to take hold with the increasing realization that evolution can occur over ecological time

71 scales (Schoener, 2011, 2013; DeLong et al. 2016). In 2007, Fussmann et al. surveyed the literature for

72 examples that provided empirical support for eco-evolutionary dynamics using four criteria: (1) Does the

73 study document population change over several generations? (2) Is there a record of genetic frequencies

74 and their changes over time? (3) Is the mechanistic link between ecological and evolutionary dynamics

75 plausible? (4) Is there a control? Only eight studies were found that partially supported their criteria, and

76 none were experimental studies in the field. There have been numerous relevant studies since this survey,

77 some of which supported one or both of the evo-to-eco and eco-to-evo links (see especially Turcotte et

78 al., 2011 and Agrawal et al., 2013; Hendry and Kinnison 1999, Reznick and Ghalambor 2001, Hariston et

79 al. 2005, Saccheri and Hanski 2006, Ezard et al. 2009, Coulson et al. 2011; various papers this volume,

80 including Kindsvater and Palkovacs, Tuckett et al., Urban et al; recent partial reviews in Ellner [2013],

81 Hiltunen et al. [2015], Schoener [2013], Schoener et al. [2014]). However, moderately long-term,

82 substantially multi-generational experiments in natural systems of eco-evolutionary dynamics—

83 particularly how evolution affects ecology—remain elusive.

84   Beginning in 2008, we initiated a study in an entirely natural system, a set of small islands in the

85 Bahamas. The current study was preceded by several other field-experimental manipulations as well as

86 substantial observational work, providing in some cases continuous data going back to 1997. In the

87 present study, we selected 14 islands with natural populations of the lizard *Anolis sagrei* and introduced

88 the larger, mostly terrestrial lizard *Leiocephalus carinatus* (a known predator of smaller lizards [Schoener

89 et al., 1982]) onto seven randomly chosen islands, leaving the other seven islands as controls. Each year,

90 we measured properties of lizard populations—abundance, structural habitat use (perch height and

91   diameter), morphological traits, and various components of the lizard-topped food web. In addition to the

92   experimental islands, we monitored food-web components on three islands with no lizards to assess the

93   effects of lizards.

94   This experiment has yielded major abundance change (great decrease), habitat-use change (upward

95   shift to narrower perches), and other behavioral change (e.g. in signaling behavior [Steinberg et al. 2014])

96   in *A. sagrei,* as well as some food-web effects. However, it has produced no significant morphological

97   change in lizard limb length and only a suggestive change in *A. sagrei* abundance in the direction

98   predicted by adaptive ecological change. A possible explanation for these so-far negative results is the

99   severe effects of two hurricanes—Irene (2011) and Sandy (2012)—which exterminated *A. sagrei* on some

100   islands while on others greatly lowered their abundance as well as that of their predator *L. carinatus.* We

101   have taken advantage of these hurricanes to monitor the natural recolonization by lizards of islands from

102   which they were exterminated. Such disturbance must have greatly affected the strength and even

103   possibly the direction of selection, plausibly forestalling the expected morphological changes.

104   What follows is a progress report of ongoing efforts to understand the multifaceted nature of the eco-

105   evolutionary feedbacks in *A. sagrei* in response to biotic (predator additions) and abiotic (hurricanes)

106   perturbations and the cascading impacts on the rest of our island food webs. We begin by describing the

107   temporal progression of habitat use, density and morphology found for *A. sagrei* after introduction of the

108   larger predator. We then discuss effects of the manipulation on other levels of the food web: various kinds

109   of arthropods and plants. We summarize the data on natural colonization by *A. sagrei* in the wake of

110   extinctions caused by the two hurricanes, and we explore long-term data on morphological change in the

111   aftermath of hurricanes.

112   **EFFECT OF THE LARGER LIZARD ON HABITAT USE OF THE SUBJECT LIZARD.** We

113   predicted that the introduction of the ground-dwelling predatory lizard *L. carinatus* would force *A. sagrei*

114   to shift its habitat use up into the vegetation, decreasing the percentage of the time it was found on the

115   ground, increasing its average perch height and decreasing its average perch diameter. We visited each

116   island multiple times during annual fieldwork in May and recorded structural habitat use (i.e., perch

117 height and diameter in cm) for every undisturbed lizard encountered. For perch height and all other

118 response variables, we used repeated-measures MANOVA, an alternative designation for "multivariate

119 repeated measures", with treatment (*A. sagrei* with *L. carinatus* introduced, *A. sagrei* alone) as the main

120 between-subjects factor, time (2009-2015) as the repeated within-subjects factor, and the treatment-by-

121 time interaction. Sphericity was significant ($p < 0.03$) for this and all other analyses except morphology (p

122 = 0.064); therefore the multivariate approach was used in all analyses for consistency. The predicted

123 shifts occurred soon after the introduction of the predatory lizard and have been maintained over the six-

124 year period (Figs. 1 & 2). Moreover, focal behavioral surveys indicate that *A. sagrei* has altered its

125 behavior: on islands on which the predator was introduced, *A. sagrei* produces less conspicuous visual

126 displays (Steinberg et al., 2014).

127

128 **EFFECT OF THE LARGER LIZARD ON DENSITIES OF THE SUBJECT LIZARD.** Strauss et al.

129 (2008) have argued that evolutionary change in the focal species may often influence effect size of

130 treatments in ecological field experiments, given that ecological and evolutionary time can be

131 commensurate. For a negative interaction such as predation, Strauss et al. (2008) hypothesized that the

132 effect size should first increase as the prey is diminished by the predator, then decrease as the prey adapt,

133 evolving morphologies and other kinds of traits more appropriate to their new situation and thereby

134 eventually increasing the prey density. Indeed, lack of apparent change of ecological traits such as

135 population size may reflect much ongoing evolution (Kinnison et al., 2015). Although there are various

136 relevant field studies (e.g. Bassar et al., 2012; Harmon et al., 2009; Ingram et al., 2012; Palkovacs et al.,

137 2009; Simon et al. THIS VOLUME AND OTHERS CITED ABOVE), as well as numerous lab studies

138 (reviewed in Hiltunen et al., 2015; Schoener, 2013; Schoener et al., 2015), to our knowledge the specific

139 predation effect suggested in Strauss et al. (2008) is not yet demonstrated in the field.

140 To estimate population size of *A. sagrei* on entire islands (which are closed systems), we used log-

141 linear capture-recapture methods (Fienberg et al., 1999), which are promoted by an international working

142 group including Fienberg, Buckland, Seber and Cormack (Fienberg, pers. comm.). These methods have

143   been described as particularly useful for modeling the capture dependencies between censuses that

144   weather imposes on our system (Schwarz and Seber, 1999).

145   Introduction of the larger lizard resulted in a marked decrease in the density of *A. sagrei* (Fig. 3).

146   Densities first diverge and then converge: before Hurricane Sandy (which occurred in 2012) the effect of

147   *L. carinatus* on *A. sagrei* density was significant (2009-2012, $F_{1,7} = 6.9$, p=0.034), but not after Sandy

148   (2013-2015, $F_{1,7} = 1.7$, p=0.236). The time-by-treatment interaction (the test for whether a return to pre-

149   experimental densities occurs, run for the entire time series) is not significant, however (2009-2015, $F_{6,2} =$

150   5.4, p = 0.165, repeated-measures MANOVA). In view of our results on leg length, this is perhaps not

151   surprising, as there is no significant difference in leg length through the same period of time (see below).

152   Given the results in a previous experiment (Losos et al., 2006) in which survival selection did shift over

153   time toward favoring shorter limbs (Fig. 4), we predict that without further severe disturbance we will

154   eventually find a significant decrease in effect size as the lizards adapt to living in the arboreal matrix.

155   Indeed, in a different experiment undisturbed by hurricanes (Schoener and Spiller, 1999), we found a

156   similar reversal in effect size over the course of seven years: upon introduction of *A. sagrei*, plant damage

157   first increased, then decreased back to the pre-introduction value, perhaps due to in part to adaptation by

158   the herbivore prey.

159

160   **EFFECT OF THE LARGER LIZARD ON LIMB LENGTH OF THE SUBJECT LIZARD.** Both

161   comparative and biomechanical studies make clear predictions about how *A. sagrei* will adapt to its use of

162   narrower perches in the presence of *L. carinatus*: species that use broad surfaces, such as tree trunks or

163   the ground, evolve long hindlegs and tails, whereas species specialized to use narrow surfaces have

164   shorter limbs and tails. In addition, more arboreal species tend to have narrow heads and well-developed

165   toepads. These trends have evolved independently on four Greater Antillean islands and among *A. sagrei*

166   populations on islands in the Bahamas and elsewhere (Lister, 1976; Williams, 1983; Losos et al., 1994,

167   1998; Calsbeek et al., 2006); however, whether population-level changes are the result of adaptive

168   phenotypic plasticity or genetic change is always an issue. Although anoles do exhibit phenotypic

169 plasticity in limb length (Losos et al., 2000; Kolbe and Losos, 2005), in at least some of these cases

170 genetic change seems the more likely explanation (Kolbe et al., 2012).). Biomechanical models predict

171 that lizards using narrower surfaces should evolve shorter legs, narrower heads, and larger toepads

172 (reviewed in Losos, 2009). In accordance with these trends, our previous selection experiments revealed

173 that once *A. sagrei* occupied higher and narrower vegetation on islands that had the predator introduced,

174 selection favored shorter limb length (Fig. 4 taken from Losos et al., 2006]).

175

176   To characterize trait change, we collected, measured and returned lizards to their point of capture

177 within 24 hours. We analyzed skeletal morphology from images collected with a field-portable, custom-

178 built, digital x-ray system (minimum image dimensions 1500 x 1900; X-ray Associates East), which we

179 used to measure snout-vent length (SVL) and tibia length using ObjectJ

180 (https://sils.fnwi.uva.nl/bcb/objectj/), a plug-in for ImageJ (Schneider et al., 2012). We calculated mean

181 relative tibia length as the residuals of the regression of log-tibia on log-SVL, separately for each sex, and

182 then calculated a mean for islands in each year (2008-2015) with the sexes combined. Despite the strong

183 effects of the predatory lizard on *A. sagrei* habitat use and density (see above), to date there is no

184 evidence of any difference in hindlimb morphology between populations on experimental and control

185 islands (Fig. 5). We hypothesize that the lack of an effect may be the result of Hurricanes Irene and

186 Sandy. Not only did *A. sagrei* populations greatly decrease on many islands, but the populations of the

187 predatory lizard were reduced as well; consequently, for several years, the selective effect of the

188 experimental treatment may have been minimized. Indeed, there is a 0.83 ordinary Pearson correlation

189 between perch-height effect size (log treatment/control) and mean number of *L. carinatus* per island in a

190 given year. We plan to continue to monitor the islands on a yearly basis: now that the islands and their

191 populations have recovered from the hurricanes, we expect that the treatments will begin to diverge in

192 morphology.

193

194   **EFFECT OF ECO-EVOLUTIONARY CHANGE ON COMPONENTS OF THE FOOD WEB.** To

195   attempt to experimentally document evolutionary trait-mediated indirect effects (Ohgushi et al., 2013), we

196   measured a number of food web attributes: (1) Web spiders were censused by searching the entirety of

197   each island and recording the species identity and web height of each spider individual or fresh web

198   observed. (2) Relative abundance of aerial arthropods was measured on 2-3 focal buttonwood shrubs (see

199   below) on each island using sticky traps (22 x 14 cm sheets of clear plastic coated with Tangletrap®

200   adhesive and tied to the vegetation). On each shrub, one trap was tied in the upper vegetation (1-2 m

201   above ground) and one was tied lower (0.2-0.5 m). After 24 hr, body length and taxon (to order or lower

202   when possible) of each arthropod caught in each trap was recorded in the field. (3) Ground arthropods

203   were sampled with plastic bowls filled with 500 ml of water and a trace amount of detergent. Two bowls

204   were placed on the ground under each focal shrub and specimens caught after 24 hr were preserved. (4)

205   We measured leaf damage and foliage growth on 2-3 buttonwood (*Conocarpus erectus*) shrubs on each

206   island from May to December as follows. In May, on each shrub, three randomly chosen branches were

207   tagged in the upper (1-2 m above ground) and in the lower (0.2-0.5 m) vegetation layers. On each branch,

208   the most distal leaves present were marked with ink. In December, only leaves that emerged after May

209   (those more distal than the marked ones) were collected. Sampled leaves were immediately pressed and

210   then photographed. Total leaf and damaged areas were measured digitally from photographs using

211   SigmaScan Pro Image Analysis System. Percent of the leaf area damaged on each shrub was computed by

212   summing the total and damaged areas of all the leaves sampled. We categorized three difference types of

213   damage: holes, scars and lines. Growth rate per branch was the sum of the total leaf areas that emerge

214   from May to December.

215   Through 2012 only a few food-web elements showed significant changes, even though many

216   responded in previous experiments (Schoener et al., 2002, and references therein). Web-spider density

217   immediately increased on introduction islands and tended to remain higher than on islands with only *A.*

218   *sagrei* present (repeated measures ANOVA: $F_{1,13} = 6.33$, p=0.026; Effect size (log ratio) = 0.24). We

219   suggest that the positive effect of *L. carinatus* on web spiders was indirect: large lizards reduced the

220   density of the small lizard (the major web-spider predator), which increased web spiders. We found no

221   significant difference between treatments in the height of webs above the ground (repeated measures

222   ANOVA: $F_{2,12} = 1.71$, p=0.22). Numbers of cursorial spiders (mostly lycosids and salticids) were higher

223   on islands with lizards absent than on islands with only *A. sagrei* (repeated measures ANOVA: $F_{1,14} =$

224   45.21, p=0.0001; Effect size = 1.26) and were higher on *L. carinatus* introduction islands than on islands

225   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

226   negative effect of small lizards on cursorial spiders was direct, whereas the positive effect of large lizards

227   was indirect. Although there was no significant overall difference among treatments in the number of

228   springtails caught in bowls (repeated measures ANOVA: $F_{2,13} = 1.30$, p=0.31), in 2011 they were

229   noticeably lower on introduction islands than on islands with only small lizards (ANOVA: $F_{1,14} = 4.90$,

230   p=0.044; Effect size = 0.35) and on no-lizard islands than on islands with only small lizards ($F_{1,14} = 5.55$,

231   p=0.034; Effect size = 0.61). We suggest that this pattern might be caused by a 4-level trophic cascade in

232   which large lizards reduce small lizards, leading to an increase in cursorial spiders which decreases

233   springtails. We expected the more arboreal arthropods to decline with the increasingly arboreal adaptation

234   of *A. sagrei* and plant damage from arthropod herbivory to decrease disproportionately in the higher

235   vegetation, but neither happened. Nor was there an effect on foliage growth. Nothing has substantially

236   changed through 2015. Because the morphological changes are not yet in the predicted direction, it is

237   unsurprising that most food-web expectations are unfulfilled. Hence as above, we can attribute the lack of

238   response to effects of hurricanes: recall (see above) that *Anolis sagrei* populations were not only greatly

239   decreased on many islands, but the populations of the predatory lizard were greatly reduced;

240   consequently, for several years, the selective effect of the experimental treatment may have been

241   minimized.

242

243   **EFFECT OF HURRICANES ON THE EXPERIMENTAL SYSTEM.** We are currently yearly

244   monitoring 46 islands that have had *A. sagrei* in the past (all were monitored for at least six years, and

245   some for decades). Of those, 27 islands had their populations exterminated by Hurricane Sandy (as

246   determined in 2013 censuses). Only three of those 27 were recolonized in 2014 (although one of the no-

247   lizard control islands was colonized for the first time), and one was recolonized in 2015. Hurricanes have

248   had devastating effects on some islands in our experiments, but here is one benefit: by clearing all lizards

249   from relatively large islands, for the first time we are able to measure lizard recolonization of islands of

250   this size. Our genetic studies have allowed us to estimate rates of immigration onto already occupied

251   islands (Kolbe et al., 2012), and from those we might have expected relatively high recolonization rates.

252   However, the results to date do not support this expectation; recolonization rates have been very low,

253   even for islands much larger than the local threshold area for *A. sagrei* (see also Schoener and Schoener,

254   1983a,b).

255   Our current study is embedded in a much longer-term study. Over the past two decades, we have

256   been tracking *A. sagrei* morphology in 31 populations in the same region. Some islands were part of

257   previous experiments; some have never been included in any of our previous studies. Over this 19-year

258   period, mean limb length has barely changed. However, this stasis is more apparent than real, as limb

259   length has varied markedly over this period (Fig. 6). Research on Darwin's finches has illustrated how

260   long periods of little net evolutionary change can result from oscillating selection (Grant and Grant, 2014)

261   -- i.e., directional selection that alternates in direction (Gibbs and Grant, 1987). The prevalence of

262   oscillating selection is currently debated (Siepielski et al., 2009, 2013; Morrissey and Hadfield, 2012),

263   and the extent to which long-term stasis is the result of alternating selection is unclear. Our time series

264   suggests such a pattern: in years following hurricanes, limb length tends to increase, followed by a decline

265   (Fig. 6): all four years after a hurricane show an increase, and three of those four are the largest increase

266   in the time series. A Monte Carlo simulation was performed, in which we computed 1000 random

267   arrangements of the four hurricanes over the time series and computed as the test statistic the signed

268   change in limb length the year before a given year. The increase in limb length after a hurricane year is

269   unusually large: the two-tailed $P = 0.005$, that is, only 0.5 percent of 1000 random arrangements of the

270   four hurricanes over the time series give a more extreme difference in either direction than the observed.

271   We will continue to measure morphology for lizards on these islands, as well as measure the morphology

272   of any newly-established populations resulting from natural colonization (including the three recent

273   populations we have detected in the last three years). Our prediction is that limb length will decline across

274   all populations in the absence of further hurricanes but will increase if the islands are hit by another

275   hurricane.

276   **CONCLUSION.** We caution that the results herein represent an interim report. As described, certain

277   results (*A. sagrei* habitat shifts) are exceptionally strong, certain results (*A. sagrei* density changes, a few

278   food-web effects) are moderate, and certain results (*A.sagrei* morphological changes) show no trend so

279   far. Hurricanes have impacted the study site greatly during the course of the experiment, and these may

280   have slowed down some of the expected eco-evolutionary changes and food-web effects, a possibility we

281   will hopefully be able to assess in a few years. Indeed, extreme climatic events may often reset the

282   pathway that eco-evolutionary dynamics is following, a possibility explored further in a recent Gordon

283   conference keynote address (T.W. Schoener, unpublished), and which is an example of context-

284   dependence as conceptualized by Tuckett et al. (THIS VOLUME). Hurricanes have not been an

285   unmitigated negative, however: they have allowed us to gather unique data on natural recolonization rates

286   as well as study their possible effects on morphological and other traits. Our exploratory finding that *A.*

287   *sagrei* hindlimb length increases after the four hurricanes over the past 19 years generates the testable

288   hypothesis that hurricanes select for longer legs, a phenomenon that we are actively investigating both

289   empirically and theoretically. Ultimately, our goal is to tie together the effects of major disturbances, in

290   our case hurricanes, to chronic eco-evolutionary dynamics in metacommunities.

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436

437 **(FIGURE CAPTIONS)**.

438

439 Fig. 1. Mean (±SE) perch heights of *A. sagrei* shift higher ($F_{1,7}$ = 17.2, p = 0.004 repeated measures

440 MANOVA; Effect size (log ratio) = 0.79) on islands after the experimental introduction of the predatory

441 lizard *L. carinatus*. Islands on which lizards were extirpated during the course of the experiment (see

442 text) were not included in this or subsequent analyses.

443

444 Fig. 2. Mean (±SE) perch diameters of *A. sagrei* decrease ($F_{1,7}$ = 5.3, p = 0.05 repeated measures

445 MANOVA; Effect size (log ratio) = 1.27) on islands after the experimental introduction of the predatory

446 lizard *L. carinatus*.

447

448 Fig. 3. Mean (±SE) densities of *A. sagrei* on islands with and without the introduced predatory lizard *L.*

449 *carinatus*. Also included are mean (±SE) densities of *L. carinatus* after introduction. See text for

450 statistical analysis.

451

452 Fig, 4. Changes in habitat use and pattern of natural selection from Losos et al. (2006). For use of the

453 ground (top) and perch diameter (middle), data from May 2003 represents habitat use before the initiation

454 of the experiment. All data are for individuals initially measured and marked in May 2003. Lizards grew

455 throughout the experiment, probably explaining the increase in perch diameter on control islands (an

456 intraspecific relationship between body size and perch diameter is well established in *Anolis* lizards).

457 (bottom) Selection gradients were calculated for two time periods, May 2003 to November 2003 and

458 November 2003 to May 2004. Selection gradients in the figure were adjusted for log-transformed island

459 area (included in the repeated-measures analysis as a covariate) by using least squares means from the

460 ANCOVA. Open symbols indicate control islands; filled symbols, introduction islands. Error bars ± SE.

461

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.

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 9 islands sampled across the 19-year period are considered [results not shown]). Limb values increase after hurricanes (P=0.005, see text).

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492 **(AUTHOR ADDRESSES)**

493

494

495 Thomas Schoener, David Spiller: Department of Evolution and Ecology,

496 University of California, Davis CA 95616 (twschoener@ucdavis.edu,

497 daspiller@ucdavis.edu)

498

499 Jason Kolbe: Department of Biological Sciences, University of Rhode Island,

500 Kingston, RI 02881 (jjkolbe@uri.edu)

501

502 Manuel Leal: Division of Biological Sciences, University of Missouri, Columbia,
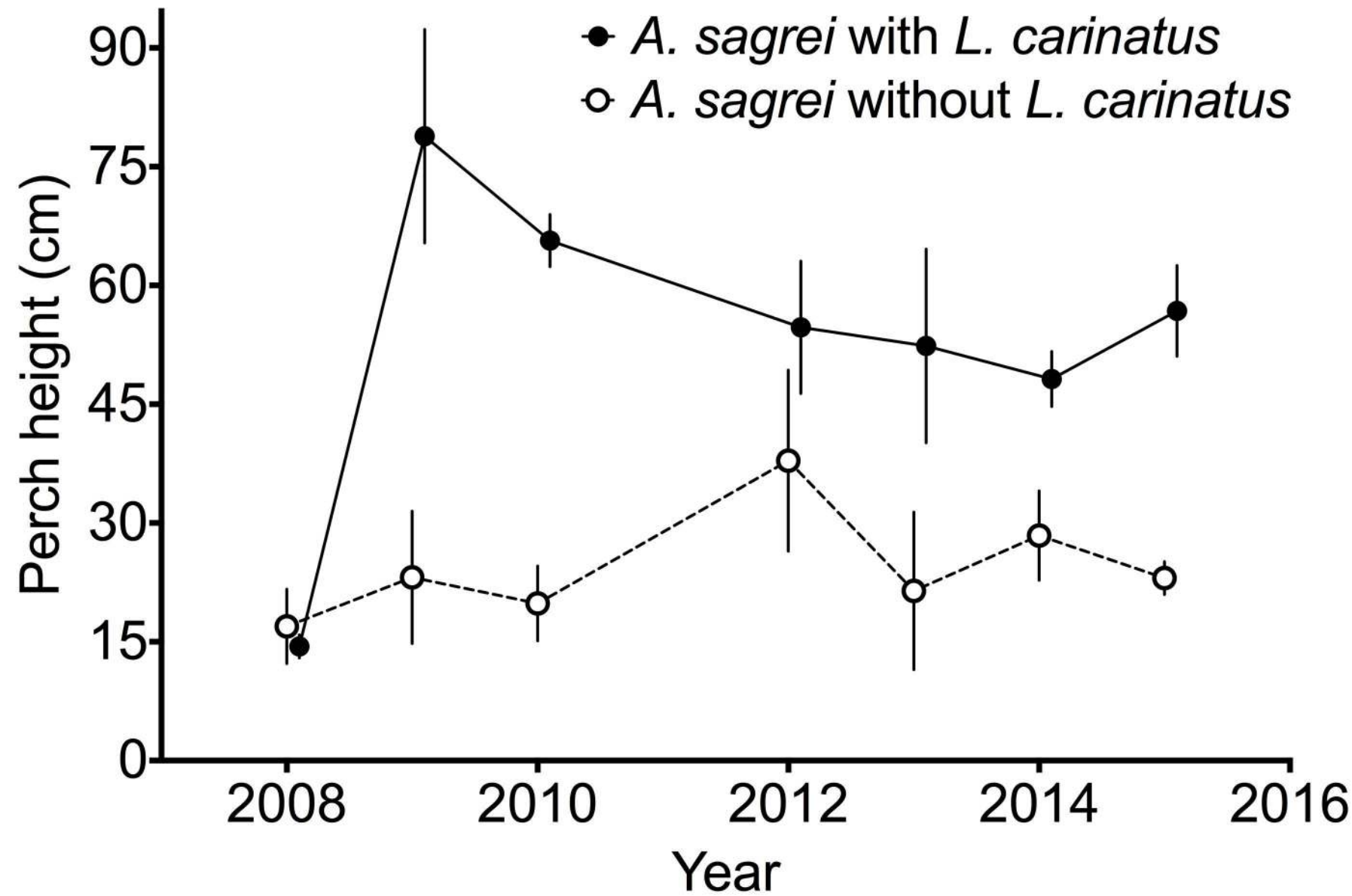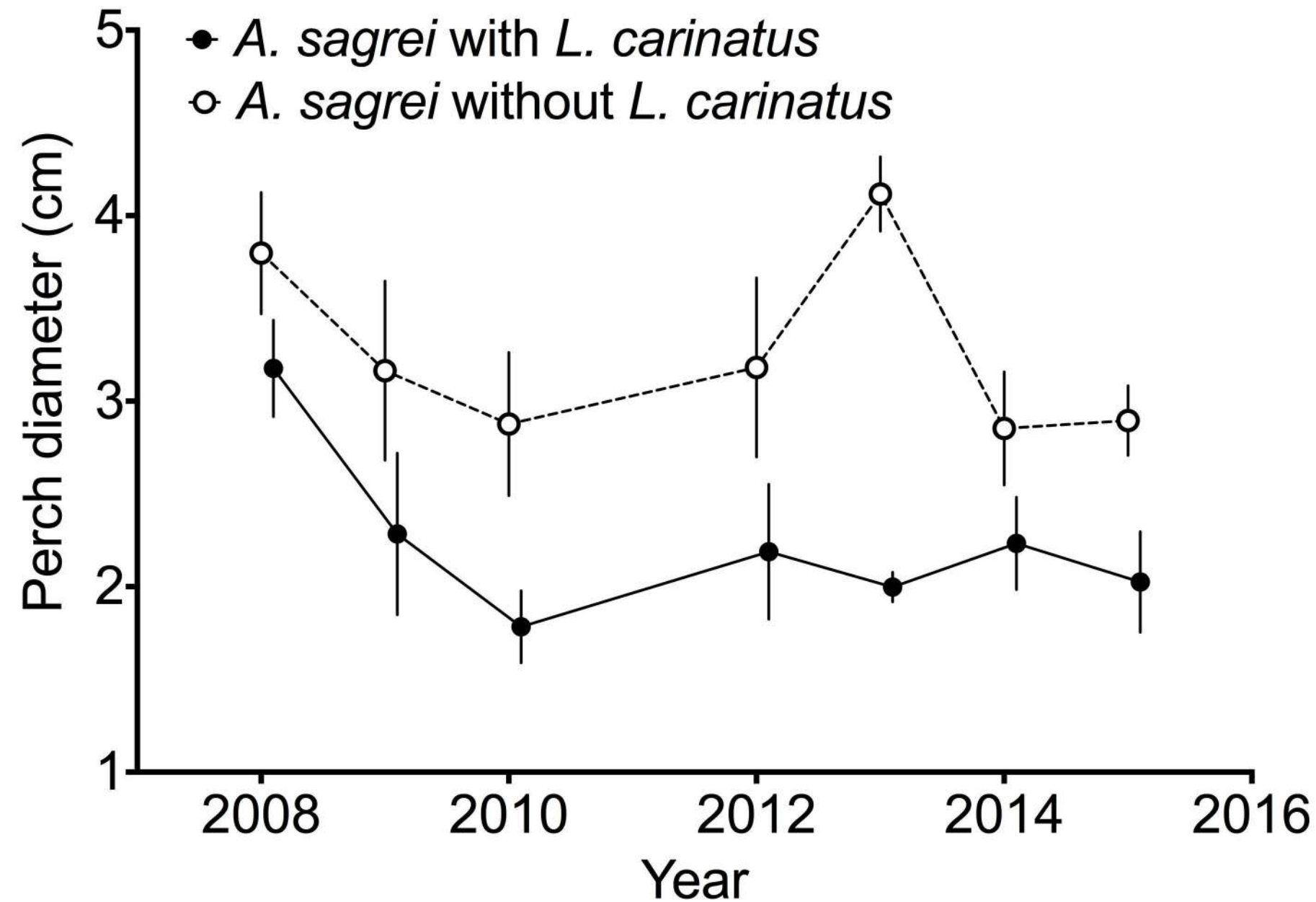
503 MO 65211 (lealm@missouri.edu)

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505 Jonathan Losos: Museum of Comparative Zoology and Department of Organismic

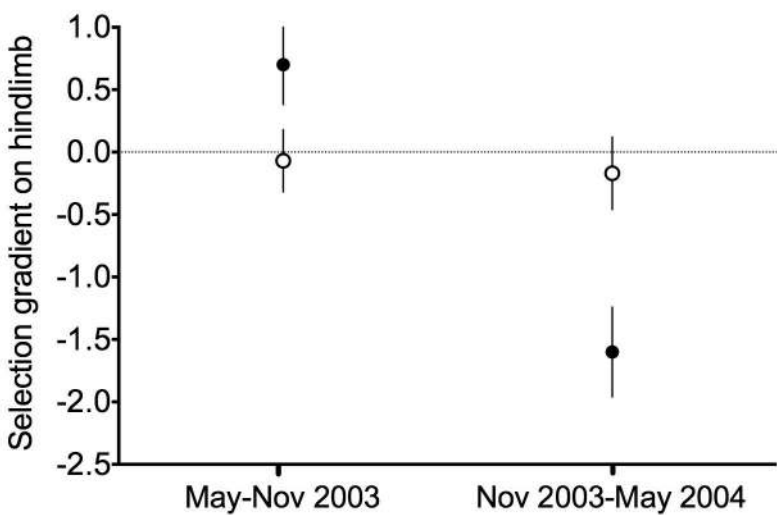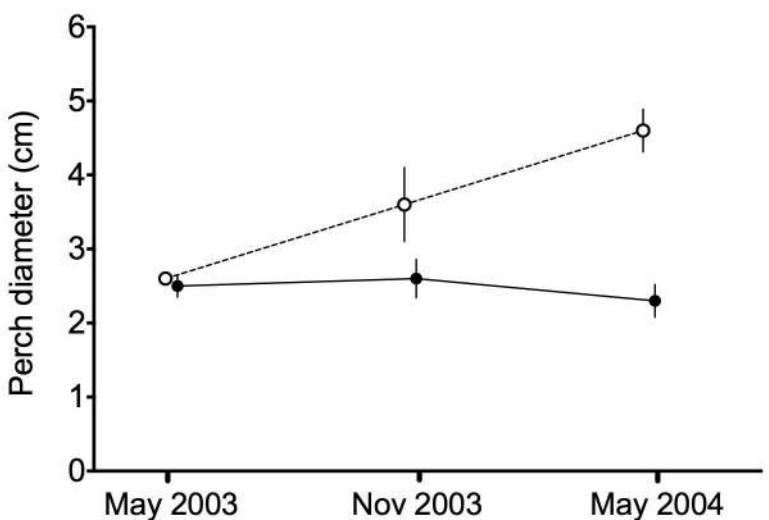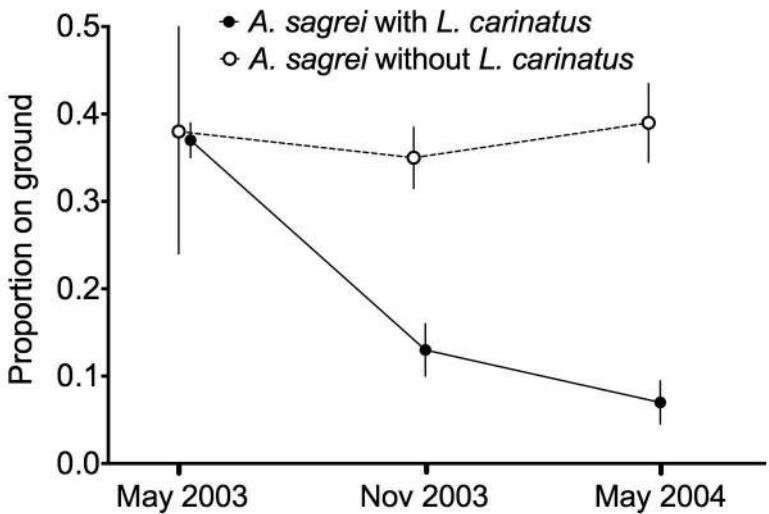506 and Evolutionary Biology, Harvard University, Cambridge, MA 02138

507 (jlosos@oeb.harvard.edu)

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A. sagrei with L. carinatus
A. sagrei without L. carinatus