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Warming increases activity in the common tropical frog *Eleutherodactylus coqui*

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ABSTRACT

Tropical ecosystems are expected to experience climate warming, with predicted increases in drying and heat extremes in the coming years. Understanding how these changes will affect terrestrial vertebrates such as amphibians is limited. The Tropical Responses to Altered Climate Experiment in the Luquillo Experimental Forest in northeastern Puerto Rico allows us to study how the tropical forest responds to warming within a replicated plot design. From September 2018 to August 2019, we used mark-recapture sampling to investigate how the spatial population ecology of the common coqui frog (*Eleutherodactylus coqui*) is impacted by experimentally increasing surface temperatures by 4 °C above ambient. We compared estimates of baseline detection, space use, and the density of frogs in control and warmed plots. Coqui space use and population density did not differ between control and warmed plots. However, coqui detection probabilities were higher in warmed plots, suggesting an increased level of activity relative to individuals in the control (unwarmed) plots. Frog detection increased in all plots with increased precipitation. Our results suggest that, at least in the short-term, the density of an ecological generalist frog like *E. coqui* does not change as a response to increased surface temperatures. However, short-term responses to warming such as changes in behavior may lead to changes in population dynamics in the long-term. Our research highlights the need to consider mutiple repsonses in order to understand the effects of climate warming on tropical vertebrates.

1. Introduction

The pattern of increasingly rich diversity of life as we move from the poles to the equator, or latitudinal diversity gradient, has been demonstrated across a range of biomes and taxonomic groups, including the vertebrates [27,39,46]. In high diversity regions near the equator, global warming is expected to result in novel, hotter climates, with an increased incidence of heat extremes [56]. Although a large body of literature has accumulated gaining insight into how species respond to climate warming (reviewed by [63,66,67]), these findings are primarily based on correlational data rather than experimental manipulations, thus limiting our ability to rule out confounding factors and apply the findings across other taxa or regions [17,36]. More recently there has been a call to better incorporate aspects of species' ecology, such as space use, behavior, and movement, into mechanistic models to allow more representative and informative predictions of how species will respond to climate change [64].

Many ecological responses of species to climate change have been documented across taxa. Changes in phenology and shifts in distribution have occurred worldwide across a wide range of taxa, including marine, freshwater and terrestrial groups [45,63]. The studies that best illustrate these changes are long-term and involve common, wide-ranging species, such as the Wood Frog (*Lithobates sylvatica* [55]), Rusty Blackbird (*Euphagus carolinus* [41]), and numerous tree species in the eastern U.S. [32]. Documenting the mechanisms that inform us of why these changes occur is more difficult because they must be observed over shorter time scales. For instance, individuals may respond to increased temperatures by altering microhabitat use in the short term, leading to population-level changes such as shifting distributions in the long term [45]. Understanding how behavioral responses to increased temperature lead to emergent population level processes will help us to examine more immediate di-

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rect effects of climate change, which may be through mismatched timing with food sources and habitat for a species [45].

The activity and performance of ectothermic vertebrates such as amphibians are affected by surface temperatures [13]. Therefore, it is not surprising that climate warming has resulted in shifts in the phenology of breeding events and reduction in body sizes ([22,55]; reviewed by [37]) and changes in anuran vocalizations [43], plus a host of indirect consequences [7,23,37]. Recent research has highlighted the poor potential of ectotherms to adapt via thermal tolerance plasticity [24,30], with small-sized organisms showing a positive relationship between ability to thermally acclimate and latitude [51]. Indeed, many amphibians in the lowland tropical Andes are less tolerant of warming than montane species [10]. Instead of plasticity and acclimation, other mechanisms must dominate to assist ectotherms in adjusting to climate warming, such as shifts in behavior or physiology [23]. Although much work has identified thermal maxima of different amphibian species in a laboratory setting [6,65] including *Eleutherodactylus coqui* [5,11], little is known about how amphibians respond to increased surface temperatures *in-situ*.

The Tropical Responses to Altered Climate Experiment (TRACE) plots, established in September 2016, offer a unique opportunity to study how tropical species respond to increased surface temperatures expected with climate warming. Within the six-plot study, three plots are heated to 4 °C above ambient temperatures using infrared heaters and three are unheated controls. To study the spatial ecology of amphibians in plots of a determined size, the ideal focal species would need to meet several characteristics, including being highly philopatric and having a small home range size. Fortunately, the common coqui frog (*Eleutherodactylus coqui*) meets these requirements [34,69]. Here, we use spatial capture-recapture methods to estimate baseline detection, space use, and density of coqui frogs within the TRACE plots. Our goal is to examine whether these aspects of the spatial ecology of this species differ between warmed and control plots. We predict that increased evaporative water loss caused by warmer temperatures in the heated plots will reduce coqui frog baseline detection, space use, and density relative to unheated, control plots.

2. Methods

2.1. Study species

The common coqui frog (*Eleutherodactylus coqui*) is ubiquitous throughout Puerto Rico, occurring in wet to dry forests as well as human-dominated areas, in low and high elevations [34]. It rests in understory vegetation by day and has been reported to move an average of 3.0 m (dry season) to 4.5 m (wet season) per night mainly to forage [69]. Population declines of coqui frogs (*E. coqui* and its congeners) have been attributed to prolonged dry periods as well as infection with chytrid fungus [7,38], both direct and indirect consequences of climate change. The common coqui is native to Puerto Rico but introduced to Hawaii, Costa Rica, the Virgin Islands and other locations [31]. The IUCN Redlist category for *E. coqui* is least concern and its population is listed as increasing [31].

2.2. Study area and environmental variables

In September 2016, six plots were established in the Luquillo Experimental Forest (LEF) in northeastern Puerto Rico (18.32630, −65.72995) at 100 m in elevation (Fig. 1A; see [35] for details on experiment installation). The plots are in secondary forest, regenerated from pasture in the 1950s [35], and the forest is characterized as subtropical wet forest according to the Holdridge Life Zone System [29]. The LEF undergoes a regular disturbance regime including hurricanes, droughts and landslides [71], allowing unique opportunities to study the resilience of tropical forest to these disturbances along with the novel disturbance of climate warming [49]. Mean annual temperature is 24° C, with little variation (4° C) between months and mean annual precipitation is 3500 mm per year [18].

Each plot (12 m^2 in area) consisted of a hexagonal array of six aluminum poles (labeled A-F) with each pole approximately 2.3 m apart (Fig 1). Plots were located a minimum of 10 m apart, within a 50 × 60 m area. Three plots (temperature treatment plots) were warmed 24 h a day using infrared heaters set to 4 °C above ambient temperatures of the average understory vegetation temperature (measured continuously by infrared thermometers) in the three unheated, control plots [35]. Thus, the warmed plots automatically adjusted to 4 °C above the control plots as daily temperature fluctuated in the control plots [35]. The infrared heaters were positioned at 3.6 m above the soil surface, which is approximately 2 m above the mean height of the understory vegetation. Infrared heaters work by warming the surfaces of vegetation; the warming of the air occurs because of the heat that is re-radiated back off of the surfaces. The nocturnal habitat of *E. coqui* generally includes tree trunks, branches, epiphytes or leaves between 0.5–3.0 m in the forest understory [58], so the warming included many surfaces that frogs utilize.

The USDA Forest Service Sabana Field Research Station has a meteorological station located near the TRACE field site [20]. We used hourly rainfall data to estimate the cumulative precipitation within a 24-hour period before the start of each survey occasion (19:00). We selected cumulative precipitation before survey events, rather than other measures of precipitation, because moisture is a primary factor determining activity in *E. coqui* [57,58] and we wanted to evaluate the effect of this abiotic factor on frog activity across the sites.

2.3. Data collection

From September 2018 to August 2019, we surveyed each plot for frogs on 22 occasions and encountered frogs in all plots on each date, except for one occasion when no frogs were encountered in plot 6 (Appendix 1). Infrared heaters were turned off for safety reasons before surveys began and were turned on after completion. We used time-constrained (15 min) visual encounter methods to search each plot for frogs between 19:00 and 21:00. We rotated the order of plots each survey occasion to reduce influence of timing on frog captures. A minimum of two weeks occurred between survey occasions to reduce potential behavioral responses to disturbance as seen in other amphibians [26,40]. Surveys were conducted by two observers, one person searching for frogs on the outside of the plot which included a 0.5 m strip around the outside of the experimental hexagon, and the other person searching the inside of the hexagon (see Fig 1). We captured all observed frogs and recorded the capture location defined as the nearest pole (or poles when captured between two poles; Fig 1). Once captured, we marked each new individual using visible implant elastomers (VIE), a widely used and safe method for amphibians [3,21], in four possible locations (near each limb) to create unique frog identifications for each frog. We identified recaptured individuals using UV light to observe the unique code. Each frog was measured to determine size (snout-to-vent length to nearest 0.1 cm), mass (using a digital scale to nearest 0.01 g) and sex (males were identified by the presence of a vocal sac or if vocalizing when captured). After measuring and marking were complete, we returned frogs to the location where they were captured, generally the following day.

2.4. Spatial capture–recapture analysis

Our capture-mark-recapture protocol generated spatial encounter histories for all detected individuals, i.e., the spatial location (nearest pole) and occasion (survey) for each individual was known. We employed spatial capture–recapture methods (SCR) to jointly estimate the parameters of both a spatially explicit encounter probability model and a density model [52]. The first is the observation model, a 2-parameter

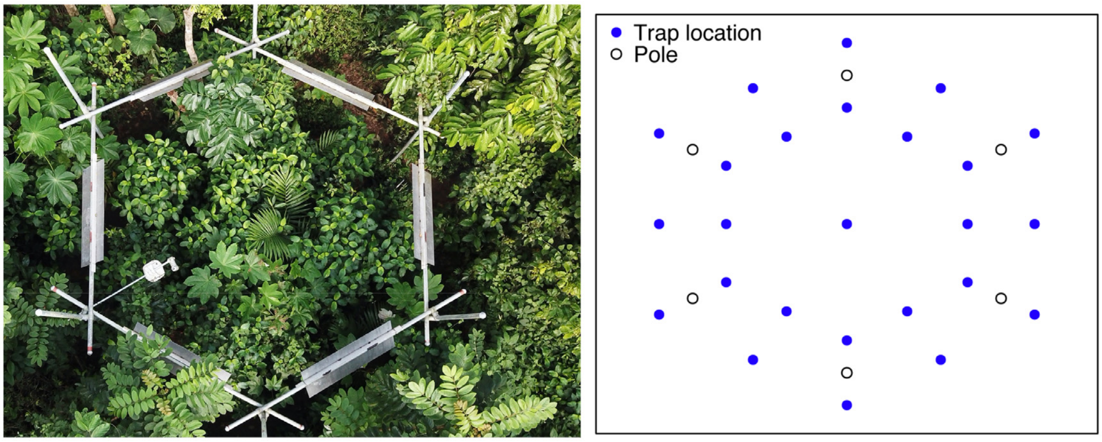

Fig. 1. On left, a hexagonal plot (12 m^2) in the Tropical Responses to Altered Climate Experiment (TRACE) in the Luquillo Experimental Forest. Photo by Maxwell Farrington, Nov. 2018. On right, the array of 25 uniquely identified trap locations (blue) within each plot.

detection function (i.e., parameters for detection and spatial decay of detection over space), and the second is the state model estimating the number and distribution of (latent) activity centers. SCR methods are hierarchical models specifically designed to analyze data from repeated sampling of individuals over a period of demographic closure to estimate detectability, space use, and density. These methods are becoming well-established in the herpetological literature [15,25,42,60] because they are robust and reduce potential biases in estimates of amphibian density and abundance from traditional capture-recapture models based solely on how individuals are encountered by sampling, disregarding spatial explicitness.

In particular, SCR methods account for individual movement and heterogeneity in detection probability by incorporating information about the spatially explicit nature of sampling, how individuals are distributed in space, and how they use space [44,53]. The location where each frog was encountered in a plot was converted into an array consisting of 25 uniquely identified trap locations; 24 trap locations located 0.5 m outward and 0.5 m inward of the aluminum hexagonal array, and 1 trap location in the middle of the array (Fig. 1, blue). The spatial encounter model describes the individual detection probability, $p[x,s]$, as a decreasing function of the distance between trap locations (x) and the individual's activity center (s):

$y_{ijk}|s_i \sim \text{Bernoulli}(p[x_j,s_i])$ Eq. (1)

$$\mathrm{p}[\mathrm{x_j},\ \mathrm{s_i}] = \mathrm{p_0} \times \exp\left(\frac{-d\left(x_j, s_i\right)^2}{2\sigma^2}\right) \tag{1}$$

where y_{ijk} indicates whether an individual i was detected at pole j in occasion k, s_i is the estimated activity center of individual i, x_j is the location of trap j, and $d(x_j,s_i)$ is the Euclidean distance between trap j and activity center s_i. In this model, p_0 is the baseline detection probability, or the probability of detecting an individual at its activity center, and σ is the spatial scale parameter that characterizes the decline in detectability with distance from an activity center. The detection probability can be interpreted as a proxy for activity as in spatial capture-recapture analyses of the red-back salamander (*Plethodon cinereus*; [25,60]). To account for behavioral responses to capture events, we included a behavioral response parameter in all models that allowed capture probability to change after the initial capture.

SCR methods include a density model describing the number and location of individual activity centers. Here we assume activity centers are distributed uniformly over a state-space S. The state-space represents the area of interest defined by a sufficiently large buffer around the trapping array containing the activity center of all individuals with non-negligible detection probabilities, and is discretized at a resolution small enough to approximate continuous space relative to the species' movement and the trap arrangement. As is standard for maximum likelihood SCR methods, we defined S as the center points of a grid with a 7 m buffer around a convex hull of the hexagonal array, each point representing the center points of equally sized 0.5 × 0.5 m pixels (total area = 289.8 m^2). Buffer selection was carried out by fitting the null SCR model with incrementally larger buffers ranging from 1 to 10 m until model parameters reached an asymptote as a function of buffer size. We selected the smallest buffer size (7 m) at the asymptote to minimize computational demand while ensuring density estimates were not biased by the size of S.

Our main interest was to expand our understanding of the environmental drivers of activity, space use, and density by fitting a set of competing models with all combinations of covariate effects that represent the alternative hypotheses we wished to test. First, we tested site effects on these variables to determine whether site (i.e., plot) was a significant factor explaining the observed variation (Appendix 2). As there were no significant site effects, we did not include this covariate in the model list. To account for variation in activity, we included a temperature treatment effect and the linear and quadratic effect of cumulative precipitation 24 hour prior to each survey occasion as covariates on baseline detection probability p_0. The quadratic effect of precipitation was added because the response of amphibians to precipitation is often nonlinear, instead optimal detection may be associated with intermediate rainfall and be lower with little or high cumulative rainfall [57]. To account for variation in movement and density, we included temperature treatment effects as a covariate on space use σ and density D. Covariates were scaled to have a mean of 0 and a 1-unit standard deviation (i.e., z-score standardization). Considering all factor combinations among p_0, σ, and D resulted in a total of 18 models (Appendix 2). We analyzed these models in R [48] using the package oSCR [61] and conducted AIC-based model selection following Burnham and Anderson [8] and Arnold [1]. We interpreted a difference of ≥ 2 AIC values to indicate that two models differed in their support. Models within 2 AIC values of the best model were further examined for number of parameters and log-likelihood. Models with an extra parameter but same log-likelihood to that of the top model were considered non-competitive. We considered the effect of covariates (i.e., beta coefficient) to be strong if the 95% confidence intervals (CI) did not overlap 0 and to be weak if otherwise.

3. Results

We captured a total of 858 frogs across all survey occasions (143 ± 7.71 [average ± SE] per plot). Control plots had a lower number of captures (132 ± 2.08) than warmed plots (154 ± 13.12; Fig. 2). The number of frogs captured per occasion ranged from 1 to 15 individuals

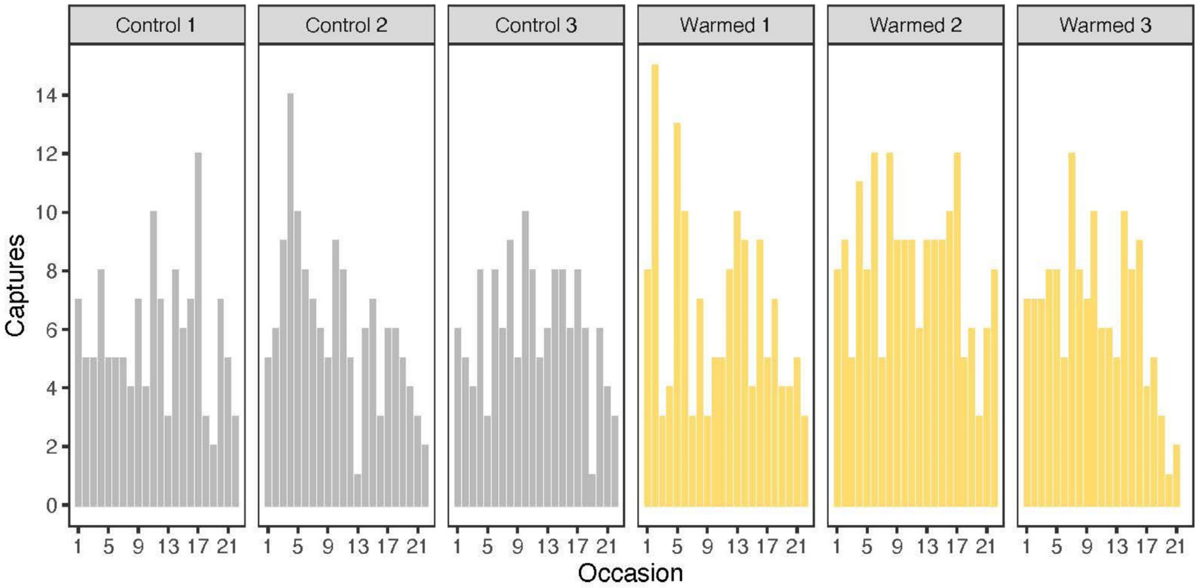

Fig. 2. Captures per plot across sampling occasions. Gray represents control plots. Yellow represents warmed plots.

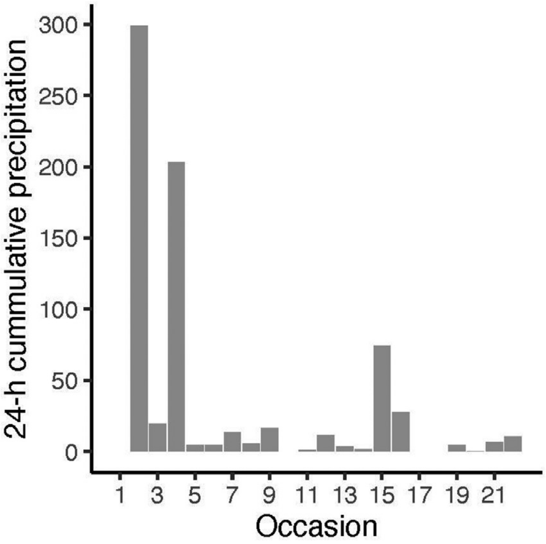

Fig. 3. Cumulative precipitation 24 h prior to the survey occasion.

per plot, and the maximum number of captures of a single individual was 10. Of all captures, 488 (56.88%) were unique or new individuals and the remaining 370 individuals were recaptures, resulting in a 43.12% recapture rate across plots.

Cumulative precipitation in the 24-hour period before survey occasions varied from 0 to 298.8 mm (Fig. 3). Rainfall occurred throughout the survey period, with occasions 2 and 4, in October and November, exhibiting the most cumulative precipitation prior to the survey date. Four surveys, in September, February, May and June, had no cumulative precipitation prior to the survey date.

We found support for treatment- and precipitation-specific differences in frog baseline detection probability, where the model accounting for temperature treatment effects and 24 h cumulative precipitation best explained the observed variation in detection (cumulative model weight = 0.23; Table 1). Uncertainty in the models was present and related to whether there is variation in density or detection by treatment (model 2 in Table 1). Regardless, the top model, with constant space use and density is more competitive, with a lower log-likelihood value.

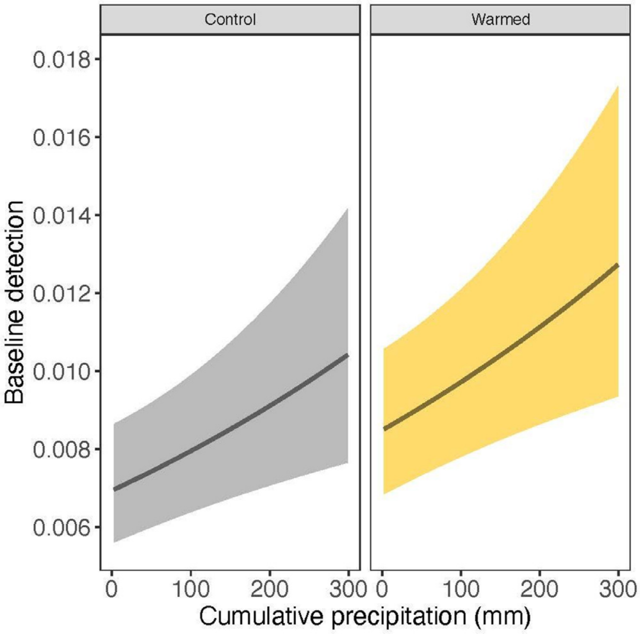

Fig. 4. Treatment-specific baseline detection probability of the coqui frog as a function of 24-h cumulative precipitation. Lines and shaded areas represent model predictions across temperature treatments and 95% CI, respectively.

Specifically, we found support for a positive effect of treatment (mean ± SE: $p_{\text{warmed}} = 0.203 \pm 0.102$), suggesting that detectability, which we use as a proxy for surface activity, is weak but higher in the treatment than in the control plots, and a strong positive effect of cumulative precipitation ($p_{\text{precip}} = 0.102 \pm 0.033$; Fig. 4), suggesting activity is higher when conditions are wet. The increase in detection with cumulative precipitation was additive, i.e., was consistent across sites. Our model also predicted an increase in detection after initial capture (positive behavioral response: $\beta_b = 1.229 \pm 0.135$; Table 2) which may explain the high recapture rate in this study. We found no covariate effects on the spatial scaling parameter σ and on density, suggesting no warming effects or precipitation effects on the extent of space use or density. The spatial scaling parameter σ was 0.637 ± 0.065 m and the estimated

Table 1

Variability in baseline detection (p_0) of the coqui frog (*Eleutherodactylus coqui*) as a function of temperature treatment and cumulative precipitation. The ~1 notation represents null or an intercept- only model with no covariate effect. Acronyms are LogL = log likelihood, K = number of model parameters, AIC = Akaike's Information Criterion, and Ω = model weights. Only top 10 ranked models presented. The superscript ^{2} represents the quadratic effect.

detection (p_0)	space use (σ)	density (D)	logL	K	AIC	ΔAIC	Ω
~*b* + treatment + precip	~1	~1	3658	6	7328	0.00	0.23
~*b* + precip	~1	~treatment	3659	6	7330	1.70	0.10
~*b* + treatment + precip + precip^2	~1	~1	3658	7	7330	1.70	0.10
~*b* + precip	~treatment	~1	3659	6	7330	1.90	0.09
~*b* + treatment + precip	~1	~treatment	3658	7	7330	2.00	0.09
~*b* + precip	~1	~1	3660	5	7330	2.00	0.09
~*b* + treatment + precip	~treatment	~1	3658	7	7330	2.00	0.09
~*b* + precip + precip^2	~1	~treatment	3659	7	7332	3.40	0.04
~*b* + precip + precip^2	~treatment	~1	3659	7	7332	3.60	0.04
~*b* + treatment + precip + precip^2	~1	~treatment	3658	8	7332	3.70	0.04

Table 2

Regression coefficients of the top model describing the variability in baseline detection (p_0), space use (σ), and density D of the coqui frog (*Eleutherodactylus coqui*) as a function of temperature treatment and cumulative precipitation. The covariates were scaled to have a mean of 0 and a 1-unit standard deviation (i.e., z-score standardization).

Factors	Estimate	SE
Detection p_0		
ß$_{p\text{(intercept)}}$	−4.920	0.110
ß$_{p\text{(b)}}$	1.229	0.135
ß$_{p\text{(warmed)}}$	0.203	0.102
ß$_{p\text{(precip)}}$	0.102	0.033
Space use σ		
ß$_{\sigma\text{(warmed)}}$	0.637	0.065
Density D		
ß$_{D(warmed)}$	−0.985	0.100

density was 1.49 ± 0.149 frogs/m^2 (Table 2). The estimated population level 95% home range radius and its associated area can be calculated from the detection function, which is an implied model of space use, as $r_{.95} = \sigma\sqrt{5.99}$ and $A_{.95} = \pi r^2$, respectively [42,60], and were 4.63 m and 67.3 m^2, respectively.

4. Discussion

Climate warming in the tropics is expected to raise surface temperatures and result in more temperature extremes [56]. In Puerto Rico, these abiotic changes will likely reduce carbon storage and tree growth resulting in alterations in forest community composition and structure [14]. The TRACE experimental design allows us to directly compare the spatial ecology of populations of *E. coqui* in warmed and control plots allowing a snapshot of what we can expect with climate warming. Artificial warming and cumulative precipitation caused *E. coqui* to increase activity but did not alter its density or space use compared to control plots. The short time period from when artificial warming started to when frog survey data were collected may be sufficient to elicit a behavioral response in *E. coqui*, but insufficient to detect changes in space use and density. Use of SCR methods by incorporating space use into our estimates of density allowed us to gain novel insights about how *E. coqui* uses space and whether such space use is influenced by warming using an experimental design. We demonstrated the ability to simultaneously account for variable and imperfect detection in order to draw inferences about the latent state variable density, allowing us to ask questions about the effects of warming on density. These insights improve our understanding of detection, space use and density of *E. coqui* in comparison to what we would have gained from traditional capture-recapture analyses.

An increase in detection probability or activity is contrary to our expectation that coqui frogs would reduce activity in warmed plots, potentially to reduce exposure to dry conditions and avoid desiccation. During periods of time with little precipitation, the warmed plots have lower soil water content than the control plots [49]. The causal mechanisms for increased activity deserve more attention.

There are several behavioral causal mechanisms that could explain the pattern of increased frog activity in warmed plots. First, frogs may be trapped in a feedback loop whereby warmer temperatures increase metabolic rates [19], which results in greater energetic demands, and as a consequence, more activity to acquire prey to meet those demands. Ultimately this feedback loop could result in increased stress and lower immune function and cause increased exposure to potential predators. These responses could have indirect consequences on demographic rates over time, as frogs redirect energy and resources from growth and development to increased activity. It is unlikely that *E. coqui* are increasing activity to forage, since they are known to be sit-and-wait predators [62]. Although the majority of short-distance frog movements in a night are related to prey acquisition, long-distance movements are between daily retreat sites and nocturnal perching sites [69]. Greater frog activity in warmed plots may be the result of increased detection of individuals as they climb into the canopy to escape the heat. Large-sized coquis, especially adult females and non-calling males are known to climb into the canopy, some to heights of 18.5 m, to forage [69]. The number of arthropods increases with height above the ground [58], which may further increase motivation to forage in the canopy. Individuals may leave retreat sites and climb above the height of the infrared heaters to reduce exposure to increased temperatures, then return to diurnal retreat sites near the forest floor. Greater frog activity in warmed plots may also be an artefact of the methodology used in sampling the frog populations. Turning off the infrared heaters during each survey event may have the unintended consequence of providing a reprieve from the heat for the frogs. Even with a temporary reprieve from the heat, the drier conditions remain in the warmed plots; therefore, frogs may be more active in an effort to access microhabitats with tolerable thermal and hydric limits as found with *Geocrinia alba* [28].

Alternatively, changes in prey availability may cause frogs to change their behavior in warmed plots. Patterns in space use by *E. coqui* are dominated by foraging opportunities, as vocalizing individuals generally remain stationary [69]. Yet, as sit and wait predators, it is unlikely that individuals would change this behavior based on prey availability. But undoubtedly, more movement would occur if the sit and wait strategy is not yielding foraging opportunities. Currently, there is no indication that invertebrate herbivore density changes in warmed plots, as foliar damage of understory woody seedlings and herbivore morphotype richness did not differ between control and warmed plots [2]. However, a more direct measurement of invertebrate density is needed in the TRACE plots in order to better understand the causal mechanism of increased frog activity in warmed plots. In general, long-term study of arthropods in the LEF indicate that populations respond to hurricane disturbance but show no clear patterns in response to climate warming [54].

Coqui frog detection and density are influenced by the density and structure of understory vegetation, as they use vegetation for retreat and calling sites [59]. If changes occur in understory vegetation in the warmed plots, we would expect changes in coqui frog detection and density either because of increased ability to detect frogs if vegetation density is lower, or increased habitat for frogs if vegetation density is higher. However, data suggest that understory cover, richness and diversity do not differ between warmed and control plots in the TRACE experiment [33]. These trends may change when examined over a longer time period, yet currently do not lend support as a causal mechanism for differences in frog activity. However, the absence of change in understory vegetation does support our findings for a lack of a difference in coqui density and space use between warmed and control plots.

Tropical ectotherms are expected to be affected by climate warming more severely than their temperate counterparts because they may be already close to their critical thermal maxima [12,30]. It is important to consider that there is species-specific variability in vulnerability to increasing temperatures [12]. Therefore, the threshold at which temperature begins to affect activity, density and space use varies by species. Since *E. coqui* is a common, widespread species, occurring across all of Puerto Rico, from wet to dry forest [34,50], it may be less vulnerable to increased temperatures than some of its congeners which prefer cooler habitat higher in elevation, such as *E. richmondi, E. gryllus* and *E. portoricensis* [9,34]. It is also important to consider that temperature sensitivity may vary within populations of a species. Recent results indicate that lowland *E. coqui* have a narrower operative warming tolerance than highland conspecifics, suggesting they are thermoconformers and that climate warming may affect populations differently (Delgado and Burrowes, unpublished data).

Density estimates at our plots (1.49 ± 0.149 frogs/m^2) are lower than invasive populations of *E. coqui* in Hawaii (2.55 ± 1.74 frogs/m^2 averaged across 3 years and 8 plots and estimated using closed capture-recapture models [4,68]). In Puerto Rico, other studies have found lower estimates of density, ranging from 0.01 to 0.40 adult frogs/m^2 across sites [16,57,59,70] and up to 2.05 frogs/m^2 when both adults and juveniles are considered [58]. These authors used both mark-recapture methods (Jolly method; [58]) and direct counts to estimate population density and stress the influence of season and habitat on their estimates. Variability in methods used to estimate density complicates our ability to make direct comparisons between locations and years.

The coqui frog home range size reported here is higher than those reported in the literature. On average, we estimated a 95% home range size of 67.3 m^2, while published estimates generally report sizes less than 25 m^2 [34,47,69]. As for density estimates, effectively comparing home range estimates across studies is challenging because multiple methodologies have been used for both data collection and analysis (e.g. one-night monitoring, traditional mark–recapture). The methods we employ here are robust and allow estimation of home ranges with less bias and higher precision. Thus, it is imperative to compare our estimate with that of other populations using spatially explicit analyses.

Our results highlight the importance of considering short-term responses to warming. Behavioral changes at the individual level, such as increased activity as we observed, may preclude changes at the population level over longer time frames, such as shifting distributions [45]. Physiological and behavioral mechanisms underlying responses to climate warming ultimately influence species interactions which culminate in performance of individuals and dynamics of populations [23]. Although experimental manipulations at the scale of the TRACE project do have limitations, in-situ experiments are the only way to verify if what we observe in a lab applies in nature. Use of technologies, such as minitransmitters, could offer clear insight into how energy budgets differ for frogs while in diurnal retreats as well as during nocturnal periods in control and warmed plots. Further work should seek to evaluate support for various short-term behavioral mechanisms, explore sublethal effects of warming on energy budgets and examine long-term trends in coqui frog response to climate warming.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

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References

[1] T.W. Arnold, Uninformative parameters and model selection using Akaike's Information Criterion, J. Wildl. Manage. 74 (2010) 1175–1178.

[2] B. Bachelot, A.M. Alonso-Rodríguez, L. Aldrich-Wolfe, M.A. Cavaleri, S.C. Reed, T.E. Wood, Altered climate leads to positive density-dependent feedbacks in a tropical wet forest, Glob. Change Biol. 26 (2020) 3417–3428, doi:10.1111/gcb.15087.

[3] L.L. Bailey, Evaluating elastomer marking and photo identification methods for terrestrial salamanders: marking effects and observer bias, Herpetol. Rev. 35 (2004) 38–41.

[4] K.H. Beard, R. Al-Chokhachy, N.C. Tuttle, E.M. O'Neill, Population Density Estimates and Growth Rates of Eleutherodactylus coqui in Hawaii, J. Herpetol. 42 (2008) 626–636.

[5] C.A. Beuchat, F.H. Pough, M.M. Stewart, Response to simultaneous dehydration and thermal stress in three species of Puerto Rican frogs, J. Compar. Physiol. B 154 (1984) 579–585.

[6] B.H. Brattstrom, P. Lawrence, The rate of thermal acclimation in anuran amphibians, Physiol. Zool. 35 (1962) 148–156.

[7] P.A. Burrowes, R.L. Joglar, D.E. Green, Potential causes of amphibian declines in Puerto Rico, Herpetologica 60 (2004) 141–154.

[8] K.P. Burnham, D.R. Anderson, Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd edition, Springer, New York, 2002.

[9] Campos-Cerqueira and Aide, Lowland extirpation of anuran populations on a tropical mountain, PeerJ 5 (2017) e4059, doi:10.7717/peerj.4059.

[10] A. Catenazzi, E. Lehr, V.T. Vredenburg, Thermal physiology, disease, and amphibian declines on the eastern slopes of the Andes, Conserv. Biol. 28 (2014) 509–517.

[11] K.A. Christian, F. Nuñez, L. Clos, L. Díaz, Thermal relations of some tropical frogs along an altitudinal gradient, Biotropica 20 (1988) 236–239.

[12] H. Duarte, M. Tejedo, M. Katzenberger, F. Marangoni, D. Baldo, J.F. Beltrá, D.A. Martí, A. Richter-Boix, A. Gonzalex-Voyer, Can amphibians take the heat? Vulnerability to climate warming in subtropical and temperate larval amphibian communities, Global Change Biol. 18 (2012) 412–421, doi:10.1111/j.1365-2486.2011.02518.x.

[13] W.E. Duellman, L. Trueb, in: Biology of Amphibians, Johns Hopkins University Press, Baltimore, MD, 1986, p. 670.

[14] X. Feng, M. Uriarte, G. Gonzalez, et al., Improving predictions of tropical forest response to climate change through integration of field studies and ecosystem modeling, Glob. Change Biol. 24 (2018) e213–e232, doi:10.1111/gcb.13863.

[15] J. Fleming, E.H. Campbell Grant, S.C. Sterrett, C. Sutherland, Experimental evaluation of spatial capture-recapture study design, Ecol. Appl. (2021) e02419.

[16] J.H. Fogarty, F.J. Vilella, Population dynamics of Eleutherodactylus coqui in Cordillera Forest Reserves of Puerto Rico, J. Herpetol. 36 (2002) 193–201.

[17] J. Franklin, J.M. Serra-Diaz, A.D. Syphard, H.M. Rega, Proc. Natl Acad. Sci. 113 (14) (April 5, 2016) 3725–3734 first published February 29, 2016, doi:10.1073/pnas.1519911113.

[18] A.R. García-Martino, G.S. Warner, F.N. Scatena, D.L Civco, Rainfall, runoff and elevation relationships in the Luquillo Mountains of Puerto Rico, Caribbean J. Sci. 32 (1996) 413–424.

[19] J.F. Gillooly, J.H. Brown, G.B. West, V.M. Savage, E.L. Charnov, Effects of size and temperature on metabolic rate, Science 293 (2001) 2248–2251.

[20] Grizelle González, Ashley E. Van Beusekom, Carlos R. Estrada, Luquillo Experimental Forest Sabana weather station scaffold tower 2018-2020 data, Fort Collins, CO: Forest Service Research Data Archive (2021), doi:10.2737/RDS-2021-0030.

[21] E.H.C. Grant, Visual implant elastomer mark retention through metamorphosis in amphibian larvae, J. Wildl. Manag. 72 (2008) 1247–1252, doi:10.2193/2007-183.

[22] D.M. Green, Amphibian breeding phenology trends under climate change: predicting the past to forecast the future, Global Change Biol. 23 (2017) 646–656, doi:10.1111/gcb.13390.

[23] A.R. Gunderson, B. Tsukimura, J.H. Stillman, Indirect effects of global change: from physiological and behavioral mechanisms to ecological consequences, Integr. Comp. Biol. 57 (2017) 48–54.

[24] A.R. Gunderson, J.H Stillman, Plasticity in thermal tolerance has limited potential to buffer ectotherms from global warming, Proceedings of the Royal Society B: Biological Sciences 282 (2015) 20150401 pmid:25994676.

[25] R. Hernández-Pacheco, C. Sutherland, L.M. Thompson, K.L. Grayson, Unexpected spatial population ecology of a widespread terrestrial salamander near its southern range edge, R. Soc. Open Sci. 6 (2019) 182192, doi:10.1098/rsos.182192.

[26] K.M. Hesed, Uncovering salamander ecology: a review of cover board design, J. Herpetol. 46 (2012) 442–450, doi:10.1670/10-220.

[27] H. Hillebrand, On the generality of the latitudinal diversity gradient, Am. Nat. 163 (2004) 192–211.

[28] E.P. Hoffmann, K.L. Cavanough, N.J Mitchell, Low desiccation and thermal tolerance constrains a terrestrial amphibian to a rare and disappearing microclimate niche, Conservation Physiology 9 (1) (2021) coab027.

[29] L.R. Holdridge, Life Zone Ecology, Tropical Science Center, San Jose, Costa Rica, 1967.

[30] R.B. Huey, C.A. Deutsch, J.J. Tewksbury, L.J. Vitt, P.E. Hertz, H.J. Álvarez Pérez, T. Garland Jr, Why tropical forest lizards are vulnerable to climate warming, Proceedings of the Royal Academy of Sciences B 276 (2009) 1939–1948, doi:10.1098/rspb.2008.1957.

[31] IUCN SSC Amphibian Specialist Group. 2021. Eleutherodactylus coqui. The IUCN Red List of Threatened Species 2021: e.T56522A3041672. https://dx.doi.org/10.2305/IUCN.UK.2021-1.RLTS.T56522A3041672.en. Downloaded on 30 April 2021.

[32] L.R. Iverson, A.M. Prasad, Potential changes in tree species richness and forest community types following climate change, Ecosystems 4 (2001) 186–199.

[33] D.K. Kennard, D. Matlaga, J. Sharpe, C. King, A.A. Alonso-Rodriguez, Reed SC, M.A. Cavaleri, T.E. Wood, Tropical understory herbaceous community responds more strongly to hurricane disturbance than to experimental warming, Ecol Evol 10 (2020) 8906–8915, doi:10.1002/ece3.6589.

[34] R.L. Joglar, in: Los Coquíes de Puerto Rico Su Historia Natural y Conservación, Universidad de Puerto Rico, San Juan, PR, 1998, p. 232.

[35] B.J. Kimball, A.M. Alonso-Rodríguez, M.A. Cavaleri, S.C. Reed, G. González, T.E. Wood, Infrared heater system for warming tropical forest understory plants and soils, Ecology and Evolution 8 (2018) 1932–1944, doi:10.1002/ece3.3780.

[36] L. Korell, H. Auge, J.M. Chase, S. Harpole, T.M Knight, We need more realistic climate change experiments for understanding ecosystems of the future, Glob. Change Biol. 26 (2020) 325–327, doi:10.1111/gcb.14797.

[37] Y. Li, J.M. Cohen, J. Rohr, Review and synthesis of the effects of climate change on amphibians, Integrative Zoology 8 (2013) 145–161.

[38] A.V. Longo, P.A. Burrowes, Persistence with chytridiomycosis does not assure survival of direct-developing frogs, Ecohealth (2010), doi:10.1007/s10393-010-0327-9.

[39] R.H. MacArthur, Patterns of species diversity, Biol. Rev. 40 (1965) 510–533.

[40] D.M. Marsh, M.A Goicochea, Monitoring terrestrial salamanders: biases caused by intense sampling and choice of cover objects, J. Herpetol. 37 (2003) 460–466, doi:10.1670/98-02A.

[41] C.J.W. McClure, B.W. Rolek, K. McDonald, G.E. Hill, Climate change and the decline of a once common bird, Ecology and Evolution 2 (2012) 370–378, doi:10.1002/ece3.9.

[42] D.J. Muñoz, D.A.W. Miller, C. Sutherland, E.H.C. Grant, Using spatial capture–recapture to elucidate population processes and space-use in herpetological studies, J. Herpetol. 50 (2016) 570–581.

[43] P.M. Narins, S.W.F. Meenderink, Climate change and frog calls: long-term correlations along a tropical altitudinal gradient, Proc. R. Soc. B 281 (2014) 20140401, doi:10.1098/rspb.2014.0401.

[44] D.L. Otis, K.P. Burnham, G.C. White, D.R. Anderson, Statistical inference from capture data on closed animal populations, Wildlife Monographs 62 (1978) 31–35.

[45] C. Parmesan, Ecological and evolutionary responses to recent climate change, Annu. Rev. Ecol. Evol. Syst. 37 (2006) 637–669.

[46] E.R. Pianka, Latitudinal gradients in species diversity: A review of concepts, Am. Nat. 100 (1966) 33–46.

[47] F.H. Pough, T. Taigen, M. Stewart, P. Brussard, Behavioral modification of evaporative water loss by a Puerto Rican Frog, Ecology 64 (1983) 244–252.

[48] R Development Core TeamR: a Language and Environment For Statistical Computing, R Foundation for Statistical Computing, Vienna, 2018.

[49] S.C. Reed, R. Reibold, M.A. Cavaleri, A.M. Alonso-Rodríguez, M.E. Berberich, T.E. Wood, Soil biogeochemical responses of a tropical forest to warming and hurricane disturbance, in: Advances in Ecological Research, 62, Academic Press, 2020, pp. 225–252, doi:10.1016/BS.AECR.2020.01.007.

[50] J.A. Rivero, in: Los Anfibios y Reptiles De Puerto Rico, Editorial Universitaria, Universidad de Puerto Rico, SanJuan, P.R., 1978, p. 152. pg + lam.

[51] J.R. Rohr, D.J. Civitello, J.M. Cohen, E.A. Roznik, B. Sinervo, A.I. Dell, The complex drivers of thermal acclimation and breadth in ectotherms, Ecology Letters 21 (2018) 1425–1439.

[52] J.A. Royle, R.B. Chandler, R. Sollmann, B. Gardner, Spatial Capture–Recapture, Elsevier, Amsterdam, The Netherlands, 2013.

[53] J.A. Royle, A.K. Fuller, C. Sutherland, Unifying population and landscape ecology with spatial capture-recapture, Ecography 41 (2018) 444–456, doi:10.1111/ecog.03170.

[54] T.D. Schowalter, P. Manoj, S.J. Presley, M.R. Willig, J.K. Zimmerman, Arthropods are not declining but are responsive to disturbance in the Luquillo Experimental Forest, Puerto Rico, Proc. Natl Acad. Sci. 118 (2) (2021) e2002556117, doi:10.1073/pnas.2002556117.

[55] J.A. Sheridan, N.M. Caruso, J.J. Apodaca, L.J. Rissler, Shifts in frog size and phenology: Testing predictions of climate change on a widespread anuran using data from prior to rapid climate warming, Ecol Evol 8 (2018) 1316–1327, doi:10.1002/ece3.3636.

[56] Shukla, P.R., J. Skea, E. Calvo Buendia, V. Masson-Delmotte, H.-.O. Pörtner, D.C. Roberts, P. Zhai, R. Slade, S. Connors, R. van Diemen, M. Ferrat, E. Haughey, S. Luz, S. Neogi, M. Pathak, J. Petzold, J. Portugal Pereira, P. Vyas, E. Huntley, K. Kissick, M. Belkacemi, J. Malley. 2019. IPCC: Climate Change and Land: an IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems. Accessed 2/24/21 https://www.ipcc.ch/srccl/

[57] M.M. Stewart, Climate driven population fluctuations in rain forest frogs, J. Herpetol. 29 (1995) 437–466.

[58] M.M. Stewart, L.L. Woolbright, Amphibians, in: D.P. Reagan, R.B. Waide (Eds.), The Food Web of a Tropical Rain Forest, University of Chicago Press, Chicago, 1996, pp. 363–398.

[59] M.M. Stewart, F.H. Pough, Population density of tropical forest frogs: relation to retreat sites, Science 221 (1983) 570–572.

[60] C. Sutherland, D.J. Muñoz, D.A.W. Miller, E.H.C. Grant, Spatial capture-recapture: a promising method for analyzing data collected using artificial cover objects, Herpetologica 72 (2016) 6–12.

[61] C. Sutherland, J.A. Royle, D.W. Linden, oSCR: a spatial capture–recapture R package for inference about spatial ecological processes, Ecography (2019).

[62] T.L. Taigen, F.H. Pough, Prey preference, foraging behavior, and metabolic characteristics of frogs, Am. Nat. 122 (1983) 509–520.

[63] C.D. Thomas, Climate, climate change and range boundaries, Diversity and Distributions 16 (2010) 488–495.

[64] M.C. Urban, G. Bocedi, A.P. Hendry, J.-.B. Mihoub, G. Péer, A. Singer, J.R. Bridle, L.G. Crozier, L. De Meester, W. Godsoe, A. Gonzalez, J.J. Hellmann, R.D. Holt, A. Huth, K. Johst, C.B. Krug, P.W. Leadley, S.C.F. Palmer, J.H. Pantel, A. Schmitz, P.A. Zollner, J.M.J. Travis, Improving the forecast for biodiversity under climate change, Science 353 (2016) aad8466, doi:10.1126/science.aad8466.

[65] R. von May, A. Catenazzi, R. Santa-Cruz, A.S. Gutierrez, C. Moritz, D.L. Rabosky, Thermal physiological traits in tropical lowland amphibians: Vulnerability to climate warming and cooling, PLoS One 14 (8) (2019) e0219759, doi:10.1371/journal.pone.0219759.

[66] G. Walther, Community and ecosystem responses to recent climate change, Phil. Trans. R. Soc. B 365 (2010) 2019–2024, doi:10.1098/rstb.2010.0021.

[67] S.R. Weiskopf, M.A. Rubenstein, L.G. Crozier, S. Gaichas, R. Griffis, J.E. Halofsky, K.J.W. Hyde, T.L. Morelli, J.T. Morisette, R.C. Muñoz, A.J. Pershing, D.L. Peterson, R. Poudel, M.D. Staudinger, A.E. Sutton-Grier, L. Thompson, J. Vose, J.F. Weltzin, K.P. Whyte, Climate change effects on biodiversity, ecosystems, ecosystem services, and natural resource management in the United States, Sci. Total Environ. 733 (2020) 137782, doi:10.1016/j.scitotenv.2020.137782.

[68] G.C. White, K.P. Burnham, Program MARK: Survival estimation from populations of marked animals, Bird Study 46 (sup1) (1999) S120–S139, doi:10.1080/00063659909477239.

[69] L. Woolbright, Patterns of nocturnal movement and calling by the tropical frog Eleutherodactylus coqui, Herpetologica 41 (1985) 1–9.

[70] L.L Woolbright, The impact of Hurricane Hugo on forest frogs in Puerto Rico, Biotropica 23 (1991) 462–467.

[71] J. Zimmerman, Tana E. Wood, Grizelle González, Alonso Ramirez, Whendee L. Silver, Maria Uriarte, Michael R. Willig, Robert B. Waide, Ariel E. Lugo, Disturbance and resilience in the Luquillo Experimental Forest, Biol. Conserv. 253 (2021) 108891, doi:10.1016/j.biocon.2020.108891.