Chapter 13
Effects of Acute and Chronic Environmental Disturbances on Lizards of Patagonia

Nora R. Ibargüengoytía, Erika Kubisch, Facundo Cabezas-Cartes, Jimena B. Fernández, Fernando Duran, Carla Piantoni, Marlin S. Medina, and Barry Sinervo

Abstract The extent of stress caused by acute and chronic environmental disturbances depends on the adaptive ability of organisms to behaviorally and physiologically adjust to change and on the timing and magnitude of the disturbances. This resilience is a result of numerous exposures to perturbations throughout the evolution of the species. In Patagonia, volcanic eruptions have caused larger and variable perturbations on populations and communities. The 2011 eruption of the Puyehue-Cordón Caulle volcano dispersed 100 M tons of pyroclastic material and accumulated ash layers of 30 cm. At the same time, a gradual but chronic increase in temperature, intensified by ozone depletion, affected especially taxa sensitive to thermal fluctuations. Nevertheless, species from cold temperate environments like Patagonia and the Andean mountains could benefit from warming as their body temperatures are commonly below preferred and optimum temperatures for performance. Eventually, cold temperate environments may provide refuge for northern or lowland species that while shifting their geographic ranges will potentially impact

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N. R. Ibargüengoytía (✉) · E. Kubisch · F. Cabezas-Cartes · J. B. Fernández · F. Durán
Instituto de Investigaciones en Biodiversidad y Medioambiente, Consejo Nacional de Investigaciones Científicas y Técnicas (INIBIOMA-CONICET),
San Carlos de Bariloche, Río Negro, Argentina
e-mail: norai@comahue-conicet.gob.ar; jimenafernandez@comahue-conicet.gob.ar; fernandoduran@comahue-conicet.gob.ar

C. Piantoni
Physiology Department, Bioscience Institute, University of São Paulo, São Paulo, Brazil

M. S. Medina
Centro de Investigación Esquel de Montaña y Estepa Patagónica, Consejo Nacional de Investigaciones Científicas y Técnicas (CIEMEP-CONICET), Universidad Nacional de la Patagonia San Juan Bosco, Esquel, Chubut, Argentina

B. Sinervo
Department of Ecology and Evolutionary Biology, University of California,
Santa Cruz, CA, USA

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local populations by competing for resources and transporting novel pathogens. In this chapter, we summarize studies on physiological traits of Patagonian lizards and discuss the biotic and abiotic factors involved in the evolution of these species. We integrate concepts of thermal biology, analyzing the relationship between the immune system and body temperature, and examining the thermal sensitivity and plasticity of locomotion, development, and growth rates using different geographic and temporal scales. The complex interplay of the ecophysiological strategies in Patagonian lizards is discussed based on their legacy of survival, having withstood and recovered from the extreme thermal fluctuations and catastrophic events for over ~140 Ma.

Keywords Liolaemidae · Volcanic ash · Climate Change · Lizards · Ecophysiology · Extinctions

13.1 Acute and Chronic Disturbances on Lizard Populations

Organisms respond to acute and chronic disturbances according to their resilience and to the magnitude of environmental impacts (Ruggiero and Werenkraut 2014; Mora and Labra 2017; Wild and Gienger 2018). Stressful environments can influence genotypic variability, via mutation and recombination, providing a source of new variation upon which natural selection can act, optimatizing plastic responses to environmental conditions (Hoffmann and Parsons 1997; Badyaev 2005; Wild and Gienger 2018). For example, genes controlling the expression of novel characters can be activated when the environment is stressful but downregulated under optimal environmental conditions conferring resilience to populations (Hoffmann and Parsons 1997).

Lizards from Patagonia on either side of the Andes experience interrelated acute and chronic disturbances (Boretto et al. 2014; Cabezas-Cartes et al. 2014; Ibargüengoytía et al. 2016; Mora and Labra 2017). Acute disturbances, such as volcanic eruptions and long droughts, can occur alone or in concert, affecting fire frequency in the Patagonian steppe and forests (Veblen et al. 2003). Key chronic disturbances are global warming and ozone layer depletion, both becoming more noticeable in Patagonia, particularly over the past 20 years (Barros et al. 2014). The expected increase in temperature for the coming decades will occur at twice the speed of the last 60 years, and precipitation is expected to be dramatically reduced, especially in western Patagonia (Barros et al. 2014).

However, the environmental challenges that Patagonian lizards have experienced, such as high fluctuation of temperature over the last 100 million years, suggest that many species could have a legacy of resilience that allows them to cope with these anthropogenic and natural environmental changes in diverse ways. Whereas individuals may adjust through phenotypical plasticity (Gause 1947; Bradshaw 1965; Wild and Gienger 2018) through buffer mechanisms such as modifying certain behaviors (thermoregulation), the timing for different tasks, or the diet and associated physiological processes, populations will depend on their genetic variability and capacity of adaptation to cope with change (Via and Lande 1985). However, if plasticity and adaptation are insufficient to keep pace with chronic change, organisms might instead shift, when possible, their geographic range to more suitable environments (Bonino et al. 2015, Minoli and Avila 2017, Minoli et al. 2019).

When exploring new environments is not an option, organisms must face the environmental disturbances that, at an individual level, may result in temporary but reversible ecophysiological responses (Boretto et al. 2014) involving aspects of life history (Warner and Shine 2008; Fernández et al. 2017) and potentially causing retraction and extirpation of local populations (Bestion et al. 2015). Lizards are constantly exposed to biotic (e.g., predators, competitors) and abiotic (e.g., large-scale disturbances) pressures that threaten their survival. Floods, drought, volcanic eruptions, hurricanes, and severe fires can be critical as they modify habitat and cause mortality and potentially local extinction (Lugo 2008; Elizalde 2014). In the last century, anthropogenic activities have enhanced climate change as well as the frequency in which these disturbances occur (Van Aalst 2006). In this regard, research on the effect of acute and long-term changes in the environment on organisms has become of paramount importance in biological conservation (Van Aalst 2006; Podolskiy 2009; Huang and Cheng 2013).

13.2 Effects of Volcanic Ash on Lizard Populations

In Patagonia, episodic volcanic activity has been prominent since the initial uplift of the Andes (Castro and Dingwell 2009). At present, there are many active volcanoes in the region (Dzierma and Wehrmann 2012) frequently producing pyroclastic ash during the Holocene (Singer et al. 2008; Stern 2008). Volcanic eruptions can modify entire landscapes through a diversity of geophysical disturbances including the precipitation of ash or tephra that may cover extensive areas (e.g., Mount St. Helens, >100,000 ha; Dale et al. 2005). As a consequence, in Patagonia, ashfall is not only a recurrent disturbance but also a medium- to long-term disturbance because ash remains in the environment for several years and its remobilization can be a dominant feature of posteruptive landscapes (Ayris and Delmelle 2012).

Particulate ash can have negative health effects on both animals and plants (Marske et al. 2007; Unno et al. 2014). In plants, the accumulation of ash on leaves induces damage that reduces photosynthetic activity (Seymour et al. 1983; Biondi et al. 2003; Ayris and Delmelle 2012) and, therefore, plant productivity (Tognetti et al. 2012; Chaneton et al. 2014). Also, insect-dependent plant reproduction can be negatively affected because pollinators are not able to locate flowers covered by ash (Morales et al. 2014). Insecticidal effects on herbivorous insects were also observed in the aftermath of some eruptions, which was attributed to dehydration, mechanical abrasion of cuticles, and accumulation of ash in their digestive and respiratory systems (Edwards and Schwartz 1981; Gersich and Brusven 1982; Buteler et al. 2014;

Elizalde 2014; Chaneton et al. 2014; Fernández-Arhex et al. 2013, 2015). In addition, those organisms that survive an eruption must face a radically changed environment in which much of their food is buried or covered with volcanic ash (Elizalde 2014; Fernández-Arhex et al. 2017). It has been reported that vertebrates also experience adverse effects attributable to the food shortage and difficulties in finding food in an ash-covered landscape (Wilson et al. 2011a, b; Pedersen et al. 2012).

Some Patagonian lizard populations seem to be well adapted to cope with the effects of intermittent eruptions during the last 11,500 years (Singer et al. 2008; Stern 2008). The massive eruption of the Puyehue-Cordón Caulle volcanic complex (2236 m a.s.l., 40° S; 70° W) in June of 2011 was a great opportunity to analyze the responses of lizard populations to this kind of disturbance. This particular eruption affected a considerable part of Patagonia, expelling into the atmosphere large amounts of pyroclastic material of variable particle size and texture that, due to the prevailing westerly winds, were deposited in an eastern trajectory toward the Atlantic Coast (Cremona et al. 2011; Gaitán et al. 2011). Several hundred million tons of volcanic tephra were dispersed over c. 25,000 km^2, along a west-to-east gradient (Gaitán et al. 2011) of the Argentine provinces of Neuquén, Chubut, and Río Negro and reaching areas just south of Buenos Aires (Bermudez and Delpino 2011). The locality of Ingeniero Jacobacci, in Río Negro, was one of the most affected sites (Fig. 13.1). This area is characterized by a high diversity and abundance of lizards, especially of the genus *Phymaturus* (Scolaro 2006; Perez et al. 2011; Chap. 9).

Studies of *Phymaturus* populations performed before and after the eruption were used to analyze the effect of ash deposition and relative abundance of predators on ecophysiological parameters related to fitness and survivorship, such as reproductive output (Boretto et al. 2014) and running performance of lizards (Cabezas-Cartes et al. 2014; Ibargüengoytía et al. 2016). Studies conducted during the first-year posteruption found that ash reduced sprint speed decreasing the locomotor performance of *Phymaturus excelsus* (= *P. spurcus*) (Ibargüengoytía et al. 2016) and was detrimental to locomotor performance, reproduction, and body condition of *P. spectabilis* (= *P. spurcus*) (Boretto et al. 2014; Cabezas-Cartes et al. 2014). Specifically, the negative effect on body condition was related to changes in the abundance of insects (Buteler et al. 2011; Morales et al. 2014; Fernández-Arhex et al. 2013, 2014) and food availability (Siffredi et al. 2011; Ghermandi and González 2012). However, an unexpected result showed that long-term effects of ashfall produced a decrease in the abundance of predators that feed on lizards and a decrease in herbivores that compete with lizards (Butcher 1981; Arendt et al. 1999; Dalsgaard et al. 2007). As a consequence, populations of *P. excelsus* and *P. spectabilis* (= *P. spurcus*) exhibited better body conditions and larger litter sizes in the second-year posteruption (Boretto et al. 2014; Ibargüengoytía et al. 2016; Chap. 12). The dramatic recovery of the population was probably the result of the increased availability of flowers and fruits resulting from the high mortality of livestock (i.e., sheep and goats), caused by the abrasive effects of ash on their intestines (Robles 2011; Boretto et al. 2014).

The environment can be tragically modified sometimes, but lizards seem to be resilient to this extreme impact on the ecosystem. Another example corresponds to

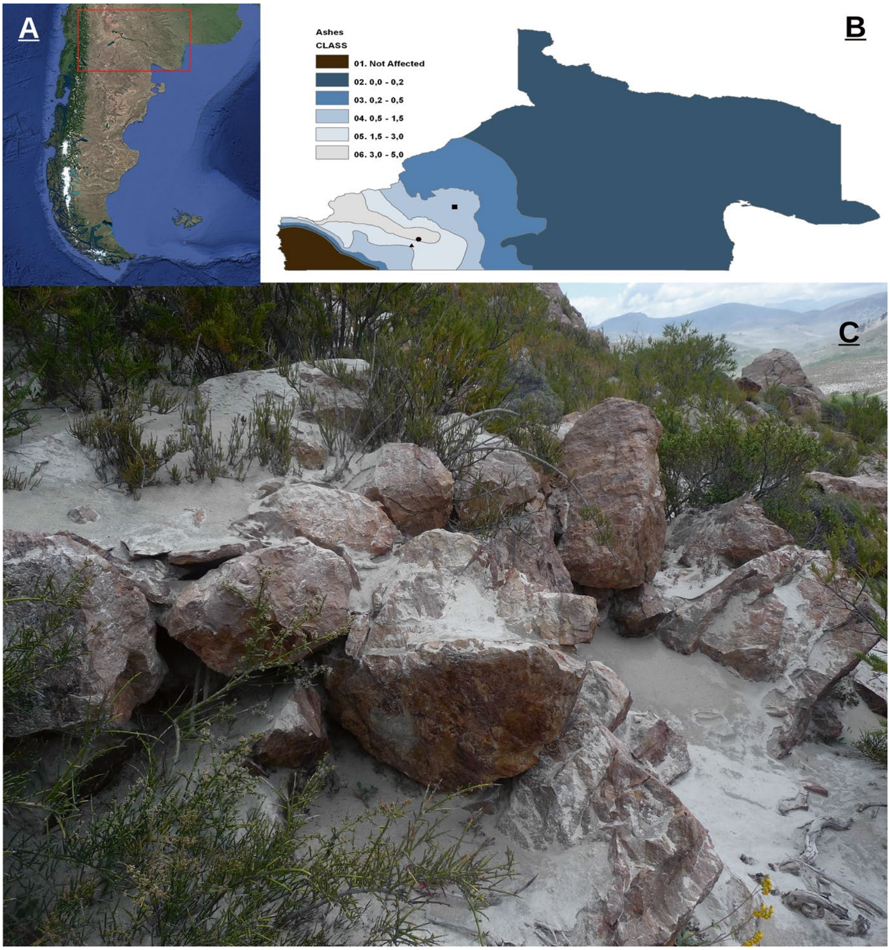


Fig. 13.1 (**a**) Relative situation of Río Negro Province in the context of Patagonia. (**b**) Map of Río Negro Province showing the amount of ash deposited (cm) in *Phymaturus* localities near Ingeniero Jacobacci (square *P. sinervoi* locality; triangle *P. excelsus* (= *P. spurcus* Barbour 1921, *sensu* Becker et al. 2019) locality; studied in Ibargüengoytía et al. 2016) and the locality of *P. spectabilis* (= *P. spurcus* Barbour 1921, *sensu* Becker et al 2019) (circle) studied by Cabezas-Cartes et al. (2014), (**c**) Photograph taken 6 months after the eruption of Puyehue-Cordón Caulle volcanic complex in the type locality of *P. spectabilis* (= *P. spurcus*)

Liolaemus lemniscatus and *L. pictus* from Chile, which seem to cope well with ash produced by volcanoes or fire. After ash deposition, lizards were able to emerge from their burrows, search for and feed on insects by following their tracks in the ash, suggesting starvation might not be the main source of immediate mortality after a disturbance (Mora and Labra 2017). In general, arthropod abundance decreased with volcanic disturbance, but the short-term effects of Cordón Caulle volcano ash on arthropod populations were according to ash grain shape, size, deposit thickness, and density in the air (Fernández-Arhex et al. 2013; Elizalde 2014). Effects were subtle on some groups like beetle assemblages protected by tree canopy in mountain forests (Ruggiero and Werenkraut 2014). Moreover, some lizard species may have been favored with the environmental changes produced by ashfall such as *Phymaturus sinervoi* that attained higher maximum sprint speeds over ash than over other substrates (Ibargüengoytía et al. 2016, probably related to their ancestral psammophilous habits; unpublished data).

13.3 Climate Change Effects on Lizards' Populations

Climate change has been noticeable in Argentina with greater temperature extremes, heat waves, and a remarkable reduction in precipitation in the Andes mountains and across most of Patagonia (Barros et al. 2014). In terms of temperature, Patagonia can be defined as a temperate or cold temperate region (Paruelo et al. 1998). Mean annual temperature ranges from 12 °C in the northeast to 3 °C in the south. However, toward the southwest, absolute minimum temperatures can reach values lower than −20 °C. In Patagonia, mean annual daily thermal amplitude varies with latitude (16 °C in north-central Río Negro Province and 5 °C in the southern extreme of Patagonia, Paruelo et al. 1998; Chap. 4). The Representative Concentration Pathway (8.5 scenario, IPCC 2014) for the next 50 years for this area estimates increases of 3.5–4 °C in annual means with the greatest change occurring in summer (Barros et al. 2014). In addition, the incremental warming rate is expected to be about five times greater than that experienced during the twentieth century (Meehl et al. 2007).

Patagonia shows a dramatic transition of environments and climate from the Andes to the Atlantic coast. The combined effects of seasonal movement, of the low- and high-pressure systems, and the ocean currents moving to an equatorial direction result in strong and prevailing westerly winds. The influence of the Pacific air masses and the topographic barrier of the Andes, parallel to the Pacific coast, results in a strong west–east gradient of precipitation (Barros et al. 1979, 2014). Most of the precipitation is discharged in the coastal mountains of Chile and on western slopes of the Andes, and the air warms and dries as it descends on the Argentine side of the Andes, an area whose mean annual rainfall ranges from 1200 mm in the northwest to 100 mm in the desert plains of southeastern Patagonia (Barros et al. 2014). The climatic trend observed during the last century, characterized by an increment in precipitation in northern Argentina and a reduction in the southwest, will be accelerated with a reduction in winter precipitation in response to increased greenhouse gas concentrations (RCP 4.5 and 8.5 scenarios, Intergovernmental Panel on Climate Change – IPCC 2014; Alexander et al. 2013; Barros et al. 2014).

Recent climate change projections led biologists to classify the threat to biodiversity at high altitudes in the Andes as severely threatened, because of the reduction in water availability due to receding glaciers, land degradation, and desertification (IPCC 2014; Barros et al. 2014). The alteration of fire regimes in the forest and steppe has an aggravated impact on the biota. In Patagonia, between 1999 and 2005, 2.7 M ha burned in 17,000 fires, with 85% of the surface affected and 82% of the fires concentrated in Río Negro province (de Torres Curth et al. 2008). Thus, the changes that are possible within accepted scenarios for Patagonia could be critical for lizard populations by directly or indirectly affecting their opportunities to move to refuges (Robinson et al. 2013), reproduce, and forage (Sinervo et al. 2010; Kearney 2013), resulting in the extirpation of some local populations (Kubisch et al. 2016a) and retractions of others (Vicenzi et al. 2017).

Nevertheless, the impact of climate change on lizards depends on extrinsic abiotic factors like temperature, thermal amplitude, precipitation, and biotic factors like predators, competitive interaction with invasive species (Mack et al. 2000), an influx of pathogens (Lafferty 2009), changes in vegetation, and food availability (Gilbert and Miler 2016). Among intrinsic factors, the physiological sensitivity and plasticity and the efficiency in thermoregulation can mitigate the impacts of climate change (Williams et al. 2008; Deutsch et al. 2008; Piantoni et al. 2016). In fact, if adaptive responses are slow relative to global warming, then changes in habitat suitability and increases in fragmentation will isolate populations and increase their vulnerability in the coming decades (Chevin et al. 2010; Huey et al. 2010; Sinervo et al. 2010; Pincheira-Donoso et al. 2013).

The general tendency shows that species are changing their distribution toward higher latitudes or altitudes (Chen et al. 2011). The cold temperate environment represents a potential thermal refuge for many lizard populations that live in warmer environments at lower latitudes and altitudes (Cabezas-Cartes et al. 2019; Piantoni et al. 2016). In northern Patagonia, *Liolaemus elongatus*, mostly known from steppe environments (Cei 1986), was observed in 1998 for the first time in the transition forest in sympatry with *L. pictus* (Ibargüengoytía and Cussac 1998), and in 2018 it was first seen at 2050 m a.s.l. in sympatry with *L. lineomaculatus* (Ibargüengoytía, unpublished data).

13.4 Immune State: Effects on Thermal Biology and Running Performance

Rapid shifts in geographic range when seeking for cooler environments may result in threats in the form of new competitors and pathogens (Cahill et al. 2012). In addition, in temperate environments, shorter and milder winters would trigger an increase in the spread of new diseases (Harvell et al. 2002). Nevertheless, the resilience of lizard populations to novel host–pathogen interactions will be governed by the interplay of immune state and the behavioral and physiological plasticity to adjust to the new challenges (Graham et al. 2011). Traits such as thermoregulation and running performance are usually linked directly to ecophysiological adaptation and can be affected by pathogens exerting selection pressures on their hosts (Graham

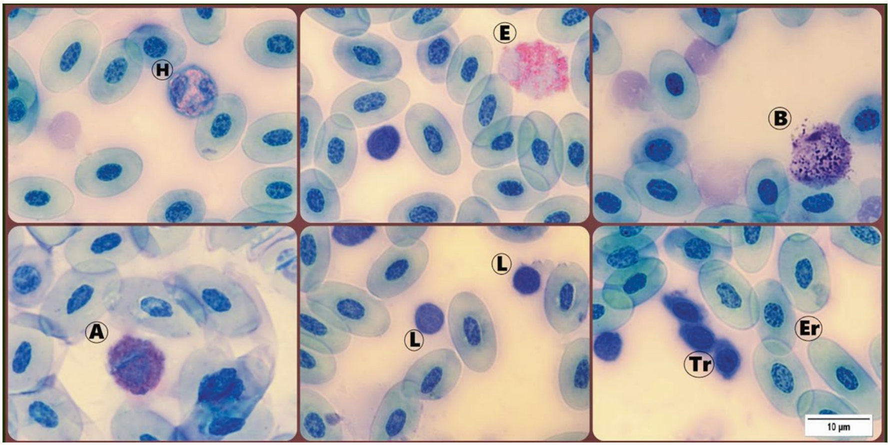


Fig. 13.2 Selected photographs of the blood cells found in *Liolaemus sarmientoi*. Leukocytes: heterophil (H), eosinophil (E), basophil (B), azurophil (A), and lymphocytes (L) erythrocytes (Er) and thrombocytes (Tr). May-Grünwald Giemsa stain. Bars = 10 µm

et al. 2011; Zamora-Camacho et al. 2014). Lizards can balance the benefit of an immune response and the cost of thermoregulation (a consequence of the effect of higher body temperatures of free-ranging lizards (T_b) on metabolic rate). This trade-off leads populations to exhibit high variability in the magnitude and efficiency of immune responses (Schmid-Hempel 2011).

In the same way, recent studies show that thermoregulation and locomotor performance of individuals of *L. sarmientoi* varied according to the leukocyte profile, suggesting a physiological adjustment to enhance the immunological response to infection, disease, or stress (Duran et al. 2019). Lizards selected high temperatures in thermal gradients in laboratory free from restriction related with temperature, predators, or social interactions (T_{pref}, sensu Hertz et al. 1993) while showing a high percentage of some leukocytes like eosinophils and basophils or a low percentage of monocytes (Fig. 13.2). In addition, Duran (unpublished data) found that individuals of *Liolaemus kingii* injected with LPS (lipopolysaccharide of the cell wall of *Escherichia coli*, treatment) thermoregulated accurately and at stable temperatures within T_{set} (interquartile of T_{pref}). Conversely, lizards injected with phosphate-buffered saline (PBS, control) showed a variable and lower T_{pref} (Fig. 13.3). These preliminary studies performed on *L. sarmientoi* and *L. kingii* suggest that lizards experiencing an immune response maintain temperatures higher than T_{pref} or within T_{set} and more stable than healthy lizards, probably to improve phagocytic activity by thermoregulation, a widespread mechanism in vertebrates (Zimmerman et al. 2010).

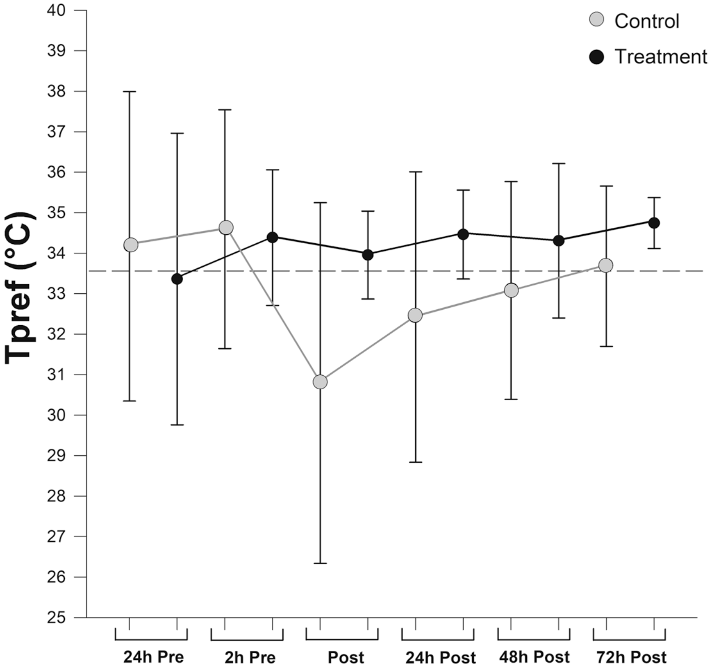


Fig. 13.3 Effects of injection on thermoregulation (T_{pref}) of two groups of adult male of *Liolaemus kingii*, from 24 h before and 72 h after injection. A group injected intraperitoneally with a saline solution as control group (PBS), free of antigens ($N = 10$, gray dots and lines), and another group injected with lipopolysaccharide of the cell wall (LPS, 2.5 μg endotoxin/g body mass), as treatment group ($N = 10$, black dots and lines). Means ± standard errors are indicated. Dashed lines indicate the mean preferred body temperature (T_{pref})

13.5 Environmental Restriction for Effectiveness of Thermoregulation

Temperature is particularly relevant because of its vital role over the biochemical and physiological functions, which affect the organism at all levels, from the rate of biochemical reactions at cellular level to whole organism physiological processes (Tattersall et al. 2012). Thus, most of physiological functions are thermally sensitive including digestion (Angilletta Jr et al. 2002), respiration (Al-Sadoon 1986, 1987), circulation (de Vera Porcell and Gonzalez 1986), locomotion (Bauwens et al. 1995), feeding (Van Damme et al. 1991), growth (Sinervo 1990; Kubisch et al. 2012; Gutiérrez et al. 2013), development (Castilla and Swallow 1996), and, hence, social behavior and reproduction (Sinervo et al. 2010; Tattersall et al. 2012). Knowledge of the body temperatures of free-ranging lizards (T_b), the preferred body temperatures using thermal gradients in laboratory (T_{pref}), and the effect of immunological states on lizard T_b-values allow us to infer how they will cope with predicted environmental changes (Paranjpe et al. 2014).

The ability of most lizards to control T_b within relatively narrow ranges through behavioral thermoregulation (De Witt 1967; Huey et al. 2003; Bartholomew 2005; Kearney et al. 2009) allows them to partially avoid or buffer increased temperatures (Kearney et al. 2009; Clusella-Trullas and Chown 2011). In this regard, it is necessary to know the operative environmental temperatures that represent the availability of thermal microenvironments for thermoregulation (T_e, Porter et al. 1973; Bakken 1992), also defined as the T_b that a non-thermoregulating lizard might experience in their natural environment (Hertz 1992). These parameters allow the calculation of the deviation of T_b of an individual from the set point range ($d_b = \sum|T_b - T_{set}|$), the mean thermal quality of a habitat from an organism's perspective ($d_e = \sum|T_e - T_{set}|$), and the effectiveness of thermoregulation in a given habitat [$E = 1 - (\text{Mean } d_b/\text{Mean } d_e)$; sensu Hertz et al. 1993]. Thus, the effectiveness of thermoregulation (E) will depend not only on the behavioral and intrinsic characteristics of the individuals but also on the heterogeneity of the thermal environments (Medina et al. 2009; Gutiérrez et al. 2010; Clusella-Trullas et al. 2011; Piantoni et al. 2016; Duran et al. 2018). Furthermore, there is a complex interplay among ecological and physiological traits that imposes limitations on thermoregulation and on the geographic distribution of the species, such as food availability, competition (Labra 1995), nesting sites, and predator abundance (Huey 1982), together with the reproductive (Medina et al. 2011) and immunological demands of the lizards (Tracy and Christian 1986).

Intraspecific comparative studies of thermal biology of *Liolaemus* populations from different latitudes and elevations (Medina et al. 2009, 2011) show that some species from the steppe maintain similar body temperatures and a common pattern of low variability in their effectiveness of thermoregulation by using different thermal microenvironments (Medina et al. 2009; Ibargüengoytía et al. 2010; Medina et al. 2011; Piantoni et al. 2016; Fig. 13.4; Table 13.1). For example, a study at two locations of three sympatric species, *Liolaemus bibronii*, *L. boulengeri*, and the viviparous *L. lineomaculatus* (Esquel 43° S 70′ W at 1400 m a.s.l.; Perito Moreno 46° S 71° W 263 m a.s.l.), shows that they compensate for the differences in the substrate and air temperatures and during cold windy conditions, they use different heat sources and exhibit differing activity timetables (Medina et al. 2011). *Liolaemus boulengeri* and *L. bibronii*, even when they are syntopic, choose different microenvironments that offer diverse challenges impelling lizards to find different behaviors for heat gain, and the populations at lower latitude of *L. bibronii*, *L. boulengeri*, and *L. lineomaculatus* are mainly heliothermic, while at higher latitude, the same species acquire heat by thigmothermy. Maintenance of similar T_bs at different latitudes suggest that lizards from colder environments at high latitude spend more time finding appropriate microenvironments for thermoregulation in detriment to other activities such as feeding and reproduction, and consequently they could be more exposed to predators (Pianka and Pianka 1970; Avery 1976; Huey and Slatkin 1976; Hertz and Huey 1981). In the same way, the southernmost lizards of the world (50–52° S), the psamophilous *L. magellanicus* and the saxicolous *L. sarmientoi*, show opportunistic thermoregulatory behavior and behave as heliotherms when air temperature is cold during the morning but gain heat from the substrates

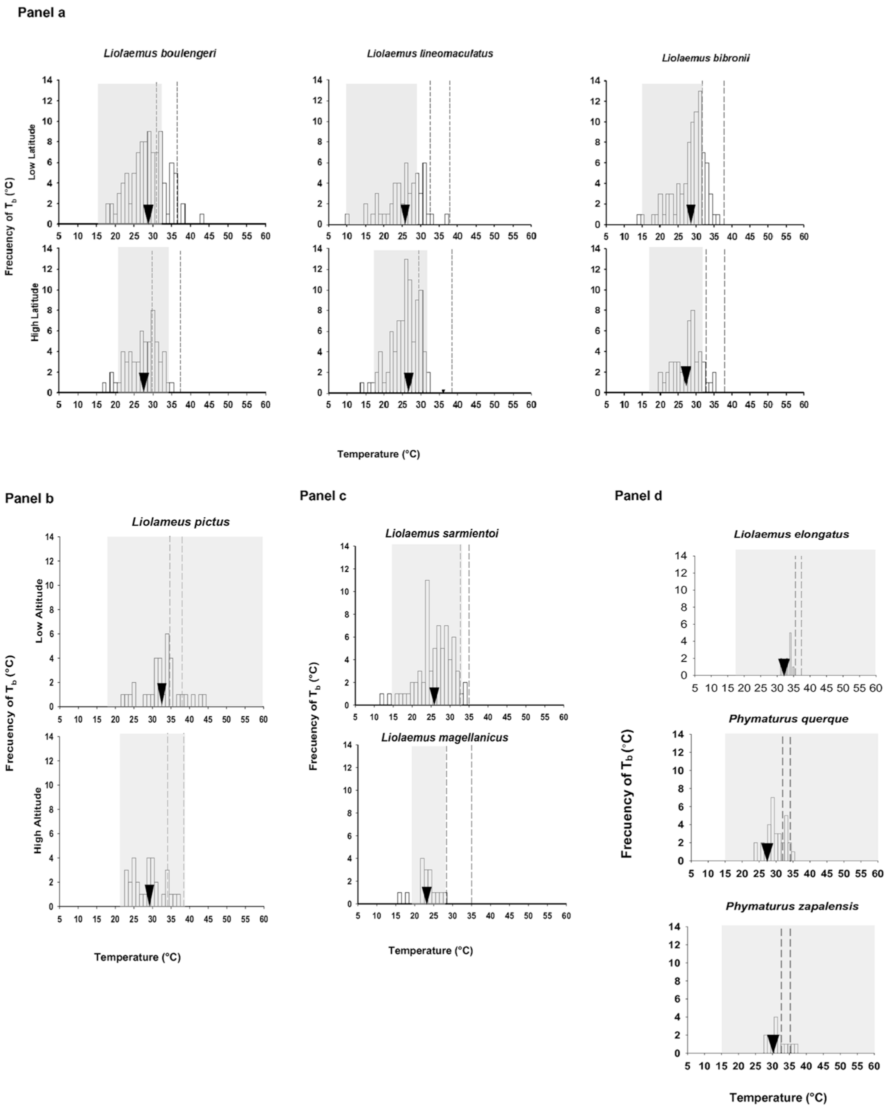


Fig. 13.4 (Panel **a**) Distribution of body temperature (T_b) of *Liolaemus boulengeri*, *L. lineomaculatus*, and *L. bibronii* at low (upper graphs) and high latitude (lower graphs) in Esquel and Perito Moreno, respectively; studied by Medina et al. (2011). (Panel **b**) Distribution of body temperature (T_b) of *L. pictus argentinus* at 771 m a.s.l. (Melipal Beach, Lake Nahuel Huapi, upper graph) and at 1615–1769 m a.s.l. (Chalhuaco Mountain, lower graph); studied by Gutiérrez et al. (2010). (Panel **c**) Distribution of body temperature (T_b) of *L. sarmientoi* (upper graph) and *L. magellanicus* (lower graph); studied by Ibargüengoytía et al. (2010). (Panel **d**) Distribution of body temperature (T_b) of *L. elongatus*, *Phymaturus querque* and *P. zapalensis* from 39° S latitude and 824–1312 m a.s.l.; studied by Duran et al. (2018). The gray area indicates range of operative temperatures (T_e) at capture; the dashed lines indicate the lower and upper set points of the preferred body temperature (T_{set}), and the black triangles indicate the mean T_b

Table 13.1 Descriptive data of individual deviation of T_b from T_{set} (d_b), the index of the average thermal quality of a habitat from an organism's perspective (d_e), and the effectiveness of temperature regulation (E), for *Liolaemus* and *Phymaturus* of Patagonia

	d_b	d_e	E
Liolaemus bibronii			
Low latitude (43°S 70°W, 626 m a.s.l.)	4.7 ± 0.7 (46)	8.42	0.44
High latitude (46°S 71°W, 263 m a.s.l.)	5.9 ± 0.7 (47)	10.87	0.45
Liolaemus boulengeri			
Low latitude (43°S 70°W, 626 m a.s.l.)	3.3 ± 0.5 (44)	8.2	0.59
High latitude (46°S 71°W, 263 m a.s.l.)	3.1 ± 0.5 (46)	6.2	0.5
Liolaemus lineomaculatus			
Low latitude (42°S 71°W, 1400 m a.s.l.)	6.9 ± 0.8 (53)	12.6	0.45
High latitude (46°S 71°W, 263 m a.s.l.)	4.5 ± 0.4 (73)	7.7	0.41
Liolaemus pictus argentinus			
Low altitude (41°S 71°W, 771 m a.s.l.)	5.6 ± 0.8 (27)	9.47	−0.24
High altitude (41°S 71°W, 1700 m a.s.l.)	6.5 ± 1.0 (30)	5.20	0.4
Liolaemus sarmientoi			
50°S 72°W, 980 m a.s.l.	6.8 ± 0.6 (53)	9.9 ± 0.5	0.30
Liolaemus magellanicus			
51°S 70°W, 133 m a.s.l.	5.4 ± 1.3 (36)	5.15 ± 1.85	−0.04
Liolaemus elongatus			
39°S 70°W, 824–1312 m a.s.l.	2.29 ± 0.51 (10)	6.95 ± 1.45	0.67
Phymaturus querque			
39°S 70°W, 824–1312 m a.s.l.	4.97 ± 0.50 (32)	8.89 ± 0.70	0.44
Phymaturus zapalensis			
39°S 70°W, 824–1312 m a.s.l.	3.28 ± 0.70 (14)	6.21 ± 1.12	0.47

Mean ± standard error and sample size (N)

(thigmothermy) during the early afternoon, when rocks and soil have warmed up (Ibargüengoytía et al. 2010).

Another comparative study yielded different results. Observation of two populations of *L. p. argentinus* at different elevations (771 and 1700 m a.s.l.) in northwestern Patagonia, Argentina (41° S 71° W), shows that both environments impose strong effects on the efficiency of thermoregulation displayed by lizards. *Liolaemus pictus argentinus* is a viviparous and insectivorous species with a wide distribution in the Patagonian Andes of Neuquén, Río Negro, and Chubut provinces of Argentina (39–43° S and 520–1600 m a.s.l., Cei 1986; Scolaro 2005). The high-elevation population inhabits the shady understory of a closed forest dominated by *Austrocedrus* and *Nothofagus* near the summit of Chalhuaco Mountain and attains only a low mean T_b (29 °C). At the low-altitude site, *L. p. argentinus* lives by the lakeshore in a rocky microenvironment with greater exposure to sunlight. These lizards attain a higher T_b (33 °C) probably because they can bask and be active during longer periods taking advantage of thermal inertia of the rocky substrate (Gutiérrez et al. 2010). In the high-altitude environment, the forest challenges thermoregulatory ability (high d_e), and lizards behave as moderate efficient thermoregulators ($E = 0.4$). Meanwhile, lizards in the low-latitude site showed an E-value of −0.24, suggesting that even microenvironments available in the range of their T_{set} are not selected. This anomaly likely occurs because of non-energetic factors such as disturbances by people on the public beach, predators hunting for lizards basking in the open, or concentrations of food in habitat patches otherwise unsuitable for thermoregulation.

The capacity to reach and maintain body temperatures within a range that allows activity and optimizes physiological performance depends not only on the availability of suitable microhabitats for thermoregulation but also on the spatial arrangement of the thermal resources (Sears et al. 2016). *Phymaturus* lizards are robust rock dwellers with flattened bodies that can shelter in small rock crevices where they spend most of their time (Cei 1986, 1993). *Phymaturus* are conservative in many aspects of their biology, being predominantly herbivorous, viviparous, and saxicolous (Cei 1986, 1993; Espinoza et al. 2004; Ibargüengoytía 2005; O'Grady et al. 2005; Boretto and Ibargüengoytía 2006, 2009). In the same way, it has been demonstrated that the thermal biology of *Phymaturus* is remarkably similar across a wide geographic range suggesting that it may be evolutionarily or ecologically constrained (Ibargüengoytía et al. 2008; Cruz et al. 2009) probably because of their low vagility and the similarity in their habitat (Debandi et al. 2012). In this regard, a comparative study of two sympatric species showed that *Phymaturus querque* ($E = 0.44$) and *P. zapalensis* ($E = 0.47$) behave as moderately efficient thermoregulators and specialists using narrow and deep cracks in the rocks as shelters. It is noteworthy that the two syntopic species selected thermal microenvironments colder than their T_{pref} during summer although warm microenvironments were available, probably to avoid overheating (Duran et al. 2018; Fig. 13.4, panel C). On the other hand, a population of *Phymaturus tenebrosus* from southwestern Río Negro behaves as a poor thermoregulator presenting the lowest E of all *Phymaturus* ($E = 0.19$) and also present operative temperatures lower than their optimal temperatures for locomotion (Cabezas-Cartes et al. 2019). As a result, the rising temperatures related to global climate change would favor the thermal physiology and locomotor performance of this species, possibly favoring its survival to global warming (Cabezas-Cartes et al. 2019).

Thermoregulatory behavior typically increases with latitude and altitude (except for the two southernmost liolaemids, *L. sarmientoi* and *L. magellanicus*, at 51° S) and that tropical and lowland lizards generally behave as thermoconformers (e.g., genera *Anolis* and *Tropidurus*; Piantoni et al. 2016), suggesting that species from lower latitudes and altitudes are more vulnerable to warming than temperate climate species (Huey et al. 2009; Piantoni et al. 2016). In tropical environments, the large proportions of individuals with T_b and T_e that exceed the population's T_{set}, together with the thermoconformity or poor thermoregulatory capacities, represent a risk of overheating and could restrict the hours of activity (Sinervo et al. 2010; Medina et al. 2016). In contrast with the tropics, lizards from Patagonia are characterized by having T_{pref} values much higher than the T_b and T_e, pointing out that in temperate environments, lizards face a greater challenge to raise body temperatures (Fuentes and Jaksic 1979; Medina et al. 2009, 2011; Ibargüengoytía et al. 2010; Piantoni et al. 2016; Cabezas-Cartes et al. 2019). Thus, it is expected that temperate-zone populations may experience improved thermal conditions during global warming by having more thermoregulatory opportunities to improve their physiological performance (Ibargüengoytía et al. 2010; Fernández et al. 2011, 2017; Duran et al. 2019, also see Paranjpe et al. 2014; Cabezas-Cartes et al. 2019).

13.6 Prediction of Population Extirpations and Changes in the Distribution Ranges Due to Global Warming

The high and conservative T_{pref} observed in most liolaemids (Labra 1998; Ibargüengoytía 2005; Rodriguez-Serrano et al. 2009; Ibargüengoytía et al. 2010; Moreno-Azócar et al. 2013; Medina et al. 2012) suggest that warming could be neutral or beneficial to many populations (Piantoni et al. 2016). Nevertheless, local extirpations of liolaemids have been already observed from 1975 to 2010, including at least three populations in South America. Affected species include *Liolaemus lutzae*, *L. fittkaui*, and *Phymaturus tenebrosus* (Sinervo et al. 2010). Sinervo et al. (2010) showed that one of the main mechanisms that could drive lizard populations to extinction is the increase in the hours of restriction (H_{r}), considered to be the daily time span lizards stay sheltered due to temperatures exceeding their thermal preferences (Sinervo et al. 2010; Kubisch et al. 2016a; Vicenzi et al. 2017). The physiological limit to which a species is adapted is reflected by the most extreme hours of restriction observed across the species range (e.g., at the warm temperature limit) during the breeding season. When the local hours of restriction climb above this value, local extinction and extirpation is predicted because the retreat into cooler shelters has detrimental effects on sociality, feeding, and reproduction (Sinervo et al. 2010).

For lizards of Patagonia, Kubisch et al. (2016a) estimated the current and future H_{r} under a global warming scenario for three species and predicted the proportion of populations to be extirpated by 2080 as 20% in the nocturnal gecko *Homonota darwinii*, 15% in *L. pictus*, and 26% in *L. elongatus*. In addition, a species distribution model performed for 14 Patagonian species, corresponding to three *Liolaemus* clades, predicted that future range boundaries would shift toward higher altitudes and latitudes (Bonino et al. 2015). Most of these species (*L. coeruleus*, *L. petrophilus*, *L. kriegi*, *L. escarchadosi*, *L. hatcheri*, *L. lineomaculatus*, *L. sarmientoi*, and *L. baguali*) may suffer a decrease in the size of their geographic range and may be seriously affected. But four of these species (*L. fitzingerii*, *L. xanthoviridis*, *L. boulengeri*, and *L. elongatus*) may increase their range with suitable climatic conditions (Bonino et al. 2015). However, this increase of area and expansion of the species distribution is not ensured, mainly because of their limited dispersal ability and geographic barriers. Case in point, *Phymaturus palluma*, an endemic lizard from the Central Andes, is expected to experience reductions in the number of suitable microhabitats in its current range, and, although such microhabitats may increase in availability in areas to the south and west, they may not be able to get there because of an inhospitable habitat matrix in between (Vicenzi et al. 2017). Whether lizards can move toward more suitable habitat patches will depend on their vagility, plasticity in behavioral habitat selection, and the presence of habitat continuity or corridors (Buckley et al. 2013). For example, the high degree of morphological and physiological specialization of *Phymaturus* species that occupy isolated rock promontories in the steppe, the rapid environmental change rate as the product of global warming, and the fact that much of the intervening lands are modified for agriculture or ranching (Feeley and Silman 2010) prevent dispersion of these species to more suitable areas (e.g., *P. palluma*, Vicenzi et al. 2017).

13.7 Performance and Physiological Plasticity

The trade-offs among thermal biology, performance, and ecology are shaped by intrinsic factors (genetic and epigenetics) and extrinsic pressures imposed by biotic (predators, food resources, competition) and abiotic (temperature, relative humidity). This complex interplay will determine whether lizards need to maximize performance in one function over another trait in nature (Huey and Stevenson 1979), and this system can vary temporally (seasonally), geographically (latitude, elevation), during ontogeny, or according to reproductive demands (adult vs juvenile, pregnant vs nonpregnant, Fernández et al. 2017). Individuals can select optimal temperatures that maximize some physiological functions, in detriment of having suboptimal temperatures for other functions (Huey and Stevenson 1979).

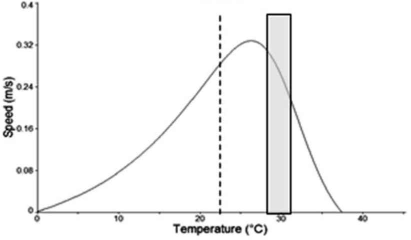
The knowledge of optimal temperatures for running performance combined with the temperature that lizards experience in their environment (T_b) allows the inference of how close species are to their thermal limits in nature and is essential to predict potential responses to a changing climate (Huey and Kingsolver 1989, 1993; Tattersall et al. 2012). In ectotherms the speed of locomotion depends on several factors like morphology (Irschick et al. 2005; Kubisch et al. 2011), reproductive status (Sinervo et al. 1991; Kubisch et al. 2011), sex (Irschick et al. 2005), substrate (Tulli et al. 2012; Cabezas-Cartes et al. 2014), habitat use (Irschick et al. 2005), the time of the day (Ibargüengoytía et al. 2007), and immune state (Paranjpe et al. 2014; Duran et al. 2019), among others. The most influential variable affecting running performance is temperature (Angilletta Jr et al. 2002; Tattersall et al. 2012). Thermal performance curves (Huey and Stevenson 1979) extend within the thermal critical minimum (CT_{min}) and the thermal critical maximum (CT_{max}) limits (i.e., where performance equals zero). From CT_{min}, lizards' locomotor performance increases and reaches a peak (i.e., maximum speed) at the optimal body temperature (T_o), and then decreases rapidly as temperature approaches CT_{max} (Huey and Stevenson 1979; Hertz et al. 1983; Huey and Bennett 1987; Angilletta Jr et al. 2002). The performance breadth corresponds to the range of temperatures over which an animal performs at a selected proportion of their maximal performance (e.g., 80% or 95%, Angilletta Jr et al. 2002; Tattersall et al. 2012; Huey et al. 2012). In the austral *Liolaemus*, the T_o for running performance is higher than the body temperature they can achieve in their natural environments (Bonino et al. 2011; Fernández et al. 2011; Fig. 13.5). Displacement to colder environments of these austral species in the past could have led to lower locomotor capacities, possibly mitigated only in part by subsequent adaptation (Fernández et al. 2011). Therefore, it is expected that an increase in temperature would favor performance of many lizard cold temperate populations (Fernández et al. 2011; Cabezas-Cartes et al. 2019).

For example, for the southernmost species, *L. sarmientoi*, and especially for *L. magellanicus*, there is a great difference between thermal optima for locomotor performance and body temperature that lizards can achieve by thermoregulation in nature (Fernández et al. 2011; Fig. 13.5d, e). These lizards presented the lowest body temperatures obtained for the genus *Liolaemus* (27 °C, Jaksic and Schwenk 1983; 23–26 °C, Ibargüengoytía et al. 2010), but the T_{pref} values obtained in the laboratory for both species (32–34 °C, Ibargüengoytía et al. 2010) were similar to those of congeners (Labra 1998; Medina et al. 2009). The same pattern was observed in the southernmost nocturnal gecko *Homonota darwinii* (Ibargüengoytía et al. 2007; Fig. 13.5a), the saxicolous *L. elongatus* (Kubisch et al., unpublished data; Fig. 13.5c), and *Phymaturus tenebrosus* (Cabezas-Cartes et al. 2019). However, in the north of Patagonia, *L. pictus argentinus* shows average body temperatures in the field higher than the T_o ($T_b = 32$ °C, $T_o = 26$ °C, Kubisch et al. 2016b). Thus, *L. pictus* seems to be the most vulnerable as its capacity to disperse, forage, and perform social activities is expected to be affected under an increment of environmental temperature (Kubisch et al. 2016b). In addition, the thermal safety margin (TSM) for physiological performance of *L. pictus* ($T_o -$ mean T_e, sensu Deutsch et al. 2008; Logan et al. 2013) was 0.43 °C in long runs and 0.64 °C in sprint runs suggesting that the environmental temperatures are already close to the physiological optimal temperature in this species (Kubisch et al. 2016b). It is noteworthy that the TSM in *L. pictus* was lower than in four tropical species of *Anolis* (TSM ranging from 1.5 to 5.5 °C, Logan et al. 2013). Nevertheless, *L. pictus* can run at 80% or more of its V_{max} around a wide range of temperatures close to T_o ($B_{80} = 17$ °C, Fig. 13.6), and the warming tolerance (WT = mean $T_e - CT_{max}$, sensu Deutsch et al. 2008, Logan et al. 2013) is much higher than those found for four tropical *Anolis* species (WT = 3.1 − 7.8 °C, Logan et al. 2013). The high WT in *L. pictus* (WT = 17.71 °C, Kubisch et al. 2016b) shows that this species could attenuate the impact of global warming on performance even though they show a very low TSM (Fig. 13.6).

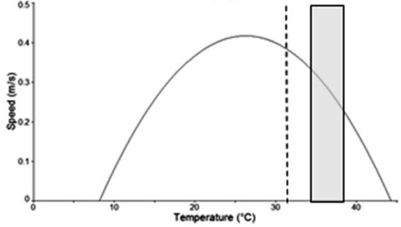
In addition, it is expected that lizards, when possible, select temperatures that maximize physiological performance (T_{pref} near the T_o). A review (Martin and Huey 2008) of 63 species from the northern hemisphere showed T_o is often above T_{pref}. In Patagonian lizards, the same was found in *L. elongatus* (Kubisch et al., unpublished data; Fig. 13.5c), *L. kolengh*, and *L. hatcheri* (Bonino et al. 2011). Nevertheless, other studies of lizards of Patagonia showed that their optimal temperatures for maximum locomotor performance are near or below the lowest T_{set}, as is the case for *Homonota darwinii* (Ibargüengoytía et al. 2007; Aguilar and Cruz 2010; Fig. 13.5a),

Fig. 13.5 Estimated performance curves of the relationship between speed and body temperature in five species of Patagonian lizards from northern to southern latitude: (**a**) *Homonota darwinii*, (**b**) *Liolaemus pictus*, (**c**) *L. elongatus*, (**d**) *L. sarmientoi*, and (**e**) *L. magellanicus*. Vertical dashed line indicates the mean field body temperature. The gray rectangle indicates the set point range of preferred temperatures

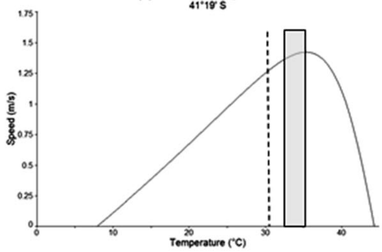
(a) Homonota darwini
41°05′ S



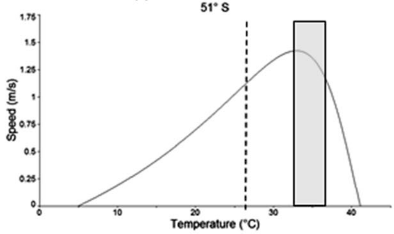
(b) Liolaemus pictus
41°07′ S



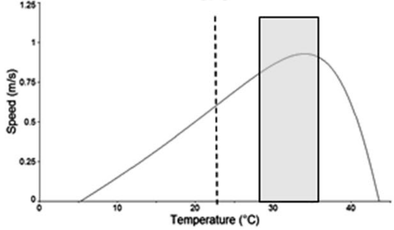
(c) Liolaemus elongatus
41°19′ S



(d) Liolaemus sarmientoi
51° S



(e) Liolaemus magellanicus
51° S



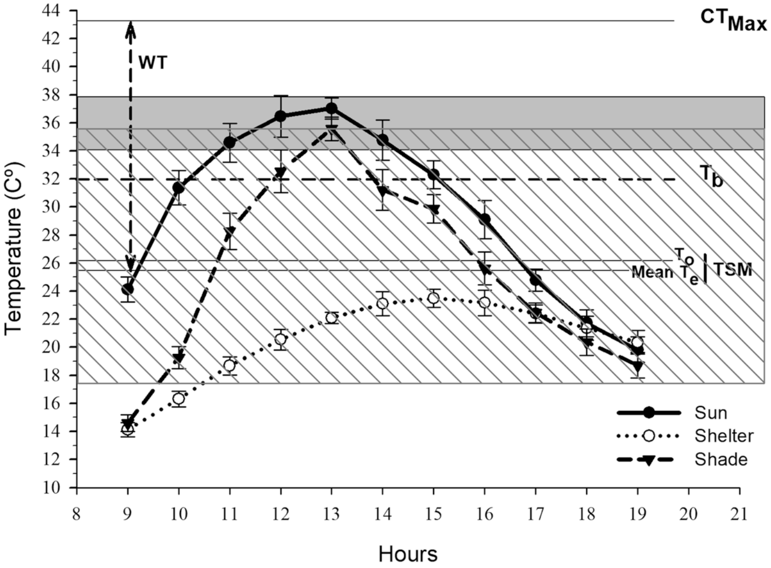


Fig. 13.6 Operative temperature (mean ± standard error) every hour during activity span, obtained from plastic models placed in different thermal microenvironments. The mean operative temperature (T_e), the critical thermal maximum (CT_{Max}), the mean body temperature in field (T_b), and the optimal performance temperature (T_o) of *Liolaemus pictus* are indicated with horizontal lines. The warming tolerance (WT) and the thermal safety margin for physiological performance (TSM) are indicated with arrows. The gray rectangle represents the set point range of the preferred body temperature in laboratory that corresponds to the 25 and 75% quartiles. The rectangle with diagonal stripes corresponds to the thermal performance breadth (B_{80} = range of body temperature over which the lizard can run at 80% or faster of its maximum speed)

L. sarmientoi (Fernández et al. 2011; Fernández, unpublished data; Fig. 13.5d), *Liolaemus pictus* (Kubisch et al. 2016b; Fig. 13.5b), *L. baguali*, *L. escachardosi*, *L. gallardoi*, *L. kingii*, *L. lineomaculatus*, and *L. zullyi* (Bonino et al. 2011). For the southernmost reptile, *Liolaemus magellanicus*, the T_o is included in their set point range of preferred temperatures (Fernández et al. 2011; Fernández, unpublished data; Fig. 13.5e) even though they are very unlikely to find in nature.

However, the thermal performance curve can vary as an individual acclimates to the temperature and time of exposure in a particular environment (Somero 2010; Tattersall et al. 2012), and this physiological plasticity allows ectotherms to exploit novel environments (Huey and Kingsolver 1989, 1993). The changes in the performance curves are considered acclimatization if they occur by natural changes in the environment, but they are called acclimation if they are consequence of manipulation in the laboratory (Huey et al. 2012). Acclimation capacity of thermal physiology in lizards (Paranjpe et al. 2013) can potentially ameliorate projected extinctions due to climate change by upward of 10% (Sinervo et al. 2018). The "beneficial acclimation assumption" postulates that physiological plasticity confers advantages to the organism and should elicit a change in the phenotype that improves performance in the new environment (Leroi et al. 1994).

Although physiological plasticity is expected to occur mainly in higher-latitude species because their environments have greater seasonal amplitude (Stillman 2003), several Patagonian lizards like *Liolaemus sarmientoi*, *L. pictus*, *L. elongatus*, and *Homonota darwinii* show low plasticity in their performance variables during acclimation (Aguilar and Cruz 2010; Fernández and Ibargüengoytía 2012; Kubisch 2013; Kubisch et al. 2016b). *Liolaemus pictus* and *L. elongatus* showed limited plasticity in some physiological variables like the T_{pref}, the panting threshold (T_{panting}; the body temperature at which the individual opens its mouth to lose heat by evaporation; Kubisch et al. 2011), and the critical minimum temperature ($\mathrm{CT}_{\mathrm{min}}$; the body temperature at which the individual is no longer able to right itself when placed on its back) when lizards were acclimated to low temperatures (21 °C in *L. p. argentinus* and 22 °C in *L. elongatus*) or high temperatures (31 °C in *L. p. argentinus* and 30 °C in *L. elongatus*, Kubisch 2013; Kubisch et al. 2016b). The only case of plasticity reported for *Liolaemus*, which involves *L. pictus pictus* from Chile (Artacho et al. 2017), found plastic responses in T_{pref} among three populations acclimated at different temperatures.

Regarding running speed, Aguilar and Cruz (2010) also suggest a low acclimation capacity in *Homonota darwinii*, since they did not find maximum speed differences among groups acclimated to temperatures ranging from 18 to 33 °C. In *L. sarmientoi*, acclimation to a higher temperature (21 °C, higher than their mean natural environmental temperature during their activity period) resulted in a decrease in running speed (Fernández and Ibargüengoytía 2012), while in *L. pictus* and *L. elongatus*, the different acclimation temperatures (21 °C and 31 °C for *L. pictus* and 22 °C and 30 °C for *L. elongatus*) did not affect locomotor performance (Kubisch 2013; Kubisch et al. 2016b). The same pattern of limited acclimation plasticity exhibited by *H. darwinii*, *L. sarmientoi*, *L. pictus*, and *L. elongatus* was observed in the desert night lizard (*Xantusia vigilis*) to either 20 °C or 30 °C (Kaufmann and Bennett 1989), and this phenomenon has been seen in amphibians after metamorphosis (Wilson and Franklin 2000; Marvin 2003). Therefore, organisms experiencing a rapid increase in environmental temperature due to climate change may not be significantly plastic in their ability to behaviorally compensate their locomotor performance, which could influence directly their ability to escape from predators, forage, or do social activities. But *L. elongatus* showed partial acclimation in long runs, since the test group acclimated at 30 °C ran faster than that acclimated to 22 °C when run at 40 °C (Kubisch 2013). This result is congruent with the "beneficial acclimation assumption." In this way, *L. elongatus* could dampen the effects of global warming in long runs.

13.8 Embryo Survivorship and Newborn Fitness

Environmental temperature also exerts a powerful effect on physiology during the embryonic development in reptiles. Reptile phenotypes are thus significantly plastic, and therefore they are a good biological model for the study of environmental effects on their life history strategies (Adolph and Porter 1993; Shine 1995; Elphick and Shine 1998; Shine and Elphick 2001; Lourdais et al. 2004; Cadby et al. 2014). Constraints on time of activity during the breeding season may affect the reproductive output and cause local extinctions (Sinervo et al. 2010, 2011; Kubisch et al. 2016a; Vicenzi et al. 2017). This mechanism occurs because embryos and juvenile lizards are particularly vulnerable to both acute and chronic disturbances at high temperatures, since they have lower thermal tolerance ranges than adults and lower thermal inertia (Buckley and Huey 2016). A chronic increase of temperature in early stages of ontogeny can influence the locomotor performance and behavior patterns that persist over time, affecting the biological adaptation of the species (Aidam et al. 2013; Angilletta Jr et al. 2013; Buckley and Huey 2016). For this reason, in particular, Pincheira-Donoso et al. (2013) predict that viviparous *Liolaemus* that inhabit temperate cold climates of the Andes are the most prone to suffer extirpations or major extinctions in the next half century, because viviparity evolved in the genus in cold climate environments and is probably adaptively restricted to such environments.

However, as mentioned above, in the austral and viviparous species *L. sarmientoi* (from 51° S), the T_e and T_b were much lower than their T_{set}, but the T_o for both short and long runs was within their T_{set} (Fernández et al. 2011; Fernández, unpublished data; Fig. 13.5d). Furthermore, recent studies show that the T_{pref} for pregnant *L. sarmientoi* females provides an optimal environment for embryo development in this viviparous lizard (Fernández et al. 2017). The T_b values that pregnant females attain by thermoregulation in a thermal gradient (T_{pref}) enhances offspring traits related to fitness, such as shorter gestation period, locomotor performance, and body condition, in contrast with the temperatures they would be exposed to if oviparous. In females exposed to temperatures that simulated natural environments for a potential nest, it was observed that their reproductive success decreases drastically and they produced low-quality offspring (Fernández et al. 2017). Similar results were found for other species such as the phrynosomatid lizard *Sceloporus virgatus* (Qualls and Andrews 1999) and in the soft-shelled turtle *Pelodiscus sinensis* (Du and Ji 2003). In addition, pregnant females of *L. sarmientoi* thermoregulate differently than nonpregnant females and achieve higher and more stable body temperatures compared to environmental temperatures suggesting that they precisely thermoregulate to promote successful embryonic development (Fernández et al. 2017).

Pregnant females also reduce their risk of predation and optimize energy expenditure (Lin et al. 2008; Fernández personal observation). If the variability of the T_{pref} tends to be lower in pregnant than in nonpregnant females, the optimum temperature range for embryonic development is also narrow, avoiding potentially lethal limits for embryos (Webb et al. 2006). In this way, when females reach optimum thermal levels for development, they maximize the benefits with relatively low reproductive costs (Wang and Dillon 2014). These results point out that this austral species is not well adapted in relation to the running ability and offspring development (Fernández et al. 2017). These results, in contrast with predictions of Pincheira-Donoso et al. (2013), show that at least some populations of viviparous liolaemids could benefit from higher environmental temperatures and therefore bear a lower risk of local extinction (Fernández et al. 2011, 2017).

13.9 Effects of Climate Change on Growth Rates, Age at Sexual Maturity, and Longevity

It has been demonstrated that increased climatic temperature can affect several life history traits such as clutch size (Winkler et al. 2002), fecundity (Barbraud and Weimerskirch 2001; Sanz et al. 2003), growth rates, and survival (Bestion et al. 2015). However, global warming effects might be reduced or mitigated in species with shorter generation times that would allow faster adaptation. Accelerated rates of warming would curtail such adaptive change. In contrast, in species with long generation times like some Patagonian lizards, the rate of temperature change may be too fast for lizard populations to cope with. Indeed, the *Phymaturus* and *Liolaemus* species of Patagonia studied so far exhibit delayed sexual maturity (3–9 years, Gutiérrez et al. 2013; Cabezas-Cartes 2016) and long life spans (7–16 years, Gutiérrez et al. 2013; Cabezas-Cartes 2016). In addition, all these species have mean reproductive outputs that are among the lowest in lizards (Chap. 12). These life history traits yield long generation times, which limits the rate of evolutionary change in these species. As a result, populations of Patagonia would be less able to adapt to the rapid increase in temperature as a consequence of global warming and more likely to become extinct in a short- or medium term (Sinervo et al. 2010; Kubisch et al. 2012).

The lizards living in temperate climates have cyclic seasonal growth, with rapid growth during the period of activity and an arrest of growth during brumation (Boretto et al. 2018). This is recorded in the long bones of lizards as annual growth rings that appear as broad layers (fast growth), concentric, and adjacent to narrower layers (slow growth). Through the histological examination of these patterns (skeletochronology), it is possible to estimate the individual age, longevity, age at sexual maturity, and age-specific growth rate (Saint Girons et al. 1989; Castanet and Báez 1991; Piantoni et al. 2006; Gutiérrez et al. 2013; Boretto et al. 2015; Cabezas-Cartes et al. 2015; Chap. 12). Furthermore, when longevity and age at sexual maturity are analyzed together with other characteristics, like clutch size and reproductive cycles, it is possible to make inferences about fecundity and the evolution of life history tactics in cold and warm environments (Piantoni et al. 2006; Chap. 12).

Preserved museum specimens were analyzed using skeletochronology by Kubisch et al. (2012) in order to understand how increased environmental temperature may affect populations, comparing individual growth rates, longevity, age at sexual maturity, and reproductive output from specimens obtained in 1941 and 2010 from two sites, one warmer continental site and one cooler and more coastal. Their results suggest that, under a scenario of global warming, the nocturnal gecko *H. darwinii* would not exhibit a negative fitness response but would increase growth rates and reproductive output, as was shown by the difference between the 1941 and 2010 samples at both sites. The effects of climate change over this 69-year time frame are still negligible when compared with the present-day continental-to-coastal differences in temperature, that is, those related to the proximity to the Andes vs. the coastal location. However, the three populations reached adult size at a minimum age of 3 years, but the maximum life span at the warm site was up to 9 years in the 1941 sample but only 5 years in the 2010 sample (Kubisch et al. 2012). These results corroborate the findings of Bestion et al. (2015) showing that warmer climate can be detrimental for the survival of older individuals and that the annual survival of adults and yearlings was lower in warm-climate environments (Bestion et al. 2015).

13.10 Conclusions

The origin of the family Liolaemidae dates from ~62 Ma (Townsend et al. 2011) and has passed through climatic and geological events resulting in acute and chronic disturbances for this clade. For example, reconstruction of the Pleistocene versus Eocene temperature regimes indicates that the family Liolaemidae has experienced long-term mean temperatures 6 °C lower than and up to 14 °C greater than recent relative means (1960–1990, IPCC 2014). Nevertheless, they may experience a greater increasing temperature rate (up to 7 °C higher than average) in the next 80 years that could drive several populations to extinction. In particular, if we consider the slow-lane lifestyle of Patagonian lizards (Boretto et al. 2018), we expect them to have less opportunity to adapt to rapid environmental changes. In Patagonia the family Liolaemidae is represented by the genera *Phymaturus* and *Liolaemus* (Donoso-Barros 1966; Cei 1986; Pincheira-Donoso et al. 2008), and the most extensive radiation in the family occurred in the genus *Liolaemus*, most probably boosted by a series of episodes of Andean uplift during the last ~25 Ma (Pincheira-Donoso et al. 2015). The Andes became a barrier to atmospheric circulation, changing the patterns of precipitation and seasonal heating, and was the main cause of the global cooling trend observed since the Eocene (Gregory-Wodzicki 2000). Since the Andean uplift, there has been a succession of earthquakes, volcanic eruptions, and fires that have depleted several lizard populations with a resulting legacy of a great diversity of life history traits in Liolaemidae, *Phyllodactylidae*, and Leiosauridae.

The Patagonian steppe has been subjected to a variety of volcanic eruptions since the Miocene, 23.3 Ma (Giacosa and Heredia 2004; Giacosa et al. 2005), and volcanism continues at the present. In particular, the Puyehue-Cordón Caulle volcanic complex (with a 2.5 km diameter) has been active the last 11,500 years with several explosive pulses (Lara et al. 2004). Recent eruptions were registered in 1893, 1914, 1919, 1921–1922, and 1960 (Singer et al. 2008). Following the most recent eruption in 2011, we found evidence of ecophysiological adaptations to volcano ash in lizard populations of *Phymaturus* in steppe environments (Ibargüengoytía et al. 2016) in Argentina and also to fire ash in *Liolaemus pictus* and *L. lemniscatus* on the other side of the Andes in the Austral forests of Chile (Mora and Labra 2017).

The present review shows that lizard populations from Patagonia experience both acute catastrophic events such as ashfall and chronic events such as the gradual increase in ambient temperature due to global warming, without drastic changes in locomotor performance, thermoregulatory capacity, or growth dynamics. Some species, like *L. elongatus* and the southernmost lizards of the world, *L. sarmientoi* and *L. magellanicus*, could benefit to some extent from global warming as warmer temperatures would reduce their costs of thermoregulation, improve locomotion, and enhance immunological performance (Fernández and Ibargüengoytía 2012; Duran et al. 2019). In addition, an increase in environmental temperatures in cold environments would increase the availability of thermal microenvironments favoring pregnant *L. sarmientoi* females, in which higher and stable temperatures are necessary to ensure newborn fitness and survivorship (Fernández et al. 2017). Although increased temperatures may help pregnant females in some species and reduce the costs of thermoregulation in others, it may harm other life stages or phenological events.

Climate change can force lizards to refuge several additional hours each day, decreasing the amount of time available for reproductive activity, feeding, and social behaviors (Sinervo et al. 2010; Kubisch et al. 2016a; Vicenzi et al. 2017). Thus, shifts are expected in the geographic ranges of lizard populations under a global warming scenario (Bonino et al. 2015), but this is strongly dependent not only on their vagility and dispersal behavior but also the speed of adaptive changes in traits such as habitat and diet selection. The general question is whether such range shifts and adaptations would occur quickly enough to prevent the collapse of populations due to the energetic restrictions imposed by global change (Vicenzi et al. 2017). For example, it is expected that in Patagonia global warming would affect in particular the genus *Phymaturus*, because it is highly specialized to live in rock promontories in the steppe environments (Scolaro 2005, 2006), an herbivorous diet (Espinoza et al. 2004) and a slow pace-of-life reproductive schedule (Boretto et al. 2018). Extirpations of populations have been observed already in the genus *Phymaturus* (Sinervo et al. 2010). In *Liolaemus* and the gecko *Homonota darwinii*, studies predict 15–26% of the populations to become extinct by the year 2080 (Kubisch et al. 2016a), and most *Liolaemus* species studied may suffer range reductions (Bonino et al. 2015).

In Patagonia, consideration of the actual low operative temperatures T_e, compared to the T_b values that lizards attain by thermoregulation in the field, and the high T_{pref} characteristic of the Liolaemidae family, explains why the genus *Liolaemus* has experienced low rates of extinction and why such rates are predicted to continue through 2080 despite global warming, compared to 12 other families of heliothermic lizards (Sinervo et al. 2010). Meanwhile, species located at lower latitudes in northern Argentina and Chile, and in Brazil, are considered more vulnerable to global warming (Piantoni et al. 2016). However, the fact that the environments in Patagonia represent a potential refuge for northern species may constitute a challenge for current-day Patagonian populations in terms of new predators, competitors, and pathogens (Paranjpe et al. 2014; Duran et al. 2019). The biodiversity of Patagonia and the high Andean habitats could be severely threatened not only by receding glaciers but also by land degradation, the desertification aggravated by the alteration of fire regimes in the forest and the steppe, and rapid global climate change (IPCC 2014; Barros et al. 2014).

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