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Impact of climate change and habitat degradation on two endangered reptiles: the Guatemalan beaded lizard and the Olive Ridley sea turtle

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Dedication

I want to dedicate this work to the loving memory of my mother, Elsa who give me the foundations of curiosity, observation, determination, and love for life in all its forms. Mom, how I wish you can see what your son has achieved, but I know you might feel my happiness whenever you are. I also want to dedicate this work to my father Carlos, who has been crucial in developing my interest in nature and science. I also want to dedicate this work to my life companion, my wife Johana, as she has been my shelter in difficult moments, my strength when weakness arises, and most of all, my soulmate through this journey of life.

Preface

To develop ecology science of endangered species is a challenge but is a must to develop better conservation strategies. Preserving nature and the beauty of the world around us is probably the main quest for a transcendent purpose for humanity. It is our moral duty to preserve planet Earth and all the living forms that inhabit it. We have been the cause of the extinction of hundreds of species, but we are also the only beings with the ability to save them.

> "*We come from an egg much smaller than a pinhead, and we inhabit a stone that revolves around a dwarf star and will eventually crash against that star. But we've been made of light, plus carbon and oxygen and shit and death and stuff, and after all, we've been here ever since the beauty of the universe needed someone to see it*."
>
> – Eduardo Galeano. Writer

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Abstract

Climate change and habitat degradation are the main threats to non-avian reptiles. Non-avian reptiles are a clade of ectothermic vertebrates that include turtles, alligators, lizards, amphisbaenians, and snakes. As ectotherms, their behavioural ecology is constrained by their thermal physiology which indeed is potentially affected by climate change and habitat degradation. This thesis examines how climate change and habitat degradation affect the ecology of endangered reptiles using two model species, one terrestrial (Guatemalan Beaded Lizard (Heloderma charlesbogerti)) and one marine species (Olive Ridley sea turtle (Lepidochelys olivacea)). First, I investigated the effects of seasonality and forest cover on the home range size, movement patterns, and habitat selection of the Guatemalan Beaded Lizard. Dry season home ranges and core areas were substantially smaller, and its associated lizard movement patterns showed shorter step lengths and smaller turning angles than those of the wet season. Larger lizards also had larger home ranges. When estimating dry forest selection within their home ranges, lizards with larger annual home range size and more forest cover within their home range showed higher selection for dry forest habitat. Second, I investigated how the strongest global interannual pattern of climate seasonality, El Niño Southern Oscillation (ENSO), can disrupt the annual phenological cycle of the Olive Ridley sea turtle in northern Central America. As proxies for nesting abundance, I analysed a 16-year period of Olive Ridley sea turtle nesting data. I found a clear overall upward trend in Olive Ridley sea turtle nesting abundance but no clear effect of ENSO variability on the numbers of nesting tracks and eggs buried in hatcheries. However, a decrease in the net change of eggs buried in hatcheries occurred in the respective years after the two extreme ENSO events during the study period. In the second year after those events, nesting abundance bounced back to resume the overall ascending trend. Third, this thesis examines how climate change can affect movement- related thermoregulation and activity intensity of the Guatemalan Beaded Lizard using GPS tags and triaxial accelerometry. I found a clear positive effect of ambient temperature on activity intensity and step-length of lizard movements. The movement also became more directional with increasing ambient temperatures. I propose that these patterns are indicative of internal state changes in the animals, as they move from a state of hunger, eliciting foraging, which is enhanced by lower temperatures and rainfall to a thermally stressed state, which initiates shelter-seeking. My findings highlight the sensitivity of this species to temperature change and indicate that predicted regional increases in temperature and reduction in rainfall are likely to negatively impact this species by reducing the width of their operational thermal window. Fourth, I also studied how vegetation loss and urbanization may affect the thermal profile of two Olive Ridley sea turtle nesting beaches with dark volcanic sand in northern Central America, and how sea turtle breeding ecology could be affected. Average sand temperatures at nesting beaches were almost always above the pivotal temperature, and either close to or above the thermal maximum tolerance of sea turtle embryos over longer periods. I found that higher air temperatures led to higher sand temperatures, and high relative humidity and precipitation led to lower sand temperatures. As expected, sand temperatures in plots covered by vegetation were lower than those without vegetation cover. Plots close to concrete structures showed the highest sand temperatures. My results highlight the relevance of vegetation and undisturbed nesting beaches in buffering the effects of high air temperatures, low relative humidity, and low precipitation rates at the study site, which will have profound implications for the resilience of Olive Ridleys to climate change. At last, I discuss perspectives on future research lines that can help improve our understating of the impacts of climate change and habitat degradation on non-avian reptiles. The combined results in this thesis may inform better conservation strategies for the two studied endangered model species.

Keywords: Global warming, habitat destruction, accelerometry, behavioural ecology, lizards, sea turtles, movement, dry forest, and volcanic sand beaches.

List of papers

Article 1

Ariano-Sánchez, D., Mortensen, R., Reinhardt, S., & Rosell, F. (2020). Escaping drought: Seasonality effects on home range, movement patterns and habitat selection of the Guatemalan Beaded Lizard. Global Ecology and Conservation, 23, e01178. doi: 10.1016/j.gecco.2020.e01178

Article 2

Ariano-Sánchez, D., Muccio, C., Rosell, F. & Reinhardt, S. (2020). Are trends in Olive Ridley sea turtle (*Lepidochelys olivacea*) nesting abundance affected by El Niño Southern Oscillation (ENSO) variability? Sixteen years of monitoring on the Pacific coast of northern Central America. Global Ecology and Conservation, 24, e01339. doi: 10.1016/j.gecco.2020.e01339

Article 3

Ariano-Sánchez, D., Mortensen, R., Wilson, R., Bjüreke, P., Reinhardt, S., & Rosell, F. (2022). Temperature and Barometric Pressure Affect the Activity Intensity and Movement of an Endangered Thermoconforming Lizard. Ecosphere, 13(3), e3990. doi: 10.1002/ecs2.3990

Article 4

Ariano-Sánchez, D., Nesthus, A., Rosell, F. & Reinhardt, S. (2022). Developed black beaches - too hot to emerge? Factors affecting sand temperatures at nesting grounds of Olive Ridley sea turtles (*Lepidochelys olivacea*). *Submitted to Climate Change Ecology.*

Table of contents

1 Introduction

Earth has entered a new human-dominated geological epoch called Anthropocene (Lewis and Maslin 2015, Laureance 2019) characterized by climate change and biodiversity loss (Dirzo et al. 2014, Cohen et al. 2018). Over the last century, global temperatures have risen by approximately 1 °C, and a further increase is expected in the future according to different climate change scenarios. Changes in precipitation will vary, with a decrease in many subtropical dry regions (IPCC 2021). Central America is identified as a climate change hot-spot (Giorgi 2006), where the impact of global warming on natural ecosystems with higher temperatures and lower precipitation will be particularly pronounced (Hidalgo et al. 2013, Hannah et al. 2017, Imbach et al., 2018). Climate change effects at the local level are exacerbated by habitat destruction and urbanization, making urban and degraded landscapes much hotter and drier than well-preserved natural landscapes (Huang et al., 2022).

Increased temperatures and a decline in precipitation will seriously affect the physiological homeostasis of a wide variety of animals, especially as temperatures reach the upper thermal tolerance limit of many species (Somero 2010, Bozinovic and Pörtner 2015, Silva et al. 2015). These effects are particularly important for ectotherms because elevated temperatures increase their metabolic rate (Garcia-Robledo et al. 2020) but also can affect their behavioural ecology (Gibert et al. 2016).

For example, ectotherms may invest large amounts of energy moving between places to maintain their body temperatures within a specific range of temperatures (Rolland et al. 2018). Climate change is thus expected to increase such thermoregulation energy expenditures in ectotherms, most particularly as many species have limited potential to change their thermal limits (Gunderson and Stillman 2015, Pinsky et al. 2019). Within vertebrate ectotherms, non- avian reptiles (turtles, crocodiles, lizards, snakes, and amphisbaenians) are particularly vulnerable to climate change and habitat degradation as both threats can show synergistically deleterious effects on their thermal physiology (Sinervo et al. 2010, Jara et al. 2019).

On the one hand, climate change causes ambient temperatures to reach species upper thermal tolerance limits (Sinervo 2010, Somero 2010, Bozinovic and Pörtner 2015, Piantoni et al. 2016) and increases seasonality in resource availability affecting home range (Castellón et al. 2018), energy expenditures (Davis and DeNardo 2010), habitat selection (Beaudry et al. 2009), movement (McCaster and Downs 2009), and phenological cycles (Cohen et al. 2018). On the other hand, habitat degradation reduces local habitat variation thus reducing the availability of thermoregulatory relevant resources (Price-Rees et al. 2014), along with a decline in resource availability (Adamski and Ćmiel 2014). Individuals living in fragmented and degraded habitats often have larger home ranges because resources are more difficult to reach, while individuals living in high-quality habitats and unfragmented landscapes exhibit smaller home ranges (Castellón et al. 2018, Young et al. 2018).

Climate change will magnify climate variability by increasing, for instance, the frequency of droughts associated with El Niño Southern Oscillation (ENSO) events (Wang et al. 2017, IPCC 2021), thus resulting in global disruption of weather patterns and ecosystem functions (McPhaden et al. 2006). ENSO involves an alternation between a phase characterized by increased sea surface temperature and decreased ocean productivity, known as El Niño, and a phase that shows contrary effects, known as La Niña (Wang et al. 2017). Drought and ENSO patterns might have profound effects on non-avian reptiles increasing their extinction risk (Böhm et al. 2013).

Non-avian reptiles can show behavioral adaptations in their thermoregulation strategies that may either amplify or mitigate the impacts of climate change and habitat degradation on their fitness (Meiri et al. 2013, Piantoni et al. 2016, Diele-Viegas et al. 2018, Jara et al. 2019). Specifically, behavioral thermoregulation in non-avian reptiles is manifest in a continuum that ranges between two very different strategies: active thermoregulation and thermoconformity (Pianka and Vitt 2003). Thermoregulating species maintain their internal body temperature within a narrow range by moving rapidly between sites according to temperature (Sannolo et al. 2019) and therefore do not show a linear relationship between overall ambient temperature and body temperature. Conversely, thermoconforming species react little to the heterogeneity in temperature at different sites and therefore have a body temperature close to ambient temperature. This last strategy reduces the metabolic costs of movement but means that the metabolic rate of thermoconformers is driven primarily by weather conditions (Herczeg et al. 2003).

The Anthropocene is not only characterized by climate change, but also by an unprecedented biodiversity loss driven mainly by habitat destruction related to agriculture and urbanization (Lunstrum and Bose 2022). Habitat destruction and fragmentation are the most important threats to vertebrates, especially in tropical regions (Tilman et al. 2017). Within vertebrates, non-avian reptiles are one of the groups most threatened with habitat loss and degradation, making them a group of big concern, as nearly one in five species are threatened with extinction (Böhm et al. 2013). As an example, 31 species of reptiles had had become extinct since 1500, all of them having in common habitat loss as the main driver of their extinction (Cox et al. 2022). Non-avian reptiles are particularly susceptible to the patch size of the remaining natural habitat, habitat fragmentation, and urbanization (Thompson et al. 2015, Amburgey et al. 2020). Lizards and snakes that are forest or shrubland specialists are particularly sensitive to habitat fragmentation and degradation (Keinath et al. 2017). Even small changes in microhabitat composition such as the availability or distribution of rocks and crevices that function as thermal suitable shelters within the landscape can have huge effects on lizard and snake diversity (Goode et al. 2005, Michael et al. 2020).

Habitat loss and fragmentation have been shown to have synergistic effects with climate change, especially for large-sized reptiles, as they are probably more vulnerable to overheating in sun-exposed environments, such as forest edges (Pfeifer et al. 2017). Climate change and habitat destruction are thus expected to increase such movement-related thermoregulation energy expenditures as many species have limited potential to change their thermal limits (Kearney et al. 2009, Hoffmann et al. 2013, Paaijmans et al. 2013, Gunderson and Stillman 2015, Pinsky et al. 2019). The understanding of how climate change and habitat loss may affect non- avian reptile behavioural traits and breeding ecology is crucial to understand whether an individual will be able to compete with other individuals of its species to get access to suitable habitat (Castellón et al. 2018) or successfully find food or mates (DeGregorio et al. 2011). Furthermore, behavioural ecology research in the context of global change will give innovative insights on how to adapt wildlife management and implement better conservation strategies for endangered species.

In order to understand how animals adapt their movement patterns in response to increased variability in resource availability, movement ecology has developed two useful measures that can be used for this purpose: step length and turning angles (Thurfjell et al. 2014). Step length is defined as the straight distance between consecutive locations in time, and the turning angle is the angle between the vectors of three consecutive locations (Ironside et al. 2017). In landscapes with habitat destruction and fragmentation, lizards inhabiting highly fragmented landscapes exhibited smaller step lengths compared to those in unfragmented landscapes, indicating that fragmentation is a barrier to species natural movements (Young et al. 2018). Habitat destruction and fragmentation may also affect habitat selection (Santos et al. 2008). The understanding of the variables that affect habitat selection is fundamental for developing effective conservation strategies for endangered non-avian reptiles (DeGregorio et al. 2011).

Within non-avian reptiles, sea turtles and lizards are particularly vulnerable because they are affected by climate change in various ways (Hawkes et al. 2009, Sinervo 2010, Piantoni et al. 2016, Patrício et al., 2020). As an example, sea turtles lack sex chromosomes and have a temperature-dependent sex determination (TSD) (Bull 1980, Standora and Spotila 1985). Temperatures above a pivotal temperature (generally between ca. 28 °C and 31 °C; depending on the species) in the middle third of incubation (the thermosensitive period), produce more females, and temperatures below, produce more males (Yntema and Mrosovsky 1982, Bentley et al. 2020). Based on temperature monitoring at nesting grounds, and other methods to determine sea turtle sexes, several studies of sea turtle populations from different continents and species predict an increase in the already frequent female-biased sex-ratio of hatchlings (Laloë et al. 2016, Jensen et al. 2018, Tanner et al. 2019), leading to a feminization of sea turtle populations. Also, possible temperature-induced increased mortality rates of sea turtle embryos have been observed or are predicted for the future (Fuentes et al. 2011, Maulany et al. 2012, Santidrián Tomillo et al. 2012, Pike 2013). Based on early studies and literature reviews (Yntema and Mrosovsky 1982, Howard et al. 2014), the maximum thermal tolerance of sea turtle embryos is frequently cited as 35°C but may vary depending on the species and other external factors, such as location (Hawkes et al. 2009). However, these thermal tolerances are given as mean temperatures, nest temperatures can exceed 35°C by up to several degrees for shorter periods, and eggs may still hatch successfully. Therefore, time spent at stressful temperatures is more crucial for the survival of the embryos, than high temperatures over short periods (Howard et al. 2014).

Climate change and habitat destruction will increase the energy expenditures associated with behavioural thermoregulation in non-avian reptiles and may affect the thermal profiles of their nesting grounds thus affecting their long-term survival. Unfortunately, little research has been conducted on the behavioural ecology of this group, especially with the most endangered species, as many of these species are too elusive, too small, or with very low population numbers representing serious methodological limitations for their study. The present thesis is an effort to overcome these difficulties in order to provide a better understanding of how climate change and habitat degradation can affect the movement and nesting ecology of non- avian reptiles. To achieve this, I have used two endangered non-avian reptiles as model species, the Guatemalan Beaded Lizard (*Heloderma charlesbogerti*) and the Olive Ridley sea turtle (*Lepidochelys olivacea*).

2 Objectives

The overall aim of this thesis was to assess how climate change and habitat destruction affect the movement and nesting ecology of endangered reptiles using two model species, one terrestrial (Guatemalan Beaded Lizard) and one marine (Olive Ridley sea turtle).

2.1 Effects of seasonality and habitat destruction on home range, movement patterns and habitat selection of the Guatemalan Beaded Lizard (article I)

Understanding the effects of seasonality on the home range size of endangered species is crucial to assess the risks associated with habitat degradation and climate change. To date, the effects of seasonality and habitat destruction on the spatial ecology of the Guatemalan Beaded Lizard have not been studied. In article I, I analysed telemetry data collected in 2007–2008 to produce the first quantitative analysis of the factors affecting the movement patterns and habitat selection of the endangered Guatemalan Beaded Lizard in a fragmented landscape. I aimed to analyse how the extrinsic factors of season and forest cover affect home range size, movement patterns, and habitat selection of Guatemalan Beaded Lizards.

2.2 Effects of climate change on the nesting trends of Olive Ridley sea turtles (article II)

In article II, I present the first long-term study in northern Central America of the nesting abundance trends of a hatchery-managed Olive Ridley sea turtle population and how it is affected by ENSO variability. My objectives were to estimate the trends of the nesting abundance of Olive Ridley sea turtle and to assess the effects of ENSO on their nesting abundance on the Pacific coast of Guatemala for the period 2003–2018.

2.3 Effects of climate change on the activity intensity and movement of the Guatemalan Beaded Lizard (article III)

In article III, I investigate how local weather could affect the energy expenditures associated with behavioural thermoregulation in the Guatemalan Beaded Lizard. Specifically, I studied how these animals modify their movement patterns according to ambient temperature and barometric pressure, discussing the potentially deleterious effects of climate change on this species thermal biology.

2.4 Effects of climate change and habitat destruction on the thermal profile of Olive Ridley sea turtle nesting beaches with dark volcanic sand (article IV)

In article IV, I studied how sand temperatures of Olive Ridley sea turtle nesting beaches respond to the weather, vegetation cover, and urbanization. I hypothesized that local weather, location, and annual cycle factors, will have a pronounced effect on sand temperatures, thus potentially affecting hatching success and sex ratios of Olive Ridley sea turtle embryos in *in-situ* nests.

3 Materials and methods

3.1 Study area

Guatemala is located in northern Central America, and despite being a relatively small country (108,889 Km^2), it is formed by a very complex terrain, composed of various habitats that support a particular diversity of life forms. Guatemala is one of the countries with the highest biodiversity worldwide, attributed to its topographic complexity and its location between the Nearctic and Neotropical regions (Campbell and Vannini 1989). Unfortunately, this biodiversity is highly threatened mainly by habitat loss, climate change, and overexploitation (CONAP 2008). Non-avian reptiles are one of the most diverse groups in Guatemala with 264 species recorded including 25 endemic species (Acevedo et al. 2010, Ariano-Sánchez 2022). Of these, 246 species had been evaluated by the IUCN red list, showing that 17% of Guatemalan non-avian reptiles are listed under a threatened category, with climate change and habitat destruction as their main drivers of extinction (Ariano-Sánchez 2022).

The data for all four articles were collected from two study areas located in Guatemala. The first study area was the seasonally dry tropical forest of Heloderma Natural Reserve and the surrounding areas (14.86266°N, 89.78982°W, elevation 300–950 m) (Figure 1a). Rainfall is seasonal in this area, with the wet season lasting from May to October and the dry season from November to April. The landscape is highly fragmented with forest remnants composed mainly of dry forest species such as the Cudjoe-wood (*Bonellia macrocarpa*), Naked Indian (*Bursera simaruba*), Huilihuiste (*Karwinskia calderonii*), Zacapa Collins Lead (*Leucaena collinsii*), Quebracho (*Lysiloma divaricatum*), Old Man Cactus (*Pilosocereus leucocephalus*), Pitayo Organ Pipe Cactus (*Stenocereus pruinosus*), and Hog Plum (*Ximenia americana*). Elevations range from 310 to 950 m. The topography is mostly undulating, with steep slopes clustered in the range of 40–70%. The nearest weather station to the study site is La Fragua Station, from the Instituto Nacional de Sismología, Vulcanologia, Meteorologia e Hidrología (Ariano-Sánchez and Salazar 2007).

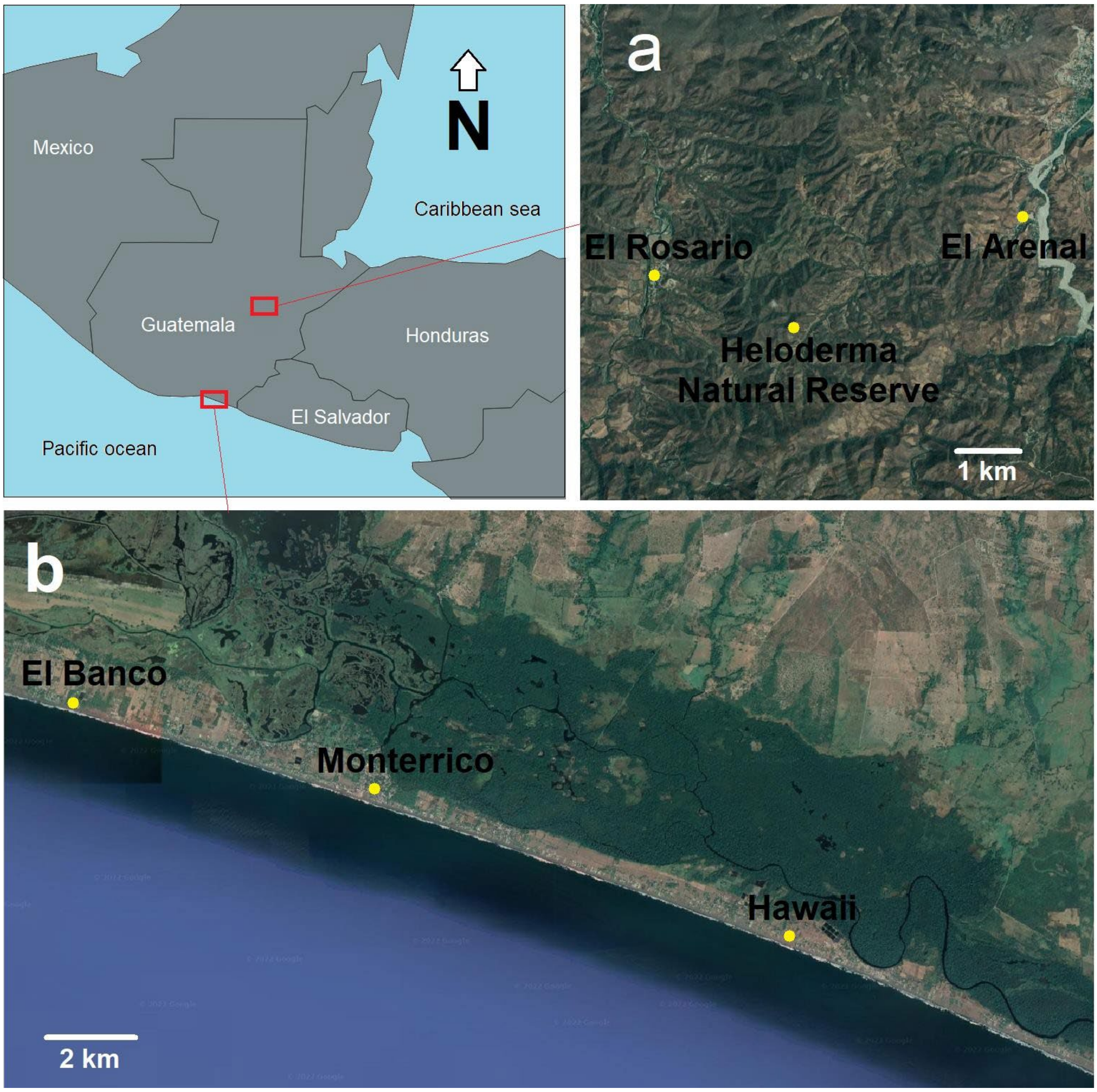

Figure 1. Map of Guatemala. Inset maps show the study areas: Heloderma Natural Reserve in Motagua Valley (a) and El Banco, Monterrico, and Hawaii beaches on the Pacific coast (b).

The second study area comprised the beaches known as El Banco, Monterrico, and Hawaii, a 14 km dak volcanic sand shoreline located between the village of El Banco (13.903123°N, 90.524111°W) and Las Mañanitas (13.866981°N, 90.416238°W), on the Pacific coast of eastern Guatemala (Fig. 1b). These beaches include several villages along the coastline with strong touristic and residential development. Only a few portions of the shoreline still have native vegetation cover (Brittain et al. 2007).

3.2 Model species

3.2.1 Guatemalan Beaded Lizard

Within fossorial reptiles, the Guatemalan Beaded lizard (Fig. 2) is one of the most endangered and elusive lizards in the world with less than 500 individuals left in the wild (Campbell and Vannini 1988, Ariano-Sánchez 2006, Reiserer et al. 2013, Auliya et al. 2017). This species is classified as Endangered by the IUCN Red List of Threatened Species (Ariano-Sánchez and Gil-Escobedo 2021).

The Guatemalan Beaded lizard is endemic to the seasonally dry tropical forests of the valleys of eastern and southern Guatemala (Ariano-Sánchez and Salazar 2007, Domínguez-Vega et al. 2012), and is part of the venom-producing clade of non-avian reptiles (Fry et al. 2006). Bites by this lizard are extremely rare, but envenomation is known to produce severe local pain, dizziness, diaphoresis, vomiting, paresthesia, and hypotension (Ariano-Sánchez 2008). The Guatemalan Beaded lizard is a vertebrate nest specialist predator feeding mainly on bird and reptile eggs (Campbell and Vannini 1988; Ariano-Sánchez and Salazar 2012).

Figure 2. Guatemalan Beaded Lizard (*Heloderma charlesbogerti*) in the dry forest of Motagua Valley, Guatemala. Snout-vent length 392 mm, total length 690 mm. Photo: Daniel Ariano.

Among the species of Beaded lizards (consisting of five species within Helodermatidae), only the Mexican beaded lizard (*H. horridum*) and the Gila monster (*H. suspectum*) had substantial research effort. These studies have resulted in descriptions of home ranges (Beck 1990, Beck and Lowe 1991) and habitat use (Beck and Jennings 2003, Kwiatkowski et al. 2008). The breeding season of Beaded lizards is related to the appearance of rainfall in the dry forest and has been reported from September to November (Beck and Lowe 1991). Most of these studies utilized VHF transmitters but failed in detailed recordings of relevant behaviour of free-ranging individuals such as mating, nesting, feeding, digging, and inside burrow behaviour.

3.2.2 Olive Ridley sea turtle

The Olive Ridley sea turtle is the most common sea turtle that nests on the sandy beaches of the Pacific Coast of Guatemala. This species is catalogued as Vulnerable by the IUCN Red List of Threatened Species (Abreu-Grobois and Plotkin 2008). The Olive Ridley sea turtle has a circumtropical distribution along Earth´s oceans (Seminoff et al. 2015). It is one of the smallest sea turtles, rarely exceeding 45 kg, with an average weight of around 35 kg (Pritchard 1979). Olive Ridley sea turtles display two different types of nesting behavior: arribada or synchronized mass nesting, and solitary nesting (Plotkin et al. 2006). Olive Ridley sea turtle nesting in Guatemala occurs between June and October with peak activity in August and September (Fig. 3a), although sporadic nesting occurs year around and is composed only of solitary nesting (Brittain et al. 2007).

Olive Ridley sea turtles have a maximum of two nesting events per year spaced between 16 to 25 days (Barrientos-Muñoz et al. 2014). *In-situ* incubation of nests is almost non-existent on the Guatemalan Pacific coast, as egg harvesting is an important local economic activity and local villagers sell the collected eggs to the hatcheries for their re-burial (Fig. 3b), along with the conservation quota stated by the governmental regulations (Brittain et al. 2007).

Figure 3. Olive Ridley sea turtle (Lepidochelys olivacea) nesting at Hawaii beach, in Guatemala (a), and inside view of the Hawaii sea turtle hatchery, where relocated eggs are incubated under protected and controlled conditions (b). Photo on the left by José Ubico, and photo on the right by Colum Muccio.

3.3 Field methods

I used data I collected from April 2007 to April 2008 to determine the effects of seasonality and habitat destruction on home range, movement patterns, and habitat selection of the Guatemalan Beaded Lizards. Eighteen adult Guatemalan Beaded Lizards (eight males and ten females) were fitted with CHP-5P radio tags (Telonics). One tag was sutured to each lizard with absorbable surgical thread at the base of the tail and then wrapped with duct tape to prevent entanglement with vegetation. Transmitters weighted less than 5% of the lizard’s body mass following animal welfare recommendations (Naef-Daenzer et al. 2005). Each individual was released in the place of capture and after the study period, tags were taken off and recovered if they were still transmitting.

I located and tracked the lizards using the homing-in method (Millspaugh and Marzluff 2001), with a sampling regime of a fix every 6 days. The radio signal was detected using a hand-held ATS FieldMaster FM100 Receiver with a foldable 3-element Yagi antenna. Some lizards were not located as frequently due to logistic constraints, resulting from long-distance movements over a very harsh habitat that make the signal difficult to locate. During each tracking event, I recorded the geographic location of each lizard with a GPS.

I evaluated ENSO variability using the Revised Multivariate ENSO Index (MEI.v2) which is a composite of sea level pressure, sea surface temperatures, 10-m surface zonal wind, 10-m surface meridional wind, and outgoing longwave radiation (Zhang et al. 2019) in order to determine how ENSO variability affects the nesting trends of the Olive Ridley sea turtle. I estimated the average of MEI.v2 for the nesting season (July–December) of each year during the study period. The MEI.v2 data were obtained from the Physical Sciences Laboratory (PSL) of the National Oceanic and Atmospheric Administration (NOAA) of the United States of America.

I used nesting tracks (Fig. 4a) at the study site as an indicator of the abundance of nesting of Olive Ridley sea turtle females. Nesting track data was obtained from ARCAS, a Guatemalan non-governmental organization that realizes sea turtle monitoring at the study site. The data was gathered by daily early-morning nesting track count patrols, carried out between July 1st and December 31st along Monterrrico-Hawaii beach for the period 2003–2018. Trained surveyors hired from local villages identified Olive Ridley sea turtle nesting tracks according to their shape, flipper pattern, and depth. After recording, the tracks were erased, to prevent repeated counting. Nesting tracks for 2012 were not recorded because of logistical difficulties with the trained staff that year.

Figure 4. Olive Ridley sea turtle (*Lepidochelys olivacea*) nesting track at Hawaii beach, in Guatemala (a) and Olive Ridley sea turtle eggs ready to be buried at El Banco sea turtle hatchery, where relocated eggs are incubated under protected and controlled conditions (b). Photos by Daniel Ariano.

Additionally, I used the number of eggs buried in hatcheries (Fig. 4b) as a secondary indicator of the abundance of nesting females of Olive Ridley sea turtle at the study site. The number of eggs harvested or collected is considered an effective estimate to monitor the relative abundance of nesting sea turtles according to the State of the World´s Sea Turtles Program Scientific Advisory Board (2011). I used official data on the total number of eggs collected and re-buried in all the sea turtle hatcheries along the 254 km of the Pacific coast of Guatemala, compiled by the National Council of Protected Areas of Guatemala. Eggs from different nests are often combined in the process of collection and transfer, therefore I analysed the total number of eggs buried in all the operating sea turtle hatcheries for every given year during the 16-year study period, rather than the number of nests, as a proxy for nesting trends.

To determine the effects of temperature and barometric pressure on the activity intensity and movement of the Guatemalan Beaded Lizard, I tracked twelve adult free-ranging Guatemalan Beaded Lizards (five males and seven females) from May to September 2019. Snout-vent length (SVL) was measured for each individual, and they were weighed, sexed, and permanently marked with passive integrated transponder (PIT) tags (AVID microchips) inserted subcutaneously at the level of the right scapula.

I designed and produced 3D-printed (Ultimaker 3) backpack cases that were specifically tailored to the lizards' dorsal region. The backpacks contained a 2 GB Thumb Daily Diary tag (Wildbyte Technologies Ltd) with a triaxial accelerometer, triaxial magnetometer, thermometer, barometer, a battery (Omnicel 3.6 V, 750 mAh), and a VHF tag (CHP-5P Telonics). Each backpack was glued to a rectangular piece of denim and then glued to the dorsal region of the lizards following a method like the one described by Flesch et al. (2009). The VHF tag was included in the backpack system for recovery in case the backpack fell off. Additionally, a µGPS tag with a temperature sensor (PinPoint Beacon 240) was glued to the proximal portion of the tail of each lizard. Thus, each individual was equipped with a µGPS logger and a backpack system (Fig. 5a, b).

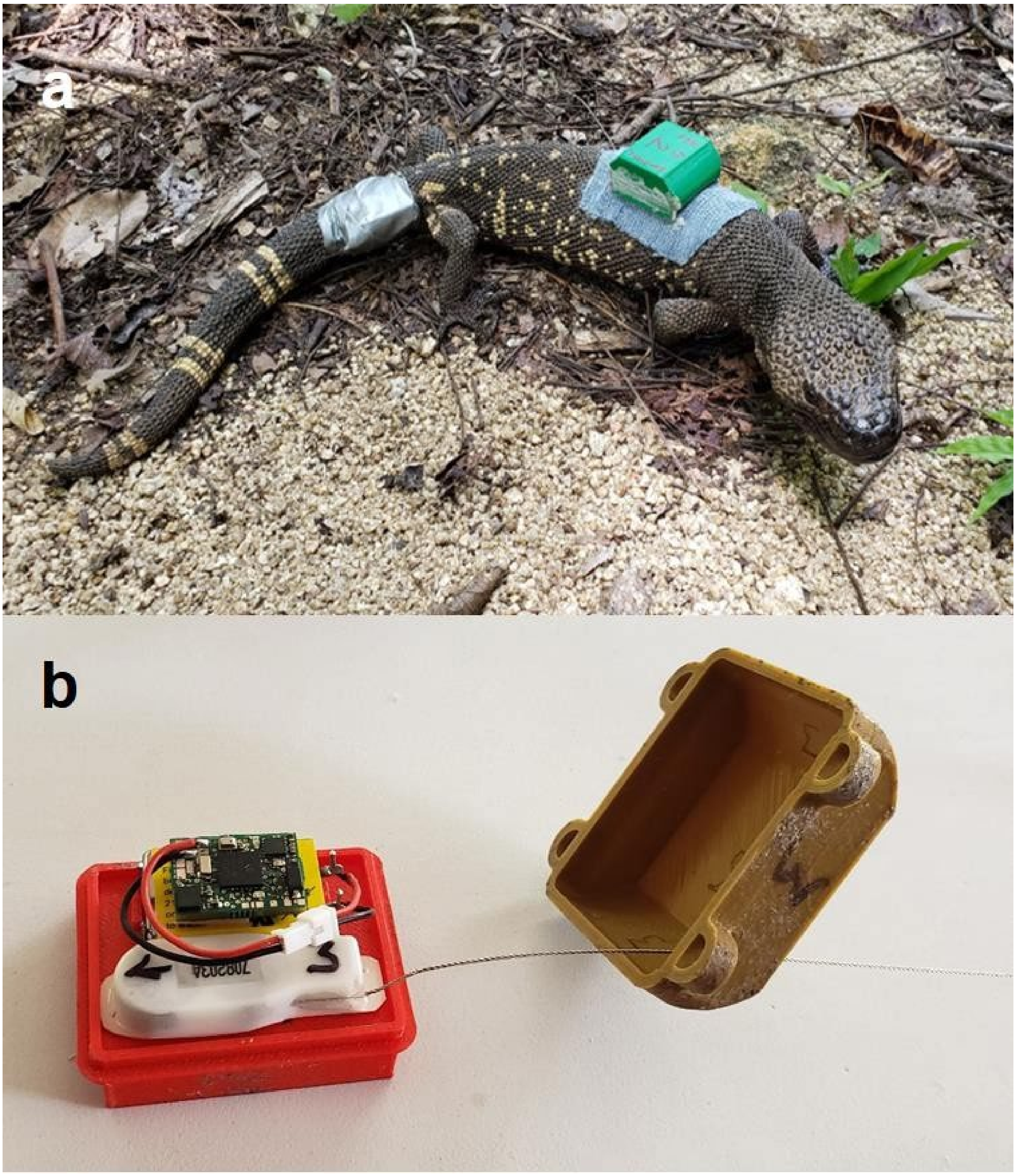

Figure 5. Guatemalan Beaded Lizard (*Heloderma charlesbogerti*) with the 3D printed backpack case glued to its back and the GPS logger attached to the base of its tail (a) and internal configuration of the backpack system showing the VHF transmitter, Daily Diary, and battery (b). Photos by: Daniel Ariano.

The total weight of the backpack and the GPS tag was 33 ± 0.1 g representing less than 5 % of the average body weight of the lizards. The backpack system containing the Thumb Daily Diaries was programmed to record acceleration at 10 Hz, while temperature and barometric pressure were recorded at 1 Hz. The µGPS tag schedule was programmed to record 37 fixes and temperature records per day for 15 days, to maximize battery lifetime. Before analysis, I discarded unreliable GPS location records (horizontal dilution of precision greater than 8.9).

To determine how weather, vegetation cover, and urbanization can influence the thermal profile of Olive Ridley sea turtle nesting beaches with dark volcanic sand, I collected sand temperature data from July 2018 to December 2019, covering two nesting seasons and one intermediate period, at the sea turtle nesting beaches of Hawaii and El Banco. LogTag Trix-8 temperature loggers (measurement range -40°C to +85°C, accuracy ±0.5°C for -20°C to +40°C) were used for temperature recording. The loggers were programmed to record temperature simultaneously every hour. From July 2018 to December 2019, they were placed along two transects (one at Hawaii, one at El Banco) parallel to the shoreline, and on average one meter away from the high tide line, in the zone were, according to previous observations, most sea turtles place their nests (Fig. 6). Each transect stretched over 1 km and consisted of ten plots 100 m apart from each other. At each plot, temperatures were measured in the sand at 30 and 50 cm below the surface. These depths were corresponding to the natural depths of Olive Ridley sea turtle nests (Plotkin et al. 2006), assuring that both loggers were placed at depths where egg incubation under natural conditions would occur. Weather data on air temperature, precipitation, and solar radiation were collected from Instituto Privado de Investigación sobre Cambio Climático (ICC 2020). The nearest weather stations were La Candelaria for the El Banco transect, and La Máquina for the Hawaii transect.

3.4 Data analyses

To determine the effects of seasonality and habitat destruction on the home range, movement patterns, and habitat selection of the Guatemalan Beaded Lizards, I calculated the home range and core area for 12 lizards tracked between 2008 and 2009. I estimated home ranges and core areas using the package adehabitatHR (Calenge 2006). I divided the data (relocations) into the dry season and the wet season. I consider the home range as the 95 % coverage region of the kernel density estimator (KDE) for the probability distribution of all possible locations, as determined from the distribution of all possible paths (Fleming and Calabrese 2017). Within home range estimation, the identification of core areas in which animals spend most of their time can be achieved using 50% KDE (Wilson et al. 2010). At last, 95% minimum convex polygons (MCP) were also calculated for each lizard just for comparison with older studies that used this method on helodermatid lizards, combining all relocations no matter of season (Beck 1990, Beck and Lowe 1991, Beck and Jennings 2003, Kwiatkowski et al. 2008). I calculated step lengths and turning angles between consecutive relocations for each lizard using the R package amt (Signer et al. 2019). Step lengths were divided by days between relocations to account for the sampling effort. As an indicator for the extent of habitat destruction to which each lizard is exposed, I merged the 95% KDE home ranges over a land-use type map of the area, to calculate the percentages of dry forest cover within each lizard´s home range. I created 20 random availability points for each relocation within each seasonal home range to analyze the habitat selection (Signer et al. 2019).

To evaluate how ENSO variability affects the nesting trends of Olive Ridley sea turtles, I used the net change of eggs buried in hatcheries between consecutive years (in percentage). This was used as a descriptive tool for visualizing annual changes in nesting abundance according to the occurrence of ENSO events.

To assess the effects of temperature and barometric pressure on the activity intensity and movement of the Guatemalan Beaded Lizard, I collected two different datasets coming from the lizards tracked in 2019: one consisting of triaxial acceleration, ambient temperature (the air temperature surrounding the body of the lizard), and barometric pressure obtained from the backpack system, and another consisting of ambient temperature (defined as above) and GPS fixes obtained from the µGPS loggers. Vectorial dynamic body acceleration (VeDBA) and ambient temperature data obtained from the backpack system were averaged by the minute. I derived the static acceleration for each axial sensor by using a running mean over 8 seconds which I used to calculate the VeDBA (Wilson et al. 2006, Shepard et al. 2008). I analyzed both datasets as the GPS tag only registered ambient temperature when a GPS fix was able to be taken, while the

Daily Diary tag recorded temperature at a fixed rate. Step-lengths and turning angles were obtained from the GPS fixes to be used as proxies of above-ground activity and were estimated using the R package adehabitatLT (Calenge 2006), while navigation bearings of movements were calculated using the R package circular (Agostinelli and Lund 2017). Data were resampled into movement steps by hour that expressed movement behavior concerning step-length and turning angle. The elevation of each GPS fix was obtained from the digital elevation model (DEM) for Guatemala.

To determine how weather, vegetation cover, and urbanization can influence the thermal profile of dark volcanic sand Olive Ridley sea turtle nesting beaches I received weather data of air temperature, precipitation, and solar radiation from Instituto Privado de Investigación sobre Cambio Climático (ICC 2020). The nearest weather stations to both sites were used; La Candelaria for the El Banco transect, and La Máquina for the Hawaii transect. I estimated the daily average of all sand temperature records. The type of surrounding was defined as follows: sand surrounding was a plot with no vegetation cover on top and not close to concrete edifications, vegetation surrounding was a plot with vegetation cover, and concrete surrounding was a plot with concrete edifications in its proximities (< 2 m distance).

3.5 Statistical analyses

All data analyses were performed using R, using version 3.5.1 for article I, version 3.6.2 for article II, and version 4.0.3 for articles III and IV (R Core Team 2021). Visual representations of the results were produced using the ggplot2 package (Wickham 2016). I developed a list of candidate models based on my hypotheses to prevent the inclusion of uninformative parameters and overfitting (Fisher et al. 2018, Leroux 2019). Candidate models were analyzed with the MASS package (Venables and Ripley 2002). In the case of Linear Mixed Models (LMM) and Generalized Linear Models (GLM), model selection was carried out based on Akaike's Information Criterion corrected for small sample size (AICc, Burnham and Anderson 2002) to obtain the most parsimonious models and parameter estimates using the MuMIn package (Barton 2020). When multiple candidate models showed the same level of performance (Δ AICc < 2), I performed model averaging to examine the overall effect size of the predictor variables (Harrison et al. 2018, Leroux 2019). In the cases where Circular Mixed Models were used, model selection was based on Watanabe-Akaike Information Criterion (WAIC) using the R package bpnreg (Cremers 2020) to obtain the most parsimonious models. I used the procedures of Cremers et al. (2018) for parameter estimation. Parameters that included zero within their 95% confidence interval (CI) were considered uninformative (Arnold 2010, Cremers and Klugkist 2018, Leroux 2019). The fixed effects used in all the analyses were not correlated (Pearson r coefficient < 0.5), and variance inflation factor values were < 3 (Harrison et al. 2018). Residuals plots were analyzed using the R package DHARMa (Hartig 2020). The specific statistical analyses for each article are described below.

3.5.1 Article 1 – seasonality and seasonality and habitat destruction on the home range, movement patterns, and habitat selection of the Guatemalan Beaded Lizards

I tested the effect of season, body length, and forest cover within the home range, on 95% KDE home range sizes and core areas, by using a generalized linear model (GLM) weighted by seasonal individual relocations, to determine the effects of seasonality and habitat destruction on the home range, movement patterns, and habitat selection of Guatemalan Beaded Lizards. Home range sizes and core areas were log-transformed to meet assumptions of normality. Sex was not included in any analysis because of my low sample size.

Movement patterns were analyzed using linear mixed models (LMM) with individual lizards as a random effect. I tested how step length and turning angles of the movement patterns of each lizard were affected by season, body length, home range size (95% KDE), core area size (50% KDE), and forest cover within their home ranges. In order to analyze the directionality of the lizards' relocations, I first took the absolute turning angles and thereafter subtracted them from π if the angle was larger than π/2. This produced angles from zero to π/2. Angles closer to zero indicated a movement in a more straight or backward direction from the previous relocation whereas angles closer to π/2 indicated movement in a more perpendicular direction from the previous relocation.

I used resource selection functions to analyze habitat selection within annual 95% KDE home ranges by the lizards (Manly et al. 2007). I fitted a weighted GLM with Bernoulli distribution and logit link as a dependent variable (1 = used relocation, 0 = available relocation) to each individual for dry and wet seasons. Used relocations were assigned a weight of 1 and randomly available relocations were assigned a weight of 1000. Individual within-home range selection coefficients were hereafter related to animal-specific characteristics by using a linear model (LM) weighted by seasonal individual relocations to investigate the effects of season, body length, home range size, and forest cover within seasonal home ranges to explore functional responses. Selection coefficients could not be calculated when the home ranges did not include any agricultural fields, and these cases were excluded from the analysis.

3.5.2 Article 2 – Effects of ENSO variability on the nesting trends of Olive Ridley sea turtles

I examined the annual trends of nesting tracks and eggs buried in hatcheries with generalized linear models (GLM) with negative binomial distribution to correct for overdispersion (Lindén & Mäntyniemi 2011), using year and MEI.v2 as fixed effects to assess how ENSO variability affects the nesting trends of Olive Ridley sea turtles. Interaction between the fixed effects was included in the list of candidate models to expand the understanding of the relationship between year and MEI.v2 values.

3.5.3 Article 3 – Effects of temperature and barometric pressure on the activity intensity and movement of the Guatemalan Beaded Lizard

I used Linear Mixed Models (LMM) to analyze how step-lengths and VeDBA were affected by ambient temperature, using individual lizards as a nested random effect within the month of sampling to correct for any intergroup differences in environmental conditions during my field research to evaluate the effects of temperature and barometric pressure on the activity intensity and movement of the Guatemalan Beaded Lizard. I corrected for elevation, snout- vent length (SVL), and sex in the step-length models (obtained from the µGPS tags), and barometric pressure, SVL, and sex in the VeDBA models (obtained from the Backpack system). VeDBA and step-lengths were log-transformed to meet assumptions of normality.

Considering that circular variables (e.g. angles, bearings) require analysis methods that are different from those used for linear data (Pewsey et al. 2014, Cremers et al. 2018), I fitted Circular Mixed-effects Models (CMM, Cremers and Klugkist 2018) to test the effects of ambient temperature (using sex, SVL, and elevation as covariates) on the turning angles and bearings of lizards' movements. I used individual lizards as random effects in the models. I choose 3000 output iterations (its = 3000), a burn-in period of 1000 iterations (burn = 1000), and a lag every third iteration (n.lag = 3) to make sure that the Markov Chain Monte Carlo (MCMC) sampler converged and to prevent possible autocorrelation between the parameter estimates. These CMMs were fitted using the R package bpnreg (Cremers 2020).

3.5.4 Article 4 – Effects of weather, vegetation cover, and urbanization on the thermal profile of Olive Ridley sea turtle nesting beaches

I tested eight candidate models to assess the effects of local weather (air temperature, precipitation, and relative humidity), location (beach, depth, and type of surrounding), and annual cycle (year and season) variables on sand temperatures to determine how weather, vegetation cover, and urbanization can influence the thermal profile of Olive Ridley sea turtle nesting beaches with dark volcanic sand, The effects of air temperature (daily average), precipitation (daily average), relative humidity (daily average), beach (Hawaii and El Banco), depth (30 cm and 50 cm), type of surrounding, year (2018 and 2019), and season (rainy and dry season) on the sand temperatures were analysed with linear mixed models (LMM). Julian day and the individual datalogger identity were considered as random effects with temporal autocorrelation to correct for the diurnal cycle of the weather variables and the temporal autocorrelation of these variables with Julian day (Silk et al. 2020). Beach and year were treated as fixed effects because they consist of only two levels each, making it impossible to use them as random effects (Harrison 2015). Relevant interactions were not included to avoid an unnecessary increase in the complexity of the models evaluated (Duncan and Kefford 2021).

3.6 Ethics statement

All work was legally approved and done following The National Council of Protected Areas of Guatemala (CONAP) regulations (permits 8-2006, 11-2007, 13-2015, and 12-2021). The work carried out during this study followed the “Guidelines for use of live amphibians and reptiles in field and laboratory research” approved by the American Society of Ichthyologists & Herpetologists (Herpetological Animal Care and Use Committee 2004). All efforts were made to reduce the stress of the animals involved in the study. Animal welfare and ethics approval was obtained from the University of South-Eastern Norway and Universidad del Valle de Guatemala.

4 Results and discussion

This thesis examines how climate change and habitat degradation affect the behavioural and nesting ecology of endangered reptiles using two model species, one terrestrial (Guatemalan Beaded Lizard) and one marine (Olive Ridley sea turtle). My findings confirmed most of the hypotheses and predictions tested about climate change and habitat degradation effects on the behavioural and nesting ecology of the model species studied (Table 1). I considered that for a hypothesis to be supported, at least half of its related predictions needed to show an effect as expected (Y).

Table 1. Hypotheses and predictions tested about habitat degradation and climate change effects on the movement and nesting ecology of two endangered reptiles (GBL: Guatemalan Beaded Lizard; ORST: Olive Ridley sea turtle) with a summary of outcomes.

Hypothesis	Predictions	Model species	Prediction supported	Hypothesis supported	Article
1. Home range size is affected by extrinsic factors such as seasonality and habitat destruction.	1.1 Home ranges and core areas are smaller in the dry season compared to the wet season.	GBL	Y	Y	I
	1.2 Individuals with less forest cover in their home ranges have larger home ranges and core areas than those with more forest cover in their home ranges.	GBL	N		I

Hypothesis	Predictions	Model species	Prediction supported	Hypothesis supported	Article
2. Home range size is affected by the intrinsic factor of body length.	2.1 Larger lizards have larger home ranges than smaller lizards.	GBL	Y	Y	I
3. Movement patterns are affected by extrinsic factors such as seasonality and habitat destruction.	3.1 Lizards have shorter step lengths during the dry season compared to the wet season.	GBL	Y	Y	I
	3.2 Lizards move more straightforwardly (with smaller turning angles) during the dry season compared to the wet season.	GBL	Y		I
	3.3 Individuals with more forest cover in their home ranges or core areas move farther and more erratically than those with more forest cover in their home ranges.	GBL	Y		I
4. Movement patterns are	4.1 Larger lizards have greater step	GBL	N	N	I

Hypothesis	Predictions	Model species	Prediction supported	Hypothesis supported	Article
affected by the intrinsic factor of body length.	lengths and turning angles than smaller lizards.				
5. Habitat selection is affected by extrinsic factors such as seasonality and habitat destruction.	5.1 Lizards have a higher selection for dry forest during the dry season compared to the wet season.	GBL	Y	Y	I
	5.2 Lizards with more forest cover within their annual home range have a higher selection for the dry forest.	GBL	Y		I
6. Habitat selection is affected by intrinsic factors such as body length and annual home range size.	6.1 Larger lizards have a higher selection for dry forest available within their home range than smaller lizards.	GBL	N	Y	I
	6.3 Lizards with larger annual home range sizes have a higher selection for dry forest than those with smaller home ranges.	GBL	Y		I

Hypothesis	Predictions	Model species	Prediction supported	Hypothesis supported	Article
7. The El Niño Southern Oscillation (ENSO) seasonality effects on the nesting trends of sea turtles are compensated by hatchery conservation efforts.	7.1 There is a negative effect of ENSO seasonality on the nesting abundance of sea turtles.	ORST	N	Y	II
	7.2 Sea turtles will show an upward trend in the abundance estimates of annual nesting females.	ORST	Y		II
8. Air temperature does not affect the movement ecology of a thermoconforming reptile.	8.1 Activity intensity and movement paths won´t change as a function of ambient temperature	GBL	N	N	III
9. Barometric pressure will have an effect on the movement ecology of a thermoconforming reptile.	9.1 Decreasing barometric pressure should increase their activity intensity and modify their movement paths as rainfall increases the movement, and	GBL	Y	Y	III

Hypothesis	Predictions	Model species	Prediction supported	Hypothesis supported	Article
	therefore availability of their prey				
10. Sand temperatures at dark volcanic sand beaches can pose a threat to sea turtle embryo survival.	10.1 Sand temperatures exceed regularly the pivotal and the upper thermal critical maximum reported for sea turtle embryos.	ORST	Y	Y	IV
11. Sand temperatures at dark volcanic sand sea turtle nesting beaches are affected by local weather factors such as air temperature, precipitation, and relative humidity.	11.1 Sand temperatures increase along with air temperature.	ORST	Y	Y	IV
	11.2 Sand temperatures decrease as precipitation increases.	ORST	Y		IV
	11.3 Sand temperatures decrease as relative humidity increases.	ORST	Y		IV
12. Sand temperatures at dark volcanic sand	12.1 Sand temperatures are similar in the two	ORST	Y	Y	IV

Hypothesis	Predictions	Model species	Prediction supported	Hypothesis supported	Article
sea turtle nesting beaches are affected by location-related factors such as beach, depth, vegetation available, and urbanization at the surface.	dark volcanic sand beaches studied.				
	12.2 Sand temperatures decrease at increasing depth.	ORST	Y		IV
	12.3 Sand temperatures are lower at plots with vegetation compared to plots with no vegetation cover or plots with urban development in their proximities.	ORST	Y		IV
13. Sand temperatures at dark volcanic sand sea turtle nesting beaches are affected by annual cycle factors such as year and season.	13.1 Sand temperatures differ over years.	ORST	Y	Y	IV
	13.2 Sand temperatures are higher during the dry season compared to the rainy season.	ORST	Y		IV

In article I, I was interested in understanding the effects of seasonality and forest cover on the home range size, movement patterns, and habitat selection of the Guatemalan Beaded Lizard. As seen in Table 2, dry season home ranges and core areas were substantially smaller and its associated lizard movement patterns showed shorter step lengths and smaller turning angles

than those of the wet season. Larger lizards also presented larger home ranges. When estimating dry forest selection within their home ranges, lizards with larger annual home range size and more forest cover within their home range showed higher selection for dry forest habitat.

Article II focused on how the strongest global interannual pattern of climate seasonality, El Niño Southern Oscillation (ENSO), can disrupt the annual phenological cycle of the Olive Ridley sea turtle in northern Central America. I found a clear overall upward trend in Olive Ridley sea turtle nesting abundance but no clear effect of ENSO variability on the numbers of nesting tracks and eggs buried in hatcheries (Table 2).

In article III, I examined how climate change can affect movement-related thermoregulation and activity intensity of the Guatemalan Beaded Lizard using µGPS tags and triaxial accelerometry. I found a clear positive effect of ambient temperature on activity intensity (measured as VeDBA) and step-lengths of lizard movements (Table 2).

Lastly, in article IV, I studied how vegetation loss and urbanization may affect the thermal profile of two Olive Ridley sea turtle nesting beaches with dark volcanic sand in northern Central America and how sea turtle nesting ecology could be affected. I found a clear positive relationship of air temperatures and a clear negative relationship of humidity and precipitation with sand temperatures at the study site (Table 2). As expected, sand temperatures in plots covered by vegetation were clearly lower than those without vegetation cover.

The results of the most parsimonious models tested are shown in Table 2. Based on the magnitude of the effect sizes (β) of the fixed factors included in the tested models, seasonality, vegetation cover, precipitation, and air temperature are the most relevant variables affecting the behavioural ecology of the model species studied. These variables are proxies that can be used for a better understanding of the effects of climate change and habitat destruction on the movement and breeding ecology of the Guatemalan Beaded Lizard and the Olive Ridley sea turtle.

Table 2. Effect size (β), standard error (SE), lower (LCI), and upper (UCI) 95 % confidence interval of the explanatory variables for the most parsimonious models tested for climate change and habitat destruction effects in two endangered reptiles: Guatemalan Beaded Lizard (*Heloderma charlesbogerti*) and Olive Ridley sea turtle (*Lepidochelys olivacea*). Parameters with clear effects are given in bold.

Model evaluated / Parameters	Effect size (β)	SE	LCI	UCI
Effects of seasonality and habitat destruction on the home ranges of the Guatemalan Beaded Lizard (Article I)				
Intercept	-0.1	1.99	-3.22	4.62
Season (Dry)	-2.29	0.48	-1.36	-3.22
Body length (mm)	0.09	0.04	0.01	0.17
Forest cover in home range (%)	-0.84	1.65	-4.07	2.39
Effects of seasonality and habitat destruction on the core areas of the Guatemalan Beaded Lizard (Article I)				
Intercept	-0.56	1.81	-4.11	2.99
Season (Dry)	-2.43	0.49	-1.48	-3.38
Body length (mm)	0.06	0.05	-0.04	0.16
Effects of seasonality and habitat destruction on the step-lengths of the movement paths of the Guatemalan Beaded Lizard (Article I)				
Intercept	1.93	0.70	0.56	3.30
Season (Dry)	-2.23	0.14	-1.96	-2.50
Forest cover within 95 % KDE (%)	-0.28	0.8	-2.11	0.69
Forest cover within 50 % KDE (%)	-0.36	0.62	-2.09	0.91
Effects of seasonality and habitat destruction on the turning angles of the movement paths of the Guatemalan Beaded Lizard (Article I)				

Intercept	0.49	0.03	0.43	0.55
Season (Dry)	-0.21	0.05	-0.12	-0.31

Model evaluated / Parameters	Effect size (β)	SE	LCI	UCI
Effects of seasonality and habitat destruction on the habitat selection of the Guatemalan Beaded Lizard (Article I)				
Intercept	-7.48	3.09	-13.53	-1.44
95% KDE home range size (ha)	0.004	0.001	0.002	0.007
Forest cover in 95 % KDE (%)	8.59	3.62	1.50	15.68
Effects of ENSO variability on the nesting trends of Olive Ridley sea turtle (nesting tracks) (Article II)				
Intercept	-92.24	15.86	-123.33	-61.16
Year	0.05	0.01	0.03	0.06
MEI.v2 a	-0.002	0.01	-0.03	0.03
Effects of ENSO variability on the nesting trends of Olive Ridley sea turtle (Number of eggs buried in hatcheries) (Article II)				
Intercept	-295.34	14.56	-323.87	-266.82
Year	0.15	0.01	0.14	0.17
MEI.v2a	-0.0004	0.01	-0.02	0.02
Effects of temperature and barometric pressure on the activity intensity (VeDBA) of the Guatemalan Beaded Lizard (Article III)				
Intercept	2.651	0.51	1.657	3.638
Air temperature	0.166	0.0013	0.164	0.169
Barometric pressure	-0.013	0.0005	-0.014	-0.012
Effects of temperature and barometric pressure on the step-lengths of the movement paths of the Guatemalan Beaded Lizard (Article III)				
Intercept	0.523	0.49	-0.447	1.554

Air temperature	0.07	0.01	0.053	0.096
Elevation	0.0009	0.0005	-0.00024	0.0020
Effects of temperature on the turning angles of the movement paths of the Guatemalan Beaded Lizard (Article III)				
Intercept	-4.19	1.97	-8.21	-0.46

Model evaluated / Parameters	Effect size (β)	SE	LCI	UCI
Air temperature	0.07	0.01	0.04	0.10
Sex (Male)	0.17	0.23	-0.27	0.62
SVL	0.06	0.05	-0.03	0.16
Effects of temperature on the bearings of the movement paths of the Guatemalan Beaded Lizard (Article III)				
Intercept	-0.84	0.59	-2.03	0.23
Air temperature	0.02	0.01	-0.01	0.05
Elevation	0.00065	0.001	-0.00046	0.0017
Effects of weather, vegetation cover, and urbanization on the thermal profile of Olive Ridley sea turtle nesting beaches with dark volcanic sand (Article IV)				
Intercept	24.04	1.49	21.12	26.97
Air temperature	0.47	0.04	0.39	0.55
Precipitation	-0.65	0.25	-1.15	-0.16
Relative humidity	-0.03	0.01	-0.05	-0.03
Beach (Hawaii)	0.02	0.05	-0.09	0.12
Depth (50 cm)	-0.53	0.04	-0.62	-0.44
Surrounding (Vegetation)	-1.48	0.08	-1.64	-1.31
Surrounding (Sand)	-0.70	0.08	-0.85	-0.55
Season (Dry)	1.15	0.12	0.91	1.38
Year (2018)	-0.14	0.07	-0.27	-0.01

4.1 Effects of seasonality and habitat destruction on home range, movement patterns and habitat selection of the Guatemalan Beaded Lizard (article I)

On the topic of climate change effects on the movement ecology of the Guatemalan Beaded Lizard, I found a strong influence of seasonality of precipitation in the home ranges and movement paths of Guatemalan Beaded Lizards. Home range size and step-lengths were substantially smaller during the dry season compared to those of the wet season.

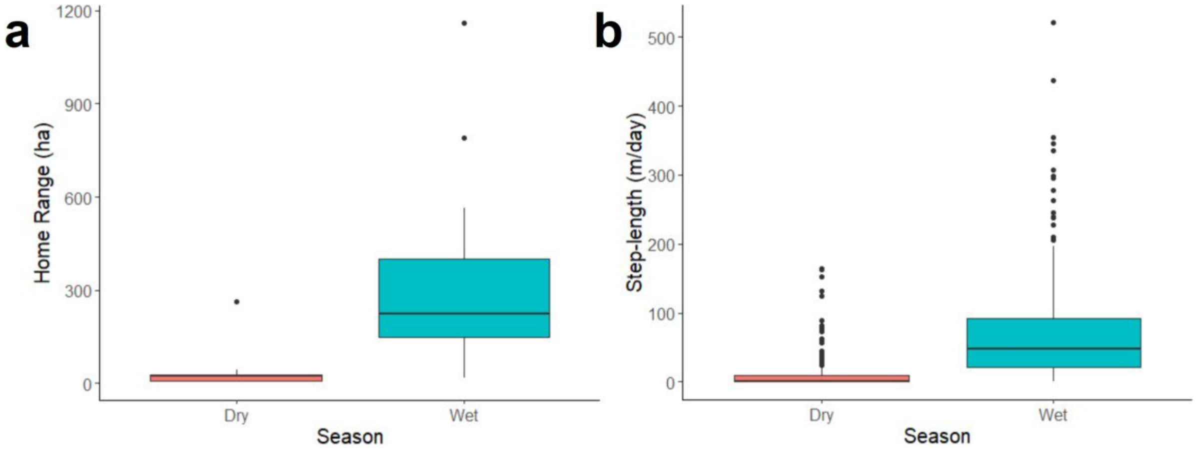

Figure 6. Differences in home range size defined as 95% Kernel Density Estimator (a), and in step-lengths (b) of Guatemalan Beaded Lizard (*Heloderma charlesbogerti*) movements between dry and wet seasons in Motagua Valley, Guatemala.

This reduction in home range size and step-length when resources are scarce such as during the dry season is rare in vertebrates, but it is a common feature of species inhabiting xeric habitats (Braham et al. 2015, Pérez-Pérez et al. 2017, Castellón et al. 2018). Usually, most vertebrates show an increase in their home ranges and movement patterns when resources are scarce such as during the dry season (Morales-Mávil et al. 2007, Brandt and Cresswell 2008, Volampeno et al. 2011, Morellet et al. 2013, Tuqa et al. 2014). The clear decrease in home range size and step-lengths during the dry season could help the lizards to cope with seasonal droughts by reducing energy expenditures related to movement when resources such as food and water are almost inexistent. Despite this behavioural adaptation to seasonality, the increased drought recurrence and the consequent shortage in food and water availability that is expected in the area as a product of climate change (Hidalgo et al. 2013, Pons et al. 2018), will probably affect the future resilience of the species by reducing the time of activity above the surface in which these animals can search for food or mates. Climate change is also expected to increase the recurrence of droughts and wildfires, especially for seasonally dry tropical forests (Laurance and Williamson 2002, Feng et al. 2013), which in turn can reduce the population viability of species inhabiting these habitats with the increasing risk of dead due to forest fires along with severe dehydration because of droughts (Domínguez-Vega et al. 2012).

Concerning habitat destruction effects on the movement ecology of the Guatemalan Beaded Lizard, I found that lizards with larger home ranges and with more available dry forest within their home ranges also showed higher selection for this habitat, especially during the dry season (Fig. 7 a,b). Habitat destruction clearly affects habitat selection in Guatemalan Beaded Lizards. Individuals with less availability of dry forest within their home ranges showed lower selection for this type of habitat, probably because the energy expenditure needed to cross the agricultural matrix and reach other forest patches is too high, especially during the dry season. This reduction in dry forest habitat selection in lizards inhabiting degraded habitats makes them highly vulnerable to predation and aversive hunting, as they spend more time within the agricultural matrix compared to those inhabiting areas with more availability of dry forest. My results highlight the importance of the conservation of seasonally dry tropical forests for the population resilience of the Guatemalan Beaded Lizard. Lizards that live in xeric habitats are very susceptible to habitat destruction and climate change as their survival depends on finding suitable habitats for aestivation in the hot and dry period of the year (Kearney 2002, Wone and Beauchamp 2003). Restoration of seasonally dry tropical forest habitat may be fundamental for the permanence of the populations of this species in the context of climate change.

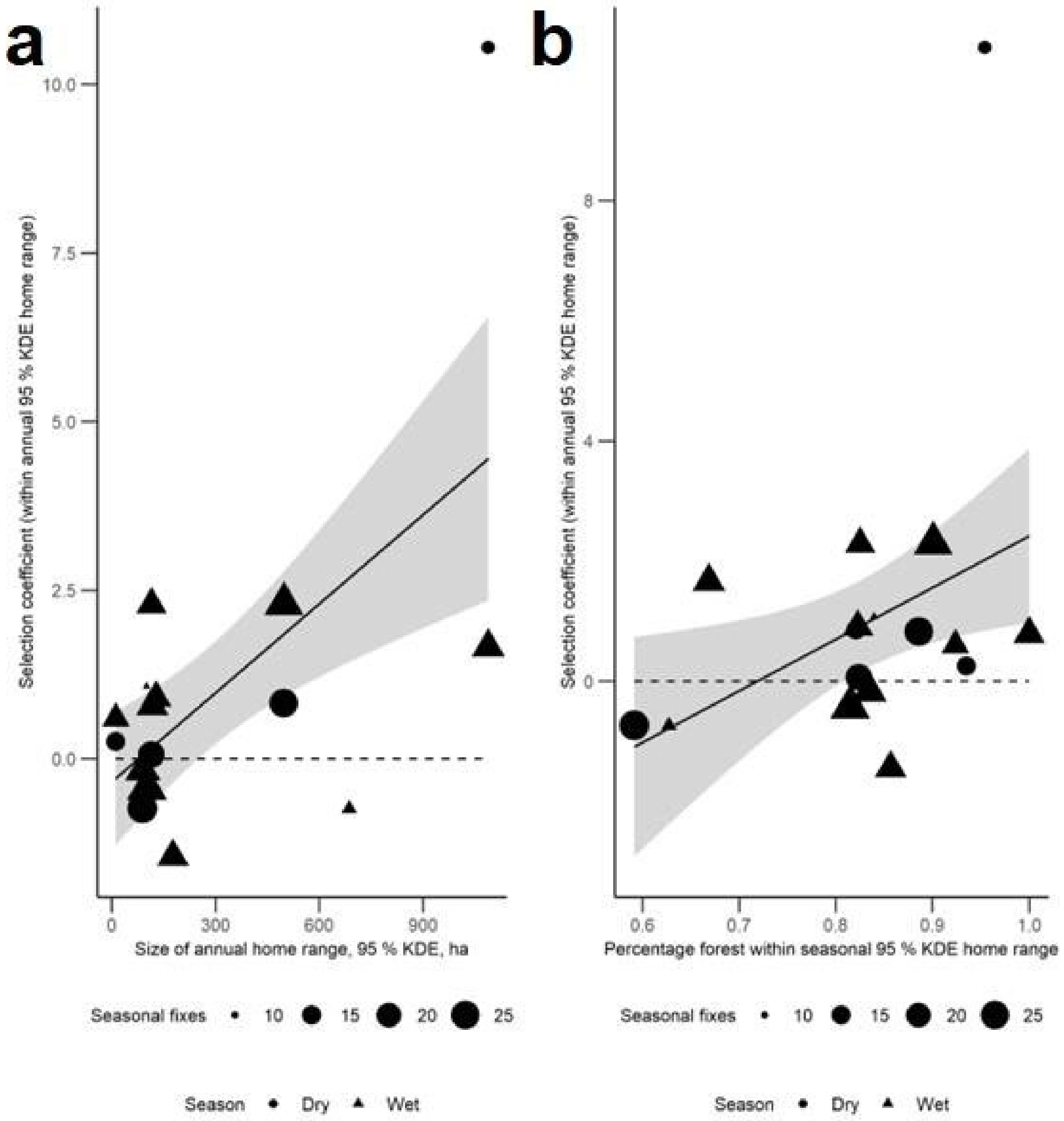

Figure 7. Effects of home range sizes (a) and availability of forest within their home ranges (b) on the selection coefficient for dry forest habitat of the Guatemalan Beaded Lizard (*Heloderma charlesbogerti*). Lower and upper 95% confidence intervals are shown.

4.2 Effects of climate change on the nesting trends of Olive Ridley sea turtles (article II)

Regarding climate change effects on the breeding biology of Olive Ridley, my results suggest decreases in nesting marks numbers the year after an ENSO event but with no clear patterns on which type of ENSO events affects the abundance of nesting marks (Fig. 8a). On the other hand, I found a small decrease in the number of eggs buried in hatcheries in the respective first year after the extreme ENSO events recorded. Despite this, egg numbers bounce back to an increasing trend in the following two years after the decrease (Fig. 8b).

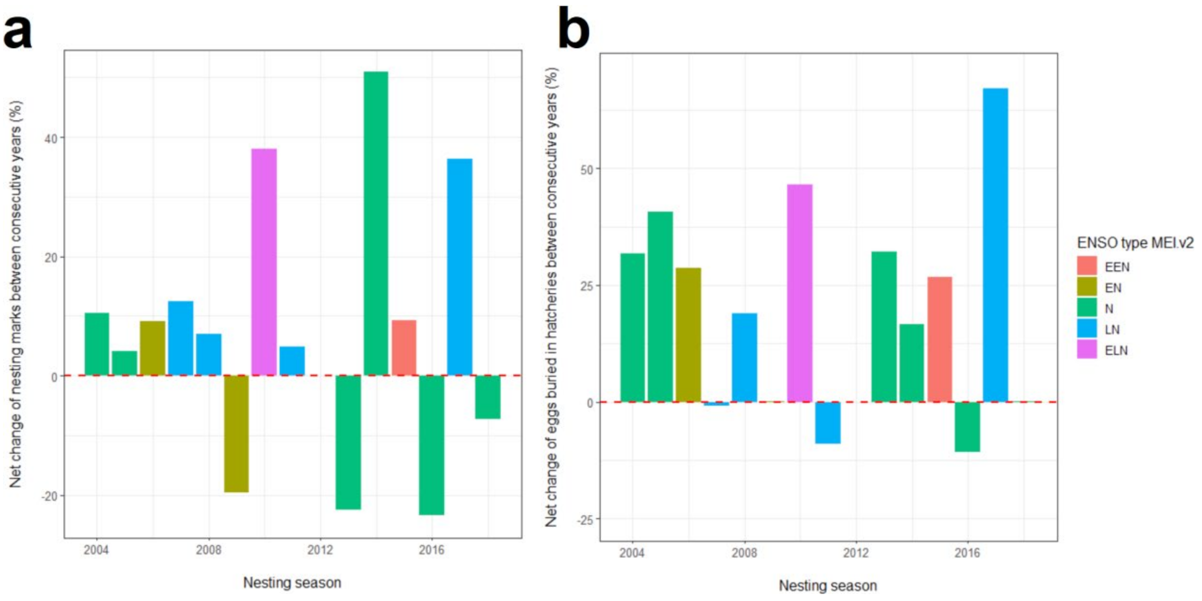

Figure 8. Relative percentage changes in nesting marks at Hawaii beach (a) and the number of eggs buried in hatcheries (b) for Olive Ridley sea turtle between consecutive years along the Pacific coast of Guatemala reported for the period 2003–2018. Bars are coloured according to El Niño Southern Oscillation (ENSO) type based on the Revised Multivariate ENSO Index (MEI.v2). Data from 2012 was not registered because of logistic problems in that year. EEN: extreme El Niño, EN: El Niño, N: neutral years, LN: La Niña, ELN: extreme La Niña.

Overall, my results show a clear upward trend in the nesting abundance of the Olive Ridley sea turtle population, based both on nesting marks at Hawaii beach (Fig. 9a) and on the number of eggs buried in hatcheries along the Pacific coast of Guatemala (Fig. 9b) over the last 16 years that is resilient to ENSO variability. The upward trend is consistent with positive population trends reported for other sea turtle species such as the Green Turtle (Troëng and Rankin 2005, Seminoff et al. 2015, Silva et al. 2017), and for Olive Ridleys itself in the last decades at several nesting beaches (Da Silva et al. 2007, Eguchi et al. 2007, Hernández-Echeagaray et al. 2012, Ocana et al. 2012, Valverde et al. 2012, Honarvar et al. 2016, Sosa-Cornejo et al. 2021).

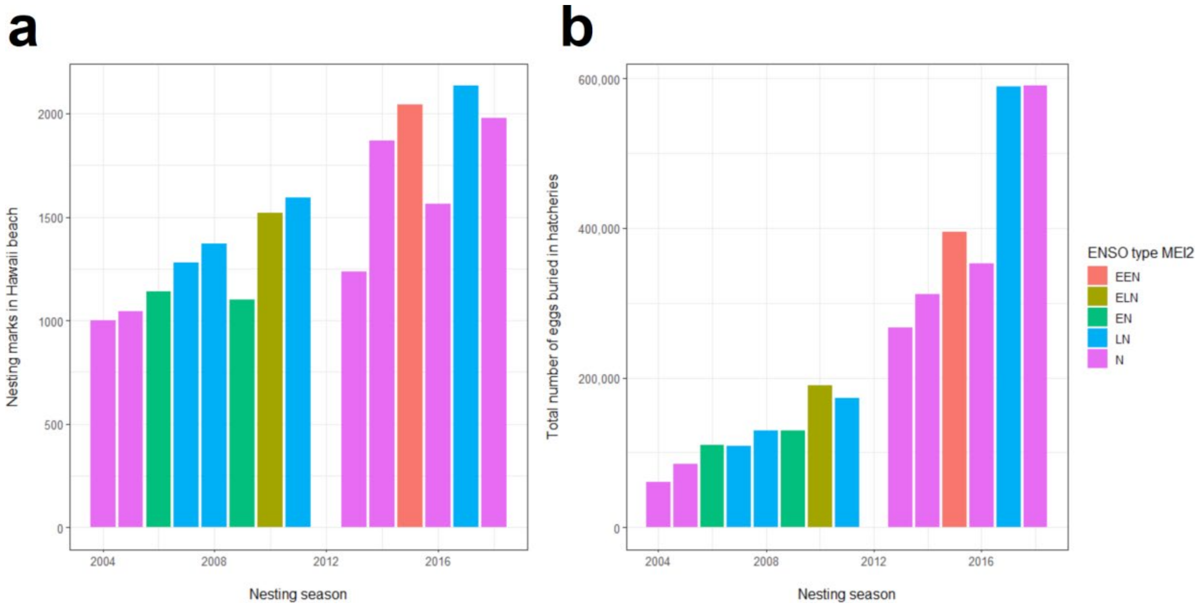

Figure 9. Number of nesting marks at Hawaii beach (a) and the number of eggs buried in hatcheries (b) for Olive Ridley sea turtle between consecutive years along the Pacific coast of Guatemala reported for the period 2003–2018. Bars are coloured according to El Niño Southern Oscillation (ENSO) type based on the Revised Multivariate ENSO Index (MEI.v2). Data from 2012 was not registered because of logistic problems in that year. EEN: extreme El Niño, EN: El Niño, N: neutral years, LN: La Niña, ELN: extreme La Niña.

4.3 Effects of climate change on the activity intensity and movement of the Guatemalan Beaded Lizard (article III)

On the subject of the potential effects of climate change on the movement ecology of the Guatemalan Beaded Lizard, I found evidence that ambient temperature and barometric pressure (related to the probability of precipitation) have a positive relationship with the lizardsactivity intensity and movement patterns (Fig. 10).

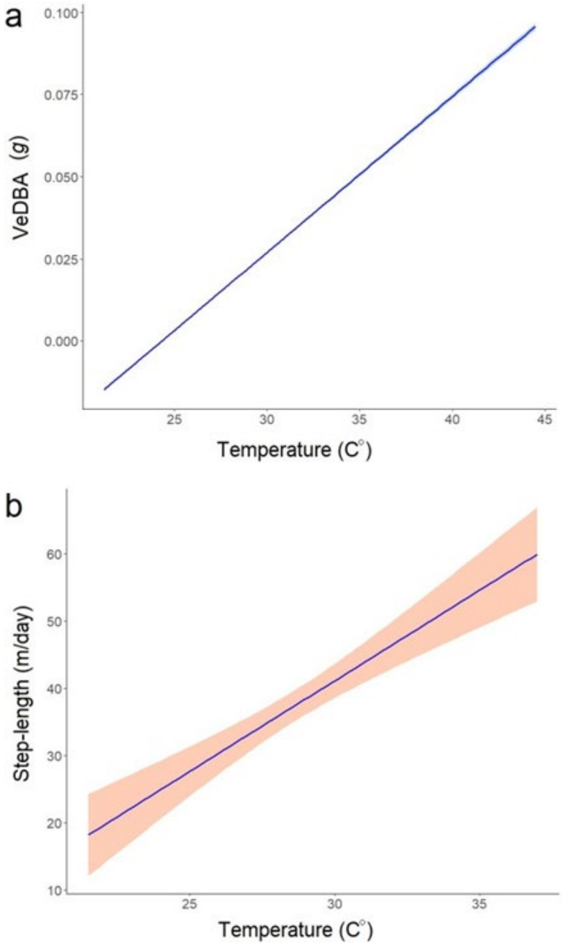

Figure 10. Vectorial dynamic body acceleration (VeDBA) (a) and step-length (b) predicted relationship with air temperature ± 95 % confidence interval in a Guatemalan Beaded Lizard population at Motagua Valley, Guatemala.

It is well documented that increases in ambient temperature are related to an increase in activity in many thermoregulatory lizards until they reach their critical thermal maximum (Sound and Veith 2000, Clusella-Trullas and Chown 2014, Gibert et al. 2016, Kirchhof et al. 2017, Cabezas-Cartes et al. 2019). I found that lizards followed a straighter path (smaller turning angles) and longer step-lengths at higher ambient temperatures than at lower ambient temperatures (Fig. 11).

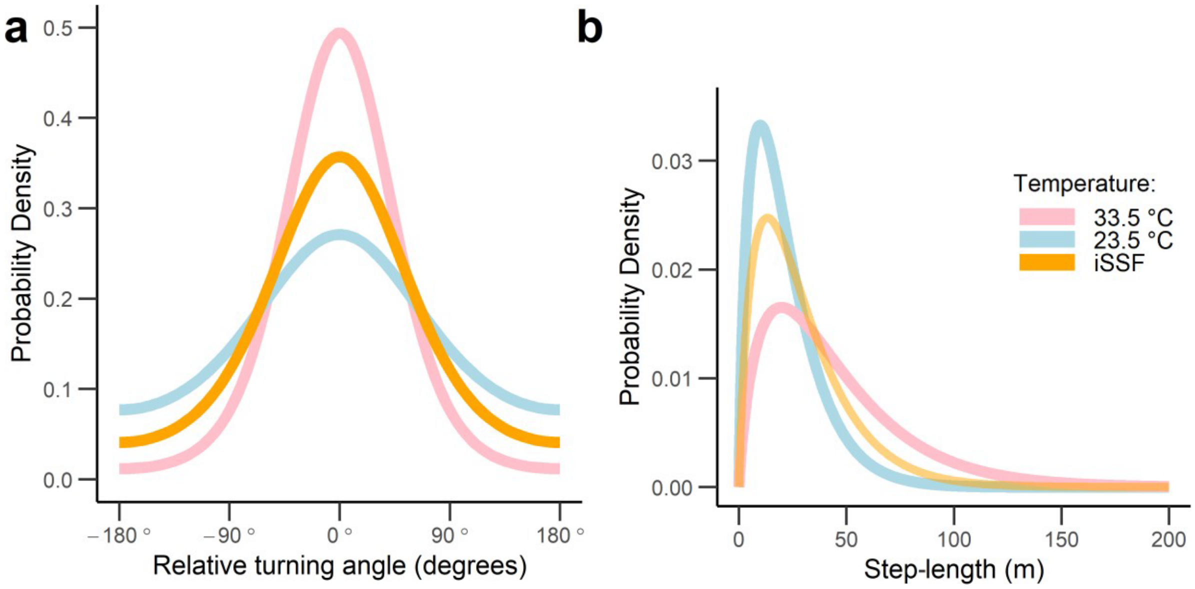

Figure 11. Predicted relationship of turning angles (a) and step-lengths (b) with ambient temperature and the relative probability of use according to the integrated step-selection function (iSSF) in a Guatemalan Beaded Lizard population at Motagua Valley, Guatemala.

My results highlight the effects of climate change in the increase of energy expenditures related to movement in thermoconforming lizards such as the Guatemalan Beaded Lizard. Climate models predict an increase of 3–4 °C in the average daily temperature and a reduction of 100–200 mm in the monthly average rainfall during the wet season at the xeric Motagua Valley region in Guatemala (García-Morales 2019), resulting in a hotter and more arid region by the end of this century (Pons et al. 2018). Climate change is expected to reduce the operative thermal window within which the Guatemalan Beaded Lizard can forage or search for mates. An increase in ambient temperature should also reduce the suitability of many current thermal shelters.

Conservation of good-quality habitat that provides enough resources (such as thermal shelters) is essential for the survival of these lizards in the long term. Unfortunately, seasonally dry tropical forests are disappearing by leaps and bounds because of agriculture and cattle ranching, thus reducing the availability and quality of suitable habitats (Portillo-Quintero and Sánchez-Azofeifa 2010, Gillespie et al. 2012).

4.4 Effects of climate change and habitat destruction on the thermal profile of Olive Ridley sea turtle nesting beaches with dark volcanic sand (article IV)

Regarding the effects of climate change on the thermal profiles of Olive Ridley sea turtle nesting beaches, I found that average sand temperatures were above the pivotal temperature, and either close to or above the thermal maximum tolerance reported for Olive Ridley sea turtle embryos. Overall, the daily mean sand temperatures were above 32 °C except for plots surrounded by vegetation during the rainy season (Fig. 12). The highest daily mean sand temperatures were recorded in plots near concrete structures (above 33.5 °C).

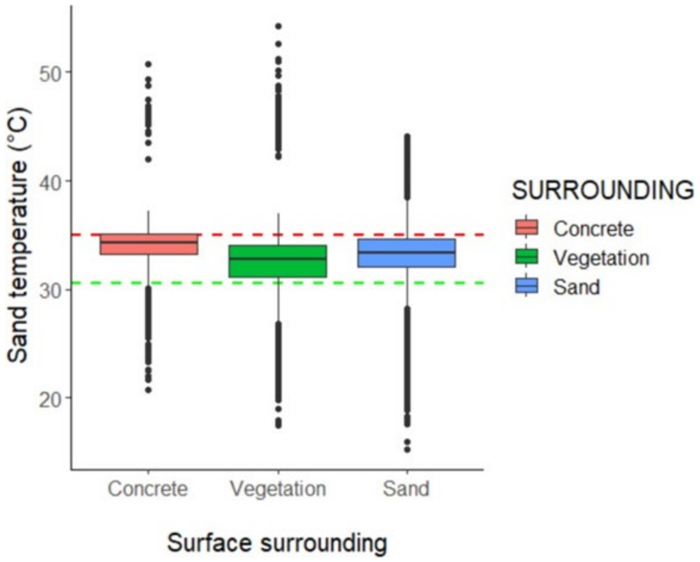

Figure 12. Daily average sand temperatures (°C) for different surface surroundings of sample plots recorded in the dark volcanic sand beach of El Banco-Monterrico-Hawaii on the Pacific coast of Guatemala from May 2018 to November 2019. The thermal critical maximum for Olive

Ridley sea turtle embryos is shown as a red dashed line (35°C). The pivotal temperaturefor the Olive Ridley sea turtle is shown as a green dashed line (30.5 °C).

As predicted, sand temperatures were positively correlated with air temperatures, while negatively correlated with precipitation and relative humidity (Fig. 13). Also, the portions of the beach covered by vegetation showed lower sand temperatures compared to those areas not covered at all, or that are close to urban infrastructure (Fig. 12). Regional climate models predict an increase of 4 °C in the average daily temperature, and a reduction of 200 mm in the monthly average precipitation on the Pacific coast of Guatemala by the end of this century, resulting in a hotter and more arid environment (Pons et al. 2018, García-Morales 2019). Higher air temperatures, along with less precipitation will result in higher sand temperatures increasing the number of days above the critical thermal maximum of Olive Ridley sea turtle embryos all over the year. This may drastically reduce Olive Ridley's hatching success of nests in the dark volcanic sand beaches of the Pacific coast of Guatemala. Local weather variables affected by climate change could act synergistically with dark sand colour resulting in a dramatic decrease in the hatching success of *in situ* Olive Ridley sea turtle nests on the Pacific coast of Guatemala.

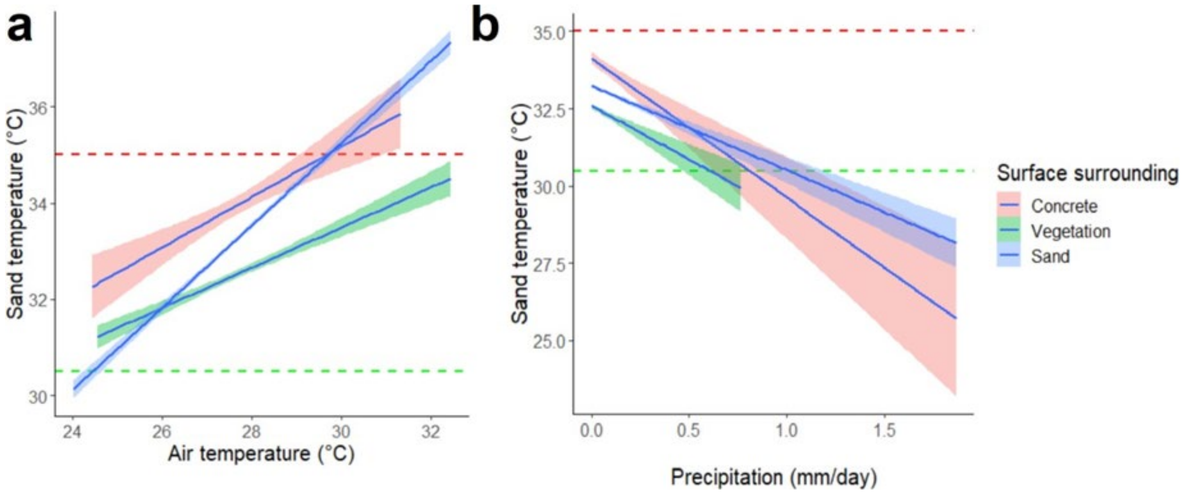

Figure 13. Relationship of air temperatures (a) and precipitation (b) with sand temperatures recorded in the dark volcanic sand beach of El Banco-Monterrico-Hawaii on the Pacific coast of Guatemala from May 2018 to November 2019, categorized in different types of surface surroundings (Concrete, vegetation, and sand). The thermal critical maximum for Olive Ridley

sea turtle embryos is shown as a red dashed line (35°C). The pivotal temperature for the Olive Ridley sea turtle is shown as a green dashed line (30.5 °C).

High sand temperatures, as I measured in my study, have earlier been measured in Ostional Beach, Costa Rica (Valverde et al. 2010), and do seem to impose a problem for successful *in situ* incubation on beaches, especially those with dark volcanic sand which can be strongly affected by climate change (Patino-Martínez et al. 2022). The clear effect shown by the rainy season in decreasing sand temperatures emphasizes the relevance that the overall duration of the rainy season will have for maintaining sand temperatures low enough to reach pivotal temperatures and have successful hatchings in Olive Ridley sea turtle nests. However, shorter rainy seasons with rainfall concentrated at shorter periods and an increase in tropical storm recurrence as expected under climate change scenarios will probably reduce offspring production of sea turtles (Montero et al. 2018). Overall, my results stress the possible impacts that global warming can have on Olive Ridley's hatching success at dark volcanic beaches in the context of climate change.

In addition, the eggs in the nest themselves will influence the incubation temperature, since they are producing metabolic heat (Gammon et al., 2020). Unfortunately, I was not able to measure temperature conditions in real nests on the beach, but considering metabolic heat, I can safely assume that the measured temperature conditions of the sand would be even warmer if the temperatures had been measured in real nests, leading to an even more pronounced increase in incubation temperatures. Given that *in situ* sand temperatures at the studied beaches often reach lethal temperatures for Olive Ridley sea turtle embryos, nest relocation to protected shaded hatcheries can be considered a useful conservation management tool for this species (Hill et al. 2015).

Concerning habitat destruction impacts in the thermal profiles of Olive Ridley sea turtle nesting beaches, my findings highlight the relevance of vegetation in buffering the effects of high air temperatures, low relative humidity, and low precipitation rates at the study site (Fig. 13). Unfortunately, beaches on the Pacific coast of Guatemala are almost devoid of vegetation near the shoreline, due to rapid urbanization and coastal development (Global Facility for Disaster Reduction and Recovery 2011). This vegetation loss and rapid urbanization of the shoreline can affect the reproductive success of sea turtles reducing the availability of suitable thermal microhabitats for nesting (Fuentes et al. 2016, Shamblott et al. 2021). One of the major changes induced by urbanization is the use of heat-absorbing construction materials such as concrete and the corresponding reduction of natural vegetation which may cause sand temperatures to rise, particularly in coastal areas (Muthamilselvan et al. 2016). Unregulated coastal development and sprawling urbanization reduce the potential for beach vegetation to buffer the impacts of climate change on the thermal profile of the dark volcanic sand beaches studied. Regulation of coastal development at nesting beaches is a vital element of the population recovery efforts for sea turtles (Fuentes et al. 2016). Consequently, the protection of urbanization-free coastal habitats is crucial for providing enough thermal niches for *in situ* sea turtles nests in Guatemala.

There were some cases in which my results were contrary to my predictions (Table 1). Those cases represent very important advances in the understanding of how habitat degradation and climate change can affect the movement and breeding ecology of the two model species studied. For example, Guatemalan Beaded Lizards showed to be highly affected by habitat degradation, independent of their size of the amount of available forest within their home ranges. Contrary to expectations, all Guatemalan Beaded Lizards studied showed much larger home ranges, longer step lengths, and greater turning angles than what has been reported for other members of the genus (Beck and Lowe 1991, Beck and Jennings 2003, Kwiatkowski et al. 2008). These lizards live within what is considered one of the most endangered habitats in the world, the thorn scrub and dry forest of the Motagua Valley in eastern Guatemala (Nájera 2006). This area has undergone severe habitat destruction with at least a 50% forest loss along with a strong degradation and fragmentation of the remaining forest patches (Ariano-Sánchez and Salazar 2007). Guatemalan Beaded Lizards have very low population densities with less than 500 individuals left in the wild (Ariano-Sánchez and Gil-Escobedo 2021). High habitat degradation at Motagua Valley may explain the larger home range sizes and longer movement paths of Guatemalan Beaded Lizards compared to other helodermatids as habitat degradation increase home range size and produced longer movement paths in non-avian reptiles (Goodman et al. 2005, Mitrovich et al. 2009, Morrison et al. 2013, Castellón et al. 2018, Young et al. 2018).

My findings, which show an increase in overall activity when ambient temperature increases, run contrary to predictions that advocate that thermoconformers such as lizards of the genus *Heloderma*, do not respond to ambient temperatures (Aranda-Coello et al. 2019). This perhaps highlights the dangers of oversimplifying how non-avian reptiles react to increasing temperatures because my model species was clearly not a passive responder to ambient temperature even though the Helodermatids are considered thermoconformers.

At last, considering that ENSO is the most important interannual pattern of climate variability and that its recurrence is expected to increase with climate change (McPhaden et al. 2006, Wang et al. 2017), I predicted a negative effect of ENSO variability on the nesting abundance of Olive Ridley. However, my results showed that Olive Ridley's nesting trends were independent of the ENSO events recorded during my study period. This pattern is consistent with the results of a recent study that found no relationship between ENSO effects and the nesting abundance of Olive Ridley sea turtles (Santidrián-Tomillo et al. 2020). Olive Ridley's trophic position as a benthic carnivorous species (Wildermann and Barrios-Garrido 2012, Colman et al. 2014) might also explain their resilience to ENSO variability as carnivorous sea turtle species are known to present less inter-annual variability than herbivorous species (Broderick et al. 2001).

5 Conclusions and perspectives

My findings reinforce that climate change and habitat destruction pose a threat to the two model species studied. In the case of the Guatemalan Beaded Lizard, increased seasonality, higher air temperatures caused by climate change, and habitat loss, have pronounced effects on its movement ecology that will increase its energy expenditures associated with searching for food, water, mates, and thermal refugia. This in turn can potentially affect the viability of these lizard populations all along the last dry forest remnants within its distribution area, especially under the prospects of climate change.

As for the Olive Ridley sea turtle, seasonality represented as ENSO variability showed only a marginal effect in the nesting output of the species. In contrast, nesting habitat destruction, represented as shoreline urbanization and coastal vegetation loss, has shown clear effects on the thermal profiles of nesting beaches, thus compromising the future hatching success of the species in the context of climate change.

Specifically, I have found that home ranges, core areas, and movement patterns of the Guatemalan Beaded Lizards have a differential response to seasonality. Lizards dramatically decrease their home range and reduce their movements during the dry season. Also, my habitat selection results show the relevance of the conservation of well-preserved dry forest remnants for these lizards. Dry forest conservation and restoration are essential for this species to cope with drought recurrence and habitat destruction.

My results suggest a clear increase in the nesting abundance of the Olive Ridley sea turtle population along the Pacific coast of Guatemala over the last 16 years. This upward trend in nesting abundance is resilient to ENSO variability during my study period. However, community-based hatchery management efforts seem to be essential for Olive Ridleys on the Pacific coast of Guatemala to cope with increased ENSO variability. Longer-term monitoring would help elucidate the effects of extreme ENSO events on the nesting abundance of Olive Ridley, as only two extreme events have occurred during the time frame of my study.

I found evidence that ambient temperature and, in less degree barometric pressure, influence the activity intensity and movement paths of a thermoconforming reptile, the Guatemalan Beaded Lizard, indicating that not all thermoconforming lizards should be considered thermal generalists. It is likely that higher activity intensity with hotter ambient temperatures will increase the movement-related energy expenditures of beaded lizards, thus making them highly vulnerable in the context of climate change.

I found that average sand temperatures almost always, and over longer periods, were above the pivotal temperature, and either close to or above the thermal maximum tolerance reported for Olive Ridley sea turtle embryos. As predicted, sand temperatures were positively correlated with air temperatures, while negatively correlated with precipitation and relative humidity. I also showed that sand temperatures were lower at 50 cm depth compared to 30 cm depth. As expected, plots covered by vegetation showed lower sand temperatures compared to plots not covered at all, or to plots close to concrete structures. Sand temperatures for 2019 were slightly higher than those of 2018, and sand temperatures were lower during the rainy season compared to those of the dry season. Overall, my study stresses the possible impacts that climate change can have on Olive Ridley sea turtle hatching success on dark volcanic beaches and suggests solutions such as undisturbed and development-free nesting habitats that may have the potential to interact with the negative impact that climate change can have on thermal conditions of sea turtle nesting beaches to a certain degree. Even more important, my results highlight the relevance of sea turtle hatcheries as a conservation tool in Guatemala, as sand temperatures in the natural setting of sea turtle nesting beaches are often above the thermal maximum tolerance reported for sea turtle embryos.

have the potential to interact with the negative impact that climate change can have on thermal conditions of sea turtle nesting beaches to a certain degree. Even more important, my results highlight the relevance of sea turtle hatcheries as a conservation tool in Guatemala, as sand temperatures in the natural setting of sea turtle nesting beaches are often above the thermal maximum tolerance reported for sea turtle embryos.

Combining the results of this thesis with future studies may provide a more comprehensive image of how climate change and habitat degradation may affect the behavioural ecology of endangered non-avian reptiles. Prolonging a study like article II may provide further insights into the role of extreme ENSO events on the nesting ecology of Olive Ridley sea turtle while expanding a study like article III to unveil dry season movement ecology of Guatemalan Beaded Lizards can give insights into how climate change and drought may affect the energy expenditures of thermoconforming lizards. Finally, prolonging a study like article IV will help to elucidate the cumulative impact of climate change on the thermal profile of sea turtle nesting beaches in northern Central America and the synergistic effects that a rise in sand temperature will have along with vegetation loss and urbanization of the shoreline.

In addition, research focused on understanding how other anthropogenic factors related to habitat destruction, such as light pollution, may affect the nesting ecology of sea turtles is highly relevant for the improvement of the conservation actions for these species. Furthermore, long-term characterization of the thermal profiles within sea turtle hatcheries is also very important to assess the future effectiveness of this conservation tool in the context of climate change. Finally, understanding how climate change will affect the thermal profile of soil where Guatemalan Beaded Lizards lay their eggs is also an unexplored and very interesting field of study regarding the potential impacts of climate change on the hatching success of terrestrial non-avian reptiles. These are only some examples of possible future next steps that can be explored after my thesis to have a better understanding of the overall effects of climate change and habitat destruction on the movement and breeding ecology of non-avian reptiles.

Overall, the combined results in this thesis may inform better conservation strategies for endangered non-avian reptiles in the context of climate change and habitat loss. These strategies may encompass the protection of remnant natural habitats that are critical for the survival of the species through participatory conservation schemes such as private protected areas or areas under forestry incentives, especially within the seasonally dry tropical forests of Motagua Valley. Also, habitat restoration in degraded lands that may increase thermal habitat suitability for endangered species is highly relevant, both in Motagua Valley and all along the Pacific coast of Guatemala.

Furthermore, developing policies oriented to the regulation of urban development at sea turtle nesting beaches are highly relevant to overcome the combined threats of climate change and loss of coastal vegetation for sea turtles. Finally, an environmental awareness program aimed at highlighting the importance of conservation is of vital importance to ensure the participation of local communities and governments in the implementation of the aforementioned strategies.

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Article 1

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Escaping drought: Seasonality effects on home range, movement patterns and habitat selection of the Guatemalan Beaded Lizard

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ABSTRACT

The relative contribution of extrinsic and intrinsic factors affecting lizard movement patterns have rarely been examined. We were interested in understanding the effects of extrinsic factors such as seasonality and forest cover, along with the intrinsic factor of body length on home range size, coarse-scale movement patterns and habitat selection of the endangered Guatemalan Beaded Lizard (*Heloderma charlesbogerti*). We predict that home ranges, core areas and movement patterns will be reduced in the dry season compared to those of the wet season. Twelve individuals (five males and seven females) were radio tracked for 4–9 months from April 2007 to April 2008. We used minimum convex polygon for home range comparison with other helodermatid studies. Guatemalan Beaded Lizards showed larger home ranges than other helodermatids. We determined annual and seasonal home range size and core areas using kernel density estimators. Turning angles and step lengths were also determined to assess the effect of the extrinsic and intrinsic factors on the movement patterns of the lizards. Dry season home ranges and core areas were substantially smaller and its associated lizard movement patterns showed shorter step lengths and smaller turning angles than those of the wet season. Larger lizards also presented larger home ranges. When estimating dry forest selection within their home ranges, lizards with larger annual home range size and more forest cover within their home range showed higher selection for dry forest habitat. These findings showed the differential response of Guatemalan Beaded Lizards to seasonality and highlights the relevance of the conservation of the remnants of well-preserved dry forest on the ability of this species to cope with drought and habitat destruction.

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1. Introduction

Seasonality in resource availability can affect non-avian reptile ecology, influencing home range (Castellón et al., 2018), physical condition (Davis and DeNardo, 2010), habitat selection (Kearney, 2002; Beaudry et al., 2009), and movement patterns (McCaster and Downs, 2009). Home range size has specifically been associated with the availability of burrows (Beck and Jennings, 2003), mates (Rismiller et al., 2010), thermoregulation sites (Hagen and Bull, 2011) and escape routes (Morrison et al., 2013). Foraging style also affects home range size. Active foraging species have larger home ranges than do sit-and-wait foragers (Verwaijen and Van Damme, 2008).

Dry season in the tropics is characterized by a decrease in resource availability for many vertebrates, and this can elicit increased home range sizes as animals roam to access resources necessary for their survival (Brandt and Cresswell, 2008; Smith and Griffiths, 2009; Volampeno et al., 2011; Morellet et al., 2013). Resource availability is also affected by factors such as habitat quality, habitat destruction and fragmentation (Adamski and Ćmiel, 2014). Individuals living in low quality or highly disturbed habitats often have larger home ranges (Castellón et al., 2018), while individuals living in high quality habitats and unfragmented landscapes exhibit smaller home ranges (Mitrovich et al., 2009). In fragmented landscapes, individuals range over larger areas than in undisturbed landscapes, because resources are more difficult to reach (Young et al., 2018).

Home ranges of animals are not used homogeneously by individuals. As a result of this, the concept of core areas emerged as a tool to identify areas of higher density use over less frequently visited areas, within an animal's home range (Wilson et al., 2010). Core area delimitation is useful to analyze habitat selection (Chamberlain et al., 2003) and territorial defense (Darden and Dabelsteen, 2008). Body length, foraging styles, seasonality, habitat destruction and fragmentation have similar effects on core areas as on home ranges (Wilson et al., 2010).

Step length and turning angles are useful measures in movement ecology to understand how animals modify their movement patterns in response to resource availability (Thurfjell et al., 2014). Step length is defined as the Euclidean distance between consecutive points in time, and turning angle is the angle between the axes of three consecutive points in time (Nouvellet et al., 2009; Ironside et al., 2017). Currently, research on step length and turning angles of squamate reptile movements has focused on differences between sexes and the effects of habitat fragmentation (Wone and Beauchamp, 2003; Young et al., 2018). Investigations found that males tend to travel further distances due to the necessity to protect territories or search for females (Kwiatkowski et al., 2008, Campbell et al., 2013). In landscapes with habitat destruction and fragmentation, lizards inhabiting highly fragmented landscapes exhibited smaller step lengths compared to those in unfragmented landscapes, indicating that fragmentation is a barrier to species natural movements (Young et al., 2018). Habitat destruction and fragmentation also affect habitat selection (Santos et al., 2008). The understanding of such factors that affect this within home range habitat selection is fundamental for developing effective conservation strategies for endangered squamate reptiles (Santos et al., 2008; DeGregorio et al., 2011).

Lizards of the family Helodermatidae are active foraging, slow-moving, venomous predators, specialized in feeding on the contents of vertebrate nests (eggs and neonates) found in seasonal habitats such as deserts and dry forests (Beck, 2005). These lizards are highly prone to dehydration, resulting in long periods of inactivity in underground shelters during hot periods, and this in turn restricts their active season to wetter periods of the year (Beck and Jennings, 2003; DeNardo et al., 2004).

Helodermatidae now comprises five species (composed by the Gila Monster and four species of Beaded Lizard) distributed along the drylands of the United States of America, Mexico and Guatemala (Reiserer et al., 2013). The Guatemalan Beaded Lizard *Heloderma charlesbogerti* is one of the most elusive, least studied, and most endangered of the species, with an estimate of less than 500 adult individuals (Ariano-Sánchez, 2006). The distribution of this large venomous lizard is now restricted to an area of ca. 150 km^2 in the Motagua Valley of Guatemala (Ariano-Sánchez and Salazar, 2007). Beaded Lizards are closely associated with seasonally dry tropical forests, and landscapes with more than 90% of forest cover (Domínguez-Vega et al., 2012).

The greatest threats to the Guatemalan Beaded Lizard are habitat destruction (Ariano-Sánchez and Salazar, 2007), wildlife traffic (Auliya et al., 2017), climate change (Sinervo et al., 2010), and aversive hunting (Domínguez-Vega et al., 2017). Aversive hunting often occurs when lizards are found in agricultural fields while moving between dry forest patches (Ariano-Sánchez and Salazar, 2007). The Guatemalan Beaded Lizard is included in CITES Appendix I, and is protected under the Guatemalan Endangered Species Act. The species is also part of a national conservation strategy sponsored by the central government and local non-governmental organizations (NGOs) (Ariano-Sánchez and Salazar, 2007).

Beaded Lizards are difficult to study because of their cryptic behavior, low population densities, and long inactive periods (Beck, 2005; Domínguez-Vega et al., 2017). There are few published papers on the spatial ecology of helodermatid lizards, with research mainly focused on Gila Monsters (Beck, 1990; Beck and Jennings, 2003; Sullivan et al., 2004; Kwiatkowski et al., 2008). Beaded Lizard studies are scarce and with usually very low sample sizes ($n < 6$) due to their rarity in the wild (Beck and Lowe, 1991). Understanding the effects of seasonality on home range size of endangered species is therefore important in order to assess the risk of threats such as habitat destruction and increased drought recurrence caused by climate change (Sullivan et al., 2004; Morrison et al., 2013, Sung et al., 2015). To date, the effects of seasonality, body length and habitat destruction on the movement patterns and habitat selection of the Guatemalan Beaded Lizard have not been studied.

In this study, we analyze relocation data collected in 2007–2008 to produce the first quantitative analysis of the factors affecting the movement patterns and habitat selection of the endangered Guatemalan Beaded Lizard in a fragmented landscape. Our aims were to analyze how the extrinsic factors of season and forest cover along with the intrinsic factor of body length, affects home range size, movement patterns and habitat selection of Guatemalan Beaded Lizards. The underlying hypotheses, and the predictions tested, are summarized in Table 1.

2. Materials and methods

2.1. Study region

The field work was conducted at Heloderma Natural Reserve (HNR) and surrounding areas (14°53′N, 89°47′W, elevation 310–950 m a.s.l.) in the Motagua Valley of Guatemala (Fig. 1). Patches of dry forest are scattered within agricultural fields of maize and industrial crops (Campbell and Vannini, 1988; Ariano-Sánchez and Salazar, 2007; Anzueto and Campbell, 2010).

This area has two clearly distinguished seasons (Fig. 1): the dry season (mid-November to mid-May) consisting of several weeks without rain, and the wet season (mid-May to mid-November) with rainfall almost every week (Nájera, 2006; Ariano-Sánchez and Campbell, 2018; Yoshimoto et al., 2019). In recent years, as a consequence of climate change the dry season is getting longer and there is a reoccurrence of droughts during the wet season (Hidalgo et al., 2013). The annual average rainfall (820 ± 178 mm), temperature (28.1 ± 0.6 °C) and relative humidity (63.5 ± 3.3%) in this region for the years 1990–2017 are typical of seasonally dry tropical forests. HNR and the surrounding forest has the largest remaining population of the endangered Guatemalan Beaded Lizard with exact numbers unknown but estimated to be around 80 adult individuals (Ariano-Sánchez and Salazar, 2007).

2.2. Study species

We captured 18 adult Guatemalan Beaded Lizards (eight males and ten females) with the help of local villagers as part of a community-based conservation program led by Heloderma Natural Reserve. Snout–vent length (SVL) and tail length (TL) were measured for each individual, and adult individuals where considered as the ones with SVL > 25.0 cm (Beck, 2005). Sex was determined through careful manual eversion of the males' hemipenes. This technique for sex determination may be inaccurate when not properly performed. To reduce potential errors in sex determination, this task was done by a very experienced person. Individuals were permanently marked with passive integrated transponder (PIT) tags (AVID microchips, Los Angeles, California, United States) inserted subcutaneously at the level of the right scapula for subsequent population studies.

2.3. Telemetry

Field work was conducted from April 2007 to April 2008. Eighteen adult Guatemalan Beaded Lizards (eight males and ten females) were fitted with radio transmitters (CHP–5P, Telonics; standard battery life ≥ 8 months). One transmitter was sutured to each lizard with absorbable surgical thread, within the 2nd and 3rd tail ring (ca. 20 mm posterior to the vent) and

Table 1
Hypothesis and predictions tested with summary of outcomes.

Hypothesis	Predictions	Prediction supported	Hypothesis supported
1. Second-order habitat selection (Home range size and core areas) is affected by extrinsic factors such as seasonality and habitat destruction.	1.1 Home ranges and core areas are smaller in the dry season.	Y	Y
	1.2 Individuals with less forest cover in their home ranges have larger home ranges and core areas.	N	
2. Second-order habitat selection (Home range size and core areas) is affected by the intrinsic factor of body length.	2.1 Home range size increase as body length increases.	Y	Y
3. Movement patterns of lizards (Step lengths and turning angles) are affected by extrinsic factors such as seasonality and habitat destruction.	3.1 Lizards have shorter step lengths during the dry season.	Y	Y
	3.2 Lizards move more straightforward (smaller turning angles) during the dry season.	Y	
	3.3 Individuals with less forest cover in their home ranges or core areas move farther and more erratically.	N	
4. Movement patterns of lizards (Step lengths and turning angles) are affected by the intrinsic factor of body length	4.1 Larger lizards have greater step lengths and turning angles.	N	N
5. Third-order habitat selection for dry forest (within annual home range) is affected by extrinsic factors such as seasonality and habitat destruction	5.1 Lizards have higher selection for dry forest during the dry season.	N	Y
	5.2 Lizards with more forest cover within their annual home range have higher selection for dry forest.	Y	
6. Third-order habitat selection for dry forest (within annual home range) is affected by intrinsic factors such as body length and annual home range size	6.1 Larger lizards have higher selection for dry forest available within their home range.	N	Y
	6.2 Lizards with larger annual home range size have higher selection for dry forest.	Y	

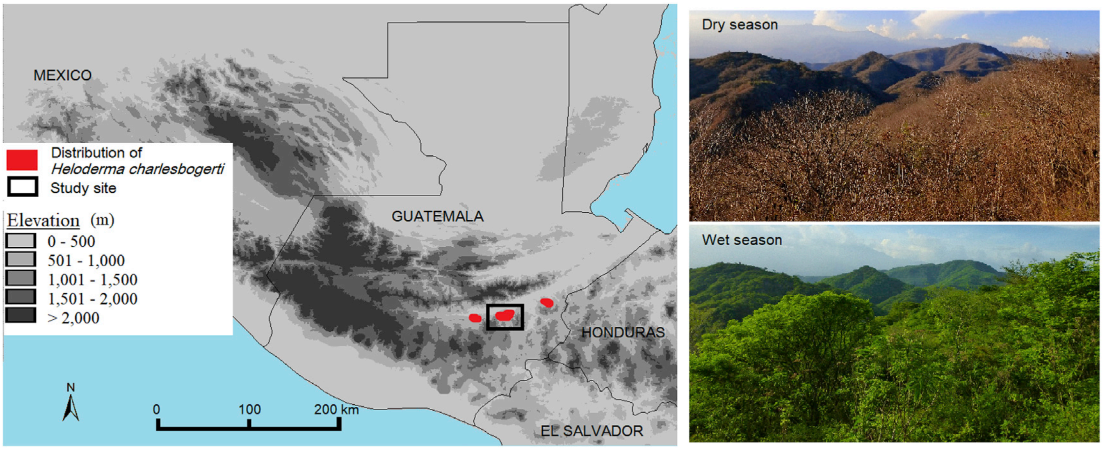

Fig. 1. Distribution of the Guatemalan Beaded Lizard (*Heloderma charlesbogerti*) in the Motagua Valley, Guatemala and the seasonality of forest foliage in the study site.

then wrapped with gray duct tape (Truper) to prevent entanglement with vegetation, carefully so as not to obstruct the vent. Transmitters weighted <5% of the lizard's body mass (Naef-Daenzer et al., 2005). Each individual was released in the place of capture within 24 h after capture. Overall health conditions of individuals were checked before release. After the study period, VHF transmitters were taken off and recovered if they were still transmitting.

Data collection started three days after release to avoid including the effects of tagging stress on activity and movement patterns of the lizards (Beck and Lowe, 1991). We located and tracked the lizards using the homing-in method (Millspaugh and Marzluff, 2001), with a sampling regime of a relocation every 6.3 ± 0.1 days. The radio signal was detected using a hand-held ATS FieldMaster FM100 Receiver with a foldable 3-element Yagi antenna (Advanced Telemetry Systems, Isanti, Minnesota, United States). Some lizards were not located as frequently due to logistic constraints, resulting from long distance movements over a very harsh habitat full of deep gullies, steep hills and uneven hollows that make the signal difficult to locate. During each tracking event, we recorded the geographic location (Universal Transverse Mercator (UTM), zone 16 N) of each lizard.

2.4. *Home range estimation and movement pattern analysis*

Home range and core area estimates were calculated for 12 of the 18 lizards attached with transmitters (five males and seven females), because six of them had too few relocations ($n < 5$) due to transmitter loss. This sample size is around 2% of the estimate of overall population size of the species (around 500 individuals) and 15% of the estimate of population size at the study site (around 80 individuals) based on population estimates by Ariano-Sánchez (2006) and Ariano-Sánchez and Salazar (2007). Raw relocation data of five of the 12 lizards analyzed in this study were included in an earlier exploratory study for the species (Ariano-Sánchez and Salazar, 2015), but without any statistical tests of underlying hypothesis.

Home ranges and core areas were produced using the package adehabitatHR version 0.4.16 (Calenge, 2019). We divided the data (relocations) into the dry season and the wet season. Dry season relocations were from April 2007 to second week of May 2007, and from third week of November 2007 to April 2008, while wet season relocations were from the third week of May 2007 to the second week of November 2007.

We consider home range as the 95% coverage region of the probability distribution of all possible locations, as determined from the distribution of all possible paths (Fleming and Calabrese, 2017). Kernel density estimators (KDE) are considered as the least biased home range estimators analysing small sample-size (Seaman and Powell, 1996; Börger et al., 2006). Using 50% KDE is also helpful to identify core areas where an animal spends most of its time, including important feeding and resting sites (Wilson et al., 2010). Seasonal (dry or wet) and annual (both seasons) home ranges for each individual were estimated as the 95% Kernel density estimator (KDE) and core areas as the 50% KDE, with reference bandwidth (href) as smoothing factor. In squamate reptile ecology, the minimum convex polygon (MCP) is the most widely used estimator (Cunha et al., 2015), but it is highly inefficient and results are subject to considerable and unpredictable biases (Laver and Kelly, 2008). However, annual 95% MCP were also calculated for each individual for comparison with older studies on helodermatid lizards that used this method, combining all relocations no matter of season (Beck, 1990; Beck and Lowe, 1991; Beck and Jennings, 2003; Kwiatkowksi et al., 2008).

The fixed kernel method was selected over the adaptive kernel method because it produces more accurate and precise home range estimates that are less sensitive to autocorrelation and small sample size (Seaman and Powell, 1996; Gredzens et al., 2014), a usual problem when tracking dryland fossorial squamate reptiles (Harless et al., 2010). Reference bandwidth was selected over least-squares cross validation (LSCV) because several lizards were found in the same burrow on many occasions, producing non-convergence problems in LSCV (Schuler et al., 2014).

Autocorrelation of the data was not considered because kernel densities do not require independence of relocations (Gredzens et al., 2014). We calculated step lengths in meters and turning angles in radians ($-\pi$ to π) between consecutive relocations for each individual as a proxy for above ground activity, using the R package amt (Signer et al., 2019). Step lengths were divided by days between relocations to account for the sampling effort.

2.5. *Habitat selection*

In ArcGIS (version 10.1 Environmental Systems Research Institute, 2012), polygons representing the two land use types, agricultural land and dry forest were constructed based on aerial orthophotos. As a proxy for the extent of habitat destruction to which each lizard is exposed, we merged the 95% KDE home ranges over the land-use type map, to calculate the percentages of dry forest cover within their home range. We created 20 random availability points for each relocation within each seasonal home range (9320 random points) to analyze the habitat selection (agriculture or dry forest) within home ranges. We also calculated the percentage of forest within 100 m radius for every point (relocations and random available points). The areas of each point were allowed to cross the border of the seasonal home ranges to estimate percentage of forest in the few seasonal home ranges which were smaller than the area of a 100 m radius circle.

2.6. *Statistical analysis*

We tested the effect of season, body length, and forest cover within the home range, on 95% KDE home range sizes and core areas, by using a generalized linear model (GLM) weighted by seasonal individual relocations. Home range sizes and core areas were log-transformed to meet assumptions of normality. Sex was not included in any analysis because of our low sample size.

Movement patterns were analyzed using linear mixed models (LMM) with individual lizards as random effect. We tested how step length and turning angles of the movement patterns of each lizard were affected by season, body length, home range size (95% KDE), core area size (50% KDE), and forest cover within their home ranges. In order to analyze the directionality of the lizards' relocations, we first took the absolute turning angles and thereafter subtracted them from π if the angle was larger than $\pi/2$. This produced angles from zero to $\pi/2$. Angles closer to zero indicated a movement in a more straight or backwards direction from the previous relocation whereas angles closer to $\pi/2$ indicated movement in a more perpendicular direction from the previous relocation.

We used resource selection functions to analyze habitat selection within annual 95% KDE home ranges by the lizards (Manly et al., 2007). We fitted a weighted GLM with Bernoulli distribution and logit link as dependent variable ($1 =$ used relocation, $0 =$ available relocation) to each individual for dry and wet seasons (Fithian and Hastie, 2013). Used relocations were assigned a weight of 1 and random available relocations were assigned a weight of 1000. Individual within home range selection coefficients were hereafter related to animal-specific characteristics by using a linear model (LM) weighted by seasonal individual relocations to investigate the effects of season, body length, home range size, and forest cover within seasonal home ranges to explore functional responses. Selection coefficients could not be calculated when the home ranges did not include any agricultural fields, and these cases were excluded from the analysis.

The fixed effects used in all analyses were not correlated (Pearson r coefficient < 0.5), and variance inflation factor values were <3 (Zuur et al., 2010). A list of candidate models was created using all combinations of fixed effects. Relevant interactions were included in the list of candidate models for the movement patterns, but not for the home range sizes, because of the limited sample size.

Model selection was based on Akaike's Information Criterion corrected for small sample size (AICc) (Burnham and Anderson, 2002) using the R package MuMIn (Barton, 2019). If ΔAICc was <2 in two or more of the most parsimonious models, we performed model averaging (Burnham and Anderson, 2002; Arnold, 2010). Parameters that included zero within their 95% confidence interval (CI) were considered as uninformative (Arnold, 2010). All analyses were conducted in R 3.5.1 (R Core Team, 2018). Mean values are given with standard error (SE).

3. Results

We have found a strong influence of seasonality on the home ranges, core areas and movement patterns of Guatemalan Beaded Lizards, along with the relevance of well-preserved dry forest habitat for this species. Our findings confirmed most of our hypotheses on the coarse-scale movement ecology of the Guatemalan Beaded Lizards (Table 1). For a hypothesis to be supported, at least half of its related predictions needed to show an effect as expected (Y).

Tracked individuals ranged in snout-to-vent length (SVL) from 25.5 to 41.5 cm. The mean duration of radio tracking per individual was 163.8 ± 29.3 days (range: 10–318). The mean number of relocations per individual was 31.8 ± 19.3 (range: 3–57). Home range sizes varied between seasons (Fig. 2). Annual weighted mean home range for the species was 264.3 ± 89.4 ha with the 95% kernel density estimate (KDE), and 75.9 ± 20.5 ha with the 95% minimum convex polygon (MCP). Annual weighted mean 95% KDE home range for females was 105.9 ± 88.0 ha and 518.3 ± 111.4 ha for males. Annual weighted mean 95% MCP home range for females was 37.5 ± 19.1 ha and 173.5 ± 24.1 ha for males (Table 2).

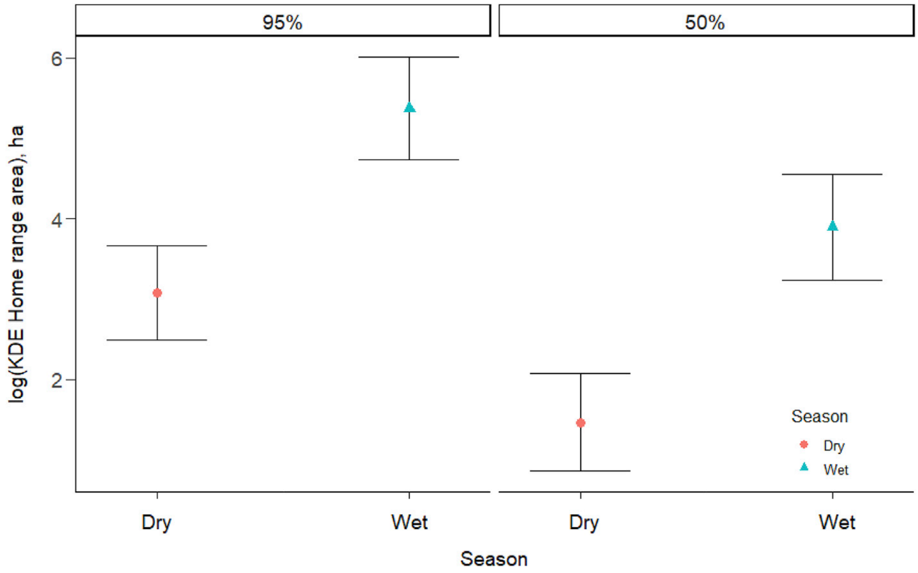

Fig. 2. Home range (95% kernel density estimate, KDE) and core area (50% KDE) log area differences of Guatemalan Beaded Lizard (*Heloderma charlesbogerti*) between seasons at Motagua Valley, Guatemala. Error bars represent the 95% confidence intervals. Dots in the box plots indicate predicted means.

Table 2
Summary of seasonal and annual home range estimates for each Guatemalan Beaded Lizard radiotracked at Motagua Valley, Guatemala.

ID	SVL	*n*	Dates of tracking	Dry season		Wet season		Annual	
	(cm)			95% MCP	95% KDE	95% MCP	95% KDE	95% MCP	95% KDE
F1	38.3	23	02/10/2007–25/02/2008	0.1	7.9	24.9	118.9	18.7	100.4
F2	38.7	35	21/07/2007–28/02/2008	4.5	25.4	22.3	223.3	26.7	128.1
F3	38.4	57	03/07/2007–30/04/2008	7.9	43.1	53.3	140.4	51.9	102.0
F4	29.5	43	02/08/2007–20/04/2008	3.0	26.7	44.5	158.3	42.1	114.7
F5	28.5	52	03/06/2007–07/04/2008	0.8	13.2	43.8	158.2	40.3	89.7
F6	25.5	33	28/06/2007–07/02/2008	1.3	7.8	3.4	16.7	3.1	11.8
F7	38.0	44	20/07/2007–04/04/2008	0.8	26.3	66.3	230.9	54.8	176.9
F8	36.9	2[a]	15/06/2007–20/06/2007	–	–	–	–	–	–
F9	33.8	3[a]	01/06/2007–27/06/2007	–	–	–	–	–	–
F10	34.5	3[a]	09/05/2007–02/06/2007	–	–	–	–	–	–
M1	39.7	54	03/04/2007–10/02/2008	27.7	264.8	143.9	565.6	180.7	498.1
M2	33.5	50	10/06/2007–23/04/2008	10.2	23.8	71.8	237.4	57.6	117.5
M3	41.0	35	04/09/2007–28/04/2008	0.5	4.9	119.5	789.5	110.4	686.5
M4	41.5	33	11/07/2007–31/01/2008	0.1	3.8	266.0	1157.9	246.0	1089.5
M5	36.5	7[b]	08/04/2007–16/05/2007	0.3	4.0	–	–	–	–
M6	38.1	4[a]	21/04/2007–30/05/2007	–	–	–	–	–	–
M7	39.2	4[a]	05/09/2007–10/10/2007	–	–	–	–	–	–
M8	39.8	3[a]	21/08/2007–12/09/2007	–	–	–	–	–	–

ID code includes sex (F for female and M for male), SVL is snout–vent length, *n* is number of relocations, home range (95% minimum convex polygon, MCP and 95% kernel density estimate, KDE) is measured in hectares. [a] individuals not included in home range analysis because of small number of relocations, [b] individual with only dry season home range estimated because of transmitter loss.

3.1. *Home ranges and core areas*

Both home ranges estimates differ between seasons (Table 2, seasonal weighted means: $\text{KDE}_{\text{dry}} = 46.2 \pm 68.3$ ha, $\text{KDE}_{\text{wet}} = 345.2 \pm 74.3$ ha, $\text{MCP}_{\text{dry}} = 6.0 \pm 14.7$ ha, $\text{MCP}_{\text{wet}} = 82.0 \pm 15.9$ ha) with dry season home ranges being smaller than home ranges during the wet season (Fig. 2). The same pattern was found for 50% KDE core areas, 4.4 ± 2.6 ha for the dry season and 34.6 ± 17.6 ha for the wet season.

We found a clear effect of season on both KDE home ranges and core areas (Table 3). Dry season home ranges and core areas were smaller than those of the wet season (Fig. 3a, Fig. 3b). Body length showed an effect on KDE home ranges but not on core areas (Table 3). No effect of forest cover within home ranges were found on home range size. Core areas of lizards were mainly restricted to dry forest habitat especially during the dry season (Fig. 3b).

Table 3
Effect size (β), standard error (SE), lower (LCI) and upper (UCI) 95% confidence interval of explanatory variables for the analyses of 95% KDE home range, core areas, cube root step length per day, absolute turning angle (radians), and within home range habitat selection coefficients in a Guatemalan Beaded Lizard population at Motagua Valley, Guatemala. We performed model averaging of the best models (ΔAICc < 2) to estimate the effect size of each variable. Informative parameters are given in **bold**.

Variables	Effect size (β)	SE	LCI	UCI
95% KDE (Home range)				
Intercept	−0.1	1.99	−3.22	4.62
Season (Dry)	**−2.29**	**0.48**	**−1.36**	**−3.22**
Body length (mm)	**0.09**	**0.04**	**0.01**	**0.17**
Forest cover within home range (%)	−0.84	1.65	−4.07	2.39
50% KDE (Core area)				
Intercept	−0.56	1.81	−4.11	2.99
Season (Dry)	**−2.43**	**0.49**	**−1.48**	**−3.38**
Body length (mm)	0.06	0.05	−0.04	0.16
Step length per day				
Intercept	1.93	0.70	0.56	3.30
Season (Dry)	**−2.23**	**0.14**	**−1.96**	**−2.50**
Forest cover within 95% KDE (%)	−0.28	0.8	−2.11	0.69
Forest cover within 50% KDE (%)	−0.36	0.62	−2.09	0.91
Turning angles				
Intercept	0.49	0.03	0.43	0.55
Season (Dry)	**−0.21**	**0.05**	**−0.12**	**−0.31**
Selection within annual[a] 95% KDE home ranges				
Intercept	−7.48	3.09	−13.53	−1.44
Annual[a] 95% KDE home range size (ha)	**0.004**	**0.001**	**0.002**	**0.007**
Forest cover within 95% KDE (%)	**8.59**	**3.62**	**1.50**	**15.68**

[a] Annual home range refers to both seasons combined.

3.2. *Movement patterns*

Season had a clear effect on the movement patterns of the lizards (Table 3). Mean step length was 66.6 ± 180.9 m/day for the dry season and 396.8 ± 398.9 m/day for the wet season. During the dry season lizards relocation steps were located within shorter distances compared to relocation steps during the wet season (Fig. 4).

Mean turning angle was 28.1 ± 30.9° for the dry season and 40.5 ± 25.9° for the wet season. Dry season turning angles between relocations had more stable azimuthal direction (straight and back) from previous relocations, compared to greater turning angles found during the wet season (Fig. 5). Turning angles closer to zero indicated a more straight-lined direction of coarse-scale movement from previous relocations, whereas angles closer to $\pi/4$ indicated a greater change in the overall coarse-scale direction between relocations.

3.3. *Within home range habitat selection*

We found that lizards with larger annual 95% KDE home range had higher selection for dry forest (Fig. 6a). Lizards with more dry forest cover within their annual 95% KDE home range also have higher selection for this habitat especially during the dry season (Fig. 6b). Neither season nor body length had an effect on the individual selection coefficients within 95% KDE annual home ranges (Table 3).

4. Discussion

4.1. *Home ranges and core areas*

Individual variation in Guatemalan Beaded Lizard home range size and core areas that we found in this study is consistent with the strong variation among individuals found in other studies of helodermatid lizards (Beck, 1990; Beck and Lowe, 1991; Beck and Jennings, 2003; Sullivan et al., 2004; Kwiatkowski et al., 2008), but we found that the overall annual home range 95% minimum convex polygon (MCP) for the Guatemala beaded lizard (75.9 ha) is much larger than those for other helodermatids such as the Mexican Beaded Lizard (21.6 ha, Beck and Lowe, 1991), or Gila Monsters (58.1 ha, Beck and Jennings, 2003; 33.1 ha, Kwiatkowski et al., 2008). The remaining populations of Guatemalan Beaded Lizards are very small (Campbell and Vannini, 1988; Ariano-Sánchez, 2006; Anzueto and Campbell, 2010), and their distributional area has undergone severe habitat destruction and fragmentation (Ariano-Sánchez and Salazar, 2007). This highly degraded and fragmented habitat along with very low population densities, may explain the larger home range sizes of Guatemalan Beaded Lizards compared to other

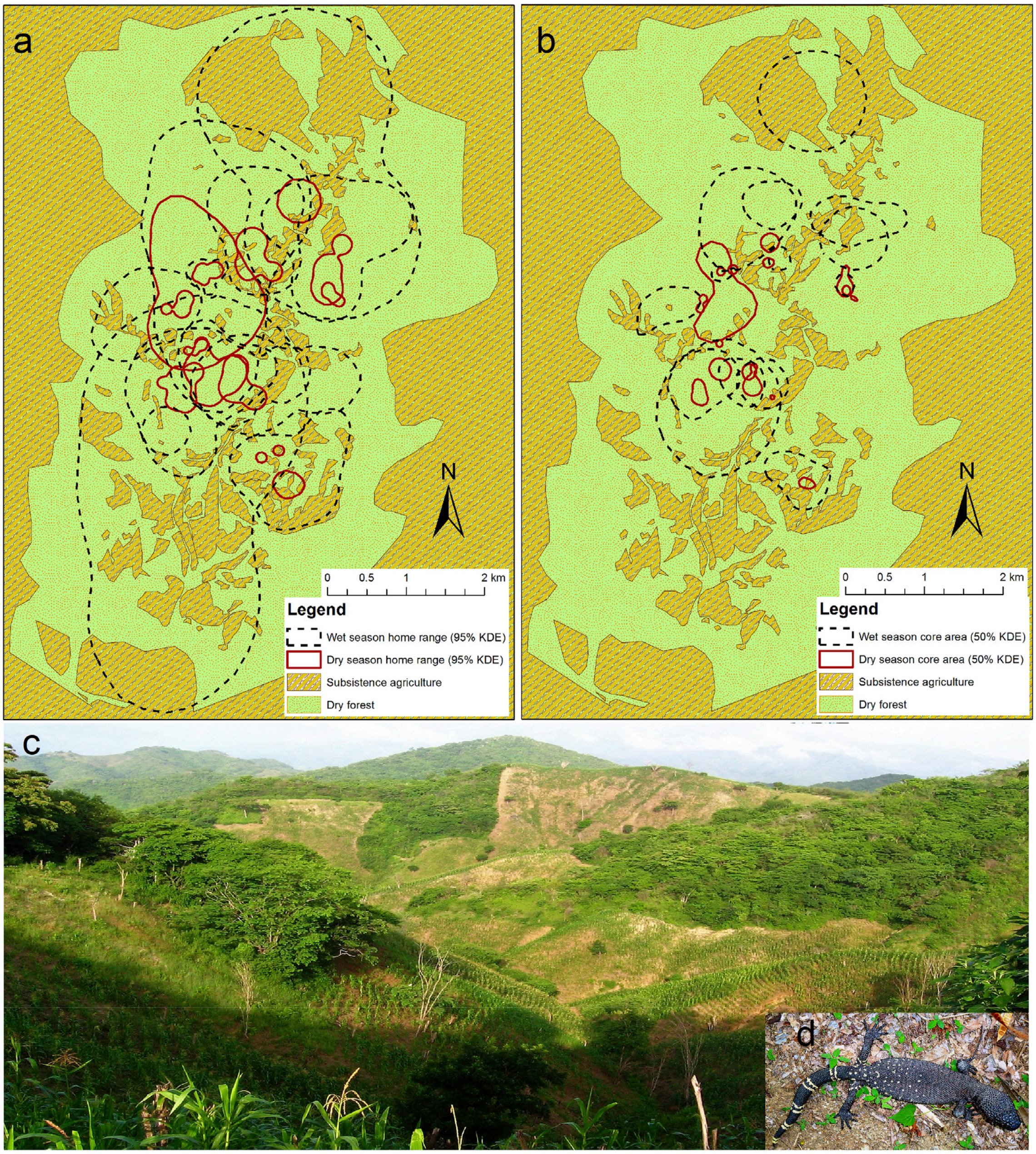

Fig. 3. Guatemalan Beaded Lizard (*Heloderma charlesbogerti*) seasonal fixed kernel home ranges (a), core areas (b), example of habitat view within home range of individual F5 (c) and lizard F5 (d) in Motagua Valley, Guatemala. KDE: kernel density estimator. Each polygon represents one lizard.

helodermatids. Population density and habitat quality are negatively related to home range size in non-avian reptiles (Goodman et al., 2005; Morales-Mávil et al., 2007; Mitrovich et al., 2009; Morrison et al., 2013; Castellón et al., 2018; Young et al., 2018).

Guatemalan Beaded Lizards showed a large reduction in home range size during the dry season, when resources are extremely scarce. This reduction in home range size when resources are scarce is rare in vertebrates but it is a common feature of species inhabiting seasonally dry habitats (Braham et al., 2015; Pérez-Pérez et al., 2017; Castellón et al., 2018). Usually most vertebrates show an increase in their home ranges when resources are scarce (Morales-Mávil et al., 2007; Brandt and Cresswell, 2008; Volampeno et al., 2011; Morellett et al., 2013; Tuqa et al., 2014). The drastic decrease in home range size and core areas during the dry season could be an evidence of aestivation in the Guatemalan Beaded Lizard. Aestivation is typically defined as a dry season dormancy triggered by arid conditions that restrict water and food availability (Storey and Storey, 2012). Accordingly, smaller home ranges and core areas can be a survival strategy used by the Guatemalan Beaded

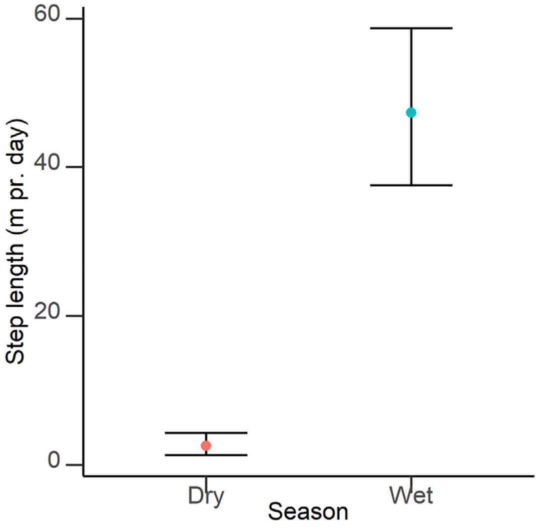

Fig. 4. Step length (meters per day) of Guatemalan Beaded Lizard (*Heloderma charlesbogerti*) movements between seasons. Error bars represent the 95% confidence intervals. Dots in the box plots indicate predicted means.

Lizard to endure arid environmental conditions. This strong reduction in home range area during the dry season could help the lizards in decreasing metabolic demands coupled with reprioritization of energy use to sustain a minimum suite of vital functions. Helodermatid lizards are known for storing energy as fat reserves in their tails, a trait that can increase survival when resources are scarce (Beck, 2005).

Our finding that larger lizards showed larger home ranges is consistent with what is known on the spatial ecology of squamate reptiles. Usually morphologically larger individuals within a population can have larger home ranges as they require more extensive foraging areas to survive (Perry and Garland, 2002; Sullivan et al., 2004; Smith and Griffiths, 2009; Cunha et al., 2015).

Active foraging lizards such as the Guatemalan Beaded Lizard are known to have larger home ranges than sit-and-wait foragers (Verwaijen and Van Damme, 2008). The Guatemalan Beaded Lizard can be considered an active forager as it feeds mainly on immobile and spatially spread food items such as eggs and nestlings (Campbell and Vannini, 1988; Beck, 2005). Larger home ranges during the wet season can result in increased opportunities for the species to find food as it coincides with the nesting and hatching of many bird species in the Motagua Valley (Fagan & Komar 2016).

Further, the breeding period of the different Beaded Lizard species occurs during the wet season (Beck, 2005). An increase in home range size during this period can be an adaptive trait for both sexes, with females increasing the chances to find enough food to achieve their metabolic requirements for egg production, and males increasing the chances of finding mates.

4.2. Movement patterns

Shorter travel distances and smaller turning angles of the Guatemalan Beaded Lizards during the dry season are probably an adaptive strategy to reduce metabolic energy expenditures in this highly seasonal habitat in which severe droughts are recurrent. DeNardo et al. (2004) suggested that helodermatids are very susceptible to dehydration despite living in arid areas. Smaller home range size, shorter distances travelled, and smaller turning angles during the dry season, can make the Guatemalan Beaded Lizard less prone to dehydration by droughts during this part of the year.

On the other hand, longer travel distances during the wet season can increase the risk for this species to wildlife trafficking and aversive hunting especially in an agricultural landscape. Aversive hunting is defined by Domínguez-Vega et al. (2017) as a radical measure of hunting aimed at species considered venomous. Guatemalan Beaded Lizards are also highly valuable in the illegal wildlife pet trade, and dozens of individuals had been captured in the last decades (Auliya et al., 2017). All the founder individuals of the captive collections of Guatemalan Beaded Lizards kept at international institutions come from wild captures (Carruth, 2015; Auliya et al., 2017).

4.3. Within home range habitat selection

Within home range habitat, dry forest areas were selected against agricultural lands in individuals with larger home ranges and with more amount of dry forest cover within their home ranges. Lizards with larger home ranges may have higher metabolic requirements that can be satisfied only with resources provided by the dry forest. This pattern has also been found in Gopher tortoises (Castellón et al., 2018). Habitat destruction is also relevant in habitat selection by Guatemalan Beaded

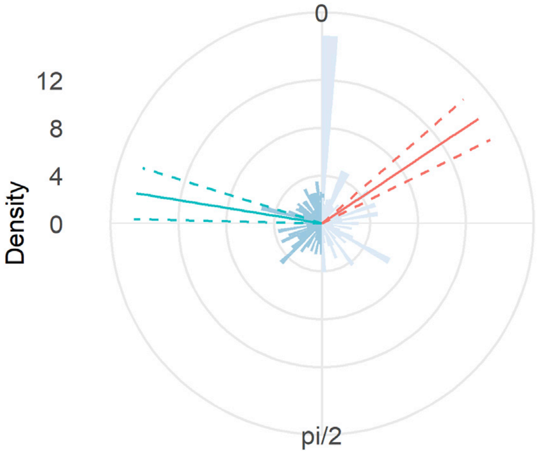

Fig. 5. Effect of season on the turning angles between relocations of radio tracked Guatemalan Beaded Lizards (*Heloderma charlesbogerti*). Bars represent density of individuals' turning angles. Solid lines represent predicted means in each season (dry season shown in red and wet season in blue). Dashed lines represent 95% confidence intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

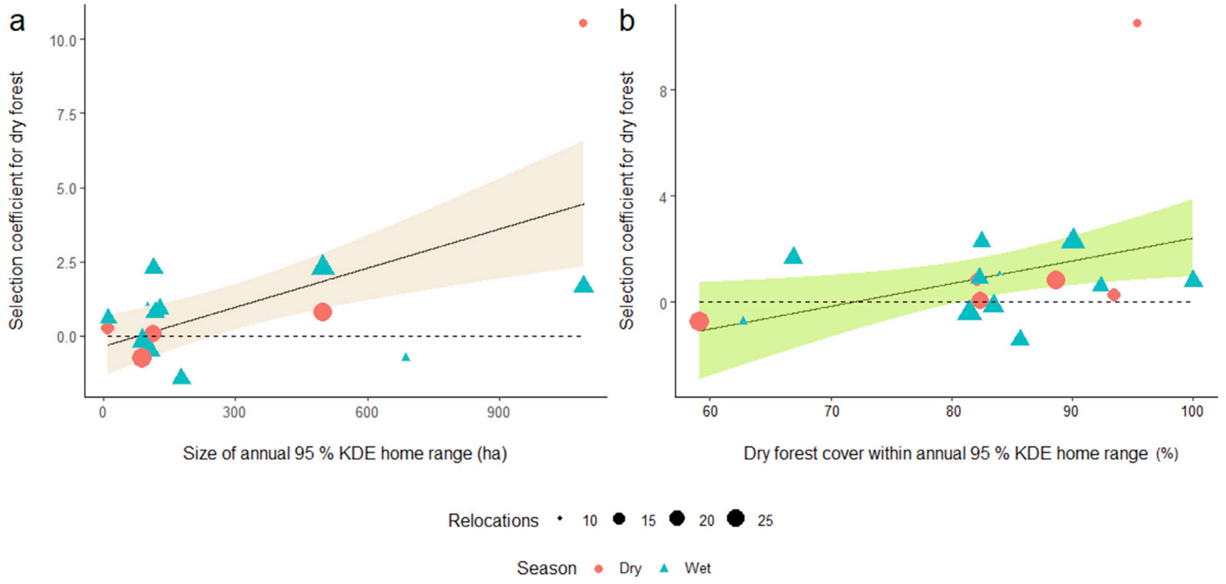

Fig. 6. Effects of annual 95% KDE home range size (a) and dry forest cover within annual 95% KDE home range (b) on the selection coefficient for dry forest habitat of the Guatemalan Beaded Lizard (*Heloderma charlesbogerti*). Lower and upper 95% confidence intervals are shown.

Lizards. Individuals with less forest cover within their home ranges showed lower selection for dry forest, probably because the energy expenditure needed to cross the agricultural matrix and reach other forest patches is too high, especially during the dry season. This highlights the relevance of well-preserved dry forest as a limiting factor for Guatemalan Beaded Lizard permanence.

4.4. *Relevance of dry forest for conservation of Guatemalan Beaded Lizard in the context of increased drought recurrence*

Squamate reptiles that live in highly seasonal habitats are very susceptible to habitat destruction and climate change as their survival depends on finding suitable habitats for aestivation in the hot and dry period of the year (Douglass and Layne, 1978; Kearney, 2002; Wone and Beauchamp, 2003). Recent models of the impacts of climate change on several lizard families showed that Helodermatidae may have an extinction risk of 91% in 2080 due to global warming (Sinervo et al., 2010). Climate change is expected to increase recurrence of droughts and wildfires over many parts of the tropics especially for seasonally dry forests (Laureance and Williamson, 2002; Feng et al., 2013). In recent years, northern Central America has shown an increase in reoccurrence of droughts and an extension in the length of the dry season with extreme reductions in precipitation as a consequence of climate change (Hidalgo et al., 2013). This may cause an increase in metabolic stress that can imperil the survival of the Guatemalan Beaded Lizard for the long term. Climate change is expected to diminish the population viability of species inhabiting arid environments through increasing metabolic expenditures (Tuqa et al., 2014). Restoration of dry forest habitat may be fundamental for the permanence of the populations of this species in the context of climate change.

Habitat destruction may reduce the access to prey items and shelters for the Guatemalan Beaded Lizard and may also increase its risk to aversive hunting. Only about 0.01% of Guatemalan Beaded Lizard original habitat remains with an average patch size of 20 ha (Ariano-Sánchez and Salazar, 2007). As the percentage of dry forest is reduced within the landscape, Guatemalan Beaded Lizards are forced to move into agricultural lands to reach other patches of forests to obtain resources needed for their survival. This increases the chances to be found by farmers and so, the probability of being killed by aversive hunting.

The clear reduction observed in home range size, core area, step length and turning angles during the dry season (an evidence of aestivation) may have a buffering effect on the susceptibility of the Guatemalan Beaded Lizard to drought recurrence caused by climate change during this critical period. Nevertheless, these lizards as dry forest specialists can also be more vulnerable to wildfires during the dry season, especially in an agricultural landscape such as the Motagua valley. Fire is normally a rare event in dry forests (Santiago-García et al., 2008), but as habitat destruction advance and transforms dry forest in a landscape of slash and burn agriculture, this risk would probably increase. Dry forest conservation, habitat restoration and the adoption of sustainable agroforestry practices are fundamental for the long term survival of the Guatemalan Beaded Lizard in the wild.

Our study indicated that Guatemalan Beaded Lizards could adjust their home range size and movement patterns according to seasonality, although based on a relatively small sample size. Small sample size is a common limitation of endangered species research (Goodman et al., 2005; Knapp and Owens, 2005; Braham et al., 2015; Beauchamp et al., 2018). However, considering that our sample represents a relevant proportion of the estimated species' population, our results give valuable insights on the factors affecting the movement patterns of this endangered and elusive lizard.

5. Conclusions

Our findings suggest that home ranges, core areas and movement patterns of the Guatemalan Beaded Lizards have a differential response to seasonality. Lizards dramatically decrease their home range and reduce their movements during the dry season. Also, our habitat selection results show the relevance of the conservation of well-preserved dry forest remnants for these lizards. Dry forest conservation and restoration is essential for this species to cope with drought recurrence and habitat destruction.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2020.e01178.

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Article 2

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Are trends in Olive Ridley sea turtle (*Lepidochelys olivacea*) nesting abundance affected by El Niño Southern Oscillation (ENSO) variability? Sixteen years of monitoring on the Pacific coast of northern Central America

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ABSTRACT

Long-term monitoring is essential for the identification of population trends, and to understand how these trends are affected by climate variability. The El Niño Southern Oscillation (ENSO) is the strongest global interannual pattern of climate variability, resulting in the disruption of the annual phenological cycles of sea turtles. Among sea turtles, the Olive Ridley (*Lepidochelys olivacea*) is the most abundant, and on many beaches their nests are relocated to hatcheries as part of conservation management, especially in northern Central America. However, Olive Ridley nesting abundance trends in northern Central America and the effects of ENSO variability on these trends are still not fully understood. Here, we present the first long-term study of this subject. We predicted an upward trend in Olive Ridley nesting abundance on the Pacific coast of Guatemala, and a negative effect of increasing ENSO variability on nesting abundance. As proxies for nesting abundance, we analysed two different data sets; a 16-year period of Olive Ridley nesting data, using nesting tracks from one index beach (Hawaii in Guatemala), and the yearly number of eggs buried in the 25–35 hatcheries that operate along the Pacific coast of Guatemala. Revised Multivariate ENSO Index values were applied to estimate annual ENSO variability. During this 16-year study period, ENSO variability was distributed in eight neutral years, two normal El Niño years, four normal La Niña years and two extreme ENSO events; an extreme La Niña in 2010 and an extreme El Niño in 2015. We found a clear overall upward trend in Olive Ridley numbers of nesting tracks and eggs buried in hatcheries but no clear effect of ENSO variability on these nesting abundance proxies. However, a decrease in the net change of eggs buried in hatcheries occurred the respective years after the two extreme ENSO events during the study period. In the second year after those events, the net change of eggs buried in hatcheries bounced back to resume the overall positive trend. Our results suggest a clear upward trend, resilient to ENSO variability, of the nesting abundance of the Pacific coast Olive Ridley population in Guatemala. Community-based hatchery management efforts seem to be effective for Olive Ridley conservation on the Pacific coast of Guatemala. However, longer term monitoring

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including additional nesting beaches in northern Central America are necessary to further elucidate the effects of ENSO variability on the nesting abundance of Olive Ridley.

1. Introduction

An increase in climate variability caused by current climate change is greatly affecting biodiversity and annual phenological cycles of many animal species (Cohen et al., 2018). Data series obtained through series of successive observations along several years can reveal long-term trends that may reflect climatic or anthropogenic influences (Sukhotin and Berger, 2013). Long-term monitoring permits the separation of these trends from the noise of highly variable natural data and is especially relevant for the assessment of conservation actions in the context of climatic change (Sukhotin and Berger, 2013; Cheney et al., 2014; Rodríguez-González et al., 2017; Guerra et al., 2019). The El Niño Southern Oscillation (ENSO) is the strongest interannual pattern of climate fluctuation in the world, resulting in global disruption of weather patterns and ecosystem functions (McPhaden et al., 2006; Santoso et al., 2017). Climate change is expected to double the frequency of ENSO events compared to pre-industrial levels, maintaining an increasing trend that will persist long after the stabilization of greenhouse warming (Cai et al., 2014, 2015b; Wang et al., 2017). ENSO involves an irregular alternation between El Niño phases, which consist of increased sea surface temperature and decreased ocean productivity (Cai et al., 2014), and La Niña phases, which show contrary effects (Cai et al., 2015b). Extreme El Niño and La Niña are characterized by even warmer/colder sea surfaces, with Extreme El Niño phase originating in the eastern equatorial Pacific while extreme La Niña phase originates in the central Pacific (McPhaden et al., 2006; Cai et al., 2015a).

Increased climate variability, such as ENSO patterns, might have profound effects on ectothermic organisms such as sea turtles, since environmental cues largely dictate their metabolic rate, sex ratios, migration patterns and affect their phenological cycles (Hawkes et al., 2009; Quiñones et al., 2010; Castro et al., 2012; Patrício et al., 2019; Godley et al., 2020). Sea turtles are known to have clear interannual variability in the number of females nesting at their breeding beaches as females typically do not nest in consecutive years, and spend time feeding at sea between successive nesting years (Broderick et al., 2001; Solow et al., 2002). El Niño events have shown some influence on the interannual variability of the nesting abundance of Leatherbacks (*Dermochelys coriacea*), which is under severe decline in the Pacific, due to egg harvesting and bycatch in fisheries (Saba et al., 2007; Reina et al., 2009; Santidrián-Tomillo et al., 2012, 2020). A recent study carried out over 7 years at six beaches in Costa Rica found no clear correlation between El Niño events and the nesting abundance of Green Turtles (*Chelonia mydas*) and Olive Ridleys (*Lepidochelys olivacea*) but highlighted the relevance of conducting longer term site-specific analyses for these species (Santidrián-Tomillo et al., 2020). However, Green Turtles and Olive Ridleys in the eastern Pacific are showing encouraging populations recoveries in recent years (Ocana et al., 2012; Seminoff et al., 2015; Bézy et al., 2016). The effects of La Niña and overall ENSO variability on the nesting numbers of other sea turtle species has not been studied.

The Olive Ridley is the most abundant sea turtle species in the world (López-Castro et al., 2004; Plotkin et al., 2006; Eguchi et al., 2007; Plotkin, 2010; Dornfeld et al., 2015), and is classified as Vulnerable in the IUCN Red List of Threatened Species (Abreu-Grobois and Plotkin, 2008). In Central America, harvesting of Olive Ridley eggs for local consumption is considered to be one of the species' major threats (Juarez and Muccio 1997; Fonseca et al., 2009; Valverde et al., 2012; Bézy et al., 2016), therefore nest relocation to protected hatcheries is considered an effective conservation management tool for this species (García et al., 2003). The oldest of these hatcheries in Guatemala was established in 1979 and is located at Hawaii beach (Juarez and Muccio, 1997). In recent years, upward trends in sea turtle populations in areas with ongoing long-term sea turtle conservation programs were reported (Ceriani et al., 2019; Godley et al., 2020; Laloë et al., 2020). The identification of proxies of essential variables for long-term monitoring of population trends of endangered species is fundamental for the optimization of conservation efforts in the context of increased climate variability (Guerra et al., 2019). In the case of sea turtles, nesting tracks and number of eggs collected at index beaches are commonly used as effective proxies of their nesting abundance following the Index Nesting Beach Survey (INBS) protocol (SWOT Scientific Advisory Board, 2011).

Herein, we present the first long-term study of Olive Ridley population trends and potential relationships with ENSO variability in northern Central America, using nesting tracks and numbers of eggs buried in hatcheries as proxies of their nesting abundance. Our objectives were to (1) estimate the trend of the nesting abundance of Olive Ridley females, and (2) evaluate the effects of ENSO variability on the nesting abundance of Olive Ridleys on the Pacific coast of Guatemala over a 16-year period (2003–2018). We predicted an upward trend in the abundance estimates of annual nesting females as a result of long-term conservation efforts, such as egg harvest limits, fisheries bycatch mitigation and hatcheries, carried out on the Pacific coast of Guatemala since 1979. Also, we predicted a negative effect of ENSO variability on the nesting abundance of this species.

2. Materials and methods

2.1. Study area

The fieldwork was conducted at Hawaii Beach (13.869012°N, −90.419519°W), a volcanic sand beach located 2 km west of the village of Hawaii, Chiquimulilla, Santa Rosa, on the Pacific coast of Guatemala (Fig. 1a). This beach is located within the Hawaii Protected Area (HPA), a 4000 ha multiple-use zone declared in 2016 that includes one of the largest mangrove wetlands in the country. Five villages are located along the coastline, with small hotels and vacation homes concentrated near the village of Hawaii. Residents of these villages traditionally subsist on fishing, mangrove logging, agriculture and sea turtle egg collection, but tourism is an increasingly important economic activity. The Wildlife Rescue and Conservation Association (ARCAS) administers the HPA from its base at the Hawaii Park, also home to the Hawaii hatchery, the oldest, and historically one of the most productive sea turtle hatcheries on the Pacific coast of Guatemala. Since 1993, ARCAS has operated sea turtle hatcheries in Hawaii and in the village of El Rosario, 6 km to the east, collecting and incubating 40,000–60,000 Olive Ridley eggs per year (Juarez and Muccio, 1997; Brittain et al., 2007). Along with these efforts, ARCAS has carried out standardized nesting track surveys along a 7.5 km transect (Fig. 1b) for monitoring the abundance of annual nesting female Olive Ridleys (Fig. 1c) since 2003.

In-situ incubation of nests is almost non-existent on the Guatemalan Pacific coast, as egg harvesting is an important local economic activity, and local villagers sell the eggs collected to the hatcheries for their re-burial (Fig. 1d). Depending on the resources available, between 25 and 35 other sea turtle hatcheries operate per year along the 254 km Pacific coastline of Guatemala. Under a program sanctioned by the government's National Council of Protected Areas (CONAP), local villagers are permitted to harvest Olive Ridley eggs as long as they give 20% of each nest as a conservation quota, which then is distributed along the active sea turtle hatcheries for re-burial and incubation (Brittain et al., 2007). The central government lacks the resources to implement sea turtle conservation efforts on its own, and a number of private and public sector stakeholders, including non-governmental organizations (NGOs), educational institutions, universities, schools, hotels, and vacation homeowners sponsor sea turtle hatcheries. In theory, only Olive Ridley eggs are allowed for harvesting; all other species are fully protected by law.

2.2. Study species

The Olive Ridley has a circumtropical distribution, occurring in the Atlantic, Pacific, and Indian Oceans (Seminoff et al., 2015). It is one of the smallest of the marine turtles, rarely exceeding 45 kg, with average weights around 35 kg

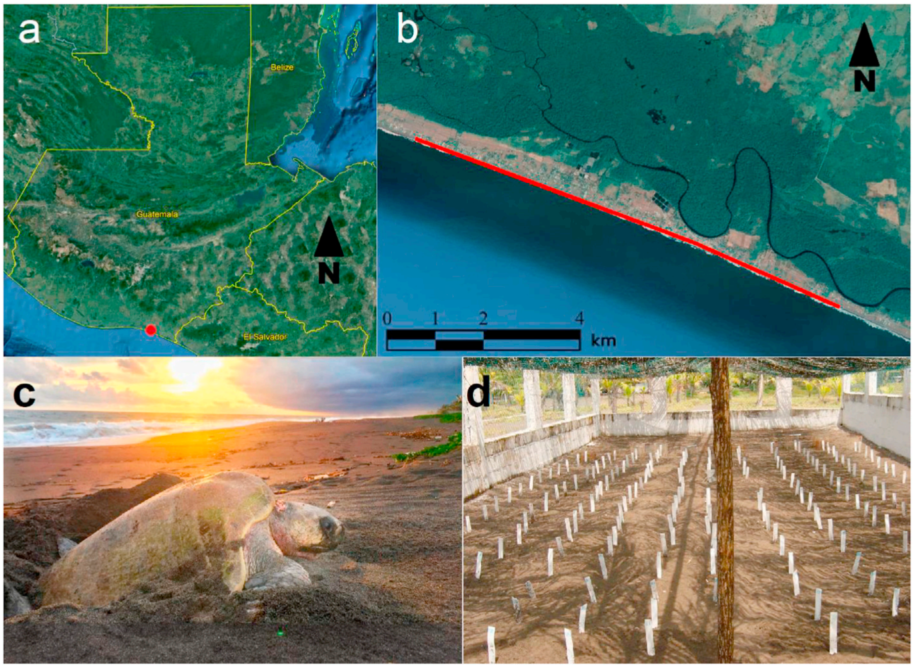

Fig. 1. Study area Hawaii beach (red dot) on the Pacific coast of Guatemala, Central America (a), location of nesting track monitoring transect (red line) at Hawaii beach (b), Olive Ridley (*Lepidochelys olivacea*) nesting at Hawaii beach, in Guatemala (c), and inside view of the Hawaii sea turtle hatchery, where relocated eggs are incubated under protected and controlled conditions (d). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

(Pritchard, 1979). The mean age at sexual maturity for this species is around 13 years (Zug et al., 2006). Olive Ridleys display two different types of nesting behavior: synchronized mass nesting, known also as arribada, and solitary nesting (Plotkin et al., 2006; Matos et al., 2012). Nesting in Guatemala consists only of solitary nesting that occurs between June and October with peak activity in August and September, although sporadic nesting occurs year around (Juarez and Muccio, 1997).

Olive Ridleys can exhibit strong nesting site fidelity (Matos et al., 2012). They have a maximum of two nesting events per year, every two years with an internesting period ranging from 16 to 25 days (Barrientos-Muñoz et al., 2014). In other parts of Central America, the average clutch size for the species is around 100 eggs per clutch (Da Silva et al., 2007; Valverde et al., 2012), although in Guatemala, clutch size is reported to be 92.7 ± 7.4 eggs (Muccio, 2019).

2.3. El Niño Southern Oscillation variability

We evaluated El Niño Southern Oscillation (ENSO) variability using the Revised Multivariate ENSO Index (MEI.v2) which is a composite of five variables: sea level pressure, sea surface temperatures, 10-m surface zonal wind, 10-m surface meridional wind, and outgoing longwave radiation (Zhang et al., 2019). MEI.v2 captures a more holistic picture of the state of ENSO than do sea surface temperature-based indices (Zhang et al., 2019). We estimated the average of MEI.v2 for the nesting season (July–December) of each year during the study period. ENSO events were considered as extreme when MEI.v2 $> +1.5$ (extreme El Niño) or MEI.v2 < -1.5 (extreme La Niña), normal El Niño when MEI.v2 was between $+0.5$ and $+ 1.5$, normal La Niña when MEI.v2 was between -1.5 and -0.5, and neutral years when MEI.v2 was between -0.5 and $+ 0.5$, during the July–December nesting season. The MEI.v2 data were obtained from the Physical Sciences Laboratory (PSL) of the National Oceanic and Atmospheric Administration (NOAA) of the United States of America (PSL, 2020).

2.4. Nesting tracks

Nesting tracks were registered as a proxy for abundance of nesting of Olive Ridley females at the study site, as they are considered an effective estimate for relative abundance of nesting sea turtles especially on beaches with solitary nesting, where the probabilities of confusing nesting tracks from different individuals are low (SWOT Scientific Advisory Board, 2011). The procedure we followed was an adaptation of the Index Nesting Beach Survey (INBS) protocol (SWOT Scientific Advisory Board, 2011). The INBS protocol has proven to be useful for nesting trend assessments and accurate comparisons between years due to fixed start and end dates, fixed time window for daily early-morning surveys, fixed survey boundaries, and specialized standardized training of the different beach surveyors that record the nesting tracks every year (Ceriani et al., 2019). Monitoring the numbers of nesting tracks has the advantages of reduced confusion in the count, and requires less effort needed to perform surveys, but as disadvantage, it doesn't account for variation in nesting success or clutch frequency (SWOT Scientific Advisory Board, 2011).

In our case, the Olive Ridley population-monitoring protocol consists of daily early-morning nesting track count patrols, carried out between July 1st and December 31st (fixed start and end dates, respectively) along the transect (boundaries fixed between 13.879112° N, −90.451536°W and 13.853776° N, −90.385770°W) at Hawaii beach for the period 2003–2018. Trained surveyors hired from local villages identified Olive Ridley nesting tracks according to their shape, flipper pattern and depth, thus confirming nests and distinguishing false crawls. The ending point (body pit) of each nesting track was marked with a GPS location. After marking, the tracks were erased, to prevent repeated counting. Nesting tracks for 2012 were not recorded because of logistical difficulties with the trained staff that year.

The probability of confusion of the species is extremely low because the vast majority (at least 99%) of the sea turtle nests recorded every year for the last 30 years on the Pacific coast have been Olive Ridleys, with infrequent Green Turtle and Leatherback nests (Juarez and Muccio, 1997; Brittain et al., 2007). The only documented nesting of a Hawksbill (*Eretmochelys imbricata*) at the Pacific coast of Guatemala was recorded in 2018 (Muccio and Izquierdo, 2019).

2.5. Number of eggs buried in hatcheries

Number of eggs buried in hatcheries were registered as a complementary proxy of abundance of nesting Olive Ridley females at the study site. Number of eggs harvested or collected are considered an effective estimate to monitor relative abundance of nesting sea turtles as they are a direct measure of their reproductive output (SWOT Scientific Advisory Board, 2011). We used official data of the total number of eggs collected and re-buried in all the sea turtle hatcheries along the 254 km of the Pacific coast of Guatemala, gathered by CONAP. Monitoring the number of eggs buried in hatcheries has the advantage that eggs harvested or collected regularly can be used to monitor relative nesting abundance but has the disadvantage that is difficult to account for variation in clutch size or clutch frequency (SWOT Scientific Advisory Board, 2011). Often, clutches that are laid on one beach are transported, and then buried in hatcheries relatively far from the nesting site. Therefore, it is not possible to make any statement on which part of the coast the eggs actually come from. Eggs from different nests are often combined in the process of collection and transfer, therefore we analysed the total numbers of egg buried in all the operating sea turtle hatcheries for every given year during the 16-year study period, rather than the number of nests, as a proxy for nesting trends on the Pacific coast of Guatemala. In addition, the net change of eggs buried in hatcheries between consecutive years (in percentage) was estimated as a descriptive tool in visualizing annual changes in nesting abundance according to the occurrence of extreme ENSO events. This net change of eggs buried in hatcheries was calculated using the following formula: (*Total number of eggs buried in hatcheries for the actual year − Total number of eggs buried in hatcheries the year before*)/*Total number of eggs buried in hatcheries the year before* * 100.

2.6. Statistical analysis

We examined the annual trends of nesting tracks and eggs buried in hatcheries with generalized linear models (GLM) with negative binomial distribution to correct for overdispersion (Lindén and Mäntyniemi, 2011), using year and MEI.v2 as fixed effects. Interaction between the fixed effects was included in the list of candidate models to expand the understanding of the relationship among year and MEI.v2 values. The fixed effects used in all analyses were not correlated (Pearson r coefficient < 0.5), and variance inflation factor values were <3 (Zuur et al., 2010). Residuals plots were analysed, showing that homogeneity and normality of residual variance were fulfilled (Zuur et al., 2010).

We developed a list of candidate models based on our hypotheses. Candidate models were analysed with the MASS package (Venables and Ripley, 2002). We carried out model selection based on Akaike's Information Criterion corrected for small sample size (AICc) (Burnham and Anderson, 2002) to obtain the most parsimonious models and parameter estimates using the MuMIn package (Barton, 2020). When multiple candidate models showed the same level of performance (cumulative Akaike weight > 0.95), we performed model averaging to examine the overall effect size of the predictor variables (Symonds and Moussalli, 2011; Dormann et al., 2018; Harrison et al., 2018). Parameters that included zero within their 95% confidence interval (CI) were considered as uninformative (Arnold, 2010). Mean values are given with standard errors (SE). All analyses were conducted in R 3.6.2 using the RStudio 1.3.959 interface (R Core Team, 2020).

3. Results

We registered 21,775 Olive Ridley nesting tracks at Hawaii beach and 3,740,009 Olive Ridley eggs buried in all hatcheries on the Pacific coast of Guatemala, over the 16-year study period. On average 1520 ± 477 Olive Ridley nesting tracks were registered annually at Hawaii beach, ranging from 906 nesting tracks in 2003 to 2134 in 2017. The mean number of Olive Ridley eggs buried annually in the hatcheries along the Pacific coast of Guatemala was 233,750 ± 172,682, ranging from 46,048 eggs in 2003 to 590,405 in 2018. During this 16-year study period, ENSO variability was distributed in eight neutral years, two normal El Niño years, four normal La Niña years and two extreme ENSO events: La Niña in 2010 and El Niño in 2015 (Table 1).

The models of best fit for predicting the nesting abundance of Olive Ridleys over the study period included year alone or both year and MEI.v2 as fixed effects. Neither MEI.v2 values alone nor the interaction between MEI.v2 values and year were good predictors of nesting abundance in our model selection procedure (Table 2 and Table 3).

3.1. Nesting abundance trends over the 16-year study period

There was a clear upward trend in the number of Olive Ridley nesting tracks and the overall number of eggs buried in hatcheries for the period 2003–2018 (Fig. 2). We found a 236% increase in the number of nesting tracks and a 1282% increase in the number of eggs buried in hatcheries during the same period (Table 1). Nesting tracks showed a wider dispersion of data than the number of eggs buried in hatcheries in our negative binomial fit. According to the effect size of year (Table 3), the

Table 1
Olive Ridley nesting tracks at Hawaii beach, number of Olive Ridley eggs buried in the hatcheries on the Pacific coast of Guatemala, and Revised Multivariate El Niño Southern Oscillation (ENSO) Index (MEI.v2) during the peak nesting season (July–December). Years of extreme ENSO events occurrence are presented in *italics*. Nesting tracks for 2012 were not recorded.

Year	Nesting tracks at Hawaii beach (n)	Total number of eggs buried in all the hatcheries (n)	MEI.v2	MEI.v2 type[a]	Net change in number of eggs buried in hatcheries (%)
2003	906	46,048	0.13	N	–
2004	1,001	60,681	0.48	N	31.78
2005	1,043	85,376	−0.35	N	40.70
2006	1,138	109,839	0.58	EN	28.65
2007	1,280	108,861	−1.03	LN	−0.89
2008	1,370	129,482	−1.03	LN	18.94
2009	1,101	129,526	0.68	EN	0.03
2010	*1,520*	*189,749*	*−2.20*	*ELN*	*46.49*
2011	1,594	172,648	−1.13	LN	−9.01
2012	–	202,310	−0.08	N	17.18
2013	1,237	267,217	−0.40	N	32.08
2014	1,867	311,503	0.18	N	16.57
2015	*2,042*	*394,699*	*1.95*	*EEN*	*26.71*
2016	1,564	352,392	−0.42	N	−10.72
2017	2,134	589,273	−0.70	LN	67.22
2018	1,978	590,405	0.25	N	0.19

[a] N: neutral, EN: El Niño, LN: La Niña, EEN: extreme El Niño, ELN: extreme La Niña.

Table 2
Summary of generalized linear models (GLM) selection for nesting abundance of Olive Ridley sea turtles showing model log-likelihood (LL), Akaike Information Criterion corrected for small sample sizes (AICc), change in AICc (ΔAICc) and AICc weight (wAICc).

Candidate models	LL	AICc	ΔAICc	wAICc
(a) Olive Ridley nesting tracks				
Nesting tracks ~ Year	−91.85	192.1	0.00	0.83
Nesting tracks ~ Year + MEI.v2[a]	−91.77	196.0	3.87	0.12
Nesting tracks ~ Year + MEI.v2 + Year*MEI.v2[a]	−90.17	197.8	5.73	0.05
Nesting tracks ~ MEI.v2	−102.30	213.0	20.89	0.00
(b) Number of Olive Ridley eggs buried in hatcheries				
Number of eggs ~ Year	−159.51	327.4	0.00	0.87
Number of eggs ~ Year + MEI.v2[a]	−159.50	331.4	4.03	0.12
Number of eggs ~ Year + MEI.v2[a] + Year*MEI.v2[a]	−159.36	336.2	8.80	0.01
Number of eggs ~ MEI.v2[a]	−185.56	379.5	52.10	0.00

[a] Revised Multivariate El Niño Southern Oscillation Index.

Table 3
Effect size (β), standard error (SE), lower (LCI) and upper (UCI) 95% confidence interval of the explanatory variables for the analyses of Olive Ridley nesting (annual nesting tracks at Hawaii beach and annual total number of eggs buried in hatcheries) on the Pacific coast of Guatemala from 2003 to 2018. Informative parameters are given in **bold**.

Variables	Effect size (β)	SE	LCI	UCI
(a) Olive Ridley nesting tracks at Hawaii beach				
Intercept	−92.24	15.86	−123.33	−61.16
Year	**0.05**	**0.01**	**0.03**	**0.06**
MEI.v2[a]	−0.002	0.01	−0.03	0.03
(b) Number of Olive Ridley eggs buried in hatcheries				
Intercept	−295.34	14.56	−323.87	−266.82
Year	**0.15**	**0.01**	**0.14**	**0.17**
MEI.v2[a]	−0.0004	0.01	−0.02	0.02

[a] Revised Multivariate El Niño Southern Oscillation Index.

upward trend was steeper in the number of Olive Ridley eggs buried in hatcheries than in the number of nesting tracks at Hawaii beach.

3.2. ENSO variability effects on nesting abundance

ENSO variability measured with the MEI.v2 values had no effect on the upward trend in Olive Ridley nesting abundance proxies (number of nesting tracks and the number of eggs buried in hatcheries) for the period 2003−2018 (Table 3).

The annual patterns in the net change of eggs buried in hatcheries showed a decrease occurring in the respective first year after the two extreme ENSO events that happened during our study period (Fig. 3). The year after the extreme La Niña event of 2010 showed a decrease of 9.01% (2011) and the year after the extreme El Niño event of 2015 showed a decrease of 10.71% (2016) in the total number of eggs buried in hatcheries between consecutive years. Despite these two yearly decreases, the net change of eggs buried in hatcheries increased again in the second year after those extreme ENSO events, resuming the overall upward trend in the numbers of eggs buried.

4. Discussion

Our findings provide evidence of an increasing trend in the nesting abundance of Olive Ridley sea turtles on the Pacific coast of Guatemala during the 16-year study period. There was no clear effect of ENSO variability measured with the MEI.v2 index on Olive Ridley nesting tracks. A more detailed exploration of the annual net change of eggs buried in hatcheries according to the ENSO type of each year showed a decrease occurring in the respective first year after the extreme ENSO events during our study period. However, the net change of eggs buried in hatcheries bounced back to positive values two years after these extreme events.

4.1. Nesting abundance trends over the 16-year study period

The upward trend in the nesting abundance of Olive Ridleys on the Pacific coast of Guatemala is consistent with the recovery of other populations of sea turtle species, as for example, at several disjunct Green Turtle nesting beaches all around the world with long-term, community-based conservation programs (Troëng and Rankin, 2005; Seminoff et al., 2015; Silva et al., 2017; Patrício et al., 2019). In recent years, more examples of modest upward trends in population numbers have

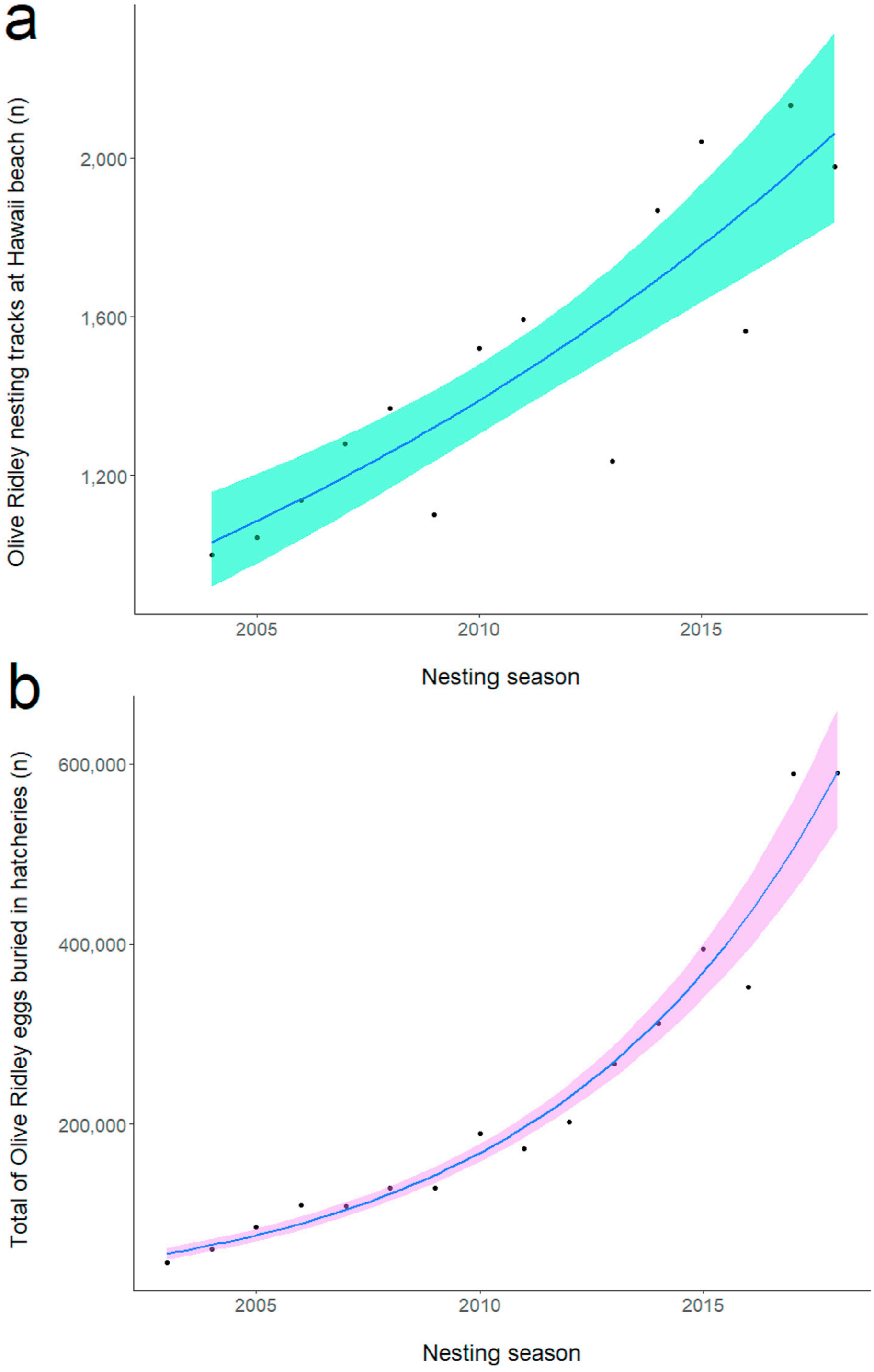

Fig. 2. Annual trends in Olive Ridley nesting tracks at Hawaii beach (a) and number of eggs buried in hatcheries along the Pacific coast of Guatemala (b) during the period 2003−2018. Predicted values by the most parsimonious models are shown in solid blue line with 95% confidence intervals shaded in color. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

also been reported, among many others, for Hawksbills at American Samoa and Marianas islands in the western Pacific (Becker et al., 2019) and Loggerheads (*Caretta caretta*) at Cape Verde archipelago in western Africa (Laloë et al., 2020). These upward trends in sea turtle populations at the local level are believed to be a result of long-term conservation programs that involve beach protection, mitigation of fisheries bycatch and the use of hatcheries for nest translocation (García et al., 2003;

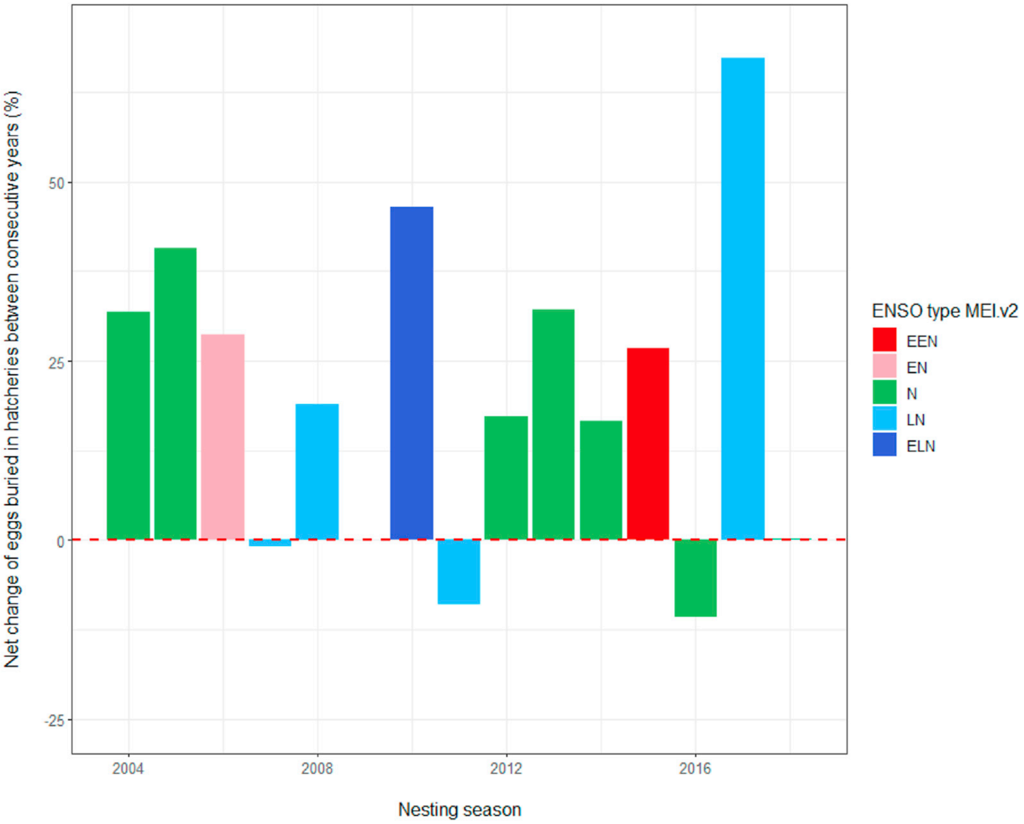

Fig. 3. Annual net change in percentage of Olive Ridley eggs buried in hatcheries between consecutive years along the Pacific coast of Guatemala reported for the period 2003–2018. Bars are colored according to El Niño Southern Oscillation (ENSO) phase type based on the Revised Multivariate ENSO Index (MEI.v2). EEN: extreme El Niño ($MEI.v2 < -1.5$), EN: El Niño ($+0.5 < MEI.v2 < +1.5$), N: neutral years ($-0.5 < MEI.v2 < +0.5$), LN: La Niña ($-1.5 < MEI.v2 < -0.5$), ELN: extreme La Niña ($MEI.v2 < -1.5$) in the corresponding nesting season year.

Ceriani et al., 2019; Godley et al., 2020). However, among sea turtles, Leatherbacks have shown dramatic declines presumably due to overharvesting of eggs, fisheries interactions in the open ocean and climate change (Saba et al., 2007; Reina et al., 2009; Santidrián-Tomillo et al., 2012).

Of the extant sea turtle species, the Olive Ridley is one of the species that have shown more robust population recovery in recent years (Eguchi et al., 2007; Peavey et al., 2017) after extremely low numbers in the past century (Fonseca et al., 2009). A very notable recovery documented for Olive Ridleys has occurred at Escobilla beach, in Oaxaca Mexico, which in the 1980s was almost decimated and has since recuperated to become one of the largest arribada sites in the world (Hernández-Echeagaray et al., 2012; Ocana et al., 2012). Other sites with notable Olive Ridley recoveries are Ostional, in Costa Rica (Valverde et al., 2012; Bézy et al., 2016), La Flor, in Nicaragua (Honarvar et al., 2016), Sergpipe, in Brazil (Da Silva et al., 2007) and Gahirmatha, in India (Behera et al., 2010).

Our findings show that the nesting population of Olive Ridleys at the Hawaii beach in Guatemala might also be recovering, after over-harvesting of eggs caused extremely low nesting numbers that were first documented in the late 1990s (Juarez and Muccio, 1997). Taking into account that Olive Ridleys reach sexual maturity at an age of approximately 13 years (Zug et al., 2006), we consider our 16-year study period as representative to detect nesting population trends at the site. *In-situ* nest incubation of Olive Ridleys has almost been non-existent in Guatemala during the last decades, which suggests the positive nesting trends are likely the result of almost 30 years of intensive, participatory, hatchery-based conservation efforts. Long-term conservation efforts that include beach protection and nest relocation to hatcheries have also contributed to reversing nesting declines of endangered sea turtle populations such as Green Turtles at Tortuguero, Costa Rica (Troëng and Rankin, 2005) and Olive Ridleys at Playa Cuixmala, México (García et al., 2003). However, our results need to be interpreted with caution as they represent only a fraction of the Olive Ridley population, the nesting females, at the Pacific coast of Guatemala, and conservation actions, such as the 20% conservation quota for egg collectors, must be maintained on site.

4.2. ENSO variability effects on nesting abundance

The absence of clear ENSO effect measured with the Multivariate ENSO Index (MEI) on the nesting abundance of Olive Ridleys is consistent with the findings of a 7-year period study (2011–2018) carried out in Costa Rica (Santidrián-Tomillo et al., 2020). These authors consider that the lack of correlation between MEI and the nesting numbers of Green Turtles and Olive Ridleys in their study may be explained by too few study years to identify long-term patterns and the prevalence of average neutral ENSO conditions (only two non-neutral ENSO years). In our 16-year study period, we encompass eight non-neutral ENSO years, but still face limitations since the ENSO variability was distributed in eight neutral years, two El Niño years, four La Niña years and only two extreme ENSO events: La Niña in 2010 and El Niño in 2015. However, the absence of clear ENSO effects on the nesting abundance of Olive Ridleys may also be explained by the species' trophic position as benthic carnivores. They feed on crabs, shrimps, bivalves, and benthonic fishes, which are generally present in some form during all years, allowing them to switch prey items to maximize energy intake and thus maintain nesting output (Wildermann and Barrios-Garrido, 2012; Colman et al., 2014; Poggio et al., 2014). Benthic carnivorous sea turtle species such as Loggerheads are known to present less interannual variability than herbivorous species such as Green Turtles (Broderick et al., 2001).

Our results showed a decrease in the annual net change of Olive Ridley eggs buried in hatcheries in the first year following an extreme ENSO event, but no decrease in the net change of nesting track numbers. Unfortunately we were unable to determine if these reductions are consistent over time due to the small number of extreme ENSO events (extreme La Niña of 2010 and extreme El Niño of 2015) during the study period. The decrease in the annual net change of eggs buried in hatcheries without a clear reduction of nesting tracks the year after the extreme ENSO events can be a product of a decrease in the number of eggs per clutch laid by females, while the numbers of nesting females at the site remain the same. A similar decrease in the reproductive output was found in Green Turtles during and after extreme ENSO events (Santidrián-Tomillo et al., 2020). Reduced marine food abundance is a common effect of extreme ENSO events (Chavez et al., 2011), and this could prevent sea turtles from accumulating sufficient body fat for the breeding season of the following year, leading to a reduction in reproductive output and average number of eggs per clutch (Bjorndal et al., 2017). Alternatively, the impact of extreme ENSO events on Olive Ridley populations may not be significant given the multiple breeding events during their long lifetime (Santidrián-Tomillo et al., 2020), their relatively short time for reaching sexual maturity (Zug et al., 2006), and their migratory flexibility to adapt to their large dynamic marine ecosystem (Plotkin, 2010; Peavey et al., 2017). Additionally, Olive Ridley populations that are subject to hatchling production in managed hatcheries may be more resilient to the long-term effects of ENSO variability on nesting trends, as these hatcheries artificially control nest temperatures and protect against nest predation.

The identification of proxies of essential variables for long-term monitoring is useful for the optimization of available operational resources (Guerra et al., 2019). We suggest a continuing long-term monitoring of both proxies of Olive Ridley nesting abundance (number of eggs buried in hatcheries and nesting tracks) as both are complementary and can provide a clearer picture of the nesting population trend and its relationship to extreme ENSO events at the study site. On the one hand, the number of eggs buried in hatcheries has a lower dispersion of data during the study period and are a more direct measurement of the reproductive output than nesting track counts. On the other hand, nesting tracks are independent of the capacity of the hatcheries to purchase eggs in addition to the 20% conservation quota, although they are subject to the abilities of local patrollers to accurately detect nesting tracks. In the end, community-based monitoring of nesting beaches is often considered as the only feasible and low-cost approach for assessing sea turtle populations in developing countries (Olendo et al., 2019).

4.3. Relevance of community-based conservation efforts of sea turtle hatcheries

Although sea turtle conservation has taken a largely non-consumptive approach over the last decades, there is a clear need to adapt conservation strategies to include sustainable use by local communities (Valverde et al., 2012; Godley et al., 2020). In recent years, sea turtle hatcheries on the Pacific coast of Guatemala have incorporated local egg collectors in their management and have also benefitted from increased support from hotels and vacation home owners for the purchase of eggs for the hatcheries. Since 2017, most sea turtle egg collectors have preferred to sell the remnant 80% of the eggs they collect to hatcheries, instead of selling them for human consumption, knowing that the eggs sold to hatcheries are contributing to the conservation of the species. This has evolved into a win-win relationship between local egg collectors and sea turtle hatcheries. Locals receive economic benefits from their egg collection work, and sea turtle hatcheries receive increased numbers of eggs for *ex-situ* incubation, raising the number of Olive Ridley hatchlings released every year. This increased capacity of hatcheries to buy eggs in addition to the 20% conservation quota may explain the steeper increase in the number of eggs buried in hatcheries particularly shown in the last three years, compared to the increase in the number of nesting tracks over the same period.

In developing countries, the empowerment of local communities has shown to be fundamental for success in natural resources management, especially when conservation actions contribute to create local livelihoods (Barrientos-Muñoz et al., 2014; Nilsson et al., 2016; Olendo et al., 2019). Olive Ridley eggs make a significant contribution to the local economies of the villages at the Pacific coast of Guatemala. Thus, we recommend the continuation of the 20% conservation quota along with the strengthening of the win-win relationship between sea turtle hatcheries and local eggs collectors.

Further studies are required to determine if the current hatchling production in the hatcheries along the Pacific coast of Guatemala is sufficient to maintain a stable Olive Ridley population. Age-specific mortality rates, sex ratios, shoreline habitat destruction and numbers of pelagic adults are still unknown factors for this population. However, strengthening the community-based conservation efforts at Guatemalan sea turtle hatcheries seems fundamental to ensuring the resilience of Olive Ridleys to ENSO variability and other aspects of climate change.

5. Conclusions

Our results suggest a clear increase in nesting abundance of the Olive Ridley sea turtle population along the Pacific coast of Guatemala over our 16-year study period. This upward trend in nesting abundance was resilient to ENSO variability. Given only two extreme events occurred during the time frame of our study, continued long term monitoring will better elucidate the possible effects of extreme ENSO events on the nesting abundance of Olive Ridleys. Nonetheless, community-based hatchery management efforts seem to be essential for this population to cope with increased ENSO variability.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2020.e01339.

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Article 3

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ARTICLE

Climate Ecology

Temperature and barometric pressure affect the activity intensity and movement of an endangered thermoconforming lizard

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Abstract

Global warming is expected to affect movement-related thermoregulation in ectotherms, but the likely effects on thermoconforming lizards, which spend little energy in thermoregulation behavior, are unclear. We used the Guatemalan beaded lizard (*Heloderma charlesbogerti*) as a model thermoconforming species to investigate the effects of ambient temperature and barometric pressure (a cue for rain in the study area) on activity intensity and the structure of movement paths. We tracked 12 individuals over a total of 148 animal days during the wet season of 2019 using Global Positioning System tags and triaxial accelerometry. We found a clear positive effect of ambient temperature on activity (using vectorial dynamic body acceleration [VeDBA]) and step length of lizard movements. The movement also became more directional (longer step lengths and smaller turning angles) with increasing ambient temperatures. There was a small negative effect of barometric pressure on VeDBA. We propose that our patterns are indicative of internal state changes in the animals, as they move from a state of hunger, eliciting foraging, which is enhanced by lower temperatures and rainfall to a thermally stressed state, which initiates shelter-seeking. Our findings highlight the sensitivity of this species to temperature change, show that not all thermoconforming lizards are thermal generalists, and indicate that predicted regional increases in temperature and reduction in rainfall are likely to negatively impact this species by reducing the width of their operational thermal window.

KEYWORDS
accelerometry, barometric pressure, climate change, Daily Diaries, dry forest, ectotherms, global warming, *Heloderma charlesbogerti*, movement ecology, reptiles, thermal biology, vectorial dynamic body acceleration

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Stefanie Reinhardt and Frank Rosell contributed equally to this study.

INTRODUCTION

Global warming will seriously affect the physiological homeostasis of a wide variety of animals, especially as temperatures reach species upper thermal tolerance limits (Bozinovic & Pörtner, 2015; Silva et al., 2015; Somero, 2010). These effects are a particular cause for concern in ectotherms such as marine invertebrates (Johnson & Hofmann, 2020; Lefevre, 2016; Stuart-Smith et al., 2015), insects (Sales et al., 2018; Zeuss et al., 2014), fishes (Alfonso et al., 2021; Lema et al., 2016; Weber et al., 2015), amphibians (Rohr & Palmer, 2013; Scheffers et al., 2013; Thurman & Garcia, 2017), and reptiles (Nowakoski et al., 2020; Rodgers et al., 2015; Sinervo et al., 2010) because elevated temperatures not only increase metabolic rate (Garcia-Robledo et al., 2020) but also initiate changes in behavior (Gibert et al., 2016). For example, ectotherms may invest large amounts of time and energy moving between places to maintain their body temperatures within a specific range of temperatures, thereby attempting to optimize physiological processes (Ohlberger, 2013; Rolland et al., 2018). Global warming is thus expected to increase such movement-related thermoregulation energy expenditures in ectotherms, most particularly as many species have limited potential to change their thermal limits (Gunderson & Stillman, 2015; Hoffmann et al., 2013; Kearney et al., 2009; Paaijmans et al., 2013; Pinsky et al., 2019).

Within vertebrate ectotherms, lizards show behavioral adaptations in their thermoregulation strategies that may either amplify or mitigate the impacts of global warming on their survival (Diele-Viegas et al., 2018; Jara et al., 2019; Lara-Reséndiz et al., 2021; Meiri et al., 2013; Piantoni et al., 2016; Sinervo et al., 2010). Specifically, behavioral thermoregulation in lizards is manifest in a continuum of behavioral adaptations that ranges between two very disparate strategies: active thermoregulation and thermoconformity (Huey & Slatkin, 1976; Pianka & Vitt, 2003). The most actively thermoregulating lizards maintain their internal body temperature within a narrow range by moving rapidly between sites according to temperature (Sannolo et al., 2019), and therefore do not show a linear relationship between overall ambient temperature and body temperature. Conversely, the most thermoconforming lizards react little to the heterogeneity in temperature at different sites on short timescales and therefore have a body temperature close to ambient temperature. This strategy reduces the metabolic costs of movement but means that the metabolic rate of thermoconformers is driven primarily by ambient conditions (Herczeg et al., 2003). Importantly though, even thermoconforming lizards react to changes in the environment to some degree, so across the spectrum of lizard thermoregulators and thermoconformers, the extent of species-specific movement due to local temperature depends on temperature heterogeneity across time and space and species-specific strategies.

Understanding the strategies behind the movement ecology of any animal is challenging anyway (Nathan et al., 2008) but is particularly so in lizards, where multiple abiotic movement elicitors such as irradiation, temperature, surface water, and humidity play an important role (Cabezas-Cartes et al., 2019; DeNardo et al., 2003; Diele-Viegas et al., 2018; Lara-Reséndiz et al., 2021; Pianka & Vitt, 2003) above and beyond other biological movement elicitors such as predation and foraging (Du et al., 2000; Sannolo et al., 2019).

Helodermatid lizards are good models to explore the effects of rising temperatures on the movement strategy of thermoconforming lizards due to the simplicity of the major drivers of their movements. During the dry season, they aestivate as they show low tolerance to high body temperatures, even though they inhabit hot and xeric environments (Aranda-Coello et al., 2019; Beck, 2005; DeNardo et al., 2003). During the wet season, their movements are primarily driven by three internal states (Nathan et al., 2008): finding mates, finding food, and locating thermal refugia underground for post-movement habitation or presumably when it becomes too hot (Ariano-Sánchez et al., 2020; Beck & Jennings, 2003).

Accordingly, we used the Guatemalan beaded lizard (*Heloderma charlesbogerti*), an endangered Helodermatid with a restricted range within Guatemala in Central America (Mata-Silva et al., 2019), as a model species to investigate the change in state that should occur with rising daily temperatures that should eventually lead to heat avoidance. Specifically, we studied how these animals switch from a hunger state, inciting foraging, to a temperature avoidance state, which would cause individuals to move to thermal shelters. We precluded mate-seeking during our study period because we worked in May to September when no breeding activity, which occurs in October and November, takes place (Ariano-Sánchez & Salazar, 2013), with the rest of the wet season (May to September) being dedicated to weight gain (Ariano-Sánchez & Salazar, 2015).

Barometric pressure is another relevant factor that will affect lizards' movement because decreasing pressure often heralds rainfall (Petersen et al., 2015), and aside from being another local weather condition that is expected to be affected by globally changing weather patterns in the tropics (Feng et al., 2013), it is relevant for many reptiles because it changes food availability (Hume et al., 2020). To quantify activity and movement, we used animal-mounted triaxial accelerometers (Wilson et al., 2008) together with GPSs (Clemente et al., 2016). The accelerometers allow calculation of dynamic body acceleration (DBA) metrics (Wilson et al., 2020), which have been used to quantify the energetics of animal movement (Halsey et al., 2011; Halsey & Bryce, 2021; Qasem et al., 2012; Wilson et al., 2020) and the general intensity of activity (Bograd et al., 2010), and have even been used to examine the extent to which animals react to environmental variables such as temperature and barometric pressure (Parlin et al., 2018). GPS-derived variables, such as step length and turning angles, can be used to examine how animals adapt their movement paths to different environmental variables (Ironside et al., 2017; Parlin et al., 2018).

We hypothesized that ambient temperature does not affect the movement ecology of a thermoconforming reptile such as the Guatemalan beaded lizard. We also hypothesized that barometric pressure will have an effect in the movement ecology of this lizard. We further predict that activity intensity and movement paths will not change as a function of ambient temperature, but that decreasing barometric pressure should increase their activity intensity and modify their movement paths as rainfall increases the movement and therefore availability of their prey.

METHODS

Study area

The fieldwork was conducted in a seasonally dry tropical forest at Heloderma Natural Reserve and the surrounding areas (14°53′N, 89°47′W, elevation 310–950 m) in rough terrain with steep slopes at the Motagua Valley of Guatemala (Figure 1a,b). Rainfall is seasonal in this area, with the wet season lasting from May to October and the dry season from November to April (Nájera, 2006). Vegetation is typical of seasonally dry tropical forests, including several species of cacti of the genera *Stenocereus* and *Opuntia* (Cotí & Ariano-Sánchez, 2008). The nearest weather station to the study site, which is located 15 km to the east at an elevation of 330 m, is La Fragua Station, from the Instituto Nacional de Sismología, Vulcanologia, Meteorologia e Hidrología.

Study species

The Guatemalan beaded lizard is a large endangered venomous lizard (mean total length = 61 ± 11 cm) with a very low population size (approximately 500 existing mature individuals in the wild), which is endemic to the seasonally dry tropical forest of Guatemala (Ariano-Sánchez, 2006; Campbell & Vannini, 1988; Mata-Silva et al., 2019). It shows a distinct seasonality in its movement patterns, with a dramatic decrease during the dry season in home range size (wet season home range = 82.0 ± 15.9 ha vs. dry season home range = 6.0 ± 14.7 ha) and movements (wet season step length = 396.8 ± 398.9 m/day vs. dry season step length = 66.6 ± 180.9 m/day), a period that comprises from November to April (Ariano-Sánchez et al., 2020). This species is semi-fossorial, spending up to 90% of time hidden in underground shelters (Ariano-Sánchez & Salazar, 2015), and thus is hardly ever encountered in the wild (Beck, 2005). It is a specialist predator of vertebrate nests, feeding mainly on birds and reptile eggs (Ariano-Sánchez & Salazar, 2012).

Accelerometry and GPS data

Twelve adult free-ranging Guatemalan beaded lizards (five males and seven females) were gathered with the help of local villagers from May to September 2019 (Table 1). Snout–vent length (SVL) was measured for each individual, and they were weighed, sexed, and permanently marked with passive integrated transponder tags (AVID microchips, Los Angeles, CA) inserted subcutaneously at the level of the right scapula.

We 3D-printed (Ultimaker 3) backpack cases that were specifically tailored to the lizards' dorsal region. The backpacks were designed to contain a 2-GB Thumb Daily Diary (Wildbyte Technologies Ltd, Swansea University, Swansea, UK) with triaxial accelerometer/magnetometer, temperature (degree Celcius) and barometric pressure (hectopascal) sensors, a battery (Omnicel 3.6 V, 750 mAh, EF651625, Phoenixville, PA), and a VHF transmitter (CHP-5P Telonics, Mesa, AZ, USA). Each backpack was glued to a rectangular piece of denim and then glued to the dorsal region of the lizards following a method similar to the one described by Flesch et al. (2009). The VHF transmitter was included in the backpack system for recovery in case the backpack fell off. Additionally, a micro-GPS logger with a temperature sensor (PinPoint Beacon 240 Lotek, Wareham, Dorset, UK) was glued to the proximal portion of the tail of each lizard. Thus, each individual was equipped with a micro-GPS logger and a backpack system (Figure 1c). The total weight of the backpack and the GPS tag was 33 ± 0.1 g representing 3.31% of the average body weight of the lizards we used in this study, which follows the recommendations that equipment attached to reptiles has to weigh less than 5% of the total body weight (Naef-Daenzer et al., 2005). Each individual was released in the vicinity of the place of capture, and the overall health of all the

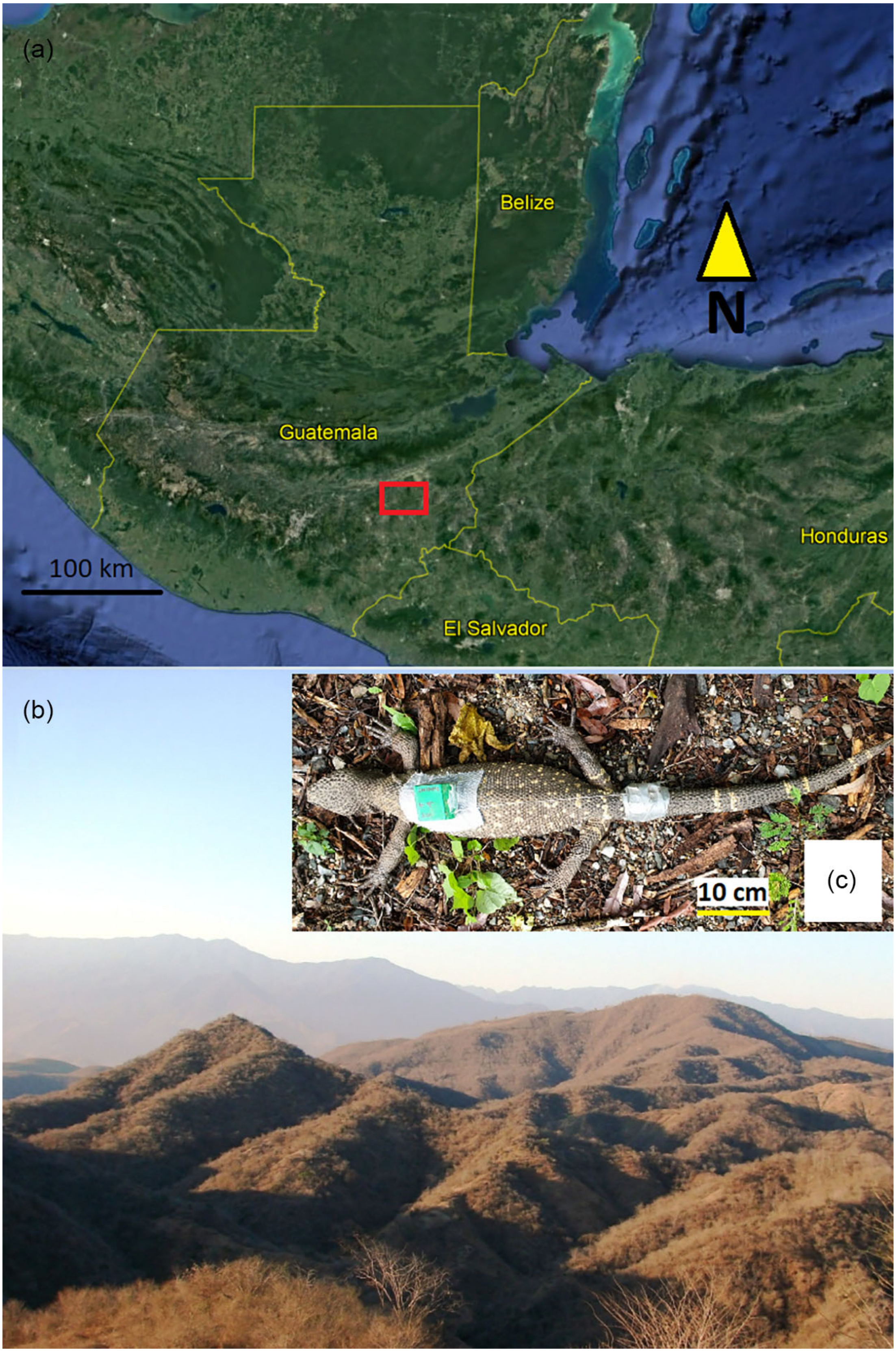

FIGURE 1 (a) Location of the study area in Motagua valley in Guatemala (red rectangle), (b) view in south–north direction of the dry forest steep terrain landscape in the study site at Heloderma Natural Reserve, and (c) Guatemalan beaded lizard *Heloderma charlesbogerti* showing the attachments of the backpack system and Global Positioning System tag

TABLE 1 Sex, snout–vent length (SVL), tracking period, number of Global Positioning System (GPS) fixes, and number of minutes with averaged triaxial acceleration and temperature recordings from each Guatemalan beaded lizard biologged in Motagua Valley, Guatemala

Lizard ID	Sex	SVL (cm)	Weight (g)	Start of tracking (d/m/y)	End of tracking (d/m/y)	Days tracked (*n*)	GPS fixes (*n*)	Minutes from Daily Diaries (*n*)
America	Female	41.0	950	15/06/19	25/06/19	11	152	12,146
Angelito	Male	34.0	1100	09/07/19	23/07/19	15	28	Failed
Cheja	Female	38.0	1050	17/05/19	29/05/19	13	64	Failed
Chica	Female	41.5	1100	11/07/19	23/07/19	13	113	9963
Chumpita	Female	38.0	900	10/07/19	23/07/19	14	59	19,923
Ericka	Female	39.0	1150	09/07/19	21/07/19	11	40	17,531
Kasperina	Female	38.0	900	12/06/19	17/06/19	6	160	Failed
Lionidas	Male	36.0	750	11/06/19	21/06/19	11	137	13,025
Majito	Female	38.5	1100	10/07/19	22/07/19	13	75	18,686
Neco	Male	36.0	900	29/08/19	13/09/19	16	147	21,585
Peder	Male	39.0	950	12/06/19	19/06/19	8	86	13,235
Yaje	Male	41.0	1100	29/08/19	14/09/19	17	Failed	22,632

individuals was considered good before release. Lizards were recaptured after approximately one to 2 weeks to recover the backpack and micro-GPS logger for data collection. All the study animals were rereleased into the wild in good health after the study.

The backpack system containing the Thumb Daily Diaries was programmed to record acceleration data at a frequency of 10 Hz, while temperature and barometric pressure were recorded at a frequency of 1 Hz. The micro-GPS logger schedule was programmed to record 37 fixes and temperature records per day for 15 days, to maximize battery lifetime. These daily fixes and temperature registers were divided into four recording periods: every 15 min from 7:00 AM to 11:00 AM; every 30 min from 11:30 AM to 1:00 PM; every 15 min from 3:45 PM to 6:00 PM; and every 30 min from 6:30 PM to 9:00 PM. These hours were selected according to the periods of activity reported for Helodermatids (Beck, 2005; García-Grajales et al., 2020). Prior to analysis, we discarded unreliable GPS location records (horizontal dilution of precision greater than 8.9).

Effects of ambient temperature and barometric pressure

For each lizard, we collected two different datasets: one consisting of triaxial acceleration, ambient temperature (the air temperature surrounding the body of the lizard), and barometric pressure obtained from the backpack system, and another consisting of ambient temperature (defined as above) and GPS fixes obtained from the micro-GPS loggers. Vectorial DBA (VeDBA) and ambient temperature data obtained from the backpack system were averaged by minute. We derived the static acceleration for each axial sensor by using a running mean of over 8 s, which we used to calculate the VeDBA (Shepard et al., 2008; Wilson et al., 2006). We analyzed both datasets as the GPS tag-only registered ambient temperature when a GPS fix was able to be taken, while the Daily Diary tag recorded temperature at a fixed rate. Step lengths and turning angles were obtained from the GPS fixes to be used as proxies of aboveground activity were estimated using the R package adehabitatLT (Calenge, 2006), while navigation bearings of movements were calculated using the R package circular (Agostinelli & Lund, 2017). Data were resampled into movement steps by hour that expressed movement behavior with respect to step length and turning angle. Bearings were analyzed for circular uniformity using Watson's test (Landler et al., 2018), and their reflective symmetry was analyzed using an ad hoc bootstrap test due to the small sample size (Pewsey et al., 2014). Elevation of each GPS fix was obtained from the digital elevation model for Guatemala.

We used linear mixed models (LMMs) to analyze how step lengths and VeDBA were affected by ambient temperature, using individual lizards as a nested random effect within the month of sampling to correct for any intergroup differences in environmental conditions during our field research. We corrected for elevation, SVL, and sex in the step length models (obtained from the micro-GPS loggers), and barometric pressure, SVL, and sex in the VeDBA models (obtained from the backpack system). VeDBA and step lengths were log-transformed to meet assumptions of normality.

Considering that circular variables (e.g., angles and bearings) require analysis methods that are different from those used for linear data (Cremers et al., 2018; Pewsey et al., 2014), we fitted circular mixed-effects models (CMMs; Cremers & Klugkist, 2018) to test the effects of ambient temperature (using sex, SVL, and elevation as covariates) on the turning angles and bearings of lizards' movements. We used individual lizards as random effects in the models. We choose 3000 output iterations (its = 3000), a burn-in period of 1000 iterations (burn = 1000), and a lag every third iteration (n.lag = 3) to make sure that the Markov chain Monte Carlo sampler converged and to prevent possible autocorrelation between the parameter estimates. These CMMs were fitted using the R package bpnreg (Cremers, 2020).

We developed a list of candidate models based on our hypotheses to prevent the inclusion of uninformative parameters and overfitting (Fisher et al., 2018; Leroux, 2019). Candidate models were analyzed with the MASS package (Venables & Ripley, 2002). For the LMMs, we carried out model selection based on Akaike's information criterion corrected for small sample size (AIC_c; Burnham & Anderson, 2002) to obtain the most parsimonious models and parameter estimates using the MuMIn package (Barton, 2020). When multiple candidate models showed the same level of performance ($\Delta AIC_c < 2$), we performed model averaging to examine the overall effect size of the predictor variables (Harrison et al., 2018; Leroux, 2019; Symonds & Moussalli, 2011). For the CMM, model selection was based on the Watanabe-AIC using the R package bpnreg (Cremers, 2020) to obtain the most parsimonious models. We used the procedures of Cremers et al. (2018) for parameter estimation. Parameters that included zero within their 95% confidence interval were considered uninformative (Arnold, 2010; Cremers & Klugkist, 2018; Leroux, 2019). The fixed effects used in all the analyses were not correlated (Pearson's r coefficient < 0.5), and variance inflation factor values were <3 (Harrison et al., 2018). Residual plots were analyzed (Zuur et al., 2010) using the R package DHARMa (Hartig, 2020).

Step selection analyses

We analyzed the factors that affect step selection of the beaded lizards by using conditional logistic regressions in an integrated step selection analysis (iSSA) (Avgar et al., 2016; Forester et al., 2009). Data were resampled into movement steps of <35 min that expressed movement behavior regarding step length and turning angle. The time difference between steps was on average 20.0 ± 7.1 min (range: 12.7–32.1 min, median = 15.1 min). Each used location of the beaded lizards was compared with 10 available locations randomly sampled from a distribution of observed steps using the R package amt (Signer et al., 2019). Observed steps were described using gamma distribution of step length and a von Mises distribution of turning angles (Duchesne et al., 2015).

Following Muff et al. (2020), we fitted mixed conditional logistic Poisson's models with stratum-specific fixed intercepts to model how ambient temperature affected beaded lizard movement. We included step length, the natural logarithm of step length, cosine of turning angle in all candidate models, and combinations of their interactions with ambient temperature at starting point as covariates to model the movement behavior of the beaded lizards (Avgar et al., 2016; Duchesne et al., 2015; Fieberg et al., 2021). We incorporated individual-specific slopes for all covariates to accommodate interindividual heterogeneity in the iSSA (Duchesne et al., 2010; Muff et al., 2020). We selected the most parsimonious models with ΔAIC_c <2.

To assess individual differences, we fitted conditional logistic Poisson's models with stratum-specific fixed intercepts to each individual (Fieberg et al., 2010). Using univariate Gaussian generalized linear models (GLMs), we analyzed the individual variations in movement selection coefficients as a function of sex and body size. We included the inverse variance of the response variable as weight in all models to account for uncertainty in parameter estimates (Scrafford et al., 2018).

Mean values are given with SEs. All analyses were conducted in R 4.0.3 using the RStudio 1.3.959 interface (R Core Team, 2020).

Ethics statement

This research was supported by the University of South-Eastern Norway, Universidad del Valle de Guatemala, Heloderma Natural Reserve, and Zootropic. All work was legally approved and done following the National Council of Protected Areas of Guatemala. The work carried out during this study followed the "Guidelines for use of live amphibians and reptiles in field and laboratory research" approved by the American Society of Ichthyologists and Herpetologists (Herpetological Animal Care and Use Committee, 2004).

RESULTS

Tracked individuals (n = 12) had a mean SVL of 38.3 ± 2.2 cm (range: 34.0–41.5 cm) and mean body mass of 995.8 ± 121.5 g (range: 750–1150 g). The mean number of GPS fixes per individual ($n = 11$) was 98.2 ± 51.6 (range: 36–169). The mean duration of tracking per individual was 12.3 ± 3.2 days, before being recaptured to recover the backpack and micro-GPS logger for data collection. The mean number of minutes with averaged recordings of triaxial acceleration and ambient temperature per individual ($n = 9$) was 16,525 ± 4547 (range: 9963–22,632). One of the micro-GPS tags and three backpack systems (Thumb Daily Diaries) failed, and we were not able to recover any data from these devices (Table 1).

The climatic data recorded by the nearest weather station during the study period showed that the average daily air temperature was 30.5 ± 1.4°C (range: 25.6–34.3°C), the average maximum daily air temperature was 36.5 ± 1.9°C (range: 31.8–46.0°C), and the average minimum daily air temperature was 23.6 ± 1.3°C (range: 21.0–29.0°C). The average ambient temperature measured with the GPS tag was 28.6 ± 2.9°C (range: 21.5–37.0°C), while the average ambient temperature measured at a higher frequency (4 Hz) with the Daily Diary tag was 27.4 ± 2.2°C (range: 21.2–44.5°C; Appendix S1: Figure S1). The mean elevation used by the lizards was 608.0 ± 78.0 m (range: 426–740 m). The barometric pressure had a mean of 951.0 ± 7.1 hPa (range: 930.7–989.7 hPa).

Activity intensity and movement paths

Mean VeDBA was 0.01472 ± 0.02963 g (range: 0.00000–1.20964 g). Mean step length was 37.5 ± 39.0 m (range: 1.1–604.7 m, median = 27.7 m). Turning angle was on average 0.26 ± 156.55° (range: −180 to 180, median = 0.77°). The circular median direction of the bearings was 358.7°, showing reflective symmetry with bearings directed in a north–south direction. Bearings were not uniformly distributed along the circle according to Watson's tests for circular uniformity ($W = 1.15$, $p < 0.01$). The bearings of the movement paths of the lizards were directed mainly toward either the north (America, Chica, Ericka, Peder), south (Angelito, Cheja, Chumpita, Kasperina), or equally distributed between north and south bearings (Lionidas, Majito, Neco). Only a few of the lizards' movements were directed toward the east or the west (Figure 2).

Temperature and barometric pressure effects on activity intensity

The model of the best fit for predicting the VeDBA of the movement of each lizard was the one that included ambient temperature and barometric pressure as fixed effects. The model of the best fit for step lengths of each lizard was the one that included ambient temperature and elevation as fixed effects (Table 2). We found a strong positive effect of ambient temperature on VeDBA and step lengths of the lizards' movements (Figure 3). We found a weak negative effect of barometric pressure on VeDBA. There was no effect of elevation in the step lengths (Table 3).

Temperature effects on movement paths

The model of the best fit for predicting the turning angles of the movement paths of the lizards was the one that included ambient temperature, sex, and SVL as fixed effects. The model of the best fit for the bearings of the movement paths of the lizards was the one that included ambient temperature and elevation as fixed effects (Table 4). We found a clear effect of ambient temperature in the turning angles of the movement paths of the lizards' movements. There was no effect of any of the covariates on the bearings of the lizards' movements (Table 5). The lizards followed a straighter path (smaller turning angles) at higher ambient temperatures than at lower ambient temperatures (Table 6, Figure 4). At lower ambient temperatures, lizards showed a more diverse pattern in the turning angles of their movement paths.

Temperature effects on step selection

Although lizards had, overall, short movement steps, step lengths increased with ambient temperature (Table 6, Figure 5). We found no clear effects of sex or body size on step selection among the individuals and no statistically clear general selection for any turning angle pattern among the lizards (Table 6, Figure 4).

DISCUSSION

Temperature and barometric pressure effects on activity intensity and movement paths

It is well documented that increases in ambient temperature escalate general activity and increase movement step lengths in many thermoregulatory lizards until they reach their critical thermal maximum (Cabezas-Cartes et al., 2019; Clusella-Trullas & Chown, 2014; Du et al., 2000; Gibert et al., 2016; Kirchhof et al., 2017;

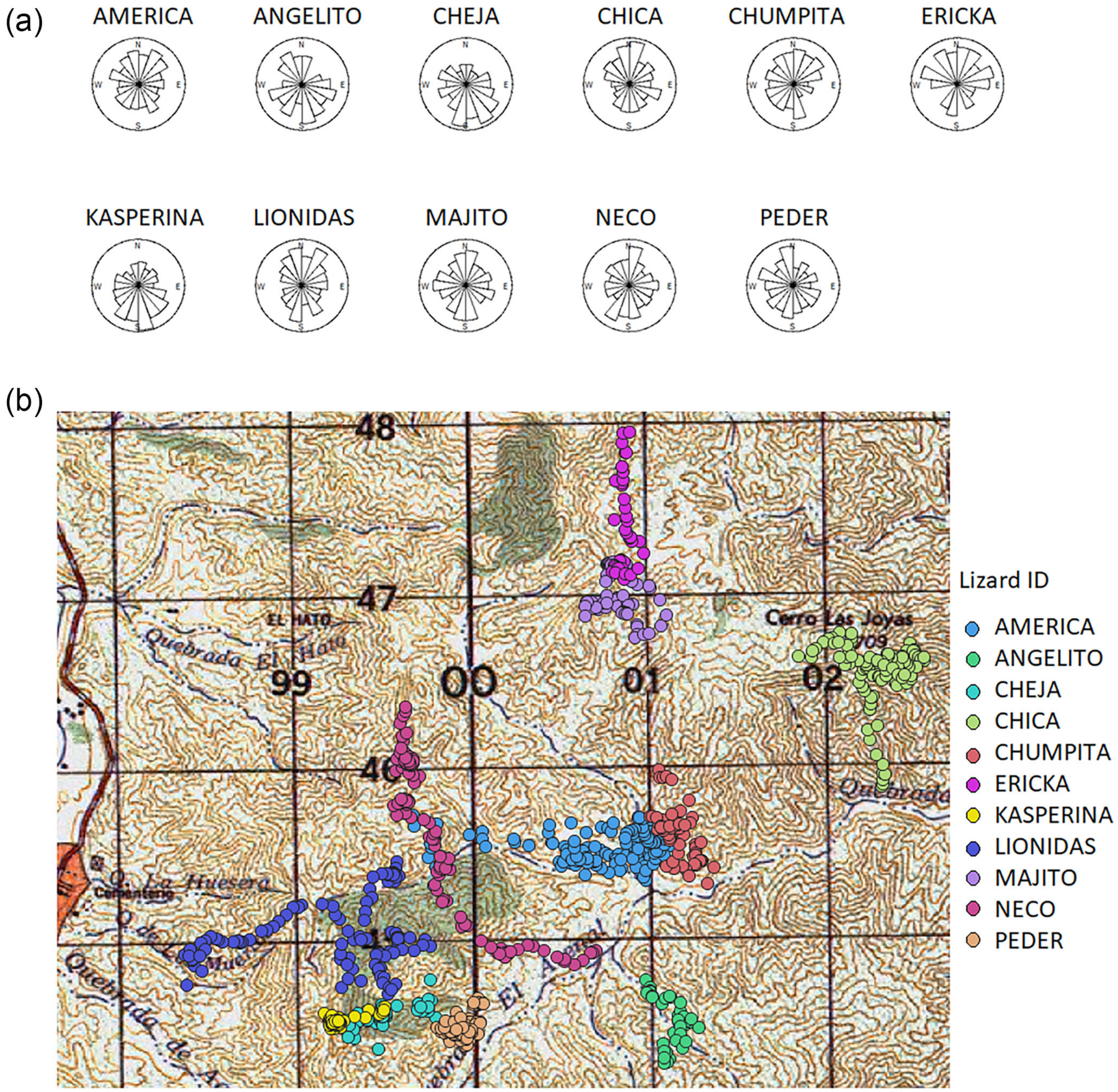

FIGURE 2 (a) Rose diagrams showing the bearings of the movement paths and (b) location of Global Positioning System fixes for 11 Guatemalan beaded lizards tracked in Motagua Valley, Zacapa, Guatemala, showing 20-m elevational gradient lines from May to October 2019. Each square in the map represents 1 km^2

Sound & Veith, 2000). However, our findings, which show increasing activity in VeDBA and step lengths when ambient temperature is higher and barometric pressure is lower, run contrary to predictions that advocate that thermoconformers such as the Guatemalan beaded lizard do not respond to ambient temperatures (Aranda-Coello et al., 2019; Beck, 2005). This perhaps highlights the dangers of oversimplifying how reptiles react to changing temperatures because our species was clearly not a passive responder to ambient temperature even though the Helodermatids are considered typical of thermoconformers. In fact, our finding that Guatemalan beaded lizards increase activity intensity (both VeDBA and step lengths) with increasing ambient temperatures (Figure 3), a pattern usually expected for thermoregulating lizards (Sannolo et al., 2019), contradicts the results of the only study that has analyzed the effects of ambient temperature on the step lengths of another thermoconforming lizard, the blue-tongued skinks (*Tiliqua* spp.), where ambient temperature had no effect on movement (Price-Rees et al., 2014). The critical question here, though, is the extent to which the

TABLE 2 Summary of linear mixed model selection for vectorial dynamic body acceleration (VeDBA) and step lengths of Guatemalan beaded lizard movements showing model log likelihood (LL), Akaike's information criterion corrected for small sample sizes (AIC_c), change in AIC_c (ΔAIC_c), and AIC_c weight (ωAIC_c)

Candidate model	LL	AIC_c	ΔAIC_c	ωAIC_c
Vectorial dynamic body acceleration (VeDBA)				
Log(VeDBA) ~ Ambient temperature + Barometric pressure	−222,649.7	445,311.5	0.00	0.996
Log(VeDBA) ~ Ambient temperature + Barometric pressure + Sex + SVL	−222,653.4	445,322.8	11.28	0.004
Log(VeDBA) ~ Ambient temperature + Sex + SVL	−223,126.8	445,914.0	602.48	0.000
Step length				
Log(Step length) ~ Ambient temperature + Elevation	−1372.4	2756.9	0.00	0.677
Log(Step length) ~ Ambient temperature + Sex + SVL	−1371.8	2759.7	2.77	0.170
Log(Step length) ~ Ambient temperature + Elevation + Sex + SVL	−1372.9	2759.9	2.97	0.153

Note: Lizards' identity and month of sampling were used as nested random effects in all the models.
Abbreviation: SVL, snout–vent length.

temperature in the blue-tongued skink study ever reached levels that might induce changes in movement because few, if any, species will not respond to detrimental temperatures.

Since we could preclude any breeding activity in our study (Ariano-Sánchez & Salazar, 2013), we presume that our measures of activity intensity on our lizards can only be a product of two different behaviors: searching for food or searching for shelters. Helodermatids are chemosensory-guided predators where foraging behavior consists of slow, short, stop-and-go food searching movements (Beck, 2005) and presumably some sinusoidal component in the movement path as the animals travel up a concentration gradient of chemical cues to find food and avoid predators (Baeckens et al., 2017). By contrast, search for thermal shelter involves straighter, directed, faster movements to take the animals rapidly to shelter (Beck & Jennings, 2003). Both these observations in Helodermatids were represented in our data, with our lizards showing reduced intra-lizard activity (via VeDBA), high turn angles, and short step lengths at low temperatures and low barometric pressures, which are indicative of foraging. Against this, animals increased VeDBA, which is a good proxy for speed, and step lengths while decreasing turn angles at higher ambient temperatures, which minimizes the time and energy invested in travel (Munden et al., 2021), especially in complex landscapes with steep slopes (Dunford et al., 2020), which is the case of the landscape at our study site. Despite the extremely rugged terrain at our study site, lizards do not follow ridgelines or streams, and move crossing gulleys and hilltops, which represent high energetic costs related to movement within the landscape. Consequently, we suggest that these patterns are specifically related to a switch in the internal state for the lizards, with them changing from food-seeking behavior, enhanced by the likelihood of rain and temperatures that present no thermal stress, to shelter-seeking behavior when temperatures become critically high.

That there is an expected reaction to temperature in our Guatemalan beaded lizards is indicated by the dependence of Helodermatid lizards on underground thermal shelters (Beck, 2005; Beck & Jennings, 2003). In fact, the average ambient temperature at which our lizards roamed in the wild during our study is similar to the preferred body temperature reported for the Chiapan beaded lizard (*Heloderma alvarezi*) in captivity (27.0 ± 2.2°C; Aranda-Coello et al., 2019), but clearly lower than the average daily air temperature of the study area. This gives credence to the idea that animals should, with rising temperatures, search for suitable shelters that serve them as thermal refugia during the hottest parts of the day to avoid overheating (Beck & Jennings, 2003).

The relatively small negative relationship we observed for barometric pressure with VeDBA is contrary to that reported in blue-tongued skinks, which clearly increase their movement with the occurrence of high-pressure systems as a product of these lizards preferring fine weather (dry air, clear skies, hot daytime, and lower nighttime temperatures) for their dispersive movements (Price-Rees et al., 2014). Against this, in our study, the decrease in

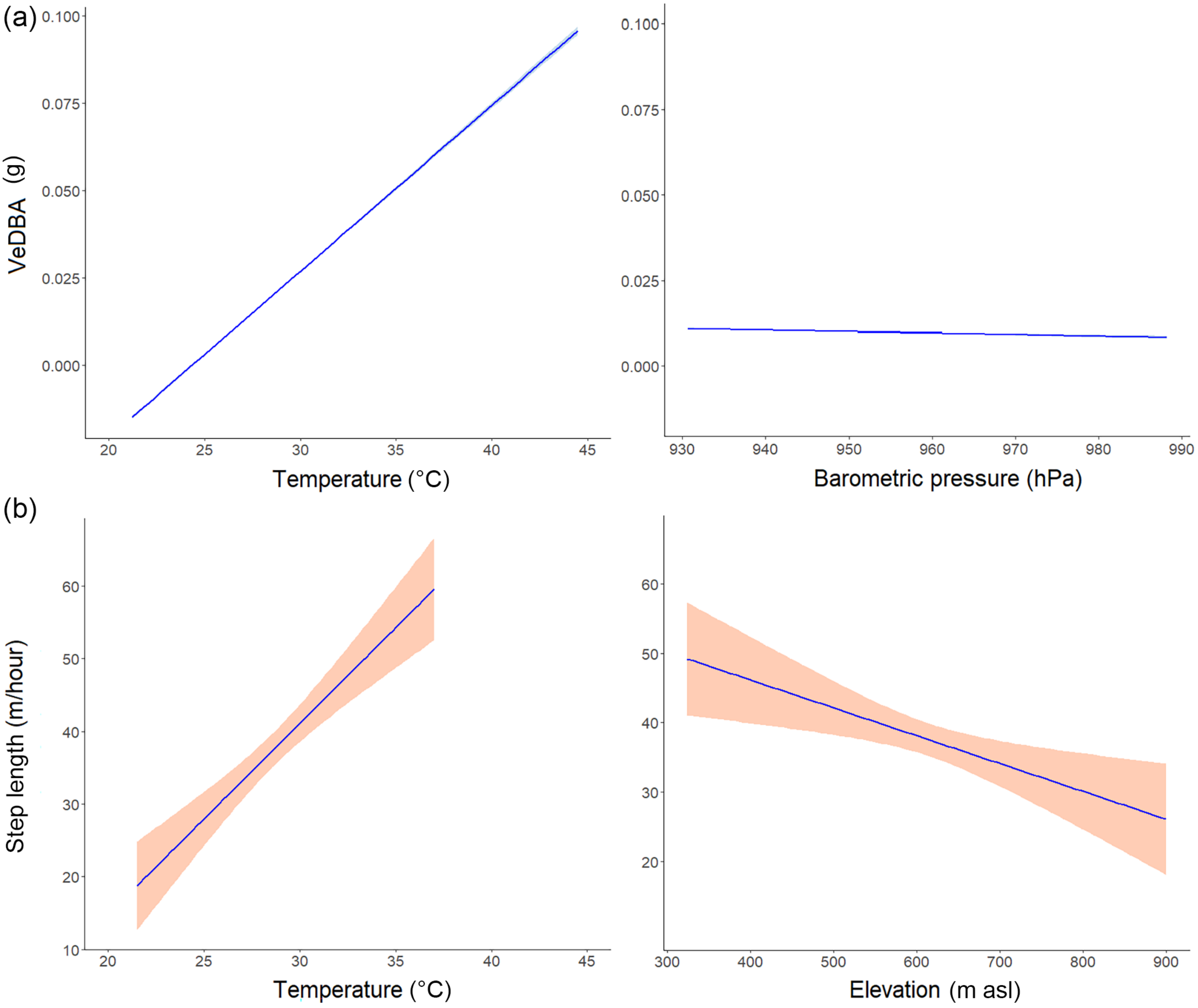

FIGURE 3 (a) Vectorial dynamic body acceleration (VeDBA) and (b) step length predicted relationship ±95% confidence interval between ambient temperature, barometric pressure, and elevation in a Guatemalan beaded lizard population at Motagua Valley, Guatemala

TABLE 3 Effect size (β), SE, and lower (LCI) and upper (UCI) 95% confidence intervals of the explanatory variables for the most parsimonious models of vectorial dynamic body acceleration (VeDBA) and step lengths of Guatemalan beaded lizard movements

Variable	Effect size (β)	SE	LCI	UCI
Log (VeDBA)				
Intercept	**2.651**	**0.51**	**1.657**	**3.638**
Ambient temperature	**0.166**	**0.0013**	**0.164**	**0.169**
Barometric pressure	**−0.013**	**0.00052**	**−0.014**	**−0.012**
Log(Step length)				
Intercept	0.523	0.49	−0.447	1.554
Ambient temperature	**0.07**	**0.01**	**0.053**	**0.096**
Elevation	0.0009	0.0005	−0.00024	0.0020

Note: Lizards' identity and month of sampling were used as nested random effects. Informative parameters appear in **boldface**.

barometric pressure (i.e., local low-pressure system) produces cloudy skies, increases relative humidity, and is considered a good predictor of impending rainfall (Petersen et al., 2015) and therefore has some predictive potential for Guatemalan beaded lizards to benefit from cloacal, and general body, evaporative cooling, helping maintain relatively low body temperatures while moving across the landscape. The ability to sense and respond to declining barometric pressure is a common adaptive trait in both vertebrates (Breuner et al., 2013) and invertebrates (Zagvazdina et al., 2015). Thus, given that excessive temperatures have deleterious effects on muscle performance of ectotherms (James & Tallis, 2020), the probability of benefitting from evaporative cooling could explain the barometric pressure-linked increase in activity with a reduced likelihood of overheating (DeNardo et al., 2003). The strength of the relationship between barometric pressure and VeDBA needs to be taken with caution as the effect we found is relatively small, and further research in other ectothermic lizards will be helpful to clarify this relationship.

TABLE 4 Model selection based on the Watanabe-Akaike information criterion (WAIC) of the circular mixed-effects models for turning angles and bearings of Guatemalan beaded lizard movements

Candidate model	WAIC	ΔWAIC
Turning angles		
Turning angles ~ Temperature + Sex + SVL	3734.35	0.00
Turning angles ~ Temperature + Elevation	3736.37	2.02
Turning angles ~ Temperature + Elevation + Sex + SVL	3739.51	5.16
Bearings		
Bearings ~ Temperature + Elevation	3821.33	0.00
Bearings ~ Temperature + Elevation + Sex + SVL	3823.89	2.56
Bearings ~ Temperature + Sex + SVL	3825.52	4.19

Note: Lizards' identity was used as random effect in all the models.
Abbreviation: SVL, snout–vent length.

TABLE 5 Posterior estimates of the mean (M), mode (Mo), SD, and lower bound (LB) and upper bound (UB) of the 95% highest posterior density (HPD) interval obtained through the slope at the mean approach for parameter estimation of the effects of the explanatory variables on the turning angles and bearings of Guatemalan beaded lizard movements in Motagua Valley, Guatemala

Variable	M	Mo	SD	LB HPD	UB HPD
Turning angles					
Intercept	−4.19	−4.35	1.97	−8.21	−0.46
Temperature	**0.07**	**0.07**	**0.01**	**0.04**	**0.10**
Sex (male)	0.17	0.23	0.23	−0.27	0.62
SVL	0.06	0.05	0.05	−0.03	0.16
Bearings					
Intercept	−0.84	−0.81	0.59	−2.03	0.23
Temperature	0.02	0.02	0.01	−0.01	0.05
Elevation	0.00065	0.00058	0.00056	−0.00046	0.0017

Note: Lizards' identity was used as random effect. Informative parameters appear in **boldface**.
Abbreviation: SVL, snout–vent length.

TABLE 6 Effect size (β), SE, and lower (LCI) and upper (UCI) 95% confidence intervals of explanatory variables for the step selection analysis with individual-specific slopes in a Guatemalan beaded lizard population at Motagua Valley, Guatemala

Variable	Estimate	SE	LCI	UCI
Step length	**−0.012**	**0.005**	**−0.023**	**−0.001**
ln(Step length)	**0.262**	**0.133**	**0.002**	**0.522**
cos(Turning angle)	0.013	0.111	−0.205	0.231
Step length × Temperature	**0.004**	**0.001**	**0.003**	**0.005**
cos(Turning angle) × Temperature	**0.116**	**0.022**	**0.074**	**0.159**

Note: Informative parameters appear in **boldface**.

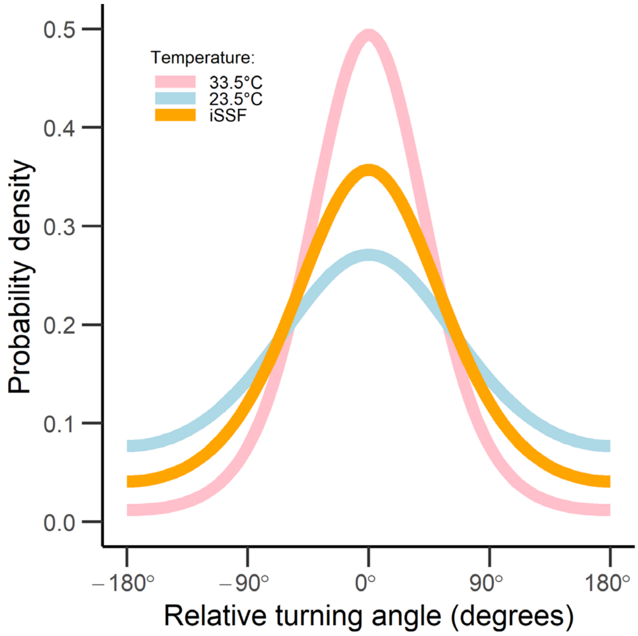

FIGURE 4 Predicted relationship ±95% confidence interval (represented by the width of the lines) between turning angle, ambient temperature, and relative probability of use according to the integrated step selection function (iSSF) among 11 individuals in a Guatemalan beaded lizard population at Motagua Valley, Guatemala

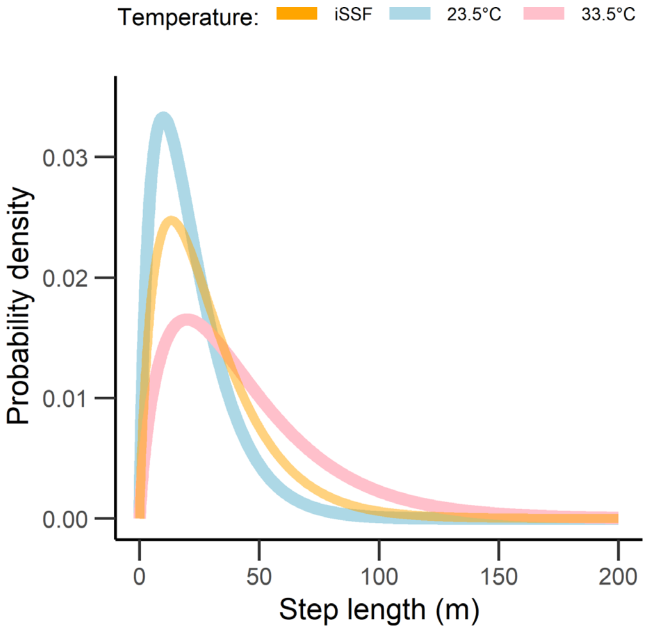

FIGURE 5 Predicted relationship ±95% confidence interval (represented by the width of the lines) between step length, ambient temperature, and relative probability of use according to the integrated step selection function (iSSF) among 11 individuals in a Guatemalan beaded lizard population at Motagua Valley, Guatemala

Changes in Guatemalan beaded lizard heading

It was particularly perplexing that most of the lizards' movement paths were directed along the north–south magnetic axis, with only a few movements directed toward the east–west magnetic axis. Such an alignment with the magnetic north–south axis has also been described in two lacertid lizards, the wall lizard, *Podarcis muralis*, and the Balearic lizard, *Podarcis lilfordi* (Diego-Rasilla et al., 2017). It has been suggested that magnetic alignment might assist animals in improving their mental map of space optimizing the time invested while navigating through the landscape (Begall et al., 2013), thus reducing fitness costs of movement behavior (Diego-Rasilla et al., 2017) and obtaining a constant directional reference while they are performing different survival-related tasks (Červený et al., 2011). Helodermatid lizards are known to have strong shelter fidelity, usually reusing thermal shelters within their home ranges on multiple occasions and for long periods (Ariano-Sánchez & Salazar, 2012, 2015; Beck & Jennings, 2003). Therefore, north–south magnetic axis directional preference of the bearings in the lizards' movements may be also an adaptive trait of these lizards to have a constant directional reference that may help them to reduce some fitness-related costs such as the increased risk of predation or overheating while searching for suitable thermal shelters, associated with moving in a complex steep landscape. This may also explain the absence of a relationship between the bearings of the lizards and ambient temperature or any other covariate, as there might be strong pressure for a directional preference in their movement. Further studies are needed to determine the actual mechanisms involved in magnetoreception in these lizards.

Conservation implications in the context of global warming

Although our study is restricted to a relatively small sample size, this is a common limitation when working with rare and elusive endangered species. Additionally, in the case of Helodermatidae, encounters with these lizards are very uncommon, making it difficult to obtain adequate sample sizes of individuals that meet the size and weight requirements needed for attaching biologgers on them. Despite these methodological constraints, we encourage conservation ecologists to study the movement ecology of rare and elusive endangered species as data obtained can be fundamental to inform conservation measures. Our results highlight the potentially deleterious effects of global warming for thermoconforming lizards inhabiting xeric environments. Climate models predict an increase of 3–4°C in the average daily temperature and a reduction of 100–200 mm in the monthly average rainfall during the wet season at the xeric Motagua Valley region in Guatemala (García-Morales, 2019), resulting in a hotter and more arid region by the end of this century (Pons et al., 2018). This increase in temperature, along with the reduction in rainfall, is expected to reduce the thermal window within which the Guatemalan beaded lizard can forage effectively, and will also have deleterious effects on their metabolic performance. It should also specifically cause a foraging-to-shelter state change sooner in animals that have left their shelter to forage while giving them fewer opportunities to benefit from evaporative cooling. It may also reduce the suitability of many current thermal shelters. Conservation of good-quality habitat that provides enough resources (such as shelters) has been shown critical for lizards to have a chance of survival in the context of climate change (Ariano-Sánchez et al., 2020). Unfortunately, seasonally dry forests are vanishing due to pervasive forest loss and fragmentation caused by agriculture and cattle ranching, reducing the availability and quality of thermally suitable habitat (Gillespie et al., 2012; Portillo-Quintero & Sánchez-Azofeifa, 2010; Sinervo et al., 2010), which are especially relevant for thermoconforming lizards (Palmeirim et al., 2017).

CONCLUSIONS

We found evidence that ambient temperature and, in less degree, barometric pressure influence the activity intensity and movement paths of a thermoconforming reptile, the Guatemalan beaded lizard, indicating that not all thermoconforming lizards should be considered as thermal generalists. It is likely that higher activity intensity with hotter ambient temperatures will increase the movement-related energy expenditures of beaded lizards, thus making them highly vulnerable in the context of global warming.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and code (Ariano-Sánchez & Mortensen, 2021) are available from Zenodo: https://doi.org/10.5281/zenodo.5500659.

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SUPPORTING INFORMATION

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Article 4

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Developed black beaches - too hot to emerge? Factors affecting sand temperatures at nesting grounds of Olive Ridley sea turtles (*Lepidochelys olivacea*)

Running title: Sand temperatures of nesting beaches

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Abstract

Sea turtles are particularly vulnerable to global warming because their breeding ecophysiology is highly dependent on the sand temperatures of their nesting beaches, affecting traits such as hatching success and sex ratios. Most research has focused on the impact of climate change on sex ratios, while the thermal ecology of natural nesting grounds has received less attention. Many nesting beaches are highly affected by weather conditions, vegetation loss, and urbanization which in turn may affect their thermal profile, particularly at beaches with dark volcanic sand. We studied the sand temperatures on two urban-developed volcanic sea turtle nesting beaches in Guatemala, and their potential effect on the thermal ecology of sea turtle nests, by using the Olive Ridley as model species. We hypothesized that local weather, location, and annual cycle variables along the studied beaches will have a pronounced effect on sand temperatures, potentially affecting the hatching success of sea turtles. We found that higher air temperatures led to higher sand temperatures, and a high relative humidity and precipitation led to lower sand temperatures. As expected, sand temperatures at 50 cm depth or in plots covered by vegetation were clearly lower than those at 30 cm depth or in plots without vegetation cover. Plots close to concrete structures showed higher sand temperatures compared to plots with no building structures close by. Average sand temperatures at nesting beaches were almost always above the pivotal temperature, and either close to or above the thermal maximum tolerance of sea turtle embryos over longer periods. Our results highlight the relevance of vegetation and nest depth in buffering the effects of high air temperatures, low relative humidity, and low precipitation rates at the study site, which will have profound implications for the resilience of Olive Ridleys to global climate change.

Keywords

Marine turtles, volcanic beach, incubation temperatures, temperature-dependent sex determination, female-biased sex ratios, lethal temperatures.

Introduction

Climate change, with increased temperatures and changes in precipitation patterns, along with coastal vegetation loss and urbanization, are direct and indirect threats to numerous species inhabiting or using shoreline habitats (Bulleri and Chapman 2010, Hubbard et al. 2014, Sundblad and Bergström 2014, Pacifici et al. 2015, Beaugrand and Kirby 2018). Additionally, climate change and shoreline development have been shown to have synergistic effects that may jeopardize the resilience of coastal associated species (Schaler et al. 2016, Machado et al. 2017).

Sea turtles are particularly vulnerable because they are affected by climate change in various ways (Hawkes et al. 2009, Patrício et al. 2018), also due to their dependence on different habitat types throughout their life history. However, since sea turtles migrate and forage over huge spatial distances, they are expected to be more resilient to climate change during their life stages in the oceanic habitat than during their life stages in the coastal habitat (Hawkes et al., 2009), although time spent on land is a very short period compared to time spent in the sea. On land, climate change entails several threats to sea turtles. Sea turtles can become affected by sea level rising, which can lead to the loss of nesting areas

(Yamamoto et al. 2015, Butt et al. 2016, Patrício et al. 2018, Varela et al. 2018). Also, sea turtle nests may be washed out during extreme weather events (Ross 2005, Prusty et al. 2007, Van Houtan and Bass 2007, Rivas et al. 2018). Another impact of climate change on sea turtle populations on land is increased sand temperature on nesting beaches and the resulting consequences for the incubation of eggs in the nests (Hawkes et al. 2009).

Sea turtles lack sex chromosomes and have a temperature-dependent sex determination (TSD) (Bull 1980, Standora and Spotila 1985, Janzen and Paukstis 1991). Temperatures above a pivotal temperature (generally between ca. 28 °C and 31 °C; depending on the species) in the middle third of incubation (the thermosensitive period), produce more females, and temperatures below, produce more males (Ackermann 1997, Wibbels 2003, Bentley et al. 2020). Based on temperature monitoring at nesting grounds, and other methods to determine sea turtle sexes, several studies of sea turtle populations from different continents and species predict an increase in the already frequent female-biased sex ratio of hatchlings (Laloë et al. 2016, Jensen et al. 2018, Colman 2018, Tanner et al. 2019), leading to a feminization of sea turtle populations.

The consequences of female-biased sex ratios still need to be researched in detail. Long-term studies of sex ratios are lacking (Witt et al. 2010), and so are also measurements of background sex ratios, i.e. sex ratios not influenced by climate change. After all, sea turtles are considered survivors of a changing climate in the past, descending from very old lineages that already existed around 100 million years ago (Kear and Lee 2006). However, today sea turtles also face other anthropogenic threats additionally to climate change, such as habitat destruction, overharvesting, and pollution. These threats may reinforce the effects of climate change (Witt et al. 2010) and can make potential compensations for the impact of climate change on sex ratios, such as shifts in geographical ranges (towards higher latitudes) (Rabon et al. 2003, Hawkes et al. 2009, Pike 2013a, Pike 2013b, Esteban et al. 2016, Jensen et al. 2018), phenological adaptation (nesting during cooler periods of the year) (Weishampel et al. 2004), or nesting site selection (in the shade) (Witt et al. 2010) more difficult. Other studies suggest that female-biased hatchling sex ratios can lead to more optimal operational sex ratios, because of more frequent mating by males compared to females (Wright et al. 2012; Hays et al. 2014; Hays et al. 2017; Santidrián-Tomillo et al. 2020).

Many studies have been focusing on the impact of climate change on sex ratios in sea turtles, while maximum thermal tolerances of sea turtle embryos in natural settings have not been considered that much. Extreme high temperatures in the nest will, due to overheating, result in the mortality of the clutch. Increased mortality rates, possibly caused by high temperatures have been observed or are predicted for the future (Fuentes et al. 2011, Maulany et al. 2012, Santidrián-Tomillo et al. 2012, Pike 2013c). Based on early studies and literature reviews (Yntema and Mrosovsky 1982, Ackermann 1997, Howard et al. 2014), the maximum thermal tolerance of sea turtle embryos is frequently cited as 35 °C, but may vary depending on the species and other external factors, such as location. Hays et al. (2017) found that the hatching success decreases already at 30 °C, and is halved at ca. 32 °C. However, these thermal tolerances are given as mean temperatures, nest temperatures can exceed 35°C by up to several degrees for shorter periods, and eggs may still hatch successfully. Therefore, time spent at stressful temperatures is more crucial for the survival of the embryos, than high temperatures over short periods (Howard et al. 2014). Thermal tolerances to high incubation temperatures seem also to vary from species to species with Green Turtle (*Chelonia mydas*) and Loggerhead Turtle (*Caretta caretta*) embryos being more tolerant to high temperatures than Leatherback (*Dermochelys coriacea*) and Olive Ridley (*Lepidochelys olivacea*) embryos (Howard et al. 2014).

Sand temperatures on sea turtle nesting beaches are known to be positively correlated with air temperature and negatively correlated with precipitation and relative humidity, also showing a seasonal variation (Hays et al. 2003, Glen and Mrosovsky 2004, Laloë et al. 2016, Montero et al. 2018, Laloë et al. 2021). Over the last 100 years, global temperatures have risen by approximately 1 °C, and a further increase is expected in the future according to different climate change scenarios. Changes in precipitation will vary, with a decrease in many subtropical dry regions (IPCC 2014, IPCC 2021). Central America is identified as a climate change Hot-Spot (Giorgi 2006), where the impact of climate change on natural ecosystems with higher temperatures and less precipitation will be particularly pronounced (Hannah et al. 2017, Hidalgo et al. 2017, Imbach et al. 2018). The expected local weather changes, potentially leading to higher sand temperatures, will be particularly severe for sea turtle populations that nest at beaches with dark volcanic sand (Hays et al. 2001, Laloë et al. 2014, Bentley 2020). Such beaches have a lower albedo, which is the ratio between reflected and incoming solar radiation, than beaches with white sand. Lower albedo results in higher sand temperatures because more solar radiation is transformed into thermal energy warming up the sand (Laloë et al. 2016). Other aspects that are important for nesting temperatures on the beach are shading (by vegetation for instance) (Kolbe and Janzen 2002, Kamel 2013), and the depth of the nest (Marco et al. 2018, Rivas et al. 2018).

Global warming effects at the local level are exacerbated by vegetation loss and urbanization, resulting in urban landscapes being hotter and drier than natural landscapes (Huang et al. 2022). Rapid urbanization with the consequent loss of coastal vegetation cover is part of the main threats to the ecological resilience of coastal ecosystems (Zhai et al. 2020). Many beaches are highly affected by vegetation loss and urbanization, which may lead to higher sand temperatures potentially affecting the reproductive success of sea turtles (Glen and Mrosovsky 2004, Kamel 2013, Fuentes et al. 2016, Montero et al. 2018). The synergistic effects of weather variables, coastal vegetation cover, and urbanization on sand temperatures at nesting grounds of sea turtles on dark volcanic sand beaches have not been evaluated before.

We used the Olive Ridley, the most abundant sea turtle species in the world (Valverde et al. 2012), as a model species to investigate how local weather variables, coastal vegetation, and urbanization affect sand temperatures on dark volcanic nesting beaches on the Pacific coast of northern Central America. Specifically, we studied how sand temperatures respond to local weather (air temperature, precipitation, and relative humidity), location (beach, depth, and type of surface surrounding), and annual cycle (year and season) variables. We then looked at the potential effect of these variables on the nesting thermal ecology of Olive Ridleys. We hypothesized that local weather, location, and annual cycle factors, will have a pronounced effect on sand temperatures, thus potentially affecting hatching success and sex ratios of Olive Ridley embryos in *in-situ* nests. We predicted that sand temperatures on dark volcanic beaches: 1) increase along with air temperature but decrease as precipitation and relative humidity increase, 2) are similar on the two dark volcanic sand beaches studied, 3) decrease with increasing depth in the sand, 4) are lower in plots with vegetation cover compared to plots with no vegetation cover, 5) are higher in plots with urban development in their proximities compared to plots without urban development in their proximities, 6) differ for the two study years, 7) are higher during the dry season compared to the rainy season, and 7) exceed regularly the pivotal temperature, as well as the upper thermal critical maximum reported for Olive Ridley embryos.

Material and methods

Study area

The study was conducted on the Pacific coast of Guatemala in Central America, on two important sea turtle nesting beaches, El Banco (13.905685°N, -90.536711°W) and Hawaii (13.869012°N, -90.419519°W) (Figure 1 a, b). The two beaches are located ca. 12 km apart from each other, with the town of Monterrico in between. Hawaii beach is situated in a moderately developed area, being more densely populated than the beach at El Banco. In Hawaii, there are housing estates, and holiday resorts with smaller hotels bordering the beach directly, while El Banco has more forested and open patches of land. Both beaches consist of dark sand, resulting from volcanic activities in the area. The slope of the beach at El Banco is steeper than the beach in Hawaii.

The climatic conditions can be described as warm and humid with pronounced rainy and dry seasons. The average yearly temperature is around 27 ºC with the highest temperatures of 30 ºC in April, however, the fluctuations throughout the year are relatively little. Historical climate data has shown that the air temperature at the Pacific coast of Guatemala has increased by 1 ºC since 1980, and is expected to increase between 2.5 and 4.1 ºC by 2070 (MARN and PNUD 2018). The rainy season lasts from July to December, with a yearly precipitation of up to approximately 2000 mm (MARN and PNUD 2018). In the last years, the rainy season has become shorter and interrupted by longer dry periods, with more extreme rain events. This trend is expected to continue in the future, resulting in a water deficit and converting the Pacific coast into an area with a semiarid climate by 2070 (Pons et al. 2018). Relative humidity varies between 68 and 85 % with a yearly average of 76 %. The wind direction is east/southeast with an average wind speed of 2.7 km/h throughout the year (Siguenza 2017).

In the Guatemalan Pacific Ocean, five of the seven sea turtle species are present: Green Turtle, Hawksbill Turtle (*Eretmochelys imbricata*), Leatherback, Loggerhead Turtle, and Olive Ridley. Nesting has been documented for three of these species. Olive Ridleys are the most abundant with an estimation of 22,328 nests on the Pacific coast of Guatemala in 2018 (Muccio 2019), also showing a pronounced upward trend in nesting abundance in recent years (Ariano-Sánchez et al. 2020). The nesting of Leatherbacks is minuscule with 0-4 nests every year, and decreasing (Muccio 2019). In 2018, the first Hawksbill turtle nesting on the Pacific coast of Guatemala was documented (Muccio and Izquierdo 2019), approximately 1 km away from our study transect at El Banco. In Guatemala only solitary nesting of Olive Ridleys occurs, while in other parts of the world, the species can display arribada nesting behaviour (synchronous mass nesting) (Plotkin et al. 1997, Bernardo and Plotkin 2007). The main nesting season of Olive Ridleys in the study area lasts from August to October (Higginson 1989), with most eggs being hatched between August and November. Thus, nesting coincides mainly with the rainy season. However, nesting of Olive Ridleys also occurs sporadically off-season. Green turtles are assumed to nest somewhat earlier, and Leatherbacks from December until February.

On the Pacific coast of Guatemala, there are ca. 25-30 operating sea turtle hatcheries, and a hatchery is located on each of the study beaches (Arcas Parque Hawaii – the oldest one in Guatemala, and Tortugario El Banco – with most incubated eggs in recent years) (Muccio 2019). *In-situ* incubation of sea turtle eggs is almost not occurring on the Pacific coast of Guatemala, due to nearly all eggs being harvested since they account for an important part of the economic income of local villagers. However, in Guatemala, a quota of 20% of sea turtle eggs has to be donated to hatcheries for re-burial and *ex-situ* incubation, according to Guatemalan legislation (Brittain et al. 2007). In recent years, the number of eggs, incubated at hatcheries has increased (Ariano-Sánchez et al. 2020), since the villagers to an increasing extent sell eggs to the hatcheries, instead of selling them to markets for consumption. The Guatemalan authorities consider changing the management strategies to reburying a certain percentage of eggs on the beach, and not in the hatcheries.

Data sampling

Sand temperature data was collected from July 2018 to December 2019, covering two nesting seasons and one intermediate period, on the sea turtle nesting beaches of Hawaii and El Banco (Ariano-Sánchez et al. 2022). LogTag Trix-8 temperature loggers (measurement range -40°C to +85°C, accuracy ±0.5°C for -20°C to +40°C) were used for temperature recording. The loggers were programmed to record temperature simultaneously every hour. From July 2018 to December 2019, they were placed along two transects (one at Hawaii, one at El Banco) parallel to the shoreline, and on average one meter away from the high tide line, in the zone were, according to previous observations, most sea turtles place their nests. Later, the type of surrounding was defined as follows: “sand surrounding” was a plot with no vegetation cover and not close to concrete structures, “vegetation surrounding” was a plot with vegetation cover, and “concrete surrounding” was a plot with concrete structures in its proximities (< 2 m distance) either covered with vegetation or not. Each transect stretched over 1 km and consisted of ten plots 100 m apart from each other. At each plot, temperatures were measured in the sand at 30 and 50 cm below the surface. These depths were corresponding to the natural depths of Olive Ridley nests (Santidrián-Tomillo et al. 2017), assuring that both loggers were placed at depths where egg incubation under natural conditions would occur.

Due to limited storage capacity, loggers were retrieved after half a year in December 2018, data were extracted, and a set with new loggers was placed at the original plots. Additionally, to the original transects, one more transect per study beach was established. Those new transects were placed parallel, further away from the shoreline, at a distance of 2 m to the respective first original transect at each beach, assuring that many of the plots of the new transect were covered by beach vegetation. In those new transects, loggers were buried in the same way as in the original transect (10 plots per transect, 20 loggers, measuring depths 30 and 50 cm). Temperatures at the new transect were also measured hourly from December 2018 to December 2019.

Weather data of air temperature, precipitation, and relative humidity were collected from Instituto Privado de Investigación sobre Cambio Climático (ICC 2020, Ariano-Sánchez 2022). The nearest weather stations to both sites were used; La Candelaria for the El Banco transect, and La Máquina for the Hawaii transect.

Data analyses

We estimated the daily average of all sand temperature records. Then, a list of eight candidate models was created to assess the effects of local weather (air temperature, precipitation, and relative humidity), location (beach, depth, and type of surrounding), and annual cycle (year and season) variables on sand temperatures. The effects of air temperature (daily average), precipitation (daily average), relative humidity (daily average), beach (Hawaii and El Banco), depth (30 cm and 50 cm), type of surrounding (sand, vegetation, and concrete), year (2018 and 2019), and season (rainy and dry) on the sand temperatures were analysed with linear mixed models (LMM). Julian day and the individual datalogger identity were considered as random effects with temporal autocorrelation to correct for the diurnal cycle of the weather variables and the temporal autocorrelation of these variables with Julian day (Silk et al., 2020). Beach and year were treated as fixed effects because they consist of only two levels each, making it impossible to use them as random effects (Harrison, 2015). Relevant interactions were not included to avoid an unnecessary increase in the complexity of the models evaluated (Duncan and Kefford 2021). None of the fixed effects used in all models were correlated (Pearson r coefficient < 0.5), and variance inflation factor values were < 3 (Zuur et al. 2010).

Model selection was based on Akaike's Information Criterion corrected for small sample size (AICc) (Burnham and Anderson 2002, Leroux 2019) using the dredge function in the R package MuMIn (Barton 2020). There was no need for model averaging as ΔAICc was > 2 in all the other models compared to the most parsimonious one (Burnham and Anderson 2002, Arnold 2010, Leroux 2019). Parameters that included zero within their 95% confidence interval (CI) were considered uninformative (Arnold 2010). We used residual and quantile-quantile plots to check the validity of our model (Zuur et al. 2010). Mean values were given with standard deviation (±), and all analyses were conducted in R 4.0.2 (R Core Team, 2020). To illustrate sand temperature in relation to Olive Ridley incubation temperature thresholds, we used a pivotal temperature of 30.5 °C reported for Olive Ridleys on another Central America beach (Wibbels et al. 1998), while the thermal critical maximum of Olive Ridley embryos was set to 35 °C (Valverde et al. 2010).

Results

Sand temperatures during the study period

A total of 13,078 daily mean sand temperature records from 47 plots for the study period from May 2018 to November 2019 were estimated (Figure 2). The daily mean sand temperature was 33.2 ± 2.7 °C (range: 15.3 to 54.2 °C), the daily mean air temperature was 27.6 ± 1.1°C (range: 24.0 to 32.5 °C), the daily mean precipitation was 0.03 ± 0.12 cm of rainfall (range: 0.0 to 1.87 cm of rainfall), and the daily mean relative humidity was 81.4 ± 6.9 % (range: 35.8 to 100%). Overall, the daily mean sand temperatures were above 32 °C except for plots surrounded by vegetation during the rainy season (Table 1). The highest daily mean sand temperatures were recorded in plots near concrete structures (above 33.5 °C).

The percentage of days recorded above the thermal critical maximum of Olive Ridley embryos (> 35°C) was greater in the plots with dataloggers buried 30 cm deep with concrete infrastructure in the surrounding (41.0 %) compared to plots surrounded by vegetation (18.1 %) or surrounded by sand (27.7 %). On the contrary, the percentage of days recorded below the pivotal temperature for Olive Ridleys (< 30.5 °C) was greater in the plots covered with vegetation (17.5 %) compared to plots surrounded only by sand (10.1 %) or with concrete infrastructure in the surroundings (4.8 %). The same patterns for thermal critical maximum and pivotal temperatures were found in plots with dataloggers buried 50 cm deep but with smaller differences in the percentage of days between types of surroundings (Table 2).

The model of best fit for predicting sand temperatures on the Pacific coast of Guatemala included air temperature, precipitation, relative humidity, beach, depth, type of surrounding, year, and season as fixed effects (Table 3). We found clear positive effects of air temperature, the presence of concrete structures in the surface surroundings, and dry season on sand temperatures (Table 4). We found a strong negative effect of precipitation, relative humidity, depth, year, and surface surroundings covered with vegetation or only with sand, on the sand temperatures of the monitored beaches. The beach locality was not informative.

Impact of local weather variables on sand temperatures

Air temperature was positively correlated with sand temperature (Table 4) for all three types of surface surroundings (Figure 3). Precipitation clearly reduced sand temperature (Table 4) for all three types of surface surroundings (Figure 4) and has shown to be the only weather variable that can reduce sand temperatures below the pivotal temperature of Olive Ridleys. Also, relative humidity showed a clear negative relationship with sand temperature (Table 4) for all three types of surface surroundings (Figure 5). Plots covered with vegetation showed consistently lower sand temperatures than the other types of surroundings, especially at higher air temperatures, lower precipitation, and lower relative humidity (Figure 5).

Impact of location variables on sand temperatures

We found no effect of beach locality on sand temperatures (Table 3). El Banco beach mean sand temperature was 33.1 ± 2.7 °C, and Hawaii beach mean sand temperature was 32.9 ± 2.9 °C. Sand temperatures decreased with depth (Table 4), at 50 cm depth sand temperatures were clearly lower (32.6 ± 2.8 °C) compared to 30 cm depth (33.3 ± 2.7 °C) (Figure 6). This effect was stronger during the dry season (Table 1). At 30 cm depth sand temperatures were mainly distributed above the pivotal temperature reported for Olive Ridley, and near the thermal critical maximum that Olive Ridley embryos can survive. Sand temperatures recorded at plots with surface surroundings covered by vegetation or only by sand were clearly lower than at plots with concrete structures in their surroundings (Table 4, Figure 7). Plots with vegetation cover showed lower sand temperatures (32.5 ± 2.8 °C) than plots without vegetation (33.1 ± 2.6 °C) and plots close to concrete structures (34.0 ± 3.2 °C). The sand temperatures in plots close to concrete structures were mainly near the thermal critical maximum of Olive Ridley embryos.

Impact of annual cycle variables on sand temperatures

We found a clear effect of year on sand temperatures (Table 4), with temperatures recorded during 2019 (33.14 ± 2.87 °C) slightly higher than those from 2018 (32.73 ± 2.4 °C). Sand temperatures clearly below pivotal temperature were recorded only during the two biggest tropical storms that affected the Pacific coast of Guatemala during the 2-year period of our study (Figure 2). In both years sand temperatures were distributed mainly near the thermal critical maximum of Olive Ridley embryos (Figure 8). The seasonal effect on sand temperatures was also clear (Table 4), with lower sand temperatures during the rainy season (July – December: 32.4 ± 3.1 °C), compared to those recorded during the dry season (January – June: 33.7 ± 2.0 °C). Dry season sand temperatures were distributed mainly near the thermal critical maximum of Olive Ridley embryos and showed lover variation in sand temperatures compared to those of the rainy season (Figure 9).

Discussion

In our study of sand temperatures on nesting beaches on the Pacific coast of Guatemala, we found that average sand temperatures almost always, and over longer periods, were above the pivotal temperature, and either close to or above the thermal maximum tolerance reported for Olive Ridley embryos. All our hypotheses and predictions were confirmed. As predicted, sand temperatures were positively correlated with air temperatures, while negatively correlated with precipitation and relative humidity. We also showed that sand temperatures were lower at 50 cm depth compared to 30 cm depth. As expected, plots covered by vegetation showed lower sand temperatures compared to plots not covered at all, or to plots close to concrete structures. Sand temperatures for 2019 were slightly higher than those of 2018, and sand temperatures were lower during the rainy season compared to those of the dry season. We found no clear effect of beach locality.

Measured sand temperatures and their significance for in-situ incubation on volcanic beaches

Our results show that *in-situ* incubation of sea turtle eggs on the studied nesting beaches would mainly lead to the development of female hatchlings. This bias towards female hatchlings is also observed at other Olive Ridley nesting beaches, both in Central America (Heredero Saura et al. 2022) and in other parts of the world (Tanner et al. 2019), potentially leading to a feminization of the global sea turtle population. The studied population on the Pacific coast of Guatemala, and very likely also neighbouring populations do therefore depend on an exchange of reproductive individuals from beaches where males hatch frequently and survive until their reproductive age. The closest beach where this is observed is La Escobilla, in the state of Oaxaca, Mexico (Hernández-Echeagaray et al. 2012), which is 730 km northwest of our study sites

The relatively high sand temperatures at the studied nesting beaches do not only impose a threat due to the feminization of the sea turtle population, but the even more prompt threat of many turtle eggs not hatching in case of *in-situ* incubation, as lethal incubation temperatures were reached often, and over longer periods. High sand temperatures as we measured in our study have earlier been measured in Ostional Beach, Costa Rica (Valverde et al. 2010), and do seem to impose a problem for successful *in-*

situ incubation on beaches with dark volcanic sand (Patino-Martínez et al. 2022). As an example, at Ascension Island in the South Atlantic, sand temperatures at dark beaches were 4.2 °C warmer compared to white sand beaches (Hays et al. 1995). A later study in Cyprus found that the daily minimum sand temperatures on dark sandy beaches rarely dropped below the daily maximum temperatures on white sandy beaches (Hays 2001), showing also that incubation of sea turtle nests at dark sandy beaches can be strongly affected by global warming (Patino-Martínez et al. 2022).

However, in our study, we only measured sand temperatures but not temperatures in actual sea turtle nests. Therefore, it needs to be considered that eggs will have an additional impact on the temperature of the nest since they are producing metabolic heat (Matsuzawa et al. 2002, Gammon et al. 2020). Metabolic heat generally becomes pronounced towards the end of embryonic development, in the last third of the incubation period, and is therefore considered not to influence sex determination, which occurs in the second third of incubation (Howard et al. 2014). Metabolic heat is found to affect the nests' microclimate with a temperature increase of 2.5 °C in the centre of a clutch during the final third of the incubation period (Gammon et al. 2020). Since we did not measure temperature conditions in natural nests on the beach, we assume that the measured temperature conditions would be even warmer if the temperatures had been measured in real nests, leading to an even more pronounced approximation, and exceeding the thermal limits during the final third of the incubation period. Given that *in-situ* sand temperatures on the studied beaches often exceed the critical thermal maximum for Olive Ridley embryos, nest relocation to protected hatcheries that provides shading and watering can be considered a useful conservation management tool for this species (Hill et al. 2015).

Impact of weather and location on sand temperatures and consequences of climate change

Our results were consistent with findings from other sea turtle nesting beaches in which air temperatures showed positive relationships with sand temperatures, while rainfall precipitation and relative humidity showed the inverse effect (Fuentes et al. 2009, Lolavar and Wyneken 2015). Regional climate models predict an increase of 4 °C in the average daily temperature, and a reduction of 200 mm in the monthly average precipitation on the Pacific coast of Guatemala by the end of this century, resulting in a hotter and more arid environment (Hannah et al. 2017, Hidalgo et al. 2017, Imbach et al. 2018, Pons et al.

2018, García-Morales 2019). According to our model output, higher air temperatures, along with less precipitation and lower relative humidity will result in higher sand temperatures increasing the number of days above the critical thermal maximum of Olive Ridley embryos all over the year. This may circumvent Olive Ridley's hatching success of *in-situ* nests on the Pacific coast of Guatemala. Local weather variables affected by global warming could act synergistically with dark sand colour resulting in a dramatic decrease in the hatching success of *in-situ* Olive Ridley nests on the Pacific coast of Guatemala.

The absence of clear differences in sand temperatures between the two sampled beaches is expected as both have dark volcanic sand and similar weather conditions, indicating that our results are representative of larger sections of the nesting beaches at the Pacific coast of Guatemala and neighbouring countries. Depth has shown a clear effect on sand temperatures. Natural Olive Ridley nests are 30-50 cm deep (Muccio 2019). In our study, sand temperatures at 30 cm depth almost always exceed the pivotal temperatures and do often exceed the maximum thermal tolerance reported for Olive Ridley embryos as well (35°C, Valverde et al. 2010). Eggs in the lower part of the nest may therefore be buffered to a larger degree to global warming than eggs in the upper part of the nest.

Additionally, our findings highlight the relevance of vegetation in buffering the effects of high air temperatures, low relative humidity, and low precipitation rates at the study site. Beaches on the Pacific coast of Guatemala experience rapid urbanization development and are almost devoid of natural coastal vegetation near the shoreline (GFDRR 2011). This vegetation loss and rapid urbanization can affect the reproductive success of sea turtles not only directly by reducing the available coastal area and through disturbance that beach development involves, but also through affecting the thermal microhabitats (Fuentes et al. 2016, Shamblott et al. 2021). Another change induced by development and urbanization is the use of heat-absorbing construction materials such as concrete which may cause sand temperatures to rise (Mazaris et al. 2009, Muthamilselvan et al. 2016). Regulation of coastal development at nesting beaches is a vital element of the population recovery efforts for sea turtles (Fuentes et al. 2016). Consequently, the protection of urbanization-free coastal habitats is crucial, not only to minimize direct disturbance of nesting sea turtles but also for providing enough thermal niches for *in-situ* sea turtles nesting on the Pacific coast in Guatemala.

Impact of annual cycle variables on sand temperatures and future prospects

The slightly higher sand temperatures of 2019 compared to 2018 may reflect an annual variation in weather conditions. Thus, to study the potential effects of climate change on sand temperatures, longer sand temperature monitoring at our study sites is recommended to be able to determine the long-term effects of global warming on sand temperatures at dark volcanic beaches. However, long-term monitoring of sand temperatures as Schumacher and Reece (2016) suggest might prove to be difficult on the Pacific coast of Guatemala due to unstable sociopolitical conditions. Another useful approach to assess future sand temperatures could be quantitative modeling (Fuentes et al. 2009).

The clear effect shown by the rainy season to decrease sand temperatures supports our finding of the negative effect of precipitation on sand temperatures. It also emphasizes the relevance that the overall duration of the rainy season does play an important role in maintaining sand temperatures low enough to reach pivotal temperatures and have successful hatching in Olive Ridley nests. While shorter rainy seasons with rainfall concentrated at shorter periods with possibly higher intensity, such as tropical storm recurrence as expected under climate change, will probably reduce offspring production of sea turtles (Montero et al. 2018). Overall, our study stresses the possible impacts that global warming can have on Olive Ridley hatching success on dark volcanic beaches and suggests solutions such as undisturbed and development-free nesting habitats that may have the potential to interact with the negative impact that climate change can have on thermal conditions of sea turtle nesting beaches to a certain degree.

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Table 1. Summary of sand temperatures (°C) recorded from May 2018 to November 2019 on two volcanic sandy beaches on the Pacific coast of Guatemala.

Factor	Level of factor	# Plots	# Records	Daily mean sand temperatures (°C)		
				Whole study period	Rainy season	Dry season
All plots		47	13 078	33.2 ± 2.7	32.4 ± 3.1	33.7 ± 2.0
Depth	30 cm	27	7 429	33.3 ± 2.7	32.7 ± 2.9	34.0 ± 2.2
	50 cm	20	5 649	32.6 ± 2.8	32.0 ± 3.3	33.3 ± 1.6
Surrounding	Vegetation	13	4 235	32.5 ± 2.8	31.3 ± 3.5	33.5 ± 1.6
	Sand	30	7 805	33.1 ± 2.5	32.7 ± 2.7	33.9 ± 2.2
	Concrete	4	1 038	34.0 ± 3.2	33.8 ± 3.9	34.2 ± 2.1

Table 2. Summary of number and percentage of days and plots above the thermal critical maximum that Olive Ridley embryos can survive, and below pivotal temperature (male producing temperatures), recorded from May 2018 to November 2019 on two volcanic sandy beaches on the Pacific coast of Guatemala.

Depth	30 cm			50 cm		
Type of surrounding	Vegetation	Sand	Concrete	Vegetation	Sand	Concrete
Mean number of days (n) above the thermal critical maximum (> 35°C)	59.0 ± 17.7	91.5 ± 52.9	106.5 ± 35.5	40.4 ± 25.1	39.7 ± 31.6	54.0 ± 6.0
Percentage of days (%) recorded above the thermal critical maximum (> 35°C)	18.1	27.7	41.0	10.9	9.4	20.8
Number of plots (thermal critical maximum)	5	16	2	7	6	2
Mean number of days (n) below pivotal temperature (< 30.5 °C)	57.0 ± 22.4	26.6 ±17.5	12.5 ± 1.5	57.1 ± 25.6	32.9 ± 20.3	28.0 ± 9.0
Percentage of days (%) recorded below pivotal temperature (< 30.5 °C)	17.5	10.1	4.8	17.5	14.4	10.8
Number of plots (pivotal temperature)	5	20	2	8	11	2

Table 3. Summary of Linear Mixed Models (LMM) selection of sand temperatures (°C) showing model log-likelihood (LL), Akaike Information Criterion corrected for small sample sizes (AICc), change in AICc (ΔAICc), and AICc weight (ωAICc). Datalogger identity and Julian day were used as nested random effects with temporal autocorrelation in all the models.

Candidate models	**LL**	**AICc**	**ΔAICc**	**ωAICc**
Sand temperature ~ Air temperature + Precipitation + Relative humidity+ Beach + Depth + Surrounding + Season + Year	-17473.7	34973.5	0.0	1.0
Sand temperature ~ Beach + Depth + Surrounding	-17654.4	35324.8	351.3	0.0
Sand temperature ~ Air temperature + Precipitation + Relative humidity	-17688.2	35390.4	417.0	0.0
Sand temperature ~ Air temperature + Precipitation	-17721.5	35454.9	481.5	0.0
Sand temperature ~ Air temperature	-17725.6	35461.2	487.8	0.0
Sand temperature ~ Season + Year	-17806.5	35625.0	651.6	0.0
Sand temperature ~ Precipitation	-17836.7	35683.5	710.1	0.0
Sand temperature ~ 1	-17852.8	35713.6	740.1	0.0

Table 4. Effect size (β), standard error (SE), lower (LCI), and upper (UCI) 95 % confidence interval of the explanatory variables for the most parsimonious models of sand temperature. Datalogger identity and Julian day were used as nested random effects with temporal autocorrelation in all the models. Parameters with no clear effects are given in **bold.**

Variables	**Effect size (β)**	**SE**	**LCI**	**UCI**
Intercept	24.04	1.49	21.12	26.97
Air temperature	0.47	0.04	0.39	0.55
Precipitation	-0.65	0.25	-1.15	-0.16
Relative humidity	-0.03	0.01	-0.05	-0.03
Beach (Hawaii)	**0.02**	**0.05**	**-0.09**	**0.12**
Depth (50 cm)	-0.53	0.04	-0.62	-0.44
Surrounding (Vegetation)	-1.48	0.08	-1.64	-1.31
Surrounding (Sand)	-0.70	0.08	-0.85	-0.55
Season (Dry)	1.15	0.12	0.91	1.38
Year (2018)	-0.14	0.07	-0.27	-0.01

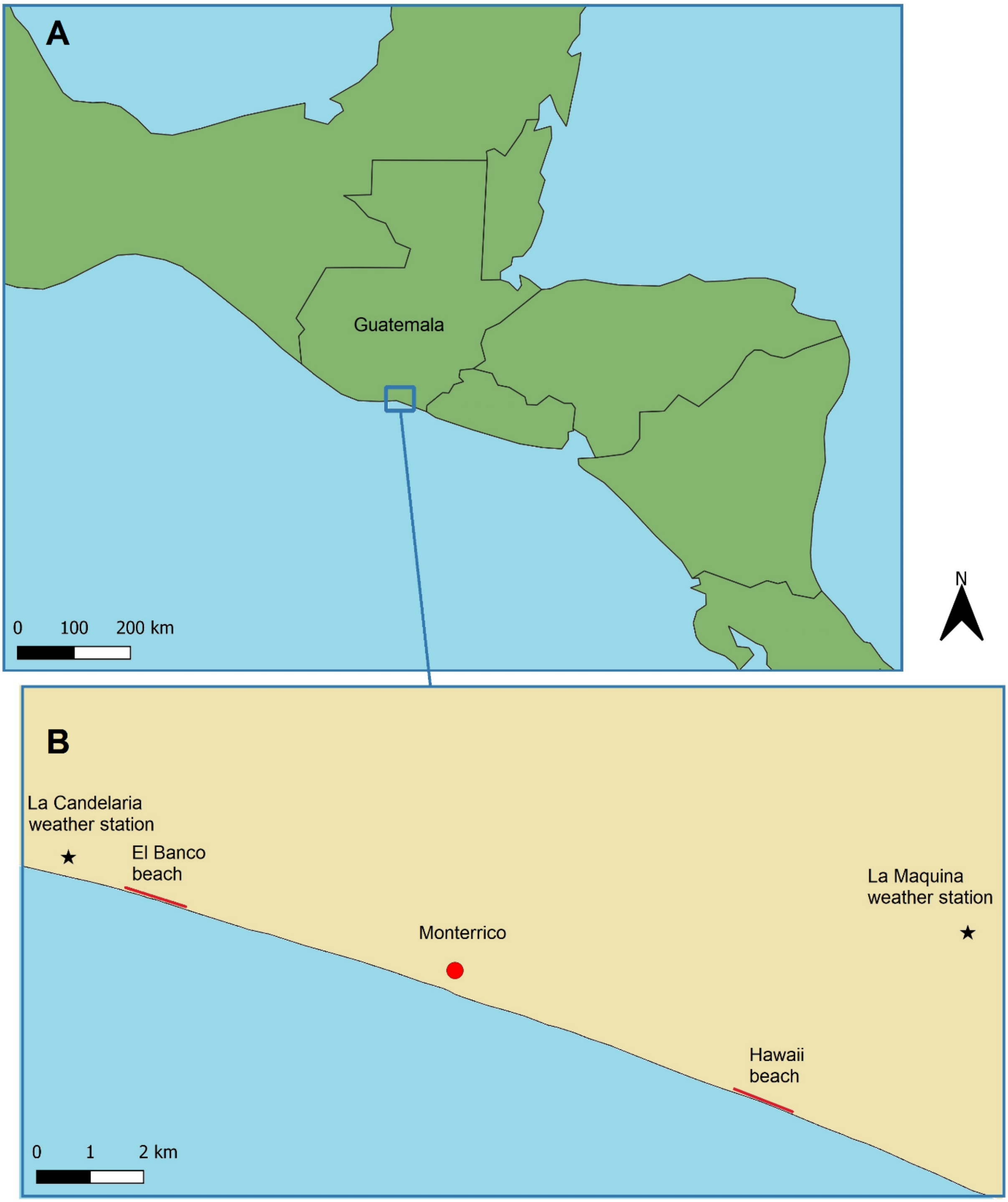

Figure 1. A. Location of the study site on the Pacific coast of Guatemala, Central America. B. The two study transects (red lines), where sand temperatures were measured, on the sea turtle nesting beaches of El Banco and Hawaii close to the town of Monterrico on the Pacific coast of Guatemala. The weather stations La Candelaria and La Maquina (black stars) provided waether data.

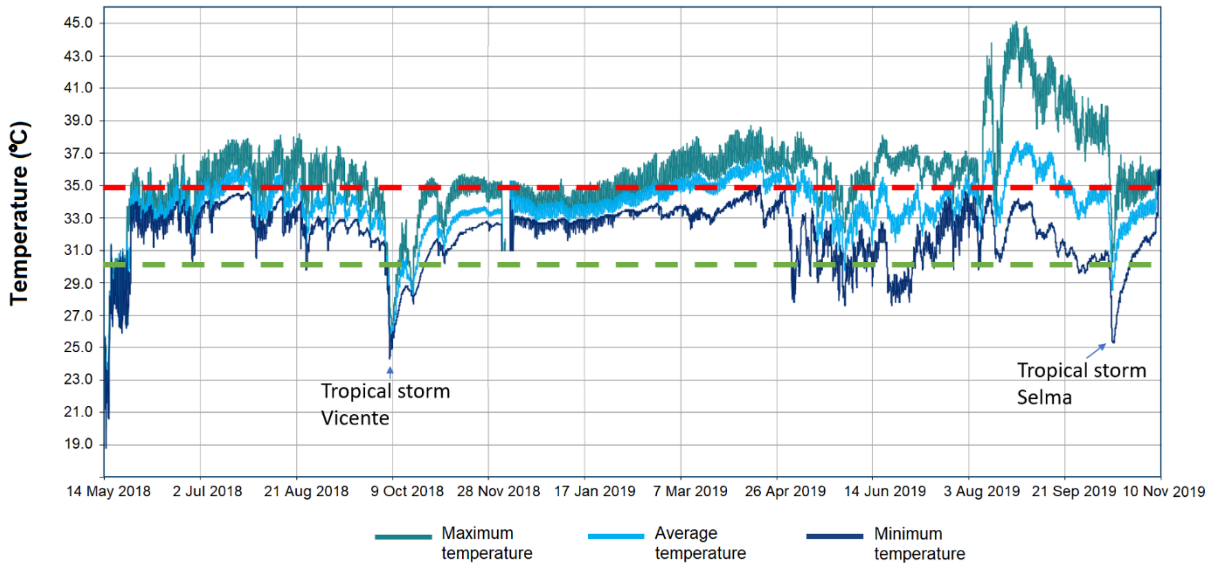

Figure 2. Sand temperatures (daily maximum, average, and minimum) recorded on the Pacific coast of Guatemala from May 2018 to November 2019. The thermal critical maximum for Olive Ridley embryos is shown as a red dashed line (35°C, Valverde et al. 2010). The pivotal temperature for Olive Ridley is shown as a green dashed line (30.5 °C, Wibbels et al. 1998). Two strong tropical storms (Vicente and Selma) that occurred during the study period are indicated with arrows.

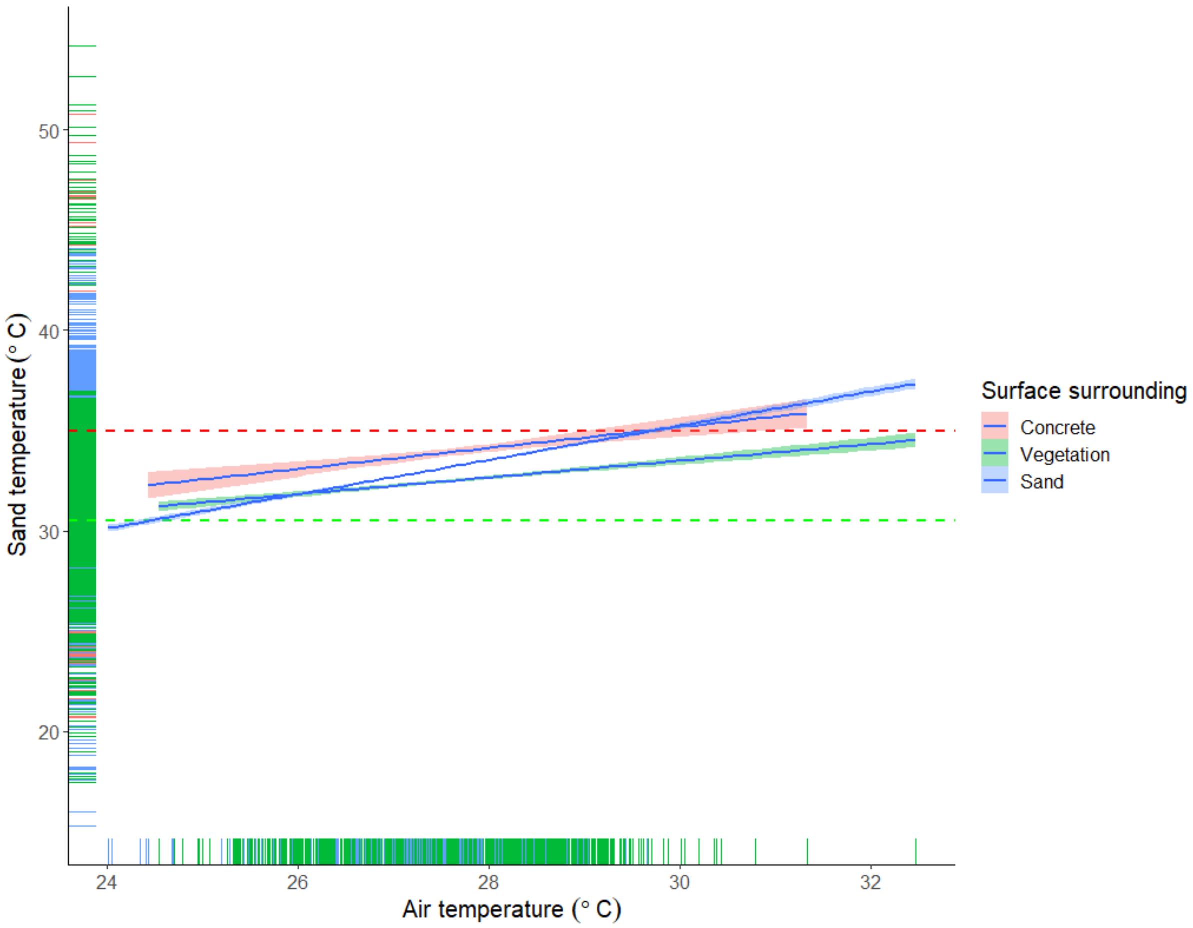

Figure 3. Relationship between air and sand temperatures (°C) categorized in different types of surface surroundings, recorded on the Pacific coast of Guatemala from May 2018 to November 2019. The thermal critical maximum for Olive Ridley embryos is shown as a red dashed line (35°C, Valverde et al. 2010). The pivotal temperature for Olive Ridley is shown as a green dashed line (30.5 °C, Wibbels et al. 1998).

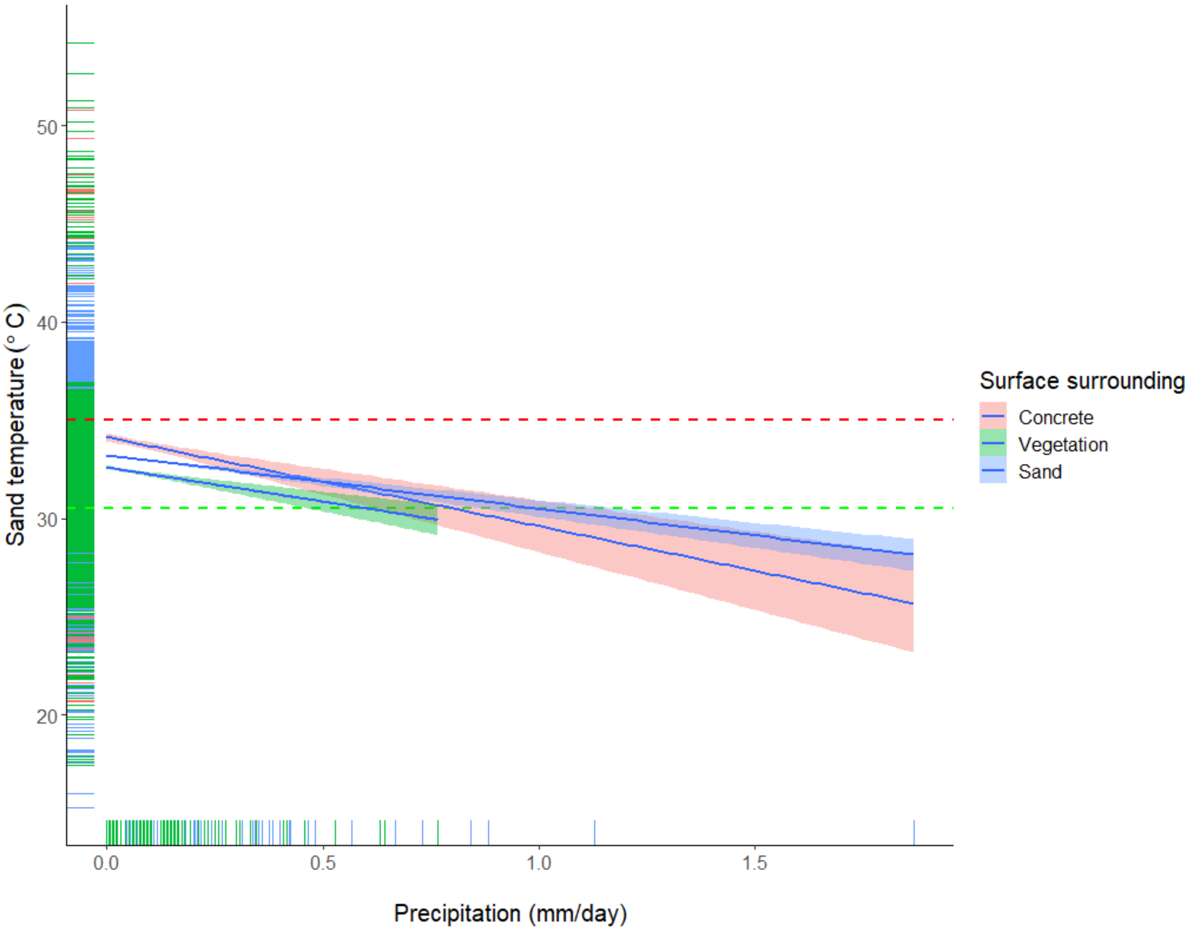

Figure 4. Relationship between precipitation (mm/day) and sand temperatures (°C) categorized in different types of surface surroundings recorded on the Pacific coast of Guatemala from May 2018 to November 2019. The thermal critical maximum for Olive Ridley embryos is shown as a red dashed line (35°C, Valverde et al. 2010). The pivotal temperature for Olive Ridleys is shown as a green dashed line (30.5 °C, Wibbels et al. 1998).

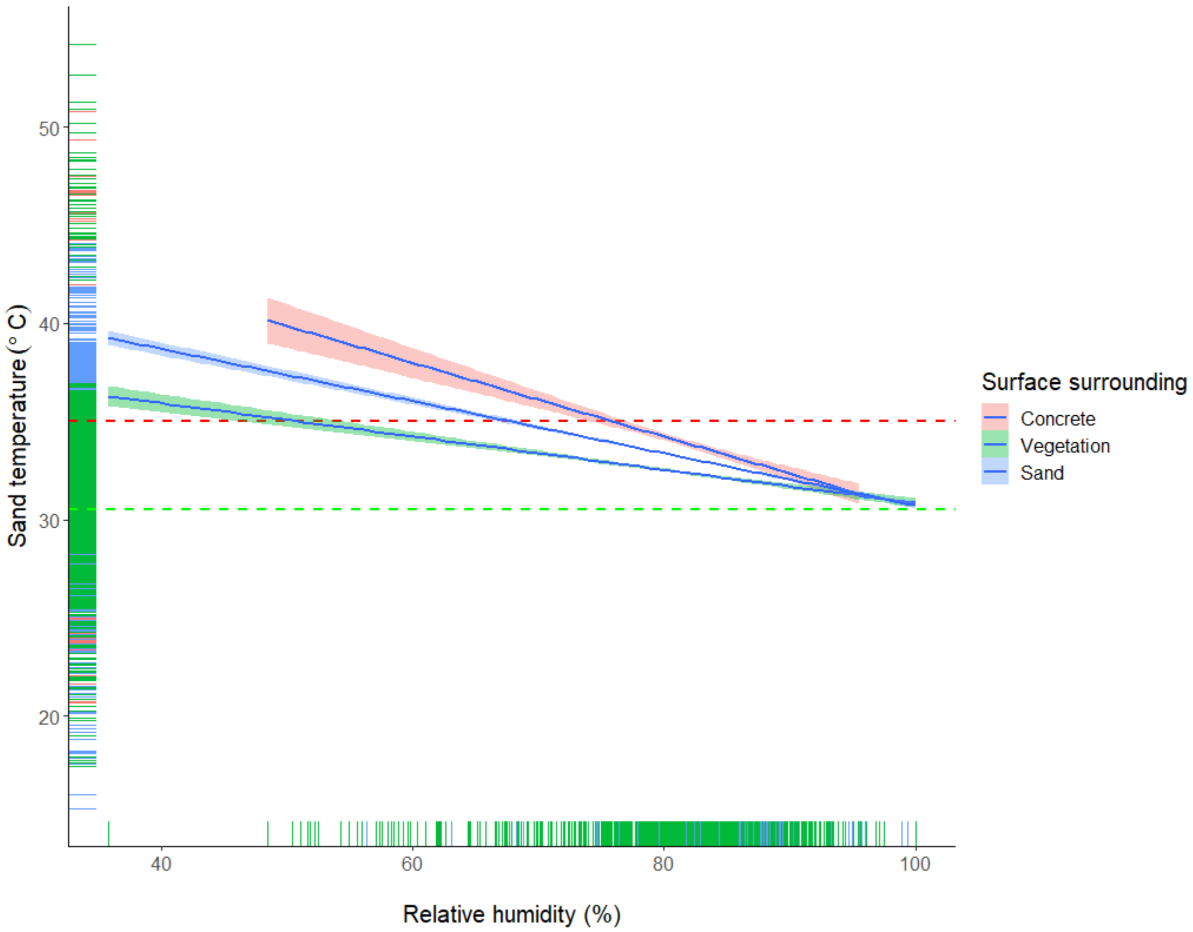

Figure 5. Relationship between relative humidity (%) and sand temperatures (°C) categorized in different types of surface surroundings recorded on the Pacific coast of Guatemala from May 2018 to November 2019. The thermal critical maximum for Olive Ridley embryos is shown as a red dashed line (35°C, Valverde et al. 2010). The pivotal temperature for Olive Ridleys is shown as a green dashed line (30.5 °C, Wibbels et al. 1998).

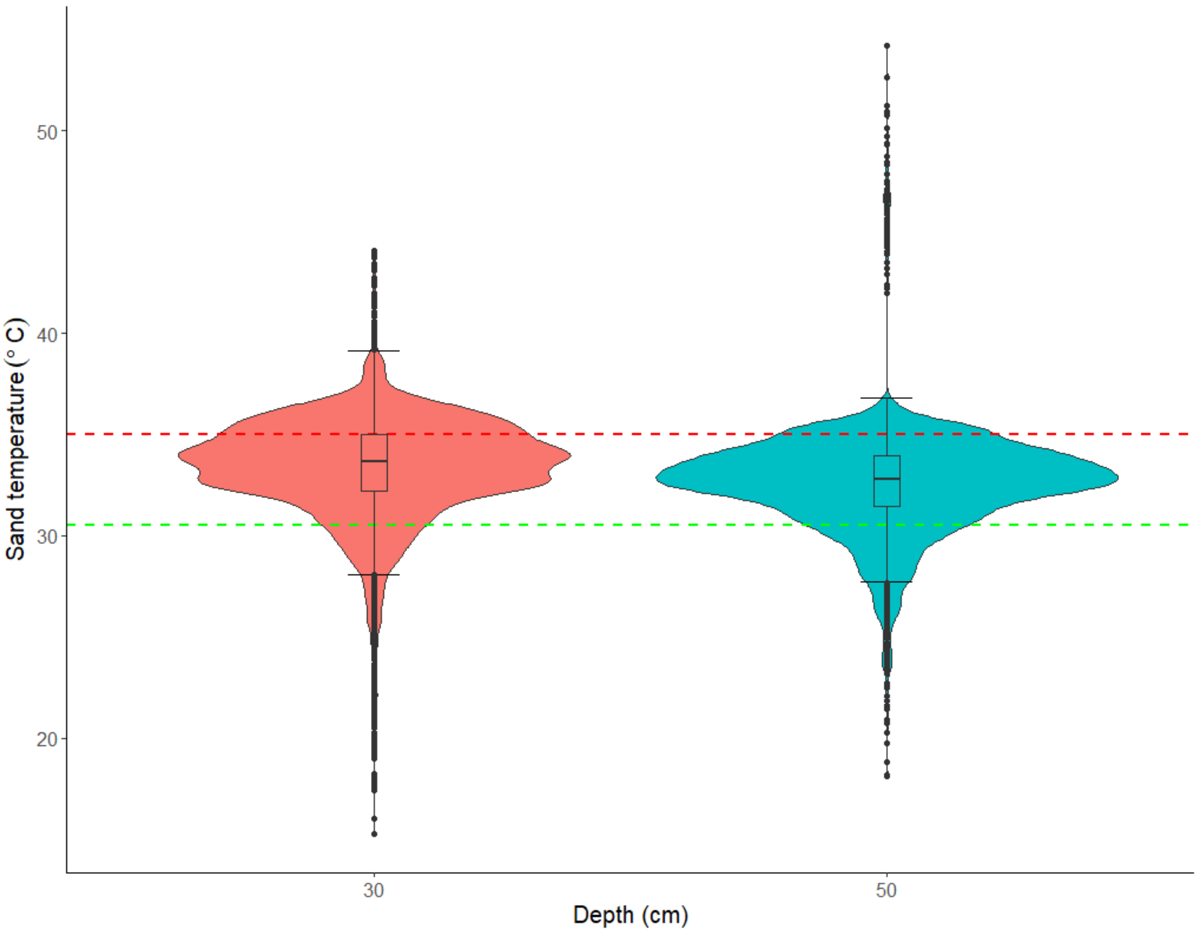

Figure 6. Violin plot of the daily average of sand temperatures (°C) recorded at 30 cm and 50 cm depths below the surface, at the Pacific coast of Guatemala from May 2018 to November 2019. The thermal critical maximum for Olive Ridley embryos is shown as a red dashed line (35°C, Valverde et al. 2010). The pivotal temperature for Olive Ridleys is shown as a green dashed line (30.5 °C, Wibbels et al. 1998).

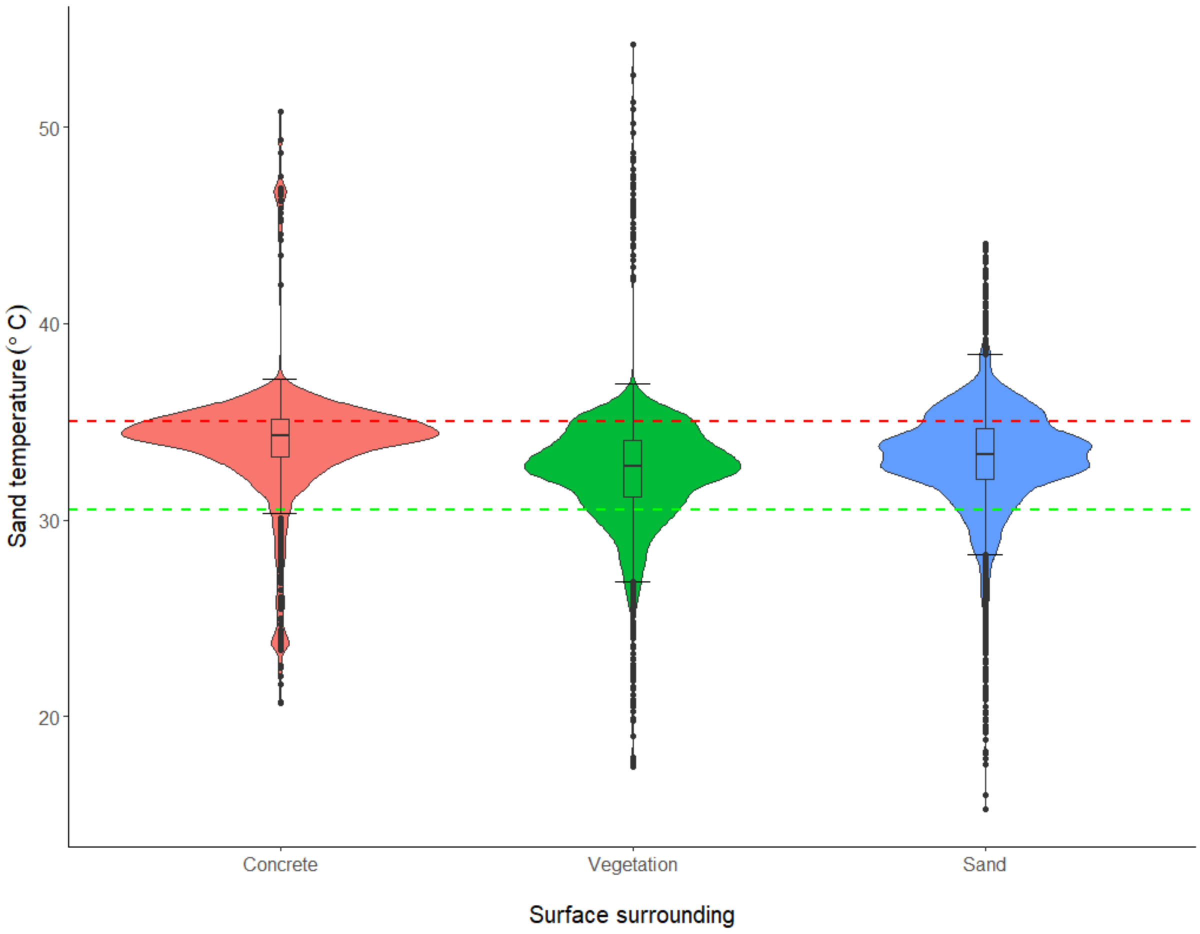

Figure 7. Violin plot of the daily average of sand temperatures (°C) for different surface surroundings of sample plots recorded on the Pacific coast of Guatemala from May 2018 to November 2019. The thermal critical maximum of Olive Ridley embryos is shown as a red dashed line (35°C, Valverde et al. 2010). The pivotal temperature for Olive Ridleys is shown as a green dashed line (30.5 °C, Wibbels et al. 1998).

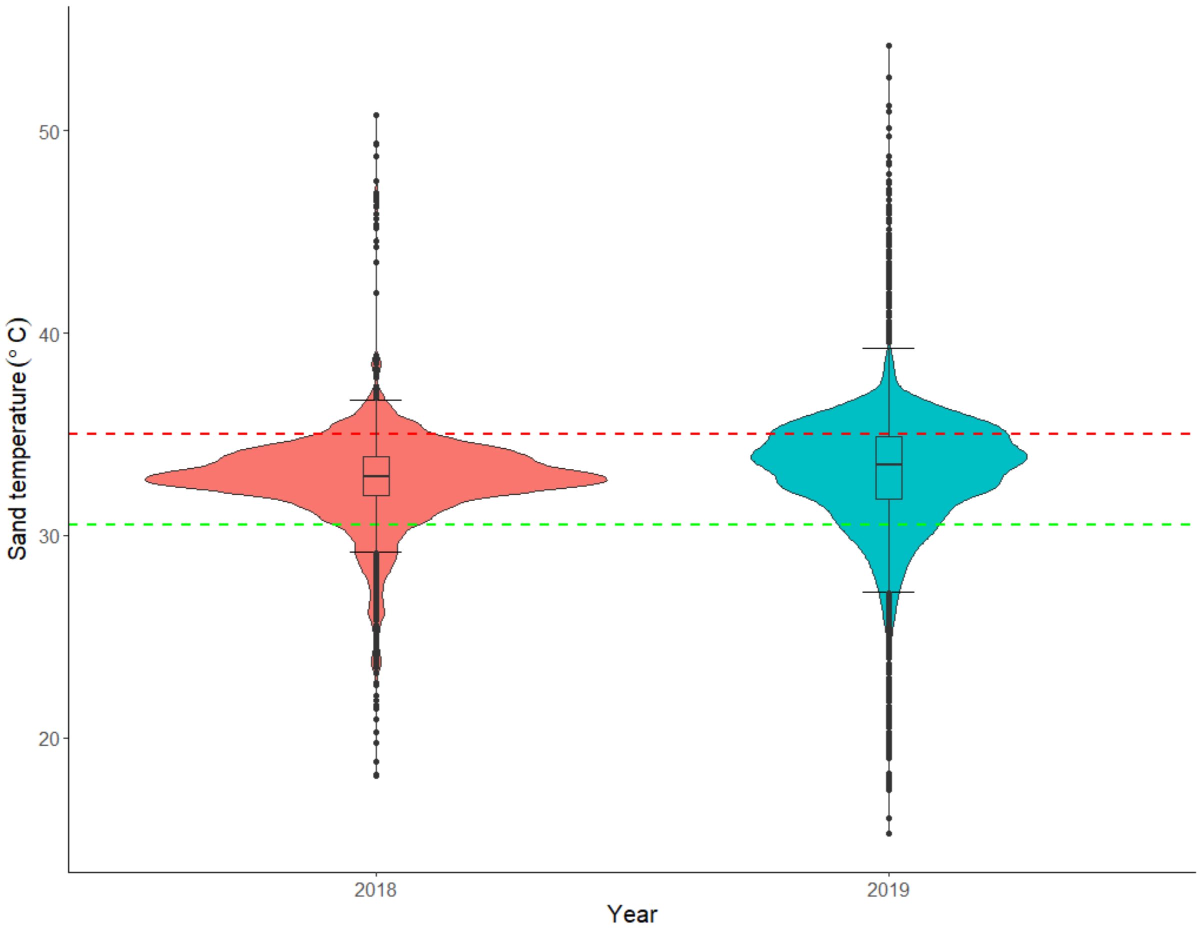

Figure 8. Violin plot of the daily average of sand temperatures (°C) for 2018 and 2019 recorded on the Pacific coast of Guatemala from May 2018 to November 2019. The thermal critical maximum for Olive Ridley embryos is shown as a red dashed line (35°C, Valverde et al. 2010). The pivotal temperature for Olive Ridleys is shown as a green dashed line (30.5 °C, Wibbels et al. 1998).

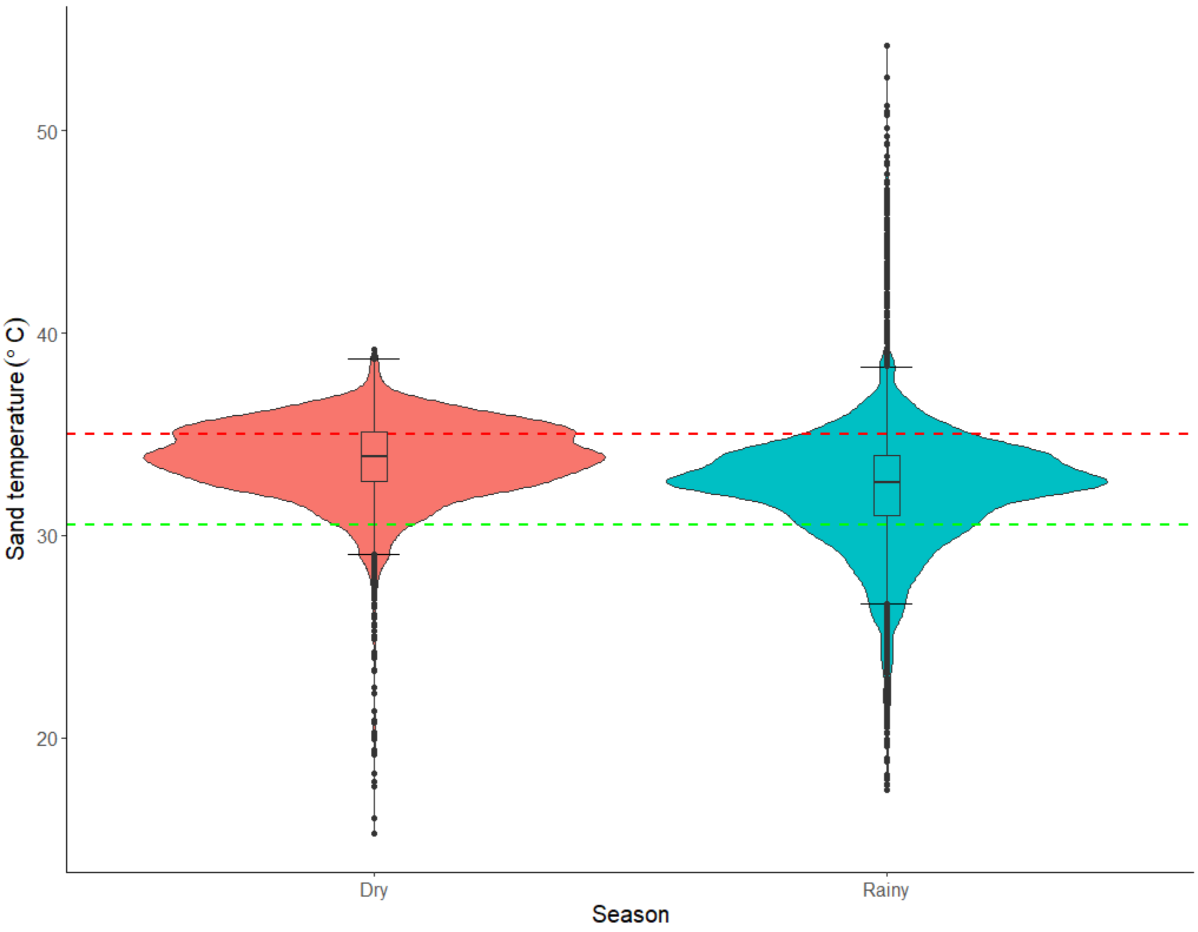

Figure 9. Violin plot of the daily average of sand temperatures (°C) classified into dry and rainy season, recorded on the Pacific coast of Guatemala from May 2018 to November 2019. The thermal critical maximum for Olive Ridley embryos is shown as a red dashed line (35°C, Valverde et al. 2010). The pivotal temperature for Olive Ridleys is shown as a green dashed line (30.5 °C, Wibbels et al. 1998).

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