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Authors
Piovia-Scott, Jonah
Yang, Louie H
Wright, Amber N
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1 **The effect of lizards on spiders and wasps: variation with island size and marine**

2 **subsidy**

3

4 Jonah Piovia-Scott[1†], Louie H. Yang[2], Amber N. Wright[3], David A. Spiller[4], Thomas W.

5 Schoener[4]

6

7 [1] School of Biological Sciences, Washington State University, 14204 NE Salmon Creek

8   Avenue, Vancouver, WA 98686, USA

9 [2] Department of Entomology and Nematology, University of California, One Shields

10   Avenue, Davis, CA 95616, USA

11 [3] Department of Biology, University of Hawaii, Manoa, 2500 Campus Road, Honolulu,

12   HI 96822

13 [4] Department of Evolution and Ecology, University of California, One Shields Avenue,

14   Davis, CA 95616, USA

15

16 [†]jonah.piovia-scott@wsu.edu

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18

Abstract

Introduced predators can have dramatic effects on island ecosystems, the magnitude of which are likely to vary with island characteristics. We investigated the influence of two important properties of islands – size and amount of resource subsidy – on the effects of an introduced predatory lizard (*Anolis sagrei*) on three groups of arthropod prey. Lizards were experimentally introduced to 16 islands that spanned gradients in vegetated area and seaweed deposition (a marine resource subsidy); 16 similar islands served as lizard-free controls. The abundance of web spiders, salticid spiders, and wasps was estimated prior to lizard introduction and again four months after lizard introduction. Lizard introduction reduced the average abundance of all three groups of arthropods. The effect of lizards on salticid spiders – which was very large (94% reduction in salticid abundance) – decreased with island size. In contrast, the effect of lizards on wasps – which was also very large (88% reduction in wasp abundance) – tended to increase with island size, but with only marginal significance. There was no evidence for variation in the effect of lizards on web spiders with island size. This variation between prey taxa may be related to the relative importance of environmental stress (such as wind and wave exposure, which tend to be more pronounced on smaller islands) in determining abundance. Salticids seem to tolerate the stressful environmental conditions that characterize smaller islands, allowing for larger lizard effects; wasps seem to be limited by these conditions (either directly, or indirectly via reduced prey availability), minimizing lizard effects on smaller islands. There was a marginally significant tendency for the effect of lizards on salticid spiders to be weaker on islands with more seaweed deposition, suggesting that subsidies may play a role in reducing predator effects on islands. Our results highlight the importance of

42 ecological context in determining the top-down effects of introduced predators and

43 underscore the need to extend existing theories relating island area and community

44 characteristics towards an explicit consideration of species interactions.

45

46 **Key words:** context dependence; food web; predator-prey interactions; resource subsidy;

47 top-down control.

48

49 **Introduction**

50 Introduced predators can have dramatic effects on ecological communities (Salo et al.

51 2007, Simberloff 2013). While there is increasing recognition that the strength of species

52 interactions depends on environmental context (Bronstein 1994, Agrawal et al. 2007,

53 Afkhami et al. 2014, Hoeksema and Bruna 2015), our understanding of how habitat

54 characteristics influence the impact of introduced predators is still being developed (e.g.,

55 Baxter et al. 2004, Snyder and Evans 2006). The top-down effects of introduced

56 predators are often particularly pronounced on islands (e.g. Schoener and Spiller 1996,

57 Wiles et al. 2003, Croll et al. 2005, Fukami et al. 2006, Rogers et al. 2012). For island

58 food webs, two of the most important axes of environmental variation are island size

59 (Schoener 1989, Holt et al. 1999, Takimoto et al. 2008, Holt 2010) and resource

60 subsidies, i.e., resources that move into the island ecosystem from the surrounding

61 aquatic habitat (Polis and Hurd 1996b, Croll et al. 2005, Fukami et al. 2006, Young et al.

62 2010). Here, we use experimental introductions of predatory lizards on small islands to

63 investigate the influence of island size and resource subsidies on predator-prey

64 interactions.

65

66   Relatively few studies have investigated how the strength of predator-prey interactions

67   changes across gradients of island size. Elton (1958) argued that invasive species have

68   greater impacts on island food webs than those of continental ecosystems, and Ebenhard

69   (1988) found that invasive mammals and birds tend to have larger impacts on prey on

70   oceanic islands than on continental shelf islands and continents. More recently,

71   mathematical modelling studies have shown that the top-down effects of consumers may

72   be more pronounced in smaller habitat patches, primarily because the capacity for spatial

73   heterogeneity to stabilize consumer-resource interactions is lost (McCann et al. 2005,

74   Tunney et al. 2012). While there is some empirical support for larger predator effects on

75   smaller islands (Lomolino 1984, Schoener and Spiller 1999b, 2010), Schoener et al.

76   (2016) recently proposed a hump-shaped relationship between island area and the

77   strength of predator effects. In their conceptual model, interaction strength on large

78   islands is diminished primarily by biological complexity (e.g. compensating predators,

79   which can limit the effect of any single type of predator by maintaining lower prey

80   abundance) and spatial heterogeneity (which can increase the availability of prey

81   refugia), while interaction strength on small islands is diminished by stressful

82   environmental conditions, such as increased exposure to wind, waves, and storm surges

83   (which can limit both predator and prey abundance), demographic stochasticity (which

84   can decouple abundance from ecological interactions), and resource subsidies from

85   surrounding habitats (which can provide alternative resources for predators).

86

87   There has been increasing recognition that resource subsidies influence food-web

88   processes. For example, subsidies can have major impacts on the top-down effects of

89   predators in the recipient community (e.g., Polis et al. 2004, Piovia-Scott et al. 2011).

90   Subsidies can both increase and decrease the strength of these predator effects (Takimoto

91   et al. 2009). The impact of subsidies on top-down effects of predators effects can depend

92   on which trophic level(s) consume the subsidy (Leroux and Loreau 2008), as well as the

93   type of predator response to subsidy -- increases in predator effects are usually driven by

94   increases in predator density (Polis and Hurd 1996a, Henschel et al. 2001, Murakami and

95   Nakano 2002), while decreases are usually driven by changes in predator diet and

96   behavior (Nakano et al. 1999, Sabo and Power 2002, Baxter et al. 2005, Spiller et al.

97   2010). In short-term studies where predator behavior is likely to be more important than

98   predator numerical responses, subsidies are expected to decrease the effect of predators

99   on *in situ* prey by causing the predators to focus on the alternate resource (Takimoto et al.

100   2009, Piovia-Scott et al. 2011).

101

102   To investigate the influence of island area and resource subsidies on the strength of top-

103   down effects, we performed a predator-introduction experiment across gradients of island

104   area and seaweed deposition in a Bahamian island system. We focus on the common

105   carnivorous lizard *Anolis sagrei*, and the term "lizard" will hereafter refer to this

106   particular species. We evaluated the effects of lizards on three groups of arthropods: web

107   spiders, salticid spiders, and wasps. The effects of lizards on web spiders have been

108   extensively documented in this system (e.g. Spiller and Schoener 1988, 1994) and vary

109   with island size (Schoener and Spiller 1999b, 2010, Schoener et al. 2016), showing a

110 positive relationship with island area over the range of island sizes used in the current

111 study (Schoener et al. 2016). Reduced lizard effects on web spiders on the smallest

112 islands are thought to be due to marine subsidies, stressful abiotic conditions, and

113 demographic stochasticity, but the relative importance of these factors is unknown. By

114 decoupling island size from seaweed deposition, the current study will shed light on the

115 role of subsidies in driving the relationship between island size and lizard effects. Salticid

116 spiders have not been the focus of previous studies in this system but are also likely to be

117 strongly affected by lizard predation because they (1) occupy the same habitats as lizards

118 (e.g. stems, branches, ground), (2) are a suitable size for consumption by lizards, and (3)

119 are active during the day. We expect the effect of lizards on salticids to be constrained by

120 the same factors influencing lizard effects on web spiders. The effect of lizards on

121 parasitoid wasps is more equivocal, with positive or neutral relationships between lizards

122 and wasps observed in some cases (Schoener et al. 1995, Schoener and Spiller 1999a,

123 Spiller and Schoener 2007). Parasitoid wasp abundance increases with island area

124 (Schoener et al. 1995), perhaps due to more pronounced effects of environmental

125 disturbance on smaller islands. Thus, we expected the effects of lizards on wasps to

126 increase in strength with island size.

127

128 Our study was abruptly terminated when Hurricane Sandy, a Category 1 storm hit our

129 field site approximately five months after lizards were introduced (and one month after

130 our first post-introduction survey). Hurricane Sandy extirpated all of the introduced lizard

131 populations and most of the web spiders (unpublished data). Hence, we report lizard

132 effects over a ~4 month time period. The relatively short duration of this study is

133   important, as certain lizard effects (e.g., on web spiders, Schoener and Spiller 1996,

134   1999a) can take longer to develop. In addition, changes in lizard behavior and diet in

135   response to seaweed deposition occur rapidly (on the scale of days or months), while

136   reproductive responses generally take a year or longer (Spiller et al. 2010, Wright et al.

137   2013, unpublished data), suggesting that seaweed is likely to reduce the top-down effects

138   of lizards in the current study (as in Piovia-Scott et al. 2011).

139

140   **Methods**

141   *Study system and experimental design*

142   Our study was conducted on 32 small islands (vegetated area: $4 - 157 \text{ m}^2$; Table S1)

143   fringing the much larger island of Great Abaco, Bahamas, between May and September

144   2012. Importantly, seaweed deposition and island size were not strongly correlated on the

145   set of islands used in our study ($\rho=-0.16$), allowing us to disentangle the relative impacts

146   of these environmental drivers on lizard effects. At the beginning of our experiment, none

147   of the study islands had lizards on them, although lizards are known to occur sometimes

148   on similar islands in this area (Schoener et al. 2001). Half of the 32 islands were

149   randomly selected for lizard introductions, while the other half served as lizard-free

150   controls. In order to ensure that lizard treatments were evenly distributed across the

151   gradient of island sizes, we established four blocks of eight islands, each with similarly

152   sized islands, and randomly assigned four out of the eight islands in each block to the

153   lizard-introduction treatment. We introduced lizards to each island in May 2012. In order

154   to maintain roughly equivalent lizard densities on all lizard-introduction islands, the

155   number of lizards introduced to each island scaled with vegetated area (roughly 0.2

156   lizards m^{-2}), with a target ratio of 2 females:1 male (mean across all lizard-introduction

157   islands: 2.001:1). For islands with very small vegetated area, we introduced a minimal

158   population of colonists consisting of two females and one male lizard. Because we did

159   not introduce fewer than three lizards to any island, the smallest block of islands had

160   higher lizard densities than the other three blocks (Appendix S1). Because of this, we

161   repeated the analyses described below with a dataset from which we had removed the

162   smallest block of islands. The results of this set of analyses were generally similar to

163   those with all islands (Appendix S1: Table S2); we indicate in the results where the

164   significance of a particular test (for $\alpha = 0.05$) differed between the two sets of analyses.

165

166   We used vegetated area as our measure of island size. We calculated vegetated area as the

167   product of total area and the proportion of the total area that was vegetated for each

168   island. We estimated total area by measuring the length and width of each island and

169   assuming islands were elliptical in shape (total area = 0.25*length*width*π), and we

170   estimated proportion vegetation by taking the mean of at least two independent (different

171   people) visual estimates. We used visual estimates to measure seaweed biomass (Spiller

172   et al. 2010) on each island in May and September 2012; these estimates were divided by

173   vegetated area to calculate seaweed density. We used the mean of the May and

174   September seaweed density estimates to assign a seaweed deposition category: low

175   seaweed (0 – 0.15 kg m^{-2}) or moderate seaweed (0.15 – 0.80 kg m^{-2}); we call this second

176   category moderate because much higher levels of seaweed deposition (>5 kg m^{-2}) have

177   been observed in this system (Spiller et al. 2010). We chose the threshold of 0.15 kg m^{-2}

178   dividing low and moderate seaweed deposition because it effectively distinguished the

179 islands with notably higher seaweed density and because it created a balanced

180 experimental design -- while we did not take seaweed deposition into account when we

181 assigned lizard treatments, we did end up with an even split between lizard and no-lizard

182 islands in both the moderate seaweed category (four lizard, four no-lizard) and the low

183 seaweed category (12 lizard, 12 no-lizard) (Appendix S1: Table S1).

184

185 *Data collection*

186 We conducted web-spider censuses on each island by counting the number of intact webs

187 present and recording species identity. We estimated salticid spider abundance using

188 bowl traps. Yellow plastic bowls filled with 500 ml of water and a trace amount of

189 detergent were placed on the ground in vegetated areas of each island. After 24 h, the

190 traps were collected, and the number of salticid spiders was counted. In order to attain

191 representative samples from each island, we set more traps on larger islands

192 (approximately one trap per 15 m^2 of vegetated area). We estimated wasp abundance

193 using sticky traps -- 22 x 14 cm sheets of clear plastic coated with Tangletrap adhesive

194 (Contech Inc., Victoria, British Columbia, Canada). Sticky traps were tied onto the

195 branches of shrubs about 0.5 m above ground. After 24 h, the traps were collected, and

196 the number of wasps was counted. The number of sticky traps set on each island was

197 equal to the number of bowl traps.

198

199 *Statistical analyses*

200 We evaluated how the effect of lizard introduction on the abundance of salticid spiders,

201 wasps, and web spiders was influenced by vegetated area and seaweed density using

202 generalized linear models. The models featured log(vegetated area), seaweed density

203 category (moderate vs. low), and lizard treatment (introduced vs. absent) as predictors. In

204 order to test for effects of island area and seaweed deposition on the strength of lizard

205 predation we evaluated lizard*log(vegetated area) and lizard*seaweed interactions.

206 Because arthropod abundances were represented by counts, we used generalized linear

207 models with a log link function, a Poisson error distribution, and an offset term for

208 sampling effort (number of traps for salticid spiders and wasps, island area for web

209 spiders). This approach allows for analyses of abundance per unit sampling effort (i.e.,

210 density) without the biases introduced by using a ratio as a response variable, and

211 features an error distribution that is appropriate for count data. For hypothesis testing, we

212 used chi-squared likelihood ratio tests. All analyses were performed using R version 3.3.2

213 (R Development Core Team 2016); raw data and code are available in the appendices.

214 We used Cameron and Trivedi's (1990) method to test for overdispersion. We did not

215 find evidence for overdispersion in the analyses of salticid spiders and wasps ($P>0.26$ in

216 both cases), but there was evidence for overdispersion in the analysis of web spiders

217 ($P=0.02$). Because of this, we added an island-level random effect to the model of web

218 spiders (Harrison 2014); the model with an island-level random effect had a better AIC

219 score than a zero-inflated model.

220

221 In order to determine whether or not there were pre-existing differences in salticid spider,

222 wasp, and web-spider abundance between islands selected for lizard introductions and

223 control islands, we used the statistical approach described above to model abundances in

224 May 2012, prior to lizard introductions. While the May 2012 model included lizard

225 treatment, vegetated area, and seaweed category as predictors, it did not include

226 interactions between lizard treatment and the other predictor variables, as the lizard

227 treatment had not yet taken place. This analysis found no evidence for pre-existing

228 differences in arthropod abundance between islands selected for lizard introduction and

229 controls ($P>0.34$ in all cases).

230

231 **Results**

232 Lizard introduction led to a 94% reduction in salticid spider abundance (Fig. 1; lizard

233 effect: χ^2=13.1, df=1, P=0.003; log response ratio = -2.9). The effect of lizards was

234 greater on smaller islands than it was on larger islands (Fig. 2; lizard*area interaction:

235 χ^2=5.2, df=1, P =0.02). This change in lizard effect with island area was associated with

236 reduced salticid abundance on larger islands in the absence of lizards (area effect in

237 absence of lizards: χ^2=5.1, df=1, P =0.02) and a tendency for higher salticid abundance

238 on larger islands in the presence of lizards, although this latter result was only marginally

239 significant (area effect in presence of lizards: χ^2=3.1, df=1, P =0.08). There was also a

240 marginally significant trend for the effect of lizards on salticids to be greater on islands

241 with lower seaweed deposition (Fig. 3; lizard*seaweed interaction: χ^2=3.3, df=1, P =0.07;

242 lizard effect on low seaweed islands: χ^2=14.4, df=1, P =0.0001; lizard effect on moderate

243 seaweed islands: χ^2=0.15, df=1, P =0.70).

244

245 Lizard introduction led to an 88% reduction in wasp abundance (Fig. 1; lizard effect:

246 χ^2=41.9, df=1, P <0.0001; log response ratio = -2.1). There was a marginally significant

247 tendency for greater lizard effects on large islands (Fig. 2; lizard*area interaction: χ^2=2.7,

248   df=1, P =0.098); this effect was significant (P =0.039) when the smallest block of islands

249   was removed from the analysis (Appendix S1: Table S2). Wasp density was higher on

250   larger islands (Fig. 2; area effect: χ^2=16.7, df=1, P <0.0001), and there was a marginally

251   significant tendency for higher wasp density on islands with low seaweed deposition

252   (Fig. 3; seaweed effect: χ^2=3.4, df=1, P =0.06). The lizard*seaweed interaction was not

253   significant for wasps (χ^2=0.9, df=1, P =0.35).

254

255   Lizard introduction led to a 58% reduction in web spider abundance (Fig. 1; lizard effect:

256   Z=1.8, P=0.07; log response ratio = -0.88); this effect was significant (P=0.04) when the

257   smallest block of islands was removed from the study (Appendix S1: Table S2). Web

258   spider density was higher on islands with more seaweed deposition (Fig. 3: seaweed

259   effect: χ^2=4.5, df=1, P =0.03). We did not detect an effect of area on web spider

260   abundance (Fig. 2; area effect: χ^2=0.65, df=1, P =0.42) nor interactions between lizard

261   treatment and island area (χ^2=0.15, df=1, P =0.70) nor seaweed deposition (χ^2=0.26,

262   df=1, P =0.61). A single species, *Eustala cazieri*, accounted for the majority (68%) of

263   spiders and webs seen in our study.

264

265   **Discussion**

266   Lizard introduction reduced the abundance of all three taxa of arthropod predators and

267   parasitoids. Island area had important consequences for the strength of this top-down

268   effect. For salticid spiders, the effect of lizards was reduced on larger islands. In contrast,

269   the effect of lizards on wasps tended to be greater on larger islands, and there was no

270   indication that the lizard effect varied with island area for web spiders. There was only

271   limited support for the hypothesis that moderate levels of seaweed deposition influenced

272   lizard effects. Specifically, there was a marginally significant trend for a reduced effect of

273   lizards on salticid spider abundance on islands with more seaweed.

274

275   The influence of island area on the top-down effects of lizards was not consistent across

276   arthropod taxa. For salticids, lizard effects decreased with island area. This pattern is

277   consistent with certain models (e.g., McCann et al. 2005, Tunney et al. 2012), but did not

278   match our expectations. We expected the effects of lizards on salticids to be weaker on

279   smaller islands due to stressful environmental conditions and demographic stochasticity.

280   In contrast, we found that lizard effects on salticids were stronger on small islands, in part

281   because salticids achieve high densities on small islands in the absence of lizards and in

282   part because lizards are not as effective at eliminating salticids on larger islands. We

283   hypothesize that high dispersal rates and low abundance of alternate predators (such as

284   wasps; Fig. 2) (Schoener et al. 2016) help explain high salticid abundance on small,

285   lizard-free islands, and thus are partially responsible for the stronger effects of lizards on

286   small islands. In addition, increased spatial and resource heterogeneity, including

287   increased refuge availability, on larger islands (McCann et al. 2005, Schoener and Spiller

288   2010, Tunney et al. 2012, Schoener et al. 2016) likely contributed to the persistence of

289   some salticids in the presence of lizards and hence weaker lizard effects. In contrast to

290   salticids, the effect of lizards on wasps tended to increase with island size. This pattern

291   was associated with the fact that wasp abundance was low on smaller islands, giving

292   lizards little opportunity to reduce their abundance further. It seems likely that low wasp

293   abundance on smaller islands is due to an increased effect of environmental disturbance,

294   in the form of tropical storms (Spiller and Schoener 2007), and perhaps also to a lack of

295   suitable prey resources (Schoener et al. 1995). Thus, stressful environmental conditions

296   may help explain weak effects of lizards on wasps on small islands (Appendix S2).

297

298   Why didn't we observe a hump-shaped relationship in effect sizes, as hypothesized by

299   Schoener et al. (2016)? One explanation is that the current study did not consider large

300   islands (i.e., $> 1000 \text{ m}^2$; the range of island sizes in the current study was $4 - 157 \text{ m}^2$),

301   where the decreasing relationship between island area and lizard effects was most

302   apparent. For example, we detected a trend for increasing lizard effects on wasps on

303   larger islands, but were not able to determine whether this trend was reversed on still

304   larger islands. In addition, our short-term experiment may not have allowed enough time

305   for stressful environmental conditions and demographic stochasticity, factors mentioned

306   by Schoener et al. (2016), to limit the size of lizard effects on small islands. For example,

307   the strong effects of lizards on salticids on the smallest islands was associated with the

308   high abundance of salticids on lizard-free islands in this size class; over longer time

309   scales average salticid abundance on these islands may be reduced by stressful

310   environmental conditions and demographic processes.

311

312   Our results suggest that marine subsidies may play a role in reducing the effects of lizard

313   predators on arthropod prey. Because our study was conducted over a relatively short

314   time period (which limits lizard reproductive responses) and because our study took place

315   on small islands (which limits aggregative responses) we predicted that lizard effects

316   would be reduced on islands with more seaweed due to changes in diet (Spiller et al.

317 2010, Piovia-Scott et al. 2013) and foraging behavior (unpublished data). Consistent with

318 this hypothesis, there was a marginally-significant trend for weaker lizard effects on

319 salticids on islands with more seaweed. There was a similar trend for wasps, but the

320 lizard*seaweed interaction term was not significant, and there was no support for

321 seaweed-based differences in top-down effects for web spiders. We suggest that the

322 absence of stronger relationships between seaweed deposition and lizard effects in the

323 current study is likely due to the relatively low rate of seaweed deposition on our study

324 islands. Previous studies applied seaweed experimentally at a rate of 2.5 kg m^{-2} to mimic

325 the amounts of seaweed deposited during "pulse" events (often associated with large

326 storms). In contrast, the maximum rate of seaweed deposition in the current study (which

327 did not include any pulse events) was only 0.8 kg m^{-2}, and it may take more seaweed to

328 cause more substantial reductions in the effects of lizards on arthropod prey.

329

330 In conclusion, we have demonstrated that the short-term effects of introduced lizards on

331 certain arthropod predators and parasitoids depends on island size. However, the nature

332 of this relationship was not consistent across taxa – lizard effects on salticid spiders are

333 greater on smaller islands, whereas effects on wasps tended to be greater on larger

334 islands. These differences were associated with pronounced relationships between island

335 size and arthropod abundance – salticids can achieve high abundance on small islands in

336 the absence of lizards, facilitating stronger lizard effects, while wasps have very low

337 abundance on small islands, weakening lizard effects – although there was also some

338 evidence that lizards are not as effective at limiting salticid spider abundance on larger

339 islands. We also found some evidence that seaweed deposition can reduce the short-term

340   top-down effects of lizards, suggesting that marine subsidies may play a role in

341   weakening predator effects on small islands. Thus, while introduced predators can have

342   devastating impacts on island communities, the strength of those effects can vary

343   dramatically based on both island characteristics and the biology of the specific prey

344   species. More generally, our study underscores the need to extend existing theories

345   relating island area and community characteristics such as diversity (Connor and McCoy

346   1979, Schoener 2009) and food-chain length (Schoener 1989, Post 2002) towards an

347   explicit consideration of species interactions (Holt 2010). This endeavor is likely to

348   provide valuable insight into ecosystem function that cannot be gleaned from descriptive

349   community metrics alone.

350

358

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500

501

Figure legends

Figure 1. Effects of lizards on the mean abundance of salticid spiders, wasps, and web

spiders. Means and standard errors are shown for 16 islands to which lizards were

introduced (solid circles) and 16 no-lizard control islands (open circles) in May 2012

(just prior to lizard introduction) and September 2012 (four months after lizard

introduction). The dashed vertical line denotes the date of lizard introduction. *P*-values

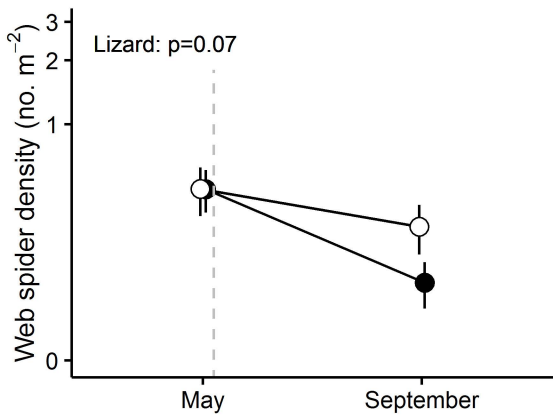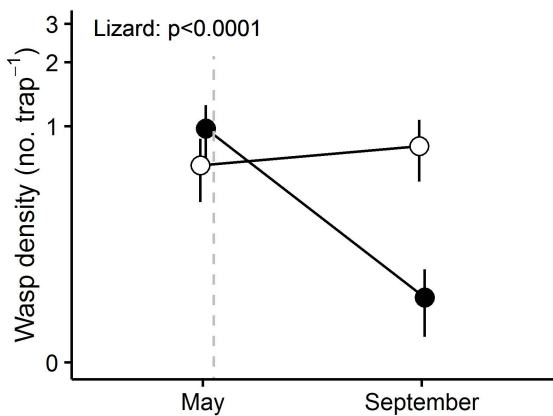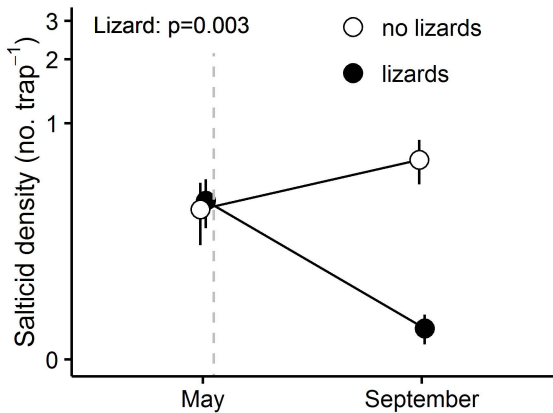for lizard effects are from models described in the text. Note log scale on y-axis.

Figure 2. Effects of lizards on the abundance of salticid spiders, wasps, and web spiders

across gradients of island size. The symbols represent individual islands (solid circles for

lizard-introduction islands and open circles for no-lizard islands); *P*-values for the

lizard*area interaction and prediction lines are derived from generalized linear models

with a log link function and a Poisson error distribution as described in the text. Note log
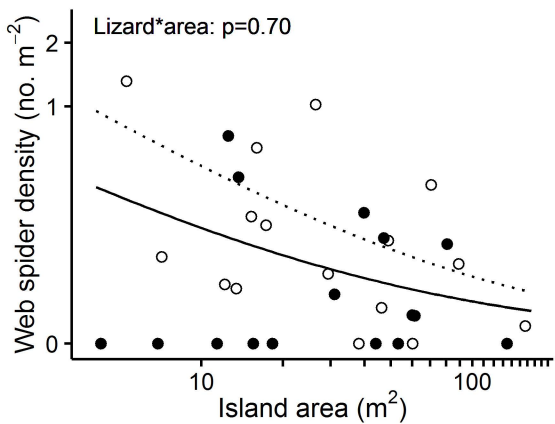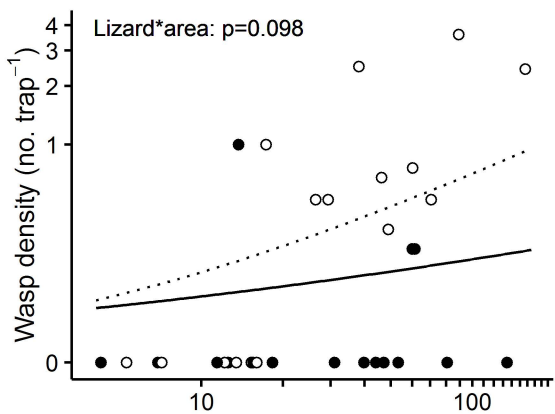
scale on both axes.

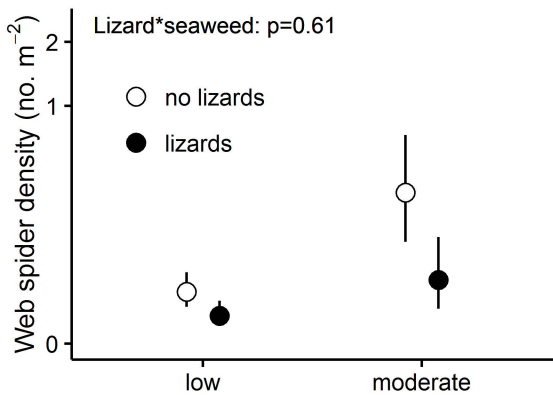**Figure 3.** Effects of lizards on the abundance of salticid spiders, wasps, and web spiders

on islands with different levels of seaweed deposition. Estimates (solid circles for lizard-

introduction islands and open circles for no-lizard islands), standard errors, and *P*-values

for the lizard*seaweed interaction are derived from the generalized linear models

described in the text. Note log scale on y-axis.

Top panel: Lizard*area: p=0.02. Y-axis: Salticid density (no. trap^{-1}). Legend: ○ no lizards, ● lizards.

Middle panel: Lizard*area: p=0.098. Y-axis: Wasp density (no. trap^{-1}).

Bottom panel: Lizard*area: p=0.70. Y-axis: Web spider density (no. m^{-2}). X-axis: Island area (m^2).

Saltcid density (no. trap^{-1})

Lizard*seaweed: p=0.07

Wasp density (no. trap^{-1})

Lizard*seaweed: p=0.35

Web spider density (no. m^{-2})

Lizard*seaweed: p=0.61

○ no lizards
● lizards

low   moderate
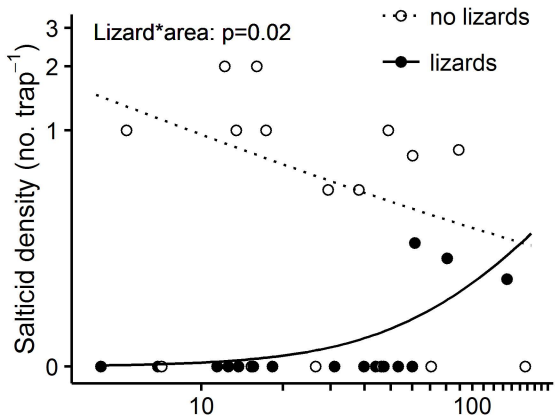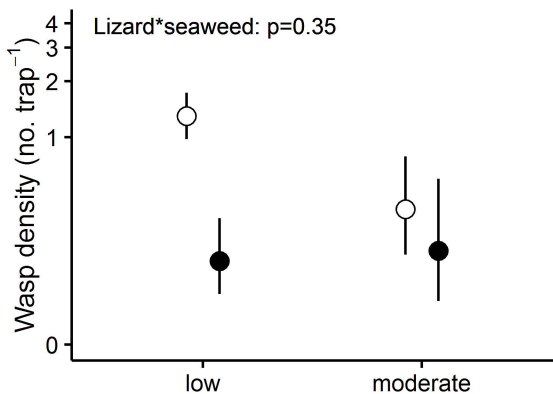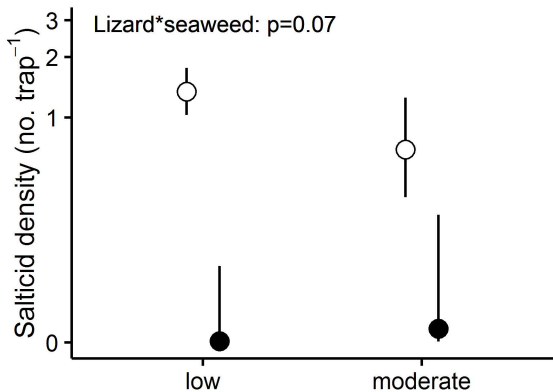
Seaweed deposition

The effect of lizards on spiders and wasps: variation with island size and marine subsidy

Jonah Piovia-Scott, Louie H. Yang, Amber N. Wright, David A. Spiller, Thomas W. Schoener

Appendix S1: Supplementary Analyses

Analyses of lizard effects on invertebrate prey with the smallest block of islands removed

Our experiment featured four blocks of islands, with each block containing islands with similar areas. We introduced a minimum of three lizards (one male and two females) to each lizard-introduction island, as we intended to create a reproductively viable population on each island. Because of this, the block with the smallest islands had a higher density of lizards than the other three blocks (ANOVA on log(lizard density), block effect: $F_{3,12}$=5.31, P=0.01; Figure S1, Table S1). In order to see whether this difference in lizard density distorted our assessment of lizard effects, we conducted a set of analyses similar to those described in the main text with the smallest block of islands removed.

As in the analyses described in the methods section, the models presented below feature log(vegetated area), seaweed density category (high vs. low), and lizard treatment (introduced vs. absent) as predictors. In order to test for effects of island area and seaweed deposition on the strength of lizard predation we evaluated lizard*log(vegetated area) and lizard*seaweed interactions. Because arthropod abundances were represented by counts we used generalized linear models with a log link function, a Poisson error distribution, and an offset term for sampling effort (number of traps for salticid spiders and wasps, island area for web spiders). For hypothesis testing, we used chi-squared likelihood ratio tests. All analyses were performed using R (R Development Core Team 2014). As in other analyses, we used an island-level random effect to the model of web spiders to account for overdispersion.

The results of these models (Table S2) are generally similar to the results presented in the main text. The only qualitative changes are as follows: 1) in the model with all islands there is a marginally significant effect of area on salticid abundance (P=0.08), this effect is not apparent in the model with small islands removed (P=0.24); 2) in the model with all islands there is a marginally significant tendency for effects of lizards on wasps to be more pronounced on larger islands (lizard*area interaction: P=0.098), this effect is significant in the model with small islands removed (lizard*area interaction: P=0.039); 3) in the model with all islands there is a marginally significant trend towards lower web spider abundance on islands with lizards (P=0.07), this effect is significant in the model with small islands removed (P=0.042).

Analyses of lizard effects on web spiders with block as predictor instead of island area

Our analysis of web spider abundance is complicated by the fact that we use island area as an offset (because we searched the entire island for spiders) and also as a predictor variable (because we are interested in evaluating whether spider abundance varies with island size). It is our impression that this approach is valid, as the offset is assigned a fixed parameter value while the parameters associated with area as a predictor variable is estimated by the model. However, we conducted supplementary analyses in which block was used as a predictor instead of island area, while island area was retained as an offset. This analysis avoids any problems that might arise from using area as both offset and predictor. The results of this analysis are similar to those presented in the main text in that there is a significant effect of seaweed and a marginally significant effect of lizards (Table S3).

Table S1. Characteristics of study islands.

Island	Vegetated area (m²)	Total area (m²)	Seaweed biomass (kg)	Seaweed density (kg m⁻²)*	Seaweed category	Lizards introduced	Lizard density (m⁻²)*
A21	4.3	29.3	0.05	0.012	low	3	0.705
A24	5.3	21.4	4.25	0.803	moderate	0	0
I04	6.9	20.9	0.30	0.043	low	3	0.434
M01	7.1	20.4	2.13	0.298	moderate	0	0
R02	11.4	13.4	0.05	0.004	low	3	0.263
P05	12.2	34.9	1.50	0.123	low	0	0
A20	12.6	31.4	0.10	0.008	low	3	0.239
W11	13.4	40.7	1.05	0.078	low	0	0
R03	13.7	41.5	1.25	0.091	low	3	0.219
N07	15.3	18.0	1.75	0.115	low	0	0
P06	15.5	31.0	2.75	0.177	moderate	3	0.193
X20	16.0	30.2	5.00	0.312	moderate	0	0
P03	17.3	38.5	1.05	0.061	low	0	0
X08	18.3	30.4	0.20	0.011	low	3	0.164
I01	26.4	88.0	1.28	0.048	low	0	0
X02	29.4	41.9	0.55	0.019	low	0	0
A23	31.0	38.7	0.30	0.010	low	5	0.161
W10	38.1	69.3	0.70	0.018	low	0	0
EB03	39.9	79.7	5.50	0.138	low	6	0.151
S01	44.0	62.9	0.05	0.001	low	7	0.159
S02	46.2	77.0	1.50	0.032	low	0	0
X23	47.1	62.8	9.25	0.196	moderate	7	0.149
B100	49.0	65.4	1.00	0.020	low	0	0
R01	53.3	71.0	2.25	0.042	low	8	0.150
N200	60.1	164.7	5.00	0.083	low	9	0.150
X07	60.2	100.3	0.15	0.002	low	0	0
N100	61.4	76.8	17.00	0.277	moderate	9	0.147
X22	70.5	84.9	12.50	0.177	moderate	0	0
X26	80.7	124.1	15.00	0.186	moderate	12	0.149
P02	89.1	99.0	0.28	0.003	low	0	0
J06	134.2	183.4	16.00	0.119	low	20	0.149
X01	156.8	178.1	4.00	0.026	low	0	0

*Densities calculated using vegetated area

Table S2. Results of statistical analyses of lizard effects on three guilds of invertebrate prey with the block containing the smallest islands removed from the data set used for analysis.

Prey guild	Effect	χ^2	P^a
Salticids	Lizard	8.97	0.003**
	Area	1.38	0.24
	Seaweed	0.26	0.61
	Lizard*Area	4.34	0.03*
	Lizard*Seaweed	2.12	0.15
Wasps	Lizard	41.90	<0.0001*
	Area	10.61	0.001*
	Seaweed	3.56	0.059
	Lizard*Area	4.25	0.039*
	Lizard*Seaweed	0.65	0.42
Web spiders	Lizard	4.14	0.042*
	Area	1.25	0.26
	Seaweed	3.86	0.0495*
	Lizard*Area	0.00	0.96
	Lizard*Seaweed	0.15	0.70

[a]All P-values are based on tests with 1 degree of freedom.

Table S3. Results of statistical analyses of lizard effects on web spider with block representing island area.

Prey guild	Effect	χ^2	P^a
Web spiders	Lizard	3.70	0.054
	Block	3.70	0.30
	Seaweed	6.10	0.01*
	Lizard*Block	1.02	0.80
	Lizard*Seaweed	0.23	0.63

Figure S1. Initial lizard density on lizard-introduction islands in four different size classes (blocks).
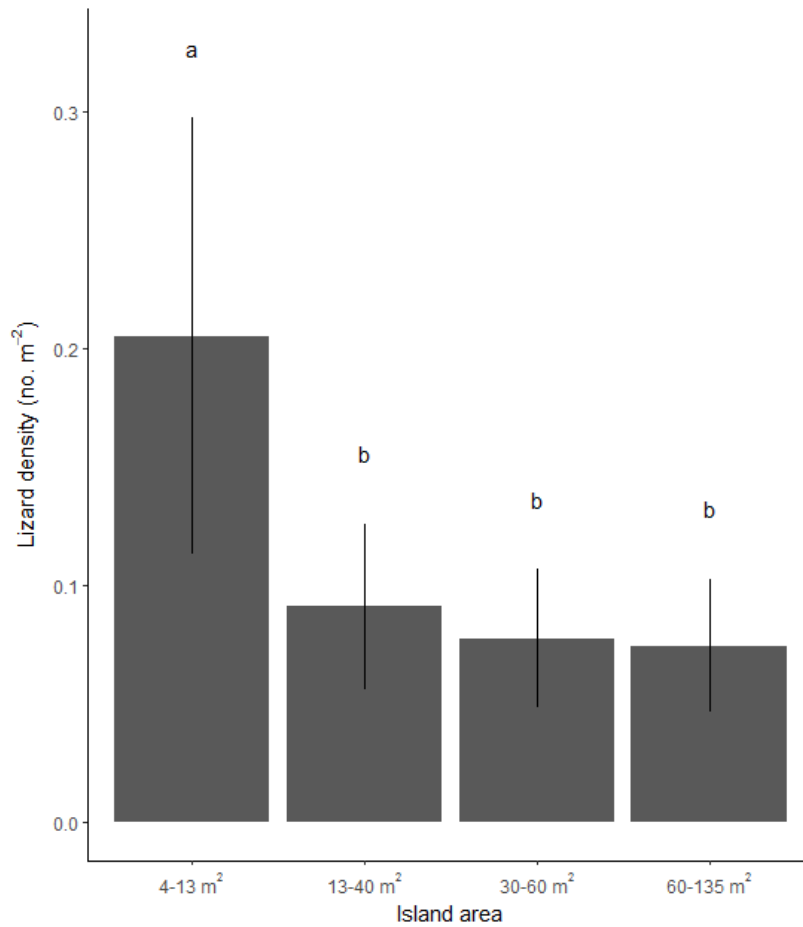
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Spiller, D. A., and T. W. Schoener. 1990. Lizards reduce food consumption by spiders: Mechanisms and
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Spiller, D. A., and T. W. Schoener. 2007. Alteration of island food-web dynamics following major
    disturbance by hurricanes. Ecology 88:37-41.

The effect of lizards on spiders and wasps: variation with island size and marine subsidy

Jonah Piovia-Scott, Louie H. Yang, Amber N. Wright, David A. Spiller, Thomas W. Schoener

Appendix S2: Supplementary Text

The negative effect of lizards on wasps observed in the current study is not consistent with previous studies showing that wasp abundance is higher on islands with lizards (Schoener et al. 1995, Schoener and Spiller 1999a, Spiller and Schoener 2007). However, the effects in these previous studies were most striking when comparing islands on which lizards were present or absent naturally, rather than comparing islands to which lizards were experimentally introduced and control islands, and wasps and lizards may tend to co-occur based on shared habitat preferences (Schoener et al. 1995, Schoener and Spiller 1999a). In addition, the majority of the wasps captured in previous studies were small (none > 4mm in Schoener and Spiller 1999a), while most of the wasps captured in the current study tended to be larger (mean: 4.3 mm, range 1-7 mm), making them more suitable prey for lizards (Spiller and Schoener 1990).

The tendency for reduced lizard effects on wasps on smaller islands was driven largely by the fact that wasp abundance was lower on smaller islands, giving lizards little opportunity to reduce their abundance further. Reduced wasp abundance on smaller islands may be driven by disturbance. For example, previous studies in this system have shown that wasp abundance is reduced by hurricanes (Spiller and Schoener 2007), and our study area was hit by Hurricane Irene in August 2011, about one year before the current study was conducted. It is likely that the effects of hurricane disturbance are more pronounced on smaller islands, as they are lower and thus more exposed to storm surge and wave action, and they are less likely to have enough vegetation or topography to create areas sheltered from high winds. It is also possible that wasps may not be as abundant on smaller islands due to the absence of suitable prey resources.

In contrast to previous studies (Schoener and Spiller 1999b, Schoener et al. 2016), we did not find evidence for variation in the effect of lizards on web spiders across an island size gradient. While the islands used in the current study encompass just a fraction of the island size gradient explored in previous studies, they include the same range of island areas across which an important transition from inconsistent lizard effects to consistently strong negative effects occurred (Schoener et al. 2016). However, the overall effect of lizards on web spider abundance in the current study appeared to be weaker than that observed in previous studies (Schoener and Spiller 1996, Spiller and Schoener 1996), which could have impeded our ability to detect patterns associated with island size. It is possible that stronger effects would have developed over a longer time period – Schoener and Spiller (1996) found that lizard effects on web spider abundance developed gradually during the first year after lizard introduction, a delay that was particularly pronounced for *E. cazieri* (Schoener and Spiller 1999b), the most common species observed in the current study.

Schoener, T. W., and D. A. Spiller. 1996. Devastation of prey diversity by experimentally introduced predators in the field. Nature 381:691-694.

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Ecosphere

The effect of lizards on spiders and wasps: variation with island size and marine subsidy

Jonah Piovia-Scott[1†], Louie H. Yang[2], Amber N. Wright[3], David A. Spiller[4], Thomas W. Schoener[4]

[1] School of Biological Sciences, Washington State University, 14204 NE Salmon Creek Avenue, Vancouver, WA 98686, USA
[2] Department of Entomology and Nematology, University of California, One Shields Avenue, Davis, CA 95616, USA
[3] Department of Biology, University of Hawaii, Manoa, 2500 Campus Road, Honolulu, HI 96822
[4] Department of Evolution and Ecology, University of California, One Shields Avenue, Davis, CA 95616, USA

[†]jonah.piovia-scott@wsu.edu

DataS1.csv: Raw data

Column heading	Description
ExperimentalUnit	Island identifier
NumberTraps	Number of bowl traps and sticky traps set on each island
VegArea_m2	Vegetated area (m^2)
block	Block (1-4)
LizardTreatment	Lizard treatment: present (i.e., introduced) or absent
swCat	Seaweed deposition category: low or moderate
swDens_kgm2	Seaweed density (kg m^{-2})
numberSalticids	Number of salticid spiders in September 2012 (after lizard introduction)
numSaltMay2012	Number of salticid spiders in May 2012 (before lizard introduction)
area.logc	Ln(vegetated area); centered so that the mean value = 0
numberWasps	Number of wasps in September 2012 (after lizard introduction)
numWaspMay2012	Number of wasps in May 2012 (before lizard introduction)
numberwebs	Number of web spiders in September 2012 (after lizard introduction)
numWebMay2012	Number of web spiders in May 2012 (before lizard introduction)

Ecosphere

The effect of lizards on spiders and wasps: variation with island size and marine subsidy

Jonah Piovia-Scott[1†], Louie H. Yang[2], Amber N. Wright[3], David A. Spiller[4], Thomas W. Schoener[4]

[1] School of Biological Sciences, Washington State University, 14204 NE Salmon Creek Avenue, Vancouver, WA 98686, USA
[2] Department of Entomology and Nematology, University of California, One Shields Avenue, Davis, CA 95616, USA
[3] Department of Biology, University of Hawaii, Manoa, 2500 Campus Road, Honolulu, HI 96822
[4] Department of Evolution and Ecology, University of California, One Shields Avenue, Davis, CA 95616, USA

[†]jonah.piovia-scott@wsu.edu

DataS2.r: R code for analyses