

**Title: 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 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.

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).

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

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

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

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

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

## **METHODS**

### **Study system**

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

Marine subsidies, such as decomposing seaweed, are most abundant near the lower shore edges of islands (Kenny *et al.* 2017). The uneven spatial distribution of these resources creates a risk trade-off for foraging brown anoles. On one hand, marine subsidies attract a higher abundance of arthropods, especially detritivores. Brown anoles can benefit substantially from consuming those arthropod prey feeding on marine subsidies (Piovia-Scott *et al.* 2011). On the other hand, since marine subsidies deposited on island edges are farther away from the safety of vegetation on which anoles commonly perch, foraging on marine resources increases the risk of being captured by ground predators, such as curly-tailed lizards. The effects of predation by curly-tailed lizards on brown anoles are well-documented, and include population size reduction, changes in

microhabitat use (i.e. their perch height), decreased survival rates as well as natural selection on both their morphology and risk-taking behavior (Schoener *et al.* 2002; Losos *et al.* 2004; Lapiedra *et al.* 2018). In contrast to the trunk and ground dwelling brown anoles, curly-tailed lizards are primarily ground-dwelling (Losos 2009). Food webs on our experimental islands are relatively simple and comparable to those of previously studied nearby island ecosystems (Schoener 1968; Schoener *et al.* 1982, 2002a; Piovia-Scott *et al.* 2011). These food webs include herbivores which consume terrestrial foliage, detritivores that consume decomposing marine subsidies on the island edges, spiders that can prey upon those arthropods, brown anoles that consume all arthropods, and curly-tailed lizards which also consume brown anoles in addition to arthropods (Schoener *et al.* 2002b; Kenny *et al.* 2017). These islands are an ideal setting to study how rapid changes in predation pressure alter trophic interactions. Moreover, they can also help reveal how new ecological interactions impact the existing network of interactions at the ecosystem level (Fig. 1).

## **Experimental design**

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

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

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

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

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

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.

We captured 156 lizards across seven experimental islands. For each captured anole, we collected approximately 1.5 cm of their tails for stable isotope analysis. All founder anoles had previously had their tail tips removed in the initial 2016 translocation, so all tail samples taken in this 2017 study reflect their diets during the period since the start of the experiment. We performed stable isotope analyses to characterize the diet of lizards from our experimental islands. We estimated the marine component in diet by analyzing differences in assimilated  $\delta^{13}\text{C}$  in each lizard (Post 2002).  $\delta^{13}\text{C}$  is relatively rare in comparison to the lighter  $\delta^{12}\text{C}$  (Fry 2006). Here we used  $\delta^{13}\text{C}$  as an indicator of marine content accumulated in organisms, as marine plants and seaweed are more enriched in  $\delta^{13}\text{C}$  than  $\text{C}_3$  terrestrial plants (Post 2002; Spiller *et al.* 2010), and  $^{13}\text{C}$  remains in the tissues of organisms that consume these resources.  $\text{C}_4$  plants are scarce in our study area (Spiller *et al.* 2010). Stable isotope values are represented as a ratio of sample isotopes to a reference standard isotope (Formula S1). We followed Fry (2006) to obtain this ratio (Formula S1 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.

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

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

### **Collecting individual-level behavioral data**

Individual variation in risk-taking behavior of anoles, which has previously been shown to be consistent through time and in different contexts (Lapiedra *et al.* 2017, 2018) might impact their foraging ecology. We hypothesized that, on predator-free islands, brown anoles that are more willing to take risks by leaving their perches to hunt for arthropod prey on the ground would obtain more food derived from marine resources in the intertidal. Conversely, on islands with predators, anoles that leave the safety of their perches to search for prey risk being captured by ground-dwelling curly-tailed lizards. To study if risk-taking behavior affected diet composition for individual lizards, we assessed variation in risk-taking behavior for all individuals captured in this study. Behavioral assays consisted of two phases: a five-minute exposure period to a caged curly-

tailed lizard, and a 30-minute experimental period. We first placed each captured anole in a refuge and covered their refuge for five minutes following Lapiedra *et al.* (2018). After this, we placed a curly-tailed lizard inside a transparent plastic container in front of the refuge. We remotely lifted the cover on the refuge and allowed the anole to observe the curly-tailed lizard inside its cage. After five minutes of exposure to the curly-tailed lizard, we covered the anole's refuge for five more minutes and removed the curly-tailed lizard from the experimental enclosure. Then, we removed the refuge cover and allowed the lizard to explore its environment for 30 minutes. We recorded the length of time between when the lizard's entire body left its refuge to the time when it reached the rocks, perch, or retreated back into the refuge (*time exposed on the ground*).

## **Statistical analyses**

To assess which factors explained variation in the proportion marine diet, we performed generalized linear mixed model (GLMM) analyses using the 'lme' function of the R package 'nlme' (Pinheiro *et al.* 2017). We performed mixed effects linear model analyses including those factors that were hypothesized to possibly influence diet of brown anoles. To assess which factors explained differences in proportion of marine diet, we assigned the ratio of marine diet as the dependent variable and included experimental treatment (predator-free vs. predator), sex (females vs. males), and lizard generation (founders vs. offspring) as fixed factors. Island ID was included as a random factor in all models to account for additional potential intrinsic differences on each island that could impact the proportion of marine diet. Models not including this random factor in the model provided similar results, although the effect of predator presence on diet was even stronger (Table S5). We used similar linear mixed model analyses to assess if the proportion of 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).

## RESULTS

### *Prey availability between predator regimes*

We quantified arthropod prey diversity and abundance as well as seaweed availability on each island to test if these factors differed between predation regimes. Arthropod prey biomass (Wilcoxon-test;  $W = 11$ ,  $p = 0.11$ ) and arthropod diversity (Wilcoxon-test;  $W = 10$ ,  $p = 0.23$ ) did not differ between islands in the presence or absence of ground predators ( $n=1,346$  arthropods sampled; Fig. S2). In addition, islands from different predation regimes did not differ in their abundance of seaweed (Wilcoxon-test;  $W = 9$ ,  $p = 0.89$ ; Fig. S3). These results suggest that brown anole diet differences between islands with and without ground predators are unlikely to be driven by differences in seaweed abundance or arthropod availability or diversity.

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>).

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

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

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

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

### ***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 marine-derived diet ( $p = 0.79$  for the interaction term of a model including sex, not shown in Table 2).

## **DISCUSSION**

Our study shows that a predator-driven behavioral shift altered resource-flow dynamics between adjacent ecosystems. First, the arrival of a ground predator caused anoles to perch higher on vegetation and use the ground less than on islands without these predators. This behavioral shift was associated with a weakened body condition in both sexes one year after experimental translocation. Our findings indicate that the aversion of brown anoles to leave the safety of their perches to capture arthropod prey on the ground limited their ability to obtain marine-derived food resources on islands with ground predators. The productivity of these coastal systems depends considerably on pulsed marine subsidies (Yang *et al.* 2008; Spiller *et al.* 2010; Piovia-Scott *et al.* 2013; 2019; Wright *et al.* 2020). Moreover, brown anoles rapidly increase ground use after experimental seaweed deposition (Kenny *et al.* 2017). Thus, lower body condition on experimental islands with predators present likely emerges from reduced consumption of seaweed-feeding 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.

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

Several pieces of evidence indicate that our findings correspond to foraging niche shifts rather than differences in resource availability between islands from different predator regimes. First, average seaweed abundance did not differ between predator-free versus predator islands. Second, our estimates of relative consumption of marine-derived resources of brown anoles included an island-specific correction of  $\delta^{13}\text{C}$  values relative to a baseline for both terrestrial (buttonwood) and marine (seaweed) resources (Post 2002; Spiller *et al.* 2010). Brown anoles on predator-free islands seem to be capturing comparatively more marine-derived prey due to the 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).

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

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

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

An unexpected observation was that lizards hatched on the experimental islands (i.e., first-generation 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

ontogenetic differences remains unknown and it is beyond the aim of this paper. Since all lizard tail tips were removed before translocation, and differences in diet are apparent in stable isotope analysis of tail samples around six months (Spiller *et al.* 2010), the  $\delta^{13}\text{C}$  values measured in this analysis should describe the diet of founder lizards exclusively after translocation. Alternatively, differences between founder and offspring lizards might partly explained by tissue differences in the stable isotope composition of different tissues; diet composition in founder lizards was quantified from regenerated tails, which is mostly cartilage and lacks bone, in contrast to the mostly un-regenerated tails of offspring.

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

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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484

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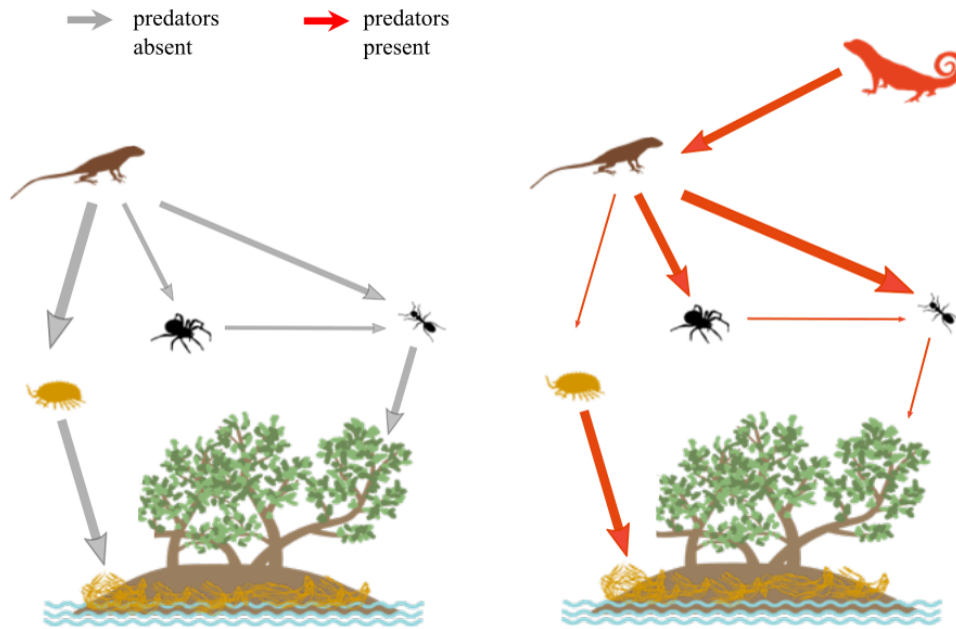
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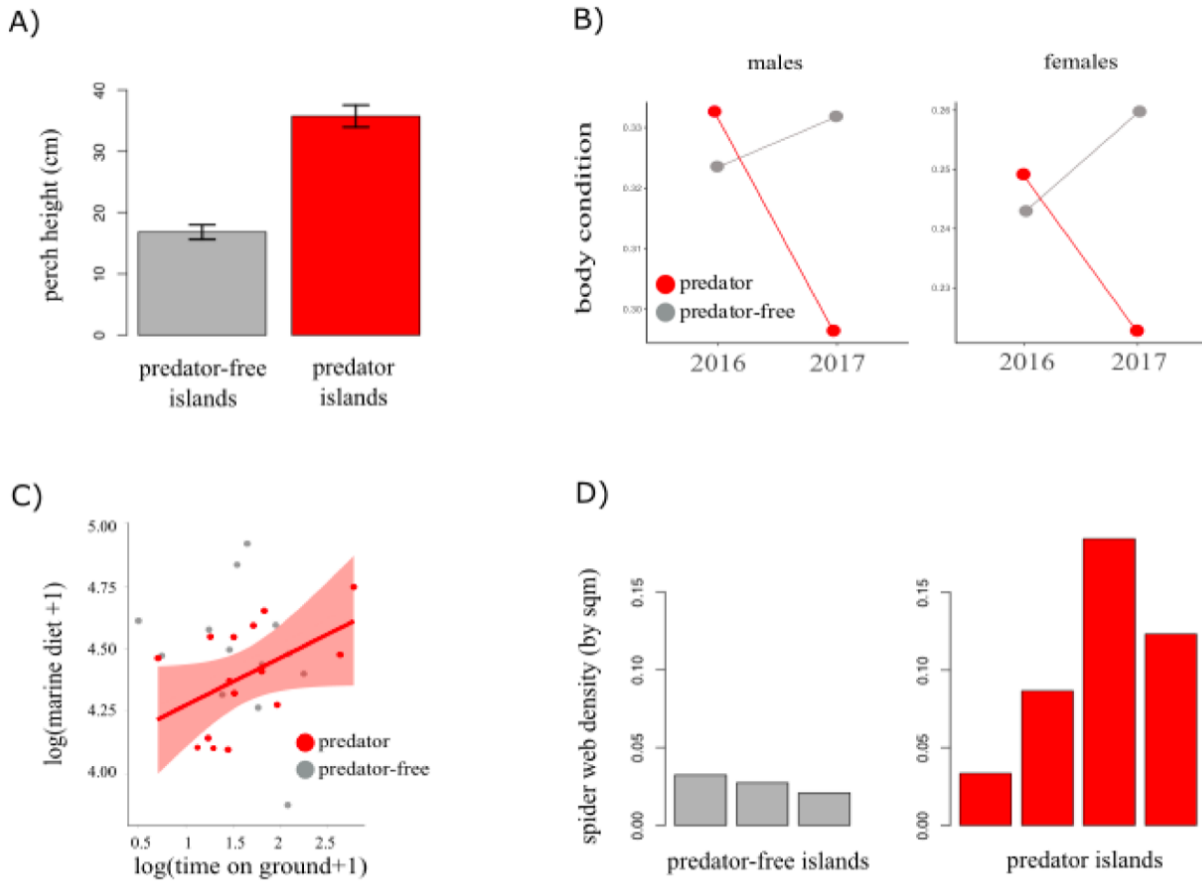
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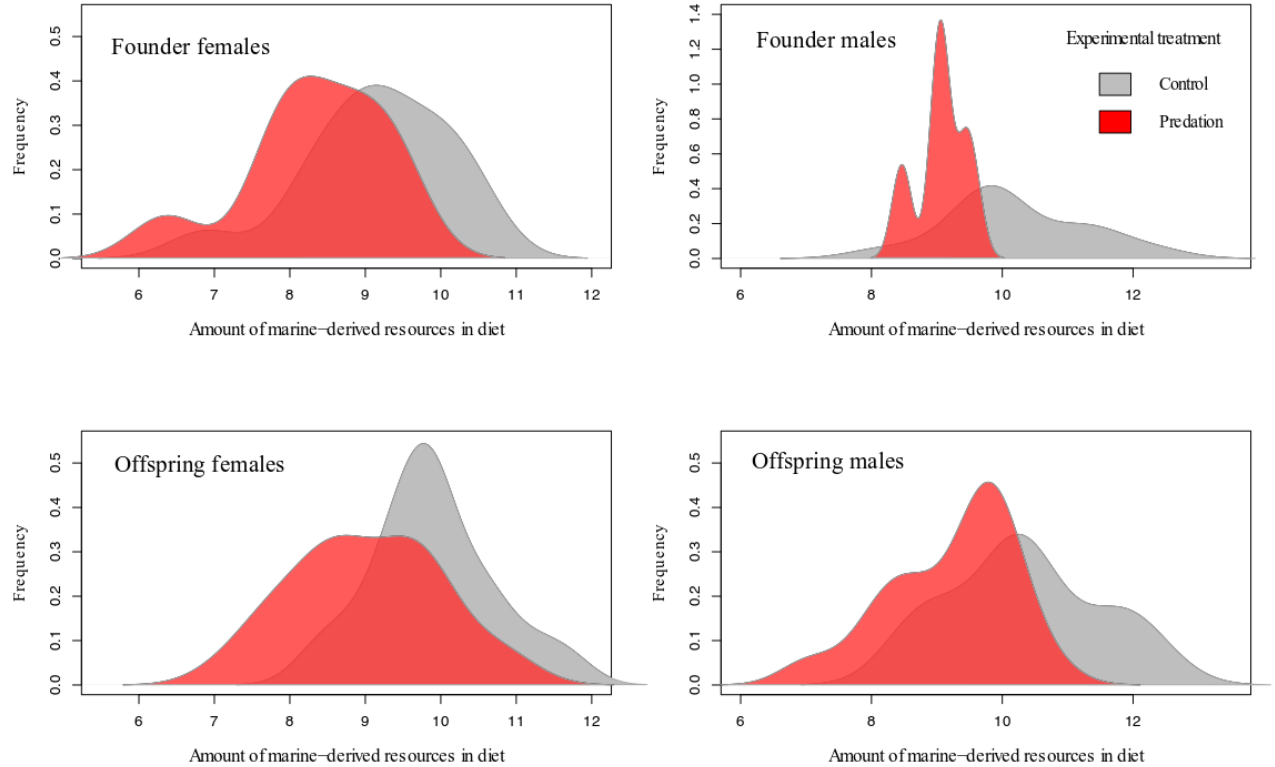
## Figures and Tables



**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.



**Fig. 2:** **A)** Mean ( $\pm$ SE) perch height (in cm) used by brown anoles on predator-free versus predator islands one year after experimental translocation. **B)** Changes in body condition for founder individuals from the start of the experimental translocation in summer 2016 compared to when lizards were recaptured in 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 marine component of diet for female brown anoles in the presence (red) vs. absence (grey) of ground predators. **D)** Differences in web spider density (number of webs by square meter) by island for the two predation regimes. Each bar represents an individual island.



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

**Table 1:** Brown anoles on islands with ground predators had lower marine components of their diet than 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 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