REPRODUCTIVE PHENOLOGY, FECUNDITY, SURVIVAL AND GROWTH OF PUERTO RICAN ANOLIS LIZARDS IN THE CONTEXT OF CLIMATE WARMING.

By

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ABSTRACT

Anolis lizards are vulnerable to climate warming because, like other ectotherms, their basic physiological functions (e.g., locomotion, growth and reproduction) are strongly influenced by environmental temperature. However, before trying to understand the effects of climate warming on these tropical organisms, we need to understand the natural history of the species, what traits can be considered sensitive or vulnerable, and do so at scales that are relevant for the species. This approach allows the construction of baseline databases that can be useful in assessing the effects that current and future climate change will have on the biology and ecology of ectotherms.

In this research, we will focus on studying life history traits that we hypothesize to be sensitive to the effects of climate change (particularly climate warming) that have already occurred on Puerto Rican Anolis lizards: reproductive phenology, fecundity, survivorship and growth rates. The first goal of this dissertation is to describe the effects of recent climate warming on the reproductive phenology of Puerto Rican Anolis lizards (Chapter I). Given the temperature increase that has occurred in Puerto Rico due to climate warming, we evaluated if warming has changed the reproductive phenology of Anolis cristatellus and Anolis gundlachi in Puerto Rico in nature. We found that recent climate warming has stimulated reproductive cycles in upland populations while lowland population cycles has been depressed.

Since reproductive cycles varied at a regional scale and are very sensitive to environmental temperatures, we decided to evaluate if these cycles would differ between different habitat types (Chapter II). We followed the reproductive cycles of females Anolis cristatellus inhabiting open and forest habitats in two localities (Punta Salinas and Monagas,
Puerto Rico) and found a higher proportion of reproductive females in the warmer open environment where lizards can thermoregulate more effectively compared with the forest habitat.

In the third chapter we evaluate if other life history traits such as survivorship and growth rates are also sensitive to the observed differences in thermal environment between open and forest habitat. We estimated the survival, body condition and growth rates of *Anolis cristatellus* for more than a year in two contiguous but thermally distinct habitats (open and forest) in Punta Salinas using capture-mark-recapture methodology. We found that survivorship and body condition are higher in the open habitat, while growth rates are higher in the forest habitat for females (males showed no difference between the two habitats).

Results of this dissertation show the importance of considering traits that are vulnerable to climate change (such as reproductive cycles in Puerto Rican *Anolis* lizards) and most importantly, that local effects can interact with global patterns of climate change to produce complex and unexpected effects in life history traits of tropical ectotherms.
Dedicatoria

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GENERAL INTRODUCTION

The global and regional changes

During recent years a lot of attention has been given to the effects that climate change has on biodiversity. A search on google scholar with the words "climate+change+biodiversity" gives back about 516000 results when restricting the search to the range of years 2005-2015. When doing the same search for the years 1994-2004, we obtain about 90000 results. Thus, the interest and effort on understanding climate change and its effects on biodiversity has increased considerably during the last decade.

However, the amount of information produced so far is not equally distributed among either taxonomical groups or geographical areas (Parmesan, 2006; Pacifici et al., 2015). A recent study shows that the taxonomic focus of vulnerability assessments is biased towards birds, mammals and plants, and when looking at geographical patterns, temperate zones contain most of the information and research that has been done, while tropical areas remain relatively understudied (Pacifici et al., 2015), (Parmesan, 2006), (Colwell et al., 2008), (Dillon et al., 2010).

Warming has already occurred in the tropics, and precipitation patterns have changed in some regions (Malhi & Wright, 2004), (Jiménez-Muñoz et al., 2013), (IPCC, 2007). Since the mid-70s, temperatures have warmed 0.26 C per decade in tropical rainforest regions, probably as a consequence of the anthropogenic greenhouse effect. Climate models suggest that a warming of between 2 and 5° C can be projected in tropical rainforests over this century (Hulme et al., 2001), (Cramer et al., 2004), (Malhi & Wright, 2004), a change that seems likely to have a
substantial impact on tropical rainforest functionality (Lewis et al., 2004) (Clark et al., 2013) (Corlett, 2011) and even food security (Battisti & Naylor, 2009), (Wheeler & von Braun, 2013) (Easterling et al., 2007; cited in Vermeulen et al., 2012) . Also, unprecedented climates are expected to occur earlier in the tropics and among low-income countries, highlighting the vulnerability of global biodiversity and the limited governmental capacity to respond to the impacts of climate change (Mora et al., 2013). For example, projections based high-resolution dynamical models consistently indicate that greenhouse warming will cause the globally averaged intensity of tropical cyclones to shift towards stronger storms, with intensity increases of 2–11% by 2100 (Knutson et al., 2010).

Climate in the Caribbean region has also changed (Taylor et al., 2012). Studies demonstrate that the numbers of days having extremes maximum temperatures have increased significantly since the late 1950s , while the percent of days with very cold temperatures have decreased (Alexander & Eischeid, 2001), (Peterson, 2002), (Taylor et al., 2012). Also, the maximum number of consecutive dry days is decreasing and the number of heavy rainfall events is increasing (Peterson, 2002), (Neelin et al., 2006). In Puerto Rico, analysis of weather data indicates a significant warming trend (Jennings et al., 2014), which has also been associated with the decline of amphibians in the island (Burrowes et al., 2004). Analyses show significant increases in annual and monthly average temperatures in Puerto Rico. A rise of 0.012 °C/yr to 0.014 °C/yr (0.022 to 0.025 °F/yr) has occurred from 1900 to present. Therefore, Puerto Rico does follow the larger-scale trend in warming (0.6° C) (Taylor et al., 2012), although some locations on the island are warming faster than others (PRCCC, 2012).
Effects on biodiversity

How global changes, particularly global warming is going to affect the biodiversity inhabiting the Caribbean? Individuals, populations and communities respond differently to this change, according to their regional and local conditions. Furthermore, the warming itself is asymmetric (different places get warmer at different rates), increasing the complexity of the effect by causing even more heterogeneity within ecological dynamics (Walther et al., 2002). For example, (Deutsch et al., 2008) detailed that warming in the tropics, although relatively small in magnitude, is likely to have the most deleterious consequences because tropical ectotherms are relatively sensitive to temperature change, and because in their thermal tolerance range, the "start" temperatures in the tropics are already warm relative to their optimal temperature. A broad range of organisms with diverse geographical distributions have already been affected by global warming (Walther et al., 2002), (Root et al., 2003), (Parmesan, 2006), (Huey et al., 2009), (Sinervo et al., 2010), (Raxworthy et al., 2008), (Whitfield et al., 2007), (Pounds et al., 1999), (Pounds et al., 2006), (Stapley et al., 2015), (Sheridan & Bickford, 2011); (Moritz et al., 2008), (Chen et al., 2009), (Narins & Meenderink, 2014).

Warming during the last century has had significant effects on the population and natural history of organisms. Recent climate change has led to both increases and declines in population size (McCarty, 2001), (Cahill et al., 2012), and there are a few “tropical” examples. Among these few, is a correlational study in “La Selva” biological station in Costa Rica where (Whitfield et al., 2007) recorded declines of reptiles and amphibians over the last decades. Considering that some of these declines and local extinctions have occurred in pristine habitats, the authors suggest that climate shifts in the past 35 years have caused reductions in standing litter mass, a major proximate determinant of abundance for leaf litter amphibians and reptiles (Whitfield et
In “La Selva”, ecosystem functions would have been altered by the increase of temperature and wet conditions, which could negatively influence standing litter mass by affecting rates of litterfall or litter decomposition (Whitfield et al., 2007). Another tropical example is given by Pounds et al (2006). They reported *Atelopus* extinctions associated with pathogens outbreaks (such as *Batrachochytrium dendrobatidis*), which are influenced by warmer highland temperatures caused by climate warming. In the case of amphibian populations, recognition has been given to the deleterious effects of synergies between climate change, diseases outbreaks and habitat modification (Burrowes et al., 2004). Also, Raxworthy et al. (2008) documented upslope shifts on the distribution of reptiles and amphibian species in a Madagascar mountain chain.

*What about climate warming and Anolis lizards?*

*Anolis* lizards are one of the most conspicuous, abundant and diverse group of vertebrates inhabiting terrestrial ecosystems of the West Indies. They are diurnal, predominantly arboreal, and generally insectivorous (Williams, 1972), (Losos, 2009).

*Anolis* and lizards in general, are vulnerable to climate warming because, like other ectotherms, their basic physiological functions (e.g., locomotion, growth and reproduction) are strongly influenced by environmental temperature (Deutsch et al., 2008); (van Berkum, 1986); (Gorman & Licht, 1974), (Licht & Gorman, 1970), (Angilletta, 2009). Different species of *Anolis* occupy open and warmer habitats whereas some species occupy forests and cooler habitats (Ruibal & Williams, 1961).
Open-habitat species thermoregulate carefully and have high body temperatures; forest species are thermoconformers and have low body temperatures (Huey, 1974). For these forest lizards, which typically have low heat tolerance, the temperature range they can live within is small (Huey et al., 2009), hence even a slight increase on environmental temperature could cause heat stress, leading to a reduction in their activities (Kearney et al., 2009). This increase in environmental temperature could be harmful for these lizards during summer, but beneficial during winter (Huey et al., 2009). The major challenge for tropical species will be to “stay cool” during summer (Kearney et al., 2009). The impact of global warming on thermoregulation in ectotherms will depend critically on how changes in vegetation alter the availability of shade as well as the lizards’ capacity to alter their seasonal timing of activity and reproduction. Warmer environments also may increase maintenance energy costs while simultaneously constraining activity time, putting pressure on mass and energy budgets (Kearney et al., 2009); (Sinervo et al., 2010).

In the case of anole lizards, some neotropical populations declines have been attributed to climate change. Some Anoline populations, which are sensitive to rainfall variability, have declined in association with mist frequency patterns in the highland forest of Costa Rica and western Panama. The cloud forest anole, Norops tropidolepis, and the montane anole, N. altae began to decline in the late 1980s and disappeared in these Central America forests by 1996 (Pounds et al., 1999). After over 40 years of monitoring, Anolis apletophallus (formerly A. limifrons) decreases have been observed in its abundances in Barro Colorado Island, Panama, probably due to local climatic changes (Stapley et al., 2015).

However, not everything is bad news for Anolis lizards. Some species are likely to cope successfully with climate change due to their physiological plasticity or adaptation capability.
Anolis cristatellus for example shows increased fecundity and survivorship in warm environments compared to forested cooler ones (Otero et al, 2015; in press). This species was studied by Gunderson and Leal (2012) who compared the critical thermal maximum (CTmax), and the critical thermal minimum (CTmin) of an introduced population in Florida (introduced about 35 years ago), with the original/source population from Cabezas de San Juan, Puerto Rico (Kolbe et al., 2007). These authors found a difference of 3°C between the CTmin’s of the two populations, with the Florida introduced population being capable of tolerating significantly colder temperatures than the Puerto Rican source population; however, CTmax did not differ (M. Leal & Gunderson, 2012). Probably this difference is adaptative, since an increased tolerance to cold temperature would benefit the lizards from Florida by increasing their survival during the winter. These results supported the labile hypothesis in thermal ecology, which sustains that the thermal sensitivity of physiological performance can vary within and among species and that change in the performance can happen due to acclimation or evolution (Angilletta et al., 2002), (M. Leal & Gunderson, 2012).

Some caveats while trying to study the effects of climate warming: the importance of understanding natural history.

Research done so far focusing on understanding the effects of climate change on biodiversity have used different approaches. One method is to generate models that incorporate natural history and biological data with projections of the biotic and abiotic (e.g., climatic) variables that are expected to change (Kearney et al., 2009; Sinervo et al., 2010). A second is to experimentally simulate the conditions that organisms will face with the current and future changes. A third is to use long term monitoring data or replicate research work done previous to
recent warming and then determining whether any observed changes might be a consequence of climate warming. Each approach has its advantages and disadvantages, and are complementary (see Pacifici et al., 2015). The most appropriate approach will depend in the organism’s biology, the question being asked, the amount of information available from past studies, and the researcher’s capacity and budget to perform any of these alternatives methodologies.

A limitation of studies focusing on understanding the effects of climate warming on tropical lizards is that it is not clear which factors are causing declines: food availability, reproductive phenology, ecological interactions (both at population and community level), or behavior could all be involved. One of the most important points made by Cahill et al (2012), is that even though climate change is now recognized as a major threat to global biodiversity that has already caused widespread local extinctions, the proximate mechanisms and specific causes of these present and future extinctions are much less clear (Cahill et al., 2012). Thus, scientists need to understand these causes, and investigate the proximate mechanisms by which animals are affected by climate change and whether they are able to cope with it. We need then to understand the natural history of the species we consider sensitive or vulnerable, and build baseline databases that can be useful in assessing the effects that current and future climate change will have.

Numerous studies have supported the idea that to determine species vulnerability to climate change, life-history traits are more important than taxonomy and distribution (see Pacifici et al., 2015). So, how can we gain more knowledge about the effects of climate warming on *Anolis* lizards? We need to focus on natural history traits that are sensitive to climate warming, but we need to do that considering what is ecologically relevant for the species we are studying.
In the case of *Anolis* lizards, Logan et al (2013) have demonstrated the importance of looking at environmental variables at relevant scales. For example, most of the models predicting how climate warming will affect ectotherms are based on ambient temperature data gathered from weather stations. However, body temperatures of ectotherms result from a complex interaction between many biophysical parameters (including convection, conduction, and radiation) and thus consistently diverge from ambient conditions (Bakken, 1992), so predictive models should use temperature variations at a much smaller scale (often less than 5 m²; Barlett & Gates, 1967; Sears et al., 2011). Other abiotic variables should be considered. Topography for example, might be related with the performance curves of some *Anolis* populations: populations in areas with higher topographic complexity are speculated to have broader performance curves, and for this reason previous assumptions of thermal homogeneity in tropical forests have been probably overstated (Logan et al., 2013). Likewise, humidity and wind speed are two important abiotic variables to consider. Both have been associated (positively or negatively depending on the species studied) to activity levels of tropical lizards (Logan et al., 2015); emphasizing the idea that if we want to predict the response of tropical ectotherms to climate change we need models that consider habitat-specific effects, since those that only include changes in mean temperature are likely to be inaccurate (Logan et al., 2015).

So, if we want to understand the effects of climate change, or climate warming specifically, what traits should we study?: We need to investigate those traits that are sensitive to changes of those abiotic environmental variables that are expected to vary with climate change. For example, limited dispersion capacity, habitat specialization, low reproductive rates, specialized dietary requirements, restricted distribution and narrow physiological tolerances are traits that make a species vulnerable to climate change.
In this research, we will focus on studying traits that we think are helpful in understanding the effects that climate change (particularly climate warming) already had, and probably will have, on Puerto Rican Anolis lizards: reproductive phenology, fecundity, survivorship and growth rates.

In chapter 1, I describe the effects of recent climate warming on the reproductive phenology of Puerto Rican anolis lizards. In the West Indies, seasonal variation of temperature plays a major role determining the length of the breeding season. In general, those species living at northern latitudes and at higher elevations have shorter breeding seasons (Licht and Gorman, 1970; Gorman and Licht, 1974). In Puerto Rico, reproduction patterns are highly influenced by environmental temperature: reproduction peaks in summer and drops in winter. The effect of environmental temperature on reproductive phenology was not well understood until 1975, when Licht and Gorman made translocation experiments with Puerto Rican Anolis adult males and the role of environmental temperature was better understood: males from lowland translocated to higher altitudes had a cessation of spermatogenesis and androgenesis earlier than males in the lowlands, suggesting that reduced temperatures (probably combined with short daylengths) are the major cue for the timing and magnitude of gonadal regression (Licht and Gorman, 1975). Therefore, according to Gorman and Licht (1974), Licht and Gorman, 1975) both sexes of Puerto Rican Anoles show a marked altitudinal effect on gonadal cycles, even over ranges of 150m, due to different thermal environments.

Given the temperature increase that has occurred in PR due to climate warming, we evaluated if warming has changed the reproductive phenology of Anolis cristatellus and Anolis gundlachi in Puerto Rico in nature. We hypothesized that if climate warming has altered lizard
reproduction, then: 1) lizards will be reproducing more and we will find a higher percentage of gravid females during the winter because it is warmer, or 2) lizards will be reproducing less in summer due to heat stress.

We did this by repeating the methodology employed by Gorman and Licht (1974) (including their 7 field sites) and comparing their results with the ones we obtained. Knowing if a higher or lower proportion of lizards are reproducing more or less than 40 years ago allowed us to understand the consequences of climate warming on these tropical lizards’ reproductive cycles.

In chapter 2, I describe the reproductive cycles of female *Anolis cristatellus* inhabiting two different kinds of habitats in two localities: Punta Salinas and Monagas, Puerto Rico. At both localities, these habitats are contiguous but are thermally distinct.

Reproductive cycles (and their intensity) often vary intraspecifically over geographic scales, in part because environmental factors that drive reproduction vary geographically. Some species like *Anolis cristatellus* occupy environmentally distinct habitats even at single localities. Open-habitat lizards thermoregulate relatively carefully to achieve body temperatures ($T_b$) that are relatively high and which overlap with thermal preferences measured in laboratory gradients (Huey, 1974; Lister, 1976). Forest species are thermoconformers and have lower $T_b$ (Ruibal, 1961; Rand, 1964). Whether individuals living in such habitats have different reproductive cycles (local scale variation) is unstudied in lizards. Since temperature drives reproductive cycles in this species we expect to find differences on the cycles of females inhabiting thermally different habitats: open and forest. Since these lizards are highly territorial, we assume that there is no exchange of individuals between habitats (Leal, coms pers). We hypothesized that if local habitat affects reproductive patterns, then we would find significantly different cycles: we
expected to have a higher proportion of reproductive females in the warmer open environment where lizards can thermoregulate more effectively, we also expected a longer breeding season compared with the forest habitat. We surveyed for more than two years open and forest habitats in two lowland sites at northeast Puerto Rico: Punta Salinas and Monagas. The results helped us understand the consequences different thermal habitats have on reproductive phenology and fecundity and discuss future implications considering how landscapes in Puerto Rico and around the globe are being continuously modified and fragmented.

In chapter 3 we estimated the survival and growth rates of Anolis cristatellus for more than a year in two contiguous but thermally distinct habitats using capture-mark-recapture methodology, also in Punta Salinas.

One of the main challenges when trying to document climate-related population declines, is that most species lack data on population parameters over time (Cahill et al., 2012). Some populations have been the focus of long-term monitoring and research, facilitating detailed studies of climate change impacts. Unfortunately, this is not the case for Puerto Rican Anolis lizards. Thus, it is important to set a background or baseline information that can be used in making projections and future comparisons.

Since we knew the relationship between the different thermal habitats and the reproductive cycles of Anolis cristatellus, we decided to study two important life history traits: survivorship and growth rates, through a capture-mark-and-recapture study in two contiguous but thermally distinct habitats. Understanding vital rates such as survivorship is key if we want to comprehend the population dynamic of the species, even at small spatial scales such as the presented in this research. Moreover, survivorship estimates are necessary for the construction of
population projection matrices and complete demographic analysis, which provide important tools for conservation biology.

Our goal is to provide baseline information about life history traits of Puerto Rican Anolis lizards. We think this information can be useful in understanding the past and future consequences climate change had and will have on these species, and we want to emphasize the importance of studying traits or biological aspects that are ecologically relevant for the model species.

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CHAPTER I

Effects of Recent Climate Warming on the Reproductive Phenology of Puerto Rican Anolis Lizards

Abstract

Annual reproductive cycles of Puerto Rican Anolis lizards are seasonal and highly influenced by seasonal variation in environmental temperatures: female reproduction peaks in summer and drops in winter, especially at higher elevations. This makes the reproductive phenology of Puerto Rican Anolis particularly vulnerable to climate warming. Here we test the prediction that higher fall and winter temperatures should promote female reproductive output especially at high elevation, but that warmer summers should depress female reproduction particularly at low elevation as a result of associated heat stress. To test these hypotheses we obtained contemporary data on female reproductive phenology (percentage gravid) in multiple populations of Puerto Rican Anolis lizards at monthly intervals over three years, and compared these data with historical data documented for some of the same sites and species sampled by Gorman and Licht in the early 1970's. We found that during summer months female reproduction did not differ in intensity between contemporary and historical periods, but in fall and winter months, females at some sites -- notably mid and high-elevations -- were more likely to be reproductive at present times, than in the 1970's. These results suggest that recent climate warming has not had a
negative effect on reproduction of Puerto Rican Anolis in summer but appears to have benefited reproduction in fall and winter, when cool temperatures reduce female reproduction.

**Introduction**

The effect of recent climate warming on organisms inhabiting tropical zones is relatively understudied and not well understood (Parmesan, 2006), (Colwell et al., 2008), (Dillon et al., 2010). Even though climate warming occurs at a lower rate in the tropics than at higher latitudes (Williams et al., 2007), (Deutsch et al., 2008), (Dillon et al., 2010), its effects on tropical organisms are extremely important to understand because the tropics host most of the biodiversity of the world. Moreover, tropical organisms are more sensitive to temperature changes than temperate ones, because tropical species generally have relatively narrow tolerance ranges and reduced acclimation capacities (Colwell et al., 2008), (Deutsch et al., 2008), (Bonebrake & Deutsch, 2011), (Dillon et al., 2010), (Ghalambor et al., 2006), (Angilletta, 2009), (McCain, 2009), (Buckley et al., 2013), (Bonebrake & Mastrandrea, 2010); although many recently it has been described that many species around the world possess the capacity for thermal acclimation (Seebacher et al., 2015).

Understanding the effects of climate warming requires the integration of different kinds of information. For example, past versus present comparisons have proven to be a very useful way to evaluate whether warming has caused changes in organismal natural history, or in population and community ecology (Thuiller, 2007), (Parmesan, 2006), (Dawson et al., 2011), (Parmesan et al., 2013), (Walther et al., 2002). Although this approach has some disadvantages (changes in taxonomy, researchers' biases, and modification or disappearance of original field
sites among others), it has been effectively used during the last decades, resulting in an important amount of information elucidating the effects of recent climate warming on both temperate and tropical biodiversity (Moritz et al., 2008), (Raxworthy et al., 2008), (Walther et al., 2002), (Chen et al., 2009), (Narins & Meenderink, 2014), (Camille Parmesan, 2006), (Sheridan & Bickford, 2011), (Bickford, 2014-ATBC).

For this study, we used this methodology to search for potential effects of recent climate warming on the reproductive phenology of Puerto Rican Anolis lizards. We used the extensive research conducted by Gorman and Licht in Puerto Rico in the 1970's as our historical baseline. Anolis lizards are potentially sensitive to climate warming, because like other ectotherms, their basic physiological functions--such as locomotion, growth and reproduction-- are strongly influenced by environmental temperature (Huey, 1983), (van Berkum, 1986), (Licht & Gorman, 1970), (Gorman & Licht, 1974). Within this group, declines in some neotropical populations have already been attributed to climate change. For example, Central American Anoline lizard populations, which are sensitive to rainfall variability, have declined in association with mist frequency patterns in the highland forest of Costa Rica and western Panama (Pounds et al., 1999). The cloud forest anole, Norops tropidolepis, and the montane anole, N. altae began to decline in the late 1980s and disappeared from these Central American forests by 1996 (Pounds et al., 1999). Anolis apletophallus (formerly A. limifrons) also showed abundance decreases in a study based on 40 years of data collection from Barro Colorado Island (BCI) in Panama (Stapley et al., 2015).

For decades, Caribbean Anolis lizards have been the subject of extensive research in evolution, thermal biology, natural history, ecology, behavior, physiology, and reproductive biology (Losos, 2009). Recently, they have been used as models to test and understand the
effects of recent climate warming on ectotherms (Huey et al., 2009), (Gunderson & Leal, 2012), (Logan et al., 2013). *Anolis* lizards are probably the most conspicuous, abundant, and diverse taxon of vertebrates inhabiting terrestrial ecosystems in the West Indies. They are diurnal, predominantly arboreal, and generally insectivorous (Williams, 1972), (Leal & Rodriguez-Robles, 1997). In Puerto Rico their reproductive cycles are cyclical and are highly sensitive to environmental temperature: reproduction peaks in summer (which is also the wet season) and drops during autumn and winter (the dry season). The autumn-winter decline in reproduction in both males and females is especially marked at higher altitude (Licht & Gorman, 1970) (Gorman & Licht, 1974). According to Gorman and Licht (1974) both sexes of Puerto Rican Anoles show a marked altitudinal effect on gonadal cycles, even over ranges as small as 150 m, presumably in response to ambient temperature variations associated with elevation (Janzen, 1967).

We sampled female reproduction almost every month for three years (2011-2014) at some of the same sites used by Gorman and Licht (1974). By comparing contemporary with historical data, we can look for shifts in phenology -- specifically whether they are consistent in direction with those predicted. This allowed us to determine if recent climate warming in Puerto Rico (Narins & Meenderink, 2014), (Taylor et al., 2012), (Schall et al., 2000), (Burrowes et al., 2004), (Alexander & Eischeid, 2001) has affected the reproductive cycles of these lizards in *their natural habitats*.

Considering that there is a lack of comprehensive analysis of the capacity for physiological plasticity across taxonomic groups and geographic regions, it is hard to predict the impacts of climate warming (Seebacher et al., 2015). We need then to assess traits that can help us understand physiological plasticity and the adaptations organisms can undergo, and in this sense, ectotherms such as *Anolis* lizards can provide a lot of information. For example, relatively recent
research has demonstrated that changes in thermal tolerance in *Anolis cristatellus* have occurred relatively rapidly, which suggests that the thermal physiology of this tropical lizard is more likely to change than previously proposed (Leal & Gunderson, 2012). Thus, Puerto Rican anoles offer an opportunity to evaluate the potential impact of recent warming on traits such as reproductive cycles. Given the relationship between environmental temperatures and the reproductive cycles in these lizards, by comparing historical and contemporary data we can test hypotheses about the effects of recent climate warming.

We hypothesize that if climate warming has altered reproductive cycles, then: 1) now that winters are warmer, lizards will reproduce more, and we will find a higher percentage of gravid females, and 2) now that summers are also warmer than in the past, lizards will reproduce less because of heat stress. Our results show that there is little change in reproduction of females during summer at any of the field sites, suggesting that these lizards are not heat stressed. However, we did detect some differences in reproductive phenologies during fall and winter months, especially in mid and upland populations where there was a higher proportion of reproductive females compared to those in the 1970s. Thus, recent climate warming may be promoting reproduction in mid and upland *Anolis* lizards in Puerto Rico.

**Field Methods and Analyses**

**Study species**

We studied the annual reproductive cycles of females of *A. cristatellus* and *A. gundlachi* for three years (July 2011-August 2014), following the general methodology previously used by Gorman and Licht. *A. cristatellus* is a medium-sized, trunk-ground anole that is widely
distributed from sea level to mid-elevations in Puerto Rico (Rand, 1964), (Rivero, 1998). At lowland sites it is abundant in both open and forest habitats; but at higher elevations, it is restricted to warmer open areas (Hertz, 1992), (Huey, 1974), (Huey & Webster, 1976), (Lister, 1981). It is a thermoregulator in open habitats but a thermoconformer in forests (Huey & Webster, 1976), (Huey, 1974), (Hertz, 1992), (Gunderson & Leal, 2012). *Anolis gundlachi* is also a medium sized trunk-ground anole that is common in deeply forested areas from low to high elevations in Puerto Rico. It is a thermoconformer (Huey & Webster, 1976)) and is restricted to shaded forested areas. The reproduction (Gorman & Licht, 1974); (Lister, 1981), behavior (Leal, 1999), (Leal & Rodríguez-Robles, 1995), habitat selection (Chandler & Tolson, 1990), and thermal biology (Gunderson & Leal, 2012), (Heatwole et al., 1969), (Hertz et al., 1979), (Hertz, 1992), (Huey & Webster, 1976), (Huey, 1974), (Lister, 1981), (Rand, 1964), of these two species are well known.

**Field sites**

We resurveyed the same field sites studied by Gorman and Licht (1974). Figure 1 shows the localities in Puerto Rico where the two species were studied during 1971 and 1972, and again between 2011 and 2014. A total of 5 populations were sampled at 5 different localities:

*El Verde field station:* This protected rainforest is located in the northern slope of El Yunque National forest, at 360 m (N 18°19.263’- W 65°49.146’). It is a well regenerated secondary forest where *Anolis gundlachi* is very abundant.
**Ranger House:** This field site is located at one of the northern entrance of El Yunque National Forest, at km 22 of road PR186, at an elevation of ~120m, (N 18°20.362’- W 065°49.512’). It is mostly a rural area where lowland and upland forests converge. We collected *A. cristatellus* at houses, fences, and other artificial structures at the edges of the road where often perches. In 1972 it was present in the forest as well as in the open (Huey and Webster 1976), though Gorman and Licht collected only in open areas. Since 1972 it has been replaced in the forest by *A. gundlachi*.

**Hacienda Rosas:** This site is located near Utuado, at kilometer 34.2 of road PR140, at an elevation of 320 m (N 18.119’ – W 66° 35.573’). It used to be a coffee plantation in the 1970’s. The plantation was abandoned and a secondary forest has grown, so it is physically very different from what Gorman and Licht (1974) surveyed four decades ago. *A. cristatellus* seems to have been displaced from the forest by *A. gundlachi*, so it is now common only in the open and warmer areas of the Hacienda. Because of major habitat shifts at this site, any reproductive differences can not readily be attributed to climate warming.

**Guanica:** This dry forest site is located in the southwest of Puerto Rico. Most samples were taken in the Playa Tamarindo area at the end of the road PR333, essentially at sea level. *A. cristatellus* is very abundant, especially in shady forest patches (N 17° 57.228’ – W 66° 50.842’). *A. cooki* is abundant in the more open areas, but was not studied by Gorman and Licht (1974).

**Río Piedras, University of Puerto Rico campus:** This is also an urban field site located within the San Juan metropolitan area, at the University of Puerto Rico campus, at 14 m (N 18°24.207’- W
A. cristatellus is also very abundant here in small patches of vegetation, open areas, houses and other artificial perch substrates.

Materials and Methods

We resurveyed the same field sites Gorman and Licht studied back in 1971 and 1972 almost every month from July 2011 through August 2014, and Hacienda Rosas from October 2011 through July 2012 and again from August 2013 until December 2013. To assay female reproduction at each monthly census, we captured 15 to 93 females in each habitat, measured their body temperature ($T_b$) using a Miller-Weber cloacal thermometer (and following standard precautions), size (SVL in mm), weight (mass in g), and palpated females to determine their reproductive condition (see below). We also recorded time of day, perch height, sun exposure (full sun, partial sun, or shade), and weather (sunny, cloudy, sunny-cloudy, or rainy). We marked all captured individuals with a temporary paint dot (Elmer’s non-toxic paint markers) so that we would not recapture them during a given census.

We classified females as “non-reproductive” (Class I) if they had no eggs in oviducts or had follicles no larger than 3mm; "reproductive" if they had enlarged follicles (Class II) and as "gravid" if they had one (Class III) or two eggs (Class IV) in their oviducts (see Gorman and Licht, 1974; Lister, 1981). Note that Gorman and Licht (1974) sacrificed females and determined reproductive condition via dissection, whereas we palpated and then released all females. LMO did all palpating. During July 2011, she correctly assigned reproductive status to every lizard
(verified by dissections) in a test series of 33 females of *A. cristatellus* and *A. gundlachi* from various localities in Puerto Rico.

In our surveys some of the animals we captured were subadult females, so we established the minimum size (SVL) of adult females (i.e., reproductive) as described in Gorman and Licht (1974) before computing reproductive frequency (i.e., percentage of adult females that were gravid) in the sites. This was done to avoid including specimens that had not yet reached maturity. The smallest (SVL) *A. cristatellus* and *A. gundlachi* female that were gravid were 40 mm and 40 mm respectively, in all populations studied. Thus, following Gorman and Licht (1974), we set the minimum size of adult females at 2 mm larger than these levels.

To compare historical versus contemporary reproductive cycles, we plotted the proportion of reproductive females by month (those with reproductive classes II, III and IV), and added 95% confidence intervals. Unfortunately, Gorman and Licht's original data set was lost, so it was not be possible to determine whether the observed differences are statistically significant (we would need their sample sizes besides their observed proportions). We based our past versus present comparisons on the data presented on the graphs of their paper (Gorman and Licht, 1974), and considered results as 'important', depending on whether confidence intervals overlapped or not.

To explore whether female reproduction might be responding to environmental temperature, we plotted the percentage of gravid females at each field site each month against the median Tb of the lizards caught and calculated the correlation coefficients. Given the observed relationship between reproduction and environmental temperatures (Gorman and Licht, 1974; Licht & Gorman, 1975), we expect to find a positive correlation between the percentage of gravid females and their body temperatures.
Results

Overall, contemporary annual female reproductive cycles of Puerto Rican Anolis lizards follow the same annual pattern described in the 1970’s: female reproduction peaks in late spring and summer, drops in autumn, and remains low in winter, especially at high elevation (see Table 1). However, we found mixed results when comparing historical versus contemporary data for the cool months of the year. At some lowland localities the proportion of gravid females has decreased, while in some highland localities there has been an increase in the proportion of gravid females (Fig. 1, 2 and 3). Below, we briefly describe the patterns found at each field site.

El Verde: at this mid to high-elevation site we found that there is an important increase in the proportion of gravid Anolis gundlachi females during the months of November and December for one of the years, and a smaller increase during the beginning of the year when comparing historical vs contemporary data (see Fig. 2). Also, during some summer months we found a non-significant higher proportion of gravid females compared to the historical data.

Ranger House: at this mid elevation site we found that the general seasonal pattern holds as for the other A. cristatellus populations. We found an important increase in the proportion of gravid females during the month of December in relation to the historical data (see Fig. 3). There is also a slight increase on the proportion of gravid females during the months of November and January compared to the historical records.

Hacienda Rosas: at this higher elevation site we found that there is an important increase in the proportion of gravid females during the month of November when comparing historical vs
contemporary data (see Fig. 4). And for some summer months, the proportion of gravid females was slightly higher than in the 1970’s (although not significant). Unfortunately, Gorman and Licht did not sample during the first months of the year, so we don’t know whether this difference holds for the other cool months of the year.

Guanica: overall, female reproduction peaks in summer but drops in winter as for the other Anolis populations, but at this site we found more current variability among years (2011-2014) compared to the other sampled sites (see Fig. 5). Also, it seems that the reproductive peak occurs later in summer (at least during two years) compared to the other A. cristatellus sites. However, we found an important lower proportion of gravid females compared to what Gorman and Licht reported in the 1970’s, especially during late summer, fall and winter months. Unfortunately they only sampled during three months in 1972.

Rio Piedras: at this urban low elevation site we also found an important lower contemporary proportion of gravid females compared to what Gorman and Licht reported in the 1970’s, especially for the fall months (see Fig. 6).

For both species, it seems that the contemporary proportion of gravid females has increased during fall and winter months for mid and higher elevation sites, but the opposite has occurred at the lowland sites. Body temperatures were positively correlated with the proportion of gravid females (except in Río Piedras) (see Figures 7-11), and all contemporary lizards populations showed higher body temperatures during summer months (Table 1).
Discussion

For both *A. cristatellus* and *A. gundlachi*, the proportion of gravid females has increased during fall and winter months for mid and higher elevation sites compared with the proportions observed four decades ago. Conversely, the opposite pattern is observed at the lowland sites. These differences in reproductive cycles among locations may be attributable to the changes that have occurred at each site during the last four decades, and changes in habitat types (i.e. vegetation) within the localities where the samples were taken. Hacienda Rosas for example, was a coffee plantation in the 1970’s, but after it was abandoned, a closed canopy secondary forest has grown; thus, the site is very different from what it was when Gorman and Licht worked there four decades ago. At this site *A. gundlachi* has displaced *A. cristatellus* from the forest, so now *A. cristatellus* is common only in the open and warmer areas of the Hacienda. These changes affect the replicability of our work, and the comparison between historical and contemporary data. Furthermore, over the last decades Puerto Rico has had many land use and land cover changes that have caused reforestation in most of the island, especially in those areas that had been used for agriculture (Aide et al., 1995), (Rivera & Aide, 1998).

Still, the current higher proportions of gravid females observed at sites like El Verde (which is warmer now than in the 1970's) are most likely due to recent climate warming. Preliminary analysis (Huey, personal communication) done with the weather data collected at El Verde field station, have shown an increase in the environmental temperatures over the last decades. We know that seasonal temperature differences play a very significant role in annual seasonal reproductive cycles of numerous *Anolis* lizards in the Greater Puerto Rico Bank (Gorman and Licht, 1974; Licht and Gorman, 1975), and this was experimentally demonstrated with translocation experiments done with *A. cristatellus*. How exactly higher temperature
stimulate an increase in reproductive readiness is unknown, but future works evaluating activity hours, food intake, and metabolic rates would be helpful elucidating this.

For places like Rio Piedras and Ranger House the heterogeneity of the landscape at each site might play an important role in the changes we have documented. Both sites include small patches of forests and open urban areas with artificial structures, so there are many different types of suitable habitats where the lizards perch. Otero et al (2015; in press) demonstrated that reproductive condition and reproductive cycles of *Anolis cristatellus* females differ strikingly between open and forest areas, probably because of differences in the thermal characteristics of each habitat. Thus, the comparison between historical and contemporary data for these two sites is probably unreliable, since Gorman and Licht (1974) did not record in detail the type of habitat where they collected each lizard, simply because the effect of habitat on the reproduction of these lizards (Otero et al. 2015; in press) was unknown and unsuspected during the early 1970’s.

We think that our past vs. present comparisons have more validity in Guanica and El Verde. Both sites are within protected areas and have not changed much structurally during the last decades (except for hurricanes, from which these habitats have recovered- Hogan et al., 2004). However, results between these two sites differed dramatically over the contemporary collecting time. The proportion of *A. gundlachi* gravid females has increased during the cooler months of the years (fall and winter) at El Verde (350 m) when comparing the historical and contemporary data. On the other hand, at Guanica (1m asl), a lower proportions of *A. cristatellus* females were gravid during the fall months when comparing the historical and contemporary data. This might reflect a negative effect of warming, but this population had notably more variable cycles between years than did or other *A. cristatellus* populations (fig 5). Why reproductive cycles of *A. cristatellus* in Guanica differ so much from other lowland populations
(e.g., Rio Piedras, as well as open habitats at Punta Salinas and Monagas, see Otero et al., 2015; in press). These differences in reproductive cycles might be a consequence of the physiological plasticity of this species and the fact that Rio Piedras and Guanica are very different habitats.

Still, ongoing genetic studies suggest that *A. cristatellus* populations in the southwest of Puerto Rico are genetically distinctive (McElroy, comm pers). Also, the characteristic lack of precipitation in the dry forest could account as an abiotic stressor affecting the reproductive cycles of these Guanica populations.

Behavior could also play an important role in how these lizards deal with a warmer environment. *Anolis cristatellus* can behave both as a thermoregulator and as thermoconformer, depending on its habitat (Huey, 1974), (Huey & Webster, 1976), whereas *Anolis gundlachi* is always a strict thermoconformer. *A. cristatellus* could use behavior to buffer higher environmental temperatures and then stay within thermal ranges close to their preferred temperatures (Kearney et al., 2009), (Huey et al., 2012). *A. gundlachi* does not have this option since it is a thermoconformer species inhabiting homogenous thermal environments. Could these two species use behavior equally to compensate for a warmer environment?; Although some populations could use behavior to diminish the effects of recent climate warming at some places, it has been pointed out that this could bring associated costs: more time thermoregulating could mean less time to feed, mate, and defend a territory among other tasks and behaviors (Kearney et al., 2009), (Sinervo et al., 2010). Whether these species have changed their behavior during the last decades to cope with climate warming is unknown.

We found that the proportions of gravid females were positively correlated with body temperatures for most populations (except in Rio Piedras; see Figures 7-11), which supports the idea of a close relationship between environmental temperatures and reproduction. The
variability in the correlation coefficients may also be due to the heterogeneity of the landscapes where the lizards were sampled.

Although recent climate warming has fostered reproductive output for some Puerto Rican Anolis populations (since there is a higher proportion of gravid females), it seems that smaller scale effects are more important and ecologically relevant for the reproductive phenology of these lizards (Otero et al., 2015; in press). Regional and local landscape changes, habitat effects and behavior may be playing a more important and complex role on reproductive cycles than global changes such as climate warming. Also, although we can relate a higher proportion of reproductive lizards with a warmer environment, is still necessary to find out the underlying processes: higher metabolisms and levels of activity?, higher food availability?, ecosystem changes?, etc. Whether these increases in reproductive output have consequences for the populations’ viability is unknown so far, but the question deserves further research and already a study looking at the population ecology of A. cristatellus at different thermal environments is being conducted (Otero et al., in prep).

The landmark paper by Gorman and Licht (1974) has provided us with an excellent opportunity to use Anolis lizards as models to evaluate the effects of recent climate warming, and hopefully some of the contemporary data presented here will serve as a baseline for future comparisons.
Tables

Table 1. Contemporary seasonality in body size and reproductive condition in *Anolis* from Puerto Rico

<table>
<thead>
<tr>
<th>Species</th>
<th>Locality</th>
<th>Seasona</th>
<th>N</th>
<th>SVL (mm)</th>
<th>Mass (g)</th>
<th>Tb d</th>
<th>% Reproductive</th>
<th>% Gravid</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>A. cristatellus</em></td>
<td>Rio Piedras</td>
<td>Winter</td>
<td>190</td>
<td>48.05 ± 0.10</td>
<td>2.79 ± 0.01</td>
<td>28.44±0.15</td>
<td>50.52</td>
<td>40.52</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Summer</td>
<td>250</td>
<td></td>
<td></td>
<td>29.28±0.12</td>
<td>86.8</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ranger</td>
<td>Winter</td>
<td>180</td>
<td>47.66 ± 0.12</td>
<td>2.92 ± 0.03</td>
<td>28.65±0.18</td>
<td>55.0</td>
<td>51.7</td>
</tr>
<tr>
<td></td>
<td>House</td>
<td>Summer</td>
<td>257</td>
<td></td>
<td></td>
<td>30.70±0.17</td>
<td>93.0</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Hacienda</td>
<td>Winter</td>
<td>109</td>
<td>45.85 ± 0.14</td>
<td>2.39 ± 0.03</td>
<td>25.91±0.27</td>
<td>25.7</td>
<td>22.0</td>
</tr>
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a Winter = Nov-Jan; Summer = May-Aug

b Reproductive includes all animals with developing ovarian follicle-those with no eggs (Class II) and those with one or two oviductal eggs-gravid (Classes III and IV).

c Mean ± standard error.

d Tb= Mean body temperature
Figures

Figure 1. Map of Puerto Rico showing the field sites where historical and contemporary data were collected. *A. cristatellus* was sampled in all the field sites except in El Verde, where *A. gundlachi* was sampled.
Figure 2. Reproductive activity of *Anolis gundlachi* measured as the proportion of gravid females (those with one or two eggs in their oviducts- Classes III and IV respectively) in El Verde Field station. Black circles represent contemporary data (July 2011-August 2014), and grey circles represent historical data collected by Gorman and Licht in 1971 and 1972.
Figure 3. Reproductive activity of *Anolis cristatellus* measured as the proportion of gravid females (those with one or two eggs in their oviducts—Classes III and IV respectively) in the mid-elevation site Ranger House. Black circles represent contemporary data (July 2011-August 2014), and grey circles represent historical data collected by Gorman and Licht in 1971 and 1972.
Figure 4. Reproductive activity of *Anolis cristatellus* measured as the proportion of gravid females (those with one or two eggs in their oviducts- Classes III and IV respectively) in the higher elevation site Hacienda Rosas. Black circles represent contemporary data (July 2011-August 2014), and grey circles represent historical data collected by Gorman and Licht in 1971 and 1972.
Figure 5. Reproductive activity of *Anolis cristatellus* measured as the proportion of gravid females (those with one or two eggs in their oviducts- Classes III and IV respectively) in the coastal Guanica. Black circles represent contemporary data (July 2011-August 2014), and grey circles represent historical data collected by Gorman and Licht in 1971 and 1972.
Figure 6. Reproductive activity of *Anolis cristatellus* measured as the proportion of gravid females (those with one or two eggs in their oviducts- Classes III and IV respectively) in lowland and urban locality of Río Piedras. Black circles represent contemporary data (July 2011-August 2014), and grey circles represent historical data collected by Gorman and Licht in 1971 and 1972.
Figure 7. Reproduction sensitivity to body temperatures of females inhabiting El Verde, Puerto Rico (correlation coefficient: 0.69).

Figure 8. Reproduction sensitivity to body temperatures of females inhabiting Ranger House, Puerto Rico (correlation coefficient: 0.55).
Figure 9. Reproduction sensitivity to body temperatures of females inhabiting Hacienda Rosas, Puerto Rico (correlation coefficient: 0.69).

Figure 10. Reproduction sensitivity to body temperatures of females inhabiting the dry forest of Guanica, Puerto Rico (correlation coefficient: 0.40).
Figure 11. Reproduction sensitivity to body temperatures of females inhabiting the urban area of Río Piedras, Puerto Rico. Correlation coefficient: -0.08

Literature Cited


CHAPTER II

A Few Meters Matter: Local Habitats Drive Reproductive Cycles in a Tropical Lizard

Abstract: Reproductive phenology often varies geographically within species, driven by environmental gradients that alter growth and reproduction. However, environments can differ between adjacent habitats at single localities. In lowland Puerto Rico, both open (sunny, warm) and forested (shady, cool) habitats may be only meters apart. The lizard Anolis cristatellus lives in both habitats: it thermoregulates carefully in the open but is a thermoconformer in the forest. To determine whether lizard reproduction differs between local habitats, we compared female reproductive cycles in open versus forest at two localities for over two years. Open females were more likely to be reproductive throughout the year than were forest females, probably because open females were able to bask and thereby achieve warmer body temperatures. These between-habitat differences in reproduction are especially marked in cool months and are equivalent to those between populations separated by elevation. Thus, environmental differences (even on a micro-landscape scale) matter to reproduction and probably to demography.
Introduction

Reproduction and life history often vary geographically and parallel environmental gradients that drive such variation (Adolph & Porter, 1993; Dunham et al., 1989; Grant & Dunham, 1990). Environmental variation can occur on micro- as well as macro-geographic scales (Christian et al., 1983; Dowd et al., 2015; Kearney et al., 2014; Porter et al., 2002; Sears et al., 2011). If individual organisms perceive heterogeneous landscapes as 'coarse grained' (Levins, 1968; Sears et al., 2011), and thus tend to stay within a given habitat type, then their reproductive cycles might well vary on a local scale (that is, micro-geographically). However, whether local environmental variation affects reproduction and ecology is rarely investigated (Dowd et al., 2015; Mitchell et al., 2009; Riechert & Tracy, 1975).

Temperature is a dominant environmental factor influencing the physiology, reproduction, and ecology of terrestrial ectotherms (Angilletta, 2009; Gorman & Licht, 1974; Huey, 1982). Environmental temperatures often vary spatially, even on local scales (Grant & Dunham, 1990; Huey, 1974; Kearney et al., 2014; Logan et al., 2013; Potter et al., 2013; Riechert & Tracy, 1975). At many Caribbean localities, for example, open habitats, which are sunny and hot, can be adjacent to forest habitats, which are shaded and warm (Hertz, 1992; Logan et al., 2013). Because temperature drives reproduction in some Caribbean anoles (Gorman & Licht, 1974; but see P. Licht & G.C. Gorman, 1970; Licht & Gorman, 1975; Lister, 1981), reproductive cycles of open versus forest lizards might differ: but this has never been investigated.

In the New World tropics, different species of Anolis lizards are often restricted either to open or forest habitats (Logan et al., 2013; Rand, 1964; Ruibal, 1961; but see Schoener, 1970). Open-habitat lizards thermoregulate relatively carefully to achieve body temperatures ($T_b$) that
are relatively warm and that overlap with thermal preferences measured in laboratory thermal
gradients, whereas forest (below canopy) species are typically thermoconformers and have lower
$T_b$ (Gunderson & Leal, 2012; Hertz et al., 1999; Huey, 1974; Lister, 1976; Logan et al., 2013;
Rand, 1964; Ruibal, 1961). However, a few *Anolis* species occur in both types of habitats (Huey,
1974; Huey & Webster, 1975; Huey & Webster, 1976; Lister, 1976). Species occupying
thermally distinct but adjacent habitats offer special opportunities to evaluate the impact of local
environmental variation on lizard reproduction.

Here we evaluate (1) whether reproductive patterns and cycles of female *A. cristatellus*
differ between adjacent (open, forest) habitats at two sites in lowland Puerto Rico and (2)
whether habitat differences in thermal environments and in opportunities for thermoregulation
might contribute to observed reproductive differences. We monitored female reproductive
condition as well as body and environmental temperatures almost every month for more than two
years. The percentage of females that were reproductive varied seasonally in both habitats and
was lowest in winter. Moreover, forest females were less likely to be reproductive than were
open females in most months, especially during October through February. In fact, the
magnitude of this between-habitat difference in reproduction frequency in winter is large and
equivalent to that between lowland versus upland females in winter (Gorman & Licht, 1974). To
our knowledge, local-scale patchiness in reproductive frequency has not previously been
documented in lizards and suggests that these lizards in these habitats -- even though separated
by only a few meters -- probably have very different demographic profiles.
**Methods**

**Study populations**

*Anolis cristatellus* is a medium sized, trunk-ground anole that is widely distributed from sea level to mid-elevation on the Puerto Rico bank (Rand, 1964; Rivero, 1998; Williams, 1972). At lowland sites it is abundant in both open and forest habitats; but at higher elevations, it is restricted to the open (Hertz, 1992; Huey, 1974b; Huey & Webster, 1976; Lister, 1981). Its reproduction (Gorman & Licht, 1974; Lister, 1981), behavior (Leal, 1999; Leal & Rodríguez-Robles, 1995), and thermal biology (Gunderson & Leal, 2012; Heatwole et al., 1969; Hertz, 1992b; Huey, 1974, 1983; Huey & Webster, 1976; Lister, 1981; Rand, 1964) are exceptionally well known.

We studied the annual reproductive cycles of female *A. cristatellus* in both open and forest habitats (separated by only a few meters) at two localities west of San Juan on the north coast of Puerto Rico: Punta Salinas (18.465°N, 66.189W, 2 m.a.s.l) and Monagas (18.407°N, 66.138°W, 13 m.a.s.l). Both sites have well developed forest and open habitats (Appendix, Fig. A1), but the open habitat at Monagas is relatively more open and sunny. At both sites open habitats are human-modified parks, and adjacent forest habitats are secondary. We sampled lizards within areas of approximately 12,400 m² (open) and 5,000 m² (forest) at Punta Salinas respectively, and 5,300m² (open) and 7,500 m² (forest) at Monagas. Open trees that we searched were 15 to 250 m from the section of the forest that we surveyed. We did not catch any individual at the forest edge. Because the two sites have somewhat different thermal and physical characteristics, as well as somewhat different sampling periods, we analyze reproductive data for each separately.
Field Methods and Statistical Analyses

We visited Pta. Salinas almost every month from July 2011 through June 2014, and Monagas from February 2012 through June 2014. We typically captured 15 to 46 females in each habitat, palpated them to determine reproductive condition, and measured body \((T_b)\) temperature (Miller-Weber cloacal thermometer, using standard precautions) and size (SVL in mm, mass in g). We classified females as "reproductive" if they had either an egg or an enlarged follicle (Gorman & Licht, 1974; Lister, 1981). [Note: Anolis lay single-egg clutches]. LMO did all palpating: she correctly assigned reproductive status a test series of 33 female \(A.\ cristatellus\) and \(A.\ gundlachi\) (from several localities) that were sacrificed, preserved, and dissected to assess reproductive condition. We did not monitor male reproduction because doing so would have required the sacrifice of many individuals. However, we did measure \(T_b\) as well as perch characteristics of males (below); and we include these data in relevant analyses.

For each lizard captured we also recorded habitat (open, forest), time of day, perch height, sun exposure (full sun, partial sun, or shade), and weather (sunny, cloudy, sunny-cloudy, or rainy). We marked all captured individuals with a temporary paint dot so that we would not recapture them during a given census (we used Elmer’s non-toxic paint markers). Identifying dots disappeared within a month, and so we likely recaptured some individuals in subsequent censuses (partial pseudoreplication). However, because the areas we sampled are large (above) and because these anoles are dense, recaptures are likely few (see below). Moreover, females are likely laying eggs frequently, at least in warmer seasons: for example, \(A.\ carolinensis\) lay an egg every 10 to 14 days under field conditions (see Crews, 1973), and \(A.\ cristatellus\) lay an egg about every 17 days in the lab at 28°C (Joel McGlothlin, personal communication). Thus
pseudoreplication involving reproduction is likely minor (see below). Original and summary data are available from the Dryad repository (doi:10.5061/dryad.669r8).

Our sample included some subadult females: thus, before computing the percentage of adult females that were reproductive at each census, we needed to establish the minimum size (SVL) of adult (i.e., reproductive) females. The smallest (SVL) females that were gravid in summer (June - August) were 38 mm and 39 mm at Punta Salinas and at Monagas, respectively, and in winter (Dec - February) were 40 mm and 40 mm, respectively. Following Gorman and Licht (1974), we set the minimum size at 2 mm larger than smallest observed reproductive female (thus 40 mm). Sample sizes (per census) of adult females in each habitat in each census were 8 to 105 in Pta. Salinas (median = 24) and 15 to 27 in Monagas (median = 20). Total captures of adult females were 1865 at Punta Salinas and 1112 at Monagas.

To compare incidence of reproduction (i.e., percentage of females that were gravid) in forest versus open habitats, we computed the number of monthly censuses in which a higher percentage of females were reproductive in the open than in the forest and then used a sign test to evaluate the overall difference. This binary analysis assumes that reproductive frequencies in adjacent months are independent (see below). We also ran a logistic regression (in R, anova with type III sums of squares) with SVL (centered), season, and habitat (Appendix, Table A1).

To compare $T_b$ of lizards in the two habitats, we computed the number of censuses in which open lizards had a higher median $T_b$ than did forest lizards and then used a sign test to evaluate difference (each site separately). Here we combined $T_b$ data on males and females, as the sexes had similar $T_b$ in summer and in winter at both sites (all $P > 0.083$, data not shown): this pattern is general in most lizards previously examined (Huey & Pianka, 2007; but see Lailvaux, 2007).
To quantify environmental (= operative, $T_e$) temperatures (Bakken, 1992), we set out at least one $T_e$ model (each with two probes) in each habitat and recorded $T_e$ every 15 minutes (Hobo U23-003) at both localities. Models were PVC (78 mm x 15 mm) painted flat grey. We did not attempt to bracket available $T_e$. We recorded $T_e$ throughout the year, except when loggers occasionally failed. [Our analyses used only time periods when data from all loggers was available.] In Monagas, the open probes were positioned on the east and west sides of a tree and thus were exposed to sun at least part of the day. In Pta. Salinas, security concerns dictated that open probes be positioned in secluded spots, and thus these probes were only occasionally exposed to full sun: consequently, open $T_e$ underestimate maximum $T_e$ available at Pta. Salinas. Because probes were few in number and rarely moved, and because security concerns prevented our placing models to bracket the $T_e$ range at both sites, our $T_e$ data should not be interpreted as randomized "thermal maps” of the two habitats (Bakken & Angilletta, 2013) but rather as general indicators of thermal conditions in each. However, in January 2012, we deployed (attempting to bracket the available range of $T_e$) eight models in the open and ten in the forest and then monitored $T_e$ over several days (Appendix, Fig. A2).

To provide an estimate of the thermal quality of the habitat (Hertz et al., 1993), we computed the percentage of $T_e$ that overlapped with preferred body temperatures ($T_p$) of Anolis cristatellus (28.6° to 30.7°C, see Hertz et al., 1993) in summer (June - August) and in winter (December - February). $T_e$ in a habitat were considered to be within the $T_p$ range if either of the two probes was within the $T_p$ range, or if the two probes bounded the $T_p$ range (such that a shuttling lizard could achieve $T_p$). Because the number of probes is small, these data should be considered only as a crude reflection of available $T_e$, especially in the open habitats, which are thermally heterogeneous (Figs. A2).
**Results**

**Reproduction**

At both localities female reproduction varied seasonally and was much higher in summer than in winter (Fig. 1; Appendix, Table A1, Ps<0.001), as in other Puerto Rican anoles (Gorman & Licht, 1974). A higher percentage of females were reproductive in the open than in the forest at both field sites (Fig. 1, 28 of 34 monthly samples at Punta Salinas, 26 of 27 samples at Monagas, both P << 0.001). The higher reproduction of open females (vs. forest ones) was especially pronounced in winter (November – February) when 47.9% (N = 313) and 59.1% (149) of open females were reproductive in Punta Salinas and in Monagas, respectively, but only 5.1% (274) and 8.1% (149) of forest females were reproductive. In effect, forest females were largely non-reproductive for several months in winter (Fig. 1).

Effects of season, habitat, and SVL on female reproduction were quantified in a logistic regression analysis (Appendix, Table A1). Seasonal and habitat effects were large at both sites (Fig. 1). The interaction between season and habitat was also large at both sites: forest females were much less likely to reproduce in winter than open females. Open females were slightly larger (SVL) on average than forest females at both sites (by 1.7 mm at Punta Salinas, by 1.9 mm at Monagas; both P < 0.001). Large adult females were slightly more likely to be reproductive than were small adult females at Punta Salinas (P = 0.018) but not at Monagas (P= 0.11). Both sites showed significant SVL by season interactions, such that small (but adult-sized) females were less likely than large females to reproductive, especially in winter.

A few females -- especially open ones -- contained two oviductal eggs. At Punta Salinas, gravid females with two oviductal eggs were infrequent in either habitat (5.0% of 576, 1.9% of
374): but even this small difference was significant (chi-square test, $P = 0.3313e-06$). At Monagas (the warmer site), relatively more gravid females in the open had two eggs than did forest females (13.3% of 430, 4.1% of 242, $P = 3.313e-06$).

**Operative temperatures**

In open habitat, $T_e$ were warmer during the day than in the forest (Fig. 2; Appendix, Fig. A2). In Punta Salinas (or Monagas) during daytime samples (0900 to 1700), an open model was warmer than either of the two forest models in Punta Salinas 94.5% (or 99.7% at Monagas) of the time. During that same time interval a much higher percentage of open $T_e$ overlapped with preferred body temperatures of *A. cristatellus* (28.6 to 30.7°C, see Huey & Webster, 1976) than did forest $T_e$ (Pta. Salinas: 41.3% vs. 25.7% Monagas: 41.3% vs. 23.0%).

**Behavioral thermoregulation and body temperature**

Lowland *A. cristatellus* are generally active from sunrise to sunset (Hertz, 1992; Huey & Webster, 1976). Prior studies based on full-day observations (Huey, 1974; Huey & Webster, 1976) have shown that open *A. cristatellus* bask in the early morning and late afternoon, but retreat to shade at midday, whereas forest lizards rarely bask. In our present study we sampled mainly at midday, when these lizards are often in shade (Hertz, 1992; Huey, 1974). Even so, a higher percentage of lizards were basking (that is, perched in sun or in sun-shade, during sunny or sun-cloudy weather only) in the open than in the forest in Pta. Salinas [34.0% (N = 808) vs. 22.1% (N = 1127); $P = 7.592e-09$] or in Monagas (32.9% (N = 429) vs. 20.2% (N = 397), $P = 5.209e-05$).
In prior studies at Pta. Salinas (in summer only), body temperatures ($T_b$) of open lizards were warmer than those of forest lizards (Huey, 1974; Huey & Webster, 1976). This pattern holds for all-year samples (Pta. Salinas: open median $T_b = 29.3^\circ$C (N = 1276); forest = 27.9$^\circ$C (N = 1704), P < 2.2e-16; Monagas: open median $T_b = 30.3^\circ$C (N = 667), forest = 28.5$^\circ$C (N = 713), P < 2.2e-16). In comparisons at each census (Fig. 3), open lizards almost always had warmer $T_b$ than did forest lizards (Pta. Salinas: 26 of 31 censuses, P = 0.00019; Monagas, 24 of 26, P = 1.049e-05).

The preferred temperature range for lowland A. cristatellus is 28.6$^\circ$C to 30.6$^\circ$C (Hertz et al., 1993). In summer, open lizards are more likely than forest lizards to have $T_b$ that are warmer than $T_p$ at both localities, especially at Monagas (Appendix, Table A2, Huey, 1974). In winter, however, open lizards were more likely than forest lizards to have $T_b$ that were within the $T_p$ range (30.8% vs. 2.9% at Punta Salinas; 37.3% vs. 3.3% at Monagas). In fact, almost all forest lizards in winter had $T_b$ below the $T_p$ range (Punta Salinas = 96.8%, Monagas = 95.9%). In spring plus fall, lizards in the two habitats had relatively similar $T_b$ patterns. Thus open habitat lizards appear too hot in summer, but forest ones appear too cold in winter.

**Discussion**

To our knowledge, this is the first study documenting that Anolis reproductive cycles (or any lizard's cycle) can differ dramatically at a micro-geographic scale. Females in shaded forests were significantly less reproductive than were females in open habitats at two localities in lowland Puerto Rico (Fig. 1). We suspect that this pattern will be observed in other tropical
ectotherms that live in both open and forest habitats (Huey, 1974; Huey & Webster, 1975; Huey & Webster, 1976; Lee, 1980; Lister, 1976)

The magnitude of these between-habitats differences in reproduction was large in most months but was especially pronounced in cooler months (October through February, Fig. 1). In fact, the magnitude of these between-habitat differences in percentage of reproduction at this time of the year is equivalent to that of open-habitat females at localities separated by several hundred meters of elevation (Gorman & Licht, 1974).

What accounts for these micro-scale differences in reproduction? Anolis require warm temperatures for reproduction (Licht, 1973); and Gorman and Licht's (1974) and Lister's (1981) analyses strongly suggest that that environmental temperatures drive seasonal and macro-geographic differences in reproduction in Puerto Rican Anolis (see also Licht & Gorman, 1975). Do the different environmental temperatures of open versus forest habitats at our sites (Fig. 2, Online Supplement Fig. A2), and thermoregulation by the lizards themselves, contribute to the conspicuous between-habitat differences in reproduction (Fig. 1)? The percentage of reproduction in a month is indeed correlated with median $T_b$ of the lizards (Punta Salinas: $r = 0.6066$; Monagas: $r = 0.677$; both $P << 0.001$). In winter, the low frequency of reproduction -- especially of forest females (Fig. 1) -- very likely relates at least in part to the relatively low $T_c$ (Fig. 2) and to the low $T_b$ of those females (Fig. 3, Supplement Table A2). As temperatures warm in spring, the percentage of reproductive females increases in both habitats and is somewhat higher in the open than in the forest (Fig. 1), consistent with warmer $T_b$ in open than in the forest at this time (Fig. 2, Appendix Table A2). In summer, open females often had $T_b$ above the $T_p$ range (Fig. 3, Appendix Table A2), consistent with behavioral observations suggesting heat
stress at midday in summer (Huey, 1974): nevertheless, open female reproduction stays high, so the elevated $T_b$ of open females doesn't appear reproductively stressful (Fig. 1).

Patterns in fall are complex. Reproduction of forest females dropped precipitously in October and November at both sites (Fig. 1). Even so, forest females maintained relatively high $T_b$ until November (Fig. 3), and most forest females in October and November had $T_b$ within the $T_p$ range (PS = 60.3%, MO = 69.1%; Appendix Table A2). Thus reproduction dropped well before activity $T_b$ did.

Temperature is, of course, not the only environmental factor that influences lizard reproduction. Photoperiod influences female reproduction in Anolis carolinensis (Licht, 1973), but open and forest females experienced the same photoperiods as did forest females, but still maintained high reproduction through late fall (Fig. 1). Potentially higher food levels in the open -- especially in fall -- might also contribute to the observed patterns. However, physiological interactions between food ration and temperature can be complex (Brett, 1971; Huey, 1982). A study that monitors feeding as well as net energy gain (between-habitats, between seasons) would be informative.

Independent of whether habitat-specific reproductive patterns are driven by temperature, food, and other factors, the forest habitats of lowland Puerto Rico appear reproductively suboptimal for A. cristatellus, though still clearly adequate for them to maintain dense populations. This habitat effect probably influences other life cycle stages, such as the egg. Schlaepfer (2003) experimentally compared the egg survival of A. limifrons in two adjacent habitats in Costa Rica: eggs in the pasture had a shorter incubation period and higher survival than did eggs in the forest: the temperature regimes for these two habitats were different (pastures were warmer), as were predation rates.
Given that traits such as reproductive frequency (herein) and egg survival (Schlaepfer, 2003) vary on a micro-landscape scale, other life history traits (e.g., growth, survival), which are also environmentally sensitive (Angilletta, 2009), are likely to also show local-scale variation. What are the consequences of such micro-scale differences in reproduction for *A. cristatellus* populations? Likely, lizards in these two habitats have different demographic profiles. Hatchlings in the open probably reach maturity faster and reproduce more frequently than do hatchlings in the forest, implying different recruitment rates in the two habitats, though potential differences in food and predation/parasitism risk could modify these predictions. A full demographic study could evaluate these issues.

Migration between adjacent habitats -- at least from an individual's perspective -- could reduce these between-habitat differences. However, *A. cristatellus* is highly territorial, and so frequent migration is unlikely (Manuel Leal, personal communication, Clark & Gillingham, 1990; Jenssen, 2002). In fact, migration of marked individuals between habitats at Pta. Salinas is rare (< 1.0%, Otero, unpublished data). Interestingly, only one of 11 recaptured individuals that had moved between habitats at Punta Salinas was male.

Overall, our data show that a few meters can matter: specifically, environmental variation on a micrographic-scale can profoundly affect body temperatures and reproduction of lizards, and by extension on the demography of lizards. Although open-habitat females appear to have reproductive advantages over forest ones (especially in winter), this advantage might eventually be reversed with climate warming. Thus even modest winter warming will likely benefit forest females. In contrast, warming in summer might induce stress open females, at least by restricting midday activity (Gunderson & Leal, 2015; Huey, 1974). However, we see no evidence of lowered reproduction in open females in summer (Figs. 2), and *A. cristatellus* are
currently thriving in xeric habitats warmer than Punta Salinas (Gunderson & Leal, 2012; Hertz, 1992a; Huey & Webster, 1976). Thus lizards at Punta Salinas and Monagas appear to have a thermal buffer from summer warming.

Finally, many landscapes in Puerto Rico and elsewhere are being modified and fragmented at different spatial (Foster et al., 1999; Peters et al., 2013), greatly altering patterns of sun and shade and thus of habitat suitability. A lesson emerging from this present study is that landscape changes that alter the thermal environment -- even at small spatial scales -- are likely to dramatically modify physiology and life history (Kearney 2013).
Figure 1: Seasonal patterns of percentage (with 95% confidence intervals) of females that were reproductive in the open (gray) vs. forest (black) females at (A) Pta. Salinas and (B) Monagas, Puerto Rico. Dates for Monagas are shifted by +2 days to eliminate overlap with data for Punta Salinas.
Figure 2. Operative temperatures in open and in forest habitats at Punta Salinas, Puerto Rico, in summer and in winter. The thermal preference range (R. B. Huey & T. P. Webster, 1976) is shaded. During the daytime lizards in open have access to preferred temperatures at both seasons, whereas those in the forest often not, especially in winter.
Figure 3. Median body temperatures of *Anolis cristatellus* in open (gray) and forest (black) habitats at A) Punta Salinas and B) Monagas, Puerto Rico. The shaded rectangle demarks the preferred body temperature range for this species.
Literature Cited


Appendix: "A Few Meters Matter: Local Habitats Drive Reproductive Cycles in a Tropical Lizard"

Figure B1. Open (left) and forest (right) habitats in Punta Salinas. Lizards in the open often have ready access to solar radiation for basking and thermoregulation, whereas lizards in the forest generally do not (R. B. Huey, 1974a).
Figure B2. Operative temperatures of eight models in open (red) and of ten models in forest habitats (blue) over five days in January 2012. Gray bars indicate nighttime. Horizontal green bar is the preferred temperature range of *Anolis cristatellus*, and the horizontal dashed line is the critical thermal maximum (P. E. Hertz et al., 1999). During the day lizards in the open have greater opportunity to achieve temperatures within their preferred range than do lizards in the forest, but have a greater risk of exposure to dangerously high operative temperatures.
Table B1. Logistic regression of SVL, season, and habitat on adult female reproduction at Pta. Salinas. Anova results are type III.

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<td>3</td>
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<td></td>
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</tr>
<tr>
<td></td>
<td>SVL</td>
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</tr>
<tr>
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<td>habitat</td>
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<td>3.625e-1</td>
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<tr>
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<td>habitat:season</td>
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<td>3</td>
<td>0.0083</td>
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</table>
Table B2. Percentage of lizards (males + females) with $T_b$ below the $T_p$ range, within the $T_p$ range, or above the $T_p$ range as functions of locality, season, and habitat. $N =$ number of individual $T_p$ per group. Winter = Dec through Feb, spring = March to May, summer = June to August, and autumn = September to November.

<table>
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<th>locality</th>
<th>season</th>
<th>habitat</th>
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<th>within $T_p$</th>
<th>above $T_p$</th>
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CHAPTER III

Survivorship and growth of Anolis cristatellus in two contiguous but thermally distinct habitats

Abstract

Reproductive cycles in Puerto Rican Anolis lizards are influenced by seasonal environmental temperatures: female reproduction peaks in summer and drops in winter. Recent studies have shown that the reproductive intensity and phenology of Anolis cristatellus differ strikingly between two types of habitats at a micro-landscape scale: females in open habitats are more likely to be reproductive throughout the year -- especially in winter -- than are females in adjacent forests. It is unknown if the population ecology of these lizards changes at this micro-landscape scale, but is likely considering the reproductive differences that female lizards show in these two habitats. We conducted a one-year mark and recapture study to assess if habitat is influencing other life history traits such as survivorship, growth rates and body condition. We obtained a total of 414 capture history profiles of juveniles, females and males Anolis cristatellus in both habitats (open and forest from June 2013 until August 2014, using visible implant elastomers (VIE-Northwest Marine Technology Inc) to mark the lizards individually. We found that survivorship and body condition of Anolis cristatellus were higher in the open habitat, but growth rates showed habitat effects only for females. Migration between the two habitats was minimal. These findings indicate a significant effect of habitat heterogeneity and of land use changes on the life history traits of this tropical lizard.
Introduction

In the new world tropics some species of *Anolis* lizards exhibit behavioral plasticity depending on the habitat they live in. Some behave as thermoconformers in shady cool habitats (and consequently have low body temperatures (Tb)), and as thermoregulators in open warmer habitats (achieving higher Tb closer to their preferred body temperature (Tp)) (Logan et al., 2013; Rand, 1964; Ruibal, 1961; but see T.W. Schoener, 1970). Examples of thermoregulator lizards in Puerto Rico are *Anolis cristatellus* and *A. cooki*, while *A. gundlachi* is a thermoconformer. However, at some localities such as the lowland areas of Puerto Rico, *A. cristatellus* can occupy both habitats, with individuals behaving as thermoregulators in open areas, and thermoconformers in the shade of the forest (Huey, 1974), (Lister, 1976).

What are the consequences of such plasticity in thermoregulatory behavior for the vital rates of the species? Recently, we demonstrated that the reproductive phenology of *A. cristatellus* differs between two contiguous but thermally different habitats: female lizards in open habitats (where they are able to thermoregulate) were warmer and more frequently gravid (i.e. carrying eggs or enlarged follicles) than were forest thermoconforming females (Otero et al, 2015; in press). This difference was very conspicuous during the coolest months of the year, when none of the forest female lizards were reproductive, but more than 20% of those in the open habitat were (Otero et al, 2015; in press). Thus, in two contiguous habitats (forest and open) with different thermal characteristics, these lizards show different behaviors and reproductive phenologies. From a reproductive perspective it seems that open warmer habitats are ‘better’ for these lizards; here, we ask if other life history traits of this species that may indicate variation in fitness vary between open habitat and forest populations. Considering that temperature is a dominant factor influencing the physiology, reproduction, and ecology of terrestrial ectotherms
(Angilletta, 2009; Gorman & Licht, 1974; Huey, 1982), and knowing that the environmental temperatures in open and close forest sites differ significantly (Otero et al., 2015 - in press), we could expect so.

One trait that probably is affected by the thermal differences between these two habitats is growth rate. Growth rates in ectothermic vertebrates are influenced by different biotic and abiotic factors (Adolph & Porter, 1996), (Arendt, 1997) such as resource availability (Tracy, 1999), (Stamps & Tanaka, 1981), environmental temperature (Niewiarowski, 2001; Niewiarowski & Roosenburg, 1993), body temperatures (Sinervo, 1990), (Autumn & De Nardo, 1995), precipitation regime (Stamps & Tanaka, 1981); (Bock et al., 2010) plus inter and intraspecific competition (Schoener & Schoener, 1978a) (Siliceo-Cantero & Garcia, 2014). In anoles, growth rates are rapid in juveniles and approach an asymptotic size shortly after maturity is reached (Schoener & Schoener, 1978a). Some differences in growth rates for island and mainland anole species have been described (Andrews, 1976), as well as differences between life stages (Schoener & Schoener, 1978a), sexes (Schlaepfer, 2006) and populations (Siliceo-Cantero & Garcia, 2014). In Anolis sagrei for example, significant differences in growth rates were reported between populations that were only a few hundred meters apart in Abaco Island, Bahamas, probably because differences in lizards density and food availability (Schoener & Schoener, 1978a). Do the different types of habitats have an effect on the growth rates of Anolis cristatellus? Are there differences between males and females of this species in terms of growth rates? Likely there are differences, given that operative temperatures in the two habitats are different (Otero et al., 2015; in press). Because Sinervo (1990) found that lizards that maintained higher Tb’s have higher growth rates than those with lower Tb’s, we hypothesize that A. cristatellus will have higher growth rates in the open habitat due to the fact that lizards in this
habitat achieve warmer body temperatures than those in the forest (see Sinervo, 1990; Otero et al., 2015; in press).

Another autecological aspect that is likely to be influenced by habitat is survivorship. Directly or indirectly, habitat can influence the survivorship of anole lizards through food availability, precipitation regime, predation rates, thermal environment, competition for territories, perch availability, diseases and parasitism among others factors (Losos, 2009) (Schoener & Schoener, 1982), (Andrews & Nichols, 1990), (Andrews, 1988). For example, in the Bahamas Schoener and Schoener (1982) found that survival of adult *A. sagrei* was higher in forested than in scrubby habitats, probably because forests provide more protection from predators. This also affected the survival rates of juveniles, since scrubby habitats usually have more available spaces to colonize compared to forests where territories are often already occupied by adult males. Also, when comparing survival rates of *Anolis sagrei* among Bahamian Islands, they found that male lizards living on small islands with relatively few bird species had higher survival rates than those on larger islands with many bird species; and that those inhabiting deep-forest sites survived better than those living in more open sites (Schoener and Schoener, 1982). Interestingly, *A. sagrei* females did not show significant differences in survival among islands, and the authors attribute this to the conspicuous social behavior of males (Schoener and Schoener, 1982).

Is there an effect of habitat type on the survivorship of *Anolis cristatellus* in lowland Puerto Rico? Do lizards in open habitats have higher or lower survival rates than those living in the forest? Are there differences in survivorship between sexes, or among body size classes? Based on the findings of Schoener and Schoener (1982) for the also trunk-ground *Anolis sagrei*, we could expect to find lower survival rates for *A. cristatellus* living in open - more exposed -
habitats. To answer these questions we employed capture-mark-recapture (CMR) methodology with a maximum likelihood approach. Survival probabilities calculated through CMR estimations have been widely used in animal population studies including lizards (Lebreton et al., 1992), (Pradel et al., 1997), (Campbell & Lagueux, 2005), (Bock et al., 2010), (McCoy et al., 2014), (Schmidt et al., 2014), (Purwandana et al., 2014) and despite some disadvantages (like its inability to distinguish between permanent emigration and death (White & Burnham, 1999), they have become an important tool for long term population studies (Fujiwara & Caswell, 2002). Considering that \textit{A. cristatellus} is a territorial species with high densities it should be a good candidate for CMR studies. The collected data also allowed us to explore possible differences between the lizards inhabiting the two habitats in terms of growth rates and body condition that can provide estimates of fitness.

\section*{Methods}

\textit{Study site and species}

We studied the growth and survivorship of \textit{A. cristatellus} in two adjacent open and forest lowland habitats, separated by only a few meters, in Punta Salinas, Puerto Rico (18.465°N, 66.189W, 2 m) (Fig. C2). The open habitat is a recreational human modified space with scattered trees. The closed habitat is adjacent to the open one, and it is secondary forest. We established two plots of approximately 500m2 at each habitat each, one within the forest and the other one in the open habitat. The edge of the forest is very well defined (Fig. C3, C4).

To characterize the thermal environment of both habitats we placed one two-probe data logger in each habitat and programmed them to record temperatures every 15 minutes for 14
months starting in May 2013. The probes had either PVC tubes or lizard copper models attached so we could obtain operative temperatures \( (T_e) \). \( T_e \)'s characterize the thermal environment as the organism perceives it independently of any physiological thermoregulation, consequently \( T_e \) provides more relevant information regarding the species thermal ecology than just air temperature (Bakken, 1992) (Angilletta 2009). For security reasons the data logger in the open habitat was hidden on a tree with shade for most of the day, so maximum operative temperatures for this habitat are underestimated. Also, in a parallel study we measured the body temperatures of hundreds of lizards in both habitats, and showed that lizards in the open habitat were warmer than forest ones (see Otero et al., 2015; in press). Precipitation data were obtained from the NOAA administered Toa Baja weather station (18.4356°N, 66.1678W°; network ID GHCND: RQC00669415 elevation 8.5m), about four kilometers away from our study site.

*Anolis cristatellus* is the most abundant lizard within the study site, and one of the most common lizards in Puerto Rico (Rivero, 1998). It is a medium sized trunk-ground anole widely distributed in the island from sea level to mid-elevation in forest and open habitats (Heatwole et al., 1969; Williams, 1972; Jenssen et al., 1984; Huey, 1974). It is also a polygynous sexually dimorphic species. Males are bigger than females, hold territories with usually several females, and sustain aggressive encounters with conspecifics and other lizard species to defend it. The species has also invaded Dominican Republic, Costa Rica and Florida (Leal & Gunderson, 2012). Its reproduction (Gorman & Licht, 1974; Lister, 1981; Licht & Gorman, 1975) behavior (Leal & Rodriguez-Robles, 1995; Manuel Leal, 1999), structural niche (Schoener, 1970), and thermal biology (Heatwole et al., 1969; Huey, 1974; Rand, 1964; Gunderson & Leal, 2012; Hertz, 1992; Huey, 1983; Huey & Webster, 1976; Lister, 1981; Gunderson & Leal, 2015) are well known.
Sampling methods

We sampled lizards every other month starting on June 2013 until August 2014, for a total of 7 censuses / 6 survival intervals over a period of 14 months. Lizards were caught by hand by one person (LMO) at each plot. Each sampling event was composed by two days of capture-mark and recapture: on the morning of day one, we caught around 50 lizards in one of the habitats that were marked and released later that afternoon. On day two, we repeated this procedure in the other habitat. We captured all the visible lizards within the plots: juveniles, adult females and males, and kept them in bags until they were marked.

Once we had around 50 lizards, we proceed to record their snout to vent length (SVL in mm), sex, and masses (± 0.1g). We used SVL and body mass to calculate an index of body condition (BIX), which is a way of assessing the general physical condition and determining if the individuals were relatively light or heavy for their body length (Tokarz et al., 1998) (Pearson, 2000). Body condition is assumed to reflect the energetic state of an animal and, by extension, a proxy of its fitness (Cox & Calsbeek, 2015). To calculate body condition, we used the allometric relationship between body length and body mass, and performed a linear regression in which the log₁₀ of mass was the dependent term, and SVL was the independent term, and then calculated the residual for each individual. We included body condition (BIX) as a covariate in our CMR models and also tested for differences in body condition between habitats.

We defined growth rates as the increase in snout vent length (SVL) divided by the number of days between each survey period. Within the group of recaptured lizards, most animals were recaptured once, but there were a few that were recaptured multiple times. For those, we used each consecutive interval as a different data point for the analysis.
To mark the lizards, we used a bio-compatible two-part elastomer material. The visible implant elastomer marking technique (VIE) has been successfully used in other Anoles during the last decade (Losos, 2009). This method involves the sub-dermal injection of a non-toxic elastomeric liquid that after injection solidifies and it is visible through the skin of the anole. To inject the VIE we used the procedure described in Kondo & Downes (2004). By using different marking sites in the lizards’ bodies (mainly the muscles of the extremities – ventral sides), and two or more marks on each individual (1-4), we were able to distinctly mark hundreds of individuals (see Fig. C5). A total of 7 colors: blue, red, green, orange, violet, yellow and pink were used. Once the elastomer was injected and the position of the marks registered (e.g: which part of the leg was marked, and the color used), the lizard was released unharmed in the plot where it was caught earlier that day.

Data set and analysis

We obtained 414 individual encounters or capture history profiles of individually identified animals. An individual encounter history is the record of all the times a marked individual was recaptured during all the censuses after it was initially marked, including its absence. For example, an individual with a history profile of “100001” was an individual captured and marked during the first census, not recaptured during the next four, but recaptured during the final one. These encounter histories were used to estimate apparent survival and encounter probabilities through maximum likelihood estimation (White & Burnham, 1999).

Lizards were classified in three groups: adult males, adult females, and undetermined. Our data were limited to lizards with a SVL larger than 28 mm, since smaller animals are hard to
encounter in the field using visual survey methods and are also difficult to mark permanently (Pike et al., 2008) (Wright et al., 2013). We considered as undetermined all those lizards with a SVL of 35 mm or less (SVL ≤ 35 mm). We established this threshold because we were unable to identify the sex of these individuals. We could readily identify the sex of those animals with SVL ≥ 36 mm.

We log transformed the growth rates and built linear models for each sex and in each one of the habitats (open and forest) with growth rates as the dependent variable and the SVL as the independent variable. We used only data from males and females individuals that grew above 36 mm of SVL. We then performed a slope test using the ‘Real Statistics Resource Pack software (Zaiontz C, 2015) to compare the slopes of the regressions within sexes and between habitats.

To obtain maximum likelihood estimates of the habitat-specific apparent survival and recapture probabilities for females, males, and juveniles of Anolis cristatellus lizards in Punta Salinas, we performed a live-captures-only model using the Comark-Jolly-Seber (CJS) model according to Lebreton et al. (1992), implemented in the program MARK 8.0 (White & Burnham, 1999). Apparent survival (Φ) is the probability that a lizard is alive and has not emigrated from the locality where we caught it, and the recapture probability (p) is the probability that a lizard is caught within the habitat patch. The term ‘Apparent’ is used because when an animal is not recaptured again it is impossible to differentiate between death and permanent emigration.

We considered the CJS model as the best approach since it applies to live captures only and to open populations (populations with emigrations, deaths and entries due to births and immigrations) (Krebs, 1999). We understand that our data set fulfills all the CJS assumptions, including that no tags were lost. Besides, all lizards were released several hours after each capture event. However, as was mentioned before, we have to keep in mind that it is not possible
to determine whether an animal that is not recaptured died or emigrated out of the sampling area, although this should not be a problem if emigration rates are low. We used the \textit{sin link function} in program MARK 8.0 to estimate the apparent survival (\( \Phi \)) and recapture probabilities (\( p \)) for the 414 lizards with encounter histories (see Table 2 for model notation).

\textbf{GoF tests and model selection}

To test whether survivorship and recapture probabilities varied among habitats and survey occasion, we first ran 16 predefined models available in MARK (Table C1) without the effects of covariates. Once we ran the 16 predefined models, we performed goodness of fit tests (GoF) on our most generalized model. With the GoF tests we looked for unexplained heterogeneity in the data set and calculates the median ‘\( \hat{c} \)’ (c-hat) as a measure of potential data overdispersion (‘\( \hat{c} \)’ > 1). Given the standard deviation of our most generalized model (time and habitat dependent survival and recaptures: \( \Phi (g^t) p (g^t) \)), we set the lower and upper bounds, the default number of intermediate points, and proceeded to calculate median c-hat. We repeated this at least five times to estimate an average - more precise median c-hat. Posteriorly, we built design matrices and ran models that included sex, SVL, weight and body condition as covariates, and adjusted all our models with the calculated median c-hat.

Since there is uncertainty in which model is the most parsimonious one, we decided to accommodate this uncertainty in the estimates we report by doing model averaging. With model averaging, MARK takes the estimates from the various models and proceeds to weight them by the relative support that each model has. The models that include covariates show the predictive effect of each covariate on survival and recapture probability, but are not specific about how
each covariate affects any of them. To have a better sense of how covariates affect the parameter estimates, we used the ‘User-specified Covariate values’ option in MARK, specified each sex, used mean values for the continuous covariates (SVL, Body Index and mass) and re-ran our most parsimonious model. For the snout to vent length (SVL), we established two size classes based on the median (large and small) for both males and females.

Finally, we used an information theoretic approach to select the most parsimonious model, based on the Akaike information criterion (lower AICc values represented models with better fit) (Burnham & Anderson, 2002). Models were ranked using the quasilikelihood AICc value (QAICc) and their respective model weights (w) estimated to evaluate their strength of model support (Anderson, Burnham, & White, 1994). Based on the QAICc values we chose the model with biological meaning that best fit our data to report the estimates for each of our groups: undetermined, adult males and adult females.

Results

Environmental variables

The open habitat was warmer and had more variable temperatures than the forest one during most of the sampling period (Fig 1 and 2; Fig C1, C3). Operative temperatures in the open habitat are underestimated since the hobos were kept in shade due to security reasons. We present data collected until April and June 2014 due to hobo malfunctioning. The total precipitation (in mm) indicated that the year 2013 had a lot more precipitation than the year 2014.
(Fig 3). In fact, the year 2013 is the 4th wettest year in the recent history of Puerto Rico (Banuchi, 2013; NWS, 2013).

**Lizards’ size, mass and condition**

Average sizes and masses of the lizards caught at each habitat are shown in Table 1. Overall, lizards in the open were larger and heavier than the ones living in the forest ($t = 1.8357$, $df = 400$, $p$-value = 0.067; $t = 2.25$, $df = 316$, $p$-value = 0.0248). We tested for differences in the body condition between habitats by establishing the allometric relationship between SVL and Log of body mass (Fig. 4). Positive residuals indicated an animal heavier than average, and negative residuals indicated an animal with reduced mass. Lizards in open habitat showed an average body index of 0.00885 while those in the forest habitat had an average body condition of -0.00998; these values were significantly different ($t = -5.2082$, $df = 374$, $p$-value = 0.0001).

Overall, it was more common to find relatively thinner lizards in the forest than in the open habitat (Fig. 5). We compared body condition of females against that of males and found no significant difference ($t = 0.3837$, $df = 377$, $p$-value = 0.7014).

**Growth rates**

Out of all the recaptured individuals, 69.3 % were recaptured only once, while 30.71% were recaptured multiple times. This resulted in 157 growth intervals, 111 from females and 46 from males. Of the recaptured individuals only 11 moved between habitats, and interestingly, only one of them was male. This represents about 8% of recaptured lizards, and there was no evidence for unidirectional movement.
As has been described for other anole species, growth rates were high in small lizards and decline with increasing size (Fig. 6, 7). Without considering habitat effects, males tended to have higher mean growth rates than females (Fig 7, 8), but when comparing the slopes of the linear models no significant differences were found (t = -1.04073; df = 153; p-value = 0.299643; Fig 9). The correlation coefficient between growth rate and SVL was higher for females than for males (adjusted female $R^2$= 0.3674; adjusted male $R^2$=0.1924).

Overall, when comparing the mean growth rates of each habitat (without taking into account the effect of sex) we found no significant differences between the open and the forest (t = 1.3923; df = 153; p-value = 0.1658; Fig. 8). But when looking at growth rates of each sex at each habitat, we found that average growth rate for females living in the forest was significantly higher than the growth rates of those inhabiting the open (t = -2.73529; df = 107; p-value = 0.007297). This was not the case for males (t = 0.100473; df = 42; p-value = 0.9204; Fig. 8). Also, when comparing the change of growth rates of females according to SVL (the slopes of the linear models, Fig. 6), we found that the slopes were significantly different too, being steeper in the forest ($y = -0.001x + 0.0889$, $R^2 = 0.1044$) than the open habitat ($y = -0.001x + 0.0788$, $R^2 = 0.4394$; $t = -2.74$; df = 107; p = 0.007). We did not detect significant differences between males ($t = -0.68$; df = 42; p = 0.50; Fig. 7).

**CMR analysis**

We built 414 encounter histories over a period of 14 months. One hundred and sixty seven of these encounter histories belonged to males, 212 to females and 35 belonged to undetermined. Within the set of predefined models (Table C1), the model that best fitted our data
(with the lowest AICc) was the time and habitat dependent model for survival (\( \text{Phi} (g^t) \)) and the time and habitat independent for recapture probability \( p(.) \) (Table C1; see Table 2 for model notation). According to this model, apparent survival depended both on the habitat and the time period when the lizards were captured, but recapture probabilities did not vary between habitats or sampling periods.

We then built design matrices and incorporated sex, snout to vent length (SVL) and body index (BIX) as covariates. We ran models where the effect of each one of these covariates was considered, as well as models where the effect of all of them combined was assessed. After adjusting our models with the estimated median \( c \)-hat (\( c = 1.22916 \)), the most parsimonious model that best fit our data was \{ \{ \text{Phi} (g+t) \} \text{ sex SVL} \} (see Table 3). According to this model, survivorship probabilities depended on the additive effect of habitat (\( g \)) and time (\( t \)) (Fig 10), whereas recapture probabilities (\( p \)) was not affected by either habitat or time. Survivorship was higher in the open habitat than in the forest, and this pattern was consistent along the entire survey period (Fig 6). Survival probabilities also varied temporally, being highest during the second census interval (August through November – 2013) and lowest during the fourth survey interval (January through March - 2014). Both survival and recapture probabilities were influenced by the effect of the covariates sex and SVL; thus, these two covariates added explanatory value to our most parsimonious model.

When considering the most parsimonious models obtained (Table 6), a common characteristic for all of them is that survivorship estimates are habitat and time dependent, either through an interaction or an additive effect. The total weight of the corrected or adjusted Akaike’s Information Criterion (AICc) for our most parsimonious model is 38.2%, but when adding the weights of the most parsimonious 7 models, it adds to 94%, indicating that indeed
there is time and habitat dependence in survival probabilities. Also, these models (except Phi \((g+t) p (g) BIX\)) support that recapture probabilities are time and habitat independent (Table 6). Average apparent survival estimates were higher in open habitat (range 80 - 95%) compared to the forest (range 60 - 88%), which is contrary to what we originally hypothesized.

According to our most parsimonious model, apparent survival probabilities for our intervals were higher for both sexes then for the undetermined in the open habitat (Table 4). Overall, undetermined lizards had the highest survival rates, followed by females and then by males (Table 5). There were not apparent differences in survival when comparing the different size classes (based on SVL) we established (Table 5).

**Discussion**

Despite there are over four hundred species of anoles that have been used as models for the study of evolution, thermal biology, and ecology, it is surprising how little information is currently available regarding some of the most basic and important life history traits of any of these species. Although very important baseline information has been produced in the past decades for Central American and Bahamian species, there is little or almost none information about Caribbean nor most of mainland species.

Even though Puerto Rican anoles have been extensively studied, to our knowledge, we present the first capture-mark-recapture (CMR) study in which survival probabilities and growth rates are estimated at two thermally distinct habitats for one of the most common species in the island: *Anolis cristatellus* (Rivero, 1998). CMR studies allow us to gain knowledge on the life history and vital rates of a species, information that is necessary to parameterize population
dynamics models that later can be used to simulate the effects of current global changes on the species, and design population management plans. Below, we compare our results for *A. cristatellus* with other *Anolis* species from other islands and regions and discuss their implications.

*Environmental variables*

Although 2013 was a particular rainy year, we cannot relate this precipitation pattern to any of the traits we evaluated in our study (such as temporal changes in survivorship). Precipitation is known to influence life cycle transitions in some Anole species. A good example involves the Jamaican *Anolis lineatopus*. For this anole, both hatchling recruitment and mean juvenile growth are highly predictable by rainfall, which is likely related to changes in arthropod abundance (arthropod abundance is higher during the wet season in tropical climates - (Losos, 2009)), and consequently influence growth rates through food availability.

Regarding operative temperatures, the open habitat showed a higher variability than the forest site (Fig 1, 2, C1, C3), and overlapped more with the range of preferred body temperatures described for the species *Anolis cristatellus* (the preferred temperature range for lowland *A. cristatellus* is 28.6°C to 30.6°C -(Hertz et al., 1993)). Of course, it is important to remember that we evaluated operative temperatures using two probes at each habitat, so probably we are not including all the thermal variability of these habitats. Still, the open habitat seems to be a better habitat - from a thermal perspective than the forest site.
**Lizards’ size, mass and condition**

*Anolis cristatellus* has been extensively studied in Puerto Rico and elsewhere during the last decades (Rivero, 1998), (Heatwole et al., 1969), (Williams, 1972), (Jenssen et al., 1984), (Huey, 1974), (Leal & Gunderson, 2012), (Gorman & Licht, 1974), (Lister, 1981), (Licht & Gorman, 1975), (Leal & Rodríguez-Robles, 1995), (Leal, 1999), (Schoener, 1970), (Rand, 1964), (Huey & Webster, 1976), (Huey, 1983), (Hertz, 1992), (Gunderson & Leal, 2012) (Gunderson & Leal, 2015). Its behavior and reproductive phenology vary depending on the habitat where the lizard is; in open habitats it thermoregulates carefully and the females are more frequently gravid, while in the forests this lizards behaves as a thermoconformer and females are not gravid as often (Huey, 1974; Otero et al, 2015; in press). In this study we demonstrate that the physical condition of the species, namely its mass, length, and the relationship between these two variables considered as a body condition, also varies depending on the habitat. Lizards in the open habitat tend to be larger and have relatively more mass per unit length than those in the forest (Fig. 5).

A positive body condition in a lizard (i.e. relatively heavier animals) could result from having more fat or muscle tissue, or perhaps simply more hydration. Open habitats might host more prey than forest habitats and thus have better fed and fatter lizards, so a study on food availability would be useful. Parasites are also known to affect body condition (Pearson, 2000) (Dunlap & Mathies, 1993). Malaria-free *Anolis gundlachi* tended to show positive body condition residuals, while infected ones tended to show negative residuals, the difference was – however - not significant (Pearson, 2000). Although the prevalence of malaria in *Anolis cristatellus* has been reported to be very low (less than 1%), (Schall & Vogt, 1993) we cannot discard the possibility that parasites and/or diseases are affecting the lizards differently in these...
two habitats. Overall, it seems that at least in terms of body condition, open habitat is ‘better’ than forest. Although we cannot establish causality to the observed differences in body condition between open and forest habitats, we hypothesize that better body condition of the anoles in open habitat could be due to higher food availability, or increased foraging and activity times allowed by the warmer temperatures in this habitat (Sinervo et al., 2010).

We did not find differences in the body condition between the two sexes, which contrasts with the results described for Anolis nebulosus and A. polylepis (Siliceo-Cantero & García, 2014), (Schlaepfer, 2006) in which females showed better body condition than males.

**Growth rates**

Significant differences were found between the growth rates of females living in the forest (faster growth) versus those living in the open (slower growth). However, the growth rate of males did not varied between habitats. Various reasons could explain these differences. For example, according to Schoener and Schoener (1978), the intrinsic growth rates for A. sagrei varied dramatically across different habitats separated by a few hundred meters, their forest site having lower growth rates in comparison to the other habitats they evaluated. They also found that the differences were positively associated with lizards’ density in the populations they studied in the Bahamas. The authors hypothesized that this was because lizard density was higher in sites with more food; this hypothesis was later supported by Wright (Wright et al.). However, if this was the case in Puerto Rico we would have also found differences between the growth rates of males inhabiting each habitat, with males having higher growth rates in the
habitat with higher lizard density. Thus, the effect that habitat is having on the growth rates of each sex is far from being clear.

As described in other studies, males had higher growth rates than females (Fig. 7, 8, 9). In lizards, this is thought to be a consequence of the territoriality and the social role of males; females in the other hand have smaller growth rates, likely due to the energy expenditure in egg production (Lewis, 1986) (Trivers, 1976).

Survivorship

Differences in survival among habitats, sexes, and life stages have been reported previously in anole lizards (Andrews & Nichols, 1990; Schoener & Schoener, 1978b; Wright et al., 2013; Schoener & Schoener, 1982; Schlaepfer, 2003; Bock et al., 2010; Andrews, 1988). The causes and consequences of such differences depend on the biotic and abiotic factors surrounding the model species, so we need to be careful when making comparisons between them. However, there are some common trends that are of interest to mention. For example, both Schoener (Schoener & Schoener, 1978b; Schoener & Schoener, 1982) and Wright (2013) found that Anolis sagrei females showed higher survival rates than males in this trunk-ground species of the Bahamas (month-to-month estimates in the Wright et al (2013) study were: females: 80%, males: 49%). For the Caribbean Anolis acutus, the mean reported annual survival was 12% for adult males and 37% for adult females (Ruibal & Philibosian, 1974). In A. cristatellus we also found that females had higher survival estimates than males according to our most parsimonious model (Table 5). Are these similarities in survivorship due to the fact that these two species are trunk ground anoles with relatively similar behaviors? Males of both species defend territories using conspicuous visual displays that make them more susceptible to predation. Meanwhile,
reported survival for the mainland species *Anolis limifrons* and *Anolis mariarum* show different patterns. Andrews and Nichols (1990) showed that survival estimates of *Anolis limifrons* were consistently similar for males and females (74 and 75% for monthly intervals), but the estimates changed among sites in Barro Colorado Island, Panama, and between survey years. For *Anolis mariarum* an interesting pattern is described: males at two sites had higher annual survivorship than females (20 and 12% respectively) (Bock et al., 2010). Undetermined individuals in our study had the highest estimates of apparent bimonthly survival (89% and 83%) for the open and forest habitat, respectively). These values appear high, and should be interpreted with caution given that survival estimates of small individuals are hard to obtain due to their small sizes and elusive biology (Pike et al., 2008).

Survivorship differences between sexes were present within each habitat: both in open and forest habitat females had higher survivorship than males, especially in the open. Why would female lizards survive more than males, especially so in the open? We can consider the hypothesis that in sexually dimorphic species larger males are able to acquire and maintain larger territories with more females but are more susceptible to mortality (Schoener & Schoener, 1982). A very interesting aspect worth considering is that females in the open are more often gravid than forest ones (Otero et al, 2015; in press). However, one of the central ideas of life-history theory is that investment in current reproduction compromises survival and consequently future reproduction (Cox & Calsbeek, 2010); in other words, the more a female reproduces in the present, the lower its survival will be in the future. Considering that *A. cristatellus* females in the open are gravid more often than those in the forest, and this is supposed to have a higher energetic cost, it seems contradictory that these females have higher survival rates. According to Cox & Calsbeek (2010), gravid females suffer reductions in stamina and sprint speed which are
known to influence survival, thus, we would expect differential mortality and survival rates for females living in both habitats, more specifically we would expect higher mortality in females living in open habitat (where they reproduce more often), which is opposite to our findings. Thus, open habitat is 'better' for female lizards, since they are able to reproduce more without apparent costs in their survivorship. Unfortunately, we cannot yet establish the causes behind these patterns. To elucidate the relationship between survivorship and reproductive condition in *A. cristatellus*, we would need to follow the survival of gravid and non-gravid females within each habitat, but that was beyond the goal of this research.

The survival differences observed could be explained from an ‘optimum environment’ point of view. Our results suggest that the forest, is a suboptimal habitat for both males and females, while the open habitat is 'better', not only in terms of reproduction for females, but also in terms of survival for both sexes (though still clearly adequate to maintain dense populations). Open habitat could ‘be better’ for different reasons: it could actually have lower predation rates than in the forest (contrary to what was reported for *A. sagrei* in the Bahamas –see (Schoener & Schoener, 1978b; Schoener & Schoener, 1982), it could have a higher prey biomass, or it could provide a more suitable thermal environment for the species that enhances different aspects of this lizard biology. Given that operative temperatures in the open habitat overlap more often with the preferred temperatures reported for the species measured in thermal gradients (Hertz et al., 1993), lizards in this habitat might be able to perform closer to a physiological optimum and cope better with life history trade-off’s (such as reproduction/survival) than those in the forest. Of course, this would need to be tested experimentally.

Overall, according to our most parsimonious model, and contrary to what we originally hypothesized based on *A. sagrei*, all lizards (undetermined, adult females and males) living in the
open exhibited higher survival than in the forest (Fig. 6, Table 4, Table 5). Another interesting pattern is that survival estimates changed through time (Fig. 6), being lower during the August-November 2013 period, and the highest during the January-March 2014 interval. Interestingly, there is no clear environmental pattern in operative temperatures that could help us explain this temporal variation in apparent survival, and no studies have been done regarding the abundance or diversity of predators in the area. Precipitation in the other hand, might be influencing survivorship rates given that the period with lowest survivorship (August-November 2013) occurred within part of the rainy season, while the period with highest survivorship falls into the dry season of Puerto Rico (Burrowes et al., 2004).

Differences in survival among habitats have been described for other life stages in *Anolis* lizards. For example, studying the demography and egg survival of *Anolis limifrons* in Panama, Andrews (1988) found the highest egg survival in youngest forests (31-53%), and the lowest in oldest forests (8-15%). In Costa Rica, Talbot (1975) (cited in Andrews, 1988) also found lower survival rates for the eggs laid in mature forests compared to successional sites; and (Schlaepfer, 2003) found in southern Costa Rica that eggs in pastures experienced a significantly reduced incubation period and significantly higher survival rates relative to eggs in forests. Whether there is a ‘habitat effect’ on the survival of eggs of *Anolis cristatellus* laid in the two habitats is unknown, but it would be an interesting question to do research on.

It seems that local habitats separated by only a few meters not only drive behavior and reproductive cycles for *A. cristatellus*, they also affect their survival and body condition. Considering how landscapes in Puerto Rico and around the globe are being continuously modified and fragmented at different spatial scales (Grau et al., 2003; Foster et al., 1999), it is important to understand how such landscape changes affect vital rates and life history.
parameters, even at small spatial scales such as the one presented in this research. Besides, survivorship estimates are used in the construction of population projection matrices and other population dynamics analysis, which provide important tools for conservation biology (e.g., Caswell, 2001; Fujiwara & Caswell, 2002) and can be used to evaluate the causes of past population declines and to predict the effect of possible future management actions (Fujiwara & Caswell, 2002). Thus, the estimation of survival and population growth rates become important subjects to study, especially for tropical ectotherm species (Tewksbury et al., 2008; Huey et al., 2009).
Tables

Table 1: Mean snout to vent length (SVL in mm) and mass (in g) values for animals caught in the two habitats at Punta Salinas.

<table>
<thead>
<tr>
<th></th>
<th>Open</th>
<th>Forest</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Females</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SVL</td>
<td>44.63 ± 0.272</td>
<td>43.20 ± 0.284</td>
</tr>
<tr>
<td>Mass</td>
<td>2.41 ± 0.517</td>
<td>2.11 ± 0.044</td>
</tr>
<tr>
<td><strong>Males</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SVL</td>
<td>55.48 ± 1.564</td>
<td>51.88 ± 0.896</td>
</tr>
<tr>
<td>Mass</td>
<td>5.82 ± 0.537</td>
<td>3.99 ± 0.217</td>
</tr>
<tr>
<td><strong>Juveniles</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SVL</td>
<td>33.0 ± 1.66</td>
<td>32.90 ± 0.375</td>
</tr>
<tr>
<td>Mass</td>
<td>1.03 ± 0.120</td>
<td>0.96 ± 0.039</td>
</tr>
</tbody>
</table>
Table 2: Explanation and notation of some of the models used in the model selection procedure:

‘Phi’ is the notation for survival probability, and ‘p’ is the notation for recapture probabilities; t denotes time variation; g denotes habitat. Sex and snout vent length (SVL) are the covariates.

<table>
<thead>
<tr>
<th>Model</th>
<th>Survival</th>
<th>Recapture</th>
<th>Num.</th>
<th>Notation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phi (g*t)</td>
<td>p (.)</td>
<td>13</td>
<td>Interaction between habitat (g) and time (t) in survivorship</td>
<td></td>
</tr>
<tr>
<td>Phi (g+t)</td>
<td>p (.)</td>
<td>8</td>
<td>Additivity between habitat (g) and time (t) in survivorship</td>
<td></td>
</tr>
<tr>
<td>Phi (t)</td>
<td>p (.)</td>
<td>7</td>
<td>Time-dependent survivorship</td>
<td></td>
</tr>
<tr>
<td>Phi (g)</td>
<td>p (.)</td>
<td>3</td>
<td>Habitat-dependent survivorship</td>
<td></td>
</tr>
<tr>
<td>Phi (.)</td>
<td>p (g)</td>
<td>3</td>
<td>Habitat-dependent recapture</td>
<td></td>
</tr>
<tr>
<td>Phi (.)</td>
<td>p (t)</td>
<td>7</td>
<td>Time-dependent recapture</td>
<td></td>
</tr>
<tr>
<td>Phi (.)</td>
<td>p (g*t)</td>
<td>13</td>
<td>Interaction between habitat (g) and time (t) in recapture</td>
<td></td>
</tr>
<tr>
<td>Phi (g*t)</td>
<td>p (g*t)</td>
<td>22</td>
<td>Interaction between habitat (g) and time (t) in both survivorship and recapture probabilities</td>
<td></td>
</tr>
<tr>
<td>Phi (.)</td>
<td>p (.)</td>
<td>2</td>
<td>Null model for both survivorship and recapture probabilities</td>
<td></td>
</tr>
<tr>
<td>Phi (g*t) sex SVL</td>
<td>p (.)</td>
<td>22</td>
<td>Interaction between habitat (g) and time (t) in survivorship. Sex and SVL influence survivorship</td>
<td></td>
</tr>
<tr>
<td>{{Phi (g*t) p (.)} sex SVL}</td>
<td></td>
<td>9</td>
<td>Interaction between habitat (g) and time (t) in survivorship. Recapture time and habitat independent. Both survivorship and recaptures probabilities influenced by sex and SVL</td>
<td></td>
</tr>
</tbody>
</table>
Table 3. List of the models that best fit our data. These models have 94% of support. Adjusted with the estimated median c-hat (\(\hat{c} = 1.22916\))

<table>
<thead>
<tr>
<th>Model</th>
<th>QAICc</th>
<th>Delta QAICc</th>
<th>AICc</th>
<th>Weights</th>
<th>Model</th>
<th>Num.</th>
</tr>
</thead>
<tbody>
<tr>
<td>{\Phi(g+t) \ p(.) } sex SVL</td>
<td>792.0747</td>
<td>0</td>
<td>0.38242</td>
<td>1</td>
<td>9</td>
<td></td>
</tr>
<tr>
<td>{\Phi(g^*t) \ p(.)} sex SVL</td>
<td>793.5081</td>
<td>1.4334</td>
<td>0.18676</td>
<td>0.4884</td>
<td>13</td>
<td></td>
</tr>
<tr>
<td>{\Phi(g+t) \ p(.) } sex SVL BIX</td>
<td>793.5966</td>
<td>1.5219</td>
<td>0.17868</td>
<td>0.4672</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td>{\Phi(g^*t) \ p(.)} sex SVL BIX</td>
<td>795.0661</td>
<td>2.9914</td>
<td>0.0857</td>
<td>0.2241</td>
<td>14</td>
<td></td>
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<tr>
<td>{\Phi(g+t) \ p(g) } BIX</td>
<td>795.5832</td>
<td>3.5085</td>
<td>0.06617</td>
<td>0.173</td>
<td>9</td>
<td></td>
</tr>
<tr>
<td>{\Phi(g+t) \ sex \ SVL \ p(.) }</td>
<td>797.3055</td>
<td>5.2308</td>
<td>0.02797</td>
<td>0.0731</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td>{\Phi(g+t) \ p(.) } sex</td>
<td>797.8345</td>
<td>5.7598</td>
<td>0.02147</td>
<td>0.0561</td>
<td>8</td>
<td></td>
</tr>
</tbody>
</table>
Table 4. Survivorship estimates calculated with model averaging. (Period 6 and 12 are not shown due to confounding effects between survivals and recapture probabilities. See (White & Burnham, 1999)

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Survey interval</th>
<th>Unconditional Estimate</th>
<th>Unconditional Variance</th>
<th>Lower CI</th>
<th>Higher CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Open</td>
<td>1</td>
<td>0.8048564</td>
<td>0.1040716</td>
<td>0.5295177</td>
<td>0.93794</td>
</tr>
<tr>
<td>Open</td>
<td>2</td>
<td>0.8116779</td>
<td>0.1474053</td>
<td>0.3943299</td>
<td>0.96614</td>
</tr>
<tr>
<td>Open</td>
<td>3</td>
<td>0.8140403</td>
<td>0.0910235</td>
<td>0.5739383</td>
<td>0.93432</td>
</tr>
<tr>
<td>Open</td>
<td>4</td>
<td>0.9568744</td>
<td>0.0519889</td>
<td>0.6525439</td>
<td>0.9962</td>
</tr>
<tr>
<td>Open</td>
<td>5</td>
<td>0.8895972</td>
<td>0.068236</td>
<td>0.6736823</td>
<td>0.96918</td>
</tr>
<tr>
<td>Forest</td>
<td>1</td>
<td>0.7850948</td>
<td>0.1025477</td>
<td>0.5260589</td>
<td>0.92322</td>
</tr>
<tr>
<td>Forest</td>
<td>2</td>
<td>0.6078872</td>
<td>0.0930081</td>
<td>0.4191286</td>
<td>0.7691</td>
</tr>
<tr>
<td>Forest</td>
<td>3</td>
<td>0.8087343</td>
<td>0.0934062</td>
<td>0.5642064</td>
<td>0.93248</td>
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<tr>
<td>Forest</td>
<td>4</td>
<td>0.889012</td>
<td>0.0854088</td>
<td>0.5948632</td>
<td>0.97763</td>
</tr>
<tr>
<td>Forest</td>
<td>5</td>
<td>0.8726024</td>
<td>0.0843168</td>
<td>0.6076806</td>
<td>0.96804</td>
</tr>
</tbody>
</table>
Table 5: Bimonthly survival probabilities according to sex and size class

<table>
<thead>
<tr>
<th></th>
<th>Open</th>
<th>Forest</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Small</td>
<td>Large</td>
</tr>
<tr>
<td>Females</td>
<td>0.877</td>
<td>0.864</td>
</tr>
<tr>
<td>Males</td>
<td>0.845</td>
<td>0.778</td>
</tr>
<tr>
<td>Juveniles</td>
<td>0.891</td>
<td></td>
</tr>
</tbody>
</table>

*Estimates are arithmetic means of time-specific survival estimates for 60-d time periods based on our most parsimonious model*
Figure 1: Operative temperatures in open habitat at Punta Salinas, Puerto Rico during the period May 2013 until April 2014. The lower and upper red lines represent the lower and upper points of the preferred temperature range reported for the species (Paul E Hertz et al., 1993)
Figure 2: Operative temperatures in the forest habitat at Punta Salinas, Puerto Rico during the period May 2013 until June 2014. The lower and upper red lines represent the lower and upper points of the preferred temperature range reported for the species (Paul E Hertz et al., 1993)
Figure 3: Total precipitation monthly values (in mm) for the Toa Baja municipality during the period May 2013 until September 2014. This weather station is very close to our study area, Punta Salinas, Puerto Rico. Data collected from [http://www.ncdc.noaa.gov/cdo-web/search](http://www.ncdc.noaa.gov/cdo-web/search). Precipitation values for August 2013 were unavailable.
Figure 4: Theoretical and estimated values for body index as the relationship between the logarithm of the mass and the Snout to vent length (SVL).

Figure 5: Frequency of body indexes for the two habitats studied at Punta Salinas, Puerto Rico.
Figure 6: Growth of females *Anolis cristatellus*. Points represent change in SVL (in mm) over time (days). Lines represent predictions from the linear model for each habitat. Red dots represent lizards living in the open habitat, while blue dots represent lizards living in the forest. Growth rates are log transformed.
Figure 7: Growth of males *Anolis cristatellus*. Points represent change in SVL (in mm) over time (days). Lines represent predictions from the linear model for each habitat. Red dots represent lizards living in the open habitat, while blue dots represent lizards living in the forest. Growth rates are log transformed.
Figure 8: Average growth rates of females and males *Anolis cristatellus* at forest and open habitats. Females at the forest had significantly higher growth rates than in the open habitats (t = -2.73529; df = 107; p-value = 0.007297). Males showed no differences.
Figure 9: Growth of females and males *Anolis cristatellus*. Points represent change in SVL (in mm) over time (days). Lines represent predictions from the linear model. Red dots represent lizards living in the open habitat, while black dots represent lizards living in the forest.
Figure 10: Change of survival estimates along time in the open (red line) and forest habitat (blue line), according to our most parsimonious model \([\Phi(g+t)p(.)|Sex SVL]\). Each survey interval corresponds to the two months period between each CMR occasion.
## APPENDIX

Table C1: List of the predefined models ran in MARK. No covariates included

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>Delta</th>
<th>AICc</th>
<th>Model</th>
<th>Num.</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phi(g*t) p(.)</td>
<td>986.923</td>
<td>0</td>
<td>0.26486</td>
<td>1</td>
<td>13</td>
<td>960.164</td>
</tr>
<tr>
<td>Phi(g*t) p(g)</td>
<td>987.061</td>
<td>0.1388</td>
<td>0.2471</td>
<td>0.933</td>
<td>14</td>
<td>958.185</td>
</tr>
<tr>
<td>Phi(t) p(.)</td>
<td>987.502</td>
<td>0.5795</td>
<td>0.19823</td>
<td>0.7484</td>
<td>7</td>
<td>973.272</td>
</tr>
<tr>
<td>Phi(g) p(t)</td>
<td>988.625</td>
<td>1.7026</td>
<td>0.11306</td>
<td>0.4269</td>
<td>8</td>
<td>972.328</td>
</tr>
<tr>
<td>Phi(t) p(g)</td>
<td>989.485</td>
<td>2.5624</td>
<td>0.07355</td>
<td>0.2777</td>
<td>8</td>
<td>973.188</td>
</tr>
<tr>
<td>Phi(.) p(t)</td>
<td>990.409</td>
<td>3.4866</td>
<td>0.04633</td>
<td>0.1749</td>
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Figure C1: Raw data of all the operative temperatures measured in open (red) and forest (blue) habitat along our survey year.

Figure C2: View of the two habitats in the Punta Salinas area.
Figure C3: Mean monthly operative temperatures in the two habitats of Punta Salinas, PR.

Figure C4: Open and forest (in the back) habitats in Punta Salinas, Toa Baja, PR.
Figure C5: Marked *Anolis cristatellus* male in the open habitat, Punta Salinas.
Literature cited


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General conclusions

After reviewing the literature about climate change and its effects on biodiversity, it is notorious how most of the articles consulted point out the lack of information regarding the proximate mechanisms by which climate change affects organisms. Authors emphasize the importance of studying life history traits that are vulnerable to climate change and doing so at scales that are ecologically relevant for the species.

In this research, we are showing that climate warming has fostered the reproductive output for some Puerto Rican Anolis populations after four decades. For both A. cristatellus and A. gundlachi, the proportion of gravid females increased during fall and winter months for mid and higher elevation sites compared with the proportions observed four decades ago. Conversely, the opposite pattern was observed at the lowland sites. These differences in reproductive cycles among locations may be attributable to the changes that have occurred at each site during the last four decades. Furthermore, we found that the proportions of gravid females was positively correlated with body temperatures for most populations, which supports the idea of a close relationship between environmental temperatures and reproduction.

Even though we followed Gorman and Licht (1974) methodology carefully, and even had one of the authors during some of the surveys, we think that our past vs. present comparisons have more validity in Guanica and El Verde, since both sites are within protected areas and have not changed much structurally during the last decades. The landmark paper by Gorman and Licht (1974) has provided us with an excellent opportunity to use Anolis lizards as models to evaluate the effects of recent climate warming, and reaffirms the importance of historical data.
Even though climate warming has influenced *Anolis* reproductive phenologies, the effect of local habitat on reproduction seems to be more important. Female lizards living in open warmer habitats were more often gravid than those living in the forest, especially during the cooler months of the years, and these differences in reproductive cycles were found in habitats that are separated by a few meters. Thus, the sensitivity of reproductive cycles to local habitat is another example indicating how important it is to consider temporal and spatial scales that are ecologically relevant for the species being studied.

Local habitat affects other life history traits of *Anolis* lizards other than reproductive cycles, like body condition, growth rates and survivorship. Body condition was higher in the open habitat. Growth rates of females differed between habitats (being higher in the forest habitat), while growth rates of males did not differ. Survivorship was higher in the open warmer habitat than in the forest. So, it seems that open warmer environments are ‘better’ for these lizards.

This ‘habitat effect’ likely has consequences for other life history traits and vital rates. Particularly, the demographic profiles of the animals living in the two habitats probably are different, so one of the most important lessons of this research is that it shows the importance of looking at the biology of the organisms at relevant scales (as the organisms perceive and interact with the surrounding environment) before trying to understand the effects global changes may have on them.