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Combating Extreme Tropical Seasonality: Use of Rock Crevices by the Critically Endangered Frog *Nannophrys marmorata* in Sri Lanka

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***Abstract.*—Kirtisinghe's Rock Frog (*Nannophrys marmorata*) is endemic to Sri Lanka and is found only on the northeastern slopes of the Knuckles Mountain Range, where a short wet season is followed by a prolonged dry season. The dry season is characterized by high air temperature, low relative humidity, and strong desiccating winds. These frogs take refuge in rock crevices during the daytime and emerge at night to forage. We monitored the body temperature of frogs while inside and outside crevices, and several environmental variables, during 4-d periods in the peak dry (August) and peak wet (December) seasons. In the peak dry season during daytime, ambient air temperature rose to 39.2° C (average) and relative humidity dropped to 27% (average). Under these conditions, the peak temperature of the rock crevices averaged 29.9° C, and the crevices served as a refuge for the frogs, whose body temperature did not exceed 27.4° C. Frogs used significantly smaller crevices (entrance height) in the dry season (10.2 mm + 1.1 SE) compared to those used in the wet season (17.9 + 1.6 mm). Frog activity outside of crevices at night was dramatically less during the dry season (98 frog-hours) than during the wet season (1,615 frog-hours). Our study shows that *N. marmorata* minimizes exposure to adverse environmental conditions in the dry season by taking refuge in rock crevices. The behavior by frogs of selecting smaller crevices and reducing activity outside of crevices during the dry season may also serve to minimize exposure to adverse conditions.**

Key Words.—amphibian; body temperature; microhabitat; Kirtisinghe's Rock Frog

Introduction

The genus *Nannophrys* (Dicroglossidae) is endemic to Sri Lanka and comprises three species: *N. marmorata* (Kirtisinghe's Rock Frog or Marbled Rock Frog), *N. ceylonensis* (Sri Lanka Rock Frog), and *N. naeyakai* (Sri Lanka Tribal Rock Frog). *Nannophrys marmorata* is categorized as a Critically Endangered species, primarily due to its restricted distribution (International Union for Conservation of Nature [IUCN] 2018). This species is found on the northeastern slopes of the Knuckles Mountain Range at elevations of 200–1,220 m, whereas *N. ceylonensis* and *N. naeyakai* live elsewhere in the country at lower elevations (Manamendra-Arachchi and Pethiyagoda 2006). The part of the Knuckles Mountain Range that includes the habitat of *N. marmorata* has been declared the Knuckles Conservation Forest (Government of Sri Lanka 2000). The Knuckles Conservation Forest and two other properties are collectively called The Central Highlands of Sri Lanka, which was added to the World Heritage list as a biodiversity hotspot in 2010 (United Nations Educational, Scientific and Cultural Organization [UNESCO] World Heritage Centre. 2018. Central Highlands of Sri Lanka. UNESCO World Heritage Centre. Available from https://whc.unesco.org/en/list/1203/. [Accessed 24 May 2018]).

Although the tropical rainforest environment is commonly perceived as relatively stable and constant over the year (Wikelski et. al. 2000), some parts of the tropics experience sharp seasonal differences (e.g., Wright and Cornejo 1990). This is seen on the northeastern slopes of the Knuckles Mountain Range, where the climate is characterized by a relatively short wet period (during the northeast monsoon) and a prolonged dry period during the southwest monsoon (which brings no rain to this part of the mountain range) and the inter-monsoonal periods (Giragama and Wickramaratne 2005). During the dry season, the atmospheric temperature rises and strong desiccating winds sweep across the area (de Rosayro 1958; Giragama and Wickramaratne 2005). Prior to the present study, observations showed that the ambient air temperature in the peak dry season approached 40° C, about 15° C hotter than that observed in the peak wet season (unpubl. data).

In ectotherms such as amphibians, the interplay of environmental temperature and relative humidity is critical in determining body temperature and water balance and hence ability of the animals to survive

Figure 1. Kirtisinghe's Rock Frog (*Nannophrys marmorata*) in the shelter of a rock crevice at Pitawala Pathana in the Knuckles Mountain Range, Sri Lanka, August 2016. (Photographed by Uvini I. Senanayake).

(Buttemer and Thomas 2003; Navas et al. 2008; Köhler et al. 2011; Titon and Gomes 2015). The terrain in the parts of the Knuckles Mountain Range where *N. marmorata* is present is rocky, and the frog has a dorso-ventrally flat body that makes it well suited to live within rock crevices (Fig. 1). Considering the extreme seasonality of the habitat and the rock crevice dwelling habit of these frogs, our study examined how this species overcomes the hot and dry conditions encountered during the prolonged dry season. We compared observations during the peak dry season (August) and the peak wet season (December) for a number of variables: ambient air temperature (hereafter referred to as air temperature) and relative humidity, temperature within the rock crevices, body temperature of the frogs when within and outside the crevices, height of entrance to the crevices occupied by the frogs, and the number of frogs that emerged onto the rock surfaces throughout the day and night. Because rock crevices may also provide shelter for other species, leading to possible predation/competition, we also recorded observations on other species.

Materials and Methods

Study site.—Our study site was located on the northeastern flank of the Knuckles Mountain Range within the Knuckles Conservation Forest, Sri Lanka, in a place known as Pitawala Pathana (7°32'58.81"N, 80°45'17.97"E; elevation 800 m; Fig. 2), which is mainly a grassland (about 26 ha in area) with scattered clumps of bushes and trees (Fig. 3). *Nannophrys marmorata* has been recorded at Pitawala Pathana (Manamendra-Arachchi and Pethiyagoda 2006). Within the grassland, the terrain in some areas is rocky, with a patchy grass cover. In our reconnaissance survey prior to the study, we observed the presence of *N. marmorata* mainly in these rocky areas. Hence, we selected a rocky area covering around 5 ha as our study site (Fig. 3). Owing to its approximately northwest to southeast orientation, the Knuckles Mountain Range directly intercepts the wind currents of both the southwest and northeast monsoons (de Rosayro 1958). This characteristic, together with the elevational gradient, results in the mountain range experiencing climatic regimes varying from wet on the southwestern and western slopes, to seasonally dry on the eastern and northeastern slopes (de Rosayro 1958). The northeastern slopes receive heavy rainfall from November to February, and this is followed by a long season of dry weather (Giragama and Wickramaratne 2005). During the wet season, a stream crosses the study site, keeping the rock surfaces moist, but the stream reduces to a trickle during the dry season. We conducted the study in 2016 during August and

Figure 2. The location of Pitawala Pathana (red-outlined polygon) in Sri Lanka. (Image from Google Earth, Google, Mountain View, California, USA; 2018).

Figure 3. The study site during the peak wet season (December, left) and the peak dry season (August, right). (Photographed by Uvini I. Senanayake).

December, which, based on available data, represents the peak dry and peak wet months, respectively, in the study region (Giragama and Wickramaratne 2005).

Frog body temperature.—In each season around mid-day, we marked 10 crevices with colored tags that were occupied by the frog *N. marmorata* and which were separated from each other by a distance of about 5 m or more. We selected the crevices in a haphazard manner to minimize bias. We measured the body temperature of frogs within the 10 marked crevices during a 4-d period in each season (19–22 August and 18–21 December). On each of the four days, we measured the body temperature of frogs in two or three of the marked crevices, starting 1000 to 1100, and we recorded data at 2-h intervals.

We measured the surface body temperature of the frog using a GM700 1.5" LCD Non-Contact Infrared Thermometer (Elecall, Zhejiang, China). We carefully pointed the infrared beam on three different points of the body (head, abdomen, and thigh) and used the mean of the three readings to indicate the body temperature. Prior to the 4-d sampling period in each season, we measured the snout-vent length of a number of *N. marmorata* frogs picked haphazardly. Snout-vent lengths ranged from 27.7 to 52.6 mm (n = 23; mean 35.0 ± 1.5 [SE] mm) in the dry season and from 28.2 to 45.0 mm (n = 20; 32.6 ± 1.0 mm) in the wet season. This information was used to determine the maximum distance from the frog at which body temperature measurements should be taken to minimize any possible impact of the substrate temperature on the measurements recorded. Accordingly, we measured body temperature from a distance of < 20 cm from the frog because the distance-to-spot size ratio of the instrument was indicated as 12:1 (specifications for GM700 1.5" LCD Non-Contact Infrared Thermometer). We calibrated the instrument daily using the ice bath method (ThermoWorks. 2016. Calibrating your infrared thermometer with a properly made ice bath. ThermoWorks. Available from https://www.thermoworks.com/infrared_tips_icebath_to_calibrate_infrared [Accessed 10 February 2016]). The accuracy of the instrument is ± 1.5° C (specifications for GM700 1.5" LCD Non-Contact Infrared Thermometer).

In all instances except one in each season, only a single frog occupied the selected crevice. For these crevices when the frog left the crevice, we continued measuring its body temperature while outside the crevice, and we continued to record its body temperature after it returned to the crevice. In all these instances, a frog that left the crevice re-entered the same crevice, and no frogs entered these marked crevices other than the ones being monitored. In two instances, one each in the wet and dry seasons, there were three frogs in the marked crevices. In these two instances, when the frog whose body temperature was being measured left the crevice before the others, we continued to take recordings on another frog within the same marked crevice. When all frogs left the crevice, we monitored the body temperature of the last frog to leave the crevice until such time as any frog re-entered the particular marked crevice, at which time we continued to monitor the temperature of this frog. In this manner we obtained 10 sets of body temperature measurements over a 24-h period for frogs in the 10 marked crevices in each season.

Air temperature, relative humidity, and crevice temperature.—We monitored these parameters over 24-h periods during the 4-d periods described above at each of the marked crevices that would be used or had already been used for measuring frog body temperatures. We used sensors to record data at 5-min intervals over a single 24-h period at each of the 10 rock crevices. To record air and crevice temperatures and relative humidity, we constructed data logging devices using commercially available sensors. We made the platform of the data logging device using the Arduino pro mini microcontroller (Atmega 328p, Atmel Corporation, San Jose, California, USA), and connected and programed three sensors: two digital thermometers (DS18B20, Maxim Integrated, San Jose, California, USA) and a digital humidity sensor

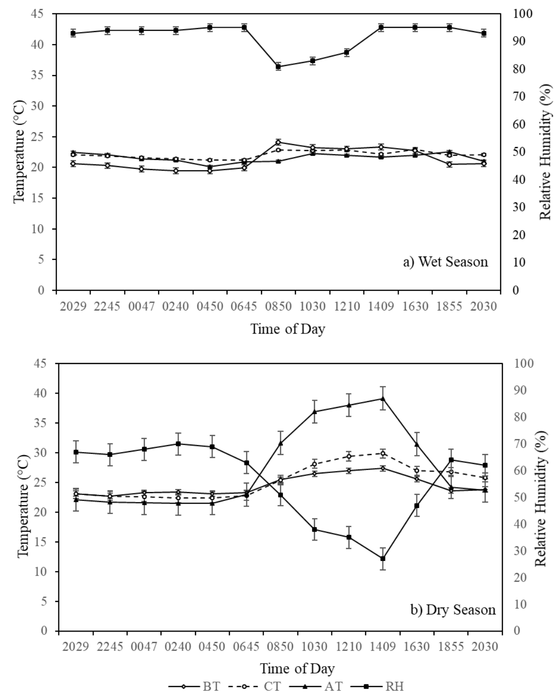

Figure 4. Air temperature (AT), crevice temperature (CT), relative humidity (RH), and body temperature of Kirtisinghe's Rock Frogs (*Nannophrys marmorata*; BT) as a function of time of day during a 4-d period in the (a) peak wet and (b) peak dry season. Data are shown for 2-h intervals; labels on X axis indicate mean time of sampling for each interval. Values are means (+ one standard error, vertical bars); n = 10 for each parameter per season. Standard error bars are not visible for some parameters due to the low values. Body temperature values include frogs both within and outside of crevices at night (see text). Sunrise times were about 0601 (dry season) and 0614 (wet season); sunset times were about 1821 (dry season) and 1755 (wet season).

(AOSONG-DHT11, Aosong Electronics Co. Ltd., Baiyung District, Guangzhou, China), alongside a Real Time Clock module (Maxim Integrated-DS3231, Maxim Integrated). A Secure Digital (SD) card reader (FUT3001, Fut-electronic Technical Co., Ltd., Shenzhen, Guandong, China), and five indicator Light Emitting Diodes (LED; 5 mm Red through hole LED, Shenzhen HanhuaOpto Co., Ltd., Guanlan, Shenzhen, China) were connected to the Arduino platform. We calibrated the temperature sensors using ice and steam point measurements (Under Water Arduino Data Loggers. 2015. Calibrating DS18B20 1-Wire Sensors with Ice and Steam point measurement. Available from https://thecavepearlproject.org/2015/03/30/using-ds18b20-one-wire-sensors-to-make-a-diy-thermistor-string-pt-2-calibration/ [Accessed 4 February 2016]). We calibrated the relative humidity sensors using the standard saturated salt method (Lu and Chen 2007). We measured air temperature and relative humidity outside the crevice at a height of about 15 cm in the shade of the sparse grass cover in a location < 1 m away from the rock crevice being monitored. We measured crevice temperature approximately 10 cm inside the rock crevice.

Rock crevice height and the occupancy of crevices.—We measured the entrance height of the 10 crevices marked in each season. In addition, in each season around mid-day (1000–1400) we haphazardly picked an additional 25 crevices (at a minimum spacing of 5 m) that *N. marmorata* occupied and took the entrance height measurements. We measured height at a point 2 cm inside the crevice entrance using a wooden tooth pick that we cut and trimmed to fit inside the rock crevice and later measured using a Vernier caliper. We used one-way ANOVA to compare the height of the rock crevices used in the two seasons. While searching for occupied crevices, we observed in the dry season that some crevices were occupied by a crab (*Ceylonthelphusa* sp.) or the Skipper Frog (*Euphylictis cyanophlyctis*). Consequently, on one day in each of the two seasons at around mid-day, we searched 35 crevices picked haphazardly that were approximately 5 m or more apart and recorded the number of crevices from among these that were occupied by either of the two frog species or the crab. We used the Chi square test to discern seasonal differences in the use of rock crevices by the three species.

Emergence from rock crevices and foraging activity.—*Nannophrys marmorata* individuals emerge from the crevices at different times during the night for foraging. In both seasons on each of the four days when we took the other measurements, we searched within the study site (5 ha) at 2-h intervals over a 24-h period and counted the number of *N. marmorata* that had emerged onto rock surfaces. We calculated the number of frog-hours outside the crevices during a 24-h period in each season by multiplying the mean number of frogs that were out at each 2-h count by 2 and summed the values. We derived times for sunrise and sunset (http://suncalc.net/#/7.5543,80.761,13/2016.12.19/11:29).

Results

Air, crevice, and body temperatures, and relative humidity.—The diurnal fluctuations in all these parameters were greater in the dry season compared to the wet season (Fig. 4). Notably, during the peak dry season, the mean air temperature fluctuated from 21.5° to 39.2° C and the mean relative humidity fluctuated from 27 to 70%, whereas in the peak wet season the fluctuations were from 19.3° to 23.4° C and from 81 to 95%, respectively. In the dry season when the air temperature peaked at 39.2° C, the crevice temperature peaked at 29.9° C, and the highest body temperature

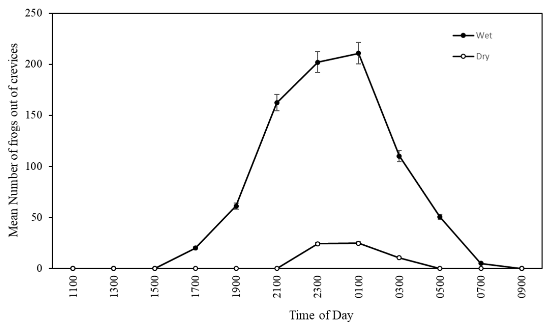

Figure 5. Mean number of Kirtisinghe's Rock Frogs (*Nannophrys marmorata*) foraging on rock surfaces as a function of time of day over a 4-d period during the peak wet (black dots) and peak dry (white dots) seasons in Pitawala Pathana, Sri Lanka. Values are means (+ one standard error, vertical bars) in each season (n = 4 days per season). Standard error bars are not visible for the dry season due to low values. Sunrise and sunset times are provided in Fig. 4.

recorded of the frogs within the crevices was 27.4° C. The difference between the maximum values of air temperature and crevice temperature was much more pronounced in the peak dry season (9.3° C) compared to the difference in the wet season (0.6° C). During the night air temperature was similar between the two seasons (about 22° C), whereas relative humidity was much lower during the dry season (about 60–70%) than during the wet season (about 95%; Fig. 4).

Occupancy of crevices.—*Nannophrys marmorata* occupied significantly smaller crevices during the dry season (mean internal height 10.2 ± 1.1 mm, n = 35) than during the wet season (17.9 ± 1.6 mm, n = 35; $F_{1,18}$ = 16.10, $P < 0.010$). *Nannophrys marmorata*, Skipper Frog, and the crab each showed considerable differences in the frequency of crevice use between the seasons, but these differences were not significant for any of the species (X^2 = 1.04, 2.28, and 2.25, respectively; all df = 1, all $P > 0.05$). In the sample of 35 rock crevices observed in each season, *N. marmorata* used 46% of the crevices in the wet season versus 26% in the dry season. The Skipper Frog used fewer than 5% of the crevices in the wet season and 17% in the dry season. The crabs did not use any crevices in the wet season, whereas they used 11% of them in the dry season.

Emergence from rock crevices and foraging activity.—The activity of *N. marmorata* frogs outside of rock crevices was dramatically less during the dry season (98 frog-hours) than during the wet season (1,615 frog-hours; data derived from Fig. 5). During the peak dry month, the maximum number of frogs foraging on the exposed rock surfaces at night at one time was 24, whereas it was 212 in the peak wet month (see Fig. 5). Moreover, the period of time when any frog was outside of crevices was much shorter during the dry month (6 h, from about 2200–0400) than during the wet month (16 h, from about 1600–0800; Fig. 5). In both seasons the number of frogs outside of crevices peaked in the middle of the night (i.e., 2300–0100).

Discussion

In conditions of extreme tropical seasonality, as occurring on the northeastern slopes of the Knuckles Mountain Range, the resident organisms must have mechanisms to deal with these conditions. Amphibians, being ectothermic and having a wet permeable skin, have limited resistance to evaporative water loss and extreme changes in humidity, temperature, and wind velocity (Keen 1984; Costa et al. 2013). Our study shows that large fluctuations occur in the dry season for two critical environmental variables, ambient air temperature and relative humidity, both of which can strongly influence body temperature of frogs (Buttemer and Thomas 2003; Navas et al. 2008; Köhler et al. 2011). During the peak dry season, air temperature reached 39° C and relative humidity dropped to 27%. At the same time, crevice temperature remained well below air temperature, and the frogs within the rock crevices maintained their body temperature nearly 12° C below air temperature. We conclude that the frogs are able to withstand the extremely hot and dry environmental conditions during the dry season by taking refuge in the rock crevices where conditions allow them to keep their body temperature at a moderate level and well below the air temperature. Behavioral changes in the selection of microhabitat use have been previously recorded in amphibians both in response to changes in environmental temperature (Meek and Jolley 2006) and relative humidity (Pough et al. 1983), thus controlling excessive rises in body temperature and desiccation, respectively.

We also observed that the frogs, which primarily forage at night, nevertheless remained for a long time within the crevices in the dry season in comparison to the wet season. The reduced time spent outside the crevices at night in the dry season would result in limited foraging activity. Both the lack of rainfall and low relative humidity have been shown to have a strong negative impact on the breeding and activity of frogs (Hall and Root 1930; Gascon 1991; Köhler et al. 2011; da Silva et al. 2012). Thus, we suggest that *N. marmorata* spends limited time foraging outside the crevices in the dry season because the environmental conditions are particularly severe during this season.

We also recorded *N. marmorata* occupying smaller crevices in the dry season than those used in the wet season. Previous studies have shown that, under extreme conditions in the tropics, burrows and other shelters provide protection against water loss in amphibians

(Schwarzkopf and Alford 1996; Andrade and Abe 1997; Seebacher and Alford 2002). It has also been shown that the type of refuge a frog selects could be related to physiological constraints relating to regulation of body temperature and desiccation (Tracy et al. 2008). The smaller crevices used by *N. marmorata* in the dry season, as observed in our study, would be less exposed to air circulation than the larger crevices used in the wet season, and hence would be less influenced by external environmental conditions. Therefore, it is possible that the selection of smaller crevices may be linked to reducing desiccation and maintaining body temperature at a moderate level in the dry season.

Previous studies have also shown that, in addition to physiological constraints, the selection of refuges by amphibians may be influenced by the presence of competitors and predators (e.g., Kronfeld-Schor and Dayan 2003; Affonso and Signorelli 2011; Pyke et al. 2013). Our study suggests that *N. marmorata* may be similarly affected. During our study we observed that in the dry season the typically aquatic freshwater crab and Skipper Frog also take refuge in rock crevices. This observation presents another plausible explanation for the use of smaller crevices by *N. marmorata* in the dry season compared to those it uses in the wet season. In the dry season, when other species also take refuge in the rock crevices to avoid extreme conditions, the relatively flat-bodied *N. marmorata* may be better adapted to occupy smaller crevices with reduced entrance height than the other two species, and thus preferentially uses the smaller crevices to reduce threats of predation or competition.

In the present study we demonstrate that *N. marmorata*, by taking refuge in rock crevices over an extended period daily in the dry season compared to the wet season, is sheltered from extreme temperatures and desiccating winds prevailing in the dry season. The preferential use we found of smaller rock crevices during the dry season compared to those used in the wet season possibly gives the frog added protection against the prevailing adverse environmental conditions while also enabling them to avoid competition from other predator/competitor species that use the rock crevices during this time. We conclude that the present study reveals that the use of rock crevices allows the Critically Endangered *N. marmorata* to overcome adverse environmental conditions related to the extreme seasonality of its natural habitat. This ability, however, may be affected by global climate change. The predicted changes in climate include a significant increase in mean annual temperatures, reduction in annual rainfall, and the extension of drought periods in Sri Lanka (de Costa 2008). Such effects may have a profound impact on tropical, restricted-range species such as *N. marmorata* that now inhabit extreme seasonal environments.

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Sahan Siriwardana is a Biologist with a B.Sc. (Honors) degree in Zoology from the University of Colombo, Sri Lanka. He has conducted a research project on developing an acoustic repellent for fruit bats in Sri Lanka, in collaboration with Department of Physics, University of Colombo. He assisted in conducting the field work in the investigation on the frog *Nannophrys marmorata*, particularly in the building, setting up, and use of the data recording instruments. He is currently working as a Research Assistant at the Department of Zoology and Environment Sciences, University of Colombo. (Photographed by Uvini I. Senanayake).

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Mayuri R. Wijesinghe is a Professor of Zoology in the University of Colombo, Sri Lanka. She obtained a Ph.D. from the University of Cambridge, UK, investigating the effects of habitat loss on, and vulnerability of, endemic species in Sri Lanka's rainforest, a biodiversity hotspot. Besides her research work in conservation biology, she has also investigated the effects of agrochemicals on fish and amphibians. Her research interest in conserving endangered species led her to the investigation on *Nannophrys marmorata*. In collaboration with Professor Weerakoon, she directed and supervised the work and wrote the paper for publication. (Photographed by Tehan Perera).