# Predator-driven behavioral shifts in a common lizard shape resource-flow dynamics from marine to terrestrial ecosystems

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#### Abstract

Foraging decisions shape the structure of food webs. Therefore, a behavioral shift in a single species can potentially modify resource-flow dynamics of entire ecosystems. To examine this, we conducted a field experiment to assess foraging niche dynamics of semi-arboreal brown anole lizards in the presence/absence of predatory ground-dwelling curly tailed lizards in a replicated set of island ecosystems. One year after experimental translocation, brown anoles exposed to these predators had drastically increased perch height and reduced consumption of marine-derived food resources. This foraging niche shift altered marine-to-terrestrial resource-flow dynamics and persisted in the diets of the first-generation offspring. Furthermore, female lizards  $\neg \neg$ that displayed more risk-taking behaviors consumed more marine prey on islands with predators present. Our results show how predator-driven rapid behavioral shifts can alter food-web connectivity between oceanic and terrestrial ecosystems and underscore the importance of studying behavior-mediated niche shifts to understand ecosystem functioning in rapidly changing environments.

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#### 51 Abstract

52 Foraging decisions shape the structure of food webs. Therefore, a behavioral shift in a single 53 species can potentially modify resource-flow dynamics of entire ecosystems. To examine this, we 54 conducted a field experiment to assess foraging niche dynamics of semi-arboreal brown anole 55 lizards in the presence/absence of predatory ground-dwelling curly tailed lizards in a replicated set 56 of island ecosystems. One year after experimental translocation, brown anoles exposed to these 57 predators had drastically increased perch height and reduced consumption of marine-derived food 58 resources. This foraging niche shift altered marine-to-terrestrial resource-flow dynamics and persisted in the diets of the first-generation offspring. Furthermore, female lizards that displayed 59 60 more risk-taking behaviors consumed more marine prey on islands with predators present. Our 61 results show how predator-driven rapid behavioral shifts can alter food-web connectivity between 62 oceanic and terrestrial ecosystems and underscore the importance of studying behavior-mediated 63 niche shifts to understand ecosystem functioning in rapidly changing environments.

Ecological interactions among organisms shape ecosystem functioning by providing biological communities with structure and stability (Valiente-Banuet *et al.* 2015). Environmental changes can alter ecosystem functioning by altering the structure and intensity of these ecological interactions within a community (Tylianakis *et al.* 2008). Examining how new species interactions "re-wire" trophic networks in nature is necessary to shed light on the ecosystem-level consequences of rapid environmental changes (Gilman *et al.* 2010; Bartley *et al.* 2019).

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72 Behavior is often the first way in which animals can modify their niches to cope with rapid 73 environmental changes (West-Eberhard 1989), and the structure of a food web is the ultimate 74 consequence of behavioral decisions made during foraging (Bartley et al. 2019). Changes in the 75 foraging niche are commonly associated with changes in competition (e.g. Van Valen 1965; 76 Svanbäck & Bolnick 2007; Bolnick et al. 2010) and predation regimes (e.g. Reznick et al. 1996; 77 Losos et al. 2004a). In these scenarios, changes in foraging behavior are most commonly 78 associated with modifications in movement and habitat use where individuals optimize their fitness 79 by altering the way they exploit food resources (Stephens & Krebs 1986; Richman & Price 1992; 80 Preisser et al. 2005; Seehausen 2006; Losos 2009; Schoener & Spiller 2012). Indeed, previous 81 research has provided important insight into how behavioral shifts can lead to rapid modifications 82 in food webs (Schmitz et al. 1997; Barton 2011; Leroux & Schmitz 2015; Jolly et al. 2019). For 83 example, the presence of predatory spiders altered feeding rates of grasshoppers, irrespective of 84 actual predation rates, with cascading effects decreasing herbivory on the herbaceous plant 85 community (Schmitz et al. 1997).

87 The arrival of new species is a major source of re-wiring of biological interactions in 88 communities (Lodge 2003; Vitousek et al. 2008; Blanchard 2015). This is particularly dramatic in 89 cases where novel predators arrive in native communities given their potential to modify the 90 structure and stability of communities through top-down effects (e.g. Vander Zanden et al. 1999). 91 Changes in habitat use are also expected to be important in the context of biological invasions. For 92 instance, following invasion by a novel ground predator, brown anoles (Anolis sagrei) in Florida 93 changed their use of the structural habitat and modified their diel activity patterns (Lapiedra et al. 94 2017). Following invasion, these niche shifts are expected to lead to changes in food-web structure. 95 This was the case after the invasion of lake ecosystems by two predatory fish that resulted in trout 96 modifying their foraging niches to consume more zooplankton and fewer littoral fish (Vander 97 Zanden et al. 1999). Understanding how behavior-driven niche shifts shape the structure and 98 connectivity of communities is of major importance for preserving ecosystem function in a rapidly 99 changing world. However, the role of behavior in re-wiring biological interactions in the context 100 of biological invasions remains largely understudied.

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102 Behavior-driven foraging niche shifts could potentially modify resource-flow dynamics 103 across ecosystem boundaries. One ecological scenario where foraging niche shifts could have 104 particularly dramatic consequences for the functioning of entire ecosystems occurs when two 105 different habitats are abutting and connected through resource-flow. For example, the energetics 106 and structure of biological communities of coastal and island habitats worldwide are often 107 influenced by marine subsidies, such as seaweed deposition (Polis & Hurd 1996; Polis et al. 2004; 108 Yang et al. 2008; Yang et al. 2010). These marine subsidies can largely determine productivity of 109 the whole island ecosystem and effectively govern the dynamics of numerous species within these

110 communities (Polis & Hurd 1996; Huxel & McCann 1998; Marczak *et al.* 2007; Spiller *et al.* 111 2010b; Piovia-Scott *et al.* 2011, 2013, 2019). Consequently, foraging niche shifts by mobile 112 generalist consumers—which forage both in the intertidal and the upland habitat—could 113 dramatically alter resource-flow dynamics between marine and terrestrial ecosystems. This pattern 114 is expected to be particularly important on small islands, where the perimeter to area ratios are 115 higher (Polis et al. 1997).

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117 Animals that modify their foraging niches in response to novel ecological interactions 118 likely face novel selective pressures. Given that generalist populations are often composed of 119 individual specialists (Bolnick et al. 2003), different individuals may interact with their 120 environment in different ways, such as taking more or less risks. Consequently, some individuals 121 could have more opportunities to obtain certain food resources than others, which should generate 122 an association between risk-taking and diet. Natural selection could favor some of these 123 phenotypic combinations over others, which could eventually modify evolutionary dynamics. 124 However, establishing a solid link between novel ecological interactions, behavior-driven foraging 125 niche shifts, and their potential to modify evolutionary dynamics is not straightforward and has 126 remained elusive for several reasons. First, it is difficult to experimentally manipulate ecologically 127 relevant selective pressures in natural populations (Toscano et al. 2016). Second, determining 128 whether behavioral variation and diet are associated requires a standardized evaluation of both 129 traits at the individual level. Finally, to understand altered niche dynamics through time, we need 130 to not only examine how the foraging niches of consumers shift under new ecological conditions 131 but also whether these changes persist into subsequent generations.

133 To better understand niche dynamics in rapidly changing environments we examined niche 134 dynamics in a replicated set of experimentally established island populations of a generalist lizard, 135 the brown anole (Anolis sagrei), in the Bahamas. We assessed habitat use, risk-taking behavior, 136 and foraging niche changes of brown anoles following experimental introduction of curly-tailed 137 lizards (Leiocephalus carinatus), a well-known terrestrial predator of anoles (Schoener et al. 138 2002a; Losos et al. 2004b; Lopez-Darias et al. 2012), on half the islands where brown anoles were 139 experimentally translocated. Brown anoles forage in the intertidal and upland habitats (Spiller et 140 al. 2010b; Piovia-Scott et al. 2019). On islands where ground predators are present, a gradient of 141 risk likely exists for brown anoles. Coastal edges where marine subsidies are most abundant 142 commonly lack vegetation and force anoles to spend more time on the ground whereas in the 143 interior of the island, where marine subsidies are scarce or absent, they spend most of their time 144 perching on vegetation above the ground. (Fig. 1). Previous work in this study system showed 145 that natural selection acted upon individual variation in risk-taking behavior of brown anoles in 146 the presence of these ground predators (Lapiedra et al. 2018). Predator-driven shifts in foraging 147 behavior could potentially alter resource flow between these two adjacent ecosystems by 148 modifying the structure and strength of existing food web interactions (Bartley et al. 2019). In this 149 study, we examine the following hypotheses: i) the arrival of a novel predator modifies habitat use 150 associated with the foraging niche of brown anoles; ii) these population-level changes in habitat 151 use result in diet shifts that decouple resource-flow dynamics between marine and terrestrial 152 ecosystems; iii) modified foraging niches persist into the next generation; and iv) individual 153 variation in the foraging niche is associated with individual variation in ecologically relevant risk-154 taking behavior.

#### 157 **METHODS**

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### 159 Study system

160 We studied resource-flow dynamics between marine and terrestrial biological communities in an 161 experimental island system in the Bahamas. In our study area, deposits of marine macrophytes 162 often accumulate on the shores of small islands especially following tropical storms (Spiller et al. 163 2010a). These nutrient-rich deposits often result in increased populations of detritivore arthropods. 164 which in turn can attract larger terrestrial predators, including the generalist brown anole lizards 165 (Spiller et al. 2010a). Brown anoles are small, semi-arboreal lizards native to the northern 166 Caribbean. They commonly use the lower portions of tree trunks near the ground and often leave 167 their perches to capture prev, predominantly terrestrial arthropods, on the ground (Schoener 1968; 168 Losos 2009; Giery et al. 2013).

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170 Marine subsidies, such as decomposing seaweed, are most abundant near the lower shore 171 edges of islands (Kenny et al. 2017). The uneven spatial distribution of these resources creates a 172 risk trade-off for foraging brown anoles. On one hand, marine subsidies attract a higher abundance 173 of arthropods, especially detritivores. Brown anoles can benefit substantially from consuming 174 those arthropod prey feeding on marine subsidies (Piovia-Scott et al. 2011). On the other hand, 175 since marine subsidies deposited on island edges are farther away from the safety of vegetation on 176 which anoles commonly perch, foraging on marine resources increases the risk of being captured 177 by ground predators, such as curly-tailed lizards. The effects of predation by curly-tailed lizards 178 on brown anoles are well-documented, and include population size reduction, changes in 179 microhabitat use (i.e. their perch height), decreased survival rates as well as natural selection on 180 both their morphology and risk-taking behavior (Schoener et al. 2002; Losos et al. 2004; Lapiedra 181 et al. 2018). In contrast to the trunk and ground dwelling brown anoles, curly-tailed lizards are 182 primarily ground-dwelling (Losos 2009). Food webs on our experimental islands are relatively 183 simple and comparable to those of previously studied nearby island ecosystems (Schoener 1968; 184 Schoener et al. 1982, 2002a; Piovia-Scott et al. 2011). These food webs include herbivores which 185 consume terrestrial foliage, detritivores that consume decomposing marine subsidies on the island 186 edges, spiders that can prey upon those arthropods, brown anoles that consume all arthropods, and 187 curly-tailed lizards which also consume brown anoles in addition to arthropods (Schoener et al. 188 2002b; Kenny et al. 2017). These islands are an ideal setting to study how rapid changes in 189 predation pressure alter trophic interactions. Moreover, they can also help reveal how new 190 ecological interactions impact the existing network of interactions at the ecosystem level (Fig. 1).

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#### 192 Experimental design

193 In June 2016, we established an experimental system consisting of translocated populations of 194 adult brown anole lizards on eight small islands off the coast of Great Abaco, Bahamas. Adult 195 male and female brown anoles were captured from larger islands around the study area and 196 distributed among the islands in proportion to the island's vegetated area (Lapiedra et al. 2018). 197 These islands were absent of anoles prior to translocation and are of similar size to islands nearby 198 that sustain brown anole populations (Losos et al. 2004). One week after the translocation of brown 199 anoles, we randomly added predatory curly-tailed lizards onto four of the islands in a proportion 200 of one predator for every 12 brown anoles following Losos et al. (2004); the other four islands 201 remained as predator-free controls (see Lapiedra et al. 2018 for more details). Data for the present

202 study were collected in May-June of 2017, one year after the field experiment was initiated. To 203 investigate if potential foraging niche shifts were persistent over time, we characterized the diets 204 of both 'founder' adult brown anoles that survived one year after experimental translocation of 205 ground predators and 'offspring' from the first generation that hatched on these experimental 206 islands. All founder lizards had been individually, permanently tagged using injectable alpha tags 207 when translocated in 2016; all untagged individuals captured in 2017 were considered offspring. 208 Additional information on how we assessed both the availability of marine resources and arthropod 209 abundance can be found in Additional Methods S1.

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## 211 Habitat use, individual tracking, and body condition

212 We measured perch height as the vertical distance between the location of a lizard and the ground. 213 After capturing each brown anole by using a lasso, we translocated them to our field laboratory at 214 the Friends of the Environment in Marsh Harbour, Bahamas. On the day after capture, we 215 conducted individual-level behavioral assays on each captured lizard (see section below). After 216 these behavioral trials, we measured their body size (i.e. snout-vent length, or SVL), body mass, 217 and determined their sex. Founder individuals were identified by reading the alpha tags that had 218 been inserted prior to translocation. After measuring each lizard, we individually tagged offspring 219 individuals with unique sub-dermic alpha tags for future identification. Then, we released each 220 lizard at the point of capture, which had been individually marked with flagging tape on each 221 island. To quantify the body condition of individual anoles, we divided log-transformed body mass 222 by log-transformed SVL and computed body condition separately for males and females because 223 these two traits co-vary differently between sexes.

#### 5 Estimating the marine component of lizard diet from $\delta^{13}$ C

To examine how predatory curly-tailed lizards alter the foraging ecology of brown anoles, we assessed habitat use of brown anoles (Schoener *et al.* 2002a; Losos *et al.* 2004; Lopez-Darias *et al.* 2012; Lapiedra *et al.* 2018) and the proportion of marine prey in anole diets (Spiller *et al.* 2010, Wright *et al.* 2020). Our prediction was that the marine component of anole diet would be reduced in the presence of ground predators. To assess how much of the diet of individual brown anoles was composed of marine-derived resources (e.g., detritivores that feed on decomposing seaweed), we measured stable isotope ratios from brown anole tissue.

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234 We captured 156 lizards across seven experimental islands. For each captured anole, we 235 collected approximately 1.5 cm of their tails for stable isotope analysis. All founder anoles had 236 previously had their tail tips removed in the initial 2016 translocation, so all tail samples taken in 237 this 2017 study reflect their diets during the period since the start of the experiment. We performed 238 stable isotope analyses to characterize the diet of lizards from our experimental islands. We 239 estimated the marine component in diet by analyzing differences in assimilated  $\delta^{13}$ C in each lizard (Post 2002).  $\delta^{13}$ C is relatively rare in comparison to the lighter  $\delta^{12}$ C (Fry 2006). Here we used  $\delta^{13}$ C 240 241 as an indicator of marine content accumulated in organisms, as marine plants and seaweed are more enriched in  $\delta^{13}$ C than C3 terrestrial plants (Post 2002; Spiller *et al.* 2010), and <sup>13</sup>C remains 242 243 in the tissues of organisms that consume these resources. C<sub>4</sub> plants are scarce in our study area 244 (Spiller et al. 2010). Stable isotope values are represented as a ratio of sample isotopes to a 245 reference standard isotope (Formula S1). We followed Fry (2006) to obtain this ratio (Formula S1 246 in Supplementary Material) and we expanded this formula to include the ratios of specific isotopes (see Formula S2). Additional information on the application of island-specific baselines,
fractionation, and lipid correction is included in Additional Methods S2.

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### 250 Stable isotope sample preparation, pre-processing, and analysis

251 To prepare samples for stable isotope analysis, we first air dried them in the field laboratory in the 252 Bahamas according to a previously established stable isotope protocol (Yang 2012). Then, we 253 stored each tail tip in an Eppendorf tube containing silica gel and tissue paper to prevent direct 254 contact with the sample (Yang 2012). Stable isotope pre-processing and analysis were done at the 255 UC Davis Stable Isotope Facility. Buttonwood and seaweed samples were ground with a SPEX 256 cryogrinder, and lizard tails were corrected for lipid content before stable isotope analysis (Yang 257 2012). Samples were then placed in a PDZ Europa 20-20 isotope ratio mass spectrometer and 258 analyzed for <sup>13</sup>C and <sup>15</sup>N with a PDZ Europa ANCA-GSL elemental analyzer.

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#### 260 Collecting individual-level behavioral data

261 Individual variation in risk-taking behavior of anoles, which has previously been shown to be 262 consistent through time and in different contexts (Lapiedra et al. 2017, 2018) might impact their 263 foraging ecology. We hypothesized that, on predator-free islands, brown anoles that are more 264 willing to take risks by leaving their perches to hunt for arthropod prey on the ground would obtain 265 more food derived from marine resources in the intertidal. Conversely, on islands with predators, 266 anoles that leave the safety of their perches to search for prey risk being captured by ground-267 dwelling curly-tailed lizards. To study if risk-taking behavior affected diet composition for 268 individual lizards, we assessed variation in risk-taking behavior for all individuals captured in this 269 study. Behavioral assays consisted of two phases: a five-minute exposure period to a caged curly270 tailed lizard, and a 30-minute experimental period. We first placed each captured anole in a refuge 271 and covered their refuge for five minutes following Lapiedra et al. (2018). After this, we placed a 272 curly-tailed lizard inside a transparent plastic container in front of the refuge. We remotely lifted 273 the cover on the refuge and allowed the anole to observe the curly-tailed lizard inside its cage. 274 After five minutes of exposure to the curly-tailed lizard, we covered the anole's refuge for five 275 more minutes and removed the curly-tailed lizard from the experimental enclosure. Then, we 276 removed the refuge cover and allowed the lizard to explore its environment for 30 minutes. We 277 recorded the length of time between when the lizard's entire body left its refuge to the time when 278 it reached the rocks, perch, or retreated back into the refuge (*time exposed on the ground*).

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#### 280 Statistical analyses

281 To assess which factors explained variation in the proportion marine diet, we performed 282 generalized linear mixed model (GLMM) analyses using the 'lme' function of the R package 283 'nlme' (Pinheiro et al. 2017). We performed mixed effects linear model analyses including those 284 factors that were hypothesized to possibly influence diet of brown anoles. To assess which factors 285 explained differences in proportion of marine diet, we assigned the ratio of marine diet as the 286 dependent variable and included experimental treatment (predator-free vs. predator), sex (females 287 vs. males), and lizard generation (founders vs. offspring) as fixed factors. Island ID was included 288 as a random factor in all models to account for additional potential intrinsic differences on each 289 island that could impact the proportion of marine diet. Models not including this random factor in 290 the model provided similar results, although the effect of predator presence on diet was even 291 stronger (Table S5). We used similar linear mixed model analyses to assess if the proportion of 292 marine diet was explained by variation in behavior by assigning risk-taking behavior (time spent *on the ground* recorded from behavioral assays) as a fixed factor. For simplicity in the interpretation of results, we ran these models separately by sex based on published evidence that this trait differs between sexes (Lapiedra *et al.* 2018).

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### 298 **RESULTS**

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# 300 Prey availability between predator regimes

301 We quantified arthropod prey diversity and abundance as well as seaweed availability on each 302 island to test if these factors differed between predation regimes. Arthropod prey biomass (Wilcox-303 test; W = 11, p = 0.11) and arthropod diversity (Wilcox-test; W = 10, p = 0.23) did not differ 304 between islands in the presence or absence of ground predators (n=1.346 arthropods sampled; Fig.)305 S2). In addition, islands from different predation regimes did not differ in their abundance of seaweed (Wilcox-test; W = 9, p = 0.89; Fig. S3). These results suggest that brown anole diet 306 307 differences between islands with and without ground predators are unlikely to be driven by 308 differences in seaweed abundance or arthropod availability or diversity.

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The abundance of web spiders, however, differs between predator vs. predator-free islands. Specifically, predator islands had higher densities of spider webs (i.e., counts of active spider webs divided by vegetated area for each island) than predator-free islands (Mann-Whitney test; W = 0, p = 0.057; Fig. 2D). The average number of spider webs on predator islands (0.107 spider webs/m<sup>2</sup> of vegetation) was nearly five times higher than that on predator-free ones (0.022 spider webs/ m<sup>2</sup>).

# 317 Changes in habitat use and body condition under different predation pressures

318 To test if brown anoles had changed their habitat use one year after experimental translocation, we 319 compared perch height on islands with and without ground predators present. We found that brown 320 anoles on predator islands perched on the ground only 6.7% of time, whereas lizards on predator-321 free islands used the ground over four times more often (31.8%). This resulted in lizards perching 322 more than twice as high as lizards on predator-free islands (average perch heights of 16.8 and 35.7 323 cm respectively, W = 9833.5; p < 0.001; Figure 2A). In addition, both males and females were in 324 worse body condition on predator islands as compared to predator-free controls (females: t = 3.91, 325 df = 68.3, p = 0.0002; males: t = 2.51, df = 89.8, p-value = 0.01) (Figure 2B).

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#### 327 The proportion of marine diet of brown anoles decreases in the presence of ground predators

328 We found that diets of brown anoles on islands with ground predators present had a lower marine 329 component than those without predators (p = 0.040; Table 1 shows the best mixed model based on 330 AICc; Fig. 3). The decreased consumption of marine-derived food resources on islands with 331 ground predators holds when restricting this analysis to lizards born on the experimental islands 332 (that is, offspring males and females; t = 2.03, p = 0.045, n=107; Fig. 3, right). In parallel, offspring 333 individuals had a higher marine component than founder lizards (p = 0.022; Table 1). Although 334 founder males tended to have a more marine-derived diet than founder females, there were no 335 overall differences in the proportion of marine diet between sexes (Fig. 3). The interaction of sex 336 with experimental treatment was not significant and was not retained in the best model.

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#### 338 Risk-taking behavior is associated with marine diet

On predator islands, we found a significant interaction showing that females exhibiting riskier behavior, measured as the amount of time spent on the ground during experimental trials, had higher proportions of marine-derived resources in their diets than females taking less risks (t = 2.50, p = 0.020, n=32; Table 2, Fig. 2C). In addition, the association between risk-taking and diet was in the same direction in both founders and offspring lizards (note a lack of interaction between these factors, Table 2). In the case of males, risk-taking did not predict the proportion of marinederived diet (p = 0.79 for the interaction term of a model including sex, not shown in Table 2).

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#### 348 **DISCUSSION**

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350 Our study shows that a predator-driven behavioral shift altered resource-flow dynamics between 351 adjacent ecosystems. First, the arrival of a ground predator caused anoles to perch higher on 352 vegetation and use the ground less than on islands without these predators. This behavioral shift 353 was associated with a weakened body condition in both sexes one year after experimental 354 translocation. Our findings indicate that the aversion of brown anoles to leave the safety of their 355 perches to capture arthropod prey on the ground limited their ability to obtain marine-derived food 356 resources on islands with ground predators. The productivity of these coastal systems depends 357 considerably on pulsed marine subsidies (Yang et al. 2008; Spiller et al. 2010; Piovia-Scott et al. 358 2013; 2019; Wright et al. 2020). Moreover, brown anoles rapidly increase ground use after 359 experimental seaweed deposition (Kenny et al. 2017). Thus, lower body condition on experimental 360 islands with predators present likely emerges from reduced consumption of seaweed-feeding 361 detritivores. Indeed, previous research found that growth rates of brown anoles were higher on islands experimentally subsidized with seaweed as compared with control islands (Wright *et al.* 2013). The lack of average differences in arthropod abundances in the presence vs. absence of ground predators suggests that body condition differences are likely driven by an increased risk of foraging bouts in the presence of these ground predators rather than by lower prey abundance.

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367 Stable isotope analyses show that anoles on predator islands reduced their consumption of 368 marine-derived resources as compared with lizards on predator-free control islands. Previous work 369 showed that higher levels of  $\delta^{13}$ C in tail tips of brown anoles are indicative of a higher use of 370 marine-based resources. Specifically, experimentally subsidized seaweed deposits at a similar 371 Bahamian field site led to a rapid increase in the marine diet proportion of brown anoles (Piovia-372 Scott et al. 2013). This higher use of marine-derived resources was associated with an increased 373 abundance of detritivores such as amphipods, which occur on seaweed deposits on the ground, as 374 compared with herbivorous arthropods, which are mostly found on foliage above the ground 375 (Spiller et al. 2010).

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377 Several pieces of evidence indicate that our findings correspond to foraging niche shifts 378 rather than differences in resource availability between islands from different predator regimes. 379 First, average seaweed abundance did not differ between predator-free versus predator islands. 380 Second, our estimates of relative consumption of marine-derived resources of brown anoles 381 included an island-specific correction of  $\delta^{13}$ C values relative to a baseline for both terrestrial 382 (buttonwood) and marine (seaweed) resources (Post 2002; Spiller et al. 2010). Brown anoles on 383 predator-free islands seem to be capturing comparatively more marine-derived prey due to the 384 absence of ground-dwelling predatory lizards. This reduced risk of predation allows brown anoles to move freely on the ground (Losos *et al.* 2004; Lopez-Darias *et al.* 2012; Lapiedra *et al.* 2018),
where marine deposits and the detritivore arthropods that feed on them are most abundant (Spiller *et al.* 2010; Piovia-Scott *et al.* 2013).

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389 There is growing interest in the ecological consequences of consistent individual variation 390 within animal populations (Bolnick et al. 2003, 2011), particularly in the context of among-391 individual variation in behavior (e.g. Sih et al. 2004, 2012; Réale et al. 2007). If certain behavioral 392 profiles are better suited to new selection pressures, they should be favored by natural selection. 393 A critical implication of among-individual variation in behavior is that these differences could 394 translate into individual differences in how individuals interact with their environment. These 395 niche changes are relevant because they could ultimately alter ecosystem functioning, especially 396 when they occur in keystone species such as brown anoles (Schoener *et al.* 2002). However, the 397 mechanisms by which among-individual variation in behavior may cascade to alter the functioning 398 of biological communities remains poorly understood. On these same experimental islands, 399 Lapiedra et al. (2018) showed that natural selection favored female brown anoles that were less 400 willing to take risks on islands with predators (i.e., females that spent less time exposed on the 401 ground in the behavioral assays had higher survival fitness). Here we found that among-individual 402 differences in behavior were associated with foraging niche variation. Specifically, females from 403 predator islands that spent a longer time exposed on the ground during our behavioral trials had a 404 significantly higher proportion of marine diet—a pattern not replicated on predator-free islands. 405 This pattern on predator islands is presumably driven by the fact that ground-dwelling predators 406 greatly decrease ground use for females. However, those females that were willing to spend a 407 longer time on the ground in behavioral trials have a greater opportunity to feed on marine-based

408 prey. In other words, most female lizards on predator islands avoid the ground, but those who were 409 able to spend more time on the ground consume higher proportions of marine-derived resources. 410 In contrast, on predator-free islands, spending more time on the ground was not associated with an 411 increased risk of predation by curly-tailed lizards (Lapiedra *et al.* 2018), which likely explains why 412 marine diet is not linked to risk-taking behavior in the absence of predators.

413

414 Individual variation in time spent on the ground was not associated with a higher marine 415 diet for males in either predation regime. It is interesting that this behavior is significantly 416 associated with marine diet for females on predation islands, but not for males on control or 417 predation islands. Previously documented differences in foraging behavior between sexes could 418 explain this difference (Losos 2009); brown anole males do not devote the majority of their time 419 to foraging, but rather spend much of their time displaying to other males and patrolling their 420 territory (Schoener 1982; Losos 2009). Thus, differences in time spent on the ground for males 421 may not be directly related to success in acquiring marine-based prey on both control and predation 422 islands.

423

An unexpected observation was that lizards hatched on the experimental islands (i.e., firstgeneration offspring) exploited a higher proportion of marine resources as compared to founder individuals. One possible explanation for this observation could be that offspring are more familiar with the spatial and temporal resource distribution on the island landscape. Learning could have allowed them to more often successfully consume more peripheral marine resources than lizards that were translocated on the islands as adults. Whether increased use of marine resources in offspring emerges from behavioral flexibility (e.g. spatial learning) or is the consequence of 431 ontogenetic differences remains unknown and it is beyond the aim of this paper. Since all lizard 432 tail tips were removed before translocation, and differences in diet are apparent in stable isotope 433 analysis of tail samples around six months (Spiller *et al.* 2010), the  $\delta^{13}$ C values measured in this 434 analysis should describe the diet of founder lizards exclusively after translocation. Alternatively, 435 differences between founder and offspring lizards might partly explained by tissue differences in 436 the stable isotope composition of different tissues; diet composition in founder lizards was 437 quantified from regenerated tails, which is mostly cartilage and lacks bone, in contrast to the 438 mostly un-regenerated tails of offspring.

439

440 There was a tendency for predator islands to have more spiders than predator-free islands. 441 This finding suggests that the presence of curly-tailed lizards has an impact on spider consumption. 442 Previous studies showed that experimentally introduced populations of brown anoles reduced 443 spider abundance on small Bahamian islands (Piovia-Scott *et al.* 2017); predation pressure from 444 curly-tailed lizards could be limiting brown anole population size and activity, including spider 445 consumption. Since we sampled vegetation-dwelling spiders on our islands, rather than ground-446 dwelling ones, the most likely explanation for the higher abundance of spiders on predator islands 447 is reduced predation pressure on spiders from brown anoles as a consequence of lower densities 448 of brown anoles on predator islands (Schoener et al. 2002) in association with lower survival rates 449 on these islands due to predation (Lapiedra et al. 2018).

450

Understanding how animal populations adjust their niches to new selective pressures is of major importance in the current context of human-induced rapid environmental change where species are often introduced into novel communities. Our study shows how the arrival of a new top-predator (topological re-wiring *sensu* Blanchard 2015) drove rapid niche shifts in brown

455 anoles. Anoles less frequently visited intertidal areas of small islands and consumed relatively less 456 marine-derived resources (i.e., interaction strength re-wiring). Understanding behavior-mediated 457 ecological alterations of consumers is of major importance because they can affect the stability of 458 ecosystems (Tylianakis et al. 2008). For example, predator-driven decreased consumption of 459 marine-derived resources in our study system not only modifies invertebrate communities on these 460 islands (Schoener et al. 2002) but, more generally, they alter resource flow between abutting 461 ecosystems. Given that the arrival of novel predators is a major driver of island biodiversity loss 462 worldwide (Simberloff 1995; Sax and Gaines 2008), shedding light on the cascading effects of 463 predator-driven behavioral responses of key consumers is essential for island biodiversity 464 conservation.

465

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- 486

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# 641 Figures and Tables





**Figure 1:** Simplified representations of island food webs in our study system based on previous studies. Arrows represent proportional consumption of resources in the presence (red arrows) vs. absence (gray arrows) of a top ground predator in the experiment study system. We predict that brown anoles will increase relative consumption of terrestrial herbivores and other mesopredators such as spiders, and markedly decrease their use of the ground in the presence of ground predators, consequently reducing the relative consumption of detritivores that mostly consume marine subsidies on the edges of our experimental islands.



652

653 Fig. 2: A) Mean (±SE) perch height (in cm) used by brown anoles on predator-free versus predator islands 654 one year after experimental translocation. B) Changes in body condition for founder individuals from the 655 start of the experimental translocation in summer 2016 compared to when lizards were recaptured in 656 summer 2017, separated by predation regime and sex, for experimental islands in the presence (red) vs. absence (grey) of ground predators. C) Individual-level association between risk-taking behavior and 657 658 marine component of diet for female brown anoles in the presence (red) vs. absence (grey) of ground 659 predators. D) Differences in web spider density (number of webs by square meter) by island for the two 660 predation regimes. Each bar represents an individual island.



663

664 Fig. 3: Population-level frequency distribution for the amount of marine component in the diet comparing 665 individuals from predator-free (grey) vs. predator present islands (red), divided by sex (females on the left 666 and males on the right) as well as whether lizards were translocated as adults (top plots, "founder lizards") 667 or hatched on the islands ("offspring lizards"). Note that translocated lizards had the tip of their tails 668 removed before the experiment, ensuring that the tissue extracted after one year was tissue regenerated 669 while these lizards were living on the experimental islands. Proportion of marine diet was square root 670 transformed before plotting. Note the range limit of "y" axis was expanded in the top right figure (founder 671 males) for visualization purposes.

- **Table 1:** Brown anoles on islands with ground predators had lower marine components of their diet than
- 674 lizards on predator-free islands. Moreover, the diets of brown anoles hatched on the experimental islands
- had a higher proportion of marine-derived prey. Finally, the diet of males contained a higher proportion of
- 676 marine-derived resources.

	Value	Std. Error	DF	t-value	p-value
Intercept	144.95	8.03	140	18.05	0
Treatment—predator	-20.51	9.14	140	-2.24	0.026
Sex-M	6.76	2.40	140	-2.82	0.005
Lizard generation—founders	-5.31	2.56	140	-2.08	0.039

Table 2: Individual brown anole females exhibiting riskier behavior in lab trials had a higher proportion of
 marine resources in their diets. This positive association was observed only on predator islands.

	Value	Std. Error	DF	t-value	p-value
Intercept	113.54	10.55	18	10.76	0
Treatment—predation	-37.09	13.62	5	-2.72	0.042
Risk-taking behavior	-7.29	2.57	18	-2.84	0.011
Lizard generation—founders	-11.02	5.74	18	-1.92	0.071
Risk-taking*Treatment—predation	10.54	2.93	18	3.59	0.021