



Rapid cross-generational changes in morphology and mate choice following an extreme climatic event

Andrew D. Cronin^{1,5} · Ryan C. Taylor^{1,2} · Rachel A. Page² · Michael J. Ryan^{2,3} · Megan A. Murphy^{1,4} · Kimberly L. Hunter¹

Received: 9 April 2024 / Accepted: 11 November 2024

© The Author(s), under exclusive licence to Springer Nature Switzerland AG 2024

Abstract

Extreme climatic events, such as hurricanes, droughts, and floods, have been implicated in altering various phenotypic traits in affected populations. The 2015 El Niño cycle led to one of the driest wet seasons recorded throughout parts of Central America. We examined the effects of this climatic event on sexual and natural selection using behavioral and morphological data from túngara frogs (*Engystomops pustulosus*) collected before, during, and after this event. In a species renowned for robust female mating preferences, we found a cross-generational reduction and loss of female mate preferences for certain male advertisement call properties following this event. We identified reductions in body length and simultaneous increases in condition during the climatic event. Reduced availability and permanence of aquatic breeding sites may explain these behavioral and morphological changes. Mate choice preferences reverted rapidly, while the restoration of body length was sex dependent following this period of drastically reduced precipitation. These findings highlight immediate and lingering effects of single climatic events and demonstrate the ability of climatic events to disrupt established mate preferences. As climate change increases the frequency and severity of extreme events, monitoring behavioral and morphological phenotypes will be imperative to fully understand the consequences of these events on animal populations.

Keywords Extreme climatic event · Climate change · Mate choice · Sexual selection · Cross-generational effects · *Engystomops pustulosus*

✉ Andrew D. Cronin
a.d.cronin@vu.nl

¹ Department of Biology, Salisbury University, Salisbury 21801, USA

² Smithsonian Tropical Research Institute, Balboa, Republic of Panama

³ The University of Texas at Austin, Austin 78712, USA

⁴ Indiana University Bloomington, Bloomington 47405, USA

⁵ Amsterdam Institute for Life and Environment, Vrije Universiteit Amsterdam, Amsterdam 1081HV, The Netherlands

Introduction

Climate change has increasingly been shown to have wide-ranging effects on organisms, including altering range distributions of populations (Chen et al. 2011) and impacting individual physiology, morphology, and behavior (Sheridan and Bickford 2011; Calabrese and Pfennig 2023). In addition to the general trend of warmer global temperatures, climate change has increased the variability of climate and weather patterns, a phenomenon most noticeable with the increase in the frequency and severity of extreme climate events (ECEs) (Jentsch et al. 2007; van de Pol et al. 2017) such as particularly strong hurricanes and monsoons, abnormally cold temperatures, heat waves, and droughts.

Similar to effects of gradually warming temperatures, single ECEs can influence animal populations (Parmesan et al. 2000; Easterling et al. 2000; Coulson et al. 2001) as well as ecosystem assemblages (Brawn et al. 2017; Ummenhofer and Meehl 2017). Climatic events have been associated with changes at various levels of organization. At a population level, ECEs have been implicated with reduced nesting success in birds (Van De Pol et al. 2010) and increased mortality in sheep (Coulson et al. 2001). Additionally, rapid changes in morphological phenotypes at the individual level have been documented in populations that have experienced ECEs (Grant and Grant 2014; Campbell-Staton et al. 2017; Donihue et al. 2018). Knowledge of the effects of ECEs on animal populations is still limited, however, and this is especially true of behavioral phenotypes.

Between 2015 and 2016, Panama experienced a historically significant El Niño Southern Oscillation (ENSO) (Kogan and Guo 2017), a major meteorological force shaping weather patterns throughout the Americas, causing hurricanes and torrential rainfall in certain regions, as well as drought and reduced rainfall in others (Neelin et al. 2003). In Panama, El Niño years are associated with reduced rainfall. While ENSO events happen relatively frequently in Central America, this specific ENSO event resulted in one of the lowest levels of precipitation on record, particularly during the normal wet season in 2015 (Bretfeld et al. 2018; Paton 2019).

We investigated the effects of this single ECE on behavioral and morphological traits in the túngara frog (*Engystomops pustulosus*), a locally abundant species that is a model for sexual selection and sexual signal evolution. Specifically, we examined female mate choice, as this behavior has significant ecological and evolutionary consequences, including dictating the reproductive success of males and influencing signal evolution, phenotypic and genetic diversity, and speciation (Ryan 1985; Seehausen et al. 2008; Rosenthal 2017). Additionally, we leveraged long-term mate choice data in this species to compare yearly female mate choice across historical averages (Ryan 1985; Ryan et al. 2019). Although females in this species demonstrate highly repeatable and robust preferences for male signals (Ryan and Rand 2003; Gridi-Papp et al. 2006; Ryan et al. 2019; Taylor et al. 2021), previous data suggests that female preferences may shift in response to an El Niño event (Ryan et al. 2019). We therefore expected that female mate choice would be altered in response to the 2015–2016 El Niño event (Table 1).

We also measured body size and condition as these morphological traits are known to be influenced by environmental conditions (Gardner et al. 2011). Both of these morphological traits have significant consequences on survivorship and reproductive fitness (Ryan 1985; Smit et al. 2019). We anticipated that both males and females would be negatively impacted by drier conditions during the 2015 El Niño event (Brodeur et al. 2012; Walls et al. 2013;

Table 1 Background, predictions, results, and implications for the túngara population after an extreme climatic event focusing on the two focal traits

	Background	Predictions	Results	Implications
Behavior	Female túngara frog mate preferences are repeatable, but may be altered by ENSO events (Ryan et al. 2019, Taylor et al. 2021).	There will be a change in female mate preference across the ENSO event.	Females preferences for previously attractive stimuli were reduced or vanished, replicating findings in the wake of the 1997-98 ENSO event (Ryan et al. 2019). Preferences returned the following year.	Extreme climatic events can alter selection on sexual signals.
Morphology	Amphibians are dependent on moisture levels; droughts can reduce foraging and induce stress (Brodeur et al. 2012, Walls et al. 2013, Rollins-Smith & Le Sage 2023).	Reduced rainfall from the ENSO event will result in smaller body sizes and poorer body condition.	Both sexes were smaller but had higher condition during the ENSO event. Return to pre-ENSO size and condition was sex dependent.	Extreme climate events can alter morphology and body condition.

Rollins-Smith and Le Sage 2023), resulting in smaller individuals with lower body condition (Table 1).

Materials and methods

General methods and study species

All behavioral and morphological data were collected in or around Gamboa, Panamá. Here we define data collected before 2015 as “pre-El Niño”, data collected in 2015 as “during El Niño”, and data collected after 2015 as “post-El Niño”. Morphological data were collected in June-August between 2013 and 2017. For behavioral data, we integrated previously published data (see below for details) with data we collected in June-August 2016 and 2017.

The túngara frog is found throughout Central America. Like many frog species, male túngara frogs form leks in highly ephemeral pools of water at night and produce reproductive advertisement calls. Túngara frogs rely exclusively on these ephemeral ponds for breeding activity, as males must be in water to successfully call and water is required for egg deposition. Due to the reliance on these water bodies, breeding activity occurs during the wet season (typically between April-December in Panama). These ephemeral ponds likely reduce predation risks from macro-invertebrates and fish. Adults likely breed in only a single season, as genetic data (Hunter, unpublished data) and mark recapture data (Ryan 1985) suggest that most frogs do not live more than one year. The male advertisement call consists of two components: a “whine” that sweeps from a higher to lower frequency, and a harmonically rich “chuck” (Fig. S1). Males always produce a whine (simple call) and can voluntarily append one or more chucks to the end of the whine, creating a complex call. Complex calls are five times more attractive to females (Gridi-Papp et al. 2006; Ryan et al. 2019). In addition, calls with lower frequency whines, longer duration whines, and higher amplitude chucks are more attractive (Ryan 1985). Female preference for specific calls, based on combinations of the previously mentioned call properties, are highly robust in experiments in which females are presented with two alternative calls differing in these

properties (Ryan and Rand 2003; Gridi-Papp et al. 2006; Ryan et al. 2019; Coss et al. 2021; Taylor et al. 2021) (Fig. S1). The sex ratio at these nighttime choruses is strongly male biased, with females sampling calling males and choosing a mate based primarily on properties of their advertisement call (Ryan 1985). A female selects a male by approaching and touching the calling male. The male then clasps the female from behind in a position called amplexus. Females then oviposit the eggs (up to several hours later) into an ephemeral water body, where the tadpoles will develop.

Meteorological data

In order to incorporate highly detailed long-term meteorological datasets, we utilized data provided by the Physical Monitoring Program of the Smithsonian Tropical Research Institute staff and by the Meteorological and Hydrological Branch of the Autoridad de Canal de Panamá (Paton 2019). Although Gamboa does have meteorological data, we utilized data collected from BCI, as several months were missing from the dataset in Gamboa, and BCI is a more robust dataset including additional environmental measurements. BCI is located near Gamboa (approximately 15 km), and overall represents a similar environment to Gamboa. To ensure that weather patterns at BCI were comparable to Gamboa, we regressed annual rainfall from 1969 to 2015 for the two locations (Fig. S2). BCI and Gamboa share similar patterns of rainfall, thus BCI served as an appropriate proxy for Gamboa rainfall. However, Gamboa receives less rainfall on average, and therefore likely experienced slightly more pronounced reductions in rainfall than BCI. BCI rainfall data were collected daily using a 260-250-A tipping bucket (NovaLynx, Grass Valley, CA, USA). To compare rainfall patterns during the 2015 El Niño event with other years, we used a Welch's two sample t-test comparing monthly rainfall within 2015 with average monthly rainfall across all other years between 1990 and 2017.

Behavioral trials

Amplexed pairs of túngara frogs were collected between 1900 and 2300 h. Each pair was placed in a plastic bag (one pair per bag) with sufficient air and moisture to maintain the health of the frogs. We placed all pairs into a cooler and transported them to a Smithsonian Tropical Research Institute laboratory. Pairs remained in a dark cooler for a minimum of 15 min in order to decrease stress from light and handling. We separated females from their males and then individually placed females under a plastic funnel in an Acoustic Systems (ETS-Lindgren, Austin, TX) sound attenuation chamber. The funnel was placed in the middle of the chamber, equidistant from two Mirage Nanostat speakers (Klipsch Group Inc. Indianapolis, IN). When testing female preferences for simple (W) vs. complex calls (WC), these speakers were separated either by 180° and 130 cm from the funnel, or by 70° and 110 cm from the funnel. The 180° angle has been the standard test protocol for phonotaxis (sound only) tests for decades (Ryan et al. 2019). The 70° angle is used when frogs are being tested for simultaneous visual and acoustic preferences (Taylor et al. 2008). We tested for potential differences in female choice between these setups and found that female responses were highly robust to trial angle, with no significant differences between the two experimental designs (Fisher's exact test, $p > 0.88$). Therefore, these data were combined in subsequent analyses. Once the female was placed under the funnel, acoustic stimuli were

played antiphonally at a duty cycle of two seconds, typical of a calling male. The female was able to move freely while under the funnel, and had an acclimatization period of two minutes in the arena. After this period, the funnel was raised, and the female was allowed to move freely around the chamber.

If a female did not move from the center of the chamber after two minutes, jumped up the wall, or did not enter a choice zone within 10 min, then she was considered a 'foul out' (Cronin et al. 2019). Females that fouled out twice were removed from the experiment, due to a presumed lack of motivation. A choice was scored once a female entered a choice zone and remained within the choice zone for three seconds. The choice zone in W vs. WC trials was 10 cm in front of the speakers and 20 cm to the sides of the speakers. In the natural call trials, the choice zone was a 10 cm around the speakers. The choice zones differed in size due to the differences in the distances between speakers. This distance was greater in the W vs. WC experiment, and therefore females were less likely to change their choice after a close approach to a single speaker.

All stimuli were calibrated each night to broadcast at 82dB SPL (re. 20 μ Pa, fast C-weighting) at the starting position of the female frog. Throughout the course of the night, speakers were recalibrated to ensure that the amplitude between the speakers did not vary. To avoid potential side bias, the stimuli were switched between the speakers throughout the course of the night.

Simple and complex calls were synthesized by averaging 15 acoustic parameters from 250 calls recorded from 50 males. The whine of the two calls was identical, but the complex call had one appended synthetic chuck (Fig. S1). These synthetic calls have been used in previous studies (Ryan and Rand 2003). The natural calls used for this experiment consisted of eight paired stimuli. These stimuli were a subset of male recordings collected from sites around Gamboa and used in previous studies, where it was determined that one group was more attractive (Ryan and Rand 2003; Taylor et al. 2021). Each of the stimulus pairings used in the current study had one attractive and one unattractive call (Fig. S1). We conducted experiments with both W vs. WC stimuli and paired natural calls as female responses to these different stimuli are likely driven by different neural processes (Wilczynski et al. 1995; Wilczynski and Ryan 2010).

Female preference for complex calls are highly robust, and has been documented repeatedly for nearly 40 years (Ryan 1985; Gridi-Papp et al. 2006). In the 19 years prior to and during the 2015 ENSO event, females showed a preference for a synthetic complex call over a synthetic simple one, with an average of 86% of females selecting the complex call (Ryan et al. 2019). Therefore, we compared the portion of females that selected the complex (WC) signal to this a priori probability of 0.86.

Similarly strong and repeatable preferences are found for natural whine-chuck calls, with females displaying preferences for longer duration, lower dominant whine frequency, higher chuck amplitudes, and lower chuck frequencies (Ryan 1980; Ryan and Rand 2003; Taylor et al. 2021) (Fig. S1). For attractive vs. unattractive natural calls (both complex), two studies conducted before the 2015 ENSO event (Ryan and Rand 2003; Taylor et al. 2021) and more than ten years apart, both revealed strong and similar preferences using the same pair of natural complex calls. The first study found a 79.37% preference (Ryan and Rand 2003) and the second, a 81.25% preference rate (Taylor et al. 2021) for the call with higher amplitude chucks and lower dominant frequencies (mean=80.3%). An additional study, conducted before the 2015 ENSO event, and published 17 years after the Ryan and Rand

2003 study, using one exemplar pair of the natural calls, also found the identical strengths of preference for that particular call pair (Coss et al. 2021), demonstrating that the preference for attractive natural calls is robust and repeatable. Therefore, female preference for “attractive” calls in our experiments were compared against the historical proportion (80.3), using a binomial exact test.

Morphological analyses

We collected snout-vent length (SVL) and mass of each female used in our experiments as well as their male mating partner. SVL was collected using calipers, and mass was collected using an electronic balance (Fig. S3). All individuals were kept in the same conditions prior to testing and measurement, ensuring that using mass would not bias our results. At the time of measuring all females were gravid.

To create a body condition index, we first calculated the residuals of a linear regression based on the cube root of body mass and SVL in SPSS (Ver. 24). These residuals were then divided by an individual's SVL (Dyson et al. 1998; Bernal et al. 2007). We analyzed data for males and females separately due to sexual size dimorphism in this species. All morphological measures, including body condition, SVL, and mass were compared between years using a mixed effects model in the R package *lme4* (version 1.1.29) (Bates et al. 2015), with year as a fixed effect and site as a random effect. We tested pairwise comparisons between years with the package *emmeans* (versions 1.7.4.1) (Lenth 2022).

Results

Climatic conditions

The 2015 ENSO was one of the most severe in recorded history. In Panama, this event also resulted in one of the longest dry seasons on record, with over 90% of the country experiencing drought during this period (Bretfeld et al. 2018; Paton 2019). This pattern was evident in our study site. The 2015 wet season (April–December) had significantly reduced rainfall compared to the previous 28 years (Welch's two-sample t-test $p=0.011$, 2015 mean monthly rainfall=169.4 mm; mean monthly rainfall for 1990–2017 (excluding 2015)=286.4 mm, standard deviation=81.11) (Fig. S4). Following the ENSO event in 2015, the following two wet seasons (2016 and 2017) were characterized by a weak La Niña and a neutral cycle; wet seasons experienced typical rainfall and typical wet-season frog breeding conditions.

Female mate preference

In the 2016 wet season following the ENSO event, we found that female preference for complex calls was significantly lower than the long-term average (binomial exact test: expected=0.86, $p=0.002$, $N=69$), with 72% of females preferring the complex call (Fig. 1). Female preference for the formerly attractive natural calls was also significantly reduced, as females chose the known attractive calls only 56% of the time (binomial exact test: expected=0.803, $p=0.002$, $N=32$). In fact, the preference for attractive natural calls

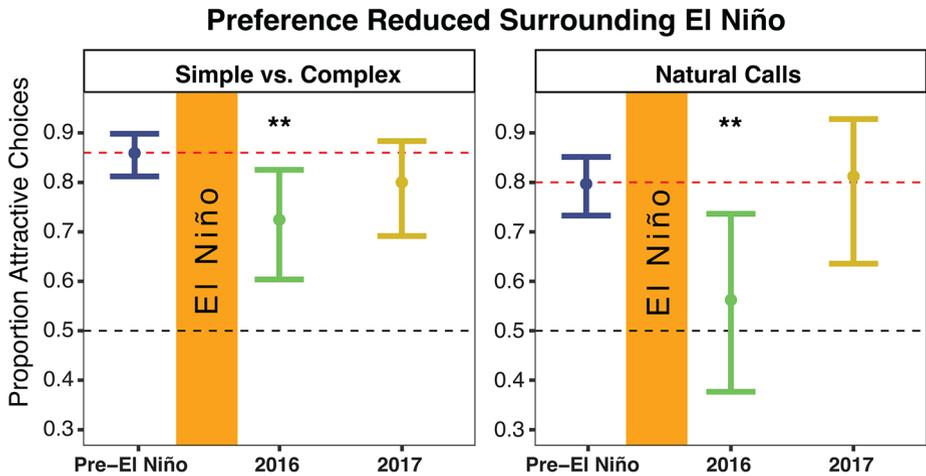


Fig. 1 Reduction of strength of female mate preference for complex and natural calls after severely reduced rainfall. Female preferences for complex calls (2016 $n=69$; 2017 $n=75$), and female preference for ‘attractive’ natural male calls (2016 $n=32$; 2017 $n=32$), showing mean preference \pm 95% confidence intervals. The dotted blue line represents random choice (0.5). The dotted red lines are expected values based on robust preferences for complex stimuli (Ryan et al. 2019), and specific attractive natural calls (Ryan and Rand 2003; Taylor et al. 2021). ** $P < 0.01$

effectively disappeared and was not different from random choice (binomial exact test: expected=0.5, $p=0.54$, $N=32$) (Fig. 1).

Surprisingly, we found that the reduction and loss of preference for attractive calls in 2016 was followed by a rapid reversion. In the 2017 rainy season, eighty per cent of females chose the complex call, which was not significantly different from the long-term average (binomial exact test: expected=0.86, $p=0.113$, $N=75$). Female responses to the attractive natural calls also returned to pre-El Niño levels; their preferences were nearly identical to prior experiments with 81.25% of females choosing the attractive call (binomial exact test: expected=0.803, $p=0.912$, $N=32$) (Fig. 1) (Ryan and Rand 2003; Taylor et al. 2021).

Body size and condition

Pairwise comparisons of snout-vent length (SVL) collected before, during, and after the 2015 ENSO event, show that both male and female SVL was significantly reduced in 2015 (Fig. 2). In the two years prior to the ENSO event, female SVL was stable, but was significantly reduced by 6.0% in 2015 (estimate = -1.805, SE=0.185, $p < 0.0001$). Males similarly had a 5.0% reduction in SVL during the 2015 ENSO event (estimate = -1.372, SE=0.203, $p < 0.0001$). In both sexes, this decline in SVL was followed by a significant increase in 2016, although the magnitude of these changes was lower than the response to the ENSO event year, with a 2.2% increase in female and a 3.2% increase in male SVL (female: estimate=0.613, SE=0.184, $p=0.008$; male: estimate=0.832, SE=0.198, $p=0.0003$). Following this increase, SVL stabilized in both sexes between 2016 and 2017. However, females still had a 4.1% reduction in SVL in 2017 compared to pre-ENSO (estimate = -1.229, SE=0.258, $p < 0.0001$) whereas males quickly reverted to pre-ENSO sizes. Although we found a decrease in SVL for both sexes during the ENSO event, body condition increased

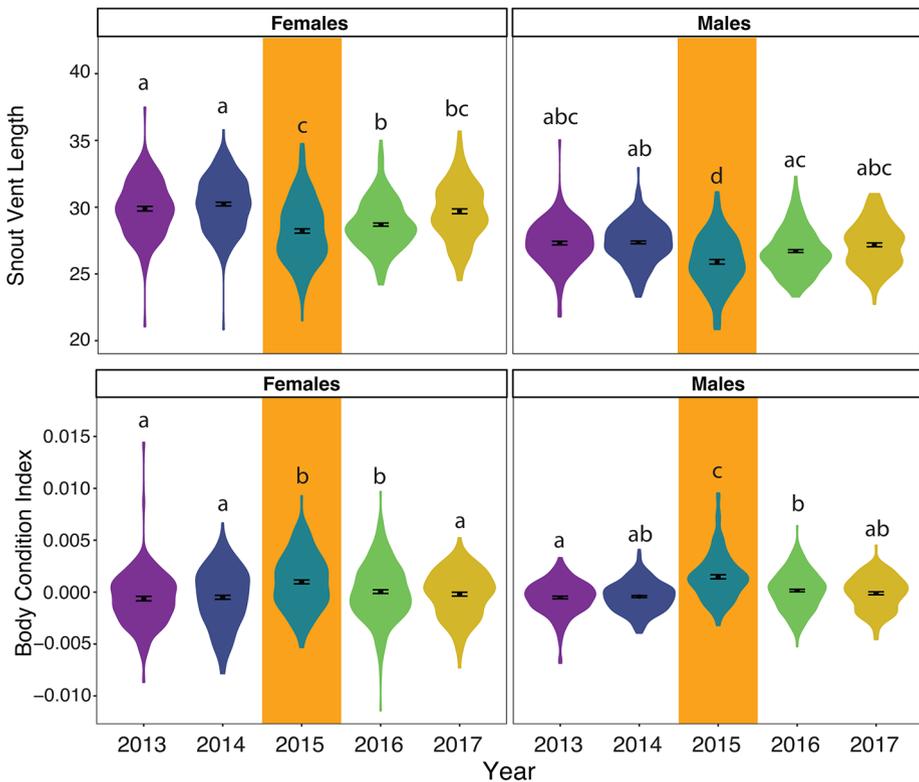


Fig. 2 Significant change in snout vent length (SVL) and body condition during the 2015 ECE (in orange), with rapid reversion to previous levels. Plots based on raw data of females and males across years with means \pm standard error. Female) 2013: $n=145$, 2014: $n=223$, 2015: $n=145$, 2016: $n=261$, 2017: $n=119$. Male) 2013: $n=164$, 2014: $n=227$, 2015: $n=143$, 2016: $n=265$, 2017: $n=65$. Distinct letters indicate a significant difference between years ($p < 0.05$). See main text for statistical details

during the ENSO compared to the year before (females: estimate=0.002, SE=0.0002, $p < 0.0001$; males: estimate=0.0018, SE=0.0002, $p < 0.0001$), largely due to stable masses of both sexes across all years (Fig. S3).

Discussion

In the wake of severely reduced rainfall during an extreme ENSO event, we documented behavioral and morphological shifts. Repeatable female mate preference for advertisement calls significantly decreased in the year following reduced rainfall, and returned the following year. Both males and females were significantly smaller during the ENSO event, with males recovering more rapidly than females. However, both males and females increased in body condition following the ENSO event.

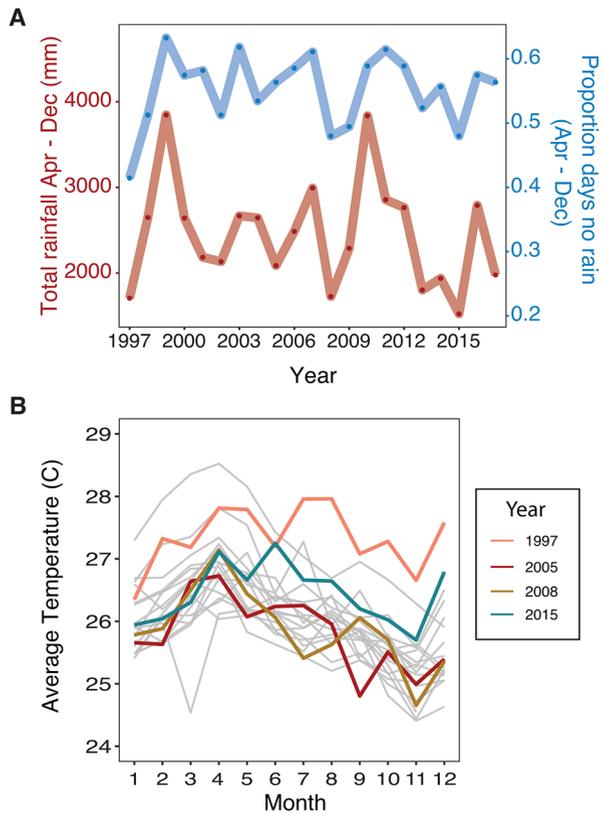
Our findings that female mate choice can change in response to a climatic event are surprising due to the robustness of female preferences in this species. In addition to consistent behavioral responses, the neural underpinnings of certain female preferences are already

known. For example, female preferences for complex calls are based on the stimulation of two inner ear organs tuned to different frequencies (Wilczynski et al. 1995; Phelps et al. 2006). The complex call stimulates both inner ear organs (the amphibian papilla (AP) and basilar papilla (BP)), whereas simple calls primarily stimulate the AP. Thus, changes in female responses to these signals as a consequence of the 2015 ENSO suggest a physiological shift at the population level. However, stronger behavioral shifts were documented when examining female preferences for natural calls, in which all presented stimuli contained one chuck. Thus, both choices available to females stimulated the BP. Therefore, the preferences for these 'attractive' stimuli are likely based on higher-level processing, not simply auditory filtering by the ear. Our understanding of specific mechanisms behind these preference changes, however, remains limited (Wilczynski and Ryan 2010). The decrease in preference for both complex and previously 'attractive' calls may be driven by different perceptual mechanisms, which suggests that this ENSO event had a profound impact on multiple processes governing female mating decisions. Additionally, most males calling together in choruses will make complex calls. Therefore, the loss of preference documented in the natural call experiments may more closely reflect female mating decisions in nature.

Although we documented significant shifts in female mate choice preferences across an extreme climatic event, one of the potential difficulties in identifying phenotypic changes in response to severe climatic events is their infrequency. Importantly, long-term data examining female mate choice by MJR documents a similar behavioral response to a previous climatic event (Ryan et al. 2019). In the wake of another period of drastically reduced precipitation induced by a strong El Niño event in 1997–1998, female preferences for the complex call dropped significantly from 91 to 70%. This is consequently the only other year that female mate preference for complex calls significantly deviated from the long term average (Ryan et al. 2019). Similarly, preferences rebounded the subsequent year to pre-El Niño levels (Ryan et al. 2019), supporting the conclusion that the behavioral shifts we document here are a result of these ENSO events.

Due to the fact that strong El Niño years can have wide ranging effects, and that reductions in precipitation could have a variety of impacts on a species, it can be difficult to determine the specific mechanisms responsible for the various behavioral and morphological changes that we discovered. However, as we previously suggested, these changes are likely explained by the lack of reliability of ephemeral ponds, which túngara frogs exclusively rely on for breeding. The prevalence and persistence of these ephemeral ponds is dependent on several factors, including the timing and amount of rainfall, as well as temperature. While the 2015 ENSO event led to a sharp decrease in overall rainfall, this event also led to changes in both temperature and the periodicity of rainfall. The 2015 ENSO event was characterized by a higher proportion of days without rain (Fig. 3A) and higher average temperatures (Fig. 3B), leading to fewer ephemeral ponds available for breeding. Many of our regular collection sites remained completely dry during the 2015 wet season, especially during one, highly unusual, 26-day dry spell between 11 June and 6 July 2015. During normal wet seasons, the number of túngara frogs breeding at ponds varies with rainfall, but individuals can be found reproducing on most nights. During the 2015 ENSO event, the lack of breeding sites meant that many nights had no túngara frog activity. The assertion that reduced access to breeding sites could play a significant role in explaining our findings is supported by the fact that two other years with low overall rainfall (2005 and 2008), did not show similar trends in behavioral mate choice preferences. Both 2005 and 2008 were

Fig. 3 Rainfall and temperature patterns show the unique climatic conditions surrounding shifts in behavioral responses in túngara frogs. **(A)** Cumulative rainfall (red) between 1997 and 2017 during the rainy season (April-December) and the proportion of days without rainfall during the rainy season (blue). **(B)** Average temperature between 1997 and 2017. All lines represent different years, with the four years with lowest rainfall highlighted. Datasets were provided by the Physical Monitoring Program of the Smithsonian Tropical Research Institute and by the Meteorological and Hydrological Branch of the Autoridad de Canal de Panamá (Paton 2019)



characterized by relatively lower temperatures and a higher proportion of days with rainfall compared to 1997 and 2015, the two years which are associated with a subsequent reduction in female mating preferences (Fig. 3). These findings suggest that a reduction in the availability and persistence of ephemeral ponds in 2015, rather than rainfall per se, may have resulted in fewer opportunities to mate and altered the developmental conditions for the next generation.

The mechanism of the female mate preference reduction following the ENSO event and returning to historical levels the following year is unresolved but is likely a result of the developmental conditions experienced in 2015. Predation rates on túngara frogs are extremely high, and mark-recapture data suggest that most individuals do not survive longer than a year (Ryan 1985). While the adult frogs we examined in 2016 experienced normal wet conditions, with above average precipitation (Paton 2019), most of these individuals would have developed during the period of reduced rainfall in 2015. With few ephemeral ponds for breeding during the 2015 ENSO, tadpoles likely developed in areas with high densities and a high risk of desiccation. The rapid dry down of larval developmental ponds during 2015 likely resulted in faster developing individuals, which could be based on selection, developmental plasticity, or a combination of these processes (Gomez-Mestre et al. 2013; Charbonnier and Vonesh 2015). Regardless of the underlying mechanisms, such changes in the rate of developmental timing can have long-lasting effects on individual morphology (Touchon et al. 2013; Charbonnier and Vonesh 2015) and survivorship (Székely et al. 2020).

Conditions during tadpole development can even lead to changes in brain size (Gonda et al. 2010), which may remain or emerge after metamorphosis in anurans (Trokovic et al. 2011). One brain region that appears to be affected post-metamorphosis by conditions during larval development is the diencephalon (Trokovic et al. 2011), which is heavily involved in auditory and sensorimotor processing (Wilczynski and Ryan 2010). Thus, there is potential that increased developmental stress during the ENSO event influenced the development of the sensorimotor processing system of female túngara frogs, leading to a change in their mate choice preferences (Ronald et al. 2017).

A lack of persistent breeding sites may also help explain the increase in body condition found in 2015. Reproductive activity is a metabolically taxing process for both males and females (Bucher et al. 1982; Ryan et al. 1983). With fewer opportunities to call in 2015, males would not expend as much energy for mate attraction. Likewise, fewer mating opportunities may lead to females producing fewer egg clutches over the course of the breeding season. This reduction in allocation of reproductive energy likely contributed to the increased body condition in both sexes during the ENSO event. However, changes in body size may be explained by alternative processes, including as a consequence of selection or due to suboptimal growth conditions for frogs collected in 2015. Crucially, ENSO events are typically associated with elevated temperatures as well as reduced rainfall in this region. Elevated temperatures have been proposed as a cause of recent global trends in body size reduction across several taxa, although this remains unsettled (Gardner et al. 2011). Alternatively, as frogs have indeterminate growth, it is possible that there may have been increased mortality of older (and therefore larger) individuals during the El Niño event in 2015.

Our findings also illustrate how rapidly populations may recover from an ECE. Notably, the change in female mate preference seen in 2016 reverted to typical preference levels in the following year, suggesting that changes in behavioral phenotypes were driven by developmental plasticity. Morphological and physiological changes in SVL and body condition also stabilized quickly following the 2015 ENSO event, although these changes remained over longer time spans, suggesting a potential role of underlying genetic processes. However, even these short-term shifts can have substantial effects on populations over time. For example, the relaxed female preferences observed in 2016, potentially driven by developmental plasticity, may have reduced sexual selection pressures on male signals and allowed for a decreased skew in reproductive success for males. Such changes could have helped maintain genetic variation within this population in the wake of environmental stress caused by the strong ENSO event in 2015. However, further investigation on the genetic make-up of this population across years would be required to test this. Overall, these data suggest that the implications of isolated ECEs may not be as devastating for resilient species with well-established populations, but may cause significant phenotypic and possibly genetic changes in less abundant or adaptable species (van de Pol et al. 2017).

Additionally, altered female mating decisions could have significant consequences on the evolution of sexual signals. Although the heritability of calling traits in this species is currently unknown, many traits important to females, like call rate and call complexity, appear to be highly flexible. In species with more heritable sexual signals (e.g. visual or chemical), changes in preferences for certain signals could have much longer lasting implications for subsequent generations. It is also difficult to overstate that female túngara frogs demonstrate highly robust preferences for certain call types. The patterns documented in this study may differ with other species that show more variable preferences. Additional studies in other

species with varying preference strengths for sexual signals would allow for a more robust understanding of the implications of extreme climatic events.

In this study, we document multiple phenotypic responses to a severe reduction in precipitation associated with a strong ENSO event, including reduced female preference for attractive mating calls, a phenomenon not previously demonstrated. Our findings refute the notion that mate choice behaviors can be assumed to be consistent across environmental gradients (Chaine and Lyon 2008; Bro-Jørgensen 2010; Candolin 2019). Additionally, we suggest that the influences of ECEs can be distinct for different life stages. In 2015, adults showed changes in morphology, whereas tadpoles developing the same year showed significant behavioral changes when they reached sexual maturity the subsequent year. Extreme weather events are becoming more common across the world, with record high global temperatures and greatly reduced precipitation again in Panamá in 2023. Therefore, it is imperative that behavioral mate choice studies on wild populations be maintained over longer time scales to better understand how climatic events alter the evolution of sexual signals and communication.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10682-024-10324-1>.

Acknowledgements We thank the Physical Monitoring Program from the Smithsonian Tropical Research Institute and the Meteorological and Hydrological Branch of the Autoridad de Canal de Panamá for providing climatic data, and would particularly like to thank Steve Paton for insightful discussion and feedback. We also thank Kyle Wilhite, Kelsey Mitchell, Laurie Adler, Whitney Handy, Hakeem Bushera, Tyler Bowling, and Kyle Davis for help with data collection.

Author contributions Conceptualization: K.L.H., R.C.T., A.D.C., M.A.M.; Methodology: K.L.H., R.C.T., A.D.C., M.A.M., M.J.R.; Investigation: A.D.C., M.A.M.; Visualization: A.D.C., M.A.M.; Funding acquisition; K.L.H., R.C.T., R.A.P., M.J.R.; Project administration: K.L.H., R.C.T. R.A.P.; Supervision: K.L.H., R.C.T.; Writing – original draft: A.D.C.; Writing – reviewing and editing: K.L.H., R.C.T., A.D.C., M.A.M., R.A.P., M.J.R.

Funding This study was supported by a National Science Foundation grant (no. 0517328) to R.C.T., K.L.H., R.A.P., and M.J.R. Travel funding for A.D.C., R.C.T., and K.L.H. was provided for by Salisbury University.

Data availability The data that support the findings of this study are openly available in Dryad at https://data.dryad.org/stash/share/Jzpo3ATPXQBLyADxh8D8044oUh9l_e-GfRFyBJEXByk.

Declarations

Ethics approval All experiments were approved by STRI Institutional Animal Care and Use Committee (protocol no. 2015-0209-2018). Permits were obtained from the Panamanian government including collecting permit numbers SE/A-30-16 and SE/AO-1-17.

Competing interests The authors declare no competing interests.

References

- Bates D, Mächler M, Bolker BM, Walker SC (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67. <https://doi.org/10.18637/jss.v067.i01>
- Bernal XE, Page RA, Rand AS, Ryan MJ (2007) Cues for eavesdroppers: do frog calls indicate prey density and quality? *Am Nat* 169:409–415. <https://doi.org/10.1086/510729>

- Brawn JD, Benson TJ, Stager M et al (2017) Impacts of changing rainfall regime on the demography of tropical birds. *Nat Clim Chang* 7:133–136. <https://doi.org/10.1038/nclimate3183>
- Bretfeld M, Ewers BE, Hall JS (2018) Plant water use responses along secondary forest succession during the 2015–2016 El Niño drought in Panama. *New Phytol* 219:885–899. <https://doi.org/10.1111/nph.15071>
- Bro-Jørgensen J (2010) Dynamics of multiple signalling systems: animal communication in a world in flux. *Trends Ecol Evol* 25:292–300. <https://doi.org/10.1016/J.TREE.2009.11.003>
- Brodeur JC, Candiotti JV, Soloneski S et al (2012) Evidence of reduced feeding and oxidative stress in common tree frogs (*Hypsiboas pulchellus*) from an agroecosystem experiencing severe drought. *J Herpetol* 46:72–78. <https://doi.org/10.1670/10-200>
- Bucher TL, Ryan MJ, Bartholomew GA (1982) Oxygen consumption during resting, calling, and nest building in the frog *Physalaemus pustulosus*. *Physiol Zool* 55:10–22. <https://doi.org/10.1086/physzool.55.1.30158439>
- Calabrese GM, Pfennig KS (2023) Climate change alters sexual signaling in a desert-adapted frog. *Am Nat* 201:91–105. <https://doi.org/10.1086/722174>
- Campbell-Staton SC, Cheviron ZA, Rochette N et al (2017) Winter storms drive rapid phenotypic, regulatory, and genomic shifts in the green anole lizard. *Science* 357:495–498. <https://doi.org/10.1126/science.aam5512>
- Candolin U (2019) Mate choice in a changing world. *Biol Rev* 94:1246–1260. <https://doi.org/10.1111/brv.12501>
- Chaine AS, Lyon BE (2008) Adaptive plasticity in female mate choice dampens sexual selection on male ornaments in the lark bunting. *Science* 319:459–462. <https://doi.org/10.1126/science.1149167>
- Charbonnier JF, Vonesh JR (2015) Consequences of life history switch point plasticity for juvenile morphology and locomotion in the túngara frog. *PeerJ* 3:e1268. <https://doi.org/10.7717/peerj.1268>
- Chen I-C, Hill JK, Ohlemüller R et al (2011) Rapid range shifts of species associated with high levels of climate warming. *Science* 333:1024–1026. <https://doi.org/10.1126/science.1206432>
- Coss DA, Hunter KL, Taylor RC (2021) Silence is sexy: soundscape complexity alters mate choice in túngara frogs. *Behav Ecol* 32:49–59. <https://doi.org/10.1093/beheco/araa091>
- Coulson T, Catchpole EA, Albon SD, Morgan BJT (2001) Age, sex, density, winter weather, and population crashes in soay sheep. *292:1528–1531*. <https://doi.org/10.1126/science.292.5521.1528>
- Cronin AD, Ryan MJ, Page RA, et al (2019) Environmental heterogeneity alters mate choice behavior for multimodal signals. *Behav Ecol Sociobiol* 73:43. <https://doi.org/10.1007/s00265-019-2654-3>
- Donihue CM, Herrel A, Fabre A-C et al (2018) Hurricane-induced selection on the morphology of an island lizard. *Nature* 560:88–91. <https://doi.org/10.1038/s41586-018-0352-3>
- Dyson ML, Henzi SP, Halliday TR, Barrett L (1998) Success breeds success in mating male reed frogs (*Hyperolius marmoratus*). *Proc R Soc B Biol Sci* 265:1417–1421. <https://doi.org/10.1098/rspb.1998.0451>
- Easterling DR, Meehl GA, Parmesan C et al (2000) Climate extremes: observations, modeling, and impacts. *Science* 289:2068–2074. <https://doi.org/10.1126/science.289.5487.2068>
- Gardner JL, Peters A, Kearney MR et al (2011) Declining body size: a third universal response to warming? *Trends Ecol Evol* 26:285–291. <https://doi.org/10.1016/j.tree.2011.03.005>
- Gomez-Mestre I, Kulkarni S, Buchholz DR (2013) Mechanisms and consequences of developmental acceleration in tadpoles responding to pond drying. *PLoS ONE* 8:1–12. <https://doi.org/10.1371/journal.pone.0084266>
- Gonda A, Trokovic N, Herczeg G et al (2010) Predation- and competition-mediated brain plasticity in *Rana temporaria* tadpoles. *J Evol Biol* 23:2300–2308. <https://doi.org/10.1111/j.1420-9101.2010.02066.x>
- Grant PR, Grant BR (2014) 40 years of evolution: Darwin's finches on Daphne Major Island. Princeton University Press
- Gridi-Papp M, Rand AS, Ryan MJ (2006) Complex call production in the túngara frog. *Nature* 441:38–38. <https://doi.org/10.1038/441038a>
- Jentsch A, Kreyling J, Beierkuhnlein C (2007) A new generation of climate-change experiments: events, not trends. *Front Ecol Environ* 5:365–374. <https://doi.org/10.1890/060097>
- Kogan F, Guo W (2017) Strong 2015–2016 El Niño and implication to global ecosystems from space data. *Int J Remote Sens* 38:161–178. <https://doi.org/10.1080/01431161.2016.1259679>
- Lenth RV (2022) emmeans: Estimated marginal means, aka least-squares means
- Neelin JD, Chou C, Su H (2003) Tropical drought regions in global warming and El Niño teleconnections. *Geophys Res Lett* 30. <https://doi.org/10.1029/2003GL018625>
- Parmesan C, Root TL, Willig MR et al (2000) Impacts of extreme weather and climate on terrestrial biota. *Bull Am Meteorol Soc* 81:443–450. [https://doi.org/10.1175/1520-0477\(2000\)081%3C:0443:IOEWAC%3E:2.3.CO;2](https://doi.org/10.1175/1520-0477(2000)081%3C:0443:IOEWAC%3E:2.3.CO;2)
- Paton S (2019) Monthly Summary_BCI, horizontal. *Smithson Trop Res Inst*. <https://doi.org/10.25573/data.10059455.v31>

- Phelps SM, Rand AS, Ryan MJ (2006) A cognitive framework for mate choice and species recognition. *Am Nat* 167:28–42. <https://doi.org/10.1086/498538>
- Rollins-Smith LA, Le Sage EH (2023) Heat stress and amphibian immunity in a time of climate change. *Philos Trans R Soc B Biol Sci* 378. <https://doi.org/10.1098/rstb.2022.0132>
- Ronald KL, Ensminger AL, Shawkey MD et al (2017) Testing a key assumption in animal communication: between-individual variation in female visual systems alters perception of male signals. *Biol Open*. <https://doi.org/10.1242/bio.028282>
- Rosenthal GG (2017) *Mate choice: the evolution of sexual decision making from microbes to humans*. Princeton University Press
- Ryan MJ (1980) Female mate choice in a neotropical frog. *Science* 209:523–525. <https://doi.org/10.1126/science.209.4455.523>
- Ryan MJ (1985) *The túngara frog: a study in sexual selection and communication*. University of Chicago Press
- Ryan MJ, Rand AS (2003) Sexual selection in female perceptual space: how female túngara frogs perceive and respond to complex population variation in acoustic mating signals. *Evolution* 57:2608–2618. <https://doi.org/10.1111/j.0014-3820.2003.tb01503.x>
- Ryan MJ, Bartholomew GA, Rand AS (1983) Energetics of reproduction in a neotropical frog, *Physalaemus pustulosus*. *Ecology* 64:1456–1462. <https://doi.org/10.2307/1937500>
- Ryan MJ, Akre KL, Baugh AT et al (2019) Nineteen years of consistently positive and strong female mate preferences despite individual variation. *Am Nat* 194:125–134. <https://doi.org/10.1086/704103>
- Seehausen O, Terai Y, Magalhaes IS et al (2008) Speciation through sensory drive in cichlid fish. *Nature* 455:620–626. <https://doi.org/10.1038/nature07285>
- Sheridan JA, Bickford D (2011) Shrinking body size as an ecological response to climate change. *Nat Clim Chang* 1:401–406. <https://doi.org/10.1038/nclimate1259>
- Smit JAH, Loning H, Ryan MJ, Halfwerk W (2019) Environmental constraints on size-dependent signaling affects mating and rival interactions. *Behav Ecol* 30:724–732. <https://doi.org/10.1093/beheco/arz009>
- Székely D, Cogălniceanu D, Székely P et al (2020) How to recover from a bad start: size at metamorphosis affects growth and survival in a tropical amphibian. *BMC Ecol* 20:1–8. <https://doi.org/10.1186/s12898-020-00291-w>
- Taylor RC, Klein BA, Stein J, Ryan MJ (2008) Faux frogs: multimodal signalling and the value of robotics in animal behaviour. *Anim Behav* 76:1089–1097. <https://doi.org/10.1016/j.anbehav.2008.01.031>
- Taylor RC, Wilhite KO, Ludovici RJ et al (2021) Complex sensory environments alter mate choice outcomes. *J Exp Biol* 224:1–9. <https://doi.org/10.1242/jeb.233288>
- Touchon JC, McCoy MW, Vonesh JR, Warkentin KM (2013) Effects of plastic hatching timing carry over through metamorphosis in red-eyed treefrogs. *Ecology* 94:850–860. <https://doi.org/10.1890/12-0194.1>
- Trokovic N, Gonda A, Herczeg G et al (2011) Brain plasticity over the metamorphic boundary: carry-over effect of larval environment on froglet brain development. *J Evol Biol* 24:1380–1385. <https://doi.org/10.1111/j.1420-9101.2011.02275.x>
- Ummenhofer CC, Meehl GA (2017) Extreme weather and climate events with ecological relevance: a review. *Philos Trans R Soc Lond B Biol Sci* 372:20160135. <https://doi.org/10.1098/rstb.2016.0135>
- Van De Pol M, Ens BJ, Heg D et al (2010) Do changes in the frequency, magnitude and timing of extreme climatic events threaten the population viability of coastal birds? *J Appl Ecol* 47:720–730. <https://doi.org/10.1111/j.1365-2664.2010.01842.x>
- van de Pol M, Jenouvrier S, Cornelissen JHC, Visser ME (2017) Behavioural, ecological and evolutionary responses to extreme climatic events: challenges and directions. *Philos Trans R Soc B Biol Sci* 372:20160134. <https://doi.org/10.1098/rstb.2016.0134>
- Walls SC, Barichivich WJ, Brown ME (2013) Drought, deluge and declines: the impact of precipitation extremes on amphibians in a changing climate. *Biology* 2:399–418. <https://doi.org/10.3390/biology2010399>
- Wilczynski W, Ryan MJ (2010) The behavioral neuroscience of anuran social signal processing. *Curr Opin Neurobiol* 20:754–763. <https://doi.org/10.1016/j.conb.2010.08.021>
- Wilczynski W, Stanley Rand A, Ryan MJ (1995) The processing of spectral cues by the call analysis system of the túngara frog, *Physalaemus pustulosus*. *Anim Behav* 49:911–929. <https://doi.org/10.1006/anbe.1995.0123>

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.