Journal of Thermal Biology 140 (2026) 104527

Contents lists available at ScienceDirect

Journal of Thermal Biology

journal homepage: www.elsevier.com/locate/jtherbio

Coping near thermal maximum: Demographic responses of the common frog species, *Eleutherodactylus coqui*, to experimental climate warming

T.J.Hawley Matlaga [a,*], P.A. Burrowes [b,e], J.E. Paterson [c], T.E. Wood [d]

[a] Susquehanna University, Selinsgrove, PA, 17870, USA
[b] University of Puerto Rico, Rio Piedras, PR, USA
[c] P.O. Box 4525, Stonewall, Canada
[d] USDA Forest Service International Institute of Tropical Forestry, Río Piedras, PR, USA
[e] National Museum of Natural History, CSIC, Madrid, Spain

ARTICLE INFO

Keywords:
Amphibian
Capture-mark-recapture
Growth
Puerto Rico
Survival
TRACE
Tropical

ABSTRACT

The effects of climate warming on phenological patterns and species distributions have been described for many species but understanding how changes in behavior and demography lead to these shifts is less understood. We followed a population of the common frog, *Eleutherodactylus coqui,* as part of an *in-situ* field warming experiment (Tropical Responses to Altered Climate Experiment; TRACE), in a humid tropical forest using capture-mark-recapture methods. We assessed how growth, body size, and survival varied by warming treatment, sex, and developmental stage of frogs. In warmed plots (+4°C above ambient), adult female frogs grew faster but attained a smaller body size than frogs in control plots, suggesting a fitness tradeoff. Growth rates of adult males and juveniles did not vary between treatments, but body size was smaller in warmed plots. Survival rates did not differ significantly between warmed and control plots for juveniles, females, or males. Our results suggest that demographic responses to warming are complex and likely to vary between sexes and stages within a population. We conclude that an increase of 4°C remains within the tolerable temperature range for *E. coqui* at lowland sites, at least within the spatial and temporal scale of our experiment. However, this temperature increase brings this frog population perilously close to its high temperature threshold, beyond which performance is likely to decline. If this threshold is reached and the species is unable to acclimate or adapt, long-term persistence could be threatened. For a common, generalist species like *E. coqui*, identifying this tipping point is crucial for understanding demographic consequences in Puerto Rico as well as for its invasive potential in locations where it has been introduced.

1. Introduction

Climate warming is driving widespread shifts in species distributions across the globe (Taheri et al., 2021; Chen et al., 2011; Thomas, 2010; Parmesan, 2006). However, before these large-scale changes in range occur, individual behavior and population demographics change in response to altered performance and fitness under new climatic conditions (Parmesan, 2006). Detecting and understanding these early responses is critical for predicting and mitigating the impacts of climate change on biodiversity (Urban et al., 2016), especially for endemic or rare species with small geographic ranges. While disproportionate attention is often given to rare species, common species with broad distributions may play larger roles in ecosystem functioning (Avolio et al., 2019; Gaston, 2010, 2011). As such, they warrant increased attention when estimating the ecological consequences of climate change.

A fundamental pattern in ecology is that ecosystems are composed of few extremely abundant species and many rare species (Gaston, 2010; Whittaker, 1965). It is generally assumed that common species exert greater evolutionary and ecological influence than rare species (Gaston, 2010). For instance, in terrestrial systems, common species are responsible for the majority of nutrient turnover and compose more biomass than rare species; therefore, their loss can dramatically disrupt ecosystem structure, function, and services (Gaston and Fuller, 2008; Grime, 2002). Common species often shape microevolution of species they interact with such as the common narrowleaf cottonwood (*Populus*

* Corresponding author. Susquehanna University, 514 University Avenue, Selinsgrove, PA, 17870, USA.
E-mail address: matlagat@susqu.edu (T.J.Hawley Matlaga).

https://doi.org/10.1016/j.jtherbio.2026.104527
Received 3 November 2025; Received in revised form 23 March 2026; Accepted 25 June 2026
Available online 26 June 2026

angustifolia) driving levels of tannin tolerance in aphids (*Pemphigus betae;* Whitham et al., 2006) or the mussel (*Mytilus californianus*), a common predator in intertidal zones, impacting microevolution of limpet (*Lottia pelta*) shell shapes (Paine, 1966). Moreover, common species are more likely to become successful invaders when introduced outside of their native range (Colautti et al., 2014; Hui et al., 2011). It follows that if common species are more tolerant of abiotic and biotic change in comparison to rare species, they may be more likely to persist when confronted with climate-related challenges. These patterns underscore the importance of better understanding how common species respond to anthropogenic change.

Species respond to climate change via a variety of demographic parameters including growth, survival, and recruitment (Chevin et al., 2013). For instance, climate warming has led to altered seasonal activity (*Anaxyrus fowleri*; Green, 2017), reduced growth rates (*Plethodon cinereus*; Muñoz et al., 2016), and changes in body size (decreased: Caruso et al., 2014 or increased: McCarthy et al., 2017 in *P. cinereus*). Smaller body size has been linked to lower monthly survival and reduced population growth rates in *P. cinereus* (Hernández-Pacheco et al., 2021). These findings suggest that climate warming is creating ecological winners and losers (Somero, 2010). Some species, such as Bechstein's bat (*Myotis bechsteinii;* Mundinger et al., 2022), thrive as warming accelerates growth, enabling earlier reproduction at a younger age and higher lifetime reproductive output. This response could result in a species that becomes more dominant in their native ecosystem and plays a larger ecological role. In contrast, other species lose with climate warming as temperature alters breeding phenology (American pika (*Ochotona princeps*; Johnston et al., 2019)) or causes reduced survival as temperatures exceed physiological limits and decrease competitive ability (Arctic fox (*Vulpes lagopus*) relative to the red fox (*Vulpes vulpes*); Elmhagen et al., 2017; Hersteinsson and Macdonald, 1992). Tropical ectotherms are predicted to generally have narrower thermal tolerances compared to species at cooler latitudes (Deutsch et al., 2008). To better predict these outcomes as our climate warms, it is crucial to understand short-term changes in amphibian growth and survival. The common frog, *Eleutherodactylus coqui*, is native to Puerto Rico and a successful invader in Hawaii (Beard et al., 2009), Costa Rica (Barrantes-Madriga et al., 2019), and the U.S. Virgin Islands (Waddle et al., 2006; MacLean, 1982). It is a fully terrestrial, direct-developing species that is abundant and widely distributed in Puerto Rico (Stewart and Woolbright, 1996), making it an ideal candidate to study how climate warming affects population dynamics.

Widespread warming and drying are expected across the eastern Caribbean, including Puerto Rico (Bhardwaj et al., 2018; Chadwick, 2017). The study of how warming affects tropical forest species using *in situ* experiments has so far been limited to short-term warming of individual trees or leaves (Brazil; Doughty, 2011; Australia; Crous et al., 2023) or warming of soil (Soil Warming Experiment in Lowland Tropical Rainforest (SWELTR) in Panama; McFarlane et al., 2024). The Tropical Responses to Altered Climate Experiment (TRACE; Kimball et al., 2018) in Puerto Rico is the only long-term experiment in the tropics using a design that actively warms the above-ground vegetation (+4°C warming; (conservative estimate of projected increase based on Khalyani et al., 2016)). Opportunities to conduct long-term studies on tropical amphibians are rare in general and the TRACE plots offer a unique opportunity to follow how the common frog *E. coqui* responds to elevated surface temperatures *in situ.* Using capture-mark-recapture methods, we assessed whether growth, survival, and body size of frogs differed between warmed and control plots, and if any effects differed by sex or developmental stage. We hypothesized that increased evaporative water loss, caused by warmer temperatures and drier conditions (Tracy et al., 2008), would reduce frog growth, survival, and body size relative to frogs in unheated control plots (Deutsch et al., 2008). However, reduction in these demographic rates depends on how individuals respond to the +4°C increase; for instance, growth rate should increase with temperature up to an upper thermal maximum, beyond which growth should decline (Huey and Kingsolver, 2019). Specifically, when temperatures are below this upper threshold, we expect digestion efficiency to be high, and as long as food demands are met, accelerated growth should occur. Above this threshold, we expected physiological stress from increased evaporative water loss and reduced foraging or digestive efficiency to suppress growth (Huey and Kingsolver, 2019). We also predicted smaller average body size in warmed plots, consistent with previous findings (Hernández-Pacheco et al., 2021; Caruso et al., 2014; Bergmann, 1847), and lower survival due to increased desiccation risk.

2. Materials and methods

2.1. Study species

The frog *Eleutherodactylus coqui* occurs throughout Puerto Rico at low and high elevations, in wet and dry forests, as well as human-dominated areas (Joglar, 1998). It reaches population densities ranging from 988 to 11,440 adult frogs/ha, with a maximum of 24,800 individuals/ha if juveniles are included (Stewart and Woolbright, 1996). It is expected to play significant ecological roles within the tropical forest food web (Beard and Pitt, 2005; Beard et al., 2003). Although native to Puerto Rico, *E. coqui* is an introduced species in Hawaii, where it is particularly bothersome and considerable efforts have been undertaken to reduce its population size, which can be as high as 91,000 frogs/ha (Beard et al., 2008, 2009; Campbell and Kraus, 2002). It was also introduced in Florida (Austin and Schwartz, 1975), Louisiana (Dundee, 1991), Guam (Christy et al., 2007), and the Dominican Republic (Joglar and Rios, 1998) but populations never established (IUCN, 2021). The IUCN Redlist category for *E. coqui* is Least Concern, with its population listed as increasing (IUCN, 2021). In Puerto Rico, population declines of highland coqui frogs (*E. coqui* and congeners) have been attributed to extensive dry periods and their interaction with chytrid fungal infection (Longo and Burrowes, 2010; Burrowes et al., 2004), which are both direct and indirect consequences of climate change. *Eleutherodactylus coqui* is well-suited for capture-mark-recapture studies because it is highly philopatric and has a very small home range size of approximately 2 m in diameter (Joglar, 1998; Woolbright, 1985). It is also the most commonly encountered amphibian in the study area and is active year-round.

2.2. Study area

Six plots (each 12 m^2 in area) were established in the Luquillo Experimental Forest (LEF) in northeastern Puerto Rico (18.32465° N, 65.73058° W; 100 m in elevation) in 2015 and artificial warming was initiated in September 2016 (see Kimball et al., 2018 for details on experiment installation). The plots are in a secondary subtropical wet forest (Holdridge, 1967), which has regenerated from pasture in the 1950s (Kimball et al., 2018). The region experiences a regular disturbance regime including hurricanes, droughts, and landslides (Zimmerman et al., 2021), along with the more novel disturbance of climate warming (Reed et al., 2020). In September 2017, Hurricanes Irma and Maria passed over the island of Puerto Rico, severely affecting forest structure at this site. Mean annual temperature is 24°C and mean annual precipitation is 3500 mm per year (Garcia-Martino et al., 1996). The forest is aseasonal with no month receiving less than 200 mm of rainfall; however, there are wetter conditions typically from April to January and a drier period that commonly occurs in February and March. A meteorological station run by the United States Department of Agriculture Forest Service Sabana Field Research Station located near the TRACE plots maintains temperature and precipitation records (González et al., 2021).

Each plot consists of a hexagonal array of six aluminum poles spaced approximately 2.3 m apart, with neighboring plots located a minimum of 10 m apart. Heating in three plots (temperature treatment plots) is via

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 (Kimball et al., 2018). The infrared heaters (Model Raymax 1010, Watlow Electric Manufacturing Co., St. Louise, MO, 480 V) function via T-FACE (temperature free-air controlled enhancement) by warming the surfaces of vegetation which in turn warms the air due to re-radiation of heat from the vegetation (Kimball et al., 2008). Calibration and maintenance plans are described thoroughly in Kimball et al. (2018). Uniformity of warming is affected by the distribution of live vegetation and plot slope, yet surface soil temperatures (0-10 cm) showed little variation within TRACE control plots (23.1 ± 0.06 (mean ± SE) or heated plots (26.4 ± 0.32) during an initial six-month testing period (Kimball et al., 2018). The nocturnal habitat of *E. coqui* includes tree trunks, branches, epiphytes, and leaves at heights between 0.5 and 3.0 m in the forest understory (Stewart and Woolbright, 1996), so the warmed surfaces are expected to include many microhabitats utilized by frogs. We compared the mean temperature in control and warmed experimental plots measured using infrared radiometers (Apogee IRT sensors) for each hour of the day from 1 September 2018 to 31 January 2020 to the critical thermal maximum of *E. coqui* (35.39 – 36.72°C; high to low elevation populations respectively (Delgado-Suazo and Burrowes, 2022).

2.3. Data collection

Between September 2018 and July 2019, we sampled the six plots for frogs twice a month, with additional single samples in August and October 2019 and three in January 2020, for a total of 26 sampling events. Two observers used time-constrained (15 min) visual encounter methods to search for frogs by walking between the poles on the exterior of each plot between 19:00 and 21:00. One person focused on the interior of the plot, while the other focused on searching up to 0.5 m outside the hexagonal plot. When we encountered a frog, we confirmed that it was *E. coqui* and then placed it in an individual plastic bag, recording the location it was found (nearest pole and inside or outside) and whether it was vocalizing on the bag. After all plots were sampled for frogs, we returned to the lab at the Sabana Field Station (less than 100 m away from the plots) to complete measurements and marking the same night and following day. At all times, frogs were housed in individual plastic bags and handled as little as possible. We identified whether each frog was a recapture or new individual by checking all limbs for visible implant elastomer (VIE) marks. New individuals were given unique VIE marks in up to four locations near each limb (Grant, 2008; Bailey, 2004). Next, we measured body size (snout-to-vent length; SVL) to the nearest 1 mm and determined the sex of adults. Male sex was confirmed by the presence of a vocal sac or if they were vocalizing when captured. We assigned all frogs equal or smaller than 24 mm SVL as juveniles, according to size and stage classes used by Fogarty and Vilella (2002). We returned frogs to the location where they were captured, generally the following day, after measuring and marking was complete.

2.4. Survival analyses

We estimated the effects of experimental warming on frog survival using a Cormack-Jolly-Seber (CJS) model (Cormack, 1989; Jolly, 1965; Seber, 1965) with the package *marked* (Laake et al., 2013). All sampling events were separated by a minimum of 9 days, except the final three (January 3, 4, and 8) which we combined into a single event for this analysis. We fit the CJS model using maximum likelihood to estimate apparent survival (Φ), the probability of an individual frog surviving to the next month and not permanently emigrating, and detection probability (p), the probability of a frog being captured during a capture event. Besides the effect of the warming treatment, we predicted that frog survival and detection probability differed between demographic groups (adult males, adult females, and juveniles; group hereafter). We fit a model where Φ varied with treatment, group, and the interaction between treatment and group. We estimated effects on p from treatment, group, and the interaction between treatment and group. There were insufficient numbers of captures to estimate the effects of plot on Φ and p. We tested the goodness-of-fit using the overall test for each demographic group separately (juveniles, females, males) in the R2ucare package (Gimenez et al., 2018).

2.5. Growth analyses

We used growth intervals to test how experimental warming affected frog growth rates. We used within-year growth rates because growth over long periods is non-linear as animals increase in size towards an approximate asymptote (Von Bertalanffy, 1957). For each frog captured more than once within a year, we fit a linear regression with SVL as the response variable and date as the predictor variable. We only included captures separated by at least 20 days because that is the interval required to detect growth at an average growth rate of 0.05 mm/day with measurements precise to 1 mm (i.e., 0.05 mm/day x 20 = 1 mm). We then used the slope estimates (growth rates; mm/day) as the response variable in a linear mixed-effects model fit with treatment, group, and the interaction between treatment and group as independent variables. We included random intercept effects of frog identity and year. We fit the linear mixed-effects model with the *lme4* package (Bates et al., 2018) and tested the main effects with type-3 F-tests.

2.6. Body size analyses

We compared body size between frogs in warmed and control plots using a linear mixed-effects model. We used SVL as the response variable, and treatment, group, and the interaction between treatment and group as fixed effects. We included random intercept effects of frog identity and year.

3. Results

3.1. General

We captured and marked 604 frogs in 963 captures (222 captures of females, 475 captures of males, 266 captures of juveniles) between 18 September 2018 and 8 January 2020. Individual frogs were captured 1-9 times (mean = 1.6 captures per frog) and 436 frogs were never recaptured (recapture rate of 27.8 %). An average of 37 ± 2 frogs were captured in each of the 26 sampling days (range 17-53). Frogs ranged in SVL from 8 to 44 mm.

Mean daily air temperature fluctuated between 25°C and 34°C in the warmed plots and 20°C and 29°C in the control plots (Fig. 1). As planned with the experimental design, temperatures in the warmed plots were 4-5°C higher than temperatures in the control plots.

3.2. Survival analyses

The overall R2ucare tests did not find significant evidence for lack of goodness-of-fit in juveniles (χ^2 = 5.21, df = 12, P = 0.95), females (χ^2 = 36.79, df = 63, P = 0.99), or males (χ^2 = 87.11, df = 82, P = 0.33) for our Cormack-Jolly-Seber model. The model estimates of apparent monthly survival (mean ± 1 SE; Table 1) did not differ between warmed (juveniles: 0.53 ± 0.19, 95 % CI: 0.20 – 0.84; females: 0.84 ± 0.04, 95 % CI: 0.74 – 0.90; males: 0.88 ± 0.02, 95 % CI: 0.84 – 0.92) and control plots (juveniles: 0.62 ± 0.13, 95 % CI: 0.36 – 0.83; females: 0.87 ± 0.04, 95 % CI: 0.75 – 0.93; males: 0.88 ± 0.02, 95 % CI: 0.83 – 0.92; Fig. 2). There was some evidence of differences in survival between juveniles, adult females, and adult males (Fig. 2) but estimates of monthly survival for all groups overlapped in 95 % confidence intervals. Detection probability of females was slightly higher in warmed plots (0.09 ± 0.02, 95 % CI: 0.06 – 0.13) than in control plots (0.06 ± 0.01, 95 % CI: 0.04 –

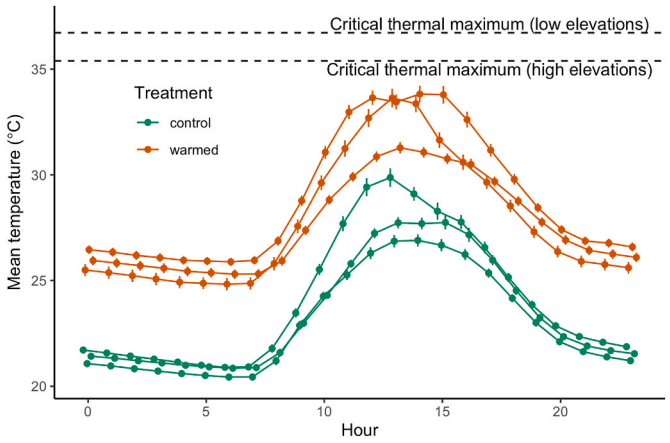

Fig. 1. The mean temperature in each of the three control and three warmed experimental plots in Puerto Rico measured using infrared radiometers for each hour of the day from 1 September 2018 to 31 January 2020. Points represent mean values and vertical lines are 95 % confidence intervals around the means. The dashed horizontal lines are estimates of critical thermal maximum for *Eleutherodactylus coqui* at high and low elevations.

Table 1
Model coefficients, standard error (SE) and 95 % confidence estimates of apparent monthly survival (Φ) and detection probability (*p*) for *Eleutherodactylus coqui* (n = 604 individuals marked and 963 captures) from six plots (3 control plots, 3 warmed plots) in Puerto Rico. Model estimates are on the logit scale.

Parameter	Coefficient	SE	Lower	Upper
$\Phi_{\text{Intercept (female)}}$	1.87	0.39	1.11	2.62
$\Phi_{\text{Warmed Treatment}}$	−0.23	0.50	−1.20	0.74
Φ_{Juvenile}	−1.37	0.67	−2.69	−0.05
Φ_{Male}	0.12	0.44	−0.75	0.99
$\Phi_{\text{Warmed Treatment:juvenile}}$	−0.15	1.07	−2.25	1.95
$\Phi_{\text{Warmed Treatment:male}}$	0.25	0.57	−0.87	1.38
$p_{\text{Intercept (female)}}$	−2.72	0.24	−3.19	−2.25
$p_{\text{Warmed Treatment}}$	0.40	0.33	−0.25	1.05
p_{Juvenile}	−0.84	0.60	−2.02	0.33
p_{Male}	0.89	0.27	0.36	1.43
$p_{\text{Warmed Treatment:juvenile}}$	−1.05	1.01	−3.04	0.94
$p_{\text{Warmed Treatment:male}}$	−0.25	0.37	−0.98	0.49

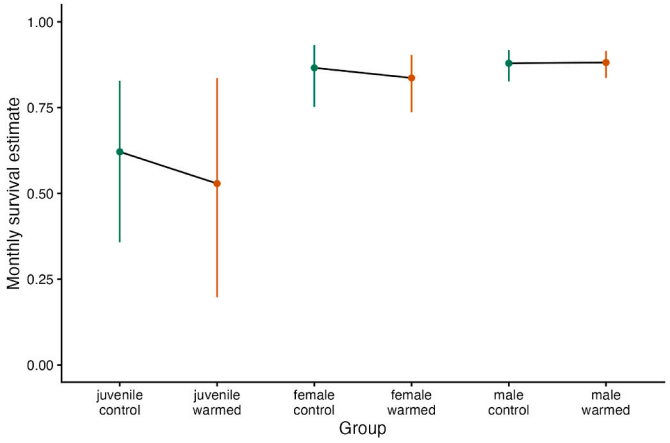

Fig. 2. Estimated apparent monthly survival (points) and 95 % confidence intervals (vertical lines) for *Eleutherodactylus coqui* in control (green) and 4°C warmed (orange) plots for juveniles, adult females, and adult males. Each point represents an estimate from three plots.

0.10). Conversely, detection probability was similar in warmed and control plots for juveniles (warmed: 0.01 ± 0.01, 95 % CI: 0.003 – 0.06; control: 0.03 ± 0.01, 95 % CI: 0.01 – 0.08) and males (warmed: 0.16 ± 0.02, 95 % CI: 0.13 – 0.19; control: 0.14 ± 0.02, 95 % CI: 0.11 – 0.17).

3.3. Growth rates

Frog growth rates were higher in warmed plots (juveniles: 0.04 ± 0.02 mm/day, 95 % CI: 0.03 – 0.05 mm/day, n = 7, females: 0.06 ± 0.01 mm/day, 95 % CI: 0.04 – 0.08 mm/day, n = 10, males: 0.01 ± 0.003 mm/day, 95 % CI: 0.002 – 0.02 mm/day, n = 54) than in control plots (juveniles: 0.04 ± 0.01 mm/day, 95 % CI: 0.01 – 0.07 mm/day, n = 5, females: 0.01 ± 0.01 mm/day, 95 % CI: −0.01 – 0.03 mm/day, n = 14, males: −0.004 ± 0.005 mm/day, 95 % CI: −0.01 – 0.005 mm/day, n = 43; $F_{1,\ 125} = 16.42$, $P < 0.001$; Fig. 3). The mean growth rate of males in control plots was negative but overlapped zero; any negative growth examples in our study likely represent measurement error rather than shrinking. Demographic groups had different growth rates ($F_{2,\ 120} = 5.03$, $P = 0.008$), with the lowest rate for males and highest rate for females. Additionally, there was evidence of an interaction between treatment and group ($F_{2,122} = 4.48$, $P = 0.01$), indicating that juvenile growth rates did not differ between treatments, the difference for males was weak, and female growth rates were higher in warmed than in control plots (Fig. 3).

3.4. Body size

Frogs differed in SVL based on demographic group ($F_{2,\ 719} = 673.34$, $P < 10^{-4}$), treatment ($F_{1,\ 757} = 11.99$, $P = 0.0006$), and the interaction between treatment and group ($F_{2,\ 777} = 12.61$, $P < 10^{-4}$; Fig. 4). Juveniles were larger in the warmed plots (16.7 ± 0.4 mm, 95 % CI: 16.1 – 17.5 mm, n = 149) than in control plots (15.2 ± 0.4 mm, 95 % CI: 14.4 – 16.0 mm, n = 117), with a similar pattern in adult males (warmed plots: 30.9 ± 0.1 mm, 95 % CI: 30.6 – 31.1 mm, n = 270; control plots: 30.3 ± 0.1 mm, 95 % CI: 30.0 – 30.6 mm, n = 205). However, females in control plots (32.8 ± 0.4 mm, 95 % CI: 31.9 – 33.7 mm, n = 121) were larger than females in warmed plots (31.0 ± 0.4 mm, 95 % CI: 30.2 – 31.9 mm, n = 101).

4. Discussion

Our study examined how survival, growth, and body size of a common frog species responded to artificial climate warming in a tropical

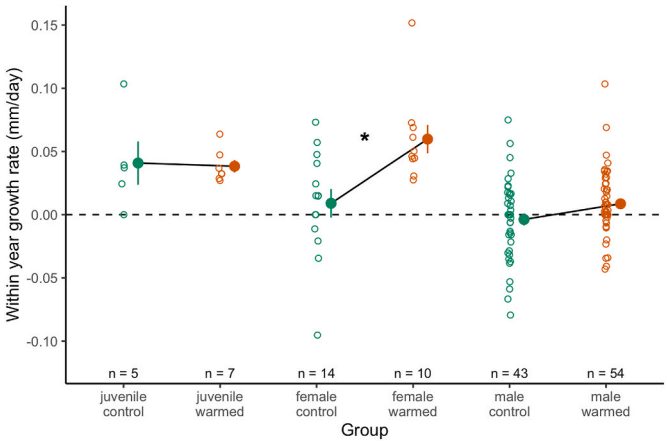

Fig. 3. Within-year growth rates (mm/day; hollow points), group means (solid points), and 95 % confidence intervals (vertical lines) for *Eleutherodactylus coqui* in control (green) and 4°C warmed (orange) plots. Each hollow point represents a frog's growth rate within one year and frogs were from 6 different plots (3 control plots and 3 warmed plots). Asterisks indicate pairwise differences from the linear mixed-effects model that do not overlap zero.

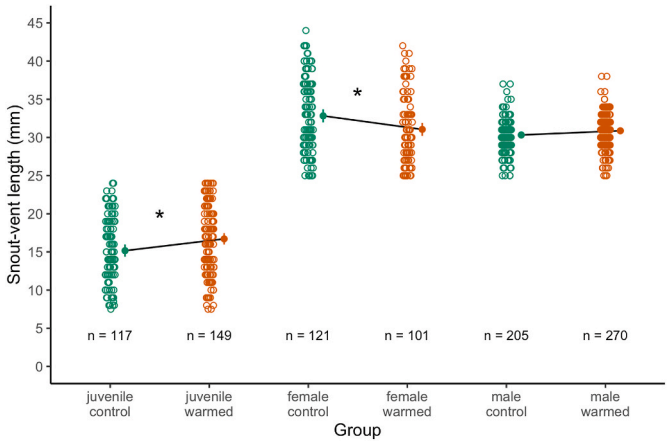

Fig. 4. Snout-vent length (mm; hollow points), group means (solid points), and 95 % confidence intervals (vertical lines) for *Eleutherodactylus coqui* in control (green) and 4°C warmed (orange) plots. Each hollow point represents a measurement of a frog's length and frogs were from 6 different plots (3 control plots and 3 warmed plots). Asterisks indicate pairwise differences from the linear mixed-effects model that do not overlap zero.

lowland forest. Frog responses varied by sex and stage, suggesting that the effects of warming are complex and difficult to generalize. We found no difference in frog survival between control and warmed plots. Female growth rates were higher in warmed plots in comparison to those in control plots, but their body size was smaller, suggesting that female fitness may be compromised by warming at this level. Larger females produce larger clutch sizes (Woolbright, 1989), and thus this effect may result in population declines over time. Identifying physiological and behavioral mechanisms altered by climate warming will allow better predictive modeling of eventual outcomes for species under expectations of continued and future global warming (Neel et al., 2021; Urban et al., 2016). Our findings have important implications for understanding the response of this common species to climate warming in its native range as well as understanding its invasive potential in locations where it is introduced.

Eleutherodactylus coqui are capable of acclimation to different elevational temperatures (Marchetti et al., 2023), so the lack of observed effects of warming on survival may be attributed to rapid local acclimation, although not directly measured with physiological markers in this study. Furthermore, at low elevation sites in Puerto Rico, *E. coqui* had a higher average critical thermal maximum (36.72°C) than those from high elevation sites (35.39°C), suggesting adaptation to recent climate warming (Delgado-Suazo and Burrowes, 2022) or local adaptation to elevation. Together these studies indicate that *E. coqui* exhibit phenotypic plasticity in response to variation in temperature and adaptation at the local scale. Alternatively, a survival response may be observed if our recapture rate (28 %) was higher. Natural mortality rates of *E. coqui* are high, with approximately 94 % of adults not surviving an entire year (Stewart and Woolbright, 1996). To improve the estimation of survival rates of *E. coqui*, future studies should consider sampling populations more frequently.

Frogs in warmed plots likely experienced temperature stress and reduced performance during the hottest hours of the day since maximum mean daily temperatures in warmed plots (34°C) approached the estimated critical thermal maximum (CTmax) values. In experimental lab settings, the jumping performance of *E. coqui* declined at temperatures above 26.7°C (Delgado-Suazo and Burrowes, 2022) and with dehydration (Rogowitz et al., 1999). Given that the mean temperature in warmed plots was above 25°C each hour of the day during the study, we expect that some reduction in individual performance was occurring. Some amphibian species are capable of adjusting cutaneous resistance, via skin secretions, to reduce evaporative water loss, allowing body temperature cooling at high air temperatures and ability to avoid reaching CTmax (Tracy et al., 2008). Experimental evidence suggests that *E. coqui* is not capable of adjusting cutaneous resistance and instead is likely to use behavioral mechanisms to maintain water balance (Rogowitz et al., 1999). Amphibians are capable of using behavior to mediate potential negative effects of climate warming (Matlaga et al., 2021; Farallo et al., 2018; Stevenson, 1985; Bogert, 1949) and this response may mask larger differences in performance of frogs in our study between warmed and control plots. In warmed plots, frogs can move away from the heaters on hot days to find a thermal refuge under vegetation or just outside of the plot. In a temperature selection experiment, the median temperature selected by low elevation *E. coqui* was 26.3°C (range 20°-33.3°C; Delgado-Suazo and Burrowes, 2022). In natural settings, *E. coqui* seek hydrated retreat locations and assume body positions that conserve water (Pough et al., 1983), yet they are also highly philopatric (home range size of 2 m in diameter) and territorial (Joglar, 1998; Woolbright, 1985; Stewart and Pough, 1983), indicating that individuals will not move far to escape heat. In addition, by the time a frog starts to experience physiological stress from heat, it may be too late to act without risking further physiological stress by moving during the day, when they are typically inactive. Frogs are more active in warmed plots and may increase movements to encounter prey items in order to meet dietary needs due to higher metabolic rates (Matlaga et al., 2021). However, increased activity could be indicative of a maladaptive response or an ecological trap (Wrensford et al., 2025; Beever et al., 2017) since moving more often or longer distances likely also increases exposure to heat or predators. A reduction in performance may be realized as reduced ability to evade a predator or altered 24-h phenology patterns, such as a reduced number of active hours each day. Additional field studies comparing daily phenology, use of microhabitat refuges, and activity rates in control and warmed plots would illuminate how frogs use behavior to thermoregulate.

The growth rate of female frogs was up to six times higher in warmed compared to control plots, indicating that a 4°C increase is accelerating growth, yet still within the range of physiological tolerance for *E. coqui*. The difference in growth between sexes was expected, as previous research showed that adult females grow faster than adult males at all body sizes, fitting the trend across most amphibians (Woolbright, 1983; Shine, 1979), with Coqui males essentially ceasing growth after reproductive size is reached (Woolbright, 1989). In control plots, frog growth in both sexes was similar to estimates in Hawaii (females in this study 0.01 mm/day, $n = 14$, females in Hawaii 0.0097 mm/day, $n = 11$, males in this study −0.004 mm/day, $n = 54$, males in Hawaii 0.0077 mm/day, $n = 90$ (Beard et al., 2008)). Increased growth rates in warmed conditions is consistent with results reported for over 80 % of ectotherms (Verberk et al., 2021; Atkinson, 1994), including numerous amphibians (Zhu et al., 2023; Blaustein et al., 2010; Browne and Edwards, 2003), as well as alpine grassland plants (Wang et al., 2020) and soil microbes (Jansson and Hofmockel, 2020). A positive growth response agrees with our hypothesis that growth will increase if temperatures experienced by an organism are within their optimal temperature range (Huey and Kingsolver, 2019; Ohlberger, 2013). Therefore, faster growth specifically for the female sex may be explained by a combination of the species-specific trend that males stop growing after reaching reproductive size (Woolbright, 1989) and the positive influence of warmer temperature in the warmed plots.

Increased growth and developmental rates are expected to lead to reduced average adult body size at age via the temperature-size rule (Atkinson, 1994; Berrigan and Charnov, 1994). In the TRACE plots, juvenile body size was 9 % larger and male body size was 2 % larger in warmed plots, but this size difference was reversed for females, with a 5 % reduction in warmed plots compared to control plots. Larger body size in warmed plots is unexpected as the general size pattern in Puerto Rico is smaller frogs in lowland (warmer) compared to highland (cooler) sites (Delgado-Suazo and Burrowes, 2022). The trends we observed in growth and size can be attributed to a strategy of increased investment

in growth to rapidly attain a critical size needed for reproduction. In warmed plots, temperature cues may suggest a mortality risk, resulting in faster growth to reach reproductive size more rapidly according to the terminal investment hypothesis (Duffield et al., 2017; Clutton-Brock, 1984). This response may be more drastic for females which need to attain a larger minimum size than males before reproductive maturity (Woolbright, 1989). Females attain a body size that is 29 % larger than that of males and this sexual dimorphism is attributed to the increased energetic costs of reproductive behavior, especially vocalizing, for males (Woolbright, 1989). At adulthood, females may continue investment in growth initially to increase body size and hence clutch size (Woolbright, 1989) but then switch to greater investment in egg production, leading to reduced average body size in warmed plots compared to control plots. Trade-offs between growth and reproduction should lead to greater lifetime reproductive output (Williams et al., 1968) and are an avenue for further study in climate warming research.

The temperature-growth rate relationship may be stronger for aquatic than for terrestrial species (Forster et al., 2012) and is hard to generalize across different species, as it is in part dependent on how species control water loss. Direct-developing, terrestrial frogs, such as *E. coqui*, are particularly susceptible to desiccation (Delgado-Suazo and Burrowes, 2022; Tracy, 1975) and are completely dependent on moisture in the forest environment. Increased temperatures typically correlate strongly with decreased environmental moisture, so it is important to study the effects of both simultaneously, as in the TRACE experimental plots. Our study demonstrates that a generalized pattern of increased negative consequences of climate warming for tropical ectotherms (Deutsch et al., 2008) does not apply to *E. coqui* within the spatial and temporal scale of our experiment.

Bioenergetic models suggest that climate warming could lead to metabolic meltdown, where ectotherms have reduced growth rates caused in part by a reduction in optimal foraging time because of sub-optimal temperatures (Huey and Kingsolver, 2019). The temperatures at which this meltdown occurs depends on species-specific physiological constraints, food availability, and food intake (Koskela et al., 1997). If species such as *E. coqui* exhibit flexibility in tolerance to temperature, then we could expect growth rates to increase until a tipping point at which the temperature becomes physiologically intolerable. There are numerous examples of species that have hit metabolic meltdown, such as the damselfly *Coenagrion puella,* which has reduced growth and survival rates under warming (Tüzün and Stoks, 2021). Other species avoid meltdown by changing phenological patterns, such as Atlantic bluefin tuna (*Thunnus thynnus*) which now spawn earlier to match larval growth with optimal prey populations and temperatures (Fiksen and Reglero, 2022). Our results suggest that although *E. coqui* in the warmed plots may not have met metabolic meltdown with a 4°C increase in temperature, this thermal regime puts them perilously near the edge of their tolerance. Furthermore, our findings offer additional evidence of the potential for *E. coqui* to exhibit behavioral and physiological plasticity and exploit a novel environment. The species' plasticity highlights the difficulty in identifying effective control measures in places where it is invasive, similar to findings by Beard et al. (2008) and Marchetti et al. (2023).

5. Conclusion

Our study examined how survival, growth rates, and body size of *E. coqui* respond to experimental warming in a tropical forest, providing insight into demographic responses of a common terrestrial ectotherm to climate change. While the inferences from some analyses may have been constrained by moderate recapture rates and limited sample sizes for specific demographic groups, these values are typical for amphibians and remain informative for detecting treatment effects. Importantly, the TRACE experiment offers a rare opportunity to evaluate complex warming responses *in situ,* where behavioral mechanisms that mediate physiological stress are preserved. Because vegetative recovery from Hurricane Maria coincided with experimental warming, our results also reflect the co-occurring disturbances that characterize contemporary tropical forests, underscoring the importance of long-term studies to determine if the trends described here persist.

To our knowledge, this is the first report of accelerated growth for female frogs in warmed conditions in an *in-situ* field experiment. Such sex-specific demographic responses are often unmeasured and overlooked until population-level changes become evident. Faster female growth has potential consequences for long-term population dynamics, including reduced age at maturity (Ohlberger, 2013; Atkinson, 1994), and reduced lifetime fertility because of smaller female body size. The divergent responses we observed among sexes and life stages for demographic measures highlight the complexity of species responses to climate warming. For populations living near the upper edge of their thermal performance curve, long-term outcomes may include shifts in phenology or geographic range, or reduced survival if physiological thresholds are exceeded.

As a common and widely distributed species, *E. coqui* has the capacity to disrupt ecological functioning if warming temperatures extend beyond tolerable limits. Because this study focused on a lowland population, future work should examine responses across elevational gradients to better capture the species' full thermal niche. Moreover, demographic responses of a focal species are also influenced by interactions with predators, competitors, and prey, rather than temperature alone (Ohlberger, 2013; Vasseur and McCann, 2005). We encourage future studies to assess warming effects on multiple interacting species over extended time periods, integrating demographic, behavioral, and physiological mechanisms to improve predictions of ecological responses to climate warming.

Funding sources

Funding for this study was received from the Department of Biology at Susquehanna University, the U.S. Department of Energy (award number 89243018S-SC-000014) and NSF award (DEB-1754713) to T.E. Wood, and NSF award IOS-2011281) to P.A. Burrowes. We also thank the USDA Forest Service International Institute of Tropical Forestry and the University of Puerto Rico-Río Piedras for additional support.

CRediT authorship contribution statement

T.J.Hawley Matlaga: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Visualization, Writing – original draft, Writing – review & editing. **P.A. Burrowes:** Conceptualization, Funding acquisition, Investigation, Methodology, Writing – review & editing. **J.E. Paterson:** Data curation, Formal analysis, Validation, Visualization, Writing – review & editing. **T.E. Wood:** Conceptualization, Funding acquisition, Methodology, Resources, Writing – review & editing.

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.

Acknowledgements

We thank IACUC at the University of Puerto Rico-Río Piedras (protocol # 3012-05-23-2018) and the Department of Natural Resources and the Environment (permit # 2018-IC-067) for giving us permission to conduct this study. We are grateful to the TRACE PIs Sasha C. Reed and Molly A. Cavaleri as well as many interns and staff who made this study possible, including Megan E. Berberich, Iana Grullón-Penkova, and William F. Mejía-García. We would also like to thank J. Pena and D. Slavick for help with field work. Funding for this study was received

from Susquehanna University Department of Biology, the U.S. Department of Energy (award number 89243018S-SC-000014) and NSF award (DEB-1754713) to T.E. Wood, and NSF award IOS-2011281) to P.A. Burrowes. We also thank the USDA Forest Service International Institute of Tropical Forestry and the University of Puerto Rico-Río Piedras for additional support.

Data availability

Data will be archived at Dryad: https://datadryad.org/stash at the time of publication.

References

Atkinson, D., 1994. Temperature and organism size-a biological law for ectotherms? Adv. Ecol. Res. 25, 1–58. https://doi.org/10.1016/S0065-2504(08)60212-3.

Austin, D.F., Schwartz, A., 1975. Another exotic amphibian in Florida, *Eleutherodactylus coqui*. Copeia 1975 188.

Avolio, M.L., Carroll, I.T., Collins, S.L., Houseman, G.R., Hallett, L.M., Isbell, F., Koerner, S.E., Komatsu, K.J., Smith, M.D., Wilcox, K.R., 2019. A comprehensive approach to analyzing community dynamics using rank abundance curves. Ecosphere 10, e02881. https://doi.org/10.1002/ecs2.2881.

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

Barrantes-Madriga, J., Parallada, M.S., Alvarado, G., Chaves, V.J.A., 2019. Distribution and invasion progress of *Eleutherodactylus coqui* (Anura: eleutherodactylidae) introduced in Costa Rica. Phyllomedusa 18, 101–107. https://doi.org/10.11606/issn.2316-9079.v18i1p101-107.

Bates, D., Kliegl, R., Vasishth, S., Baayen, H., 2018. Parsimonious mixed models. arXiv: 1506.04967. https://doi.org/10.48550/arXiv.1506.04967.

Beard, K.H., Al-Chokhachy, R., Tuttle, N.C., O'Neill, E.M., 2008. Population density estimates and growth rates of *Eleutherodactylus coqui* in Hawaii. J. Herpetol. 42 (1), 626–636. https://doi.org/10.1670/07-314R1.

Beard, K.H., Eschtruth, A.K., Vogt, K.A., Vogt, D.J., Scatena, F.N., 2003. The effects of the frog *Eleutherodactylus coqui* on invertebrates and ecosystem processes at two scales in the luquillo experimental forest, Puerto Rico. J. Trop. Ecol. 19, 607–617. https://doi.org/10.1017/s0266467403006011.

Beard, K.H., Price, E.A., Pitt, W.C., 2009. Biology and impacts of Pacific island invasive species. 5. *Eleutherodactylus coqui*, the coqui frog (Anura: leptodactylidae). Pac. Sci. 63, 297–316. https://doi.org/10.2984/049.063.0301.

Beard, K.H., Pitt, W.C., 2005. Potential consequences of the coqui frog invasion in Hawaii. Divers. Distrib. 11, 427–433. https://doi.org/10.1111/j.1366-9516.2005.00178.x.

Beever, E.A., Hall, L.E., Varner, J., Loosen, A.E., Dunham, J.B., Gahl, M.K., Smith, F.A., Lawler, J.J., 2017. Behavioral flexibility as a mechanism for coping with climate change. Front. Ecol. Environ. 15, 299–308. https://doi.org/10.1002/fee.1502.

Bergmann, C., 1847. Ueber die Verhaltnisse der warmeokonomie der thiere zu ihrer grosse. Gottinger Studien 3, 595–708.

Berrigan, D., Charnov, E.L., 1994. Reaction norms for age and size at maturity in response to temperature: a puzzle for life historians. Oikos 70, 474–478. https://doi.org/10.2307/3545787.

Bhardwaj, A., Misra, V., Mishra, A., Wootten, A., Boyles, R., Bowden, J.H., Terando, A.J., 2018. Downscaling future climate change projections over Puerto Rico using a non-hydrostatic atmospheric model. Clim. Change 147, 133–147. https://doi.org/10.1007/s10584-017-2130-x.

Blaustein, A.R., Walls, S.C., Bancroft, B.A., Lawler, J.J., Searle, C.L., Gervasi, S.S., 2010. Direct and indirect effects of climate change on amphibian populations. Diversity 2, 281–313. https://doi.org/10.3390/d2020281.

Bogert, C.M., 1949. Thermoregulation in reptiles, a factor in evolution. Evolution 3, 195–211. https://doi.org/10.1111/j.1558-5646.1949.tb00021.x.

Browne, R.K., Edwards, D.L., 2003. The effect of temperature on the growth and development of the endangered green and golden bell frog (*Litoria aurea*). J. Therm. Biol. 28, 295–299. https://doi.org/10.1016/S0306-4565(03)00006-8.

Burrowes, P.A., Joglar, R.L., Green, D.E., 2004. Potential causes for amphibian declines in Puerto Rico. Herpetologica 60, 141–154. https://doi.org/10.1655/03-50.

Campbell III, E.W., Kraus, F., 2002. Neotropical frogs in Hawaii: status and management options for an unusual introduced pest. In: Timm, R.M., Schmitz, R.H. (Eds.), Proceedings of the 20th Vertebrate Pest Conference. University of California, Davis, CA, pp. 316–318.

Caruso, N.M., Sears, M.W., Adams, D.C., Lips, K.R., 2014. Widespread rapid reductions in body size of adult salamanders in response to climate change. Glob. Change Biol. 20, 1751–1759. https://doi.org/10.1111/gcb.12550.

Chadwick, R., 2017. Sub-tropical drying explained. Nat. Clim. Change 7, 10–11. https://doi.org/10.1038/nclimate3167.

Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B., Thomas, C.D., 2011. Rapid range shifts of species associated with high levels of climate warming. Science 333, 1024–1026. https://doi.org/10.1126/science.1206432.

Chevin, L., Collins, S., Lefèvre, F., 2013. Phenotypic plasticity and evolutionary demographic responses to climate change: taking theory out to the field. Funct. Ecol. 27, 967–979. https://doi.org/10.1111/j.1365-2435.2012.02043.x.

Christy, M.T., Clark, C.S., Gee II, D.E., Vice, D., Vice, D.S., Warner, M.P., Tyrrell, C.L., Rodda, G.H., Savidge, J.A., 2007. Recent records of alien anurans on the Pacific Island of Guam. Pac. Sci. 61, 469–483. https://doi.org/10.2984/1534-6188(2007)61[469:RROAAO]2.0.CO;2.

Clutton-Brock, T.H., 1984. Reproductive effort and terminal investment in iteroparous animals. Am. Nat. 123, 212–229.

Colautti, R.I., Parker, J.D., Cadotte, M.W., Pyšek, P., Brown, C.S., Sax, D.F., Richardson, D.M., 2014. Quantifying the invasiveness of species. NeoBiota 21, 7–27. https://doi.org/10.3897/neobiota.21.5310.

Cormack, R.M., 1989. Log-linear models for capture-recapture. Biometrics 45, 395–413. https://doi.org/10.2307/2531485.

Crous, K.Y., Cheesman, A.W., Middleby, K., Rogers, E.I.E., Wujeska-Klause, A., Bouet, A. Y.M., Ellsworth, D.S., Liddell, M.J., Cernusak, L.A., Barton, C.V.M., 2023. Similar patterns of leaf temperatures and thermal acclimation to warming in temperate and tropical tree canopies. Tree Physiol. 43, 1383–1399. https://doi.org/10.1093/treephys/tpad054.

Delgado-Suazo, P., Burrowes, P.A., 2022. Response to thermal and hydric regimes point to differential inter- and intraspecific vulnerability of tropical amphibians to climate warming. J. Therm. Biol. 103, 103148. https://doi.org/10.1016/j.jtherbio.2021.103148.

Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C., Martin, P.R., 2008. Impacts of climate warming on terrestrial ectotherms across latitude. Proc. Natl. Acad. Sci. USA. 105, 6668–6672. https://doi.org/10.1073/pnas.0709472105.

Doughty, C.E., 2011. An in situ leaf and branch warming experiment in the Amazon. Biotropica 43, 658–665. https://doi.org/10.1111/j.1744-7429.2010.00746.x.

Duffield, K.R., Bowers, E.K., Sakaluk, S.K., Sadd, B.M., 2017. A dynamic threshold model for terminal investment. Behav. Ecol. Sociobiol. 71, 185. https://doi.org/10.1007/s00265-017-2416-z.

Dundee, H.A., 1991. When is an introduction not an introduction? Herpetol. Rev. 22, 122.

Elmhagen, B., Berteaux, D., Burgess, R.M., Ehrich, D., Gallant, D., Henttonen, H., Ims, R. A., Killengreen, S.T., Niemimaa, J., Norén, K., Ollila, T., Rodnikova, A., Sokolov, A. A., Sokolova, N.A., Stickney, A.A., Angerbjörnet, A., 2017. Homage to Hersteinsson and macdonald: climate warming and resource subsidies cause red fox range expansion and arctic fox decline. Polar Res. 36. https://doi.org/10.1080/17518369.2017.1319109.

Farallo, V.R., Wier, R., Miles, D.B., 2018. The bogert effect revisited: salamander regulatory behaviors are differently constrained by time and space. Ecol. Evol. 8, 11522–11532. https://doi.org/10.1002/ece3.4590.

Fiksen, Ø., Reglero, P., 2022. Atlantic bluefin tuna spawn early to avoid metabolic meltdown in larvae. Ecology 103, e03568. https://doi.org/10.1002/ecy.3568.

Fogarty, J.H., Vilella, F.J., 2002. Population dynamics of *Eleutherodactylus coqui* in Cordillera forest reserves of Puerto Rico. J. Herpetol. 36, 193–201. https://doi.org/10.2307/1565991.

Forster, J., Hirst, A.G., Atkinson, D., 2012. Warming-induced reductions in body size are greater in aquatic than terrestrial species. Proc. Natl. Acad. Sci. USA. 109, 19310–19314. https://doi.org/10.1073/pnas.1210460109.

Garcia-Martino, A.R., Warner, G.S., Scatena, F.N., Civco, D.L., 1996. Rainfall, runoff and elevation relationships in the luquillo Mountains of Puerto Rico. Caribb. J. Sci. 32, 413–424.

Gaston, K.J., 2010. Valuing common species. Science 327, 154–155. https://doi.org/10.1126/science.1182818.

Gaston, K.J., 2011. Common ecology. Bioscience 61, 354–362. https://doi.org/10.1525/bio.2011.61.5.4.

Gaston, K.J., Fuller, R.A., 2008. Commonness, population depletion and conservation biology. Trends Ecol. Evol. 23, 14–19. https://doi.org/10.1016/j.tree.2007.11.001.

Gimenez, O., Lebreton, J.-D., Choquet, R., Pradel, R., 2018. R2ucare: an r package to perform goodness-of-fit tests for capture–recapture models. Methods Ecol. Evol. 9, 1749–1754. https://doi.org/10.1111/2041-210X.13014. HYPERLINK.

González, G., Van Beusekom, A.E., Estrada Ruiz, C.R., 2021. Luquillo Experimental Forest Sabana Weather Station Scaffold Tower 2018-2020 Data, first ed. Forest Service Research Data Archive, Fort Collins, CO. https://doi.org/10.2737/RDS-2021-0030.

Grant, E.H.C., 2008. Visual implant elastomer mark retention through metamorphosis in amphibian larvae. J. Wildl. Manage. 72, 1247–1252. https://doi.org/10.2193/2007-183.

Green, D.M., 2017. Amphibian breeding phenology trends under climate change: predicting the past to forecast the future. Glob. Change Biol. 23, 646–656. https://doi.org/10.1111/gcb.13390.

Grime, J.P., 2002. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. J. Ecol. 86, 902–910. https://doi.org/10.1046/j.1365-2745.1998.00306.x.

Hernández-Pacheco, R., Plard, F., Grayson, K.L., Steiner, U.K., 2021. Demographic consequences of changing body size in a terrestrial salamander. Ecol. Evol. 11, 174–185. https://doi.org/10.1002/ece3.6988.

Hersteinsson, P., Macdonald, D.W., 1992. Interspecific competition and the geographical distribution of red and Arctic foxes *Vulpes vulpes* and *Alopex lagopus*. Oikos 64, 505–515. https://doi.org/10.2307/3545168.

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

Huey, R.B., Kingsolver, J.G., 2019. Climate warming, resource availability, and the metabolic meltdown of ectotherms. Am. Nat. 194, E140–E150. https://doi.org/10.1086/705679.

Hui, C., Richardson, D.M., Robertson, M.P., Wilson, J.R.U., Yates, C.J., 2011. Macroecology meets invasion ecology: linking the native distributions of Australian acacias to invasiveness. Divers. Distrib. 17, 872–883. https://doi.org/10.1111/j.1472-4642.2011.00804.x.

IUCN, 2021. *Eleutherodactylus Coqui*: IUCN SSC Amphibian Specialist Group: the IUCN Red List of Threatened Species 2021: E.T56522A3041672. https://doi.org/10.2305/IUCN.UK.2021-1.RLTS.T56522A3041672.en. (Accessed 24 June 2025).

Jansson, J.K., Hofmockel, K.S., 2020. Soil microbiomes and climate change. Nat. Rev. Microbiol. 18, 35–46. https://doi.org/10.1038/s41579-019-0265-7.

Joglar, R.L., 1998. Los Coquíes de Puerto Rico su Historia Natural y Conservación. Universidad de Puerto Rico. San Juan, PR.

Joglar, R.L., Rios, N., 1998. *Eleutherodactylus coqui* (Puerto Rican coqui, coquí común) in Dominican Republic. Herpetol. Rev. 107.

Johnston, A.N., Bruggeman, J.E., Beers, A.T., Beever, E.A., Christophersen, R.G., Ranson, J.I., 2019. Ecological consequences of anomalies in atmospheric moisture and snowpack. Ecology 100, e02638. https://doi.org/10.1002/ecy.2638.

Jolly, G.M., 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic Model. Biometrika 52, 225–247.

Khalyani, A.H., Gould, W.A., Harmsen, E., Terando, A., Quinones, M., Collazo, J.A., 2016. Climate change implications for tropical islands: interpolating and interpreting statistically downscaled GCM projections for management and planning. J. Appl. Meteorol. Climatol. 55, 265–282. https://doi.org/10.1175/JAMC-D-15-0182.1.

Kimball, B.A., Alonso-Rodríguez, A.M., Cavaleri, M.A., Reed, S.C., González, G., Wood, T. E., 2018. Infrared heater system for warming tropical forest understory plants and soils. Ecol. Evol. 8, 1932–1944. https://doi.org/10.1002/ece3.3780.

Kimball, B.A., Conley, M.M., Wang, S., Lin, X., Luo, C., Morgan, J., Smith, D., 2008. Infrared heater arrays for warming ecosystem field plots. Glob. Change Biol. 14, 309–320. https://doi.org/10.1111/j.1365-2486.2007.01486.x.

Koskela, J., Pirhonen, J., Jobling, M., 1997. Feed intake, growth rate and body composition of juvenile Baltic salmon exposed to different constant temperatures Aquac. Int. 5, 351–360. https://doi.org/10.1023/A:1018316224253.

Laake, J.L., Johnson, D.S., Conn, P.B., 2013. Marked: an R package for maximum likelihood and Markov Chain monte carlo analysis of capture–recapture data. Methods Ecol. Evol. 4, 885–890. https://doi.org/10.1111/2041-210X.12065.

Longo, A.V., Burrowes, P.A., 2010. Persistence with chytridiomycosis does not assure survival of direct-developing frogs. EcoHealth 7, 185–195. https://doi.org/10.1007/s10393-010-0327-9.

MacLean, W.P., 1982. Reptiles and Amphibians of the Virgin Islands. Macmillan Caribbean, London, Basingstoke, U.K.

Marchetti, J.R., Beard, K.H., Virgin, E.E., Lewis, E.L., Hess, S.C., Ki, K.C., Sermersheim, L. O., Furtado, A.P., French, S.S., 2023. Invasive frogs show persistent physiological differences to elevation and acclimate to colder temperatures. J. Therm. Biol. 114, 103590. https://doi.org/10.1016/j.jtherbio.2023.103590.

Matlaga, T.J.H., Burrowes, P.A., Hernández-Pacheco, R., Pena, J., Sutherland, C., Wood, T.E., 2021. Warming increases activity in the common tropical frog *Eleutherodactylus coqui*. Clim. Chang. Ecol. 2, 100041. https://doi.org/10.1016/j.ecochg.2021.100041.

McCarthy, T., Masson, P., Thieme, A., Leimgruber, P., Gratwicke, B., 2017. The relationship between climate and adult body size in redback salamanders (*Plethodon cinereus*). Geo 4, e00031. https://doi.org/10.1002/geo2.31.

McFarlane, K.J., Cusack, D.F., Dietterich, L.H., Hedgpeth, A.L., Finstad, K.M., Nottingham, A.T., 2024. Experimental warming and drying increase older carbon contributions to soil respiration in lowland tropical forests. Nat. Commun. 15, 7084. https://doi.org/10.1038/s41467-024-51422-6.

Mundinger, C., Fleischer, T., Scheuerlein, A., Kerth, G., 2022. Global warming leads to larger bats with a faster life history pace in the long-lived Bechstein's bat (*Myotis bechsteinii*). Commun. Biol. 5, 682. http://doi/10.1038/s42003-022-03611-6.

Muñoz, D., Miller, D.A.W., Sutherland, C., Grant, E.H.C., 2016. Using spatial capture–recapture to elucidate population processes and space-use in herpetological studies. J. Herpetol. 50, 570–581. https://doi.org/10.1670/15-166.

Neel, L.K., Logan, M.L., Nicholson, D.J., Miller, C., Chung, A.K., Maayan, I., Degon, Z., DuBois, M., Curlis, J.D., Taylor, Q., Keegan, K.M., McMillan, W.O., Losos, J.B., Cox, C.L., 2021. Habitat structure mediates vulnerability to climate change through its effects on thermoregulatory behavior. Biotropica 53, 1121–1133. https://doi.org/10.1111/btp.12951.

Ohlberger, J., 2013. Climate warming and ectotherm body size – from individual physiology to community ecology. Funct. Ecol. 27, 991–1001. https://doi.org/10.1111/1365-2435.12098.

Paine, R.T., 1966. Food web complexity and species diversity. Am. Nat. 100, 65–75. https://doi.org/10.1086/282400.

Parmesan, C., 2006. Ecological and evolutionary responses to recent climate change. Annu. Rev. Ecol. Evol. Syst. 37, 637–669. https://doi.org/10.1146/annurev.ecolsys.37.091305.110100.

Pough, F.H., Taigen, T.L., Stewart, M.M., Brussard, P.F., 1983. Behavioral modification of evaporative water loss by a Puerto Rican frog. Ecology 64, 244–252. https://doi.org/10.2307/1937072.

Reed, S.C., Reibold, R., Cavaleri, M.A., Alonso-Rodríguez, A.M., Berberich, M.E., Wood, T.E., 2020. Soil biogeochemical responses of a tropical forest to warming and hurricane disturbance. Adv. Ecol. Res. 62, 225–252. https://doi.org/10.1016/bs.aecr.2020.01.007.

Rogowitz, G., Cortés-Rivera, M., Nieves-Puigdoller, K., 1999. Water loss, cutaneous resistance, and effects of dehydration on locomotion of eleutherodactylus frogs. J. Comp. Physiol. B. 169, 179–186. https://doi.org/10.1007/s003600050209.

Seber, G.A.F., 1965. A note on the multiple-recapture census. Biometrika 52, 249–259. https://doi.org/10.2307/2333827.

Shine, R., 1979. Sexual selection and sexual dimorphism in the amphibia. Copeia 1979 297–306. https://doi.org/10.2307/1443418.

Somero, G.N., 2010. The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine 'winners' and 'losers. J. Exp. Biol. 213, 912–920. https://doi.org/10.1242/jeb.037473.

Stevenson, R.D., 1985. The relative importance of behavioral and physiological adjustments controlling body temperature in terrestrial ectotherms. Am. Nat. 126, 362–386. https://doi.org/10.1086/284423.

Stewart, M.M., Pough, F.H., 1983. Population density of tropical forest frogs: relation to retreat sites. Science 221, 570–572. https://doi.org/10.1126/science.221.4610.570.

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

Taheri, S., Naimi, B., Rahbek, C., Araújo, M.B., 2021. Improvements in reports of species redistribution under climate change are required. Sci. Adv. 7, eabe1110. https://doi.org/10.1126/sciadv.abe1110.

Thomas, C.D., 2010. Climate, climate change and range boundaries. Divers. Distrib. 16, 488–495. https://doi.org/10.1111/j.1472-4642.2010.00642.x.

Tracy, C.R., 1975. Water and energy relations of terrestrial amphibians: insights from mechanistic modeling. In: Gates, D.M., Schmerl, R.B. (Eds.), Perspectives of Biophysical Ecology. Springer-Verlag, New York, pp. 325–346.

Tracy, C.R., Christian, K.A., Betts, G., Tracy, C.R., 2008. Body temperature and resistance to evaporative water loss in tropical Australian frogs. Comp. Biochem. Physiol. A. Mol. Integr. Physiol. 150, 102–108. https://doi.org/10.1016/j.cbpa.2006.04.031.

Tüzün, N., Stoks, R., 2021. Lower bioenergetic costs but similar immune responsiveness under a heat wave in urban compared to rural damselflies. Evol. Appl. 14, 24–35. https://doi.org/10.1111/eva.13041.

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

Vasseur, D.A., McCann, K.S., 2005. A mechanistic approach for modeling temperature-dependent consumer-resource dynamics am. Nat. 166, 184–198. https://doi.org/10.1086/431285.

Verberk, W.C.E.P., Atkinson, D., Hoefnagel, K.N., Hirst, A.G., Horne, C.R., Siepel, H., 2021. Shrinking body sizes in response to warming: explanations for the temperature–size rule with special emphasis on the role of oxygen. Biol. Rev. 96, 247–268. https://doi.org/10.1111/brv.12653.

Von Bertalanffy, L., 1957. Quantitative laws in metabolism and growth. Q. Rev. Biol. 32, 217–231. https://doi.org/10.1086/401873.

Waddle, J.H., Crockett, M.E., Rice, K.G., 2006. Geographic distribution: *eleutherodactylus coqui*. Herpetol. Rev. 37, 487.

Wang, H., Liu, H., Cao, G., Ma, Z., Li, Y., Zhang, F., Zhao, X., Zhao, X., Jiang, L., Sanders, N.J., Classen, A.T., He, J.-S., 2020. Alpine grassland plants grow earlier and faster but biomass remains unchanged over 35 years of climate change. Ecol. Lett. 23, 701–710. https://doi.org/10.1111/ele.13474.

Whitham, T.G., Bailey, J.K., Schweitzer, J.A., Shuster, S.M., Bangert, R.K., LeRoy, C.J., Lonsdorf, E.V., Allan, G.J., DiFazio, S.P., Potts, B.M., Fischer, D.G., Gehring, C.A., Lindroth, R.L., Marks, J.C., Hart, S.C., Wimp, G.M., Wooley, S.C., 2006. A framework for community and ecosystem genetics: from genes to ecosystems. Nat. Rev. Genet. 7, 510–523. https://doi.org/10.1038/nrg1877.

Whittaker, R.H., 1965. Dominance and diversity in land plant communities. Science 147, 250–260. https://doi.org/10.1126/science.147.3655.250.

Williams, E.E., Highton, R., Cooper, D.M., 1968. Breakdown of polymorphism of the red-backed salamander on Long Island. Evolution 22, 76–86. https://doi.org/10.1111/j.1558-5646.1968.tb03451.x.

Woolbright, L.L., 1983. Sexual selection and size dimorphism in anuran amphibia. Am. Nat. 121, 110–119. https://doi.org/10.1098/rspb.2002.2170.

Woolbright, L.L., 1985. Patterns of nocturnal movement and calling by the tropical frog *Eleutherodactylus coqui*. Herpetologica 41, 1–9.

Woolbright, L.L., 1989. Sexual dimorphism in *Eleutherodactylus coqui*: selection pressures and growth rates. Herpetologica 45, 68–74.

Wrensford, K.C., Angert, A.L., Gaynor, K.M., 2025. Linking individual animal behavior to species range shifts under climate change. Trends Ecol. Evol. 40, 805–817. https://doi.org/10.1016/j.tree.2025.06.002.

Zhu, W., Zhao, T., Zhao, C., Li, C., Xie, F., Liu, J., Jiang, J., 2023. How will warming affect the growth and body size of the largest extant amphibian? More than the temperature–size rule. Sci. Total Environ. 859, 160105. https://doi.org/10.1016/j.scitotenv.2022.160105.

Zimmerman, J.K., Wood, T.E., González, G., Ramirez, A., Silver, W.L., Uriarte, M., Willig, M.R., Waide, R.B., Lugo, A.E., 2021. Disturbance and resilience in the luquillo experimental forest. Biol. Conserv. 253, 108891. https://doi.org/10.1016/j.biocon.2020.108891.