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LETTER

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

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Abstract

Foraging decisions shape the structure of food webs. Therefore, a behavioural 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 behaviours consumed more marine prey on islands with predators present. Our results show how predator-driven rapid behavioural shifts can alter food-web connectivity between oceanic and terrestrial ecosystems and underscore the importance of studying behaviour-mediated niche shifts to understand ecosystem functioning in rapidly changing environments.

KEYWORDS

Anolis lizards, cascading effects, d13C stable isotopes, ecological interactions, experimental ecology, food webs, niche shifts, predator–prey interactions, risk-taking behaviour, trophic interactions

Jason J. Kolbe and Jonathan B. Losos contributed equally to this work.

INTRODUCTION

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 (Bartley et al., 2019; Gilman et al., 2010).

Behaviour 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 behavioural decisions made during foraging (Bartley et al., 2019). Changes in the foraging niche are commonly associated with changes in competition (e.g. Bolnick et al., 2010; Svanbäck & Bolnick, 2007; Van Valen, 1965) and predation regimes (e.g. Losos et al., 2004; Reznick et al., 1996). In these scenarios, changes in foraging behaviour are most commonly associated with modifications in movement and habitat use where individuals optimize their fitness by altering the way they exploit food resources (Losos, 2009; Preisser et al., 2005; Richman & Price, 1992; Schoener & Spiller, 2012; Seehausen, 2006; Stephens & Krebs, 1986). Indeed, previous research has provided important insight into how behavioural shifts can lead to rapid modifications in food webs (Barton, 2011; Jolly et al., 2021; Leroux & Schmitz, 2015; Schmitz et al., 1997). 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).

The arrival of new species is a major source of re-wiring of biological interactions in communities (Blanchard, 2015; Lodge, 1993; Vitousek et al., 2008). This is particularly dramatic in cases where novel predators arrive in native communities given their potential to modify the structure and stability of communities through top-down effects (e.g. Vander Zanden et al., 1999). Changes in habitat use are also expected to be important in the context of biological invasions. For instance, following invasion by a novel ground predator, brown anoles (*Anolis sagrei*) in Florida changed their use of the structural habitat and modified their diel activity patterns (Lapiedra et al., 2017). Following invasion, these niche shifts are expected to lead to changes in food-web structure. This was the case after the invasion of lake ecosystems by two predatory fish that resulted in trout modifying their foraging niches to consume more zooplankton and fewer littoral fish (Vander Zanden et al., 1999). Understanding how behaviour-driven niche shifts shape the structure and connectivity of communities is of major importance for preserving ecosystem function in a rapidly changing world. However, the process by which behaviour re-wires biological interactions in the context of biological invasions remains largely understudied.

Behaviour-driven foraging niche shifts could potentially modify resource-flow dynamics across ecosystem boundaries. One ecological scenario where foraging niche shifts could have particularly dramatic consequences for the functioning of entire ecosystems occurs when two different habitats are abutting and connected through resource-flow. For example, the energetics and structure of biological communities of coastal and island habitats worldwide are often influenced by marine subsidies, such as seaweed deposition (Polis et al., 2004; Polis & Hurd, 1996; Yang et al., 2008; Yang et al., 2010). These marine subsidies can largely determine productivity of the whole island ecosystem and effectively govern the dynamics of numerous species within these communities (Huxel & McCann, 1998; Marczak et al., 2007; Piovia-Scott et al., 2011, 2013, 2019; Polis & Hurd, 1996; Spiller et al., 2010). 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.

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 fewer 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 favour some of these phenotypic combinations over others, which could eventually modify evolutionary dynamics. However, establishing a solid link between novel ecological interactions, behaviour-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 behavioural 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 seven experimentally established island populations of a generalist lizard, the brown anole

(*Anolis sagrei*), in the Bahamas. We assessed habitat use, risk-taking behaviour, and foraging niche changes of brown anoles following experimental introduction of curly-tailed lizards (*Leiocephalus carinatus*), a well-known terrestrial predator of anoles (Lopez-Darias et al., 2012; Losos et al., 2004; Schoener et al., 2002), on half the islands where brown anoles were experimentally translocated. Brown anoles forage in the intertidal and upland habitats (Piovia-Scott et al., 2019; Spiller et al., 2010). 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 (Figure 1). Previous work in this study system showed that natural selection acted upon individual variation in risk-taking behaviour of brown anoles in the presence of these ground predators (Lapiedra et al., 2018). Predator-driven shifts in foraging behaviour 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 changes in habitat use result in diet shifts that alter the transfer of nutrients 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 behaviour.

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., 2010). 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., 2010). 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 (Giery et al., 2013; Losos, 2009; Schoener, 1968).

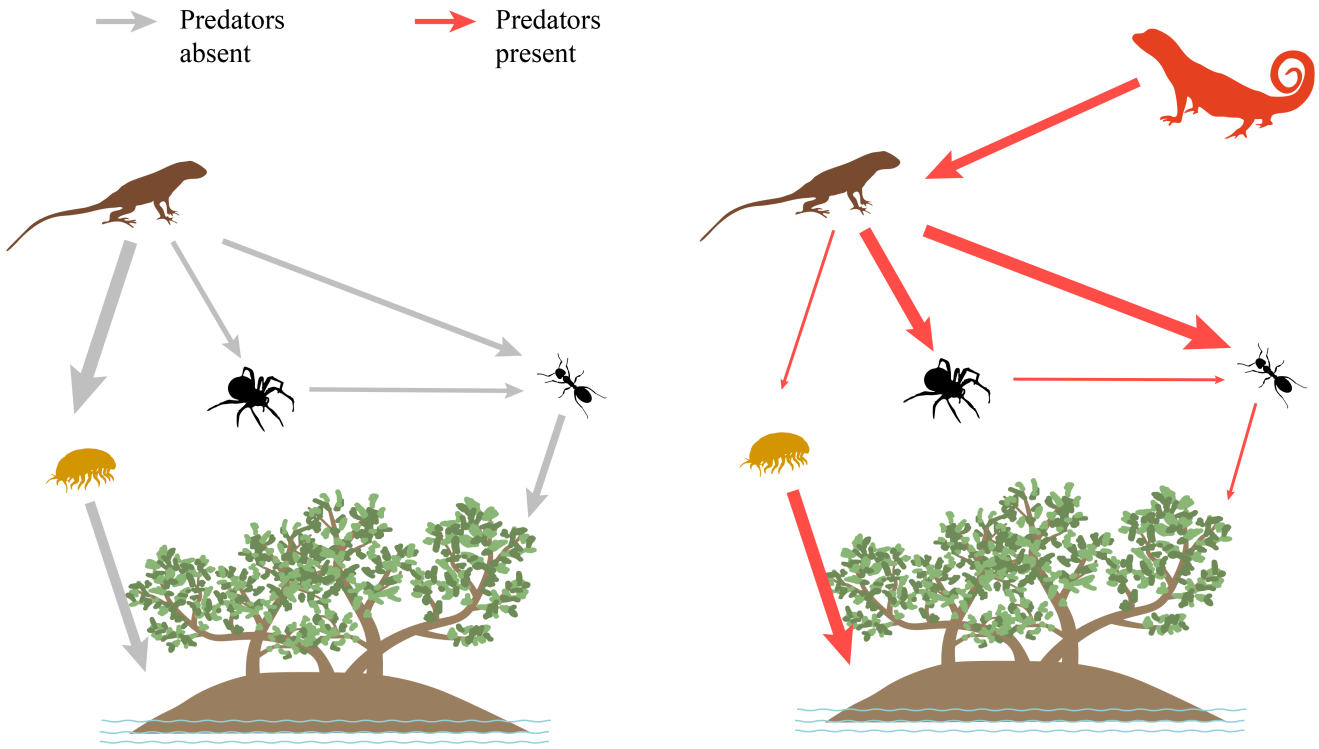

FIGURE 1 Simplified representations of island food webs in our study system based on previous studies. Arrows represent expected consumption of resources in the presence (red arrows) versus absence (grey arrows) of a top ground predator in the experiment study system. We predict that brown anoles will 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.

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 behaviour (Lapiedra et al., 2018; Losos et al., 2004; Schoener et al., 2002). 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 (Piovia-Scott et al., 2011; Schoener, 1968; Schoener et al., 1982, 2002). 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 (Kenny et al., 2017; Schoener et al., 2002). 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 (Figure 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 (Table S1; Lapiedra et al., 2018). These islands had no 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). One of these predator-free islands was excluded from this study because lizards did not have access to seaweed there (Supplementary Materials Additional Methods S1). Data for the present study were collected in May–June of 2017, 1 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 1 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 (Table S2). Additional information on how we assessed both the availability of marine resources and arthropod abundance can be found in Additional Methods S1. Research protocols were approved by IACUC at Harvard University (Protocol # 26-11, 2016). We obtained the corresponding research permit from the Bahamas Environment, Science and Technology (BEST) Commission of the Ministry of the Environment to conduct this research as well as an export specimen permit from the Bahamian Ministry of Agriculture (form #32/2017).

Habitat use, individual tracking and body condition

We measured perch height when capturing each individual in 2017 as the vertical distance between the location of a lizard and the ground ($n = 177$ lizard observations of which 156 were captured). After capturing each brown anole 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 behavioural assays on each captured lizard (see section below). After these behavioural 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, which was measured before translocation of lizards onto experimental islands, 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 $\delta^{13}C$

To examine how predatory curly-tailed lizards alter the foraging ecology of brown anoles, we assessed habitat

use of brown anoles (Lapiedra et al., 2018; Lopez-Darias et al., 2012; Losos et al., 2004; Schoener et al., 2002) 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 (75 from predator-free islands and 82 from predator 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 analysing 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 $\delta^{13}C$ as an indicator of marine content accumulated in organisms, as marine plants and seaweed are more enriched in $\delta^{13}C$ than C_3 terrestrial plants (Post, 2002; Spiller et al., 2010), and ^{13}C remains in the tissues of organisms that consume these resources. 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 Supporting Information) 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 and Tables S3–S5.

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. Then, we stored each tail tip in an Eppendorf tube containing silica gel and tissue paper to prevent direct contact with the sample. 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. Samples were then placed in a PDZ Europa 20–20 isotope ratio mass spectrometer and analysed for ^{13}C and ^{15}N with a PDZ Europa ANCA-GSL elemental analyser.

Collecting individual-level behavioural data

Individual variation in risk-taking behaviour 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, given the reduced predation risk on predator-free islands, brown anoles leaving their perches to hunt for arthropod prey on the ground would obtain more food derived from marine resources in the intertidal. 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 behaviour affected diet composition for individual lizards, we assessed variation in risk-taking behaviour for all individuals captured in this study. Behavioural assays consisted of two phases: a five-minute exposure period to a caged curly-tailed lizard, and a 30-min experimental period. We first placed each captured anole in a refuge and covered their refuge for 5 min 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 5 min 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 min. 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*). Therefore, these estimates of risk-taking behaviour were obtained for lizards that came out of their experimental refuges during the behavioural assays (Table S6).

Statistical analyses

To assess which factors explained variation in perch height, body condition and in the proportion of 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 influence the 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 intercept 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—the effect of predator presence on diet was even stronger (Table S5). We also tested the interaction of sex with experimental treatment but it was not significant and therefore not reported here and also ran a model only including offspring individuals. We employed model selection based on Akaike information criterion corrected for small sample sizes (AICc) using the 'dredge' function in the R package 'MuMIn'. We used the same model structure to assess perch height and body condition (perch height/body condition ~ predator treatment + random intercept island). An additional analysis for body condition only including founder lizards is presented in Table S11 including individual ID as a random effect. We also used linear mixed models to assess if the proportion of marine diet under different predation regimes was explained by variation in behaviour by assigning risk-taking behaviour (*time spent on the ground* recorded from behavioural assays) as a fixed factor interacting with predation regime while also including lizard generation as a fixed factor. For simplicity in the interpretation of results, we ran these models separately by sex based on published evidence that risk-taking behaviour differs between sexes (Lapiedra et al., 2018). We checked model assumptions using statistical tests for normality and homogeneity of variance and inspected model fit using residuals versus fitted value plots.

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 (Mann–Whitney test; W = 10, $p = 0.23$, $n = 7$) and arthropod diversity (Mann–Whitney *U*-test; W = 4, $p = 0.63$, $n = 7$) did not differ between islands in the presence or absence of ground predators ($n = 1346$ arthropods sampled; Figure S2). In addition, islands from different predation regimes did not differ in their abundance of seaweed (Mann–Whitney *U*-test; W = 7, $p = 0.86$, $n = 7$; Figure 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, differed between predator versus 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 *U*-test; W = 0, $p = 0.057$, $n = 7$; Figure 2d). The average number of spider webs on predator islands (0.107 spider webs/m^2 of vegetation) was nearly five times higher than that on predator-free ones (0.022 spider webs/ m^2).

Changes in habitat use and body condition under different predation pressures

To test if brown anoles had changed their habitat use 1 year after experimental translocation, we compared perch height on islands with and without ground predators present. We found that brown anoles on predator islands were found on the ground only 6.2% of the time, whereas lizards on predator-free islands used the ground over four times more often (27.5%). This resulted in lizards perching more than twice as high on predator islands (average perch heights of 40.1 and 17.8 cm, respectively, $t = 7.2$, $p < 0.001$, from $n = 177$ observations in 2017; Figure 2a, Table S10), which is not due to differences in vegetation height between islands from different predation regimes (Table S1). In addition, anoles were in worse body condition after 1 year on predator islands as compared to predator-free controls (interaction year by treatment, $t = -2.77$, $p = 0.006$, $n = 390$) in a model also including sex ($t = 13.34$, $p < 0.001$) as a fixed factor and island ID as a random intercept (see Figure 2b, but see Table S11 and Figure S4 for analyses including only founder individuals).

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 ($p = 0.042$; Table 1; Figure 3). Offspring individuals had a higher marine component than founder lizards ($p = 0.039$; Table 1). In addition, founder males had a more marine-derived diet than founder females ($p = 0.005$; Table 1; Figure 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; $t = 2.03$, $p = 0.045$, $n = 107$; Figure 3c,d).

Risk-taking behaviour is associated with marine diet

We found that females exhibiting riskier behaviour, 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. This association exists only on predator islands ($t = 2.50$, $p = 0.003$ for the interaction term, $n = 28$; Table 2, Figure 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 ($p = 0.98$ for the interaction term of a model including sex, Table S7).

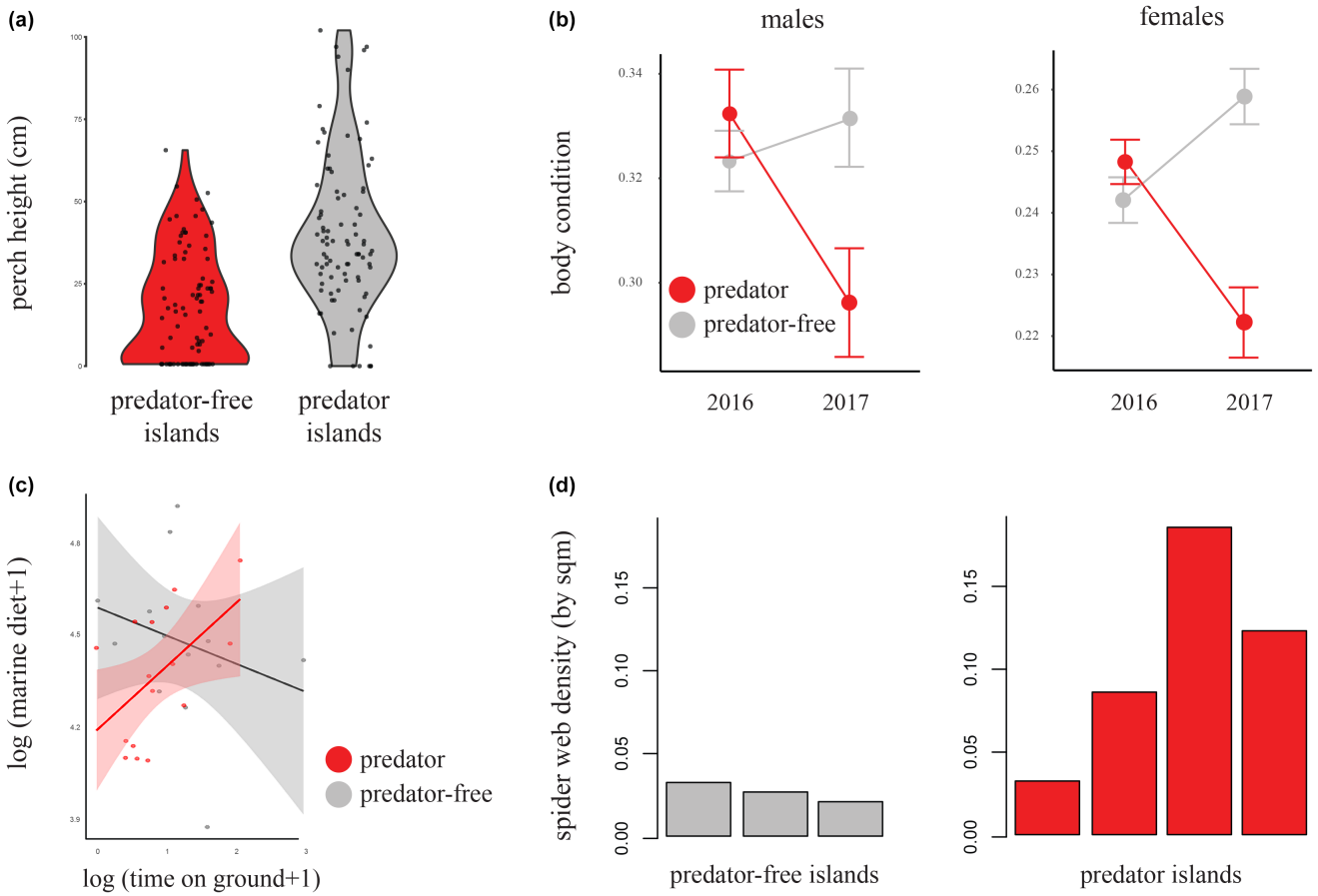

FIGURE 2 (a) Perch height (in cm) used by brown anoles on predator-free versus predator islands 1 year after experimental translocation ($n = 177$). (b) Changes in body condition for founder individuals from the start of the experimental translocation in summer 2016 compared to when lizards were recaptured in summer 2017, separated by predation regime and sex, for experimental islands in the presence (red) versus absence (grey) of ground predators ($n = 390$). (c) Individual-level association between risk-taking behaviour and marine component of diet for female brown anoles in the presence (red) versus absence (grey) of ground predators. Regression line from a linear model ($n = 28$). (d) Differences in web spider density (number of webs by square metre) by island for the two predation regimes. Each bar represents an individual island ($n = 7$ islands). Island #8 (not included) had the lowest spider web densities (0.011/sqm).

TABLE 1 Brown anoles on islands with ground predators had lower marine components of their diet than lizards on predator-free islands ($n = 150$, excluding six individuals that could not be reliably sexed out of the total of 156 lizards captured).

	Value	SE	DF	*t*-value	*p*-value
Intercept	103.26	6.66	140	15.50	0
Treatment–predator	−26.03	7.83	140	−2.05	0.042
Sex-M	6.90	2.39	140	−2.88	0.005
Lizard generation–founders	−5.30	2.55	140	−2.08	0.039
Marginal R^2	0.184				
Conditional R^2	0.509				

Note: 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. See Table S8 for details on model selection.

DISCUSSION

Our study shows that a predator-driven behavioural 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 behavioural shift was associated with a weakened body condition in both sexes 1 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 (Piovia-Scott et al., 2013, 2019; Spiller

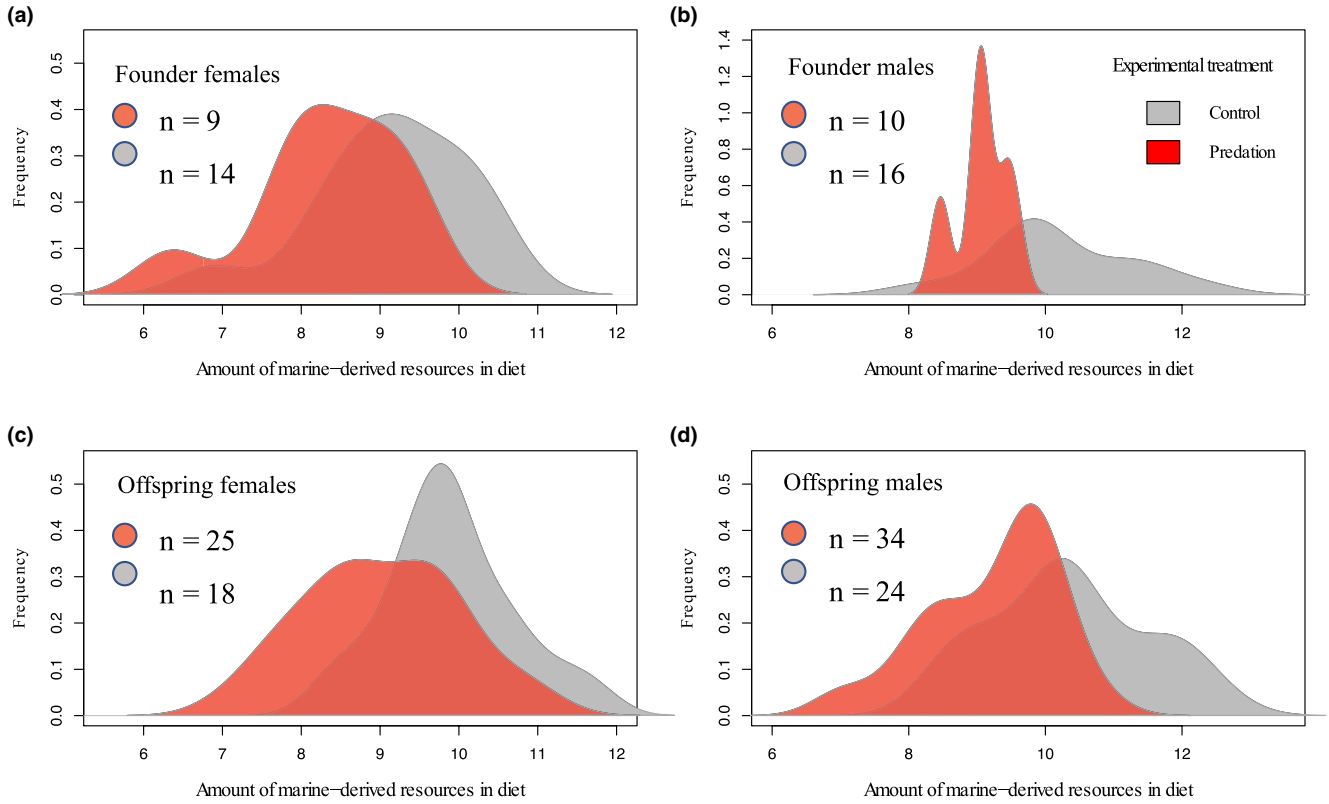

FIGURE 3 Population-level frequency distribution for the marine component in the diet comparing individuals from predator-free (grey) versus predator present islands (red) and divided by sex and whether lizards were translocated as adults or hatched on the experimental islands: (a) founder females, (b) founder males, (c) offspring females, (d) offspring males. Note that translocated lizards had the tip of their tails removed before the experiment, ensuring that the tissue extracted after 1 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 2 Individual brown anole females exhibiting riskier behaviour in lab trials had a higher proportion of marine resources in their diets (n=28). This positive association was observed only on predator islands. See Table S9 for details on model selection.

	Value	SE	DF	t-value	p-value
Intercept	119.31	10.50	18	11.36	0
Treatment–predation	−36.73	13.57	5	−2.71	0.042
Risk-taking behaviour	−6.71	2.51	18	−2.67	0.015
Lizard generation–founders	−9.75	5.63	18	−1.73	0.100
Risk-taking × Treatment–predation	9.77	2.87	18	3.39	0.003
Marginal R^2	0.290				
Conditional R^2	0.701				

et al., 2010; Wright et al., 2020; Yang et al., 2008). 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 a lower 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 versus 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 $\delta^{13}C$ 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 $\delta^{13}C$ 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 (Lapiedra et al., 2018; Lopez-Darias et al., 2012; Losos et al., 2004), where marine deposits and the detritivore arthropods that feed on them are most abundant (Piovia-Scott et al., 2013; Spiller et al., 2010).

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 behaviour (e.g. Réale et al., 2007; Sih et al., 2004, 2012). If certain behavioural profiles are better suited to new selection pressures, they should be favoured by natural selection. A critical implication of among-individual variation in behaviour 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 behaviour 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 favoured 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 behavioural assays had higher survival fitness). Here, we found that among-individual differences in behaviour were associated with foraging niche variation. Specifically, females from predator islands that spent a longer time exposed on the ground during our behavioural trials in a predatory context 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 behavioural 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 behaviour in the absence of predators.

Individual variation in time spent on the ground in behavioural trials was not associated with a higher marine diet for males in either predation regime. It is interesting that this behaviour is significantly associated with marine diet for females on predator islands, but not for males on control or predator islands. Previously documented differences in foraging behaviour 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 (Losos, 2009; Schoener, 1982). 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 predator 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 behavioural flexibility (e.g. spatial learning) or is the consequence of ontogenetic differences remains unknown and it is beyond the scope 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 6 months (Spiller et al., 2010), the $\delta^{13}C$ values measured in this analysis should describe the diet of founder lizards exclusively after translocation. Alternatively, differences between founder and offspring lizards might partly be 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 anoles. Anoles less frequently visited intertidal areas of small islands and consumed relatively less marine-derived resources (i.e. interaction strength re-wiring). Understanding behaviour-mediated ecological alterations of consumers is of major importance because they can affect the stability of ecosystems (Tylianakis et al., 2008). For example, predator-driven decreased consumption of marine-derived resources in our study system not only modifies invertebrate communities on these islands (Schoener et al., 2002) but also, more generally, they alter resource flow between abutting ecosystems. Given that the arrival of novel predators is a major driver of island biodiversity loss worldwide (Sax & Gaines, 2008; Simberloff, 1995), shedding light on the cascading effects of predator-driven behavioural responses of key consumers is essential for island biodiversity conservation.

AUTHOR CONTRIBUTIONS

OL, JBL, JJK, LHY and TWS conceived the study. OL, NCM, JJK, JBL, DF, SM, STG and JPS collected data. OL and NM performed analyses and wrote the first draft of the article; and all authors extensively discussed results and contributed to manuscript preparation.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Data and code supporting the results of this manuscript is available in Dryad repository: https://doi.org/10.5061/dryad.x95x69pqs.

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