Thermoregulatory behavior and high thermal preference buffer impact of climate change in a Namib Desert lizard

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Abstract. Knowledge of the thermal ecology of a species can improve model predictions for temperature-induced population collapse, which in light of climate change is increasingly important for species with limited distributions. Here, we use a multi-faceted approach to quantify and integrate the thermal ecology, properties of the thermal habitat, and past and present distribution of the diurnal, xeric-adapted, and active-foraging Namibian lizard *Pedioplanis husabensis* (Sauria: Lacertidae) to model its local extinction risk under future climate change scenarios. We asked whether climatic conditions in various regions of its range are already so extreme that local extirpations of *P. husabensis* have already occurred, or whether this micro-endemic species is adapted to these extreme conditions and uses behavior to mitigate the environmental challenges. To address this, we collected thermoregulation and climate data at a micro-scale level and combined it with micro- and macroclimate data across the species' range to model extinction risk. We found that *P. husabensis* inhabits a thermally harsh environment, but also has high thermal preference. In cooler parts of its range, individuals are capable of leaving thermally favorable conditions—based on the species' thermal preference—unused during the day, probably to maintain low metabolic rates. Furthermore, during the summer, we observed that individuals regulate at body temperatures below the species' high thermal preference to avoid body temperatures approaching the critical thermal maximum. We find that populations of this species are currently persisting even at the hottest localities within the species' geographic distribution. We found no evidence of range shifts since the 1960s despite a documented increase in air temperatures. Nevertheless, *P. husabensis* only has a small safety margin between the upper limit of its thermal preference and the critical thermal maximum and might undergo range reductions in the near future under even the most moderate climate change scenarios.

Key words: climate change; cost–benefit model; desert; ectotherm; Lacertidae; modeling; Namib Desert; reptile; thermoregulation.

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INTRODUCTION

Globally, some lizard populations may be at risk of extinction due to a rapidly warming climate, because ambient temperatures increasingly exceed the lizards' thermal tolerances (Huey et al. 2009, Sinervo et al. 2010). One possible mechanism is reduction in time active outside retreats, which translates ecologically into a constraint on available foraging time, particularly threatening during the reproductive season when energy demands are at their peak. Abnormally warm ambient temperatures have already been demonstrated to be associated with extinctions of local lizard populations due to what has been proposed to be an inability to balance the energetic demands of reproduction in an abbreviated period of daily activity (Sinervo et al. 2010, 2011). Despite the availability of strong circumstantial evidence, further examination of this hypothesis is warranted. In addition, expanding its application to a wider range of environments and lizard species is necessary. A combination of species-specific ecological data at a micro-scale, experimental approaches, and mechanistic species distribution modeling approaches is appropriate for such hypothesis tests.

Mechanistic species distribution models are valuable tools for testing potential threats using real ecological data (e.g., Kearney and Porter 2009, Sinervo et al. 2010, Kearney 2013). The Sinervo et al. (2010) model is based on the hypothesis that species' range edges were originally defined by the maximum operative temperatures at the outermost localities of their distribution (i.e., hottest localities for the high temperature physiological limit) before the onset of anthropogenic climate change (considered as beginning during the mid-1970s following the Intergovernmental Panel on Climate Change [IPCC; Bindoff et al. 2013). The Sinervo et al. (2010) model integrates lizard thermophysiology and in situ operative temperatures (T_e) to elucidate the interrelationships between ambient temperature and population distribution. This model relies on the premise that ambient temperatures constrain the amount of time that lizards may be active outside of their retreats (during which time lizards complete life activities such as foraging and breeding). In this model, site- and taxon-specific empirical data are used to determine species'

thermal tolerances and to estimate the thermal quality of the current environment. These data are then combined with climate change models to estimate restrictions in lizard activity in the past (before observed temperature increases beginning in the mid-1970s), present, and future.

Not all lizard species are at equal risk of extirpation from rising ambient temperatures. Several factors may interact to influence a lizard species' susceptibility to altered thermal niches arising from climate change, including the habitat requirements and characteristics, daily activity patterns, and foraging behavior (e.g., Anderson and Karasov 1981, Huey and Pianka 1981, Kearney 2013, Tingley et al. 2013, Böhm et al. 2016). It has been criticized that the model of Sinervo et al. (2010) did not explicitly include species-specific habitat affinities, their microclimatic diversity, behavior (thermoregulation, foraging strategy), or life history (Kearney 2013). These factors are potentially necessary to accurately assess climate-mediated lizard extinction risk, as has been found for the risk associated with viviparity in Mexican lizards (Sinervo et al. 2010).

Deserts are among the most extreme habitats that are occupied by lizards, due to the challenges imposed by thermal and hydric constraints. Namibia includes some of the warmest and driest regions in Africa south of the Sahara Desert, yet these arid Namibian ecosystems support a high diversity of lizard species (Thuiller et al. 2006, Herrmann and Branch 2013). In the hyper-arid Namib Desert, which stretches nearly 2000 km along the coast from southern Angola through Namibia to northern South Africa, surface temperatures often exceed 60°C (Edney 1971, Lancaster et al. 1984, Seely et al. 1990, Viles 2005, Murray et al. 2014). Terrestrial lizard species that occur here are active in extreme environmental conditions. Furthermore, the Namib Desert is home to a rich array of endemic lizard species that have specific habitat requirements and may be particularly vulnerable to changes in their environment (Sinervo et al. 2010).

Regarding foraging strategies, lizard species may be broadly characterized by using either an active or a sit-and-wait (or ambush) foraging mode (Pianka 1966). Daily foraging time and foraging strategy are strongly correlated. For example, sit-and-wait foragers usually have lower prey encounter rates and are therefore surface

active for longer periods of time than actively foraging lizard species, and have lower field metabolic rates (Anderson and Karasov 1981, Nagy et al. 1984, Brown and Nagy 2007).

We chose the diurnal, heliothermic, actively foraging lizard species *Pedioplanis husabensis* Berger-Dell'mour and Mayer 1989 (Sauria: Lacertidae) with a restricted range within the xeric western parts of central Namibia as a model to investigate thermal biology and extinction risk. This species' habitat is threatened not only by climate change but also by uranium mining, making an investigation of its ability to cope with potential abiotic threats particularly important. We apply a multidisciplinary approach combining the use of museum collections to reconstruct past distribution ranges and surveys of current population status across the majority of its distribution, with data on its thermal physiology determined in situ and experimentally. We investigate the thermal biology and estimate the thermal properties of the microhabitats used by *P. husabensis*. In addition, we assess the thermal quality of the microclimates available to this species in order to estimate how well the lizards thermoregulate across both the energy-intensive reproductive period and during non-reproductive periods. Furthermore, we apply and extend the Sinervo et al. (2010) model to assess how the historical distribution may be altered by contemporary climate warming that has already occurred (Dirkx et al. 2008) and by future climate change, across the range of *P. husabensis*. We sought evidence for local extirpations of *P. husabensis* that may have already occurred in regions where temperatures have increased (i.e., all historical collection localities), to test the hypothesis by Sinervo et al. (2010) that the physiological limits of lizard species' distributions are defined by thermal constraints experienced before anthropogenic-induced climate change. We further predict that an active forager like *P. husabensis* will be able to persist in an environment characterized by relatively long periods of time when activity is constrained by high temperatures and that it will exhibit high precision in thermoregulatory behavior.

Methods

Natural history of Pedioplanis husabensis

Pedioplanis husabensis is a medium-sized species in the family Lacertidae. Adults have a

snout-to-vent length of 45–61 mm and a mass of 1.8–4.2 g (Branch 1998). The species occurs in habitats located near the confluence of the Swakop and Khan rivers in the Namib Desert and adjacent dry savannah in central western Namibia (Berger-Dell'mour and Mayer 1989). The geographic distribution of this species encompasses <5000 km^2 (Branch 1998, Cunningham et al. 2012). Despite the restricted distribution range, *P. husabensis* is currently not listed in the IUCN Red List of Threatened Species (www.iucnredlist.org). Individuals of *P. husabensis* are diurnal and inhabit expanses of flat rock on exposed bedrock. Their activity occurs primarily on slopes where it forages for insects on rock and on loose, friable, shrub-dotted substrates (Murray et al. 2014, 2016*a*). Although it can also be found foraging away from the rocky slopes, it exploits shelters among rock crevices on the slopes (Murray et al. 2014, 2016*a*, *b*). Previous work has reported on its foraging mode, energetics, and active body temperature (Murray et al. 2014), diet (Murray et al. 2015, 2016*a*, *b*), as well as general natural history attributes (Berger-Dell'mour and Mayer 1989, Schwacha 1997, Cunningham et al. 2012). *Pedioplanis husabensis* is oviparous and breeding starts in November, with first hatchlings appearing in April (Schwacha 1997, Branch 1998). Local climatic conditions include a low, mean annual precipitation (approximately 25 mm), but additional moisture comes from the episodic fog events. Based on data from similar sites in the Namib, around 25–50 fog days per year may be expected within a range of *P. husabensis* (Olivier 1995, Haensler et al. 2011, Eckardt et al. 2013). Mean air temperature ranges from 22.3° to 24.8°C during summer and from 17.5° to 18.8°C during winter (Hijmans et al. 2005).

Thermal preference and critical thermal maximum

Lizard thermal traits are generally accepted to be species specific, although several studies have shown intraspecific daily, seasonal, spatial, ontogenetic, or sexual variation in thermal preference and critical thermal maximum with inconsistent patterns (see Clusella-Trullas and Chown 2014 for a review). This lability of thermal physiology appears to vary among taxa (reviewed by Angilletta et al. 2002). In our study, we chose the most conservative approach by sampling adult males

and non-gravid females from different populations across the geographic range and during different periods of the year to acquire data for species-specific thermal preference. To account for plasticity and potential local adaptations, we analyze the mean preferred or selected body temperature of all individuals tested (mean T_{sel}) as well as the central 50% of all individual averages (the thermoregulatory set-point range or thermal preference T_{sel}).

Sampling.—A total of 21 individual lizards (five females and 16 males) from three localities (Table 1) were captured by noosing. Sampling occurred between April 2013 and October 2014 and included both reproductive and non-reproductive seasons. We brought lizards back to the field laboratory where they were housed in glass terraria, maintained at an air temperature of 25°C with water provided ad libitum. Lizards were not fed the day before the experiment began.

Experiments.—We determined thermal preference T_{sel} as well as the critical thermal maximum

(CT_{max}) for *P. husabensis* in the laboratory at the Gobabeb Research and Training Centre (23.5611 °S, 15.0411 °E; altitude 405 m; Fig. 1; all coordinates are provided in decimal degrees). We initiated the thermal experiments within one to two days of capture.

As appropriate for a diurnal, heliothermic lizard, T_{sel} was determined in a photothermal gradient (e.g., Light et al. 1966, DeWitt 1967, Paranjpe et al. 2013, Clusella-Trullas and Chown 2014, Gilbert and Miles 2017). The commonly used experimental determination of T_{sel} using a gradient is generally preferred over field observations of body temperature (Huey 1982, Hertz et al. 1993) as the laboratory data reflect the temperature selected by an individual in the absence of costs and constraints that are present in field conditions (Hertz et al. 1993, Clusella-Trullas and Chown 2014). The experimental setup consisted of a box with eight individual tracks constructed from 5 mm thick, opaque particle board (910 × 380 × 120 mm;

Table 1. List of individuals on which data on thermal ecology were collected.

Fieldnr	Date	Sex	T_{sel}Method	Mean T_{sel} (°C)	Median T_{sel} (°C)	CT_{max} (°C)
Site 3, 22.8004 °S, 15.03801 °E, 413 m asl						
541_2013	28/04/2013	M	Cloaca	39.7	39.6	–
542_2013	28/04/2013	M	Cloaca	39.1	40.1	44.6
544_2013	28/04/2013	M	Cloaca	39.5	39.3	–
Site 4, 22.63697 °S, 15.09621 °E, 532 m asl						
588_2013	29/04/2013	M	Cloaca	39.3	40.9	45.3
592_2013	29/04/2013	M	Cloaca	38.1	39.0	–
594_2013	29/04/2013	F	–	–	–	44.5
598_2013	29/04/2013	M	Cloaca	38.8	38.9	–
602_2013	29/04/2013	M	Cloaca	38.8	38.9	–
871_2013	23/06/2013	M	Cloaca	36.8	37.3	45.4
872_2013	23/06/2013	M	Cloaca	37.6	37.3	–
873.1_2013	23/06/2013	M	Cloaca	38.4	38.1	–
873_2013	23/06/2013	M	Cloaca	37.4	36.9	–
875_2013	23/06/2013	M	Cloaca	35.5	36.6	43.6
877_2013	23/06/2013	M	Cloaca	36.3	36.7	44.0
878_2013	23/06/2013	M	Cloaca	38.5	38.3	43.6
595_2013	29/04/2013	F	Cloaca	40.6	42.2	–
597_2013	29/04/2013	F	Cloaca	39.4	39.9	–
874_2013	23/06/2013	F	Cloaca	38.3	38.0	–
876_2013	23/06/2013	F	Cloaca	37.2	38.1	44.1
Site 5, 22.63956 °S, 15.17431 °E, 685 m asl						
424_2014	23/10/2014	M	Ventral skin	36.7	37.5	–
425_2014	23/10/2014	M	Ventral skin	35.6	35.4	–
423_2014	23/10/2014	F	Ventral skin	37.4	37.8	–

Notes: The table provides information by identification number (Fieldnr) and sex and when and where data were gathered: site (see Fig. 1 for numbers), latitude, longitude, and altitude. Additionally, the method (T_{sel}Method) that was used to determine mean and median selected body temperature (mean T_{sel}, median T_{sel}) and critical thermal maximum (CT_{max}) is provided. An (–) indicates no data.
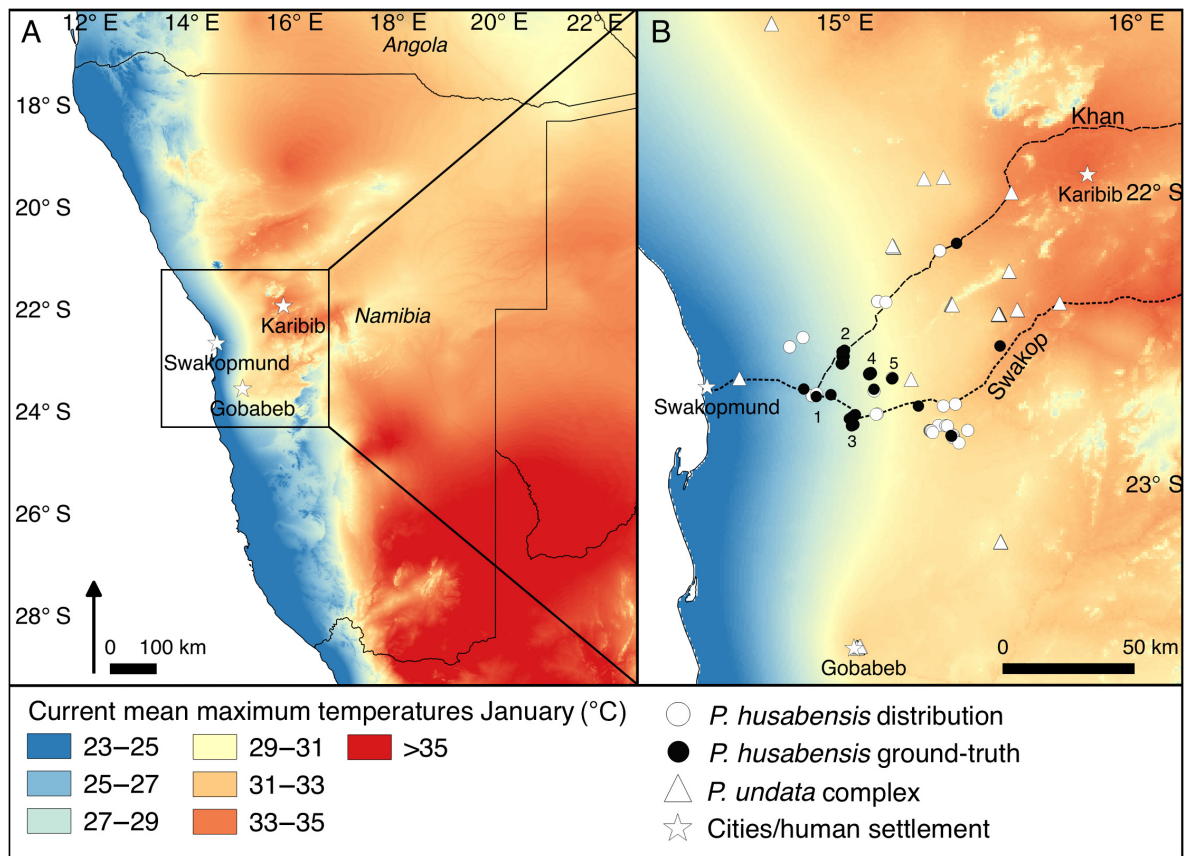
Fig. 1. Map showing contemporary monthly mean maximum air temperatures of one of the hottest months in Namibia (January) and surrounding (A) and the updated distribution range of *Pedioplanis husabensis* zoomed in (B). Depicted are all records from museum vouchers (open circles), resurveyed *P. husabensis* localities (current study; solid black circles), and records of populations belonging to the *P. undata* complex (open triangles). Stars represent cities and other human settlement (i.e., Gobabeb Research and Training Centre). The numbered solid black circles 1–5 represent the populations where ecological and temperature data were collected: Hildenhof (1), Khan Mine (2), Ida Camp, Swakop River (3), inselberg 6 km north of Husab Mountain (4), and Marble Portal (5).

length × height × width of each track) following Paranjpe et al. (2012). An incandescent 100-W light bulb (full spectrum) was suspended 30 cm above one end and a frozen gel pack placed underneath the ground plate at the other end of each track to create a thermal gradient of approximately 10° to 55°C measured at ground level with an infrared thermometer (Testo 845, accuracy ± 0.75°C, resolution 0.1°C; Testo AG, Lenzkirch, Germany). Each lizard was allowed unrestricted movement within its individual track during its normal diurnal activity period. Lizard body temperature was measured over a period of two consecutive hours. An additional 30-min acclimation time at the beginning

of each trial was discarded. In 18 individuals (Table 1), body temperature was determined by means of cloacal temperatures using a T-type thermocouple probe (diameter 1 mm inserted approximately 10 mm into the cloaca) and a digital thermometer (±0.2°C; Omega HH202A, Stamford, Connecticut, USA). Measurements were taken every 20 min. In three individuals, body temperature was determined every minute by means of ultra-thin T-type thermocouples (OMEGA 5SC-TT-T-40-72, diameter = 0.076 mm, Norwalk, Connecticut, USA) affixed with medical tape to the lizards' venter and connected to an 8-Channel USB Thermocouple Data Acquisition Module

(OMEGA TC-08, accuracy 0.2 percent $\pm 0.5°C$, resolution <0.1°C). During these trials, we conducted occasional cloacal temperature measurements to confirm that internal body temperature was represented accurately by the ventral skin measurements.

For each individual, we determined the average of all body temperature measurements. Since lizards mostly have a range of temperatures that they strive to function within, rather than a single value (Hertz et al. 1993), we used the interquartile range of the ranked individual averages as the species' thermoregulatory set-point range (thermal preference T_{sel}) ranging from T_{sel25} (lower limit) to T_{sel75} (upper limit) (Hertz et al. 1993). For the extinction risk model, we also used the species' mean T_{sel} determined as the arithmetic mean of all individual averages.

Critical thermal maximum (CT_{max}) was determined by heating individual lizards (N = 8, six males, two females, from two localities; Table 1) in an incubator (Heraeus, Hanau, Germany) at a constant rate (approximately 0.8°C/min). Prior to determining CT_{max}, we warmed individuals to the species' mean T_{sel}. Cloacal temperature was measured every minute and lizards were flipped on their back before every measurement from 40°C until either loss of the righting response and/ or muscular spasms occurred (Lutterschmidt and Hutchison 1997). When either response occurred, lizards were immediately removed from the incubator, and cooled with moist paper towels. All of the lizards tested behaved normally after being cooled in this manner within 5–10 min of ending the CT_{max} trial. While this is still the most commonly applied method to determine CT_{max}, the repeated righting response method may exhaust lizards, and results should consequently be interpreted with caution (Camacho and Rusch 2017).

Seasonal thermoregulatory efficiency and thermal quality of the habitat

To assess the thermoregulatory efficiency of *P. husabensis* and the thermal quality of its habitat, we studied a population along a dry section of the Swakop River at Farm Hildenhof (22.7008 °S, 14.9148 °E; altitude 210 m, Fig. 1). At this location, the species occurs on the extensive rocky slopes along the canyon (Murray et al. 2014, 2016*a*, *b*). We collected data for a period of ten days during the species' reproductive season in summer and another ten days during the nonreproductive season in autumn (Table 2; Schwacha 1997, Branch 1998). Weather conditions during the study period were characteristic for typical conditions during these seasons (data not shown). We quantified the thermal conditions available to lizards using operative temperatures (T_e), which represent the equilibrium temperatures of inanimate models, that is, non-thermoregulating objects whose heat-transfer properties, for example, morphology and reflectivity, approximate those of the study organism (Bakken and Gates 1975, Bakken et al. 1985). We made T_e models using empty, hollow, type *M* copper tubing (Shine and Kearney 2001, Dzialowski 2005) with a length (L) = 47 mm and wall thickness = 12.7 mm. We painted all the copper models with primer gray (Sprayon gray primer, Sprayon Paints, Cleveland, Ohio, USA) to approximate lizard reflectance (Adolph 1990, Sinervo et al. 2010) and capped both ends of the tube. A thermistor probe attached to a Hobo temperature data logger (U12-001; Onset Computer Corporation, Bourne, Massachusetts, USA) was inserted through a hole in each tube to determine the interior temperature as a substitute for a non-thermoregulating *P. husabensis* field body temperature T_b.

Table 2. Coordinates in decimal degrees and period of operative temperature (T_e) data collection for the localities (1–5; see Fig. 1) where ecological and temperature data were collected.

Site	Latitude (°S)	Longitude (°E)	Period of T_e data collection	Total no. days
1 Farm Hildenhof	22.7008	14.9148	25/12/2012–3/1/2013; 3/5/2013–13/5/2013	21
2 Khan Mine	22.5609	15.0036	16/4/2013–3/5/2013	18
3 Ida Camp, Swakop River	22.6946	14.9647	12/4/2013–2/5/2013	21
4 Inselberg 6 km north of Husab Mountain	22.6256	15.0953	11/4/2013–21/4/2013; 2/5/2013–3/5/2013; 22/6/2013	14
5 Marble Portal	22.6382	15.1753	21/10/2014–3/1/2015	75

Model temperatures were tested against cloacal temperatures of a freshly deceased adult *P. husabensis* (mass = 3.0 g) at the field site across a temperature range of 28–47°C. We found a high correlation of the temperatures recorded between the lizard and the copper model (R^2 = 0.97; P < 0.001; T_b = 1.2 × T_e − 6.52).

We obtained operative temperature data from 18 lizard T_e models deployed in three different microhabitats frequently used by the lizards. The number of models in each locality was selected to cover a representative array of available microhabitat temperatures. Microhabitat categories were as follows: (1) "rock" (N = 7), included models on rocky slopes in the canyon, in direct sunlight, and in partially/temporarily fully shaded places around and beneath shrubs; (2) "silt" (N = 3), included models on sandy flats with loose substrates and small washes, in direct sunlight, and in partially/temporarily fully shaded places around and beneath shrubs: category; (3) "crevice" (N = 8), included shaded models deployed in potential lizard shelter sites on slopes (e.g., underneath rocks, in rock crevices). Orientation of the models with regard to the path of the sun was random, although it has been shown that lizards have preferred orientations toward the sun under different environmental conditions (e.g., Seely et al. 1988). Locations of individual models did not change during the course of the study. Each logger recorded T_e every 10 min throughout each ten-day study period. Only data collected from 6:00 to 19:00 (incorporating daylight hours during both summer and autumn) were analyzed for this diurnal species. Lizards were monitored from 7.00 to 18.00 which bracketed the normal diurnal activity period of *P. husabensis*. We binned the proportion of lizards observed out of the total lizard observations during a season into time bins to estimate daily lizard activity periods (Murray et al. 2016*a*). After capturing lizards with a noose, we recorded body temperatures T_b (N = 110; as reported in Murray et al. 2014, 2016*a*) of surface active lizards immediately (within 30 s) by means of cloacal temperatures. All T_e and T_b data were subsequently analyzed in the context of the empirically determined T_{sel} and CT_{max} for this species to examine lizard thermoregulatory behavior and the thermal quality of the lizard's habitat.

We compared the effects of season and microhabitat category on mean T_e, mean maximum T_e (open habitats), and mean minimum T_e (shaded habitats) averaged across all models within each habitat type for every daylight hour of the study period, as used in previous analyses (Sinervo et al. 2010, 2011, Lara-Reséndiz et al. 2015, Kubisch et al. 2016, Vicenzi et al. 2017) with two-way ANOVAs using season and microhabitat category as factors. We also tested effect of season and microhabitat category on thermal quality (d_e) with two-way ANOVAs using season and microhabitat as factors. Thermal quality of the environment (d_e) is the summed absolute value of the difference between T_e and T_{sel}. For every value of T_e falling within the set-point range for T_{sel}, d_e equals zero. Higher or lower values were subtracted from the upper or lower limit of T_{sel} and the absolute values are reported. A large value for d_e suggests that temperatures within T_{sel} occur relatively infrequently (Hertz et al. 1993). We used two-sample t tests to investigate potential differences in lizard thermoregulatory accuracy (d_b) for individuals captured on either silt or rock substrates, as well as for lizards active during summer and autumn. Thermoregulatory accuracy (d_b) is the absolute value of the difference between lizard field active body temperatures T_b and the T_{sel} for that species (Hertz et al. 1993). Again, a value of T_b falling within the set-point range for T_{sel}, results in d_b equals zero, higher or lower values were subtracted from the upper or lower limit of T_{sel} and reported as absolute values. High values of d_b indicate that lizards did not often achieve their T_{sel}. Using these values, we calculated lizard thermoregulatory efficiency ($E = 1 − d_b/d_e$), which ranges from 0 where microclimates are used randomly (e.g., a thermoconformer) to value of 1 indicative of perfect thermoregulation. We also determined the index of thermoregulatory efficiency proposed by Blouin-Demers and Weatherhead (2001; $d_e − d_b$), which is a measure of how far animals are situated on either side of a thermoconforming situation. Negative values can be interpreted as avoidance of thermally optimal environments, whereas positive values indicated the relative magnitude of active thermoregulation (Blouin-Demers and Weatherhead 2001). Data were analyzed using SigmaPlot 8.0 (Systat Software, San Jose, California, USA), Microsoft Excel 2007 (Microsoft, Redmond, Washington, USA), SPSS 21.0 (SPSS, Chicago, Illinois, USA),

and Minitab 16.0 (Minitab, State College, Pennsylvania, USA).

Current geographic distribution

We assessed the geographic distribution of *P. husabensis* by using all available museum voucher specimens and respective publications known to us (Appendix S1: Table S1). In the case that no geographic coordinates were provided or coordinates were imprecise, we assigned coordinates based on the locality description (which was always provided) in combination with expert opinion from our local collaborators.

In addition, we resurveyed 51% of the known sites (see *Results*, Fig. 1) using visual encounter surveys with two to four people to verify extant populations on various trips between January 2013 and February 2017. Special attention was given to the hottest (based on mean monthly T_{max}; downloaded from www.worldclim.org; Hijmans et al. 2005) eastern-most localities within the known distribution. Furthermore, we surveyed additional areas inside and outside of the known distribution range for potential new records (Fig. 1). To our knowledge, all of the sites we surveyed were anthropogenically unaltered and appeared not degraded. At each locality that we resurveyed, we found *P. husabensis* over the course of the first surveying day. Average person-hours needed to record the first individual at each new locality were 0.63 h (38 min) (N = 18) (S. Kirchhof, *unpublished data*).

Extinction risk modeling

To determine extinction risk, we chose four sites in addition to Hildenhof within the distribution of *P. husabensis* where we deployed T_e models. At each of the four sites, we installed four T_e models in the microhabitat of *P. husabensis*, with two models on a southwestern slope (one in full shade and one in direct sun) and two on a northeastern slope (one in full shade and one in direct sun), thereby encompassing the extremes of prevailing temperatures at each locality. Sites were chosen across the geographic distribution of *P. husabensis* (Fig. 1, sites 2–5, Table 2) to cover the range of operative environmental temperatures occurring there (Kubisch et al. 2016). To incorporate our data into the modeling framework of Sinervo et al. (2010), we followed their standard protocol and measured operative environmental temperatures (Hobo

data loggers U23-003; Onset Computer) using models constructed from standardized hollow, empty, capped polyvinyl chloride (PVC) pipes (80 mm × 15 mm, 1 mm wall thickness) spray-painted primer gray (NEO Dur semi-matt acrylic emulsion, Pastel Base, WOT, 1 L mixed with 100 mL NEO Charcoal 122, Windhoek, Namibia). These PVC T_e models have been calibrated against live lacertid lizards of similar size to *P. husabensis* (Belasen et al. 2017; $R^2 = 0.84$, slope not significantly different from 1 and intercept not significantly different from zero). We compared the copper and PVC models by deploying both next to each other in *P. husabensis* habitat and left them for 15 d (24 June–8 July 2014) recording temperatures every 10 min. We found a high correlation of the temperatures recorded by copper (T_{cop}) and PVC (T_{PVC}) models ($R^2 = 0.99$; $P < 0.001$). For modeling, we corrected the values recorded by the copper models using the generated equation $T_{PVC} = 0.97 \times T_{cop} + 0.85$. We then selected four out of the 18 models deployed at Hildenhof from microhabitats bracketing the range of available T_e in a fashion similar to that of other four sites to include in the extinction risk model.

Ecophysiological models hypothesize that a species is optimally adapted to its local thermal conditions prior to climate change and that non-random extirpations will be concentrated at warmer range boundaries, where the velocity of climate change is most rapid, or where taxa are limited either by thermal physiology or by species interactions, for example, competition or predation (Terborgh 1973, Brown 1984). We adopted a metric of the critical daily hours of activity restriction for each species using the 95% quantile of daily hours of activity restriction h_r, similar to the model developed for lizard families (Sinervo et al. 2010). If a given site was predicted to exceed the present-day critical h_r value as computed from the 95% quantile, we assumed it would be extirpated. At each of the five study sites, we calculated h_r by summing the amount of time that mean T_e (during daylight hours) exceeded the mean T_{sel} of *P. husabensis*. We repeated the same calculation, this time using T_{sel75} instead of mean T_{sel} to account for the upper limit of the species' T_{sel}. We used concurrent daily maximum air temperatures (T_{max}) recorded by the closest weather station (79 km for the Hildenhof study site) or measured directly on site using a Hobo data

logger (at all other localities; in 2 m height exposed to the air and sheltered from direct solar radiation; WMO 1992) to determine the general species-specific relationship between daily h_r and T_{max} using the R package FLEXPARAMCURVE (Oswald et al. 2012). We calculated h_r values during the breeding season using temperature data from November to January, which comprises the major period of reproductive activity (Schwacha 1997, Branch 1998). This period also corresponds with the time when the energetic demands of adult lizards are likely to be at a maximum. From our complete *P. husabensis* locality dataset (Appendix S1: Table S1), we discarded every known record separated by 1 km or less from the next record (see resolution of temperature rasters below) to avoid pseudoreplication. We used the climate dataset for the time from 1960 to 1990 downloaded from www.worldclim.org (mean monthly T_{max}, spatial resolution 30 arc-s or 1 km^2) as a proxy for the air temperature conditions prior to the first records of increasing surface temperatures in 1975 (see Bindoff et al. 2013). The h_r values for each site in the present-day and future time points were computed from fitted sigmoidal functions $f(T_{max} - \text{mean } T_{sel})$ and $f(T_{max} - T_{sel75})$. For estimates of future T_{max}, we used the MPI-ESM-LR model (spatial resolution 30 arc-s or 1 km^2; downloaded from www.worldclim.org) of the CMIP5 Earth System Models as used in the IPCC Fifth Assessment Report (IPCC 2014). This model performed best globally in predicting future climate conditions considering the current structure of the land carbon cycle as evaluated by Anav et al. (2013). We used two different pathways for the years 2050 and 2070, namely RCP 4.5 that assumes a medium rise in CO_2 concentration and a stabilization in the year 2100 without overshoot, and RCP 8.5 that assumes a rise of CO_2 beyond the year 2100 (Moss et al. 2010).

RESULTS

Thermal preference and critical thermal maximum

Mean T_{sel} for *Pedioplanis husabensis* was $38.0° \pm 1.4°C$ (N = 21; median 38.1°C; Table 1). The thermoregulatory set-point range was 37.2°C (T_{sel25}) to 39.1°C (T_{sel75}). Average CT_{max} was $44.4° \pm 0.7°C$ (maximum 45.4°C; N = 8).

Operative environmental temperatures, thermoregulatory efficiency, and thermal quality of the habitat

Mean maximum T_e (open habitats) was much higher than mean minimum T_e (shade, crevices) during both summer and autumn (summer: $42.6° \pm 13.7°C$ vs. $29.5° \pm 7.7°C$, $t_{82} = 5.37$, $P < 0.001$; autumn: $38.3° \pm 12.0°C$ vs. $26.2° \pm 7.3°C$, $t_{82} = 5.61$, $P < 0.001$). Average daily mean T_e was similar during summer and autumn (two-way ANOVA; $F_{1,78} = 2.63$; $P = 0.11$) and did not differ by microhabitat (two-way ANOVA; $F_{2,78} = 1.03$; $P = 0.36$; Table 3). The average daily mean maximum T_e was also similar across season (two-way ANOVA; $F_{1,78} = 2.30$; $P = 0.13$) and microhabitat (two-way ANOVA; $F_{2,78} = 0.58$; $P = 0.56$; Table 3). Average daily mean minimum T_e did not vary according to microhabitat (two-way ANOVA; $F_{2,78} = 0.11$; $P = 0.89$), but autumn average daily mean minimum T_e was about 3°C lower than during summer (two-way ANOVA; $F_{1,78} = 4.19$; $P = 0.04$; Table 3). The effect of

Table 3. Average daily mean, mean maximum, and mean minimum operative temperatures (T_e) between sunrise and sunset, thermal quality of the environment (d_e), thermoregulatory accuracy (d_b), and two metrics of thermoregulatory efficiency (E and $d_e - d_b$) measured at the Hildenhof site in December (summer) and May (autumn) on rock and silt substrates, as well as in rock crevices.

Season/substrate	Mean T_e (°C)	Mean max T_e (°C)	Mean min T_e (°C)	Mean d_e (°C)	Mean d_b (°C)	E	$d_e - d_b$
December/rock	37.0 ± 11.4	42.1 ± 13.4	31.2 ± 8.4	8.7 ± 5.5	3.3 ± 1.8	0.67	5.4
May/rock	33.2 ± 10.9	39.5 ± 13.7	25.0 ± 6.5	8.4 ± 7.1	1.2 ± 1.4	0.89	7.2
December/silt	38.5 ± 13.2	46.9 ± 17.6	30.6 ± 9.2	10.3 ± 6.2	2.6 ± 1.4	0.72	7.7
May/silt	31.1 ± 11.0	37.3 ± 14.4	25.6 ± 8.9	8.8 ± 8.5	0.9 ± 1.1	0.90	7.9
December/crevice	31.3 ± 5.9	38.8 ± 8.4	26.7 ± 4.5	6.0 ± 5.7	–	–	–
May/crevice	31.8 ± 6.7	38.1 ± 7.4	27.9 ± 6.2	6.4 ± 5.7	–	–	–

Note: The (–) indicates no data.

microhabitat on seasonal minimum T_e was not significant (two-way ANOVA; microhabitat × season: $F_{2,78} = 2.00$; $P = 0.14$).

During the summer, mean operative temperatures exceeded mean T_{sel} and T_{sel75} of *P. husabensis* for 54% ($h_r = 7$) of the daylight period on rocks and for 62% ($h_r = 8$) on silt (Fig. 2). Likewise, during autumn, mean operative temperatures

exceeded mean T_{sel} and T_{sel75} for 50% of the daylight period ($h_r = 5$; both on silt and rocks) (Fig. 2). Nevertheless, in shaded areas, lizards had access to minimum operative temperatures considerably lower than T_{sel} for the majority of the day (Fig. 2). For example, during the summer, mean minimum T_e only exceeded T_{sel} for three hours on rock substrates and two hours on silt
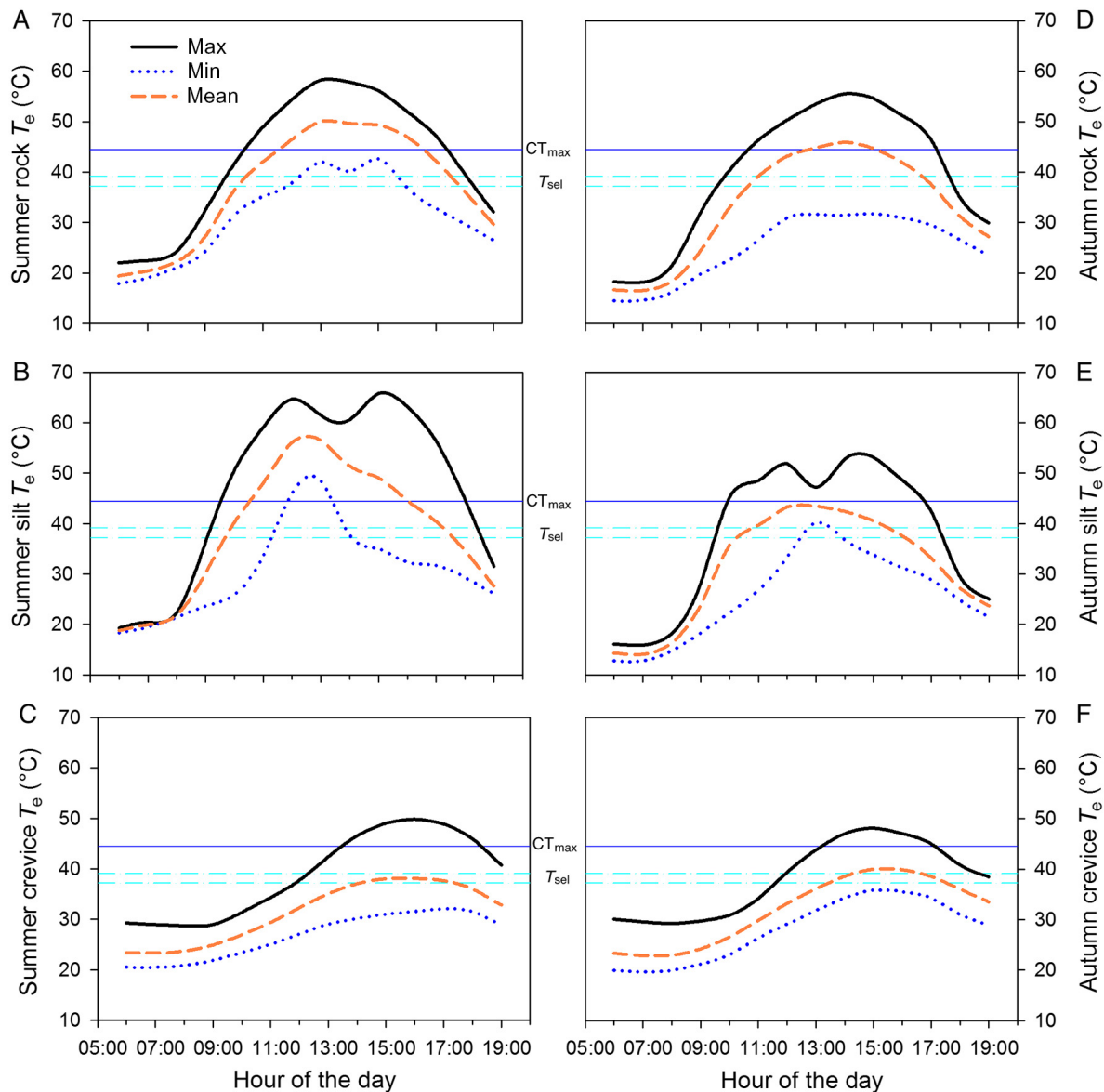
Fig. 2. Hourly mean, mean maximum (max), and mean minimum (min) operative temperatures (T_e) averaged over the study period for rock substrates, silt substrates, and rock crevices during summer (A–C) and autumn (D–F) at Hildenhof, as determined for *Pedioplanis husabensis*. The turquoise dashed horizontal lines show the thermal preference T_{sel} (37.2–39.1°C), and the solid blue line is the average critical thermal maximum CT_{max} (44.4°C).

substrates in the afternoon, exceeding CT_{max} for only two hours in the afternoon on silt (Fig. 2). During autumn, mean minimum T_e was never above CT_{max} and only exceeded T_{sel} for 1 h in the afternoon on silt substrates. Minimum crevice T_e in both seasons was always below T_{sel} (Fig. 2). Consequently, by exploiting both shaded and sunny patches (active thermoregulation through sun–shade shuttling), *P. husabensis* was able to prolong its activity periods (nine hours in summer, eight hours in autumn; translated into $h_r = 4$ and 2, respectively; Murray et al. 2016*a*) in comparison with our estimation using T_e models (five hours, summer and autumn; $h_r = 7$ and 5, respectively).

The thermal quality of silt and rock substrates (d_e) was highly variable throughout the lizard's diurnal activity period, but during both seasons there was a bimodal distribution of low d_e values (high thermal quality) separated by high d_e values (low thermal quality) during mid-day and during the early morning and evening hours (Fig. 3). Lizard surface activity periods, particularly in summer, largely corresponded to periods of high thermal quality during the morning. However, thermally optimal open surface habitats available during the late afternoon were used only rarely by lizards (Murray et al. 2016*a*). Average d_e values were similar between seasons (two-way ANOVA; $F_{1,78} = 0.10$; $P = 0.75$) and microhabitat type (two-way ANOVA; $F_{2,78} = 1.91$; $P = 0.16$; Table 3). For rock and silt substrates in the summer, the periods of optimal thermal quality occurred at 10:00–10:30 and 17:00–18:00 (Fig. 3). During autumn, the highest thermal quality became available around 11:00 and between 15:00–16:00 (silt) and 16:00–17:00 (rock) (Fig. 3). In addition, the thermal quality of rock and silt habitat during the hot mid-day remained higher (lower d_e index) during autumn than during summer (Fig. 3). The d_e index for rock crevices slowly declined through the morning hours and reached the lowest values (highest thermal quality) between 15:00 and 17:00 in the summer and between 14:00 and 17:00 during autumn (Fig. 3), suggesting these sites were good thermal refugia. Lizards were only rarely seen surface active during that time, especially in summer (Murray et al. 2016*a*). Average T_b was significantly higher in autumn (36.8° $\pm$ 1.6°C) than in summer (34.3° $\pm$ 1.7°C) (two-sample

t test; $t_{108} = 7.75$; $P < 0.001$; see also Murray et al. 2014). Both values were lower than the experimentally determined mean T_{sel} (38.0° $\pm$ 1.4°C). The thermoregulatory accuracy (d_b) of lizards on rock substrates was the same as that for lizards on silt substrates during the summer (two-sample *t* test; $t_{41} = -1.27$; $P = 0.22$). Similarly, d_b did not differ by substrate during autumn (two-sample *t* test; $t_{39} = -0.68$; $P = 0.50$; Table 3). On average, *P. husabensis* showed a thermoregulatory accuracy that was more than three times greater during autumn ($d_b = 0.9° \pm 1.1°C$) than during summer ($d_b = 2.9° \pm 1.7°C$; two-sample *t* test; $t_{108} = -7.15$; $P < 0.001$).

In general, the effectiveness of thermoregulation (*E*) was high for *P. husabensis* and was similar among substrates within a season (Table 3). However, *E* was consistently higher for lizards during autumn compared to summer (Table 3). Values for $d_e - d_b$ were similarly high across substrates, but unlike the index *E*, the value dropped less during summer in comparison with autumn (Table 3).

Distribution

We obtained distributional records for *P. husabensis* dating from 1965 in museum collections and collected 25 additional specimens over the course of the current study (Appendix S1: Table S1). Together with tissue samples that we collected from the Khan Mine, Bloedkoppie, eastern Swakop River, Farm Palmenhorst, and our records from Hildenhof (no specimens; confirmed as *P. husabensis* due to the presence of an opaque to semi-transparent lower eyelid covered with several small scales, small tympanic shield, absence of lateral row of yellow spots, and genetic analysis), our efforts resulted in a combined dataset of 99 records. The reduction in this combined dataset down to one record per km^2 resulted in a final set of 42 populations, of which we visited 22 (51%) over the course of the current study (Fig. 1). We found *P. husabensis* populations at six localities from where there were no published records until today, but all were within the known distribution (Appendix S1: Table S1). The current distribution of *P. husabensis* appeared to be mainly restricted to the canyons of the Khan and the Swakop River and nearby isolated hills surrounded by vast plains (inselbergs). It occurred in the western Swakop from around 8 km west of its
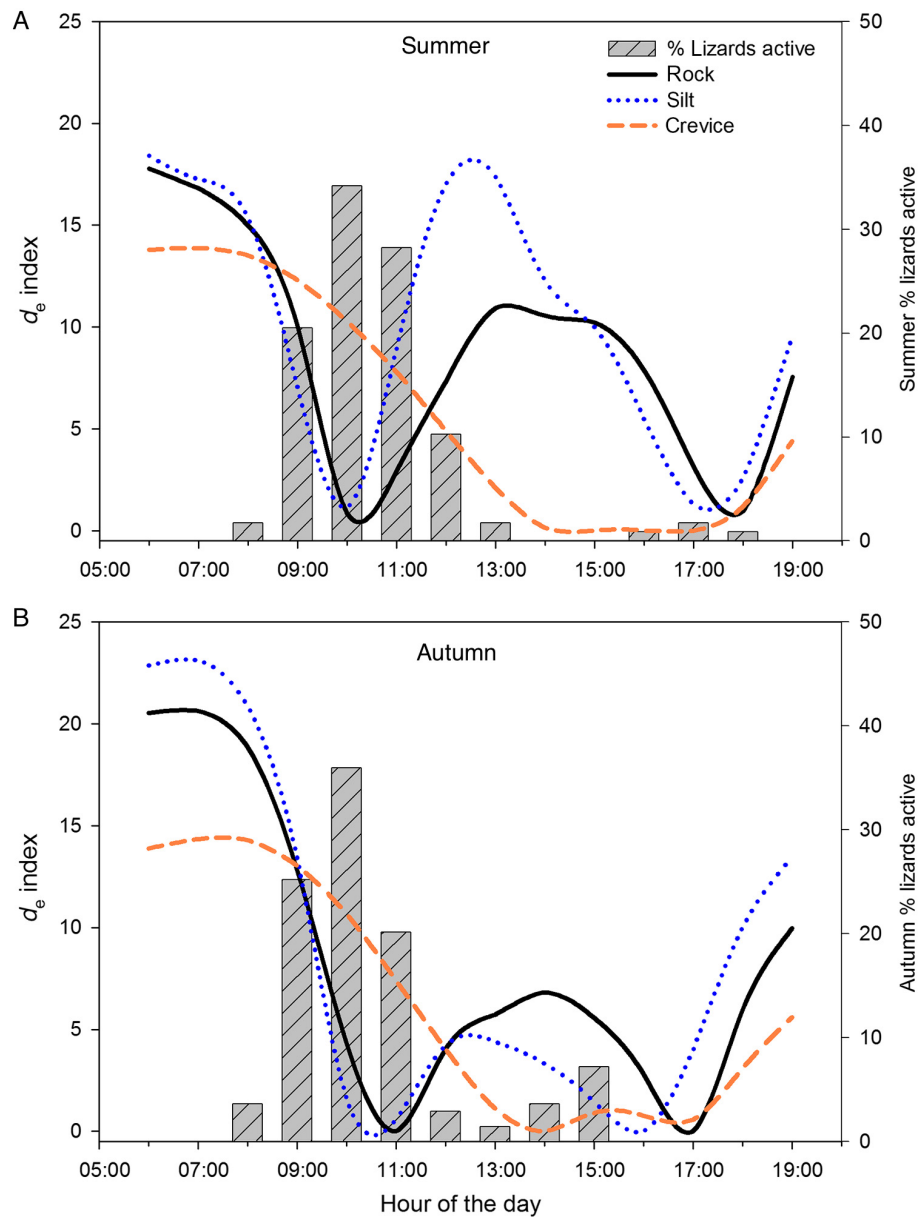
Fig. 3. Mean hourly thermal quality (d_e index) of rock and silt substrates and rock crevices during summer (A) and autumn (B) relative to the hourly distribution of active lizards observed at Hildenhof.

confluence with the Khan River (Goanikontes Rest Camp near Farm Hildenhof, voucher NHMUK 1988.510; Appendix S1: Table S1) extending eastward for roughly 75 km along both the Khan River (ZMB 83403; current study) and the Swakop River (ZMB 83405; current study). We also found vouchers collected from isolated populations outside the two riverbeds in the museum collections we examined (Roessing Mountain north of the Khan River, hills and mountains around the Langer Heinrich Mine, Tinkas and Bloedkoppie south of the Swakop River). In between the two rivers, the species occurred on isolated hills but only as far east as the Marble Portal (Fig. 1; Appendix S1: Table S1). Unfortunately, three specimens of the original paratype

series (SMR 4421, 5311, 5315) could not be located in any museum and appear to be lost. *Pedioplanis husabensis* occurred strictly parapatric to known, but as yet undescribed species belonging to the *P. undata* complex ("*P. inornata* north/central" and "*P. undata* south"; Mayer and Berger-Dell'mour 1987, Berger-Dell'mour and Mayer 1989, Makokha et al. 2007, Conradie et al. 2012).

Extinction risk modeling

The relationship of h_r as a function of T_{max} minus the mean T_{sel} of *P. husabensis* was best explained with a logistic Richard's curve function with the general equation:

$$h_r = \frac{A}{([1 + m \times \exp(-k \times ((T_{max} - \text{mean } T_{sel}) - i))]^{\frac{1}{m}}},$$

where A (8.61 ± 2.47; $P < 0.001$), k (0.17 ± 0.05; $P < 0.001$), i (−0.63 ± 3.76; $P = 0.87$), and m (0.1) are the asymptote, rate parameter, inflection point, and shape parameter, respectively (Fig. 4). By using a sigmoidal curve rather than a linear equation as used in the study by Sinervo et al. (2011), we obtained two asymptotes (one approaching zero h_r and one approaching maximum daylight hours) and prevented h_r from becoming negative or exceeding the maximum possible activity times for this diurnal species.

The maximum value of h_r averaged over the critical breeding season months for all recorded extant populations in 1975 was 2.44. This means that no population of *P. husabensis* then occurred at a locality where on average more than 2.44 h per day was thermally unsuitable during the breeding season. This maximum value was estimated from the southeastern-most population of this species along the rocky banks of a tributary to the Swakop River (vouchers ZMB 83404, ZMB 83405; current study), a locality that has one of the highest mean maximum January air temperatures where *P. husabensis* is known to occur (Fig. 1). By the year 2050, the mean T_{max} averaged for the critical reproductive period at this locality is predicted to be higher by 2.4°C (RCP 4.5) or 2.9°C (RCP 8.5) than in 1975, which would increase the h_{r2050} to 3.22 (RCP 4.5) and 3.36 (RCP 8.5), respectively. If our original hypothesis was true that the species' range edges before the onset of climate change (i.e., 1975) were defined based on the maximum temperatures occurring there, this increase in unsuitable hours for activity would push this lizard population to extinction. This ecophysiological hypothesis is a null hypothesis of sorts that the species distribution is dictated by ecophysiology per se (e.g., a concept similar to the Grinnellian niche). In October 2014, our survey confirmed this population as extant. Similarly, the two northeastern-most populations of *P. husabensis* along the rocky margins of the Khan River (voucher ZMB 83403; current study, close to SMR 7158 collected in 1987) were confirmed to be extant in 2013.
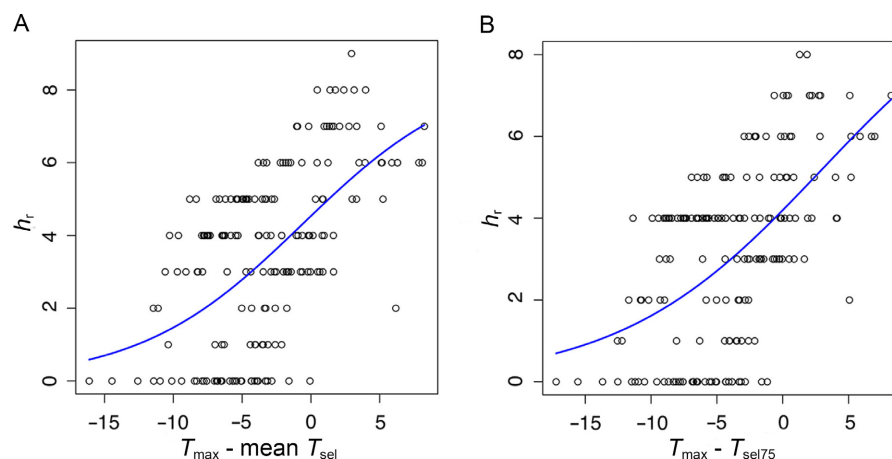

Fig. 4. Plot showing hours of average operative temperatures exceeding mean thermal preference T_{sel} (A) and the upper limit of thermal preference T_{sel75} (B) (=hours of restriction h_r) of *P. husabensis* as a function of daily maximum air temperatures T_{max} minus mean T_{sel} (A) and T_{sel75} (B), respectively.

These two sites are the next hottest localities within the species' range with $h_{r1975} = 2.40$ and 2.28, respectively. A clear cline with increasing modeled extinction risk from west to east is apparent for this species (Fig. 5).

By the year 2050, our model based on RCP 4.5 data predicts that these eastern-most populations in the two rivers will become extirpated unless they can adapt to the changing conditions. Furthermore, the model predicts extirpation of populations from the inselbergs around the Langer Heinrich Mine, Tinkas and Bloedkoppie south of the Swakop River. These patterns suggest that 14 of the 42 known populations are at risk of extirpation due to climate change (Fig. 5). If we consider the worst-case scenario regarding carbon dioxide emissions (RCP 8.5), this number rises to 17 populations (Fig. 5). By the year 2070, the predictions are even more severe: 17 (RCP 4.5) or 25 (RCP 8.5) of the 42 known populations
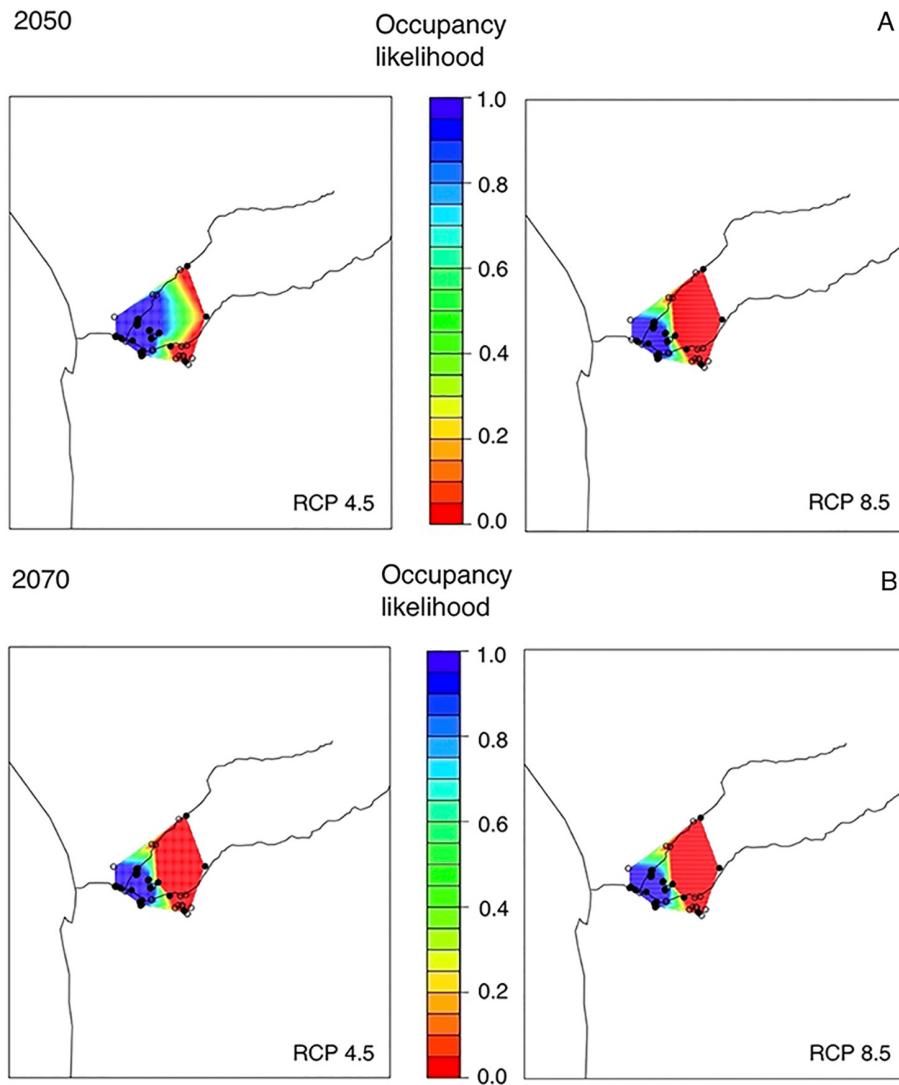
Fig. 5. Extinction risk of *P. husabensis* based on the assumption that activity restrictions due to climate warming will lead to local population extirpations. Occupancy likelihood was modeled for the years 2050 (A) and 2070 (B) under two different climate change scenarios (RCP 4.5 and 8.5). Circles represent all known, vouchered *P. husabensis* localities. Sites resurveyed in the current study are represented by solid circles; open circles stand for populations known from museum collections. Warmer colors symbolize a low occupancy likelihood, or high extinction risk.

(40% or 60%, respectively) may become extirpated as a result of rising temperatures (Fig. 5). At this point, mean T_{max} is predicted to have risen by 2.8°C (RCP 4.5) or 4.2°C (RCP 8.5) at the hottest eastern-most locality in the Swakop River, resulting in increased daily periods of unsuitable conditions by more than 1 h on average under the worst-case scenario (h_{r2070} = 3.47; RCP 8.5) in comparison with 1975. The Hildenhof site, located near the cooler western edge of the species' distribution, is modeled to have a high likelihood of persistence with an estimated h_{r1975} of 1.19 and a predicted h_r of 1.51 (2050; RCP 8.5) or 1.73 (2070; RCP 8.5) in the future (Fig. 5).

If lizards thermoregulate to achieve a range of preferred body temperatures (T_{sel}) rather than a single value (e.g., Hertz et al. 1993), then using the mean T_{sel} value as a threshold that separates suitable from unsuitable conditions tends to underestimate the potential of this species to cope with restrictions in activity due to rising temperatures. The model using T_{sel75} (39.1°C) instead of mean T_{sel} (38.0°C) as threshold resulted in a slightly different logistic Richard's curve equation:

$$h_r = \frac{10.38}{([1 + 0.1 \times \exp(-0.13 \times ((T_{max} - T_{sel75}) - 2.97))]^{\frac{1}{0.1}}}$$

with A = 10.38 ± 5.97 (P = 0.08), k = 0.13 ± 0.05 (P = 0.005), i = 2.97 ± 0.34 (P = 0.73), and m = 0.1.

However, h_r values are only marginally reduced under this scenario, that is, with the maximum h_{r1975} at the eastern-most Swakop River site decreasing to 2.17 (instead of 2.44) and reaching 2.88 (RCP 4.5) or 3.27 (RCP 8.5) in the year 2070 (instead of 3.36 [RCP 4.5] or 3.47 [RCP 8.5]). Therefore, plasticity in behavioral thermoregulation, as measured by T_{sel75} relative to mean T_{sel} (an index of thermoregulatory scope), is unlikely to have a dramatic impact on persistence.

Discussion

We found that *Pedioplanis husabensis* inhabits a thermally harsh environment, but has a high thermal preference and is not even surface active during the full range of thermally favorable periods of the day in cooler parts of its range. During the hot summer, individuals regulate at body temperatures below the species' high T_{sel} to avoid body temperature excursions near the critical thermal maximum CT_{max}. Nevertheless, our ecophysiological model predicts substantial range reductions under even the most moderate climate warming scenarios.

Operative environmental temperatures and thermal quality of the habitat

Based upon our estimation of T_{sel} of *P. husabensis*, operative temperatures T_e at the western limit of the species' range (Farm Hildenhof) would prevent this species from employing a thermoconforming strategy for substantial periods of each day. However, the ability to achieve physiologically optimal body temperatures T_{sel} is a precondition for a lizard's survival, especially during the breeding season (Sinervo et al. 2010, 2011). As a consequence, active thermoregulation (i.e., sun–shade shuttling) and eventually retreat from the surface was necessary for *P. husabensis* throughout most of each day during our study period if the species wanted to avoid lethally hot or unsuitably cold body temperatures. If air temperatures (and T_e) increase, as predicted by climate change, it is likely that *P. husabensis* activity time will be reduced to a point where local populations will become extirpated.

During times when surface T_e were unsuitable, *P. husabensis* generally had access to rocky crevices and other retreat sites where temperatures were slightly below or within its T_{sel} for a large proportion of the day, and where mean T_e never exceeded its CT_{max}. Although for some reptiles, active thermoregulation around T_{sel} may occur within retreats (e.g., Porter et al. 1973, Schall 1977), presumably engaging in feeding and social activities is impeded by staying within shelters, particularly for this heliothermic, insectivorous species. In the early morning hours, T_e was generally below T_{sel} in the overnight refugia in the crevices, and lizards became surface active around 8:00 (Fig. 3). Surface activity abruptly declined once the thermal quality of substrates decreased (rock and silt d_e in autumn, rock d_e in summer) to levels below those of refugia around mid-day. Importantly, despite a bimodal pattern of low d_e index (high thermal quality) throughout the day, surface activity pattern of *P. husabensis* was almost unimodal and the species

predominantly exploited the morning period of favorable temperatures in both seasons (Fig. 3).

Costs and benefits of thermoregulation

Cost–benefit models have been developed to assess when a thermoconforming strategy would be advantageous over thermoregulating for an ectotherm in situations when T_e was below the preferred body temperature (Huey and Slatkin 1976). Vickers et al. (2011) extended this cost–benefit model of thermoregulation to include the costs of thermoregulating in environments when available T_e exceeded the species' T_{sel} (as is the case in our study system). Fitness costs of thermoregulation are lowest when $T_e = T_{sel}$, but rise drastically when $T_e > T_{sel}$ up to CT_{max}, particularly for heliotherms (Vickers et al. 2011). This means that lizard species with higher T_{sel} would have a proportionately more rapid escalation of fitness costs, particularly since CT_{max} is more conserved across species than is T_{sel} (Sinervo et al. 2010, Araújo et al. 2013). As a result, the risk of reaching lethal body temperatures for lizards active at T_e beyond T_{sel} increases drastically with increasing thermal preference. Under this additional dimension of the Huey and Slatkin (1976) model, Vickers et al. (2011) found that thermoregulatory accuracy (d_b) increased as environmental temperatures increased for three *Carlia* skink species in an arid woodland environment in Australia. However, our results contradict their deduction that thermoregulatory accuracy should generally be highest during favorable T_e (low d_e) until the point where T_e is so high that lizards are forced to suspend surface activity. Rather, we found that thermoregulatory accuracy was significantly lower during summer when mean minimum T_e was significantly higher (by 3°C) than in autumn. In the lizard microhabitat of our study area, d_e was 2–3 times higher (worse habitat thermal quality) than in Australia (Table 3; Vickers et al. 2011). At the same time, *P. husabensis* has a much narrower thermal safety margin between its high T_{sel} and CT_{max} in comparison with the three Australian *Carlia* species with $T_{sel} = 25.4$–32.3°C and $CT_{max} = 43.6$°C (Greer 1980, Vickers et al. 2011). As a result, the determined T_b's of these skinks were often above their T_{sel} in a habitat with low thermal quality, while in *P. husabensis*, <5% of T_b measurements were above mean T_{sel} and none above T_{sel75}

(Table 3; Murray et al. 2014). A similar scenario appeared in two *Phrynosoma* species from the Chihuahuan Desert with environmental temperatures similar to the ones in our study (Lara-Reséndiz et al. 2015). These species had a lower T_{sel} (32.5–36°C and 31.1–36.5°C) and a higher CT_{max} (47.9°C; Prieto and Whitford 1971), and T_b of the species was above T_{sel} in up to 64.6% of the cases (Lara-Reséndiz et al. 2015). In these examples, the wide range between T_{sel} and CT_{max} means that the lizard can maintain a T_b above T_{sel} yet still maintain a thermal buffer minimizing the risk of approaching CT_{max}, unlike what we found for *P. husabensis*. It appears that in the hyper-arid Namib Desert, a threshold is reached for this species during summer, beyond which the risks of overheating outweigh the benefits of thermoregulating to achieve T_{sel}. Consequently, during the hottest period of the year, *P. husabensis* may rather prefer staying in the shade reaching body temperatures slightly below T_{sel} than exposing itself to the direct sun, which would increase T_b to preferable level first but then quickly reach lethal temperatures.

Other environmental factors

The almost unimodal activity pattern of *P. husabensis* indicates that thermally favorable operative temperatures were not the sole reason for surface activity. Recent work on the actively foraging teiid *Aspidoscelis exsanguis* in an arid ecosystem in New Mexico showed that the availability of moisture (in this case rainfall) influenced lizard activity and microhabitat use more than soil and air temperatures, and suggested that lizard populations will not only be impacted by temperature shifts but also by differences in moisture regimes (Ryan et al. 2015). Similarly, a long-term drought in California dramatically reduced juvenile recruitment among most known populations of the endangered blunt-nosed leopard lizard, *Gambelia sila* (Westphal et al. 2016), and future projections for reduced precipitation in California suggest it may drive extinction risk in this species. Moisture availability may also play a role in *P. husabensis* surface activity. Although not examined the current study, moisture (in this case specifically in relation to fog events) may be a factor in lack of *P. husabensis* activity during thermally favorable late afternoon periods.

Extinction risk modeling

In the future, average maximum temperatures during the summer months are predicted to increase within the geographic range of *P. husabensis*, while annual precipitation is predicted to decrease even more (Dirkx et al. 2008, Niang et al. 2014). When we apply the temperature data from our micro-scale study at Hildenhof to the extinction risk model (macro-scale), the comparatively high $h_r = 7$ at Hildenhof in January 2013 is averaged down to $h_{r1975} = 1.19$ for the period between 1960 and 1990, and $h_{r2050} = 1.51$ (RCP 8.5), respectively. At the hottest sites that *P. husabensis* currently inhabits in the Swakop River, during the reproductive season h_{r1975} was higher (2.44) than the Hildenhof h_{r1975} but lower than the $h_{r1975} = 3.1$ that was estimated for lacertids in general (Sinervo et al. 2010). That these eastern-most populations of *P. husabensis* were still present during our 2013–2017 resurveys even after the observed temperature increase (Dirkx et al. 2008) implies that this species is capable of inhabiting more thermally extreme areas than what we found at Hildenhof or what the model predicted based on the temperature changes since 1975. However, whether the lizards in these populations are able to exploit the limited hours of suitable conditions that remained or whether they were capable of counterbalancing the low thermal quality behaviorally, we cannot say. Alternatively, extinction may require several years of warm spells in succession during which impaired reproduction and recruitment may bring some but not all populations to the extinction threshold, as appears to be the case in extinctions of Mexican phyrnosomatid lizards (Sinervo et al. 2011).

The maximum h_r estimation of 3.1 for Lacertidae (Sinervo et al. 2010) is the average h_r of 36 lacertid species. Previous validation of the model and demonstration of local extinctions were conducted using mainly sit-and-wait foraging or omnivorous/frugivorous species (*Zootoca vivipara*, *Liolaemus lutzae* in Brazil, diverse liolaemid species in Argentina, diverse species of lizards in several lizard families in Madagascar, and *Liopholis* spp. in Australia), which based on measurements of field metabolic rate (Nagy et al. 1984) may have different physiological and ecological constraints compared to an active forager such as *P. husabensis*. Our results cannot

unambiguously prove that *P. husabensis* can sustain extended periods of inactivity (h_r). While our field observations suggest that the extant Hildenhof population experiences up to $h_r = 4$ during the breeding season, the extinction risk model estimates that an $h_r = 2.44$ is the maximum that a population can tolerate in the long term and remain viable. This confirms the results of a computational model incorporating different theoretical percentages of shade cover within a lizards' habitat (Kearney 2013). Kearney (2013) demonstrated that the Sinervo et al. (2010) model might over- or underestimate critical h_r limits depending on the microclimatic heterogeneity of the habitat. Without any documentation of local extinctions, we are currently unable to determine what a critical h_r value leading to extirpation for *P. husabensis* may be. Yet, if predictions are correct and temperatures increase even further in the future, local extirpations of *P. husabensis* populations are likely to occur.

The T_e models that we base our approach on here predict the equilibrium T_b of a non-thermoregulating lizard at a specific location during a particular time (Bakken 1992). Critically, we acknowledge that the full range of thermoregulatory behavior that a lizard can employ (e.g., postural changes such as orientation to solar radiation, body flattening, minimizing or maximizing body contact with a hot or cold surface by straightening/retracting the legs; physiological thermoregulation such as panting, expelling water from the cloaca) is not considered. All of these behaviors influence lizard T_b (e.g., Stevenson 1985, Seely et al. 1988, Martín et al. 1995, DeNardo et al. 2004). Consequently, without considering these behavioral changes, under the extreme conditions in the Namib, the T_e model in most instances would be likely to provide an overestimate of the lizard's body temperature. Secondly, both copper and PVC models used in our study generally underestimated lizard T_b during the calibration experiment (see *Results*). These caveats are common problems in studies using T_e models and methods still need to be improved to account for them. Nevertheless, when applied in a modeling approach as the current study, these potential sources of uncertainty are likely to be negligible (Sinervo et al. 2011).

When we thus apply our extinction risk model to the broader surroundings of the distribution of

P. husabensis (assuming that suitable rocky habitat in the fog zone of the Namib with h_r up to 2.44 is inhabitable by this species), we cannot entirely account for the small size of its current range. The small geographic extent of the species' distribution may not only be delineated through abiotic (i.e., temperature, rain/fog), but also biotic (e.g., interspecific competition, predation) constraints. As noted above, the modeling method herein tests for the action of the Grinnellian niche in driving species extinctions due to ecophysiological limits being exceeded, but does not have power to reject the action of factors related to the Eltonian niche (e.g., competition, predation, parasitism). For example, each locality with apparently suitable habitat that we surveyed adjacent to the current range edges was inhabited by morphologically similar congeneric taxa of the *P. undata* complex. These taxa have habitat requirements and thermal physiology very similar to those of *P. husabensis* (Berger-Dell'mour and Mayer 1989, Branch 1998, Cunningham et al. 2012; S. Kirchhof, *unpublished data*). The fact that a potential competitor occupies suitable areas outside of the current range of *P. husabensis* suggests that interspecific interactions may contribute toward defining current distribution boundaries for *P. husabensis*. Notable in this regard, Sinervo et al. (2010) could only accurately predict 16 of 24 extinctions of *Sceloporus* lizards in Mexico, and thus, eight extinctions were unexplained by the null model of ecophysiology for climate change extinctions. It is noteworthy that at six of these eight sites, a range expansion of a warm-adapted congener had occurred, suggesting that climate-forced extinctions of the cold-adapted species may have arisen from the action factors related to the Grinnellian niche (16 of 24 populations that went extinct) and Eltonian niche such as competition (six of the remaining eight populations that went extinct).

Conclusions

Our multidisciplinary approach (laboratory and field experiments, field surveys, utilization of museum records, and modeling) shows that behavioral and ecological data collected at a micro-scale level can greatly enhance macro-scale modeling approaches. Here, we show using museum records and ground-truthed data that despite an increase in temperatures over the past decades, the range boundaries of *Pedioplanis husabensis* apparently have not shifted, indicating that local extirpations have not yet occurred. We document that our study species is capable of prolonging daily activity beyond what we evaluated using the models by selectively moving between a heterogeneous landscape of open and sun-exposed as well as shaded patches all available on relatively small scales within its habitat. Based on our observations as well as the results of our model, the minimum amount of surface activity time necessary to sustain a viable population in this species has not yet been reached within the species' distribution. The active-foraging mode conducted by this species appears to be favorable for precise thermoregulation and allows it to exploit the environment under the extreme climatic conditions in Namibia's xeric west.

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