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Predator–Prey Reunion: Non-native Coquí Frogs Avoid Their Native Predators

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When non-native species are introduced to new areas without their native predators, they may lose their ability to detect and avoid those predators, especially if the behaviors impose some sort of cost. Few studies have investigated whether non-native populations have lost the ability to avoid their native predators. Coquí frogs, which are endemic to Puerto Rico, were introduced to Hawaii in the late 1980s. Our goal was to investigate whether Coquís from Hawaii avoid predators from their native Puerto Rico. To test this, we collected frogs from both ranges and two arthropod predators from Puerto Rico (tailless whip scorpions and tarantulas). We determined experimentally whether frogs from Hawaii and Puerto Rico exhibited the same avoidance behaviors to these predators. We found that frogs from both ranges avoid attack by moving away from predators and that there was no difference in behaviors between the two ranges. Results suggest that, after nearly 20 generations, frogs from Hawaii have not lost their ability to detect and avoid native predators. The antipredator behaviors Coquís exhibit may help them avoid novel predators in their introduced range and may have contributed to their successful invasion.

NON-NATIVE amphibians are being introduced around the world at an unprecedented rate (Kraus, 2003; Capinha et al., 2017). When amphibians are introduced, how they interact with the native community can influence whether or not they establish and spread (Adams et al., 2003; Poessel et al., 2013). Predator–prey interactions, in particular, can play a strong role in establishment success (Carlsson et al., 2009; Sih et al., 2010). Most studies have focused on how non-native predators affect novel prey (Savidge, 1987; Knapp and Matthews, 2000), but the ability of a non-native prey to avoid novel predators is also likely to contribute to successful invasion (Carlsson et al., 2009). How non-native prey respond to novel predators can depend on prior exposure, evolutionary history, and innate responses (Grason and Miner, 2012; Li et al., 2014; Kruger et al., 2019), with non-native prey more likely to avoid novel predators that are similar to those from their native range (Garcia et al., 2012).

One component of this interaction that is not particularly well studied is whether or not species lose their ability to respond to past predators once they have been introduced to a new area. If the behaviors are useful to the prey in their new range, we might expect the species to retain these anti-predator behaviors (Blumstein, 2006; Rasheed et al., 2018). However, if the behaviors are costly to maintain and not useful against novel predators, we might expect the species to lose these behaviors over time (Blumstein and Daniel, 2005; Brock et al., 2015). It also might matter if these behaviors are generalized or specialized in that behaviors that can protect the prey against a wide range of predators are perhaps more likely to be retained (Ferrari et al., 2009; Garcia et al., 2012). Species that have generalized anti-predators also may be more successful invaders (Sih et al., 2010; Carthey and Blumstein, 2018).

The Coquí (*Eleutherodactylus coqui*) is a direct-developing terrestrial frog (Townsend and Stewart, 1985), endemic to Puerto Rico, that was accidentally introduced to the island of Hawaii via the nursery plant trade in the late 1980s (Kraus et al., 1999). The Coquí is now widespread on the island of Hawaii and the focus of a massive control effort on Maui (Beard et al., 2018). Its invasion is of concern from an ecological perspective because it is an insectivore that can attain extremely high densities, up to 90,000 frogs/ha, and there are a large number of rare and endemic arthropods in Hawaii (Woolbright et al., 2006; Beard et al., 2008). In its native range, the Coquí is preyed upon by a wide variety of predators, including snakes, birds, and large arthropod predators, which likely reduce its abundance (Formanowicz et al., 1981; Stewart and Woolbright, 1996; Woolbright, 1996). Less is known about its predators in Hawaii; however, there is evidence that they are preyed upon by non-native birds, mongoose, and some arthropods (Beard and Pitt, 2006; Smith et al., 2018; Hill et al., 2019).

Two studies have measured anti-predator behaviors in Coquí frogs. One study by Formanowicz et al. (1981) documented anti-predator behaviors of Coquí in Puerto Rico in response to cane spiders, which are present in both Puerto Rico and Hawaii. In that study, pre-adult Coquí escaped after being captured by kicking free, a form of counterattack antipredator behavior (Ferreira et al., 2019). Because many Coquí predators in Puerto Rico are ambush predators (Stewart and Woolbright, 1996), it might be expected that Coquís use 'avoid detection' and 'prevent attack' mechanisms as well (Ferreira et al., 2019). Ferreira et al. (2019) studied the different forms of anti-predator behavior exhibited by Coquís in Hawaii and found that they use avoid detection mechanisms, such as camouflage and immobility, attack prevention measures, such as escape through jumping, and counterattack mechanisms, such as cloacal discharge and aggression.

Our objective was to determine whether non-native Coquí frogs in Hawaii retain their ability to recognize and avoid native predators from Puerto Rico after being in Hawaii for 20 generations. To address this objective, we investigated the behavioral response of Coquís from Hawaii and Coquís from Puerto Rico to two known arthropod predators from the native range. More specifically, we conducted a laboratory experiment where we exposed frogs from both ranges to arthropod predators, amblypygids (*Phrynus longipes*) and tarantulas (*Caribena laeta*), from Puerto Rico (Formanowicz et al., 1981; Woolbright, 1996) and monitored their behavior.

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Because both of these arthropods are ambush predators and we did not allow predators to interact with the frogs directly, we monitored avoid detection, such as immobility, and attack prevention mechanisms, such as escape. We predicted that because Coquís had been in Hawaii for over 20 generations, Coquís from Hawaii may not perceive these Puerto Rican predators as a threat and might exhibit reduced avoidance of these predators.

MATERIALS AND METHODS

Laboratory study.—Frogs were collected from two sites in Puerto Rico (El Yunque: 18°18′N, 65°46′W and Rio Abajo: 18°16′N, 66°42′W) in May 2006 and one site on the Island of Hawaii (Hilo: 19°28′N, 155°05′W) in June 2006 (n = 138 males and n = 116 females from Puerto Rico; n = 104 males and n = 73 females from Hawaii). All frogs were collected from closed-canopy forests with moderate to heavy understory of herbaceous and/or woody vegetation. The Hawaiian site is one of the oldest known populations, with Coquís occurring there since at least 1992 (Kraus et al., 1999). Because Coquís reproduce within nine months (Townsend and Stewart, 1994), it was suspected that Coquís had experienced about 20 generations in Hawaii prior to this study.

At each site, frogs were collected from high (>700 m) and low (<300 m) elevation areas (for more details see O'Neill et al., 2018). At each elevation within a site, 20 m x 20 m plots were established and divided into four, 5 m wide transects. Beginning at dusk, after Coquís had sufficient time to move to nocturnal perch sites, two people searched each transect for Coquís. Each transect was surveyed for 15 minutes, not including handling time, for a minimum total of 60 minutes per plot. All Coquís that were >25 mm snout–vent length and assumed to be adults (Woolbright, 1989) were hand-captured. At least 20 adult males and 20 adult females were collected at each site. All frogs were shipped back to the laboratory at Utah State University.

In the laboratory, each male frog was housed with a female frog from the same population in half of a 37.85 L aquarium. Frogs were given two retreat sites (15 cm PVC pipe), one small potted plant of *Pothos* sp., and moist sphagnum moss as substrate. Frogs were fed vitamin-dusted (Tree Frog Dust, T-Rex®) crickets and water *ad libitum*. Frogs were maintained in temperature-controlled rooms between 19°C and 25°C with a 12:12 L:D cycle and humidity maintained at > 90% within the aquaria.

From the field sites in Puerto Rico, three Tailless Whip Scorpions (*Phrynus longipes*) and three Puerto Rican Pinktoe Tarantulas (*Caribena laeta*), known predators of adult Coquí frogs (Stewart and Woolbright, 1996), were collected and shipped back to the laboratory. Predators were housed individually, in a separate building than frogs, in half of a 37.85 L tank, and fed vitamin-dusted crickets and water *ad libitum*.

Experiments were conducted from July to September 2006. Although both male and female frogs were collected, only males were used in the experiment to eliminate possible variance in behavior between sexes (e.g., due to differences in parental care, size, and mating behavior [Woolbright, 1989]). Of the male frogs collected from Puerto Rico (n = 67) and Hawaii (n = 62), 100 were randomly selected for the experiment. A total of 24 frogs from Hawaii and 24 frogs from Puerto Rico were introduced to whip scorpions, and 21 frogs from Hawaii and 31 frogs from Puerto Rico were introduced to tarantulas. Not all frogs were used and the numbers were not even between ranges to not disturb males during parental care (Townsend and Stewart, 1994). Testing occurred in 36.8 cm L × 21.8 cm W × 24.4 cm H plastic aquaria between 2000 and 2400 h, when lights were off in the rooms animals were housed in, and frogs would have moved from diurnal retreat sites to nocturnal perch sites in nature (Woolbright, 1985). During each test, one side of the aquarium contained a transparent, plastic cage (18.3 cm L × 10.7 cm W × 14 cm H) with a predator inside, while the opposite side of the enclosure contained the same exact cage with no predator. These cages each had 9 cm × 11.5 cm areas cut out and filled with mesh (0.76 × 0.76 cm openings) on each of the large sides of the plastic containers so that frogs could use olfaction as well as visual cues to recognize predators.

A focal frog was introduced to the center of the aquarium in a 118 mL circular Glad® container with the lid slowly removed at the start of the experiment. Frogs had access to both sides of the aquarium. Each test included a 30-minute trial during which an observer recorded the location of the frog and each time it crossed the centerline. Frog movement was recorded by the observer using a television monitor and video cassette recorder (VCR) in an adjacent room. An infrared camera was used to minimize influencing frog movement. Observers were blind to the predator's location and the frog's collection range. Videos were subsequently watched by an independent observer to confirm timings. Between trials, predator side and cage were randomly assigned, and aquaria and cages were cleaned. Individual predators were used randomly throughout the experiment. Individual frogs were never used in more than one test. Predators and frogs were not exposed to each other in the laboratory prior to the experiment.

Statistical analyses.—All statistical analyses were conducted using R (R Core Team, 2019). When placed in the center of the aquarium, the frogs responded by either remaining motionless for the duration of the trial or moved after a short period. To test whether the number of frogs that remained motionless (i.e., possible predator avoidance via immobility) versus active was different between ranges, Pearson's Chi-square tests of homogeneity of proportions were used. This test is commonly used when comparing proportions of two groups and the response is binomial (whether a frog remained motionless or not). Separate chi-square tests, one for each predator, comparing frogs from Hawaii and Puerto were conducted.

To test whether the time that Coquís spent away from predators (i.e., possible prevent attack mechanism via escape) was a function of range or predator species, a beta regression was conducted. Beta regressions are often used in place of generalized logistic regressions to analyze inherently proportional data, in our case, the proportion of time active frogs spent on the half of the aquarium without the predator versus the half of the aquarium with the predator. Range (Hawaii and Puerto Rico) and predator (tarantula and whip scorpion) were categorical predictor variables, while the proportion of time each frog spent on the half of the aquarium without the predator after moving from its initial location (time spent avoiding predator/total active time) was

Table 1. Number of Coquí frogs from Hawaii and Puerto Rico that spent more than half their time on the side of aquarium without predators (away), with predators (near), and remained motionless through the experiment.

	Tarantulas				Whip scorpions			
Range	Away	Near	Motionless	Total	Away	Near	Motionless	Total
Hawaii	11	5	5	21	12	4	8	24
Puerto Rico	14	4	13	31	11	5	8	24
Total	25	9	18	52	23	9	16	48

the response variable. Motionless frogs were excluded from this analysis. Results from planned contrasts between ranges for each predator are also presented. For our beta regression, the *betareg* function in the *betareg* package was used (Cribari-Neto and Zeileis, 2010). Results were considered significant when $P < 0.05$.

RESULTS

Of the 100 frogs released into the center of the aquaria, 34 did not move from their initial location during the 30-minute trial. Chi-square tests revealed there was no difference between the proportion of frogs from Hawaii and Puerto Rico that remained motionless in the presence of tarantulas (24% and 42%, respectively; $\chi^2 = 1.1$, df = 1, $P = 0.29$) or whip scorpions (33% and 33%, respectively; $\chi^2 = 0$, df = 1, $P = 1$; Table 1).

Of the 100 frogs released, 66 moved from the initial location and were monitored for the time spent on each half of the aquarium, either the half with or the half without the predator (Table 1). Coquís from both Hawaii and Puerto Rico spent a greater proportion of time in the half of the aquarium without tarantulas, 65% and 69% respectively, than in the half with tarantulas. Coquís from both Hawaii and Puerto Rico also spent a greater proportion of time in the half of the aquarium without whip scorpions, 66% and 60% respectively, than in the half with whip scorpions. The beta regression revealed no effect of range or predator species on the proportion of time Coquís spent in the half of the aquarium without the predator (range: $F = 0.013$, $P = 0.91$, predator: $F = 0.415$, $P = 0.52$). Planned contrasts supported that the mean proportion of time frogs spent on the half of the aquarium without either predator did not differ between Hawaiian and Puerto Rican frogs (tarantulas: $z = -0.44$; $P = 0.66$; whip scorpions: $z = 0.63$; $P = 0.53$; Fig. 1).

DISCUSSION

To our knowledge, this study is among the first to test antipredator behaviors of a vertebrate prey species from both its native and non-native ranges to its native predators. We monitored both 'prevent attack' and 'avoid detection' behaviors (Ferreira et al., 2019). Our results suggest that both Hawaiian and Puerto Rican Coquís prevent attack from Puerto Rican arthropod predators by moving away, or escaping, from the predator because Coquís spent significantly more time on the side of the aquarium without a predator. About one-third of the frogs remained motionless for the entirety of the experiment, which could be an antipredator defense mechanism to avoid detection. We also found no difference in the number of frogs from Hawaii and from Puerto Rico that remained motionless in the presence of predators. In summary, we found no difference in the predator avoidance behaviors we measured for Hawaiian and Puerto Rican Coquí, either by moving away from or remaining motionless, in the presence of arthropod predators from Puerto Rico. Thus, despite being separated from their native predators for 20 generations, Hawaiian Coquís respond in the same ways as Puerto Rican Coquís to Puerto Rican predators, which was, in general, to avoid the predators, at least as measured by this study.

Because Hawaii is not a predator-free environment, Coquí frogs may retain antipredator behaviors as predicted by the multipredator hypothesis (Blumstein, 2006; Rasheed et al., 2018). In other studies, prey populations that are isolated from predators have shown fewer or less extreme antipredator behaviors compared to populations that remain in contact with predators (Blumstein, 2006; Li et al., 2014; Brock et al., 2015; Mencía et al., 2017; Jolly et al., 2018). In Hawaii, there are Coquí predators, such as non-native mammals (Hill et al., 2019), birds (Smith et al., 2018), and a few suspected arthropod predators, such as cane spiders and centipedes (Beard and Pitt, 2006), the majority of which do not exist in their native range. The mechanisms that Coquís appear to use to avoid native predators in our study, namely escape and possibly immobility (Ferreira et al., 2019), could help them avoid these novel predators, and therefore may be beneficial in their introduced range.

Previous studies have shown that costly antipredator behaviors, such as those that are energy-intensive and reduce time foraging or mating, diminish when prey species are separated from predators for long periods of time (Blumstein

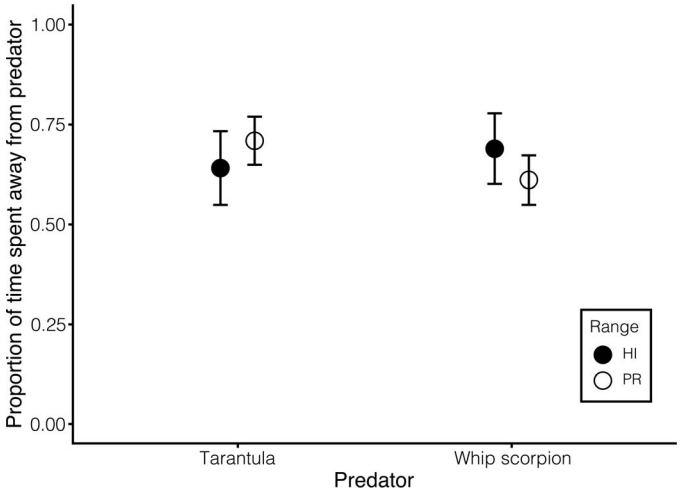

Fig. 1. Mean (± SE) proportion of time frogs from Hawaii and Puerto Rico spent on the half of the aquarium without predators versus with predators. In all cases, frogs spent more time on the half without predators. No significant difference was found between range or predator ($P > 0.05$).

and Daniel, 2005; Brock et al., 2015). We cannot conclude whether the behaviors found to diminish in other studies, for example, those by Blumstein and Daniel (2005) and Brock et al. (2015), namely vigilance and flight-initiation distance, are more or less costly than those exhibited by Coquís in our study. While reproductive behavior of male Coquí frogs (i.e., calling) does constrain their growth (Woolbright, 1989); no study has determined if Coquí antipredator behaviors impose such a cost. However, because the anti-predatory behaviors that Coquís exhibit are primarily predator-induced and therefore are not costly if there is no predator present, we suspect there is little cost to maintain this innate behavior. Future studies could determine if Coquí antipredator behaviors impose a cost and whether this cost differs between its native and non-native ranges.

There are numerous cues the Coquí could have responded to in regard to the predators in this study. While we did not identify the sensory mode by which Coquís detect predators, we suspect it may have been visual, auditory, or olfactory, or some combination of the three. Terrestrial frogs have been shown to use vision to detect predators (Bulbert et al., 2015), although we are not certain if movement, body shape, or another visual aspect of our predators could have triggered a response. Similarly, scents and vibrations produced by the predators may have triggered responses (Martín et al., 2006), although no sounds were recorded from the frogs or arthropods during the experiment. Moreover, we cannot be sure if different sensory cues would trigger different antipredator responses in Coquís.

Many of the known predators of Coquís in their native range are ambush predators, and the two arthropods we chose to use in this study are ambush predators. It has previously been shown that Coquís can avoid predation by these predators with counterattack behaviors (Formanowicz et al., 1981), but because predator and prey could not interact in our study, we could not observe these behaviors. Instead, we focused on avoid detection (i.e., immobility) and prevent attack behaviors (i.e., escape), which also could be used against ambush predators. While it is known that Coquís use avoid detection behaviors (Ferreira et al., 2019), we do not know whether or not the immobility measured in our study was in response to the predator or the frogs simply did not move. Coquís are sit-and-wait predators and often remain in the same location for extended periods (Woolbright, 1985). Future studies could test for this by having control aquaria with no predators. It was clear, however, from our study that the Coquí likely prevent attack from these predators by escaping or jumping away.

The shared behaviors shown by the native and non-native frogs is an interesting result and may suggest that Coquís employ generalized antipredator behaviors when threatened as opposed to the species-specific antipredator behaviors observed in some amphibians (Garcia et al., 2012). Ehlman et al. (2019) suggested that species with a broad diversity of native predators are more likely to recognize novel predators as a threat and respond accordingly. Coquís may have developed generalized behaviors in response to the broad diversity of predators in Puerto Rico (Formanowicz et al., 1981; Stewart and Woolbright, 1996; Woolbright, 1996). Consequently, the antipredator behaviors of Coquí frogs developed in Puerto Rico may serve them well against potential novel predators in Hawaii and may be another factor contributing to their successful invasion.

DATA ACCESSIBILITY

Data are available at https://doi.org/10.26078/y364-k307.

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