NRC Research Press

ARTICLE

Local extinction risk of three species of lizard from Patagonia as a result of global warming

E.L. Kubisch, V. Corbalán, N.R. Ibargüengoytía, and B. Sinervo

Abstract: Recently, Sinervo et al. (2010, Science, **328**: 894–899) reported declines of lizard biodiversity due to local warming trends and altered thermal niches. Herein, we applied the Sinervo et al. (2010) physiological model to predict the local extinction risk of three species of lizard from Patagonia. Whereas the previous model used a single equation (for the extinctions of Blue Spiny Lizard (*Sceloporus serrifer* Cope, 1866) in the Yucatan Peninsula) relating environmental temperatures (T_e) to hours of restriction (i.e., the period when lizards are forced into retreat sites because environmental temperatures are too high), we measured habitat-specific equations for the T_e values of each species. We analyzed the vulnerability of Darwin's Ground Gecko (*Homonota darwinii* Boulenger, 1885), Bariloche Lizard (*Liolaemus pictus* (Duméril and Bibron, 1837)), and Mountain Slope Lizard (*Liolaemus elongatus* Koslowsky, 1896) to climate change considering thermal physiological constraints on activity during the reproductive period. While Sinervo et al. (2010) predicted that the Phyllodactylidae family will not suffer from impacts of climate change, our physiological model predicted that 20% of the *H. darwinii* populations could become extinct by 2080. The physiological model also predicted that 15% of *L. pictus* populations and 26.5% of *L. elongatus* populations could become extinct by 2080. The most vulnerable populations are those located near the northern and eastern boundaries of their distributions.

Key words: Liolaemus, *Homonota*, global warming, extinction risk, physiological model, climate change.

Résumé : Sinervo et al. (2010, Science, **328**: 894–899) ont récemment fait état de diminutions de la biodiversité des lézards en raison de tendances de réchauffement locales et de la modification de niches thermiques. Nous avons appliqué le modèle physiologique de Sinervo et al. (2010) pour prédire le risque de disparition locale de trois espèces de lézards de Patagonie. Alors que le modèle précédent utilisait une seule équation (pour les disparitions du lézard bleu épineux (*Sceloporus serrifer* Cope, 1866) dans la péninsule du Yucatan) reliant les températures ambiantes (T_e) aux heures de restriction (c.-à-d. la période durant laquelle les lézards sont forcés de demeurer dans des sites de retrait parce que les températures ambiantes sont trop élevées), nous avons mesuré des équations propres à l'habitat pour les valeurs de T_e de chaque espèce. Nous avons analysé la vulnérabilité du gecko de Darwin (*Homonota darwinii* Boulenger, 1885) et des lézards *Liolaemus pictus* (Duméril and Bibron, 1837) et *Liolaemus elongatus* Koslowsky, 1896 aux changements climatiques en considérant les contraintes physiologiques thermiques sur l'activité durant la période de reproduction. Alors que Sinervo et al. (2010) prédisaient que le climat n'aura pas d'impacts sur la famille des phyllodactylidés, notre modèle physiologique prédit que 20 % des populations de *H. darwinii* pourraient disparaître d'ici 2080. Le modèle physiologique prédit également que 15 % des populations de *L. pictus* et 26,5 % des populations de *L. elongatus* pourraient disparaître d'ici 2080. Les populations les plus vulnérables sont celles qui sont situées près des limites nord et est de leur aire de répartition. [Traduit par la Rédaction]

Mots-clés : Liolaemus, *Homonota*, réchauffement planétaire, risque de disparition, modèle physiologique, changement climatique.

Introduction

Climate change to date has affected animal and plant populations in their phenology (Walther et al. 2002; Menzel et al. 2006; Parmesan 2006; Cleland et al. 2007), morphology (Harley et al. 2006; Tryjanowski et al. 2006; Yom-Tov et al. 2006; Musolin and Saulich 2012), physiology (Musolin and Saulich 2012; Oswald and Arnold 2012), behavior (Musolin and Saulich 2012), ecological interactions (Walther et al. 2002; Schweiger et al. 2008; Cornelissen 2011), and distribution (Walther et al. 2002; Parmesan 2006; Musolin and Saulich 2012). The incremental warming rate in the coming decades is expected to be about five times greater than that experienced during the 20th century (Meehl et al. 2007). In addition, the higher frequency of extreme weather events, such as heat waves (Schär et al. 2004; Diffenbaugh and Ashfaq 2010), is expected to drive local population extinctions (Huey et al. 2010). Projections of species' distributions for future climate change scenarios predicted that 15%–37% of species, which cover some 20% of the Earth's terrestrial surface, will be committed to extinction by 2050 (Thomas et al. 2004). Recent studies estimated that since 1975, 4% of local lizard populations have gone extinct worldwide as a result of climate change; by 2080, rates of local population extinction are projected to reach 39% worldwide (Sinervo et al. 2010). Those global extinction projections for lizards were validated by surveying populations across the period of warming from 1975 to 2010 and on four continents, including recorded population extinctions of three liolaemid species in South America, specifically the Lutz's Tree Iguana (*Liolaemus lutzae* Mertens, 1938), *Liolaemus fittkaui* Laurent, 1986, and the Dark Lizard (*Phymaturus tenebrosus* Lobo and Quinteros, 2005) (Sinervo et al. 2010).

Received 4 February 2015. Accepted 19 September 2015.

E.L. Kubisch and N.R. Ibargüengoytía. Departamento de Zoología, Laboratorio de Ecofisiología e Historia de vida de Reptiles, INIBIOMA–CONICET, Centro Regional Universitario Bariloche, Universidad del Comahue, Bariloche, 8400, Argentina.
V. Corbalán. Instituto Argentino de Investigaciones de las Zonas Áridas (IADIZA–CONICET), Avenida Ruiz Leal s/n, Parque General San Martín, CP 5500 Mendoza, Argentina.
B. Sinervo. Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, CA 95064, USA.
Corresponding author: E.L. Kubisch (e-mail: erikubisch@gmail.com).

Can. J. Zool. **94**: 49–59 (2016) dx.doi.org/10.1139/cjz-2015-0024

Lizards typically control body temperature (T_b) within relatively narrow ranges through behavioral thermoregulation (Huey et al. 2003; Bartholomew 2005; Kearney et al. 2009), being able to buffer the impacts of local warming only if there is sufficient heterogeneity in the thermal environment (Kearney et al. 2009; Clusella-Trullas and Chown 2011). In contrast, the possibilities for thermal microhabitat selection will be constrained if all available microhabitats have a similar "operative temperature" (T_e), which represents the availability of thermal microenvironments for thermoregulation and the body temperatures that a non-thermoregulating lizard might experience in their natural environment (Porter et al. 1973; Bakken 1992). The heterogeneity of thermal microenvironments is particularly limited in nocturnal and crepuscular lizards (Kearney and Porter 2004), in lizards that live under the canopy of forested areas (Hertz 1992), and in lizards that live in very open habitats where most soil surfaces are fully exposed to solar radiation (Grant and Dunham 1988; Kearney et al. 2009).

Nocturnal and forest lizards thermoregulate mainly by adjusting the timing of activity, rather than by moving to different microenvironments (Bustard 1967; Huey 1982). In open habitats with homogenous environments, lizards became inactive, sheltering in cooler microenvironments by going underground or inside crevices, when the temperatures exceed a threshold that might impair locomotor function and overall performance (Tewksbury et al. 2008; Sinervo et al. 2010). When lizards enter thermal refuges to avoid high temperatures and overheating and restrict hours of activity, foraging time is reduced, which may consequently limit growth and reproduction and thus increase the risk of local extinction (Sinervo et al. 2010; Ceia-Hasse et al. 2014; Lara-Resendiz et al. 2015).

It is also noteworthy that the measured contemporary extinction risk of local populations of viviparous lizards is double that of oviparous lizards, in a comparison across 48 species of Mexican phrynosomatids (Sinervo et al. 2010). In the case of viviparity, reduced opportunities for thermoregulation are hypothesized to threaten embryonic development in utero and affect offspring performance (Beuchat 1986; Shine 2005). According to predictions under current climate warming, viviparous *Liolaemus* Wiegmann, 1834 could experience not only range contraction but fragmentation, leaving populations more isolated and more vulnerable to extinctions in the coming decades (Pincheira-Donoso et al. 2013). In addition, based on evidence for irreversible parity mode (Shine 2005) or if the species do not adapt rapidly enough to global warming (Chevin et al. 2010; Huey et al. 2010; Sinervo et al. 2010), the cold-climate viviparous species would experience major extinction risk in the short and long terms (Pincheira-Donoso et al. 2013).

Patagonia has been considered an area of high endemism of vertebrate species (Lamoreux et al. 2006), particularly lizards. Approximately 45% of Argentinian lizards are endemic to Patagonia; however, their representation within the network of protected areas is very low (Chébez et al. 2005; Corbalán et al. 2011; Chehébar et al. 2013). Lizards, as ectotherms, represent an appealing biological model to predict the impact of global warming because they cannot produce appreciable physiological heat and are particularly sensitive to thermal variation (Camargo et al. 2010).

Herein, we applied the model of Sinervo et al. (2010) to predict the local extinction risk of three species of lizard from Patagonia and discuss vulnerability of these species to climate change considering thermal physiology, locomotor performance, and reproduction. The three species have been chosen to be representative of different environments, habits, and reproductive modes. The three species are sympatric in parts of their ranges in the transition environment from the most arid steppe in the northeastern Patagonia, Argentina, to the west austral rain forest, which crosses the Andes to the Pacific Coast of Chile. The southernmost nocturnal oviparous gecko, Darwin's Ground Gecko (*Homonota darwinii* Boulenger, 1885), is widely distributed in rocky outcrops in the Patagonian steppe. *Homonota darwinii* shelters during the day under small flat rocks and shows an ambush strategy and generalist feeding habit (Kun et al. 2010). *Homonota darwinii* is thigmothermic and a thermoconformer (Ibargüengoytía et al. 2007), and shows a low variance among populations in the upper thermal limit (panting threshold) and a high variance in lower thermal tolerances (critical minimum temperature) (Weeks and Espinoza 2013). This species is oviparous and reproduces annually or biennially, mating occurs from October to December, and it oviposits one egg in spring, with hatching during summer (Ibargüengoytía and Casalins 2007). The diurnal and viviparous Mountain Slope Lizard (*Liolaemus elongatus* Koslowsky, 1896) can be found sympatric with *H. darwinii* on the rocky outcrops of the steppe and is also sympatric with the Bariloche Lizard (*Liolaemus pictus* (Duméril and Bibron, 1837)) in the transitional forest (Ibargüengoytía 2004). The third species (*L. pictus*) is also a diurnal, viviparous, and insectivorous lizard, but this species is representative of the Austral forest, where they are common. They are heliothermic and can be found in bushes, on logs, or in leaf litter. *Liolaemus pictus* and *L. elongatus* show prolonged female reproductive cycles that last from 1 to 3 years, the mating season occurs in the spring, and litters of 3–7 young are produced from late January to early March (Ibargüengoytía and Cussac 1996, 1998).

We hypothesized that *H. darwinii* could be the species most affected by global warming because it is a thermoconformer, has the lowest preferred body temperature (T_{pref}) (Aguilar and Cruz 2010), and low variability in the upper thermal limit (Weeks and Espinoza 2013). However, the nocturnal habit may counteract the current effects of global warming. Besides, the two *Liolaemus* species would be more vulnerable because they are viviparous and we expect that *L. elongates*, occurring in the more open habitat, will be more affected and change its distribution toward the transition forest where they live in sympatry with *L. pictus*.

Materials and methods

Species

Homonota darwinii (Gekkota, Phyllodactylidae) is a small gecko, with mean maximum snout–vent length (SVL) of 55 mm (Cei 1986). This lizard inhabits from southern Mendoza to southern Santa Cruz provinces (32°S–52°S, 63°W–73°W; Cei 1986, 1993; Scolaro 2005), showing the southernmost distribution of the geckos of the world (Cei 1986; Scolaro 2005). *Liolaemus pictus* (Iguania, Liolaemidae) is a medium-sized lizard (SVL 23–75 mm), with a relatively long and slender body. They live at moderate to high altitudes (529–1600 m) in the Andean–Patagonian forests of Chile and Argentina. This species is distributed in western Neuquén, Chubut, and Río Negro provinces of Argentina, in the continental Chile between Vilches Alto (35°35′S, 71°05′W) and the Futaleufu National Reserve (43°15′S, 71°47′W), and in insular Chile in the islands of the archipelago of Chiloe and Mocha Island (Veloso and Navarro 1988; Pincheira-Donoso and Nuñez 2005; Elgueta et al. 2006; Vera-Escalona et al. 2010). *Liolaemus elongatus* (Iguania, Liolaemidae) is a large and insectivorous lizard (SVL 23–90 mm). It is distributed from Neuquén to Chubut, western and south-central regions of Río Negro Province, Argentina (Minoli et al. 2013).

Species' data record

The geographic distribution database of species *H. darwinii*, *L. pictus*, and *L. elongatus* was obtained from museum specimens, published literature, and fieldwork performed during this study (for details refer to the supplementary material).[1] We used

---

[1] Supplementary material is available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2015-0024.

Table 1. Mean of preferred body temperature (T_{pref}), set-point range of T_{pref}, and maximum (VT_{max}) and minimum (VT_{min}) voluntary temperatures of Darwin's Ground Geckos (*Homonota darwinii*), Bariloche Lizards (*Liolaemus pictus*), and Mountain Slope Lizards (*Liolaemus elongatus*) from different localities.

Species	Site	Mean T_{pref} (°C)	Set-point range (°C)	VT_{min} (°C)	VT_{max} (°C)	Source
Homonota darwini	Ingeniero Jacobacci	28.5	27.2–29.8	24.6	32.8	This work
	La Payunia Natural Reserve	28.5	28.4–29.8	25.5	30.0	This work
Liolaemus pictus	Cerro Chalhuaco	36.7	34.3–38.2	28.8	41.1	Gutiérrez et al. 2010
	Bariloche Playa Melipal	36.7	34.6–38.1	25.8	40.7	Gutiérrez et al. 2010
	Los Alerces National Park	36.4	35.4–37.9	31.3	39.6	This work
Liolaemus elongatus	Ingeniero Jacobacci	36.4	35.0–38.1	28.7	41.0	This work
	Laguna Blanca National Park	36.1	35.0–37.5	28.6	39.2	This work
	Bariloche Playa Melipal	35.9	35.2–37.0	29.5	38.7	This work

gazetteers from the geographic information system of the Instituto Geográfico Nacional de la República Argentina (http://www.ign.gob.ar/) and the Secretaría de Energía de la Nación (http://www.energia.gov.ar/home/) to georeference localities of each specimen of *H. darwinii* (n = 150), *L. pictus* (n = 132), and *L. elongatus* (n = 151). Any questionable or inaccurate record, or those separated by 1 km or less from the next point (defined as one population; Peterson et al. 2004; Sinervo et al. 2010), were discarded.

Preferred body temperature (T_{pref}) and interpopulation comparisons

To analyze intraspecific variation, we obtained multiple records of T_{pref} in the laboratory of (*i*) 13 individuals of *H. darwinii* captured in Ingeniero Jacobacci, Río Negro (between 40°50′S–41°32′S and 69°12′W–69°55′W; December 2010), and one specimen from the Natural Reserve La Payunia, Malargüe, Mendoza (36°13′49″S, 69°22′48″W; 1673 m above sea level (asl); November 2011); (*ii*) 15 individuals of *L. pictus* from Los Alerces National Park, Chubut (42°43′S, 71°45′W; 525 m asl; December 2011), and (*iii*) 22 individuals of *L. elongatus* from Ingeniero Jacobacci, Río Negro (between 40°50′S–41°32′S and 69°12′W–69°55′W; December 2010), 10 individuals from Laguna Blanca National Park, Neuquén (39°01′14″S, 70°24′45″W; January 2015), and 6 individuals from San Carlos de Bariloche, Río Negro (41°10′S, 71°25′W; January 2015). Additional data of T_{pref} was obtained from the literature when authors used comparable methods with those used in the present study (Table 1).

Preferred body temperatures were measured the day after capture. *Liolaemus pictus* and *L. elongatus* lizards were placed individually in an open-top terrarium (100 cm × 20 cm × 17 cm) with a thermal gradient (20–50 °C) produced by a lamp overhead (75 W) in one end of the terrarium. The T_{pref} experiments of the nocturnal *H. darwinii* were conducted overnight with individuals placed in a thermal gradient heated by Flexwatt® heat-tape at one end of the terrarium (covered with aluminium foil tape). Lizard body temperatures were measured every minute for 2 h using ultrathin (1 mm) catheter thermocouples located approximately 10 mm inside the cloaca and fastened to the base of the lizard's tail and connected to an eight-channel data logger (Measurement Computing 1.2 kHz Data Acquisition Device). For each individual, we estimated the mean and range of T_{pref}. We also estimated the set-point temperature range as the central 50% of all body temperatures selected in the laboratory and the mean of the upper bound of T_{pref} or maximum voluntary temperature (VT_{max}).

Environmental temperature (T_{e}), construction, and validation of thermal models with animals

Thermal models were designed to carefully quantify the availability of T_{e} (Bakken et al. 1985; Hertz 1992; Bakken and Angilletta 2014). The T_{e} was used to determine the availability of spatial and temporal heterogeneity of thermal microenvironments for thermoregulation (Kearney et al. 2009) and to analyze the possibilities that lizards have to achieve temperatures within the optimal physiological temperature range (Bakken et al. 1985; Bakken 1992; Dzialowski 2005; Williams et al. 2008).

We built hollow copper models (0.7 cm × 5 cm section) to estimate T_{b} of *H. darwinii* and sealed PVC dull gray (18%) models (1.5 cm × 8 cm section) to mimic the T_{b} of *L. pictus* and *L. elongatus*. Each model was connected to a thermocouple and closed at the ends with silicone (Fastix®). For thermal model validation, we used an adult specimen of each species from San Carlos de Bariloche (*H. darwinii*—male: SVL = 41.70 mm, mass = 1.6 g; *L. pictus*—male: SVL = 64 mm, mass = 8 g; *L. elongatus*—female: SVL = 70 mm, mass = 12 g). Each specimen was placed in an open terrarium (15 cm × 15 cm) with sand substrate. An ultrathin thermocouple was inserted into the cloaca attached to the base of the tail. Copper and PVC models were placed in the terrarium with the live lizard under variable thermal situations using an infrared lamp placed at 40 cm height. To discard any difference related to heat exchange between the model and the live lizards (Bakken and Angilletta 2014), we recorded the temperatures of the models and lizards simultaneously every minute during at least 2 h and the fit was tested using Pearson's product moment correlation (*H. darwinii*: $R = 0.984$, $n = 143$; *L. pictus*: $R = 0.914$, $n = 11\,211$; *L. elongatus*: $R = 0.966$, $n = 172$; $P < 0.001$). The criteria to choose the models relied on (*i*) the best-fitting model for heating and cooling phases, as well as during the stabilized phase, and (*ii*) when results were similar, we preferred the PVC model to standardize with Sinervo et al. (2010), thus allowing comparisons with several species and families around the world.

Furthermore, we have recalibrated the PVC model outdoors to confirm the steady temperature of the model with live animals set on their natural environment (Pearson's product moment correlation—*L. pictus*: $R = 0.863$, $n = 1478$; *L. elongatus*: $R = 0.871$, $n = 1478$; $P < 0.001$). The model and the organism displayed the same equilibrium temperature under natural conditions. The mean difference between lizard and model was 0.17 (SD = 0.16) for *L. pictus* and 0.31 (SD = 1.99) for *L. elongatus*.

Estimations of activity hours and restriction hours (h_{r})

To record the microenvironmental model temperatures (T_{e}), 84 thermal models connected to data loggers (HOBOTEMP® H8, four-channel external) were deployed at the extremes of the distribution of each species in different potential microenvironments such as sun, shade, under rocks, or other shelters (see Tables 2, 3, 4). Our primary goal was to simultaneously instrument as many sites as possible across each species' range. We also took into account the macroenvironments used by each species: open forest or rocky for *L. elongatus*; open forest, closed forest, high rocky outcrops, and lakeshore for *L. pictus* (Tables 3, 4). For *H. darwinii*, models were placed only in rocky outcrop environments, characteristic for the species (Table 2).

For each site, we estimated the restriction hours (h_{r}), considered to be hours that the lizards would be in their shelters due to temperatures exceeding their thermal preferences (Sinervo et al.

2010). Hours of restriction were calculated as the daily number of hours when the temperature of at least 50% of the models exceeded the mean VT_{max}, which correspond to the upper bound of T_{pref} ($T_e > VT_{max}$) and is considered to be the threshold for activity restriction. We used a more exigent threshold, VT_{max}, because we consider that lizards could still be active in the range of T_{pref} in contrast with the Sinervo et al. (2010) methodology that consider the threshold when T_e exceeded mean T_{pref}. For example, h_r for *H. darwinii* were considered to be those occurring when $T_e > 31.4$ °C; for *L. pictus*, $h_r = T_e > 40.6$ °C; for *L. elongatus*, $h_r = T_e > 39.6$ °C.

In addition, we estimated the activity hours, considered to be the hours that the lizards are outside of their shelters, performing behaviors related to basking, foraging, reproduction, and dispersal (Ibargüengoytía and Cussac 2002; Ibargüengoytía 2005). Activity hours were estimated as the daily hours that at least one model registered a T_e higher than the lowest activity temperature and lower than the VT_{max} (lowest activity $T < T_e < VT_{max}$). We assumed that the activity minimum temperatures are 25 °C for thermoregulatory species (Sinervo et al. 2010) and 20 °C for thermoconformers or nocturnal species. These activity minimum temperatures are coincident with the reported minimum body temperature for *L. pictus* and *L. elongatus* in their natural environments (Ibargüengoytía and Cussac 2002; Ibargüengoytía 2005; Gutiérrez et al. 2010). Therefore, the daily activity hours were considered to be those when the T_e was higher than 20 °C and lower than 31.4 °C for *H. darwinii*, higher than 25 °C and lower than 40.6 °C for *L. pictus*, and higher than 25 °C and lower than 39.6 °C for *L. elongatus*. For the two diurnal species of *Liolaemus*, the calculation of activity hours and h_r was conducted from 0900 to 1900. *Homonota darwinii*, even though it is predominantly nocturnal, feed on diurnal larvae of moth and ants under rocks (Kun et al. 2010); consequently, we consider h_r estimated during a 24 h period.

Relationship between hours of restriction (h_r) and maximum air temperature (T_{max})

To obtain a general function to predict extinctions (sensu Sinervo et al. 2010), we collected daily maximum temperatures (T_{max}) from http://www.tutiempo.net/ (validated for select weather stations with data from http://www.noaa.gov/) of the nearest weather station to each data-logger site to compute the functional relationship between h_r and activity time. Linear regression was performed on the hours that T_e were above VT_{max} (h_r) as a function of the difference between the maximum daily temperature and the mean maximum voluntary temperature ($T_{max} - VT_{max}$) of each site and each species:

$$(1) \qquad h_r \text{ when } T_e > VT_{max} = \text{slope} \times (T_{max} - VT_{Max}) + \text{intercept}$$

Physiological model for local extinction risk

We used global climate surfaces from http://www.worldclim.org/ (Hijmans et al. 2005) for the years 1975, interpolated 2010 (between 1975 and 2020), 2050, 2080 (IPCC IVth climate assessment with A2 scenario; IPCC 2007) to derive T_{max} at a given latitude and longitude (10 arc-minute resolution) in the corresponding breeding season months (December and January), which is considered to be the most critical period for the analysis of the population vulnerability to climate change (Sinervo et al. 2010). These 2 months were determined to be the most critical based on extensive sensitivity analysis of Mexican phrynosomatid lizards. In brief, we performed a goodness-of-fit test using all possible (consecutive) 2-month periods and all possible 3-month periods in the prediction of the observed extinctions of Mexican *Sceloporus* lizard species (for more details see the supporting online material associated with Sinervo et al. 2010). Using h_r during the 2 months of reproduction had the best-fitting χ^2 that related observed extinctions and predicted extinctions using the physiological model of extinction risk.

Table 2. Locality and environment type where thermal models were deployed for Darwin's Ground Geckos (*Homonota darwinii*).

Site	Type of environment	No. of models	Time of logger	Time interval (min)	Nearest weather station (lat., long.)	Local h_r Mean ± SE	Local h_r Median	Local activity hours Mean ± SE	Local activity hours Median	General h_r (mean ± SE)	General activity hours (mean ± SE)
San Carlos de Bariloche, Río Negro (Ea El Cóndor; 41.0937°S, 71.1320°W; 843 m above sea level (asl))	Rocky	4	9 Nov. 2010–25 Mar. 2011	25	San Carlos de Bariloche (41.15°S, 71.16°W)	3.05±0.26	2.60	8.41±0.29	12.20	4.06±0.34	9.87±0.18
Telsen, Chubut (Aguada La Escondida; 42.4659°S, 66.2134°W; 278 m asl)	Rocky	4	22 Nov. 2010–22 Apr. 2011	20	Madryn (43.2°S, 65.26°W)	5.78±0.34	6.33	12.34±0.44	7.83		
Monumento Natural Bosques Petrificados, Santa Cruz (47.7489°S, 68.1743°W; 161 m asl)	Rocky	4	27 Nov. 2010–3 Mar. 2011	20	Puerto Deseado (47.73°S, 65.91°W)	3.95±0.37	3.25	8.09±0.29	7.67		
La Payunia Natural Reserve, Mendoza (Cerro Fortunoso; 36.2267°S, 69.3766°W; 1670 m asl)	Rocky	4	7–11 Nov. 2011	2	Malargüe (35.5°S, 69.58°W)	3.07±1.24	2.20	5.57±1.57	5.13		
Malargüe, Mendoza (Observatorio Pierre Auger; 35.4638°S, 69.5848°W; 1412 m asl)	Rocky	4	30 Nov. 2010–9 Mar. 2011	20	Malargüe (35.5°S, 69.58°W)	7.49±0.29	8.00	12.33±0.35	12.00		
Ingeniero Jacobacci, Río Negro (41.4354°S, 69.7531°W; 967 m asl)	Rocky	2	1 Dec. 2011–8 Feb. 2012	6	Maquinchao (41.24°S, 68.69°W)	7.14±0.57	8.30	7.50±0.30	6.85		

Note: The mean ± SE and median values of restriction hours (h_r) and of activity hours during a 24 h period are also shown.

Table 3. Locality and environment type where thermal models were deployed for Bariloche Lizards (*Liolaemus pictus*).

Site	Type of environment	No. of models	Time of logger	Time interval (min)	Nearest weather station (lat., long.)	Local h_r		Local activity hours		General h_r		General activity hours	
						Mean ± SE	Median	Mean ± SE	Median	Mean ± SE	Median	Mean ± SE	Median
Puerto Blest, Río Negro (La Heladera; 41.0138°S, 71.8473°W; 904 m above sea level (asl))	High altitude, rocky	8	22 Nov.– 25 Dec. 2011	6	San Carlos de Bariloche (41.15°S, 71.16°W)	1.15±0.20	0.15	2.89±0.37	2.90	0.99±0.09	0.00	2.39±0.13	2.12
Puerto Blest, Río Negro (Puerto Cascada los Cántaros; 41.0229°S, 71.8171°W; 788 m asl)	Closed forest	4	22 Nov. 2011– 5 Jan. 2012	6	San Carlos de Bariloche (41.15°S, 71.16°W)	0.00±0.00	0.00	0.59±0.24	0.00				
Puerto Blest, Río Negro (41.0229°S, 71.8171°W; 788 m asl)	Lakeshore	4	22 Nov. 2011– 5 Jan. 2012	6	San Carlos de Bariloche (41.15°S, 71.16°W)	0.00±0.00	0.00	2.06±0.34	2.07				
San Carlos de Bariloche, Río Negro (Lago Moreno; 41.1099°S, 71.4768°W; 800 m asl)	Open forest	8	18 Nov. 2011– 14 Jan. 2012	2	San Carlos de Bariloche (41.15°S, 71.16°W)	1.25±0.22	0.00	3.83±0.28	3.73				
San Carlos de Bariloche, Río Negro (Cerro Challhuaco; 41.2628°S, 71.2999°W; 1546 m asl)	Open forest	4	26 Nov.– 15 Dec. 2011	4	San Carlos de Bariloche (41.15°S, 71.16°W)	1.85±0.43	1.20	3.03±0.42	2.47				
San Carlos de Bariloche, Río Negro (Cerro Challhuaco; 41.2661°S, 71.2866°W; 1476 m asl)	Closed forest	4	23 Dec. 2011– 24 Jan. 2012	6	San Carlos de Bariloche (41.15°S, 71.16°W)	0.37±0.04	0.48	1.85±0.19	1.93				
San Carlos de Bariloche, Río Negro (Cerro Challhuaco; 41.2723°S, 71.2739°W; 1435 m asl)	High altitude, rocky	4	23 Dec. 2011– 24 Jan. 2012	6	San Carlos de Bariloche (41.15°S, 71.16°W)	2.45±0.29	3.27	1.47±0.18	1.10				
Los Alerces, Chubut National Park (Puerto Chucao; 42.7304°S, 71.7595°W; 528 m asl)	Logs on the lakeshore	4	31 Oct. 2011– 27 Jan. 2012	6	Esquel (42.93°S, 71.15°W)	4.88±0.35	5.33	2.60±0.18	2.13	4.88±0.35	5.33	2.60±0.18	2.13

Note: The mean ± SE and median values of restriction hours (h_r) and of activity hours during a 24 h period are also shown.

Table 4. Locality and environment type where thermal models were deployed for Mountain Slope Lizards (*Liolaemus elongatus*).

Site	Type of environment	No. of models	Time of logger	Time interval (min)	Nearest weather station (lat., long.)	Local h_r Mean ± SE	Local h_r Median	Local activity hours Mean ± SE	Local activity hours Median	General h_r Mean ± SE	General h_r Median	General activity hours Mean ± SE	General activity hours Median
San Carlos de Bariloche, Río Negro (Moreno Lake; 41.1099°S, 71.4768°W; 800 m above sea level (asl))	Open forest	8	18 Nov. 2011–14 Jan. 2012	2	San Carlos de Bariloche (41.15°S, 71.16°W)	1.50±0.21	0.68	2.46±0.21	2.27	2.25±0.19	1.93	1.56±0.14	1.00
San Carlos de Bariloche, Río Negro (41.1233°S, 71.4427°W; 815 m asl)	Rocky	8	18 Nov. 2011–14 Jan. 2012	2	San Carlos de Bariloche (41.15°S, 71.16°W)	2.61±0.38	1.07	0.73±0.13	0.47				
San Carlos de Bariloche, Río Negro (Challhuaco; 41.2723°S, 71.2739°W; 1435 m asl)	High altitude, rocky	4	23 Dec. 2011–24 Jan. 2012	6	San Carlos de Bariloche (41.15°S, 71.16°W)	2.97±0.29	3.80	0.73±0.13	0.47				
Ingeniero Jacobacci, Río Negro (41.4354°S, 69.7531°W; 967 m asl)	Rocky	2	1 Dec. 2011–8 Feb. 2012	6	Maquinchao (41.24°S, 68.69°W)	3.27±0.42	2.25	2.86±0.33	2.15	3.27±0.42	2.25	2.86±0.33	2.15

Note: The mean ± SE and median values of restriction hours (h_r) and of activity hours during a 24 h period are also shown.

We used the R program (R Core Development Team 2013) to generate a structural regression model to predict the year of extinction of populations of lizards. Given the georeferenced database, VT_{max}, T_{max} of global surfaces, and eq. 1 for each species, we first estimated the assumed physiological limit defined by the highest h_r recorded across the species' range, which we termed "critical h_r". This differed from the value used by Sinervo et al. (2010), which was the upper 95% confidence limit for h_r across the lizard families and by Ceia-Hasse et al. (2014). Here we assume that our refined measurement of T_e across the species' range and VT_{max} more accurately assesses this key limit that is assumed under the notion of a physiological limit defining the species' distribution. If h_r (h_r = slope × (T_{max} − VT_{max}) + intercept) exceeds critical h_r for each species as estimated with the 1975 WORLDCLIM data for T_{max}, the population at the site was assumed to go extinct for the additional time periods under consideration (2010, 2050, 2080). In a test of the ability of this simple model to predict observed extinctions (Sinervo et al. 2010, 2011), we recorded an R^2 = 0.72, which indicated that the model captures a large fraction of the variation in local population extinction among sites and across eight lizard families.

Results

Preferred body temperature (T_{pref}) in the laboratory

The mean T_{pref}, set-point range of T_{pref}, and mean of maximum (VT_{max}) and minimum (VT_{min}) voluntary temperatures of *H. darwinii*, *L. pictus*, and *L. elongatus* estimated at different localities are shown in Table 1.

Predicting population extinctions

From eq. 1, we obtained general equations to predict population extinctions of each species. We generated a pooled regression estimate across all sites (Figs. 1*a*–1*c*), which gives a generic T_e relationship for each species. This regression relates h_r to T_{max} at the weather station near each deployment of T_e models, and VT_{max} for each species. Considering the georeferenced distribution points, the VT_{max}, T_{max} of global surfaces, and eq. 1 for each species, we estimated the maximum observed h_r across the entire species' distribution. We assumed that if a population exceeded this value (in future time points), then it was predicted to be too high to support a viable population according to the physiological model (sensu Sinervo et al. 2010). We estimated that 9 populations (6%) of *H. darwinii* have become extinct by 2010, 21 populations (14%) will become extinct by 2050, and 30 populations (20%) will become extinct by 2080 (Fig. 2A). We estimated that 2 populations (1.5%) of *L. pictus* have become extinct by 2010, 8 populations (6%) will become extinct by 2050, and 20 populations (15%) will become extinct by 2080 (Fig. 2B). We estimate that 4 populations (2.6%) of *L. elongatus* have become extinct by 2010, 13 populations (8.6%) will become extinct by 2050, and 40 populations (26.5%) will become extinct by 2080 (Fig. 2C).

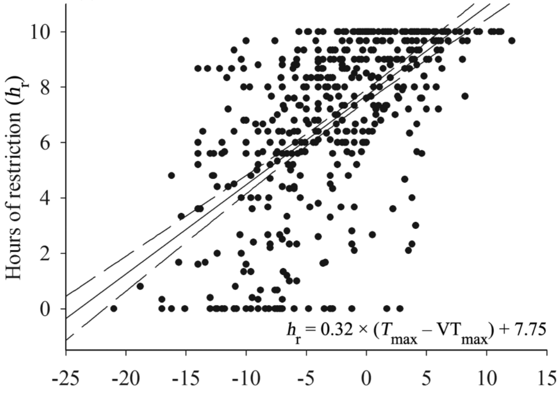
We tested whether the overall extinction risk of the thermoconformer (*H. darwinii*) was significantly different than the overall risk of extinction of the two heliotherms (*L. pictus* and *L. elongatus*) by computing a χ^2 of predicted extinct versus persistent populations of each of the two types in the years 2010, 2050, and 2080. Whereas the risk of extinction of *H. darwinii* is higher in 2010 ($\chi^2_{[1]}$ = 5.06, P < 0.01), this difference in risk rapidly disappears by 2050 ($\chi^2_{[1]}$ = 1.91, P < 0.01) and 2080 ($\chi^2_{[1]}$ = 1.73, P < 0.01).

Discussion

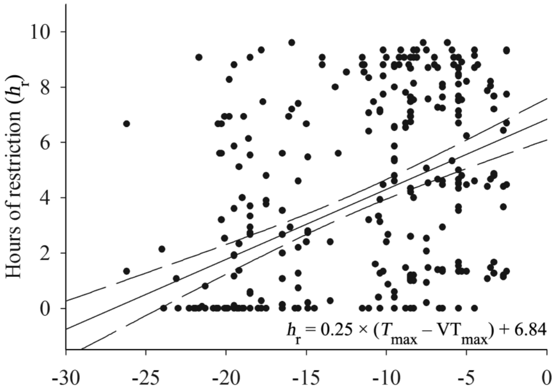
While Sinervo et al. (2010) predicts that the Phyllodactylidae family will not suffer impacts from climate change, our physiological model predicted that 20% of the *H. darwinii* populations

Fig. 1. Linear regressions of the hours of restriction (h_r; number of hours per day where the operative temperature (T_e) exceeded the maximum voluntary temperature (VT_{max}) (i.e., $T_e > VT_{max}$)) as a function of the difference between maximum daily temperature (T_{max}) and VT_{max} (i.e., $T_{max} - VT_{max}$), pooled across all sites, for (*a*) Darwin's Ground Geckos (*Homonota darwinii*), (*b*) Bariloche Lizards (*Liolaemus pictus*), and (*c*) Mountain Slope Lizards (*Liolaemus elongatus*). The regression lines and 95% confidence intervals are shown.

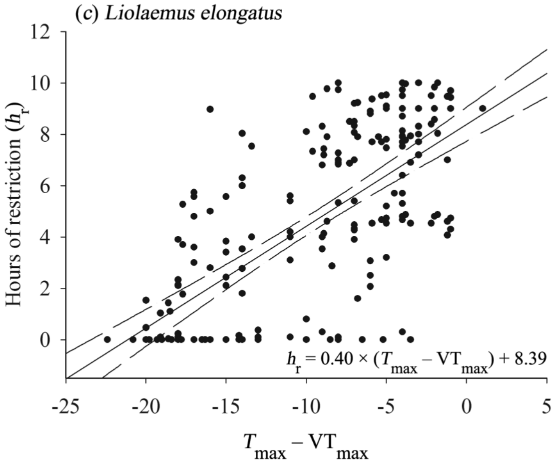
(*a*) *Homonota darwinii*



(*b*) *Liolaemus pictus*



(*c*) *Liolaemus elongatus*



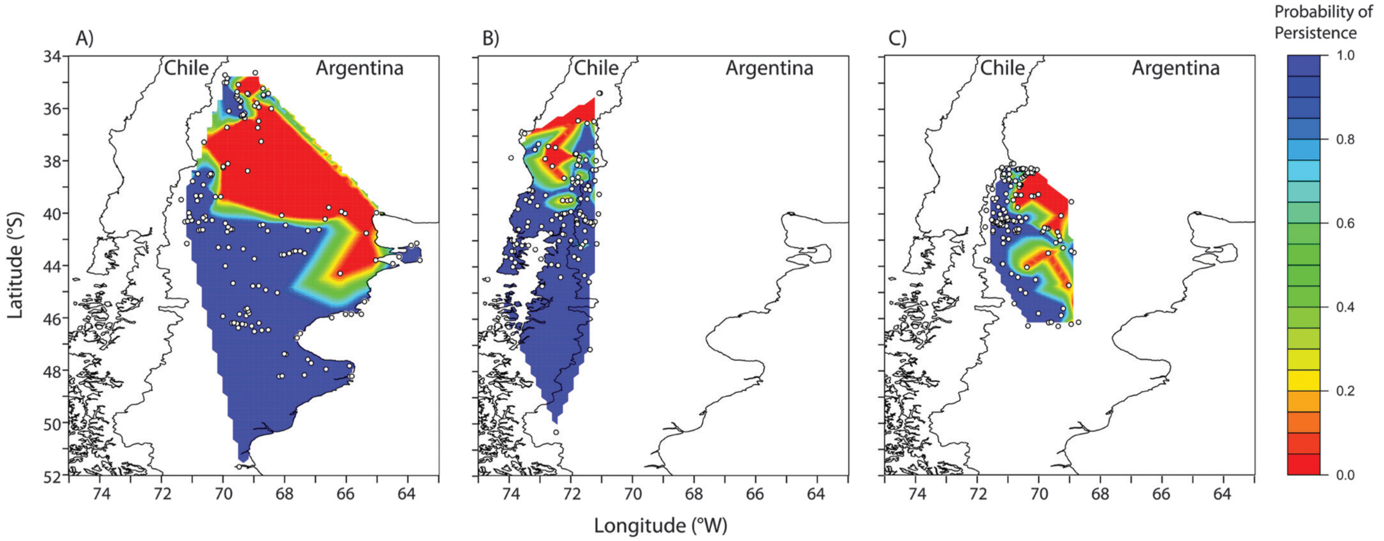
could become extinct by 2080. The physiological model also predicted that the 15% of *L. pictus* populations and 26.5% of *L. elongatus* populations could become extinct by 2080. The most-at-risk species corresponded to *L. elongatus* and *H. darwinii* that inhabit the arid steppe environments of Patagonia, in contrast to *L. pictus* that lives in the transition forest of cordilleran cypress (*Austrocedrus chilensis* (D.Don) Pic. Serm. & Bizzarri) and in the Austral southern beech (*Notophagus* Blume) forest. In addition, the prediction showed that the first populations to disappear were those located in the northern and eastern boundaries of the species' distributions.

In temperate environments, low night-time temperatures constrain the spread of nocturnal species to higher latitudes and elevations, explaining why nocturnal lizards inhabit warmer environments than diurnal ones (Meiri et al. 2013). Analyses conducted here indicate that the long-term extinction risk (e.g., 2050 and 2080) of *H. darwinii*, which is predominantly a thermoconformer and a thigmotherm (Ibargüengoytía et al. 2007; Aguilar and Cruz 2010), are nearly the same as those of the two heliotherms, even though the risk of extinction in the present is significantly higher in *H. darwinii* (e.g., 2010). These analyses are premised on the measured environmental temperatures of each species across the species' range as related to a null model of physiologically-based risk of extinction. This null model posits that the most extreme h_r observed across the species' range, during the breeding season, reflects the physiological limit to which the species is adapted. Any populations where the local h_r climbs above this value are assumed to go extinct from a physiological cause.

Physiological plasticity can help to mitigate the adverse impacts of climate change (Deutsch et al. 2008) and is expected to occur mainly in higher latitude species because they have evolved in variable seasonal environments (Stillman 2003). However, *L. pictus* and *L. elongatus* showed low acclimation capacity on locomotor performance and thermal physiological traits such as T_{pref}, panting threshold, and critical minimum temperature (Kubisch 2013). A similar response has been observed in the world's southernmost gecko (*H. darwinii*) in which the maximum locomotion speed was not affected by acclimation to different temperatures (Aguilar and Cruz 2010). In addition, Weeks and Espinoza (2013) found low variability among four *H. darwinii* populations in panting threshold. Also, organisms may mitigate the detrimental effects of warming through evolutionary change in thermal physiology or phenology (Sinervo et al. 2010).

Several studies showed patterns of rapid evolution in response to changing thermal conditions in some ectotherms like the *Anolis* Daudin, 1802 lizard (Leal and Gunderson 2012), butterfly larvae of the genus *Colias* Fabricius, 1807 (Higgins et al. 2013), the fruit fly *Drosophila melanogaster* Meigen, 1830 (Partridge et al. 1995), and other insects (Bradshaw and Holzapfel, 2006; Bonebrake and Deutsch 2012), indicating that several species can respond with rapid adaptive changes and survive thermal stress. In addition, Logan et al. (2014) showed strong directional natural selection on thermal performance traits of *Anolis* lizards. The effects of climate warming have penetrated to the genetic level in diverse organisms, but the possibilities of adaptation to new climate conditions will depend of the length of the life cycles and the population size. Small animals with short life cycles and large population sizes will probably adapt to longer growing seasons and be able to persist; however, populations with longer generation times are expected to evolve slower per generation to adapt to a given rate of environmental change and will reach extinction before they can adapt to rapid environmental change (Chevin et al. 2010). Age of maturity of *H. darwini* and *L. pictus* are 3–4 years (Kubisch et al. 2012; Gutiérrez et al. 2013), suggesting slow thermal adaptation rates. Sinervo et al. (2010) point out that the sustained intensity of selection during the period of climate change (historical (1975–2009) or future (2009–2069)) will be on the order of 0.4 for a simple trait such as the increase in thermal preference required to keep h_r below critical h_r. The breeding design for thermal preference of lizards (based on half-sibs through the sire) has shown that the additive genetic variation is near zero. The thermal preference of progeny seems to be controlled by a complex epigenetic interaction of maternal thermal preference during development and the life-history genotypes (Paranjpe et al. 2013). This suggests that adaptation in thermal preference of lizards may not be possible in the short term.

Fig. 2. Contour plots showing the levels of local extinction for (A) Darwin's Ground Geckos (*Homonota darwinii*), (B) Bariloche Lizards (*Liolaemus pictus*), and (C) Mountain Slope Lizards (*Liolaemus elongatus*). Probability of persistence by 2080 is depicted, where probability of extinction = 1 – probability of persistence.



In addition, the preferred body temperature is considered a conservative character for the genus *Liolaemus* (Rodríguez-Serrano et al. 2009; Medina et al. 2012; Moreno Azócar et al. 2013) that could lead to lower variance in body temperature, which should itself lead to lower acclimation capacity. Moreover, the T_{pref} did not show differences among populations at different distribution points observed in this study (Table 1). Therefore, plasticity in the T_{pref} is likely to have a negligible impact on the risk of extinction in other species such as the multiple T_{pref} records for single species localized in different distribution points (e.g., Side-blotched Lizard (*Uta stansburiana* Baird and Girard, 1852) has 30 records) and across diverse genera within a lizard family (Sinervo et al. 2010).

Lizards may be able to mitigate the effects of global warming by behavioral thermoregulation, moving into shadier tree habitats where T_{e} is lower, toward forest edges, or even into towns when there is greater occurrence of cool microenvironments (Huey et al. 2009, 2012; Clusella-Trullas and Chown 2011; Kearney 2013). During activity hours, lizards can feed, disperse, and breed (Tewksbury et al. 2008). However, when temperature greatly increases, lizards tend to seek refuges, e.g., deeply beneath soil, and stop their activities to avoid overheating at the expense of hours of activity. In particular, lizards currently found in open habitats are expected to move to closed forests or environments that offer shady shelters (Huey et al. 2009, 2012; Kearney 2013). This is the case for *L. elongatus*, which occurs mainly in the steppe rocky outcrops (Cei 1986), but currently shares with *L. pictus* the understory and rocks at lakeshores in the *A. chilensis* transition forest (Ibargüengoytía and Cussac 1998). A recent species' distribution model shows that *L. elongatus* may increase their area with suitable climatic conditions (Bonino et al. 2015), but this also would require a very high dispersal rate to a new habitat. Therefore, if global warming continues, then it is expected that species such as *L. elongatus* will be able to further exploit the forest as a thermal refuge and compete with *L. pictus* in the localities where they are sympatric. In steppe environments, lizards could avoid overheating by moving toward cooler sites; for example, *H. darwinii* sheltered more frequently among the rocks on the warmer slope and selected rocks of a particular size, thickness, and shape (Aguilar and Cruz 2010), suggesting that under an increment of environmental temperatures they could move to colder microenvironments. However, not all environments with extant populations of lizards offer these possibilities.

Lizards living in temperate regions may also be able to adjust to climate warming by changing hours of daily and seasonal activities (Kearney et al. 2009) and by breeding earlier (Sinervo et al. 2010) to avoid death of embryos from overheating, or h_{r}. However, global warming is predicted to be faster in spring than in summer; therefore, this solution would probably be limited by high temperatures and a shift in the activity may not mitigate the local extinction risk. In the cold environments of Patagonia, lizards produce one litter every 2 or 3 years (Ibargüengoytía 2008). This is the case for *H. darwinii* (Ibargüengoytía and Casalins 2007) and *L. elongatus* (Ibargüengoytía and Cussac 1998), which exhibit an annual–biennial female reproductive cycle, and in *L. pictus*, which exhibit a biennial–triennial reproductive cycle (Ibargüengoytía and Cussac 1996, 1998). Therefore, one would expect that an increase in temperature would extend the activity season and would reduce developmental time, which could shorten the reproductive cycles in the lizards of Patagonia, thereby ameliorating extinction risk.

The ambient temperature during the lizard activity season can also influence growth rates and, hence, the age of sexual maturity (Sinervo and Adolph 1989; Niewiarowski and Roosenburg 1993; Wapstra et al. 2001). In *H. darwinii* and in *L. pictus*, environmental temperature affect growth, body size, and age at sexual maturity (Kubisch et al. 2012; Gutiérrez et al. 2013). Thermal environment can also affect development and newborn survival, body size, morphology, and performance (Elphick and Shine 1998; Angilletta 2009). Therefore, predictions of the impacts of global warming also require consideration of the vulnerability during ontogeny (Kingsolver et al. 2011) and temperature effects during development (Amarasekare and Savage 2012). These refinements could be made to the model considered here, adding more life-cycle stages to the assessment of extinction risk, as well as demographic data and fossil records to increase the model complexity. Nevertheless, this was a first step to predict the local extinction risk of three species of lizard with different habits that take into account environmental variables such as maximum air temperature and operative temperatures across the species' range, as well as physiological variables like T_{pref}, $\mathrm{VT}_{\mathrm{max}}$, and the reproductive season. However, species' responses to global warming also depend on behavior, habitat, growth, and life history, all of which should be considered in mechanistic forecasts of local extinction risk under climate change. Our approach provides concrete predictions of extinction risk, under a null model of how restriction in activity during the breeding season sets the distributional limit of each species. All of the other potential routes by which T_e might influence performance and reproductive ecology could likely be incorporated into a more general framework to assess which traits are most important in determining physiologically-based extinction risk, especially, once surveys of extinction and persistence of local populations are conducted in *Liolaemus* lizards, as have been done with the *Sceloporus* lizards of Mexico. Such surveys are necessarily slow and laborious, requiring monitoring of populations over several years. The *Sceloporus* surveys took over a decade to complete. Nevertheless, the a priori predictions of local extinction, as presented here, may allow researchers to more rapidly survey for extinctions by focusing on sites predicted for extinction and a small set of control sites where lizards are predicted to persist.

Acknowledgements

We thank A. Scolaro for his support during this study in analyzing the georeferences of many localities. We are grateful to J. Fernández, J. Boretto, F. Cabezas-Cartes, S. Ausas, H. Pastore, and M. Gutiérrez for their help with the fieldwork. We also thank the institutions for access to the databases containing the herpetological collections. This research was supported by Universidad Nacional del Comahue (CRUB), Consejo Nacional de Investigaciones Científicas y Técnicas (PIP100271; RD2702-12), Agencia Nacional de Promoción Científica y Tecnológica (PICT 1086; 3100; 2578), MINCyT-CAPES (BR11/18), and NSF (EF-1241848) awarded to B. Sinervo, J. Pittermann, D.B. Miles, J.W. Sites, Jr., A. Bauer, and a host of international collaborators. Finally, we are indebted to J.D. Krenz, R. Cooper, and R. Lara-Resendiz for their insightful comments on the manuscript.

References

Aguilar, R., and Cruz, F.B. 2010. Refuge use in a Patagonian nocturnal lizard, *Homonota darwinii*: the role of temperature. J. Herpetol. **44**: 236–241. doi:10.1670/08-270.1.

Amarasekare, P., and Savage, V. 2012. A framework for elucidating the temperature dependence of fitness. Am. Nat. **179**: 178–191. doi:10.1086/663677. PMID:22218308.

Angilletta, M.J., Jr. 2009. Thermal adaptation: a theoretical and empirical synthesis. Oxford University Press, Oxford, UK.

Bakken, G.S. 1992. Measurement and application of operative and standard operative temperatures in ecology. Am. Zool. **32**: 194–216. doi:10.1093/icb/32.2.194.

Bakken, G.S., and Angilletta, M.J., Jr. 2014. How to avoid errors when quantifying thermal environments. Funct. Ecol. **28**: 96–107. doi:10.1111/1365-2435.12149.

Bakken, G.S., Santee, W.R., and Erskine, D.J. 1985. Operative and standard operative temperature: tools for thermal energetics studies. Am. Zool. **25**: 933–943. doi:10.1093/icb/25.4.933.

Bartholomew, G.A. 2005. Integrative biology: an organismic biologist's point of view. Integr. Comp. Biol. **45**: 330–332. doi:10.1093/icb/45.2.330. PMID:21676776.

Beuchat, C.A. 1986. Phylogenetic distribution of the urinary bladder in lizards. Copeia, **1986**(2): 512–517. doi:10.2307/1445009.

Bonebrake, T.C., and Deutsch, C.A. 2012. Climate heterogeneity modulates impact of warming on tropical insects. Ecology, **93**(3): 449–455. doi:10.1890/11-1187.1. PMID:22624199.

Bonino, M.F., Moreno Azócar, D.L., Schulte, J.A., II, and Cruz, F.B. 2015. Climate change and lizards: changing species' geographic ranges in Patagonia. Reg. Environ. Change, **15**(6): 1121–1132. doi:10.1007/s10113-014-0693-x.

Bradshaw, W.E., and Holzapfel, C.M. 2006. Evolutionary response to rapid climate change. Science, **312**(5779): 1477–1478. doi:10.1126/science.1127000. PMID:16763134.

Bustard, H.R. 1967. Activity cycle and thermoregulation in the Australian gecko *Gehyra variegata*. Copeia, **1967**: 753–758. doi:10.2307/1441885.

Camargo, A., Sinervo, B., and Sites, J.W. 2010. Lizards as model organisms for linking phylogeographic and speciation studies. Mol. Ecol. **19**: 3250–3270. doi:10.1111/j.1365-294X.2010.04722.x. PMID:20618905.

Cei, J.M. 1986. Reptiles del centro, centro-oeste y sur de la Argentina. Herpetofauna de las zonas áridas y semiáridas. Monografia IV, Museo Regionale di Scienze Naturali, Torino, Italy.

Cei, J.M. 1993. Reptiles del noroeste, nordeste y este de la Argentina: Herpetofauna de las sevas subtropicales, Puna y Pampas. Monografia XIV, Museo Regionale di Scienze Naturali Torino, Italy.

Ceia-Hasse, A., Sinervo, B., Vicente, L., and Pereira, HM . 2014. Integrating ecophysiological models into species distribution projections of European reptile range shifts in response to climate change. Ecography, **37**(7): 679–688. doi:10.1111/j.1600-0587.2013.00600.x.

Chébez, J.C., Rey, N.R., and Williams, J.D. 2005. Reptiles de los Parques Nacionales de la Argentina. Monografía, L.O.L.A., Buenos Aires.

Chehébar, C., Novaro, A., Iglesias, G., Walker, S., Funes, M., Tammone, M., and Didier, K. 2013. Identificación de áreas de importancia para la biodiversidad en la estepa y el monte de Patagonia. ErreGé y Asociados imprenta.

Chevin, L.M., Lande, R., and Mace, G.M. 2010. Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. PLoS Biol. **8**(4): e1000357. doi:10.1371/journal.pbio.1000357. PMID:20463950.

Cleland, E.E., Chuine, I., Menzel, A., Mooney, H.A., and Schwartz, M. 2007. Shifting plant phenology in response to global change. Trends Ecol. Evol. **22**: 357–365. doi:10.1016/j.tree.2007.04.003. PMID:17478009.

Clusella-Trullas, S., and Chown, S.L. 2011. Comment on "Erosion of lizard diversity by climate change and altered thermal niches". Science, **332**: 537. doi:10.1126/science.1195193. PMID:21527699.

Corbalán, V., Tognelli, M.F., Scolaro, J.A., and Roig-Juñent, S.A. 2011. Lizards as conservation targets in Argentinean Patagonia. J. Nat. Conserv. **19**: 60–67. doi:10.1016/j.jnc.2010.05.004.

Cornelissen, T. 2011. Climate change and its effects on terrestrial insects and herbivory patterns. Neotrop. Entomol. **40**: 155–163. doi:10.1590/S1519-566X2011000200001. PMID:21584394.

Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C., and Martin, P.R. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. Proc. Natl. Acad. Sci. U.S.A. **105**: 6668–6672. doi:10.1073/pnas.0709472105. PMID:18458348.

Diffenbaugh, N.S., and Ashfaq, M. 2010. Intensification of hot extremes in the United States. Geophys. Res. Lett. **37**: L15701.

Dzialowski, E.M. 2005. Use of operative temperature and standard operative temperature models in thermal biology. J. Therm. Biol. **30**: 317–334. doi:10.1016/j.jtherbio.2005.01.005.

Elgueta, E., Reid, S., Pliscoff, P., M.A., Núñez, J., and Smith-Ramírez, C. 2006. Catastro de vertebrados terrestres y análisis en seis hábitats presentes en la reserva nacional Futaleufú, Provincia de Palena, X Región, Chile. Gayana, **70**(2): 195–205.

Elphick, M.J., and Shine, R. 1998. Longterm effects of incubation temperatures on the morphology and locomotor performance of hatchling lizards (*Bassiana duperreyi*, Scincidae). Biol. J. Linn. Soc. **63**: 429–447. doi:10.1111/j.1095-8312.1998.tb01527.x.

Grant, B.W., and Dunham, A.E. 1988. Thermally imposed time constraints on the activity of the desert lizard *Sceloporus merriami*. Ecology, **69**: 167–176. doi:10.2307/1943171.

Gutiérrez, J.A., Krenz, J.D., and Ibargüengoytía, N.R. 2010. Effect of altitude on thermal responses of *Liolaemus pictus argentinus* in Argentina. J. Therm. Biol. **35**: 332–337. doi:10.1016/j.jtherbio.2010.07.001.

Gutiérrez, J.A., Piantoni, C., and Ibargüengoytía, N.R. 2013. Altitudinal effects on life history parameters in populations of *Liolaemus pictus argentinus* (Sauria: Liolaemidae). Acta Herpetol. **8**(1): 9–17.

Harley, C.D.G., Hughes, A.R., Hultgren, K.M., Miner, B.G., Sorte, C.J.B., Thornber, C.S., Rodriguez, L.F., Tomanek, L., and Williams, S.L. 2006. The impacts of climate change in coastal marine systems. Ecol. Lett. **9**: 228–241. doi:10.1111/j.1461-0248.2005.00871.x. PMID:16958887.

Hertz, P.E. 1992. Temperature regulation in Puerto Rican *Anolis* lizards: a field test using null hypotheses. Ecology, **73**: 1405–1417. doi:10.2307/1940686.

Higgins, J.K., MacLean, H.J., Buckley, L.B., and Kingsolver, J.G. 2013. Geographic differences and microevolutionary changes in thermal sensitivity of butterfly larvae in response to climate. Funct. Ecol. **28**(4): 982–989. doi:10.1111/1365-2435.12218.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., and Jarvis, A. 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. **25**: 1965–1978. doi:10.1002/joc.1276.

Huey, R.B. 1982. Temperature, physiology, and the ecology of reptiles. *In* Biology of the Reptilia. Vol. 12. *Edited by* C. Gans and F.H. Pough. Academic Press, London, UK. pp. 25–91.

Huey, R.B., Hertz, P.E., and Sinervo, B. 2003. Behavioral drive versus behavioral inertia in evolution: a null model approach. Am. Nat. **161**: 357–366. doi:10.1086/346135. PMID:12699218.

Huey, R.B., Deutsch, C.A., Tewksbury, J.J., Vitt, L.J., Hertz, P.E., Álvarez Pérez, H.J., and Garland, T. 2009. Why tropical forest lizards are vulnerable to climate warming. Proc. R. Soc. B Biol. Sci. **276**: 1939–1948. doi:10.1098/rspb.2008.1957.

Huey, R.B., Losos, J.B., and Moritz, C. 2010. Are lizards toast? Science, **328**: 832–833. doi:10.1126/science.1190374. PMID:20466909.

Huey, R.B., Kearney, M.R., Krockenberger, A.M., Holtum, J.A., Stephen, M.J., and Williams, E. 2012. Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. Philos. Trans. R. Soc. B Biol. Sci. **367**: 1665–1679. doi:10.1098/rstb.2012.0005.

Ibargüengoytía, N.R. 2004. Prolonged cycles as a common reproductive pattern in viviparous lizards species from Patagonia, Argentina: reproductive cycles of *Phymaturus patagonicus*. J. Herpetol. **38**(1): 73–79. doi:10.1670/47-02A.

Ibargüengoytía, N.R. 2005. Field, selected body temperature and thermal tolerance of the syntopic lizards *Phymaturus patagonicus* and *Liolaemus elongatus* (Iguania: Liolaemidae). J. Arid Environ. **62**: 435–448. doi:10.1016/j.jaridenv.2005.01.008.

Ibargüengoytía, N.R. 2008. Estrategias reproductivas en reptiles. *In* Herpetolgía de Chile. *Edited by* M. Vidal and A. Labra. Science Verlag, Santiago de Chile. pp. 392–425.

Ibargüengoytía, N.R., and Casalins, L. 2007. Reproductive biology of the southernmost gecko *Homonota darwini*: convergent life history patterns among Southern Hemisphere reptiles living in harsh environments. J. Herpetol. **41**: 72–80. doi:10.1670/0022-1511(2007)41[72:RBOTSG]2.0.CO;2.

Ibargüengoytía, N.R., and Cussac, V.E. 1996. Reproductive biology of the viviparous lizard, *Liolaemus pictus* (Tropiduridae): biennial female reproductive cycle? J. Herpetol. **6**: 137–143.

Ibargüengoytía, N.R., and Cussac, V.E. 1998. Reproduction of the viviparous lizard *Liolaemus elongatus* in the highlands of Patagonia: plastic cycles in *Liolaemus* as a response to climate? Herpetol. J. **8**: 99–105.

Ibargüengoytía, N.R., and Cussac, V.E. 2002. Body temperatures of two viviparous *Liolaemus* lizard species in Patagonian rain forest and steppe. Herpetol. J. **12**: 131–134.

Ibargüengoytía, N.R., Renner, M., Boretto, J.M., Piantoni, C., and Cussac, V.E. 2007. Thermal effects on locomotion in the nocturnal gecko *Homonota darwini* (Gekkonidae). Amphib.-Reptilia, **28**: 235–246. doi:10.1163/156853807780202440.

Intergovernmental Panel on Climate Change (IPCC). 2007. Climate Change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. *Edited by* S. Solomon, D. Qin, Z. Manning, Z. Chen, and M. Marquis. Cambridge University Press, Cambridge, UK.

Kearney, M. 2013. Activity restriction and the mechanistic basis for extinctions under climate warming. Ecol. Lett. **16**: 1470–1479. doi:10.1111/ele.12192. PMID:24118740.

Kearney, M., and Porter, W.P. 2004. Mapping the fundamental niche: physiology, climate, and the distribution of nocturnal lizard. Ecology, **85**(11): 3119–3131. doi:10.1890/03-0820.

Kearney, M., Shine, R., and Porter, W.P. 2009. The potential for behavioral thermoregulation to buffer "cold-blooded" animals against climate warming. Proc. Natl. Acad. Sci. U.S.A. **106**: 3835–3840. doi:10.1073/pnas.0808913106. PMID:19234117.

Kingsolver, J.G., Woods, H.A., Buckley, L.B., Potter, K.A., MacLean, H.J., and Higgins, J.K. 2011. Complex life cycles and the responses of insects to climate change. Integr. Comp. Biol. **51**: 719–732. doi:10.1093/icb/icr015. PMID:21724617.

Kubisch, E.L. 2013. Efectos del cambio climático global en el crecimiento y aptitud de tres especies de lagartos. Ph.D. thesis, Universidad del Comahue, Argentina.

Kubisch, E.L., Piantoni, C., Williams, J., Scolaro, A., Navas, C., and Ibargüengoytía, N. 2012. Do higher temperatures increase growth in the nocturnal gecko *Homonota darwini* (Gekkota: Phyllodactylidae)? A skeletochronological assessment analyzed at temporal and geographic scales. J. Herpetol. **46**(4): 587–595. doi:10.1670/10-277.

Kun, M., Piantoni, C., Krenz, J.D., and Ibargüengoytía, N.R. 2010. Dietary analysis of *Homonota darwini* (Squamata: Gekkonidae) in northern Patagonia. Curr. Zool. **56**: 406–410.

Lamoreux, J.F., Morrison, J.C., Ricketts, T.H., Olson, D.M., Dinerstein, E., McKnight, M.W., and Shugart, H.H. 2006. Global tests of biodiversity concordance and the importance of endemism. Nature, **440**: 212–214. doi:10.1038/nature04291. PMID:16382239.

Lara-Resendiz, R.A., Gadsden, H., Rosen, P.C., Sinervo, B., and Méndez-de la Cruz, F. 2015. Thermoregulation of two sympatric species of horned lizards in the Chihuahuan Desert and their local extinction risk. J. Therm. Biol. **48**: 1–10. doi:10.1016/j.jtherbio.2014.11.010. PMID:25660624.

Leal, M., and Gunderson, A.R. 2012. Rapid change in the thermal tolerance of a tropical lizard. Am. Nat. **180**(6): 815–822. doi:10.1086/668077. PMID:23149405.

Logan, M.L., Cox, R.M., and Calsbeek, R. 2014. Natural selection on thermal performance in a novel thermal environment. Proc. Natl. Acad. Sci. U.S.A. **111**(39): 14165–14169. doi:10.1073/pnas.1404885111. PMID:25225361.

Medina, M., Scolaro, A., Méndez-De la Cruz, F., Sinervo, B., Miles, D.B., and Ibargüengoytía, N.R. 2012. Thermal biology of genus *Liolaemus*: a phylogenetic approach reveals advantages of the genus to survive climate change. J. Therm. Biol. **37**: 579–586. doi:10.1016/j.jtherbio.2012.06.006.

Meehl, G.A., Stocker, T.F., Collins, W.D., Friedlingstein, P., Gaye, T., Gregory, J.M., Kitoh, A., Knutti, R., Murphy, J.M., Noda, A., Raper, S.C.B., Watterson, I.G., Weaver, A.J., and Zhao, Z.C. 2007. Global climate projections. *In* Climate Change 2007: The Physical Science Basis Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. *Edited by* S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor, and H.L. Miller. Cambridge University Press, Cambridge, UK. pp. 747–845.

Meiri, S., Bauer, A.M., Chirio, L., Colli, G.R., Das, I., Doan, T.M., Feldman, A., Herrera, F.C., Novosolov, M., Pafilis, P., Pincheira-Donoso, D., Powney, G., Torres-Carvajal, O., Uetz, P., and Van Damme, R. 2013. Are lizards feeling the heat? A tale of ecology and evolution under two temperatures. Global Ecol. Biogeogr. **22**(7): 834–845. doi:10.1111/geb.12053.

Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P., Braslavská, O., Briede, A., Chmielewski, F., Crepinsek, Z., Curnel, Y., Dahl, A., Defila, C., Donnelly, A., Filella, Y., Jatczak, K., Mage, F., Mestre, A., Nordli, O., Peñuelas, J., Pirinen, P., Remisová, V., Scheifinger, H., Striz, M., Susnik, A., Van, Vliet, A., J.H., Wielgolaski, F., Zach, S., and Zust, A. 2006. European phenological response to climate change matches the warming pattern. Glob. Change Biol. **12**: 1969–1976. doi:10.1111/j.1365-2486.2006.01193.x.

Minoli, I., Medina, C.D., Frutos, N., Morando, M., and Avila, L.J. 2013. A revised geographical range for *Liolaemus elongatus* Koslowsky, 1896 (Squamata: Liolaemini) in Argentina: review of reported and new-data based distribution with new localities. Acta Herpetol. **8**(2): 159–162.

Moreno Azócar, D.L., Vanhooydonck, B., Bonino, M.F., Perotti, M.G., Abdala, C.S., Schulte, J.A., and Cruz, F.B. 2013. Chasing the Patagonian sun: comparative thermal biology of *Liolaemus* lizards. Oecologia, **171**(4): 773–788. doi:10.1007/s00442-012-2447-0. PMID:23011849.

Musolin, D.L., and Saulich, A.Kh. 2012. Responses of insects to the current climate changes: from physiology and behavior to range shifts. Entomol. Rev. **92**: 715–740. doi:10.1134/S0013873812070019.

Niewiarowski, P.H., and Roosenburg, W. 1993. Reciprocal transplant reveals sources of variation in growth rates of the lizard *Sceloporus undulatus.* Ecology, **74**(7): 1992–2002. doi:10.2307/1940842.

Oswald, S.A., and Arnold, J.M. 2012. Direct impacts of climatic warming on heat stress in endothermic species: seabirds as bioindicators of changing thermoregulatory constraints. Integr. Zool. **7**: 121–136. doi:10.1111/j.1749-4877.2012.00287.x. PMID:22691196.

Paranjpe, D.A., Bastiaans, E., Patten, A., Cooper, R.D., and Sinervo, B. 2013. Evidence of maternal effects on temperature preference in side-blotched lizards: implications for evolutionary response to climate change. Evol. Ecol. **3**(7): 1977–1991. doi:10.1002/ece3.614.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annu. Rev. Ecol. Evol. Syst. **37**: 637–669. doi:10.1146/annurev.ecolsys.37.091305.110100.

Partridge, L., Barrie, B., Barton, N.H., Fowler, K., and French, V. 1995. Rapid laboratory evolution of adult life-history traits in *Drosophila melanogaster* in response to temperature. Evolution, **49**(3): 538–544. doi:10.2307/2410277.

Peterson, A.T., Mitchell, J.W., Beckman, W.A., and De Witt, C.B. 2004. Detecting errors in biodiversity data based on collectors' itineraries. Bull. Br. Ornithol. Club, **124**: 143–151.

Pincheira-Donoso, D., and Nuñez, H. 2005. Las especies chilenas del género *Liolaemus* Wiegmann, 1834 (Iguania: Tropiduridae: Liolaeminae): taxonomía, sistemática y evolución. Publicación ocasional Nº 59, Museo Nacional de Historia Natural, Santiago de Chile.

Pincheira-Donoso, D., Tregenza, T., Witt, M.J., and Hodgson, D.J. 2013. The evolution of viviparity opens opportunities for lizard radiation but drives it into a climatic cul-de-sac. Global Ecol. Biogeogr. **22**: 857–867. doi:10.1111/geb.12052.

Porter, W.P., Mitchell, J.W., Beckman, W.A., and De Witt, CB . 1973. Behavioral implications of mechanistic ecology: thermal and behavioral modeling of desert ectotherms and their microenvironment. Oecologia, **13**: 1–54.

R Core Development Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from https://www.r-project.org/.

Rodríguez-Serrano, E., Navas, C.A., and Bozinovic, F. 2009. The comparative field body temperature among *Liolaemus* lizards: testing the static and the labile hypotheses. J. Therm. Biol. **34**: 306–309. doi:10.1016/j.jtherbio.2009.04.002.

Schär, C., Vidale, P.L., Lüthi, D., Frei, C., Häberli, C., Liniger, M.A., and Appenzeller, C. 2004. The role of increasing temperature variability in European summer heatwaves. Nature, **427**: 332–336. doi:10.1038/nature02300. PMID:14716318.

Schweiger, O., Settele, J., Kudrna, O., Klotz, S., and Kühn, I. 2008. Climate change can cause spatial mismatch of trophically interacting species. Ecology, **89**(12): 3472–3479. doi:10.1890/07-1748.1.

Scolaro, J.A. 2005. Reptiles Patagónicos: Sur. Una guía de campo. Universidad Nacional de la Patagonia, Argentina.

Shine, R. 2005. Life-history evolution in reptiles. Annu. Rev. Ecol. Evol. Syst. **36**: 23–46. doi:10.1146/annurev.ecolsys.36.102003.152631.

Sinervo, B., and Adolph, S.C. 1989. Thermal sensitivity of growth rate in hatchling *Sceloporus* lizards: environmental, behavioral and genetic aspects. Oecologia, **78**: 411–419. doi:10.1007/BF00379118.

Sinervo, B., Mendez-de-la-Cruz, F., Miles, D.B., Heulin, B., Bastiaans, E., Villagrán-Santa Cruz, M., Lara-Resendiz, R., Martínez-Méndez, N., Calderón-Espinosa, M.L., Meza-Lázaro, R.N., Gadsden, H., Avila, L.J., Morando, M., De la Riva, I.J., Sepulveda, P.V., Rocha, C.F.D., Ibargüengoytía, N., Puntriano, C.A., Massot, M., Lepetz, V., Oksanen, T.A., Chapple, D.G., Bauer, A.M., Branch, W.R., Clobert, J., and Sites, J.W. 2010. Erosion of lizard diversity by climate change and altered thermal niches. Science, **328**: 894–899. doi:10.1126/science.1184695. PMID:20466932.

Sinervo, B., Miles, D.B., Martínez-Méndez, N., Lara-Resendiz, R., and Mendez-de-la-Cruz, F.R. 2011. Response to Comment on "Erosion of lizard diversity by climate change and altered thermal niches". Science, **332**: 537–537. doi:10.1126/science.1195348.

Stillman, J.H. 2003. Acclimation capacity underlies susceptibility to climate change. Science, **301**: 65–65. doi:10.1126/science.1083073. PMID:12843385.

Tewksbury, J.J., Huey, R.B., and Deutsch, C.A. 2008. Putting the heat on tropical animals. Science, **320**: 1296–1297. doi:10.1126/science.1159328. PMID: 18535231.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., B.F.N., Erasmus, B.F., Ferreira de Siqueira, M., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L., and Williams, S.E. 2004. Extinction risk from climate change. Nature, **427**(6970): 145–148. doi: 10.1038/nature02121. PMID:14712274.

Tryjanowski, P., Sparks, T., Rybacki, M., and Berger, L. 2006. Is body size of the water frog *Rana esculenta* complex responding to climate change? Naturwissenschaften, **93**: 110–113. doi:10.1007/s00114-006-0085-2. PMID:16514516.

Veloso, A., and Navarro, J. 1988. Lista sistemática y distribución geográfica de anfibios y reptiles de Chile. Bolletino del Museo Regionale Scienzia Naturali, Torino, **6**: 481–539.

Vera-Escalona, I.M., Coronado, T., Muñoz Mendoza, C., and Victoriano, P.F. 2010. Distribución histórica y actual de la lagartija *Liolaemus pictus* (Dumeril and Bibron, 1837) (Liolaemidae) y nuevo límite continental sur de distribución. Gayana, **74**(2): 139–146.

Walther, G., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O., and Bairlein, F. 2002. Ecological responses to recent climate change. Nature, **416**: 389–395. doi:10.1038/416389a. PMID:11919621.

Wapstra, E., Swain, R., and O'Reilly, JM . 2001. Geographic variation in age and size at maturity in a small Australian viviparous skink. Copeia, **2001**: 646–655. doi:10.1643/0045-8511(2001)001[0646:GVIAAS]2.0.CO;2.

Weeks, D.M., and Espinoza, R.E. 2013. Lizards on ice: comparative thermal tolerances of the world's southernmost gecko. J. Therm. Biol. **38**(5): 225–232. doi:10.1016/j.jtherbio.2013.02.005.

Williams, S.E., Shoo, L.P., Isaac, J.L., Hoffmann, A.A., and Langham, G. 2008. Towards an integrated framework for assessing the vulnerability of species to climate change. PLoS Biol. **6**: 2621–2626. PMID:19108608.

Yom-Tov, Y., Yom-Tov, S., Wright, J., Thorne, C.J.R., and Du Feu, R. 2006. Recent changes in body weight and wing length among some British passerine birds. Oikos, **112**: 91–101. doi:10.1111/j.0030-1299.2006.14183.x.