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ORIGINAL RESEARCH

Changes in marine iguana (*Amblyrhynchus cristatus*) heart rates suggest reduced metabolism during El Niño events

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Abstract

Marine iguanas occasionally face severe food shortages because of algal dieback during El Niño events. Research on their adaptations to these periods has highlighted their unique ability to shrink in body length, which reduces their energetic needs. Additional mechanisms, like sustaining lower body temperatures and metabolic rates, could potentially also lower energy consumption, but have never been examined. We measured 665 iguanas over an 11-year period including three El Niño events, and examined how heart rates (a proxy for metabolic rates) and body temperatures change with sea-surface temperature oscillations (Oceanic Niño Index, ONI). Heart rate (adjusting for body size, temperature, season, and study site) was negatively correlated with ONI and lower during El Niño, whereas the adjusted body temperature did not correlate with ONI or differ between El Niño and other periods. We therefore hypothesize that marine iguanas can depress their metabolic rates in response to the harsh conditions, an adaptation that is complementary to shrinking and may further enhance their survival through periods of limited food. Direct metabolic measurements are needed to test this hypothesis.

Introduction

The Galápagos marine iguana (*Amblyrhynchus cristatus*) is the world's only marine lizard (Vitousek et al., 2007). Adults feed almost solely on algae (*Centroceras*, *Gelidium*, *Spermothamnium*, and *Ulva* species), foraging underwater and on rocky shores during low tide (Vitousek et al., 2007). Food availability in the range of *A. cristatus* endemic to the Galápagos Islands, can dramatically change from year to year due to the El Niño Southern Oscillation, which is highly unpredictable but frequent (occurring, on average, every 3.8 years; NOAA, 2024). Following El Niño events, the combination of warming sea-surface temperatures and reduced upwelling of nutrient-rich water induce massive dieback of the preferred algae species (Laurie, 1989; Rubenstein & Wikelski, 2003) and overgrowth of a brown alga, *Giffordia mitchelliae*, which the iguanas cannot digest. Extreme El Niño events can result in up to 60% iguana mortality across the archipelago (Laurie, 1990), and as high as 90% on the hardest-hit islands (Romero & Wikelski, 2001; Wikelski & Wrege, 2000).

The selective pressure imposed by these irregular events gave rise to unique adaptations for coping with sudden and prolonged food shortages. Surviving individuals were observed to shrink in body length by up to 20% (6.8 cm) following El Niño events (Wikelski & Thom, 2000), a feat accomplished by resorption of body tissues (Vitousek et al., 2007). This reduces their energetic expenditure relative to their foraging capacity (Wikelski & Romero, 2003; Wikelski & Thom, 2000), until subsequent years when algae rebound and iguanas grow back to their former size. Studies on *A. cristatus* adaptations to El Niño suggest that energetic saving is achieved by shrinking, which should reduce overall metabolic needs if a constant size-dependent metabolic rate is assumed (Wikelski & Romero, 2003). To our knowledge, no study to date has tested

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for a direct reduction in the metabolic rates, or for mechanisms that can facilitate such reduction in addition to size changes.

One pathway to reduce metabolic rates, keeping dietary requirements below the threshold for survival, could be for iguanas to temporarily thermoregulate at lower selected temperatures. Ectotherm metabolic rate is directly dependent on temperature (Andrews & Pough, 1985). In *A. cristatus* metabolic rate increases almost threefold for every 10°C increase in body temperatures (Bennett et al., 1975). *Amblyrhynchus cristatus* behaviourally thermoregulate to their preferred temperature for activity (35°C) by basking (Bennett et al., 1975), and deviating from this temperature slows down functions such as running and digestion (Wikelski & Romero, 2003). However, since *A. cristatus* digestive efficiency is not affected by temperature (Wikelski et al., 1993), and impaired locomotion might be manageable due to the lack of natural predators, iguanas could benefit from selecting lower body temperatures until algal abundance rebounds. Another possible pathway to reduce metabolic rates for the duration of El Niño could be a metabolic depression, that is, 'a reduction in metabolic rate to below the normal resting value' (Guppy & Withers, 1999), by physiological and biochemical mechanisms. Metabolic regulation is temperature-dependent in ectotherms, (Seebacher, 2005), but metabolic depression beyond the effect of temperature is very common in reptiles (including other iguanians) as a seasonal phenomenon in regions where cool winters limit or prevent foraging (Dubiner et al., 2023). We investigated whether marine iguanas might be using similar mechanisms to reversibly lower their energetic needs during El-Nino events, until conditions become favorable again.

Materials and methods

We measured body temperature (T_b), snout-vent length (SVL), and heart rate of 665 iguanas from 14 sites on seven islands across the archipelago. Data were collected during 16 different trips between the years 2014 and 2024. During this period three El Niño events occurred (2015/16, 2018/19, and 2023/24). We caught the iguanas by hand on the beach (individuals of both sexes and all ages), measured their SVL (using a measuring tape), and sexed the adults (only when clearly identifiable by morphological characteristics; 98 females and 251 males, see Table 1). We measured their cloacal T_b using an EW-91219-40 thermocouple thermometer (Cole-Parmer, USA; accuracy ±0.3°C) up to a minute post-capture to avoid heating from handling (Cabanac & Gosselin, 1993; Taylor et al., 2021). Thermoregulatory accuracy was defined, according to Hertz et al. (1993), as the mean absolute deviation of field T_b from the optimal T_b of the species (Bartholomew & Lasiewski, 1965; Bennett et al., 1975). We measured heart rates using a Doppler ultrasound probe (Parks Medical Electronics Inc., Aloha, OR, USA) placed over the heart, 3 min post-capture. While heart rate can be influenced by other factors, it can nonetheless serve as a reliable proxy for estimating metabolic rates (Butler et al., 2002; Piercy et al., 2015; Tattersall et al., 2016; and see review in Green, 2011). We obtained Oceanic Niño Index (ONI) data from NOAA (2024); ONI is the 3-month mean sea surface temperature anomaly in the surface waters of the east-central tropical Pacific, prior to each trip (measured in °C, El-Niño being a period in which temperatures are warmer than ONI = 0.5).

Statistical analyses were conducted in R (version 4.4.1) and figures were created using the "ggplot2" package. We tested for a relationship between T_b and ONI using linear mixed models (LMMs, using the "lme4" package) with ONI, SVL, season (warm vs. cold, the cold season being June through November; Paltán et al., 2021), and study site as predictors. We tested for a relationship between heart rate and ONI using an LMM with ONI, SVL, T_b, season, and site as fixed factors, and individual identity as a random factor (confirmed using PIT tags, see Table S1; individuals with no PIT tag were given a unique identifier under the assumption of no recapture). In separate models we treated ONI as a dichotomous, rather than as a continuous predictor, asking whether it indicated an El Niño event (ONI > 0.5) or not (ONI < 0.5). When we added sex as an additional fixed factor in these models, it was non-significant in all models and was therefore excluded. R^2 values for the mixed models were approximated by maximum-likelihood (R^2_{lik}) using the "rr2" package in R (Ives & Li, 2018).

This study was conducted as part of a long-term research program on Galápagos marine iguanas and the veterinary hands-on Galápagos program (IslaVet), permitted by the Galápagos National Park (permits PC-75-14, PC-67-15, PC-107-16, PC-65-17, PC-59-18, PC-57-19, PC-32-21, PC-4-22, and PC-16-23) and approved by Universidad San Francisco de Quito and North Carolina State University. The study protocol was reviewed and approved by the NC State IACUC (Institutional Animal Care and Use Committee) under permit 8-009-O, ensuring compliance with ethics and animal handling protocols following standard procedures for vertebrate research and veterinary practices.

Table 1 Summary table for female and male SVL, T_b, and heart rate, in all sexed individuals (n = 98 females and 251 males)

	Non-Niño (ONI < 0.5)						El Niño (ONI > 0.5)					
	SVL (cm)		T_b (°C)		Heart rate (bpm)		SVL (cm)		T_b (°C)		Heart rate (bpm)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Female	33.38	4.66	32.15	3.95	83.67	20.08	34.78	3.37	31.49	3.01	60.00	4.24
Male	40.06	7.10	31.70	4.14	78.59	20.63	39.18	6.94	33.61	3.49	69.90	14.73

Note that these are raw values, not the adjusted values that were used for the analyses. Sex was not a significant predictor in any model and was therefore not included.

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Results

Mean SVL across the 665 individuals measured was 34.6 ± 0.3 cm (SE; range: 10.6–71.0 cm). Mean heart rate was 82.5 ± 0.9 (n = 620) beats per minute (bpm), and in the LMM it was negatively correlated with ONI (−3.96 ± 0.89 bpm/°C; R^2 = 0.66; P < 0.001; Fig. 1a) after accounting for its positive correlation with T_b (4.02 ± 0.14 bpm/°C; P < 0.001; Fig. 2a) and negative correlation with SVL (−0.06 ± 0.01 bpm/cm; P < 0.001; Fig. 2b). Heart rate in this model was not correlated with season (P = 0.630). Mean heart rate (adjusted for T_b, SVL, season, and site) in the dichotomous (i.e., El Niño vs. non-Niño)

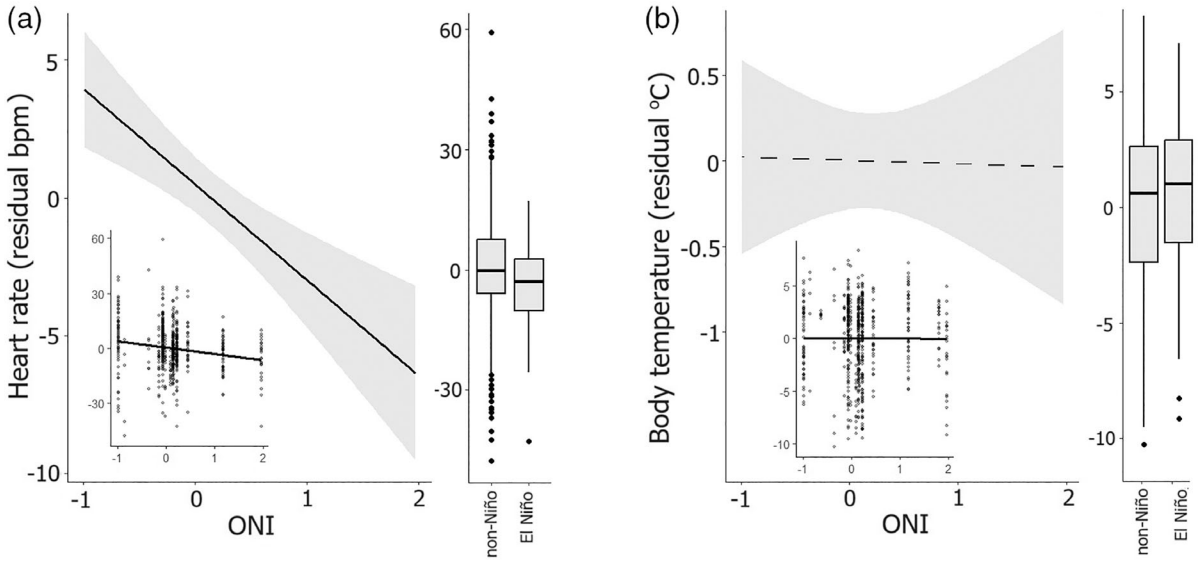

Figure 1 Model prediction for residual heart rate (a—accounting for body temperature, snout-vent length, season, and site) and body temperature (b—accounting for snout-vent length, season, and site) of marine iguanas, against ONI (Oceanic Niño Index). As sea surface temperature anomaly increases, heart rate (and therefore metabolic rate) decreases (LMM: n = 620, P < 0.001) but body temperature does not (LMM: n = 665, P = 0.948). Insets show the model prediction together with the full data (axes are the same). Boxplots (indicating median, quartiles, and outliers) show the same data in a dichotomous comparison between El Niño (ONI > 0.5) and non-Niño periods, showing lower heart rate during El Niño (LMM: n = 620, R^2 = 0.66, P < 0.001) whereas body temperature is unchanged (LMM: n = 665, R^2 = 0.21, P = 0.071).

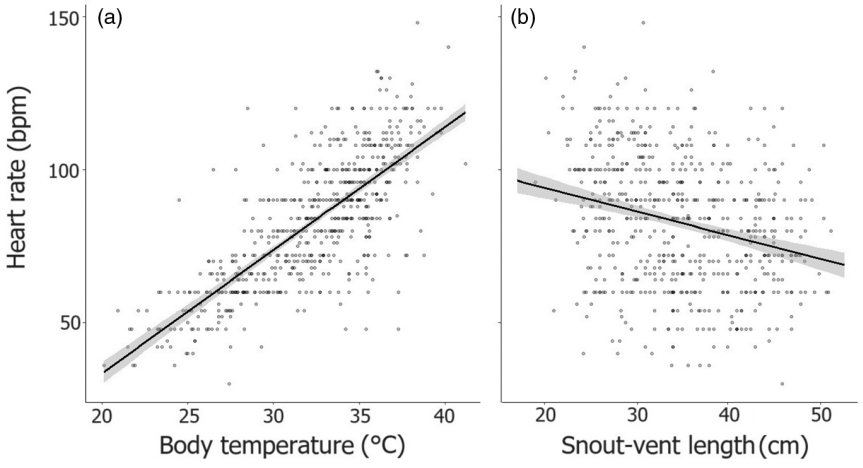

Figure 2 Heart rate plotted against body temperature (a—positive correlation of 4.06 bpm per °C; P < 0.001) and snout-vent length (b—negative correlation of −0.58 bpm per cm; P < 0.001) of marine iguanas. A few SVL outliers are not shown (10 out of n = 620) but were included in the analysis.

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LMM was 6.30 ± 1.73 bpm lower during El Niño (ONI > 0.5) compared to other periods (R^2 = 0.66; P < 0.001; Fig. 1a), but uncorrelated with season (P = 0.650).

Mean T_b was 33.8 ± 0.7°C (SE; n = 665) and was positively correlated with season (1.9 ± 0.5°C higher in the warm season; R^2 = 0.20; P > 0.001), but uncorrelated with SVL (P = 0.333) and ONI (P = 0.948; Fig. 1b). In the dichotomous LMM comparing El Niño to all other periods, T_b (adjusted for SVL, season, and site) was higher by 1.6 ± 0.5°C during the warm season, (R^2 = 0.21; P = 0.002; Fig. 1b) but uncorrelated with El Niño conditions (P = 0.071). Mean thermoregulatory accuracy (i.e., departure from the optimal T_b of 35°C; Bennett et al., 1975) was 3.6 ± 0.1°C and was independent of SVL (P = 0.781), and ONI (P = 0.848; R^2 = 0.20), but lower by 0.96 ± 0.40°C during the warm season (P = 0.018; R^2 = 0.21). The full raw data are available in Table S1.

Discussion

The heart rate of marine iguanas, when adjusted for other influencing factors, was correlated with the variation in mean sea temperature across the last decade (here represented by the Oceanic Niño Index). Lowering heart rate (a proxy for metabolic rate; Green, 2011), during the periods of reduced food availability, hints at metabolic depression (Guppy & Withers, 1999). This strategy, enabling reduction of energetic expenditure at times of low energetic intake in reptiles (Milsom et al., 2008; Sinclair et al., 2013), is known to be most efficient in warm environments (Christian et al., 1999; Giacometti et al., 2022) and for large reptiles (Dubiner et al., 2023), making it a logical mechanism for the tropical, large-bodied marine iguana. In hibernating reptiles, metabolic depression appears to be induced by the lack of food and not by cold temperatures, occurring in response to environmental change rather than in anticipation of it (Dubiner, Meiri, et al., 2024). Therefore, a similar mechanism, which is apparently ubiquitous in squamates (Dubiner et al., 2023) and involves shrinkage of internal organs (Dubiner, Meiri, et al., 2024), could be in use by *A. cristatus* in response to the unpredictable yet common food shortage. Alternative explanations for our results could hinge on the fact that marine iguana heart rate is somewhat higher during heating than during cooling (Bartholomew & Lasiewski, 1965). Thus, during periods with warmer water and less time needed to achieve the preferred T_b, a relatively higher proportion of the studied individuals would be cooling rather than heating at any given moment, leading to lower heart rates on average. Geographic or seasonal biases in heart rate are addressed in the model by including site and season as predictors and did not affect the trend. Other factors, such as stress from handling, diving prior to measurement, or cardiovascular health, could also potentially influence heart rate without necessarily reflecting metabolic rates, though these were unlikely to create a bias with respect to El Niño. Even if these or other factors lead to non-resting metabolic rates at the time of measurement, downregulating resting/standard metabolic rates is expected to also manifest a reduction in other factors such as active metabolic rate and metabolic scope (Gangloff & Telemeco, 2018; Schulte, 2015). The conclusions based on our models were required to make some assumptions: a constant scaling of metabolic rate with body size, and a direct correlation between heart rate and metabolic rate. We consider these assumptions to be well-founded (Butler et al., 2002; Piercy et al., 2015; Tattersall et al., 2016; and see review in Green, 2011), but do not rule out possible biases introduced by a possible deviation from these assumptions (Glazier et al., 2015; Green, 2011; Zuo et al., 2012).

The oscillations in mean sea surface temperature did not lead marine iguanas to correspondingly change their mean T_b while on the shore, though there were small but statistically significant differences between seasons (as expected for large, basking reptiles; Giacometti et al., 2024). Colder T_b (leading to lower metabolic rates; Andrews & Pough, 1985) is the major energy saving component enabling hibernating reptiles to survive the winter with no food (Withers & Cooper, 2010), and our results suggest that marine iguanas do not use this strategy for coping with El Niño. This could be either because they, unlike hibernators, must remain fully active year-round, and therefore need to maintain near-optimal T_b – or simply because the islands are too hot for the degree of potential cooling to be efficient, especially during El Niño as noted above. Thermoregulatory accuracy was high (and did not change with ONI, though there were small differences between seasons), as is common for heliothermic, tropical squamates that usually maintain similar T_b even across a wide range of environmental temperatures (Dubiner, Aguilar, et al., 2024; Dubiner, Meiri, et al., 2024) and for large reptiles that have high thermal inertia (Stevenson, 1985). Marine iguanas also have high control of vasomotion while basking, and are therefore efficient at maintaining high T_b (Bartholomew, 1966). Alternatively, our method of randomly measuring iguanas on the beach at a single point in time might completely miss a substantial change in T_b when averaged over the whole day, which could likely be the case (Martin Wikelski, personal communication).

Our results supported our hypothesis of energy saving during El Niño via the metabolic pathway (lower heart rate), but not the thermoregulatory pathway (no change in T_b). This could indicate that metabolic depression enables marine iguanas to deal with El Niño effects, and the next important step required to further test this hypothesis is to directly measure their metabolic rates across years, for example by indirect calorimetry. Assessing the adaptations of marine iguanas to warming-induced food shortages is important to understand, predict, and prepare for the effects future climate change will have on them. While the El Niño Southern Oscillation (ENSO) is still poorly understood (Paltán et al., 2021), two-thirds of the climatic models that are judged to provide the best ENSO simulations predict imminent changes in its variability due to climate change (Collins et al., 2010; Vecchi & Wittenberg, 2010). This may increase the intensity of these food shortages and lead to higher mortality in marine iguanas. Moreover, warming sea-surface temperatures could cause the algal community to shift or contract its range to deeper water (like many species of marine organisms; Chaikin et al., 2022; Dulvy et al., 2008), necessitating deeper diving to feed and therefore harming the smaller individuals, that do not dive as deep (Vitousek et al., 2007). The Galápagos marine iguana is

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an endemic, vulnerable species with several endangered and critically endangered subspecies (MacLeod et al., 2020), acutely exposed to the threats of climate change due to its singular ecological and dietary specialization. In addition to changes in food availability, increasing temperatures could also lead to fewer opportunities to thermoregulate. Because temperature underpins most (if not all) physiological processes in ectotherms, and because tropical ectotherms are less equipped to deal with thermal variability than non-tropical ones (Giacometti et al., 2024; Huey et al., 2009), then understanding the vulnerability of marine iguanas to ENSO becomes an ever more pressing matter. Therefore, it is important to understand how its physiology is adapted to cope with the unpredictable climatic oscillations common to its native habitat.

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Conflict of interests

The authors have no competing interests to declare.

Author contributions

Conceptualization: SD (lead), JPMP, GL (supporting); Formal analysis: SD (lead); Funding acquisition: GL (lead), SD, JPMP, KJL (supporting); Investigation: all authors (equal); Project administration: GL (lead); Supervision: EL, SM (equal); Writing – original draft: SD (lead); Writing – review & editing: SD, EL, SM, KJL (equal), all authors (supporting).

Data availability statement

All the data used in this paper are available in Table S1.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Raw data used for analysis in Dubiner et al. 'Changes in marine iguana (*Amblyrhynchus cristatus*) heart rates suggest reduced metabolism during El Niño events'.

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