Effects of climate change on a reptile community in arid Australia

Exploring mechanisms and processes in a hot, dry, and mysterious ecosystem

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Abstract (German)

Dies ist eine kumulative Dissertation, die drei Originalstudien umfasst (eine publiziert, eine in Revision, eine eingereicht; Stand Dezember 2017). Sie untersucht, wie Reptilienarten im ariden Australien auf verschiedene klimatische Parameter verschiedener räumlicher Skalen reagieren und analysiert dabei zwei mögliche zugrunde liegende Hauptmechanismen: Thermoregulatorisches Verhalten und zwischenartliche Wechselwirkungen. In dieser Dissertation wurden umfassende, individuenbasierte Felddaten verschiedener trophischer Ebenen kombiniert mit ausgewählten Feldexperimenten, statistischen Analysen, und Vorhersagemodellen. Die hier erkannten Mechanismen und Prozesse können nun genutzt werden, um mögliche Veränderungen der ariden Reptiliengesellschaft in der Zukunft vorherzusagen. Dieses Wissen wird dazu beitragen, dass unser Grundverständnis über die Konsequenzen des globalen Wandels verbessert und Biodiversitätsverlust in diesem anfälligen Ökosystem verhindert wird.

Abstract (English)

This is a cumulative dissertation comprising three original studies (one published, one in revision, one submitted; Effective December 2017) investigating how reptile species in arid Australia respond to various climatic parameters at different spatial scales and analysing the two potential main underlying mechanisms: thermoregulatory behaviour and species interactions. This dissertation combines extensive individual-based field data across trophic levels, selected field experiments, statistical analyses, and predictive modelling techniques. Mechanisms and processes detected in this dissertation can now be used to predict potential future changes in the community of arid-zone lizards. This knowledge will help improving our fundamental understanding of the consequences of global change and thereby prevent biodiversity loss in a vulnerable ecosystem.

Figure 1: View from a sand dune towards the flooded riverine woodland close to the Kinchega field station in 2012. Photo by Annegret Grimm-Seyfarth.

Figure 2: Catching Geckos through spot-lightning. Photo by Klaus Henle.

Figure 3: *Lucasium damaeum* Photo by Annegret Grimm-Seyfarth.

Acknowledgements

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List of abbreviations

Abbreviation	Description
AIC / AICc	(corrected) Akaike information criterion
ANODEV	analyses of deviance
AT	available activity time, i.e., the amount of time that an individual could be active within its operative thermal environment
CI	confidence interval
CTmax	critical thermal maximum when righting reflex cease
CTmin	critical thermal minimum when righting reflex cease
CV	coefficient of variation
ENSO	El Niño Southern Oscillation
ETT	existing thermal tolerance
EWL	evaporative water loss
(G)L(M)M	(generalized) linear (mixed) modelling
IPCC	Intergovernmental Panel on Climate Change
LRT	likelihood ratio test
N	population size
p	detection probability
pMANOVA	permutational multivariate analyses of variance
RCP	representative concentration pathway
RelAT	relative available activity time, i.e., the percentage of AT in relation to the potential available time that a species would have on that day when ignoring thermal limits
RFID	radio frequency identification tags
RWI	riverine woodland I (cracking clay, widely dispersed eucalypts, varying vegetation)
RWII	riverine woodland II (sandy clay, slightly dispersed eucalypts, herb- and shrub-layer)
S	survival probability
SDM	species distribution model
SEM	structural equation modelling
SMI	scaled mass index, an index for body condition
SOI	southern oscillation index, an index to track ENSO
station	Kinchega field station (eight huts, sandy soil, varying vegetation)
T_{air}	air temperature (1.2 m above ground)
Tb	body temperature
T_{burrow}	temperature in a burrow 15 cm below the surface
T_e	operative temperature (i.e., the potential body temperature in a non-thermoregulating individual)
T_p	preferred body temperature
T_{sel}	selected body temperature
T_{sun}	temperature on the soil in direct sunlight
Ψ	juvenile-adult-transition probability
ωAIC	AIC weights

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1 General introduction

1.1 Climate change as important driver of biodiversity change

Biodiversity is increasingly challenged by mounting global environmental change, such as land use conversion, climate change, exploitation, and pollution (Leadley et al. 2010). Among them, land use conversion and climate change are considered key drivers affecting species' population dynamics and causing species extinctions (Pereira et al. 2010). Depending on the biome under investigation, the predicted future changes in these drivers as well as their impacts on biodiversity differ in strength but their impacts will likely exceed those of other drivers of change (Sala et al. 2000). While land use conversion, exploitation, and increasing pollution levels may pose a greater threat to local biodiversity on the short-term, climate change is predicted to become the predominant driver on the long-term (Thuiller 2007, Maxwell et al. 2016). There is mounting evidence that climate change is an anthropogenically-induced phenomenon caused by increasing carbon emission rates (Hansen and Stone 2016). Thus, whereas land use conversion, exploitation, and pollution levels may be addressed at smaller scales and also directly, climate change can only be addressed indirectly, mainly through a reduction in the emission of greenhouse gases (IPCC 2014a). Unlike some of the other drivers, climate change acts at a global scale without exceptions, differing only locally in strength and direction (IPCC 2014a). Moreover, all those biodiversity threats certainly interact with each other (Côté et al. 2016) making it hard to predict their attributable impacts on local biodiversity (Maxwell et al. 2016). However, it remains important to understand effects of single drivers to refine conservation management strategies (Leadley et al. 2010). To analyse the single effects of climate change, it is necessary to study changes already observed in the biodiversity of ecosystems under constant land use in the light of a changing climate over the last decades.

According to the IPCC (2014), climate change has been manifesting through a globally rising mean surface temperature since the late 19th century, with an exceptional increase over the past three decades and an additional predicted increase of 4°C on average by 2100. This will likely cause an increase in hot temperature extremes but a decrease in cold temperature extremes. Predictions for changes in precipitation are not uniform and strongly vary across latitude, with an expected increase over wet regions and a decrease over dry regions. Extreme precipitation events will likely become more frequent and more intense. Furthermore, global systems like the monsoon system and the El Niño Southern Oscillation (ENSO) will likely also intensify (IPCC 2014a). Together, this human-induced rapid climate change is altering all ecosystems around the globe (Thuiller 2007). There is strong evidence that climate change already has considerable impact on various aspects of the ecology of species (e.g., Walther et al. 2002; Parmesan & Yohe 2003; Davey et al. 2013) and will likely operate across hierarchical levels from individual to population, species, community, ecosystem, and biome as an evolutionary selection force (Bellard et al. 2012).

Species can respond to changing local climate through either local adaptation (Urban et al. 2014, Seebacher et al. 2015) or range shifting (McCarty 2001, Walther et al. 2002, Monasterio et al. 2013, Srinivasulu and Srinivasulu 2016); otherwise they may become extinct (Devictor et al. 2008, 2012, Raxworthy et al. 2008, Cahill et al. 2014, Urban 2015). Local adaptation encompasses a local response of the species to local climate change through alteration of their seasonal or diurnal timing of key life history events, i.e., changes in phenology, or alteration of the individuals themselves, i.e., their physiology or behaviour (Bellard et al. 2012). An understanding of the mechanisms underpinning local adaptations is largely incomplete. However, these mechanisms are likely related to either genetic adaptation through micro-evolution from one generation to the next (Salamin et al. 2010) or phenotypic plasticity within or among individuals (Charmantier et al. 2008). Both genetic adaptation and phenotypic plasticity acting on phenological, morphological, physiological, and behavioural levels could mitigate the effects of climate change on species (Bellard et al. 2012, Urban et al. 2014), though plasticity could also reduce the potential for genetic adaptation (Gunderson and Stillman 2015). Effects of alternating climatic conditions may also be buffered among ecological levels within a population. As an example, life history traits and population dynamics, like enhanced/reduced reproductive rates, sexual maturity, or generational turnover, could promote resilience and recovery of a species as a whole and thus prevent it from local extinction (Williams et al. 2008). Nevertheless, the extent and ways in which species respond to rapid climate change, and whether species can really cope with it, is highly debated among ecologists and evolutionary biologists (e.g., Beebee 2002, Henle et al. 2010, Bellard et al. 2012), as it is a major prerequisite to understanding and predicting the effects of climate change on species dynamics and community composition (Pereira et al. 2010).

1.2 Hot desert ecosystems: a highly vulnerable ecosystem to climate change

Climate change will likely cause particularly severe modifications in dryland ecosystems (IPCC 2014a). Dryland ecosystems are characterised by strong water stress and hot temperatures each year (Settele et al. 2014). They cover over 40% of the global land surface area and are dominated by hot arid and semi-arid deserts (Olson et al. 2001, Millennium Ecosystem Assessment 2005; Fig. 1.1). Hot deserts cover 35% of the global terrestrial area (Settele et al. 2014). With advancing climate change, hot deserts are predicted to experience even hotter and dryer conditions (Noble and Gitay 1998, Stahlschmidt et al. 2011, Settele et al. 2014). At the same time, global phenomena like the El Niño Southern Oscillation (ENSO) are likely to intensify (Noble and Gitay 1998, Cai et al. 2014), even though, for example, changes in ENSO may not be consistently predictable (Wang et al. 2017). An intensified ENSO would lead to stronger and more frequent La Niña (i.e., cooler-than-average sea surface temperatures in the tropical Pacific) and El Niño (i.e., above-average sea surface temperatures in the tropical Pacific) events that will have continent-specific consequences including extensive droughts, bushfires, and extreme precipitation regimes followed by local flooding (Cai et al. 2014).

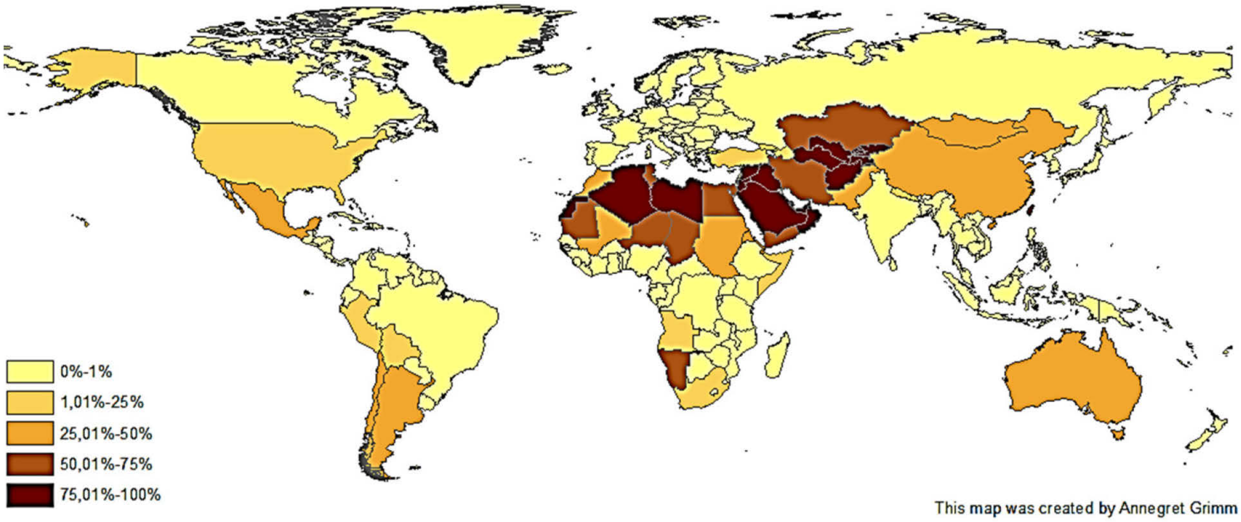

Figure 1.1: Percentage of terrestrial surface area covered by hot deserts and semi-deserts in each country. This map was created based on the ecoregions of the world, data by Olson et al. (2001).

With their extreme climatic conditions, hot deserts pose a challenge to biodiversity. For example, desert species are often exposed to climatic conditions at the limit of their tolerance thresholds (Barrows 2011). Accordingly, ecological processes in hot deserts strongly differ from those of tropical and temperate regions (Shmida et al. 1986). Hence, anticipating the impact of climate change in hot deserts cannot rely on simply extrapolating ecological findings from tropical and temperate regions. On the other hand, climate change will likely result in significant changes in the mostly endemic flora and fauna (Sala et al. 2000, Holmgren et al. 2006, Settele et al. 2014) as even small changes in temperature or precipitation in deserts may change species composition (Sala et al. 2000).

A major part of vertebrate density and diversity in deserts is represented by reptiles (Pianka and Schall 1981, Van Der Valk 1997, Powney et al. 2010). In a recent study, Roll et al. (2017) have shown that biodiversity hotspots of reptiles differ from those of other tetrapods with lizards in particular showing the highest species richness in both the tropical and arid regions. Especially in Australia, where lizard diversity is the highest worldwide (Webb et al. 2015, Roll et al. 2017), lizard richness peaks in the central inland deserts (Fig. 1.2) where the density and diversity of mammals, birds, and amphibians is particularly low (Powney et al. 2010, Coops et al. 2017). Reptile biodiversity hotspots in hot deserts are thus of high conservation importance (Webb et al. 2015). Regrettably, while several studies investigated climatic sensitivity of reptiles in (sub-)tropical and temperate regions (e.g., Aubret & Shine 2010, Brandt & Navas 2011, Huang & Pike 2011, Logan et al. 2013, Huang et al. 2014), very few studies investigated their climatic plasticity and possible adaptation mechanisms to climate change in hot drylands or deserts (Barrows 2011, Read et al. 2012, Jezkova et al. 2015, Walker et al. 2015). It is therefore of paramount importance to assess reptile species response to climate change in arid regions and to forecast future trends of a unique biodiversity component on Earth.

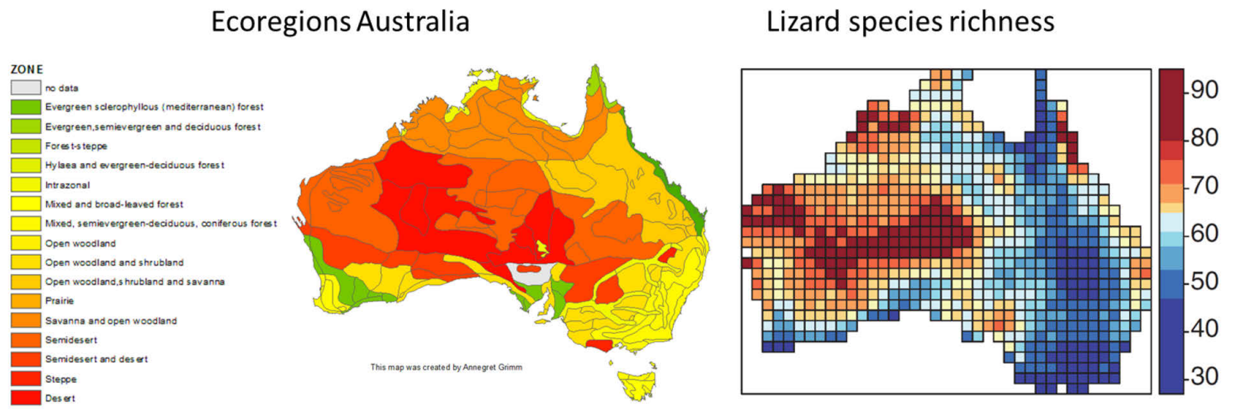

Figure 1.2: Highest lizard species richness areas are located in the most arid regions of Australia. The left map shows the ecoregions of Australia based on the data provided in Olson et al. (2001). The right map shows the lizard species richness on an equal-area Behrmann projection at a resolution of 96.49 km (approximately 1°). The colour coding refers to the number of lizard species per grid cell. This map was adapted from Powney et al. (2010).

1.3 Species responses to climate change: Reptiles in hot deserts

Reptiles are assumed to be particularly exposed to climate change (Deutsch et al. 2008, Kearney et al. 2009, Henle et al. 2010, Gunderson and Leal 2015), because most of their biology is tightly linked to external temperature (Bogert 1949, Carvalho et al. 2010; Fig. 1.3). They were recently found to have relatively low phenotypic plasticity in thermal tolerance and, together with other terrestrial ectotherms, showed high risks of overheating (Gunderson and Stillman 2015). There is mounting empirical evidence that climate change is already having various impacts on different aspects of the ecology of reptiles (e.g., Parmesan and Yohe 2003, Walther 2010). Likewise, species distribution models (SDM), which are based on the current climatic requirements of species and frequently try to match species' 'climate envelopes' with projected future climatic conditions, have suggested that many reptile species face major range shifts and a substantial threat of extinction (Wake 2007, Deutsch et al. 2008, Sinervo et al. 2010, Urban 2015). However, results of predictive models should be interpreted carefully due to a high number of uncertainties in model assumptions (Davis et al. 1998, Urban et al. 2016). Predicting the impacts of climate change on reptiles will likely not be straightforward (Clusella-Trullas et al. 2011). Hence, it is imperative to analyse recent changes in reptile populations in response to climatic fluctuations to gather information on how those species could respond in the future.

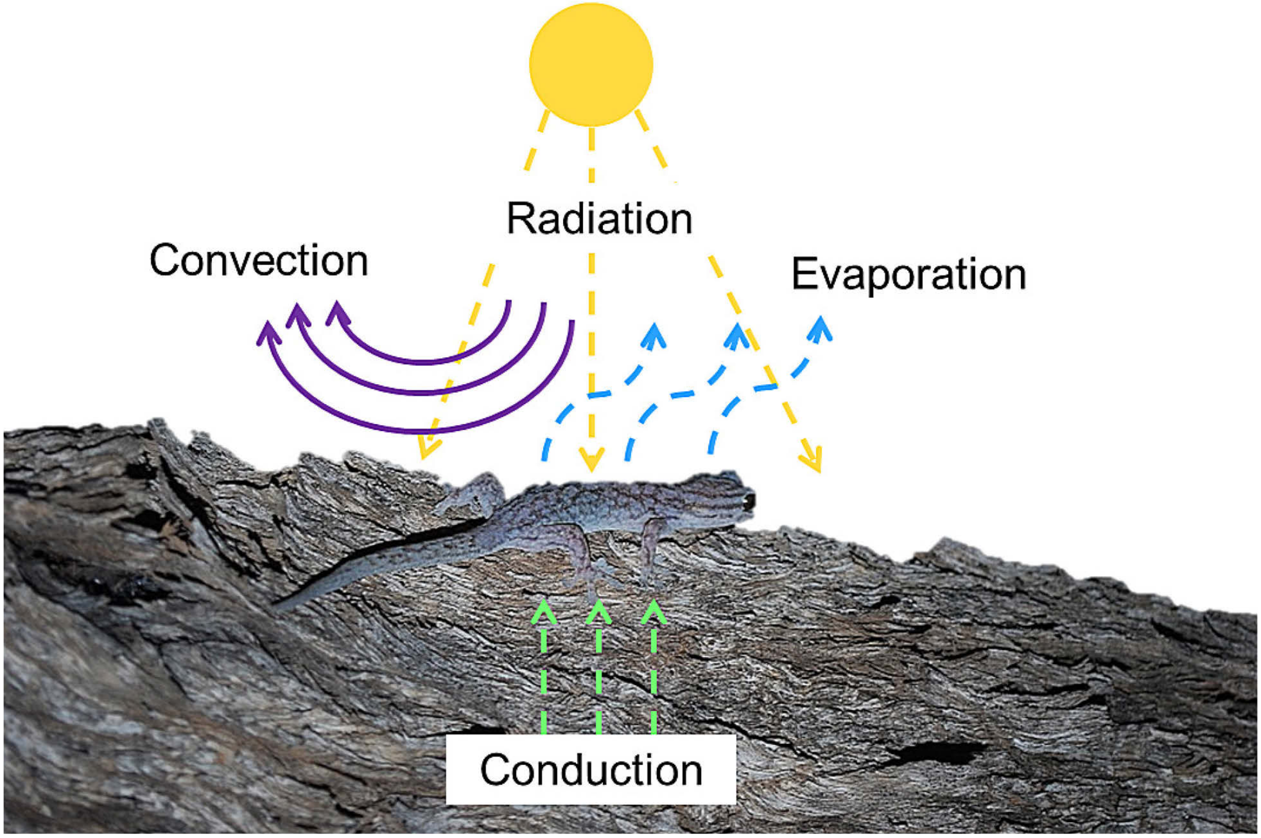

Figure 1.3: Reptiles as ectotherms are highly influenced by external temperature, especially through solar and infrared radiation, soil temperature (conduction), water loss (evaporation), and wind speed (convection). Adapted from Porter et al. (1973). Photo by Annegret Grimm-Seyfarth.

Desert reptile species will likely react asynchronously to fluctuations of local climatic conditions (Read 1995, Dickman et al. 1999, Letnic et al. 2004, Read et al. 2012). Therefore, we need a detailed understanding of the ecology and life-history of single reptile species. To date, studies that determined climatic effects on certain reptile species over time focussed mainly on specific climatic parameters, e.g. on the effects of rainfall (e.g., Dickman et al. 1999, Letnic et al. 2004, Holmgren et al. 2006, Ryan et al. 2016) or temperature (e.g., Chamaillé-Jammes et al. 2006, Massot et al. 2008, Monasterio et al. 2013). Only recently, a few studies started investigating several climatic factors simultaneously but they concentrated mainly on the effect of specific ecological processes, such as the suitable habitat niche (Barrows 2011), demography (Read et al. 2012), or activity (Walker et al. 2015). However, the relative influence of various local (rainfall, temperature) and distant (e.g., through ENSO) climatic factors might not just differ among species but also among ecological processes. It is therefore important to study these across organisational levels and at different spatial scales.

Both analyses of recent changes in reptile populations and predictions of future reptile persistence or range shifting have been mainly based on correlative approaches. In a review of 130 studies that predicted future species distributions, Urban et al. (2016) found that only 23% of them considered an underlying biological mechanism. While correlative approaches could give a general overview of what goes on with a particular system, they cannot be transferred to other species, ecosystems, or even other populations of the same species. Thus, it is not surprising that mechanistic or process-based models consistently better predict simulated species than pure correlative models (Pagel and Schurr 2012). Kearney et al. (2010a) argued that the best approach for predicting future species distributions is the use of two independent models, one correlative and one mechanistic. On the other hand, Mokany and Ferrier (2011) suggested a combination between correlative and process-based approaches into one semi-correlative approach to be able to include ecological processes into known methods under the limits of current knowledge.

Notably, even the choice of the most appropriate mechanistic model is not obvious since many possible mechanisms could influence the response of certain species to climate change. Urban et al. (2016) categorised those possible mechanisms determining species' response to climate change into six groups: (1) *Physiology*; (2) *Demography*, life history, and phenology; (3) *Dispersal*, colonisation, and range dynamics; (4) *Species interactions*; (5) *Evolutionary* potential; and (6) Responses to *environmental* variation. Our mission in contemporary ecology should be to investigate those mechanisms and their potential interactions in many species to enhance our fundamental understanding of species-specific processes. This knowledge can then be incorporated into predictions of future species responses, persistence, and range shifts which will considerably improve future conservation planning. Accordingly, we need more long-term studies in the field to investigate those mechanisms, since to date extensive field data are still lacking for most taxa and many regions of the world (Thuiller 2007, Ferreira et al. 2016, Urban et al. 2016).

For reptiles in hot deserts, one of the most critical challenges is to stay cool (Kearney et al. 2009). Consequently, desert reptiles have evolved different kinds of mechanisms, enabling them to offset the impacts of hot temperatures (Bartholomew 1964). As likely the most important mechanism, thermoregulatory behaviour can buffer climatic variations to some extent (Angilletta 2009). Thermoregulatory behaviour is likely to be present in all reptiles and includes seeking optimal thermal environments by basking, warming up on substrate, cooling down in the shade, and shuttling among thermally different microhabitats (Bogert 1949, Arribas 2010, 2013, Ortega et al. 2016). At the individual level, thermoregulatory behaviour that adjusts body temperature according to microhabitat conditions might be even more important for securing activity budgets than the environmental conditions on large spatial scales (Adolph and Porter 1993, Sears and Angilletta 2015). This mechanism is *physiological* and it can drive the extent to which a reptile species needs to thermoregulate behaviourally (Angilletta 2009). However, thermoregulatory strategies including thermoregulation effort and accuracy were found to vary strongly between hot and cold environments (Vickers et al. 2011). Especially in hot deserts, the efficiency of behavioural thermoregulation strongly depends on the availability of alternative microclimatic conditions such as shade provided by vegetation cover (Kearney et al. 2009, Kearney 2013). For example, Read et al. (2012) found that various *demographic* parameters of several desert lizard species were correlated with vegetation cover and both Letnic et al. (2004) and Dickman et al. (1999) detected that desert lizard abundance differently changed among species with changing vegetation cover and composition. However, all authors pointed out that lizard abundance and survival also responded to rainfall and temperature patterns directly, as did reproductive traits (Smith et al. 1995, Read et al. 2012). Climatic variations will clearly alter species responses on an individual (e.g., body condition, body growth) and population level (e.g., population size, survival), but also the persistence of vegetation with climatic changes could largely determine those responses. Thus, *demographic* responses to both *environmental* variation but also non-trophic *species interactions* between reptiles and vegetation are also an important mechanism for reptiles in hot deserts.

Generally, no climatic factor will affect reptiles only directly, but rather will act through multiple pathways (Ockendon et al. 2014, Deguines et al. 2017). In addition to the described non-trophic interactions between reptiles and vegetation, reptiles are affected by trophic *interactions*. This is particularly important in deserts where the longest chain lengths in food webs have been found since many species have broad diets due to high food scarcity (Pianka 1986, Van Der Valk 1997). Hence, reptiles are strongly dependent on food availability (Ballinger 1977, Dunham 1981, Pianka and Vitt 2003, Barrows 2011) while their communities are largely shaped by predation (Pianka 1986). In turn, changes in single reptile populations will likely modify the overall web of interactions at the community level (Walther 2010). Regrettably, trophic and non-trophic species interactions are largely unknown and therefore are complicated to consider when analysing reptiles in the light of climate change (Bellard et al. 2012). Especially multiple climatic and biotic relations and indirect pathways among those relations have rarely been examined collectively. However, effects from multiple pathway investigations may differ fundamentally from effects of isolated climatic or biotic factors since single factors could be enhanced by synergistic pathways or diminished by opposing pathways (Werner and Peacor 2003, Côté et al. 2016, Deguines et al. 2017). Therefore, recent calls have been made for species monitoring on multiple trophic levels to understand the overall effects of drivers of global change on single species, knowledge that is essential for optimal future conservation strategies (Ockendon et al. 2014).

1.4 Effects of climate change on a reptile community in arid Australia

As shown above, we still lack profound knowledge about the underlying mechanisms determining how reptile species respond to different climatic parameters at different spatial scales. This knowledge is necessary to predict future reptile distributions and to adapt future conservation strategies. With this thesis, my goal is to fill in some of those knowledge gaps by focussing on one reptile community in an arid-zone National Park of Australia. I took advantage of the unique opportunity provided by a detailed 30-year long-term reptile monitoring scheme that started in 1985 and which I continued from 2012 to 2016. My main objective was to investigate how reptile species respond to various climatic parameters at different spatial scales and to analyse the two main potential underlying mechanisms: thermoregulatory behaviour and interactions of species with their biotic environment. Since water availability and excessive temperatures are limiting factors for many desert organisms, I generally hypothesised that an increase in temperature might have negative effects whereas increased water availability should have positive effect at the individual and the population level. I further assumed a strong effect of non-trophic (shade, refuge) and trophic (food, predation) species interactions and similarities in responses of species with similar traits. My findings are summarised in three articles (Chapters 3-5) all of which are published or in revision for publication.

My first article entitled “Some like it hot: from individual to population responses of an arboreal arid-zone gecko to local and distant climate” is currently under the second review and considered for publication in the journal *Ecological Monographs*. In this first article, I determined the relative contribution of various local and distant climatic factors on several life-history traits at individual (body condition, body growth) and population levels (population size, survival) of an arboreal, nocturnal gecko species (*Gehyra variegata* (Duméril & Bibron, 1836)). This species is of particular interest to such investigations as it is a long-living species (up to 28 years in the study area) and responses of long-living species to climate have rarely been studied. Specifically, I investigated the effects of climatic parameters on individual traits as well as on survival and abundance of the population and whether there are intra-specific trade-offs among adaptations to climate. To investigate potential mechanistic processes which could explain the observed patterns, I further investigated the thermoregulatory behaviour during both the active (night) and the resting (day) part of the day. I found that relative effects of various local and distant climatic parameters differed depending on the ecological level considered. Plasticity in life-history traits at the individual level in response to adverse climatic conditions could partly buffer consequences on the population level by maintaining survival rates. Furthermore, only cool temperatures induced diurnal thermoregulatory behaviour likely inducing costs on fitness (e.g., greater predation risk), which could decrease performance at both individual and population level under cool temperatures. Overall, this study showed that water availability rather than high temperature is the limiting factor in our focal population of *G. variegata*.

My second article entitled “Too hot to die? The effects of vegetation shading on past, present, and future activity budgets of two diurnal skinks from arid Australia” has been published in the journal *Ecology and Evolution* in 2017 (7:6803-6813). In this article, I investigated the mechanism of thermoregulatory behaviour in two diurnal, terrestrial skink species, *Morethia boulengeri* (Ogilby, 1890) and *Ctenotus regius* (Storr, 1971). Specifically, I examined the interacting effects of vegetation on body temperatures and activity budgets to determine the activity budgets under past (1985 to now) and future (until 2090) climatic conditions. In this approach, I combined different data sets by calibrating high-resolution experimental data to longer but less accurate time series with different temporal resolutions to assess the species’ responses to climate change. I found this to be a promising approach to fill in knowledge gaps in past climatic and ecological conditions whose reconstructions create important challenges but which are imperative to address the long-term responses of species to environmental changes. With this approach I could identify that both the thermoregulatory behaviour and the activity budgets of diurnal, terrestrial desert skinks were strongly impacted by the amount of vegetation and its heterogeneity, which provided both cooling spots and heat reservoirs. Although climate change is likely to lead to a species-specific reduction in activity budgets in mid-summer, it might also provide novel temporal niches that could even contribute to an increasing annual activity budget. Moreover, with this study I highlighted that the cascading effects of vegetation, rather than climatic envelopes alone should be considered in future conservation strategies to prevent desert lizards from extinction.

My third article entitled “Eat or be eaten: Desert reptiles between prey, predators and climatic extremes” is currently under review by the journal *Global Change Biology*. In this article, I focussed on interspecific interactions in the light of climatic fluctuations. I investigated the direct and indirect effects of both climatic and biotic parameters at the individual body condition and occupancy of the eight most abundant lizard species occurring in my study area. I used structural equation modelling to disentangle single and interactive effects of climatic and biotic parameters. Additionally, I assessed whether species could be grouped in functional groups according to their responses to climatic and biotic parameters. Overall, lizard species differed strongly in how they reacted to climatic and biotic factors. Interestingly, the factor to which they responded seemed to be closely related to their functional groups. The findings of this study further highlighted key actions for future predictions of the impacts of climate change and conservation planning: (1) Inclusion of indirect pathways in SDMs to increase accuracy when predicting future species presence; (2) consideration of species functional groups for modelling since one might never obtain all mechanistic pathways on species level; and (3) conservation of natural floodplains in hot deserts to secure a natural turn-over of the community composition. With those key actions, it is possible that the effects of climate change in a desert reptile community could be buffered to a large extent.

As first author of each article, I conceptualised all studies under the commonly accepted support of my supervisors, conducted field experiments, data analyses, and predictive modelling on my own and wrote the manuscripts. All manuscripts contain suggestions from the co-authors and chapters 3 and 4 further contain suggestions from independent reviewers of the journal. Despite this dissertation will be presented in a unique format, the contents of the chapters 3-5 are identical to the articles submitted to or published in the scientific journals. This includes that no words were changed and the spelling (American or British English) requested by the journal was used. Graphs and figures were included in the Chapters, but references can be found at the end of the thesis altogether.

2 General methodology

2.1 Study area: Kinchega National Park, Australia

Australia's arid interior has experienced strong and above-average climate warming with an average temperature increase of 0.9°C since 1950 (Suppiah et al. 2007). Extreme rainfall events are rising in severity, while concomitantly dry periods are extending in time (Watterson et al. 2015). In addition, Australia's arid zones are expected to undergo major climate-related changes via ENSO (Holmgren et al. 2006). While El Niño events cause droughts during the year they occur, La Niña events cause excessive rainfall in Australia's coastal areas and the Great Dividing Range that extend through large river systems from the distant Great Dividing Range to the arid interior. This process can last up to one year (Thoms and Sheldon 2000).

The complexity of different local and distant climatic drivers, the high species richness, and the comparably undisturbed environment make Australia's arid interior, the so-called outback, a very suitable location for studying the effects of climate change on reptiles. Specifically, I continued a long-term reptile monitoring scheme which started 1985 in Kinchega National Park, New South Wales (32°28' S, 142°20' E). Kinchega is situated at the eastern margin of Australia's arid zone (Fig. 2.2). It is characterized by high summer temperatures and low, but highly variable, rainfall without seasonal patterns (Robertson et al. 1987; Fig. 2.1). Kinchega shows typical characteristics of a desert under climate change, with rising temperatures and more extreme rainfall patterns (Noble and Gitay 1998, Stahlschmidt et al. 2011). In the last 30 years, the average maximum summer temperature increased by 3.12°C (Fig. 2.1). Kinchega additionally contains floodplains with flooding being related to rainfall in inland Queensland due to La Niña events (Simpson et al. 1993, Bureau of Meteorology 2012). A huge amount of water is carried over more than 1,000 km downstream by the Darling River, part of Australia's largest river system, to Kinchega National Park.

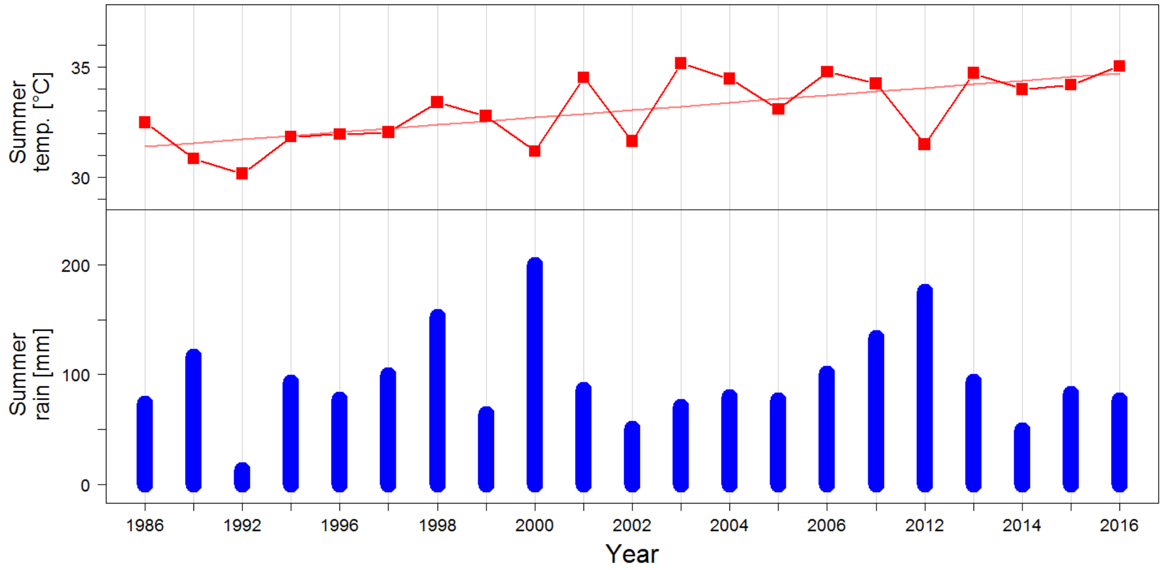

Figure 2.1: Mean maximum summer temperature [°C] and total summer rainfall [mm] in the years when summer monitoring took place from 1986 to 2016. The regression line for summer temperature over time is indicated. Data provided by the Bureau of Meterology (see Chapter 3).

In Kinchega, three main study plots representing a range of various vegetation compositions and coverages were monitored: two different riverine woodlands and the Kinchega station (Fig. 2.2). I monitored a fourth plot, the dune (Fig. 2.2), but since monitoring has only rarely been undertaken in the previous years, I excluded those data from this dissertation. Distribution and names of the plots followed Henle (1989a, 1990a). The first riverine woodland plot (RWI) was characterised by cracking clay, widely dispersed black box eucalypts (*Eucalyptus largiflorens* F. Muell), and temporally highly varying ground vegetation cover. The study plot comprised an area of approximately 140x200 m containing 60 eucalypt trees. The second riverine woodland plot (RWII) of approximately 80x25 m was characterised by sandy clay with only slightly dispersed black box eucalypts. The shrub layer was dominated to varying extents by black blue bush (*Maireana pyramidata* (Benth.) Paul G. Wilson), black rolypoly (*Sclerolaena muricata* (Moq.) Domin), cannonball burr (*Dissocarpus paradoxus* (R.Br.) F. Muell. ex Ulbr.), and Ruby Saltbush (*Enchylaena tomentosa* (R.Br.)). The herb layer coverage varied strongly among years. The third study plot was the Kinchega field station (hereafter station), which covered an area of approximately 2,000 m² consisting of seven huts in 1986/7 and of eight huts since 1991 made of corrugated iron and with sandy soil between the huts. During the 30 years, park rangers and individual researchers used the huts during varying amounts of time resulting in different light intensities during nights and a patch of irrigated grass but occasionally cut shrubs.

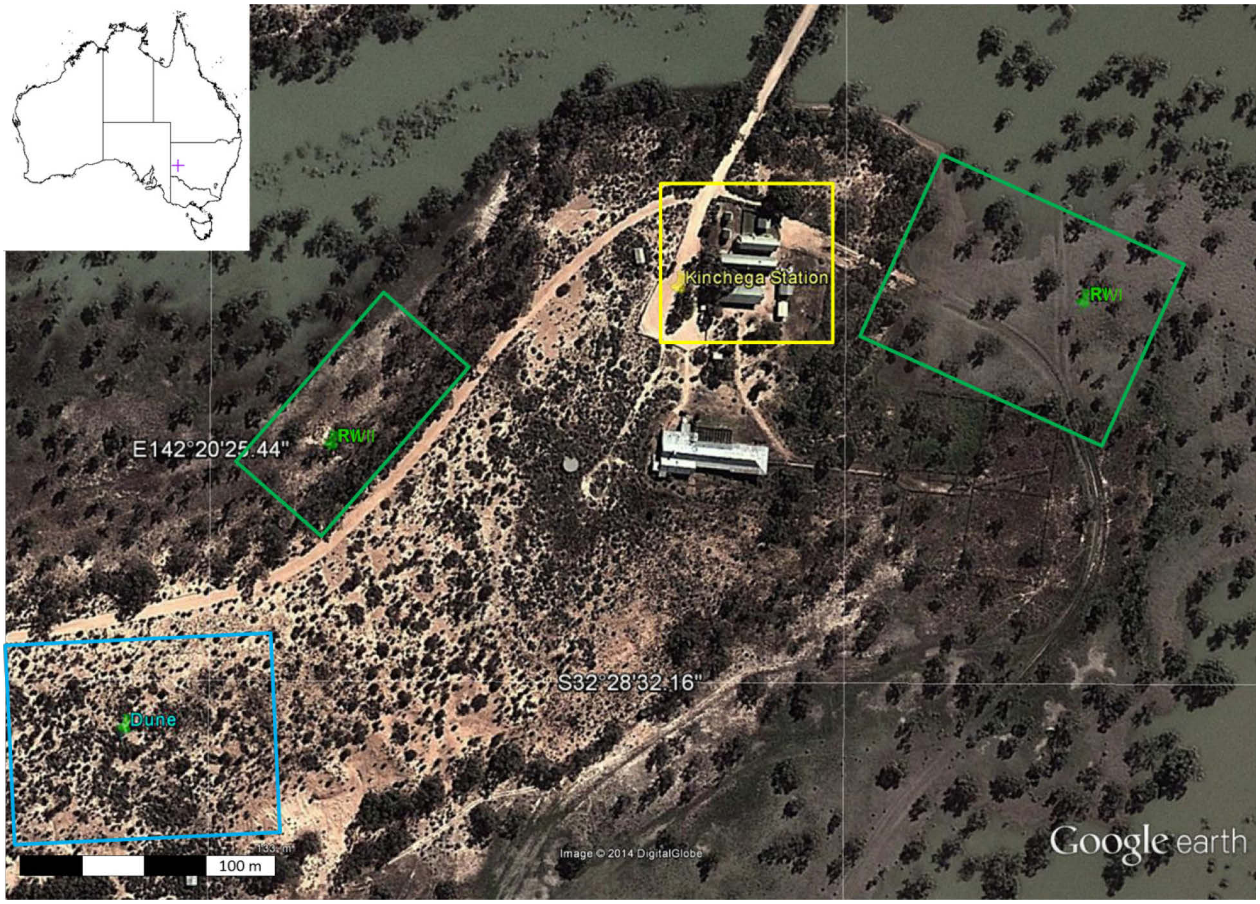

Figure 2.2: Study plots monitored in Kinchega National Park. The inserted figure shows the location of Kinchega National Park in New South Wales, Australia.

2.2 Study species

Monitoring took place on an almost annual basis at the end of the reproductive season in February or March from 1986 to 2016 except for 1988-1991, 1993, 1995, and 2008-2011. In total, 23 reptile species were caught or observed in the study plots (Table 2.1). In the whole National Park, 33 reptile species have been observed during the last 30 years. Species names follow Cogger (2014) except for one name following Greer (1990) who showed that *L. aericeps* is a synonym of *L. xanthura*.

Table 2.1: Reptile species caught or observed in the main study plots over 30 years of reptile monitoring (1985 to 2016). The eight most abundant species are highlighted in bold.

Clade	Family	Species
Sauria	Gekkonidae	***Gehyra variegata***
		Heteronotia binoei
		Lucasium damaeum
		Lucasium byrnei
		Diplodactylus tessellatus
		Rynchoedura ornata
	Scincidae	***Eremiascincus richardsonii***
		Ctenotus regius
		Morethia boulengeri
		Menetia greyii
		Lerista punctatovittata
		Lerista xanthura
		Tiliqua rugosa
	Agamidae	*Ctenophorus pictus*
		Pogona vitticeps
	Varanidae	*Varanus gouldii*
		Varanus varius
Serpentes	Typhlopidae	*Rhamphotyphlops bituberculatus*
		Rhamphotyphlops proximus
	Pythonidae	*Morelia spilota*
	Elapidae	*Pseudonaja textilis*
		Furina diadema
		Suta suta

Each species was caught during its active time of the day. The capture methods were adapted to the species that were known to occur in each study plot and therefore differed among them. We caught nocturnal geckos and *E. richardsonii* by spotlighting along transects in the RWI and at the station for at least five days per plot per season (9.8 and 6.8 days on average at RWI and station, respectively). We also checked for the presence of diurnal lizards in both study plots once per day. In the RWII plot, twenty-four 11L-icecream-containers were buried as pitfall traps in the centre of sixteen 10x10 m and eight 5x10 m quadrats. All traps were provided with a 2-3 cm soil layer to allow trapped individuals to bury themselves. Traps were checked at least once a day over at least ten days (20 days on average) and were removed between capture seasons. Additionally, *M. boulengeri* was caught by hand in the RWII plot by searching transects over at least five days (10 days on average). Every individual caught was measured, weighted, sexed and aged (if possible), photographed for long-term identification, and marked with a dorsal colour mark for short-term identification. Additionally, *M. boulengeri* and *G. variegata* were individually marked through toe-clipping which had no negative effect on either species (Hoehn et al. 2015). Elapid and pythonid snakes and goannas were not captured, except for a few juveniles that were caught in pitfall traps, but when they were observed, their estimated size and age was recorded. Analyses of this dissertation are based on the eight most abundant lizard species (Fig. 2.3). However, other species were considered when analysing species interactions (Chapter 5).

During each monitoring season, and for each study plot, we further collected information on vegetation, prey, and predator abundances. Details on collection methods and calculations of indices can be found in the methodological section of Chapter 5. Furthermore, local temperature and humidity were measured in the study plots throughout the day and year in selected years to have detailed on-site measurements for comparison with data from the closest weather station (station 047019 Menindee Post Office). Details on those measurements and how data were calibrated are described in the Appendix of Chapter 3.

Figure 2.3: The eight most abundant lizard species. Photos by Annegret Grimm-Seyfarth.

2.3 Data accessibility

All abiotic data are available online:

Climate data: Bureau of Meteorology, Australian Government, http://www.bom.gov.au/climate/data/stations, http://www.bom.gov.au/climate/current/soi2.shtml;

River height data: Department of Primary Industries, Office of Water, New South Wales Government, http://realtimedata.water.nsw.gov.au/water.stm?ppbm=DAILY_REPORTS&dr&3&drkd_url;

Sunrise and sunset data: Geoscience Australia, Australian Government, http://www.ga.gov.au/geodesy/astro/sunrise.jsp

Species data:

Own measurements of Chapter 4 are available on Dryad: https://doi.org/10.5061/dryad.jg470

Species data of Chapters 3 and 5: Data will be made available through DRYAD upon acceptance of the articles

Monitoring data were provided to National Parks and Wildlife Service New South Wales, Office of Environment and Heritage, Department of Premier and Cabinet representing the State of New South Wales, and implemented in the Atlas of Living Australia: https://www.ala.org.au/

3 Individual and population responses to climatic fluctuations

Essential processes for a mechanistic understanding of the effects of climate change on reptile species are the different effects on various ecological levels, such as individual and population levels. These processes will ultimately lead to either shifts in distribution, adaptation to changed local conditions, or extinction. Investigating these processes and linking them to abundance or distribution patterns is therefore critical for a better understanding and more reliable predictions of the effects of climate change on biodiversity and would support adjusting conservation strategies to the new challenges arising from climate change. However, such detailed investigations are only possible with extensive field data. With more than 13,000 captures and recaptures of more than 3000 individuals in two study plots, the arboreal, nocturnal gecko species *Gehyra variegata* (Duméril & Bibron, 1836) provides an excellent opportunity to determine the relative contribution of various local and distant climatic factors on several life-history traits at individual (body condition, body growth) and population levels (population size, survival). This species is of particular interest to such investigations as it is a long-living species (up to 28 years in the study area) and responses of long-living species to climate have rarely been studied. I further examined whether thermoregulatory behaviour during both the active (night) and the resting (day) part of the day can mechanistically explain these responses. I hypothesised that an increase in temperature might have negative effects whereas increased water availability should have positive effect at the individual and population levels.

Title:	Some like it hot: from individual to population responses of an arboreal arid-zone gecko to local and distant climate
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Some like it hot: from individual to population responses of an arboreal arid-zone gecko to local and distant climate

3.1 Abstract

Accumulating evidence has demonstrated considerable impact of climate change on biodiversity, with terrestrial ectotherms being particularly vulnerable. While climate-induced range shifts are often addressed in the literature, little is known about the underlying ecological responses at individual and population levels. Using a 30-year monitoring study of the long-living nocturnal gecko *Gehyra variegata* in arid Australia, we determined the relative contribution of climatic factors acting locally (temperature, rainfall) or distantly (La Niña induced flooding) on ecological processes from traits at individual level (body condition, body growth) to demography at population level (survival, sexual maturity, population sizes). We also investigated whether thermoregulatory activity during both active (night) and resting (daytime) periods of the day can explain these responses. *G. variegata* responded to local and distant climatic effects. Both high temperatures and high water availability enhanced individual and demographic parameters. Moreover, the impact of water availability was scale-independent as local rainfall and La Niña induced flooding compensated each other. When water availability was low, however, extremely high temperatures delayed body growth and sexual maturity while survival of individuals and population sizes remained stable. This suggests a trade-off with traits at the individual level that may potentially buffer the consequences of adverse climatic conditions at the population level. Moreover, hot temperatures did not impact nocturnal nor diurnal behavior. Instead, only cool temperatures induced diurnal thermoregulatory behavior with individuals moving to exposed hollow branches and even outside tree hollows for sun-basking during the day. Since diurnal behavioral thermoregulation likely induced costs on fitness, this could decrease performance at both individual and population level under cool temperatures. Our findings show that water availability rather than high temperature is the limiting factor in our focal population of *G. variegata*. In contrast to previous studies, we stress that dryer rather than warmer conditions are expected to be detrimental for nocturnal desert reptiles. Identifying the actual limiting climatic factors at different scales and their functional interactions at different ecological levels is critical to be able to predict reliably future population dynamics and support conservation planning in arid ecosystems.

3.2 Introduction

Global mean surface temperature has rapidly risen since the late 19th century, with an exceptional increase within the past three decades (IPCC 2013). Until 2100 a further increase by up to 4°C is expected. Predictions for changes in precipitation strongly vary across latitude, with an expected increase over wet regions and a decrease over dry regions (IPCC 2013). Accumulating evidence has already demonstrated considerable impact of human-induced climate change on biodiversity and a range of ecological processes (e.g., Walther et al. 2002, Parmesan and Yohe 2003, Tewksbury et al. 2008, Bellard et al. 2012, Davey et al. 2013, Cavallo et al. 2015), with many species predicted to decline or even to become extinct (Araújo et al. 2006, Wake 2007, Sinervo et al. 2010, Cahill et al. 2014).

Species can respond to climate change through local genetic adaptation and behavioral plasticity (e.g., changes in phenology, activity, and demography) (Urban et al. 2014, Seebacher et al. 2015) or range shifts (McCarty 2001, Walther et al. 2002, Monasterio et al. 2013, Srinivasulu and Srinivasulu 2016); else they may become extinct (Devictor et al. 2008, 2012, Raxworthy et al. 2008, Cahill et al. 2014). Whereas many studies have documented observed and expected range shifts and extinction risks (Araújo et al. 2006, Wake 2007, Deutsch et al. 2008, Sinervo et al. 2010), much less is known about the underlying ecological processes (e.g., Monasterio et al. 2013). Essential processes for a mechanistic understanding are the effects of climate change at the individual and population level, which ultimately will lead to either shifts in distribution, adaptation to changed local conditions, or extinction. Investigating these processes and linking them to abundance or distribution patterns is therefore critical for a better understanding and more reliable predictions of the effects of climate change on biodiversity (Jenouvrier et al. 2009, Kearney et al. 2009, Evans et al. 2013). Such knowledge would support adjusting conservation strategies to the new challenges arising from climate change.

Ectotherms are assumed to be particularly exposed to climate change (Deutsch et al. 2008, Kearney et al. 2009, Henle et al. 2010, Gunderson and Leal 2015) as most of their biology is tightly linked to external temperature (Bogert 1949, Carvalho et al. 2010). They were recently found to have relatively low phenotypic plasticity in thermal tolerance and especially terrestrial taxa like reptiles showed high overheating risks (Gunderson and Stillman 2015). Whereas several studies investigated climatic sensitivity of reptiles in (sub-)tropical and temperate regions (e.g., Aubret & Shine 2010; Brandt & Navas 2011; Huang & Pike 2011; Logan et al. 2013; Huang et al. 2014), very few studies investigated their climatic plasticity and possible adaptation mechanisms to climate change in hot deserts (Barrows 2011, Read et al. 2012, Jezkova et al. 2015, Walker et al. 2015). There, reptiles represent a major part of vertebrate density and diversity (Pianka and Schall 1981, Van Der Valk 1997, Powney et al. 2010) and are thus of high conservation importance (Webb et al. 2015). However, ecological processes in hot deserts are typically characterized by extreme climatic conditions, which strongly differ from those of tropical and temperate regions (Shmida et al. 1986). Accordingly, desert species are often exposed to climatic conditions at their tolerance limits (Barrows 2011). Hence, anticipating the impact of climate change on reptiles in such regions cannot rely on simply extrapolating ecological findings from tropical and temperate regions. Moreover, hot deserts will experience even hotter and dryer conditions in the future (Noble and Gitay 1998, Stahlschmidt et al. 2011, Settele et al. 2014), likely resulting in significant changes in mostly endemic flora and fauna (Sala et al. 2000, Holmgren et al. 2006). Anticipating these changes is of paramount importance to assess biodiversity response to climate change in arid regions, and to forecast future trends of a unique biodiversity component on Earth.

Arid Australia harbors the world’s highest species diversity of reptiles (Pianka 1968, Powney et al. 2010, Webb et al. 2015). With an average temperature increase of 0.9°C since 1950, Australia’s arid interior has experienced strong and above-average climate warming in Australia. Extreme rainfall events are rising, but simultaneously dry periods are extending (Watterson et al. 2015). In addition, Australia’s arid zones are expected to undergo major climate-related changes via the El Niño Southern Oscillation

(ENSO) (Holmgren et al. 2006). While El Niño events cause droughts within the year they appear, La Niña events cause excessive rainfall in Australia's coastal areas and the Dividing Range. Then, these exceptional amounts of rainfall spread though large river systems from the distant Dividing Range to the arid interior. This process can last up to one year (Thoms and Sheldon 2000).

While some studies already determined specific climatic effects on reptiles over time (e.g., rainfall: Dickman et al. 1999, Letnic et al. 2004, Holmgren et al. 2006, Ryan et al. 2016; temperature: Chamaillé-Jammes et al. 2006, Massot et al. 2008, Monasterio et al. 2013), only a few investigated several climatic factors simultaneously and if so, they considered exclusively one specific ecological process (e.g., Smith et al. 1995, Read et al. 2012). However, the relative influence of various local (rainfall, temperature) and distant (ENSO) climatic factors might be different among ecological processes.

In this study we take advantage of the unique opportunity provided by a 30-year long-term detailed monitoring of an arboreal, nocturnal gecko species (*Gehyra variegata* (Duméril & Bibron, 1836)) in arid Australia to determine the relative contribution of various local and distant climatic factors at individual and population levels. This species is of particular interest to such investigations as it is a long-living species (up to 28 years in our study area) and reactions of long-living species to climate have rarely been studied. Specifically we investigated (1) effects of climatic parameters on individual traits, such as body condition and body growth rate; (2) effects of climatic parameters on survival and abundance of the population, and whether there are trade-offs among adaptations to climate; and (3) whether thermoregulatory behavior during both the active (night) and the resting (day) part of the day can mechanistically explain these patterns. Since water availability and excessive temperatures are limiting factors for many desert organisms (Holmgren et al. 2006), we hypothesized that an increase in temperature might have negative effects whereas increased water availability should have positive effect at the individual and population levels.

3.3 Materials and methods

3.3.1 STUDY SITE AND STUDY SPECIES

We conducted our study in Kinchega National Park, New South Wales, Australia (32°28' S, 142°20' E). Kinchega is situated at the eastern margin of Australia's arid zone. It is characterized by high summer temperatures and low but highly variable rainfall without seasonal patterns (Robertson et al. 1987). Kinchega shows typical characteristics of a desert under climate change, such as rising temperatures and more extreme rainfall patterns (Noble and Gitay 1998, Stahlschmidt et al. 2011). It additionally contains floodplains, with flooding being related to rainfall in inland Queensland due to La Niña events (Simpson et al. 1993, Bureau of Meteorology 2012, Appendix S1.1). A huge amount of water is carried over more than 1000 km downstream by the Darling River, part of Australia's largest river system, to Kinchega National Park.

Our study area in riverine woodland contained 41 black box trees (*Eucalyptus largiflorens*) in an area of approximately 150 x 100 m; additionally, 19 trees in the vicinity were surveyed to detect moving individuals. We captured our study species, the arboreal, nocturnal gecko *Gehyra variegata* (Fig. 1), annually during their active period between February and March (except 1986 and 1987 when sampling occurred in both January and March), corresponding to the end of the reproductive season when all offspring have hatched (Henle 1990a). Sampling followed a robust design (Pollock and Otto 1983) comprising five to 19 secondary periods per year (year being the primary periods) (Fig. S3.1). In total, we sampled *G. variegata* on an almost annual basis from 1986 to 2016 except for the following years: 1988-1991, 1993, 1995, and 2008-2011.

Figure 1: The arboreal, nocturnal gecko *Gehyra variegata* from Kinchega National Park, arid Australia.

We caught geckos at night by hand, measured, sexed, and marked them by clipping the tip of the toe and with a dorsal none-toxic color mark for short-term identification (Henle 1990a). This marking method has no influence on the chance of survival in that species (Hoehn et al. 2015).

3.3.2 CLIMATE DATA

We used local climatic data from the Bureau of Meteorology, Australian Government (http://www.bom.gov.au/climate/data/stations), from the weather station closest to Kinchega (station 047019 Menindee Post Office). To ensure that these data matched with local conditions in Kinchega, we deployed data loggers in the study site and performed comparisons (Appendix S1.2). As local climatic parameters, we used monthly mean maximum temperatures, summed monthly precipitation, and numbers of days above 45°C during summer (#days>45°C). This latter parameter is a proxy of the number of days exceeding the species' average upper thermal activity range (being 45°C for this species; Henle 1990), which may impact on both individual and population level. We defined summer from the first month when all geckos were fully active during each night (November, Henle 1990) until the month when the geckos were caught (February or March). We further investigated the effect of total rainfall during the hibernation period from April to October, as this local winter rainfall has been known to affect vegetation density and biomass in Kinchega in the following summer (Robertson 1987, 1988).

Vegetation growth and biomass in Kinchega has also been shown to be affected by the Darling River, which is an important water source to the dynamic floodplains (Robertson et al. 1987). These floodplains might have influenced the entire ecosystem, including geckos. We therefore considered the monthly river height data from the closest weir to our study area (weir 32, available from the Department of Primary Industries, Office of Water, New South Wales Government; http://realtimedata.water.nsw.gov.au/water.stm?ppbm=DAILY_REPORTS&dr&3&drkd_url) as proxies for floodplain dynamics. We used averaged summer (previous October to March) and winter (previous April to previous September) river heights in our analyses. Previous analyses have already shown that the Darling River height was strongly related to ENSO phenomenon (Simpson et al. 1993, Appendix S1.1). Despite acting locally on the ecology of the gecko population, the Darling River height can be considered as a distant climatic factor induced by ENSO fluctuations. In addition, as the effects of a La Niña driven flood might have delayed consequences in the study area , we also considered the number of years after the study area was flooded (# years post flooding) as a test predictor reflecting (indirect) distant climatic parameters. Lastly, although the ENSO phenomenon has low impact on Australia's arid inland areas (Bureau of Meteorology 2012, Read et al. 2012), we investigated the direct effects of ENSO as other distant climatic parameters in comparison to the effects of local climate. We therefore calculated summer (October-March) and winter (April-September) mean indices of the Southern Oscillation Index (SOI, an index to track ENSO) using monthly time-series of the Bureau of Meteorology, Australian Government (http://www.bom.gov.au/climate/current/soi2.shtml) (Appendix S1.1).

3.3.3 BODY CONDITION AND BODY GROWTH RATES

We calculated body condition for 1917 geckos measured in Kinchega during the study period (Fig. S3.1). As an index for body condition, we used the scaled mass index (SMI) to account for growth, assuming that mass in a desert species is not only related to nutrition storage but also to water storage (Peig and Green 2009, 2010). First, we calculated the SMI calibration curve between mass and snout-vent-length by means of major axis regressions (Legendre 2014) from the measurements of a subset of 981 individuals that had a complete tail (original or regenerated, with complete tail being defined as at least as long as the snout-vent-length). Then, we obtained the SMI for all individuals by fitting the individual measurements to the calibration curve (Peig and Green 2009).

We calculated body growth rates as the relative differences in snout-vent-length in a given year in relation to the previous year (Fig. S3.1). We considered a reduced dataset of 658 geckos, since individuals need to be measured in two consecutive years for calculating a relative body growth rate.

To evaluate which climatic parameters affected body condition and body growth rate, we performed linear mixed modeling (LMM, McCullagh & Nelder 1989; Baayen 2008; Bolker et al. 2009), i.e., we considered a Gaussian error distribution and identity link function. We used the SMI and the body growth rate as response variables of independent LMMs. We used the local climatic parameters and river heights z-transformed to a mean of zero and a standard deviation of 1 as fixed effects test predictors. Since both summer and winter rainfall (Robertson 1987, 1988) and summer and winter Darling River heights (Robertson et al. 1987) could affect the vegetation and arthropod development (Kwok et al. 2016) in arid Australia, we also considered an interaction between each water related parameter and summer temperature. For comparison, we performed LMMs using direct distant (i.e., ENSO) climatic test predictors. To account for current and delay effects, we included the SOI of the current summer, the previous winter, and the previous summer. We tested every test predictor for quadratic versus linear relationships by means of AIC comparisons beforehand and chose the one which showed the lowest AIC. All local climatic parameters and Darling River parameters supported linear relationships while all SOIs supported quadratic relationships (ΔAIC > 2).

Additionally, we controlled for predictors (hereafter control predictors) that were not relevant with respect to our climate-related research questions but that may influence body condition and body growth rate in order to allow more robust and valid results (Mundry 2014). For body condition analyses, fixed effects control predictors included the day of individual measurements within a capture period (to account for the possibility of capture probability being related to body condition), the ratio of tail length by snout-vent-length (to account for energy channeled into tail regeneration), and a categorical variable combining age and sex (juveniles, subadults, adult females or adult males). Random effects control predictors controlling for pseudoreplications included the random intercepts of the gecko's ID, the year, the tree where the gecko was caught, the person who measured the individual, and the random slope of the day of measurements per year (Schielzeth and Forstmeier 2009, Barr et al. 2013). We did not consider the random slope of tree per year because we usually had a maximum of two observations per tree per year and, thus, no pseudoreplications were assumed (Appendix S3).

For analyses of body growth rates, we included the combined age-sex-variable and the random intercept of gecko's ID as control predictors. We did not include further random effects in these analyses since in the reduced dataset used for body growth rates no further pseudoreplications occurred (Appendix S3). Results for control predictors are not presented as they are part of the modeling design and strongly data-driven (Barr et al. 2013) (but see Table S3.3 for the explained variance of random effects). We did not consider any interaction between test and control predictors since control predictors describe currents states of individuals, which are unlikely to interact with climatic parameters.

For each analysis, we evaluated significance of the full models with Likelihood Ratio Tests (LRT) comparing the full models (i.e., including all test and control predictors) with the respective null models (i.e., excluding all test predictors but retaining all control predictors; Appendix S3) (Forstmeier and Schielzeth 2011, Mundry 2011). All models were significantly different from the null models unless otherwise stated. We fitted all possible model combinations out of our given set of test predictors since we did not have specific a-priori hypotheses of parameter combinations (Stephens et al. 2006). We conducted model comparisons using Akaike's Information Criterion (AIC). We considered a difference in AIC larger than 2 as a statistically different support of two models (Burnham and Anderson 2002). We calculated the relative importance of test parameters by summing up AIC weights (ωAIC) for each test predictor across models. We obtained parameter estimates and standard errors from full and most parsimonious models (Cade 2015) and their p-values with LRTs of the full model against the model without the effect in question. Although we conducted model comparisons and comparative parameter estimates using z-transformed predictors (Cade 2015), we also present untransformed coefficient estimates of the full models in the results to allow comparisons with other studies. Visual inspections of residual plots did not reveal any obvious deviations from homoscedasticity or normality assumption for both the analyses of body condition and body growth rates.

To disentangle the independent contribution of all fixed test predictors as a fraction of the total variance explained, we used hierarchical variance partitioning (Chevan and Sutherland 1991, Mac Nally 2002). For analyses of body growth rates, we conducted variance partitioning separately for all age classes as body growth rates varied considerably among age classes.

We performed all statistical analyses in R 3.1.1 (R Core Team 2016) unless otherwise stated. We used the packages *lme4* (Bates et al. 2015), *AICcmodavg* (Mazerolle 2016), *MuMIn* (Barton 2015), and *hier.part* (Walsh and Mac Nally 2013).

3.3.4 SURVIVAL AND JUVENILE-ADULT-TRANSITION PROBABILITIES

We estimated survival rates from individual recapture histories built by pooling individual capture-mark-recapture data from secondary periods (days within years) within each primary period (years) as an "ad-hoc" approach of the robust design (Fig. S3.1) (Pollock et al. 1990). We accounted for unequal time intervals by inserting non-detection ("0") in individuals' recapture histories for years when no sampling occurred and then fixing the recapture probabilities to 0 for those years. We fitted data to the standard Cormack-Jolly-Seber-model using program M-SURGE (Choquet et al. 2004).

We suspected survival to be age and sex specific. However, the sex was known for adults only since sex assignation of juveniles and subadults is impossible through visual observations. Therefore, we considered a multistate design allowing us to estimate specific annual survival and transition probabilities between the different life-stages and sex (i.e. states). We fixed the transition from juveniles (*juv*) to subadults (*sub*) to 1 for reflecting ageing but we allowed full estimation of transition probabilities from subadults to either adult females (*fem*) or adult males (*mal*). We also created an intermediate state (*int*) between subadult and adult as we observed very slow body growth in some years (i.e., individuals that were three years old but below adult size). We allowed intermediate individuals to become adult female or male in the subsequent year. We forced adult females and males to stay females or males, respectively. Such a multistate model structure allowed estimating survival (*S*) and its confidence intervals (CI) as well as juvenile-adult-transition probabilities (*Ψ*) while accounting for detection probabilities (*p*) within a single statistical framework (Lebreton and Pradel 2002).

Model selection procedure followed six consecutive steps: (1) determining the adequate age-structure by investigating different hypotheses for *S* according to the state (hypotheses: all states have identical survival, differences between *juv* + all others, *juv + sub* + all others, *juv + sub + int* + all others, *juv + sub + int + fem + mal*); (2) determining if *S* of these different states found is constant or time dependent; (3) determining whether *p* is constant throughout time or completely time dependent and if this is different between the states found; (4) determining whether *Ψ* between the states found is constant or time dependent; (5) investigating which covariates (local and distant climate factors) affect the time dependent *Ψ*; (6) investigating which covariates (local and distant climate factors) affect the time dependent *S*. We performed model comparisons using corrected AIC (AICc) scores and goodness-of-fit tests using program U-CARE (Choquet et al. 2009). We found no significant deviations from model assumptions. We assessed significance of climatic covariates in the best models in comparison to constant and time dependent models by means of analyses of deviance (ANODEV, Skalski 1996).

3.3.5 POPULATION SIZE

We used capture-mark-recapture data of secondary periods as history data for population size estimation assuming closed populations within primary periods (Fig. S3.1) (Henle 1990a). We combined consecutive secondary periods with low sampling rates to create history data minimizing the variation of capture probability over time. We estimated annual population sizes using the first sample coverage estimator accounting for individual heterogeneity (Lee and Chao 1994) as implemented in CARE-2 (Chao and Yang 2003). This estimator was already proven to fit our dataset particularly well (Grimm et al. 2014a). We further determined the coefficient of variation (*CV*) describing the individual heterogeneity present per year (Chao et al. 1992, Lee and Chao 1994).

As the annual amount of juveniles differed between February and March (hatching period), we excluded juveniles from total population size estimations, i.e., estimated total population sizes *N* refer to subadults, intermediates plus adults. In order to reflect the annual variations of juveniles, we further estimated the subadult population sizes separately (N_{sub}) and considered it as a reliable proxy of the number of juveniles that entered the population in the previous year. Since the population was monitored in January and March in 1986 and 1987, the assumption of a closed population might not hold over three months. We then averaged the estimated population sizes over both months for each year.

To assess the effects of climatic conditions on changing population sizes, we performed linear models (LM) using annual *N* or N_{sub} as response variables and the local and distant climate variables as described in the LMMs above as fixed effects test predictors. Since juveniles were excluded in the total population size *N* and populations were monitored at the end of summer, we assumed that changes in *N* were mainly driven by survival rather than by reproduction and, thus, by climatic conditions in summer and the previous winter (i.e., effects in the same year at time *t*). In contrast, we assumed that N_{sub} was mainly driven by the production of juveniles in the previous year and their survival and, thus, by climatic conditions in the previous year (i.e., one year before N_{sub} at time *t-1*). To reflect climatic conditions of the previous year, we used the same climatic factors as for all other analyses described above except that we considered summer season to stop in previous March rather than in the month of capture. In both types of analyses, we tested possible interactions between water related parameters and summer temperature beforehand by means of AICc comparisons since the limited number of observations (21) did not allow us to include all interactions. For both *N* and N_{sub}, the best full model included an interaction between summer temperature and summer rain (ΔAIC > 2) (Appendix S3). As for the analyses of individual traits, we assessed the effects of SOI separately. We had to assess drivers of total population size (survival of adults) and subadult population size (reproduction) separately using independent LMs due to the limited allowed number of predictors per number of observations (21) in an LM. Additional to these test predictors, we used the *CV* of individual heterogeneity of capture probability and the population size of the previous year as fixed control predictors in all models. Comparable to the LMMs of individual traits, we built all model combinations to assess the importance of single test predictors using summed corrected (due to small sample size) AIC weights (ωAICc). Further procedures were identical to the ones described for LMMs above.

3.3.6 THERMOREGULATORY ACTIVITY

Additional to our correlative approaches, we attempted to get a more mechanistic understanding of the gecko's thermal reactions to rising temperatures as one important driver in arid zones. We measured and analyzed thermoregulatory behavior during both the active (night) and the resting (day) part of the day. We investigated which ambient temperatures and which microhabitats determined body temperatures. However, since diurnal thermoregulation is more likely to restrict individual traits and survival of geckos than nocturnal thermoregulation (Huey et al. 1989), we focus on diurnal thermoregulation here and present analyses of nocturnal thermoregulation in Appendix S2.

For analyses of diurnal thermoregulation, we designed an experiment that aimed at comparing diurnal body temperatures of geckos hiding in hollows of eucalypts to ambient temperatures in, at, and around the tree and its microhabitat structures. In February 2015 and February 2016, we equipped 12 (6 males, 6 females) and 4 (3 females, 1 male) adult geckos, respectively, on ten different trees with unique Biomark BioThermo13 radio frequency identification tags (RFID). These tags (13 mm, 0.1 g) were attached using a small-lizard modified backpack method (Van Winkel and Ji 2014). The backpacks covered the RFIDs entirely to minimize reflectance and heating-up of the tags themselves in case the geckos were outside the trees during daytime. All trees were of identical structure and provided options for extensive within-tree movements. We scanned the eucalypts where the geckos were caught during the night the next days with a Biomark HPR.PLUS.04V1 reader and antenna to find them. We recorded the geckos' body temperatures and parameters of the geckos' locations in the tree (above-ground height, exposure, diameter of the branch) every time we located a tagged gecko. The dorsal temperatures were assumed to be a proxy for geckos' body temperatures, which should hold unless an individual would be basking (Barroso et al. 2016). We measured body temperatures between 10:30 a.m.

and 7:30 p.m. every 15 minutes for 5 and 7 days in 2015 and 2016, respectively. At the same time, we measured air temperature as well as surface and hollow temperatures on one representative tree (i.e., occupied by the species in all years) every 15 minutes using iButtons® (DS1923) wrapped in white carton. Air temperature was measured in 1.2 m height in the shade of a eucalypt tree (*Eucalyptus largiflorens*). Hollow temperature was measured at the same height but 10 cm inside the tree.

We used LMMs to determine the effects of ambient temperatures, above-ground height, exposure, and branch diameter on body temperatures following the same steps as described above. Air, surface, and hollow temperatures of the representative eucalypt tree were highly correlated. Thus, we used hollow temperatures of the eucalypt for the LMMs as this should be closest to the temperature of a gecko's location during the day. The year and random intercepts of the geckos' ID and day were included as control predictors to account for pseudoreplications.

As some of the individuals were occasionally found outside on the tree trunk during the day in 2015, we performed another Generalized LM using a binomial error distribution (1: gecko outside; 0: gecko inside) to test if the hollow temperature could explain whether a gecko was inside or outside a tree in 2015. Although no gecko was observed outside in 2016, observed movement of individuals within a tree was stronger in 2016. Thus, we performed an LM to test if the above-ground height where the gecko was observed was related to hollow temperature.

3.4 Results

3.4.1 BODY CONDITION AND BODY GROWTH RATES

We did not detect any linear temporal trend in body condition variations over the study period ($p = 0.4$), although strong variations occurred between years (Figs. 2, S3.4). Variation in body condition was affected by both local and distant climate and mainly driven by rainfall in the previous winter and the Darling River heights in both summer and winter. These parameters contributed significantly to the explanation of body condition and were part of the best LMM (Table S3.2). A model without the Darling River heights in winter ($\Delta AIC = 0.542$) as well as a model including temperature and rainfall in summer and the interactions between summer temperature and summer rain and summer temperature and winter rain ($\Delta AIC < 0.77$) were similarly supported. Importantly, summer temperature only became important when interacting with rainfall. The #days>45°C and the #years after flooding as well as interactions between summer temperature and Darling River heights in both summer and winter had a negligible effect ($\Delta AIC > 2$ for model combinations including them).

Body condition was most influenced by winter rainfall ($\omega AIC = 1$, scaled estimate = 0.192), summer Darling River height ($\omega AIC = 1$, scaled estimate = 0.124), and summer temperature ($\omega AIC = 0.74$, scaled estimate = 0.01), followed by winter Darling River height and summer rain ($\omega AIC = 0.63$ for both) (Table 1, Table S3.2). Overall, local climatic parameters were slightly more important (average $\omega AIC = 0.57$) for body condition than distant parameters (average $\omega AIC = 0.46$).

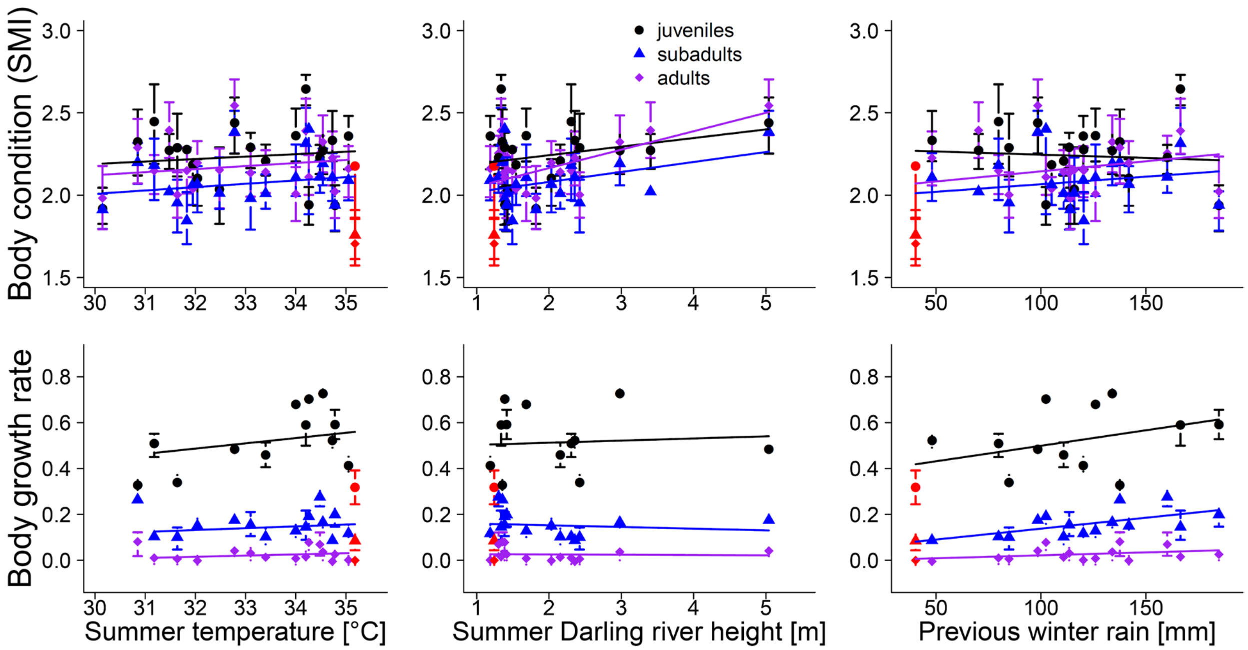

Figure 2: Correlations of body condition and body growth rates with the most important climatic parameters for the three age classes. The exceptional conditions from 2003 (simultaneously hottest and driest year) are highlighted in red. See Figure S3.4 for comparisons of the annual trends.

Among the most important parameters, summer Darling River height explained most of the variance (30.08%) followed by rainfall in winter (12.67%) and the #years post flooding (12.07%) (Table S3.2). Scaled estimates of the full and the most parsimonious model were highly similar and remained within standard errors for each predictor. All climatic predictors (summer temperature, summer and winter rain, summer and winter Darling River height) influenced body condition positively (Table 1, Fig. 2, Table S3.2). In comparison, ENSO itself only marginally influenced body condition (p(full model) = 0.05). Only the SOI of the previous summer (ωAIC = 0.62, p = 0.06) and of the previous winter (ωAIC = 0.49, p = 0.04) affected body condition with an increase SOI increasing body condition (Table S3.5). Body growth rates were always highest for juveniles (0.51 [between 0.32 and 0.73]) followed by subadults (0.15 [between 0.08 and 0.28]). Adult body growth was slightly positive in all years but 2003 and 2013 when adults were slightly shorter than in the year before (Fig. S3.4). Changes in body growth were affected by both local and distant climate and mainly driven by summer temperature, summer rain, winter rain and its interaction with summer temperature, summer and winter Darling River height and their interaction with summer temperature, and #years post flooding. All those parameters formed the best model (Table S3.2). Adding the #days>45°C (ΔAIC = 1.43) was similarly supported. AIC differences to other model combinations were >2. Darling River height in summer (scaled estimate = 0.022) and #years post flooding (scaled estimate = 0.031) as well as winter rain (scaled estimate = 0.027) and summer temperature (scaled estimate = 0.001) effected body growth rates most strongly (ωAIC = 1 for each) followed by the Darling River height in winter (ωAIC = 0.97), summer rain (ωAIC = 0.94), and the interactions between summer temperature and winter rain (ωAIC = 0.61), summer (ωAIC = 0.69) and winter Darling River height (ωAIC = 0.97) (Table 1). Distant climatic parameters (average ωAIC = 0.92) were more important for body growth rates than local parameters (average ωAIC = 0.54).

The relative independent contribution of each parameter to body growth was different for each age class. The variation for juvenile and subadult body growth was mostly driven by winter rainfall (24.07% and 37.04%, respectively). Additional variation for juvenile body growth was explained by summer temperature (14.99%) and Darling River height interacting with temperature in summer (13.15%) while variation for subadult body growth was explained by the interaction between summer temperature and winter rain (19.05%) and #years post flooding (11.68%). Most of the variance in adult body growth was explained by the interactions between summer temperature and summer (15.72%) and winter Darling River height (11.94%), winter rain (14.9%), and #years post flooding (13.02%) (Table S3.2).

Scaled estimates of the full and the most parsimonious model were highly similar and remained within standard errors for each predictor. Summer temperature, summer rain and winter rain as well as both summer and winter Darling River heights influenced body growth rates positively when at the same time temperatures are high (Table 1, Fig. 2, Table S3.2). Comparable to the importance of the Darling River, also ENSO affected body growth rates (ωAIC = 1 and p <<0.001 for every SOI) with increasing SOI advancing body growth but exceptional high SOI (>10) decreasing body growth (Table S3.5).

Table 1: Effects of climatic predictors on G. variegata. Values refer to summed AIC(c) weights. The direction of the estimate is given in brackets. Significant effects and effects of the best model are highlighted in yellow. T = temperature; P = precipitation; “:” = interaction; *# days>45°C* = number of days above 45°C; D = Darling River height; *# years p. flood* = number of years post flooding; Transition sub-ad = transition from the subadult to the adult age class; *sub. pop. size* = subadult population size. See Methods for details about statistical models and Table S3.2 for exact estimates and p-values.

Trait	T(S)	P(S)	T:P(S)	# days >45°C	P(W)	T:P(W)	D(S)	T:D(S)	D(W)	T:D(W)	# years p. flood
Body condition	0.74 (+)	0.63 (+)	0.36 (-)	0.32 (-)	1.00 (+)	0.38 (-)	1.00 (+)	0.22 (-)	0.63 (-)	0.14 (+)	0.29 (+)
Body growth	1.00 (+)	0.94 (+)	0.27 (-)	0.31 (+)	1.00 (+)	0.61 (-)	1.00 (-)	0.68 (+)	0.97 (-)	0.97 (+)	1.00 (+)
Survival juveniles	0.00 (/)	0.00 (/)	/	0.00 (/)	0.00 (/)	/	0.00 (/)	/	0.00 (/)	/	0.00 (/)
Survival subadults	0.82 (+)	0.73 (-)	/	0.01 (+)	0.001 (/)	/	0.001 (/)	/	0.001 (/)	/	0.00 (/)
Survival adults	0.00 (/)	0.00 (/)	/	0.00 (/)	0.00 (/)	/	0.00 (/)	/	0.00 (/)	/	0.00 (/)
Transition *sub-ad*	1.00 (-)	0.00 (/)	/	0.94 (-)	1.00 (+)	/	0.14 (+)	/	0.00 (/)	/	0.00 (/)
Population size (*t*)	0.99 (+)	0.62 (+)	0.61 (-)	0.04 (+)	0.02 (+)	/	0.02 (+)	/	0.90 (+)	/	0.02 (+)
Sub. pop. size (*t-1*)	0.09 (+)	0.13 (+)	0.00 (-)	0.08 (-)	0.80 (-)	/	0.33 (+)	/	0.11 (+)	/	0.09 (+)

3.4.2 SURVIVAL AND JUVENILE-ADULT-TRANSITION PROBABILITIES

Our analyses supported a three age-class structure for survival differing between juveniles, subadults, and older individuals (intermediates combined with adults) (ΔAIC = 1.7 to a model that considers intermediates separately, ΔAIC > 2 to all other possible state combinations). No differences in survival between males and females were detected. Recapture probabilities were similar among age classes but varied over years.

Juvenile and adult (including intermediates) survival was constant across years with juveniles showing a substantially lower survival rate (0.24 [CI: 0.18 - 0.31]) than adults (0.74 [CI: 0.71 - 0.76]). In contrast, subadult survival varied strongly among individuals and across years (ΔAIC = 6.2 between the best model with constant juvenile and adult but time-dependent subadult survival to the second best model with time dependent juvenile and subadult but constant adult survival). It increased significantly with higher summer temperature (ωAICc = 0.82; ANODEV, F = 36.49, $r^2 = 0.68$, $p << 0.001$) but decreased significantly with higher summer rainfall (ωAICc = 0.73; ANODEV, F = 33.01, $r^2 = 0.65$, $p << 0.001$) (Table 1; Fig. 3). No other climatic variables explained temporal fluctuations of subadult survival.

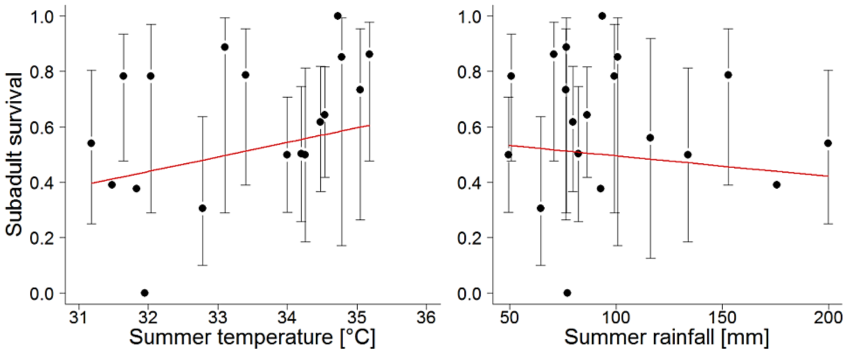

Figure 3: Subadult survival probabilities and their confidence intervals in relation to mean summer temperature (left) and summer rainfall (right). The dots represent the time-dependent subadult survival estimates. Lines show the regression line in a summer rain (left) and temperature dependent model (right).

The transition probability of subadults to become immediately adults or to go through an additional intermediate state significantly depended on summer temperatures (ωAICc = 1.00; ANODEV, F = 23.33, $r^2 = 0.58$, $p << 0.001$) and winter rainfall (ωAICc = 1.00; ANODEV, F = 11.71, $r^2 = 0.28$, $p = 0.004$). Subadults tend to become immediately adults if summer temperatures were below 34°C on average and winter rainfall was more than 100 mm (Table 1, Fig. 4). Otherwise, they might pass through an intermediate state. Likewise, we found strong indications that few subadults went through an intermediate state when more than six days in summer were above 45°C with an increasing proportion when more than nine days were above 45°C. However, these effects were not significant (ωAICc = 0.94; ANODEV, F = 3.90, $r^2 = 0.12$, $p = 0.12$). No further climatic effects were detected (Table 1). Moreover, slightly more subadults became females than males (Fig. 4) whereas almost all individuals from the intermediate state became females (86%).

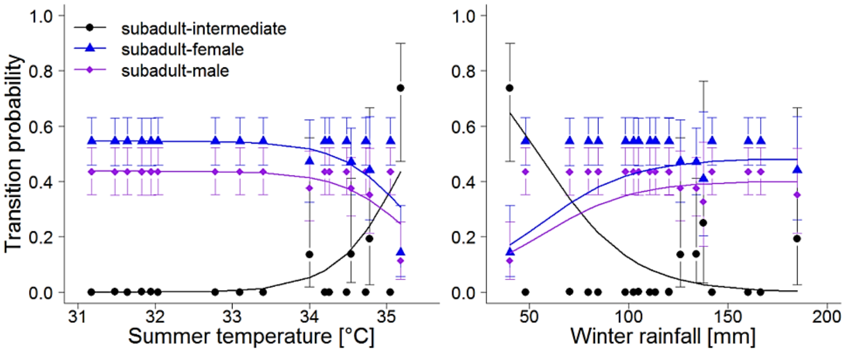

Figure 4: Transition probabilities and their confidence intervals of subadults to intermediates or adult females and males in relation to winter rainfall (left) and summer temperature (right). All symbols represent time-dependent estimates. Lines show regression lines in a model dependent on winter rainfall (left) or summer temperature (right).

3.4.3 POPULATION SIZE

Averaged total population size was approximately 79 individuals (*N* = 78.8) but strongly varied between years (from 44 to 127 individuals; Fig. 5). The averaged subadult population size was approximately 20 (N_{sub} = 20.4) and also varied between years (from 2 to 45 individuals; Fig. 6). Both total and subadult population size were more impacted by local climatic parameters (average ωAIC = 0.46 and 0.22 for local versus 0.31 and 0.18 for distant parameters, respectively). Specifically, total population size changes affected by climatic variables in the same year (at time *t*) were predominately driven by summer temperatures (ωAIC = 0.99, $p < 0.001$; Fig. 5), rainfall in summer (ωAIC = 0.62, $p < 0.001$; Fig. 5), their interaction (ωAIC = 0.61, $p<0.001$), and the Darling River height in winter (ωAIC = 0.90, $p < 0.001$) (Table 1). These parameters also explained most of the variance (31.31%, 7.66%, 34.84%, and 19.72% respectively). While the Darling River height in winter affected total population size positively, the effect of summer temperature and rainfall was interdependent due to the strong interaction: At low summer rainfall (<100 mm), higher temperatures led to higher population sizes, while at low summer temperatures (<32.5°C), higher rainfall led to higher population sizes (Table S3.2). ENSO did not affect total population size at all ($p = 0.6$) (Table S3.5).

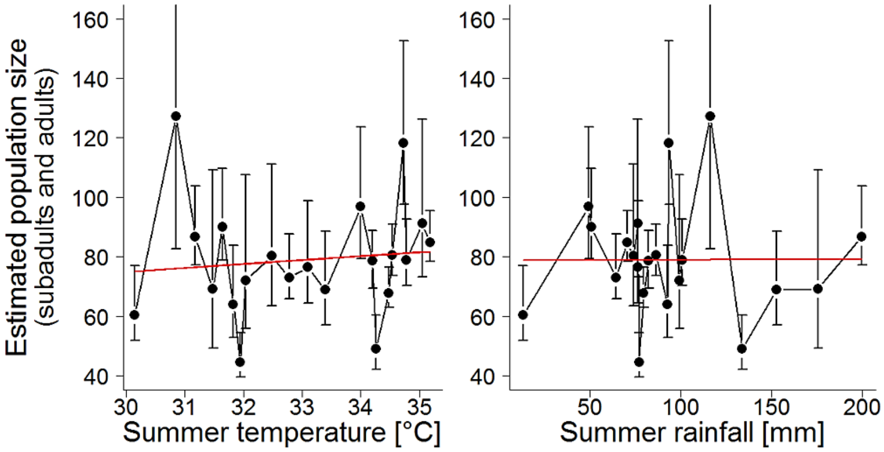

Figure 5: Total population size in relation to summer temperature (left) and summer rainfall (right) at time t as the most important explanatory variables. Confidence intervals are shown.

Subadult population size changes considering climatic variables of the previous year (at time *t-1*) where driven by winter rainfall (ωAIC = 0.80, $p = 0.003$; Fig. 6) and the Darling River height in summer (ωAIC = 0.33, $p = 0.03$; Fig. 6) (Tables 1, S3.2). Nevertheless, most of the variance was explained by summer rainfall (24.87%) followed by summer temperature (17.58%), the #years post flooding (12.09%), and summer Darling River height (9.71%). Increasing rainfall in winter slightly decreased while rainfall and Darling River height in summer increased subadult population sizes in the following year (Tables 1, S3.2). In both analyses, scaled estimates of the full and the most parsimonious model were highly similar and remained within standard errors for each predictor (Table S3.2). In contrast to the total population size, the subadult population size was also influenced by ENSO directly with increasing SOI in the previous summer increasing subadult population size (ωAIC = 0.87, p <0.001) (Table S3.5).

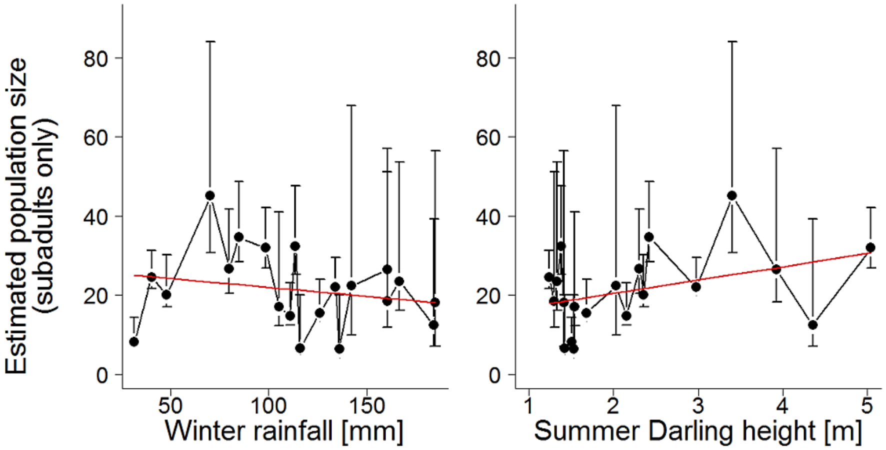

Figure 6: Subadult population size in relation to winter rainfall (left) and Darling River heights in summer (right) at time t-1 as the most important explanatory variables. Confidence intervals are shown.

3.4.4 THERMOREGULATORY ACTIVITY

Diurnal body temperatures varied less within a day (mean standard deviation = 2.74°C) than between days (standard deviation = 3.64°C). Generally, body temperatures strongly followed tree hollow temperature (Fig. 7) with hollow temperature being the most important explanatory parameter (ωAIC = 1, p<<0.001; slope: 0.75±0.03, Table 2). The location of a gecko along the tree only marginally determined its body temperature (Table 2) with body temperatures tending to increase with height above ground and with decreasing branch diameter. An LMM with hollow temperature and branch diameter explained body temperature best. Including height above ground did not improve the model fit (ΔAIC = 1.89).

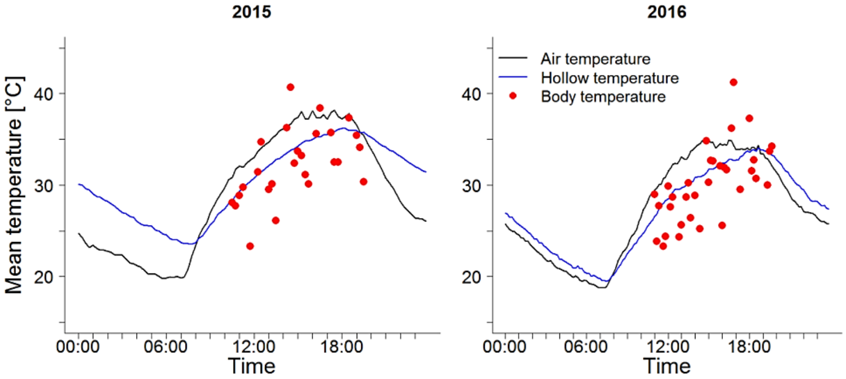

Figure 7: Averaged body temperatures of *G. variegata* during diurnal activity in comparison to air and hollow temperature in the representative eucalypt tree during the thermoregulation experiments in February 2015 (left) and February 2016 (right).

Table 2: Summary of coefficient estimates, standard errors, significance levels (p-value) and relative importance (ωAIC) of the test predictors for diurnal body temperatures in *Gehyra variegata*. T(hollow): tree hollow temperature. [x;y]: signifies the lowest and highest value obtained for this categorical variable.

Test predictor	Estimate	Standard error	p-value	Σ(ωAIC)
T(hollow)	0.75	0.03	<0.001	1
Height above ground	0.18	0.29	0.67	0.32
Branch diameter	-0.04	0.02	0.05	0.72
Exposure	[-0.23; 3.95]	[0.96; 2.00]	0.36	0.02

Behavioral thermoregulation differed between 2015 and 2016. In 2015, the location of a gecko usually did not change during the day, while in 2016 individuals changed their location frequently. Likewise, an LMM for 2015 only indicated hollow temperature to be the only significant driver of body temperature ($p << 0.01$; Table S3.6). Contrarily, an LMM for 2016 only showed that all locality parameters significantly influenced body temperature with increasing height above ground ($p = 0.02$), decreasing branch diameter ($p = 0.05$), and exposure towards North ($p = 0.002$) increasing body temperature (Table S3.7).

In a subsequent analysis, we showed that this active search for a place to thermoregulate depended on ambient temperature. In 2015, individuals were occasionally found outside the tree basking on the bark while this was not observed in 2016. In contrast, individuals moved a lot within the trees from close to the ground up to 4 m in 2016 which was not observed in 2015 (Fig. 8). Both thermoregulatory behaviors were only observed during days with low hollow temperatures. An ambient temperature below 30°C significantly increased the probability that individuals were seen outside tree hollows during the day in 2015 (binomial GLM, ωAIC = 1, $p = 0.001$) or that individuals moved up the tree in 2016 (LM, ωAIC = 1, $p << 0.001$, 7±2 cm increase in height per 1°C cooling) (Fig. 8).

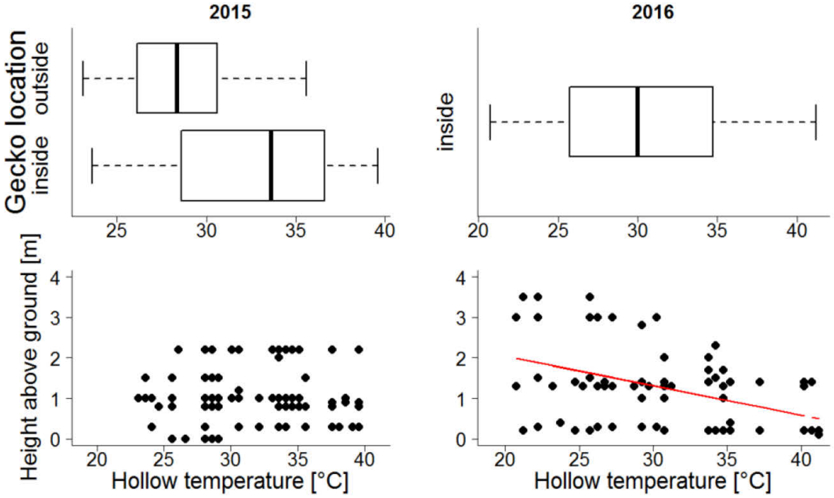

Figure 8: Geckos' response to hollow temperature in the representative eucalypt tree during the day: moving outside tree hollows in February 2015 (left) and moving up inside hollow trunks in February 2016 (right).

For comparisons, we summarized the minimum, mean, and maximum body temperatures during the day and night in Table 3. We added a summary of the nocturnal body temperature measured by Henle (unpublished data, but see analyses of the data in Henle 1990) in the same study sites. While the measurements of the present study were taken in summer only, measurements from 1985 to 1986 were taken across the year when active individuals were found (Henle 1990a). Since diurnal body temperature represents a broad range of temperatures voluntary and actively selected by individual geckos across daytime, we refer to it as selected body temperature (T_{sel}).

Table 3: Selected body temperatures (Tsel) for *G. variegata* during the day and body temperatures experienced during the night in three adjacent habitats (see Henle 1990 for details; habitat abbreviations followed this publication; RWI is the site analyzed in this study). Data were summarized for two to three years across the seasons measured. N_{ind} = number of individuals measured; $N_{measure}$ = number of measurements in total; *Min* $T_{(sel)}$ = minimum (selected) body temperature; *Mean* $T_{(sel)}$ = mean (selected) body temperature; *Max* $T_{(sel)}$ = maximum (selected) body temperature.

Habitat	Daytime	Years	Season	N_{ind}	$N_{measure}$	Min $T_{(sel)}$	Mean $T_{(sel)}$	Max $T_{(sel)}$
RWI	diurnal	2015-2016	summer	16	161	23.3	31.1	42.1
Station	nocturnal	2013-2015	summer	63	67	18.7	25.31	32.6
Station	nocturnal	1985-1986	annual	122	159	12.0	21.7	34.5
RWI	nocturnal	1985-1986	annual	55	77	12.0	24.4	32.3
RWII	nocturnal	1985-1986	spring/ summer	35	54	11.7	21.2	28.8

3.5 Discussion

Gehyra variegata was affected by various local and distant climatic factors depending on the ecological process investigated. Regarding local climatic parameters, summer and winter rain increased body condition and body growth rates. Whereas summer rain also increased total population size if temperatures were below 32.5°C, it decreased subadult survival probability. Winter rain additionally favored a direct transition from subadults to adults and decreased subadult population size in the subsequent year. Likewise, rising summer and winter Darling River heights increased body condition and, under the condition of high temperatures, body growth rates. While rising summer Darling River height increased next year's subadult population size, rising winter river height increased total population size in the same year. The number of years post flooding only enhanced body growth. Altogether, these findings may reflect the different sensitivity of species parameters to the different spatio-temporal scales: body growth rates and subadult population size were more affected on the long-term by direct or indirect distant climate whereas body condition and total population size respond on the shorter-term to local climatic conditions. This implies that ENSO has low immediate effect on nocturnal reptiles in the Australian desert and rather have strong although delayed consequences on reptiles via complex cascading impacts on local climate. Despite being mostly indirect, the effects of distant climate had a strong influence on Australian desert reptiles as a lagged effect of La Niña-induced rainfalls on the Darling River heights in Kinchega may for instance surpassed potential direct effects of local climate.

Being indifferently local or distant, climatic parameters describing water availability in Kinchega (rain and river height, respectively) were overall positively related to individual traits and demography of *G. variegata*. Insect development strongly benefiting from standing water resulting from both flooding and heavy rainfall (Birch 1953, Denlinger 1980) and increasing abundances of many arthropod species along with long-term rainfall (Masters et al. 1998, Kwok et al. 2016) may facilitated *G. variegata*, especially during their active period. Additionally, vegetation dynamics in Kinchega are known to be driven by both higher winter rain favoring growth of annual plants and higher summer rain immediately inducing flowering in perennial plants as well as the Darling River (Robertson et al. 1987). La Niña driven floods also induce leaf growth of *Eucalyptus largiflorens* (Roberts and Marston 2011), providing food and habitat for arthropods. Consequently, the biomass and the diversity of food available for *G. variegata* likely increased with both local and distant climate which supports our findings at individual and population levels. Comparably, Letnic et al. (2004) detected a strong but species-specific influence of vegetation on the abundance of various Australian lizards.

More specifically, winter rain and river heights were important drivers of both within-year (body condition, reproduction) and long-term between-year response of the geckos (body growth, direct transition of subadults to adults). This might be due to the vegetation structure within our study area which is dominated by annuals and eucalypt trees that strongly rely on winter rain and floods, respectively (Westbrooke et al. 2001). Besides, while winter rain and river heights explained most of the variance for individual traits, summer rain explained most of the variance for demographic traits. Comparably, Stamps & Tanaka (1981) found that body growth of a tropical lizard strongly depended on water and food availability and Rotger et al. (2016) that rainfall positively influenced body growth of a temperate lizard. In deserts, Dickman et al. (1999) reported that rainfall increased body growth and survival of two dragon species (*Ctenophorus nuchalis* and *C. isolepis*). In our study we found that bad climatic conditions at one scale could potentially be balanced by good conditions at another climatic scale with high body condition and body growth in years with low rainfall but comparably high river heights (e.g., 1999 and 2012, Figs. 2, S3.4). This suggests that bad conditions at one climatic scale like low amount of local rainfall could be overcompensated by floods through La Niña events (see also Appendix S1.3).

Nevertheless, despite the effect of water being mostly positive, extremely high rainfall decreased the estimated subadult population size in the following year. Both field and laboratory studies indicated that very moist conditions can prevent *G. variegata* eggs from development (Bustard 1968a, 1969) and thus, reduce total hatching success. Such an effect of humidity on geckos would lead to a reduced number of juveniles in a year with high water availability which is then mirrored in a lower subadult population size in the subsequent year as observed in this study. Nevertheless, both Smith et al. (1995) and Dickman et al. (1999) found only a positive relation of reproduction to rainfall in terrestrial lizards. Further, the negative impact of rainfall can also act though a higher vegetation cover that could increase the number of predatory arthropods (e.g., praying mantis, huntsman spider (*Isopoda immanis*), black widow (*Latrodectus hasseltii*); Henle 1990). Such increased predation pressure on juveniles and subadults could explain the negative effect of rain on subadult survival. However, there are also two other possible alternative explanations. First, subadults may grow faster under excellent conditions, entering earlier into competition with adults, and thus dispersing more. Second, both juveniles and subadults might grow very fast under high food availability. Hence, they already reached adult size by the end of summer when monitoring took place and thus were incorrectly recorded as adults instead of subadults unless the age of the individuals would have been known from previous captures. This latter hypothesis is supported since we indeed observed such extremely fast-growing individuals that have previously been captured as juveniles in an adjacent habitat in superabundant food years. This hypothesis is further supported by the observed higher direct transition rates from subadults to adults when rainfall is high. As a consequence, the negative effect of rainfall on subadult population size and survival could actually be an artefact due to faster growth rather than a true decrease in abundance. Whatever the case, it should be mentioned that not only extremely high but also extremely low rainfall induced lower subadult survival (Fig. 3) suggesting a possible quadratic relationship, although we could not detect it statistically in this study since it would require more data at extreme climatic conditions (see Methods).

Additional to precipitation, temperature affected *G. variegata* remarkably. Increasing summer temperatures enhanced body condition, (subadult) survival rate and total population size. If sufficient water is available, high temperatures enhance growth and abundance of insects (Frazier et al. 2006) and therefore potentially facilitated body conditions, reproduction, and survival through higher food availability. Comparably, previous studies demonstrated that survival of a gecko species was temperature dependent (Read et al. 2012) and that high temperatures were essential for egg development in *G. variegata* (Bustard 1969). However, direct observations of Henle (1990) also suggested that excessive heat in microhabitats can cause egg mortality.

High temperatures are also a prerequisite for body growth and thus restrict growth to summer (Greer 1989). In line with this, we detected a direct positive effect of summer temperature on juvenile and adult body growth rates and subadults even profited from a high number of excessively hot days. In addition, summer temperature was found to be particularly important when interacting with winter rain or Darling River heights in summer and winter. This interaction became extraordinary remarkable as the overall positive effect of summer temperature on both body condition and body growth was reversed for the two years with the highest summer temperatures and simultaneously lowest winter rain of the study period (2003 and 2013; see Figs. 2, S3.4). In those two years, adult body growth rates were even negative, meaning that individuals were slightly shorter than in the year before, presumably due to lower fat reserves (pers. observ.; we measured individuals at the posterior insertion of the hindleg and under low-food conditions, hindlegs were leaner than under plenty-food conditions). Notably, the small positive trend between rainfall and temperature that existed otherwise over the study period was opposite for these two years (see Appendix S1.3), underlying the quite atypical characteristic of these climatic conditions. Interestingly, when further analyzing our data by excluding records from 2003, the driest and hottest year, the effect of summer temperature on body growth rates was significantly positive (results not shown) indicating that low winter rain rather than high temperatures were responsible for low body growth in these years.

Similar temperature-rainfall-interactions might also hold for other traits, since the co-occurrence of high temperatures and low water availability not only restricted body condition and body growth but also the transition from subadult to adult stage. Such adverse climatic conditions thus maintained individuals in an intermediate state and delayed sexual maturity by one year. However, those extreme climatic conditions combining heat and water restriction did not affect survival and only marginally population sizes, suggesting that plasticity in individual traits could act as adaptive strategy off-setting unfavorable environmental conditions at the population level. Another interaction between temperature and rainfall was detected in relation to total abundance: If one climatic parameter was low, the total population size could still strongly increase if the other was high. Conversely, cold summers with low rainfall would be the worst conditions to maintain total population size. Under cold and dry conditions, food availability would likely be reduced because of decreased insect biomass and optimal digestion could not be maintained or active thermoregulation would be necessary, altogether likely increasing the energetic cost for geckos (Frazier et al. 2006, Angilletta 2009).

In conclusion, geckos seem to have a broad range of individual responses to climatic fluctuations that could potentially buffer demographic responses. While we found high potential for phenotypic plasticity, further genetic research would be necessary to investigate whether those responses are evolutionary adaptive. In any case, considering such plasticity allowing adjustments to environmental variations is of paramount importance to predict future responses to changing climate (Urban et al. 2014).

High temperatures were recently identified as the main limiting factor for terrestrial reptiles (Deutsch et al. 2008, Sinervo et al. 2010, Gunderson and Stillman 2015). However, our integrative study accounting for plastic adjustments to ecological and physiological constraints suggested that these findings cannot be generalized to all terrestrial reptiles and might not hold for instance for nocturnal desert lizards. Our results did not only support that individual traits of *G. variegata* increased with temperatures but also that demographic processes like survival and within-year changes in total population size profited from higher temperatures. Together, the positive effects of temperature might not only be a consequence of increased food availability but also of thermoregulatory activity or longer activity periods throughout a larger part of the night. We observed high activity during a night with 45°C (Henle 1990) although *G. variegata* is a strong thermoconformer during the night with body temperature strongly following ambient temperature (Appendix S2, Henle 1990). We further found active individuals voluntary tracking heat in the late afternoon exposed on stones of 45-48°C surface temperature with 43°C air temperature. Additionally, nocturnal microhabitat temperatures differed strongly and individuals could easily change the microhabitat to cool down (Kearney and Predavec 2000; Appendix S2). Moreover, night time temperatures cool down over the night and thus hot temperatures allow starting activity later and extending it further into the night. In summary, we did not detect an upper thermal limit shortening nocturnal activity. These findings are in line with Greer's (1989) assumption that geckos have extremely high critical thermal maximum temperatures and a wide physiological range. This further supports the conclusion of Huey et al. (1989) that nocturnal activity in geckos is not restricted by hot temperatures and that individuals might show reduced individual performance under cold temperatures.

Thermal constrains might rather act on diurnal activity. As proposed by Huey et al. (1989), geckos experienced higher temperatures during the day than during the night in Kinchega during our study period as well as across years in three adjacent populations (Table 3). While Huey et al. (1989) argued that geckos have to survive hot days and therefore need higher CTmax comparable to that of diurnal species, we found that geckos did not only stand the heat but rather voluntarily tracked high body temperatures during the day. Bustard (1967) already described that *G. variegata* changed their diurnal position below the bark and between trunk and bark and pressed themselves against the inner side of the bark for heating up. We even observed true basking of individuals in the sun in cool days in 2015 and movements to higher, smaller, dead, and more exposed branches on cool days in 2016. In doing so, individuals voluntarily exposed to body temperatures above 40°C. Notably, although temperature tags in backpacks might indicate less accurate body temperatures for basking than for non-basking individuals (Barroso et al. 2016), we did not find any difference in the highest body temperatures selected by individuals between years (≈ 42.1°C). Active diurnal behavioral thermoregulation is a necessary adaptation of nocturnal geckos for digestion (Bustard 1967, Greer 1989, Angilletta et al. 1999, Kearney and Predavec 2000) and for body growth (Autumn and De Nardo 1995). However, true basking behavior was previously known for larger gecko species only (Greer 1989) or for species from cooler climate, e.g. *Tarentola mauritanica* (Lisičić et al. 2012; pers. observ.). The difference observed for *G. variegata* between the two years despite similar alternatives for selecting microhabitats could be due to food availability (Stamps and Tanaka 1981). Thanks to semi-quantitative and qualitative measurements of insect density performed during capture occasions, we noted that food availability was indeed higher in 2015 than in 2016, presumably due to higher rainfall and more standing water left in the bed of Darling River in 2015. Additionally, average summer temperatures were lower in 2015 (34.2°C) than 2016 (35.05°C). Hence, in 2016 individuals were assumed to have less food to digest and, at the same time, more optimal temperatures for digestion, which should make the necessity of basking outside the tree obsolete (Abram et al. 2016). In addition, we assume that necessary movements in cool days for diurnal basking outside trees or in exposed branches of eucalypts could have decreased body condition in comparison to hot days for which no basking and thus, no movements were necessary for digestion (Angilletta 2009, Abram et al. 2016). It might also increase predator exposure and overheating risk and thus reduce survival (Angilletta 2009). Together, diurnal thermoregulatory behavior could likely explain the decreasing individual and life-history traits of *G. variegata* at low temperatures but good individual and demographic conditions under high temperatures. It also supports our hypothesis that either temperature or water availability needs to be high to maintain total population size (see above).

While several studies determining climatic effects on species in arid ecosystems focused on rainfall as a key driver in the past decades (e.g., Dickman et al. 1999, Letnic et al. 2004, Holmgren et al. 2006), more recent studies tend to focus on effects of temperature as a limiting factor for all reptile species independent of the ecosystem, neglecting both potential plastic responses to temperature and buffering effects of water availability (e.g., Wake 2007; Massot et al. 2008; Deutsch et al. 2008; Sinervo et al. 2010). However, our 30-years study instead supports the hypothesis that water availability rather than climate warming will be the limiting factor in (nocturnal) desert reptiles though nevertheless temperature was observed to be crucial in almost all life-history processes. In line with our findings, other studies provided evidence that both rainfall and temperature affect lizards in various ways with water availability being a stronger driver than temperature in most of the ecological processes (Pianka 1986, Smith et al. 1995, Read et al. 2012, García-Muñoz and Carretero 2013, Belasen et al. 2016, Rotger et al. 2016). Besides, our results highlight the need to account not only for physiological constraints such as CTmax for drawing conclusions about the effect of climate change on a whole taxonomic group, but rather to consider behavioral adjustments, phenotypic plasticity, and ecological responses balancing the effect of temperature for instance through water availability.

With advancing climate change, hot deserts are predicted to become hotter and drier (Noble and Gitay 1998, Stahlschmidt et al. 2011, Settele et al. 2014) while ENSO is likely to intensify (Noble and Gitay 1998, Cai et al. 2014), despite changes in ENSO are not consistently predictable (Wang et al. 2017). Although we found broad plasticity in *G. variegata*, our data indicate that a series of extremely hot and, especially, dry years is likely to reduce individual conditions and potentially population size remarkably. However, an intensified ENSO could increase the number of years with high water levels in the Darling River in both frequency and presumably magnitude, as well as filling rivers for a longer time as observed during the exceptionally strong back-to-back La Niña in the 1970s (Simpson et al. 1993, Green et al. 2012, see data for historic SOI at http://www.bom.gov.au/climate/influences/timeline/). In long-living species like *G. variegata*, it could be possible that improved conditions on one climatic scale (extended standing water due to higher frequencies of high Darling River heights) could compensate deteriorated conditions on another climatic scale (decreasing rainfall). Nevertheless, our findings strengthen the conclusions by Pomara *et al.* (2014) in indicating that severe droughts will have detrimental effects on both individual and population levels. These findings are particularly interesting since they can be considered as counter-intuitive given that the life history of this arboreal species is not directly depending on water. This suggests that other similar reptile species will likely encounter similar limitations. Notwithstanding, responses to changing climate can differ remarkably among (Dickman et al. 1999, Letnic et al. 2004, Read et al. 2012) and within species (Bestion et al. 2015, Belasen et al. 2016).

We showed that even within a single population, climatic responses may differ depending on the ecological level under investigation and may display complex interactions with distant and local climate. Negative responses to some climatic extremes (too much rainfall reduces reproductive success, too low rainfall prevents body growth) could likely be compensated by putting less energy in body growth and reaching sexual maturity but rather surviving to the next year. These findings are particularly important as they show that even a long-living species can exhibit short-term responses to a changing climate. In addition, another interesting finding is that delayed effects of distant climate may be interpreted as early warning signals that can be used for anticipating future impacts of climate change.

3.6 Conclusion

This study provides evidence that the relative effects of various local and distant climatic parameters differ depending on the ecological level considered. Plasticity in life-history traits at the individual level in response to adverse climatic conditions could partly buffer consequences on the population level by maintaining survival rates. Moreover, less favorable climatic conditions of a climatic parameter on one scale (e.g., low rainfall) could be compensated by favorable conditions at another scale (e.g., high Darling River height or high temperatures). Via this study we investigated several possible responses of *G. variegata* to a changing climate, though a sequence of several extremely dry years without flooding would likely cause a remarkable population decline. This stresses the need to understand the underlying mechanistic processes that link interactions between climate at different scales and ecological processes to enable us to predict species responses and successfully conserve species in arid ecosystems.

3.7 Acknowledgements

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3.8 Supporting Information

Appendix S1: Further climatic investigations

Appendix S2: Dependence of body temperatures on ambient temperatures during nocturnal activity

Appendix S3: Parameter estimates for all LMMs and annual relation graphs of the main individual traits

Figure 9: *Gehyra variegata*. Photo by Annegret Grimm-Seyfarth.

4 Effects of non-trophic interactions with vegetation coverage on thermoregulation and activity

Behavioural thermoregulation is an important mechanism allowing ectotherms to respond to thermal variations. Its efficiency might become imperative for securing activity budgets under future climate change. In the previous chapter, I investigated thermoregulatory behaviour in an arboreal, nocturnal gecko species. However, findings for nocturnal geckos could differ substantially from those of diurnal skinks with diurnal reptiles likely being more affected by hot temperatures than nocturnal ones. For diurnal lizards, thermal microhabitat variability appears to be of high importance, especially in hot deserts where vegetation is highly scattered and sensitive to climatic fluctuations. Therefore, I investigated the mechanism of thermoregulatory behaviour in two diurnal, terrestrial skink species, *Morethia boulengeri* and *Ctenotus regius*, and the interacting effects of vegetation on body temperatures and activity budgets. Specifically, I aimed at determining the effects of bush sizes, the vegetation gradient, and occasional shading from isolated trees. I combined different data sets by calibrating high-resolution experimental data to longer but less accurate time series with different temporal resolutions to determine the activity budgets under past (1985 to now) and future (until 2090) climatic conditions. Findings from this chapter will improve assessments of the potential effects of climate change on species with similar traits.

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Too hot to die? The effects of vegetation shading on past, present, and future activity budgets of two diurnal skinks from arid Australia

4.1 Abstract

Behavioural thermoregulation is an important mechanism allowing ectotherms to respond to thermal variations. Its efficiency might become imperative for securing activity budgets under future climate change. For diurnal lizards, thermal microhabitat variability appears to be of high importance, especially in hot deserts where vegetation is highly scattered and sensitive to climatic fluctuations. We investigated the effects of a shading gradient from vegetation on body temperatures and activity timing for two diurnal, terrestrial desert lizards, *Ctenotus regius* and *Morethia boulengeri*, and analysed their changes under past, present, and future climatic conditions. Both species' body temperatures and activity timing strongly depended on the shading gradient provided by vegetation heterogeneity. At high temperatures, shaded locations provided cooling temperatures and increased diurnal activity. Conversely, bushes also buffered cold temperature by saving heat. According to future climate change scenarios, cooler microhabitats might become beneficial to warm-adapted species, such as *C. regius,* by increasing the duration of daily activity. Contrarily, warmer microhabitats might become unsuitable for less warm-adapted species such as *M. boulengeri* for which mid-summers might result in a complete restriction of activity irrespective of vegetation. However, total annual activity would still increase provided that individuals would be able to shift their seasonal timing towards spring and autumn. Overall, we highlight the critical importance of thermoregulatory behaviour to buffer temperatures and its dependence on vegetation heterogeneity. Whereas studies often neglect ecological processes when anticipating species' responses to future climate change, the strongest impact of a changing climate on terrestrial ectotherms in hot deserts is likely to be the loss of shaded microhabitats rather than the rise in temperature itself. We argue that conservation strategies aiming at addressing future climate changes should focus more on the cascading effects of vegetation rather than on shifts of species distributions predicted solely by climatic envelopes.

4.2 Introduction

The strong dependence of ectotherms on temperature is frequently assumed to be a key underlying process for modelling their response to climate warming, especially through its impact on activity budgets (Angilletta 2009). However, those predictions sometimes result in contradictory findings., Caruso et al. (2014) predicted an increase in daily activity budgets in North American salamanders resulting in metabolic expenditure associated with body size reductions. Conversely, Sinervo et al. (2010) predicted a tremendous reduction in activity budgets, which could restrain metabolic functions and potentially causing up to 39% loss of lizard populations worldwide by 2080. So far, assessments of activity budgets have usually overlooked key factors, such as thermoregulation and microclimate variability (Kearney et al. 2009, Kearney 2013, Gunderson and Leal 2015). Terrestrial ectotherms such as reptiles were recently found to offset a rather low thermal plasticity by active thermoregulation (Gunderson and Stillman 2015). Thermoregulatory behaviour is likely to be present in all reptiles and includes seeking for optimal thermal environments by basking, warming up on substrate, cooling down in the shade, and shuttling between thermally different microhabitats (Bogert 1949, Arribas 2010, 2013, Ortega and Pérez-Mellado 2016). At the individual level, thermoregulatory behaviour that adjusts body temperature according to microhabitat conditions might be even more important for securing activity budgets than the environmental conditions on large spatial scales (Adolph and Porter 1993, Sears and Angilletta 2015). Moreover, thermoregulatory strategies including thermoregulation effort and accuracy were found to vary strongly between hot and cold environments (Vickers et al. 2011).

Most studies investigating the sensitivity of reptiles to climate accounting for thermoregulation or microhabitat variation were conducted in (sub-)tropical and temperate regions (e.g., Amo et al. 2007a, Arribas 2010, Aubret and Shine 2010, Huang and Pike 2011, Logan et al. 2013, Huang et al. 2014, Ortega and Pérez-Mellado 2016, Ryan et al. 2016). In contrast, only a few studies have focused on such adaptation mechanisms in hot deserts (Porter et al. 1973, Barrows 2011, Jezkova et al. 2015). However, deserts in particular are predicted to be severely impacted by climate warming (Reisinger et al. 2014). While temperate and tropical regions are covered with dense forests or grasslands, desert vegetation is usually rare and scattered while covering only a minor proportion of the. Thus, the responses of reptiles to rising temperatures in temperate or tropical regions cannot simply be transferred to deserts (see also Clusella-Trullas et al. 2011). Unlike temperate or tropical regions, one of the most critical challenge for reptiles in hot deserts is to stay cool (Kearney et al. 2009). Consequently, desert reptiles have evolved different kinds of behaviour, enabling them to offset the impacts of hot temperatures (Bartholomew 1964). These different kinds of thermoregulatory behaviour can buffer climatic variations to some extent (Angilletta 2009). Their efficiency strongly depends on the availability of alternative microclimatic conditions such as shade provided by vegetation cover (Kearney et al. 2009, Kearney 2013). To understand the available activity budgets of reptiles in such regions, it is imperative to compare the thermal conditions in the gradients of the available scattered vegetation.

In this study we investigated the effects of vegetation on body temperatures and activity budgets of two skink species in an arid region of New South Wales, Australia, to determine the activity budgets from the past (1985 to now) and the future (until 2090) climatic conditions. In our approach we combined different data sets by calibrating high-resolution experimental data to longer but less accurate time series with different temporal resolutions to assess the species' responses to climate change. We specifically aimed at disentangling the effects of bush sizes, the vegetation gradient, and occasional shading from isolated trees. Based on these findings we investigated how activity budgets have changed over time and will change in the future to assess the potential effects of climate change on species with similar traits.

4.3 Materials and methods

4.3.1 STUDY SITE AND STUDY SPECIES

The study was conducted in Kinchega National Park, New South Wales, Australia (32°28' S, 142°20' E). Kinchega is situated at the eastern margin of Australia's arid zone and characterized by high summer temperatures and low but highly variable rainfall without seasonal patterns (Robertson et al. 1987). Kinchega shows typical characteristics of a hot desert under climate change (rising temperatures and more extreme rainfall patterns). This region is projected to undergo major climate change in the future with a warming of up to 4-6°C by the end of the century (Reisinger et al. 2014).

Our study species are the terrestrial, diurnal skinks *Ctenotus regius* and *Morethia boulengeri* (Fig. 1). While Kinchega's population of *C. regius* is located at the cold edge of the species distribution range, this geographic location represents the warm edge of the distribution range of *M. boulengeri* (Fig. 1).

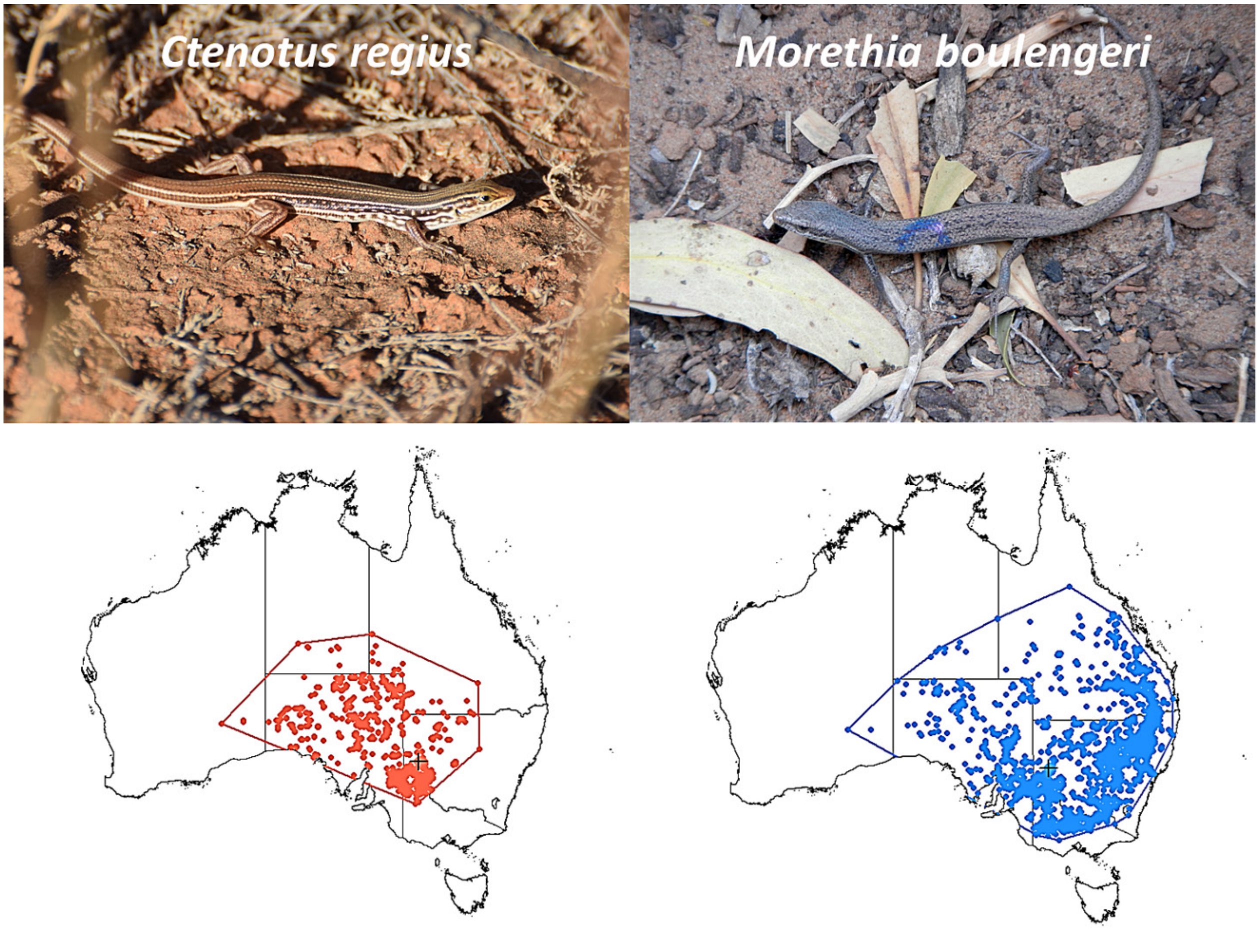

Figure 1: The terrestrial, diurnal skinks *Ctenotus regius* (left) and *Morethia boulengeri* (right). The maps show the occurrence points and a minimum convex polygon of the species in Australia (data from: http://spatial.ala.org.au/). The black cross represents Kinchega National Park.

Henle (1989a; b) found that repeated direct measurements of diurnal body temperatures of these lizards in this region is not feasible especially at hot temperatures, since individuals move too fast to be caught by hand and are too small be equipped with thermosensitive radio-transmitters. Therefore, we used copper pipe models mimicking the bodies of lizards to measure the operative temperature of individuals T_e (i.e., the potential body temperature in a non-thermoregulating individual). Copper pipe models are frequently used in field studies for the thermoregulation of small reptiles. They are assumed to have the same heat conductivity as an individual reptile (Bakken and Gates 1975) and have been found to accurately predict steady-state body temperatures of small individuals (Seebacher and Shine 2004, Kearney et al. 2009). To ensure that our copper pipe models are a true mimic individual's T_e, we followed the suggestions made by Shine & Kearney (2001) and cut the copper pipes to the respective lengths and diameters of an average adult individual for each species (*C. regius*: 6.5 cm x 1.6 cm, *M. boulengeri*: 5 cm x 1.2 cm) and sealed both ends with polystyrene caps. To mimic the species' reflectance, we dyed the copper pipes with a coloured varnish in the respective colours of the species (*C. regius*: bright ivory (RAL 1015) with a black dorsal line, *M. boulengeri*: white aluminium (RAL 9006)) (Shine and Kearney 2001). In each pipe, we placed an unwrapped and, in the case of *M. boulengeri*, sawn off iButton® (DS1923) to log the temperature every 10 minutes.

Copper pipe models were placed at different locations of the habitat where each species is most common, respectively in red sand dunes dominated by Hopbush (*Dodonaea attenuata*) and blue bush *(Maireana pyramidata*) for *C. regius*, and in a riverine woodland of black box eucalypts (*Eucalyptus largiflorens*) and small bushes dominated by blue bush (*M. pyramidata*), *Sclerolaena paradoxa*, and *Enchylaena tomentosa* for *M. boulengeri* (Henle 1989a, 1989b, 1990b). All models were loosely placed on the ground on similar soil types for each species and with a North-South orientation for all measurements in order to minimize variations in T_e due to confounding factors (Shine and Kearney 2001).

To ensure the representativeness of microhabitat conditions, we chose seven bushes of different sizes and measured T_e along the shading gradient of each bush between 3rd February and 20th February 2015 and 9th February and 24th February 2016. This bush gradient comprised of five locations, starting outside of the bush ($T_{e.sun}$) through three locations at the periphery ($T_{e.West}$, $T_{e.East}$, $T_{e.South}$) to the bush centre ($T_{e.shade}$). We placed three copper pipe models per location per bush and used means across the three replications per location per bush for higher accuracy. For each T_e measurement, we recorded the bush species, the North-South and East-West extent and the height of the bush. For measurements in the riverine woodland we also noted whether the bush could be shaded by eucalypts. This approach is generally recommended for investigations of the spatial and temporal thermal structure of habitats (Vickers and Schwarzkopf 2016).

4.3.2 CLIMATE DATA

We used iButton® temperature/humidity loggers (DS1923) to measure the environmental temperature in the air T_{air} (1.2 m above ground) and on the soil in direct sunlight T_{sun}. For comparison we measured the temperature in a burrow 15 cm below the surface T_{burrow} to evaluate whether individuals would survive in retreats. Environmental temperature measurements were conducted every 10 minutes at the same time as the measurements of T_e by the copper pipe models (February 2015 and February 2016). Additional environmental temperatures (T_{air} and T_{sun}) were measured every three hours from February 2014 to February 2016. A detailed description of the climatic parameter space over these two years can be found in Appendix S1.

In order to model T_e in years where we did not measure environmental temperatures (see below), we obtained T_{air} from local weather data from the Bureau of Meteorology of the Australian Government (http://www.bom.gov.au/climate/data/stations) from the weather station closest to Kinchega (station 047019 Menindee Post Office). T_{air} was corrected according to the temperatures in Kinchega (Grimm et al. submitted).

4.3.3 COOLING POWER OF BUSHES

We determined the cooling power of bushes at any time or day by calculating the maximum difference between $T_{e.sun}$ and T_e measured at any other location below a bush, which resulted in 22,165 measurements. To investigate whether the size of the bush influenced its cooling power, we conducted a Pearson's correlation test between the cooling power and the bush size for each skink species.

4.3.4 FROM T_E TO ACTIVITY BUDGETS

In order to extend the species-specific T_e measurements to all those days where we had only measured environmental temperatures (February 2014-February 2016), we built a linear model (LM) using the copper-pipe-measurements of February 2015 and successfully validated the model using the copper-pipe-measurements from February 2016 (Appendix S2.1). We then extrapolated T_e from any other day and time between February 2014 and February 2016. Thus, we increased our overall time scale for which we could determine activity budgets from two month to two years, enabling more robust models for activity budget predictions in the past and the future (see below). Nevertheless, T_e values between February 2014 and February 2016 were on a coarser time scale (every 3 hours compared to every 10 minutes) and had to be calculated for three different bush types: no bush (i.e., $T_{e.sun}$), small bushes, and large bushes. The size of the bushes emerged from average bush sizes measured in the field (*C. regius*: small = 4 m^2, large = 20 m^2; *M. boulengeri*: small = 3 m^2, large = 10 m^2). Moreover, T_e along the entire bush gradients, i.e. through the locations at the periphery and bush centre, was predicted.

We then calculated the corresponding activity budgets. We used two measurements for daily activity budgets: available activity time (AT) and relative available activity time (RelAT). We defined AT as the amount of time that an individual could be active within its operative thermal environment (Bakken 1992). The operative thermal environment of a species reflects the thermal conditions of a specific location at a specific point in time within the species' thermal activity range and at the appropriate time of the day (Porter et al. 1973). Following this definition, *C. regius* could be active at $19.3°C \leq T_e \leq 45.1°C$ from sunrise to sunset (Greer 1989, Henle 1989b), while *M. boulengeri* could be active at $12.7°C \leq T_e \leq 42.0°C$ from one hour before sunrise to one hour after sunset (Henle 1989a, 1989b). Data for sunrise and sunset were taken from Geoscience Australia, the Australian Government (http://www.ga.gov.au/geodesy/astro/sunrise.jsp).

For comparison, we defined daily RelAT as the percentage of AT in relation to the potential available time that a species would have on that day when ignoring thermal limits. Here, we did not differentiate between where individuals could be active but rather between whether there was any location in the vegetation gradient where they could be active. In doing so, we assumed behavioural thermoregulation of individuals since they are assumed to shuttle between the most appropriate microhabitats.

4.3.5 TEMPORAL EXTRAPOLATION OF RELATIVE AVAILABLE ACTIVITY TIME (RELAT)

As we were interested in how RelAT changed from 1985 until now and how it might change until 2050 and 2090, we first had to predict RelAT for any other day that we had not measured. Therefore, we related species- and bush-specific RelAT to the T_{air}-range of a given day between February 2014 and February 2016 (Appendix S2.2). Based on this relationship, we were able to predict RelAT on a daily basis for the last 30 years (1985-2016) using the available T_{air} time-series and by cutting the values to the range of 0-100%.

We then predicted T_{air} under climate warming according to the worst case IPCC emissions scenario RCP 8.5 in 2050 and 2090 (Appendix S2.2). These predictions resulted in a mean $T_{air.max}$ of 30.10°C in 2050 and 32.51°C in 2090. We did not consider a more benign emissions scenario because our predictions of $T_{air.max}$ were still below a continuation of the current linear trend in warming (32.42°C and 35.81°C in 2050 and 2090, respectively). We then used the predicted daily $T_{air.max}$ and $T_{air.min}$ values to predict the RelAT for every day of the year in 2050 and 2090.

To investigate whether RelAT changed over time, we finally used a linear mixed model (LMM) with RelAT as the response variable. The explanatory variables were the fixed effects of Year and the quadratic relation of the Julian Calendar Day and the random intercept of Year (Barr et al. 2013). We conducted these LMMs separately for each species, bush type and season (summer: October-March; winter: April-September) as we assumed different thermoregulatory behaviour between summer activity and winter activity (Appendix S1). Furthermore, we conducted these analyses twice – the first time to determine the past changes of RelAT (i.e. between 1985 and 2016) and the second time to include future changes of RelAT (i.e. between 1985 and 2090).

All statistical analyses were performed in R 3.1.1 (R Core Team 2016) unless otherwise stated. We used the packages *lme4* (Bates et al. 2015) and *nlme* (Pinheiro et al. 2016).

4.4 Results

4.4.1 OPERATIVE TEMPERATURES AND THE COOLING POWER OF BUSHES

Despite daily fluctuations, operative temperatures T_e showed a consistent variation pattern within locations (Fig. 2 for averages across all days). During the daytime, $T_{e.sun}$ was much higher than T_e at any other location in the bush gradient for both species. T_e was almost always coolest in the bush centre followed by T_e in the periphery with the warmest T_e always being the one under the sun's rays during the daytime. At night-time, no difference between bush locations was observed and T_e under any location of the bush gradient was slightly higher than $T_{e.sun}$, i.e. bushes were saving heat. Moreover, $T_{e.sun}$ was lower than T_{sun} throughout the night. Generally, T_e followed T_{sun} (maximal range: 13.6°C – 71.9°C) which was found to be stronger for *M. boulengeri* (maximal range: 13.5°C – 68.7°C) than for *C. regius* (maximal range: 12.4°C – 62.5°C). $T_{e.sun}$ exceeded the species' CTmax during the day (from 11:30 to 18:00 for *C. regius* and from 11:30 to 19:00 for *M. boulengeri*). However, bushes provided thermal refuges for individuals – although with species-specific differences. All locations in the bush gradient kept the temperature below CTmax at any time of the day for *C. regius*. Contrastingly, only the bush centre was found to be suitable throughout the day for *M. boulengeri* while T_e in locations of the periphery was above CTmax between at least 14:00 and 15:00 on average (Fig. 2). In comparison, we measured environmental temperatures in a burrow as a possible retreat site (T_{burrow}) to investigate whether the species could survive at times of inactivity. We found that T_{burrow} was always well below the CTmax of both species. T_{burrow} showed a low total diurnal variation with a decreasing temperature until 13:00 (minimum value measured: 27.1°C) and an increasing temperature until 19:00 (maximum value measured: 39.1°C) (Fig. 2).

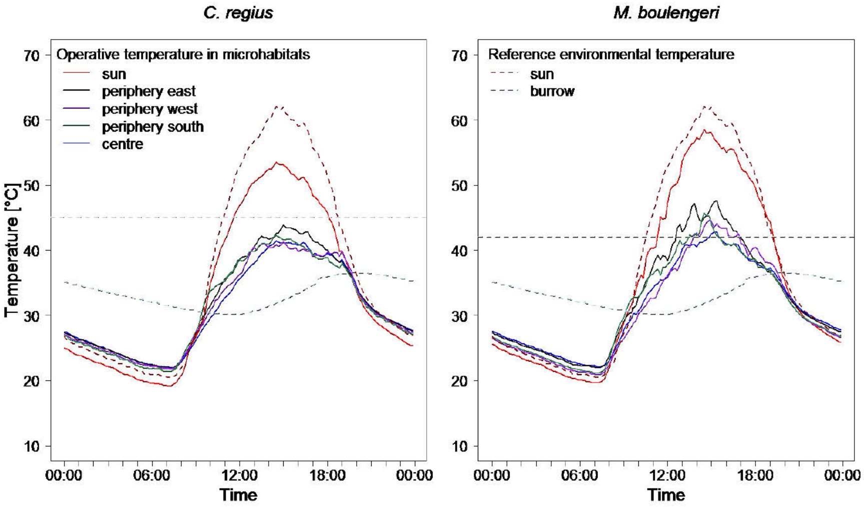

Figure 2: Average diurnal operative and en-vironmental temperatures for *C. regius* (left) and *M. boulengeri* (right) at five different microhabitat locations across all days and bushes. The horizontal dashed grey line indicates the CTmax for each species.

Bushes acted as thermal regulators buffering external temperatures for both species either by cooling during the day or by saving the heat during the night. This regulation power depended on bush size. In general, larger bushes had a higher cooling power than smaller bushes (Pearson's correlation test: t = 9.48 and 11.98 for *C. regius* and *M. boulengeri*, respectively, df = 22163, $p < 0.001$). The variation between days and bushes was largest between 12:00 and 15:00 (Fig. 3). Moreover, the cooling power for *M. boulengeri* was higher than for *C. regius* (difference to $T_{e.sun}$ up to 26.2°C and 20.5°C, respectively) in spite of the biggest bush being 10.8 m² for *M. boulengeri* and 19.35 m² for *C. regius*. Additionally, the average T_e of *M. boulengeri* was 0.82°C lower if the area was occasionally shaded by a eucalypt tree (Appendix S2.1).

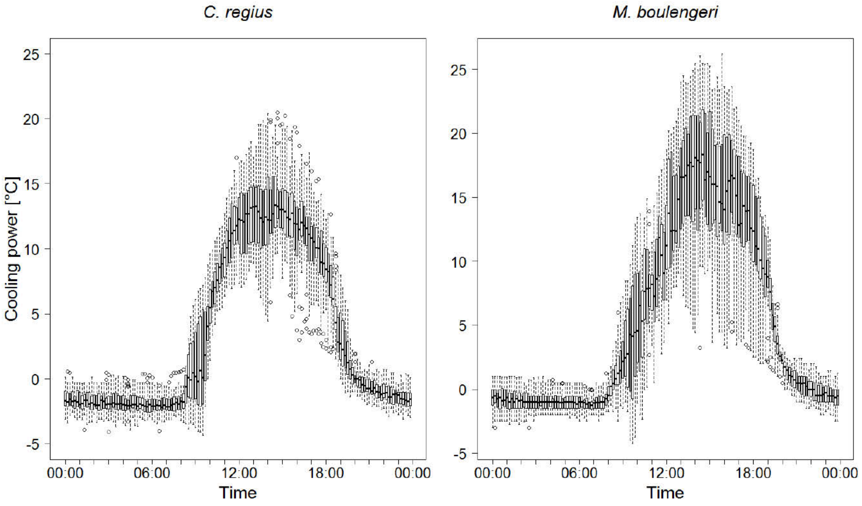

Figure 3: Average and range of the cooling power of bushes for *C. regius* (left) and *M. boulengeri* (right) throughout the day.

4.4.2 AVAILABLE ACTIVITY TIME UNDER PRESENT CONDITIONS

Heat reduced the duration of activity time (AT) in the sun for both species (Fig. 4), both on hot days (e.g., 22/02/2016, T_{air} = 21.1°C – 45.8°C, T_{sun} = 20.6°C – 70.4°C; *C. regius* and *M. boulengeri* were restricted for 7.83 and 8.67 hours, respectively) and on cool days (e.g., 04/02/2015, T_{air} = 18.2°C – 32.2°C, T_{sun} = 17.6°C – 50.5°C; *C. regius* and *M. boulengeri* were restricted for 0.17 and 6.67 hours, respectively). In shaded locations of the bush gradient, daily AT restriction varied between locations on hot days, whereas both species were able to be active at all locations on cooler days (Fig. 4). Overall, RelAT varied from 81% to 100% for *C. regius* with a mean of 95.3% (2015: 96.5%, 2016: 93.9%), and from 51.7% to 100% for *M. boulengeri* with a mean of 87.9% (2015: 92.6%, 2016: 82.8%). On the hottest days, total AT restriction (i.e. no activity at any location) was 2.5 and 7 hours for *C. regius* and *M. boulengeri*, respectively. In comparison, cold summer temperatures never restricted the AT of *M. boulengeri,* whereas the AT of *C. regius* was reduced due to the cold in the morning hours at all locations except for the bush centre (Fig. 4).

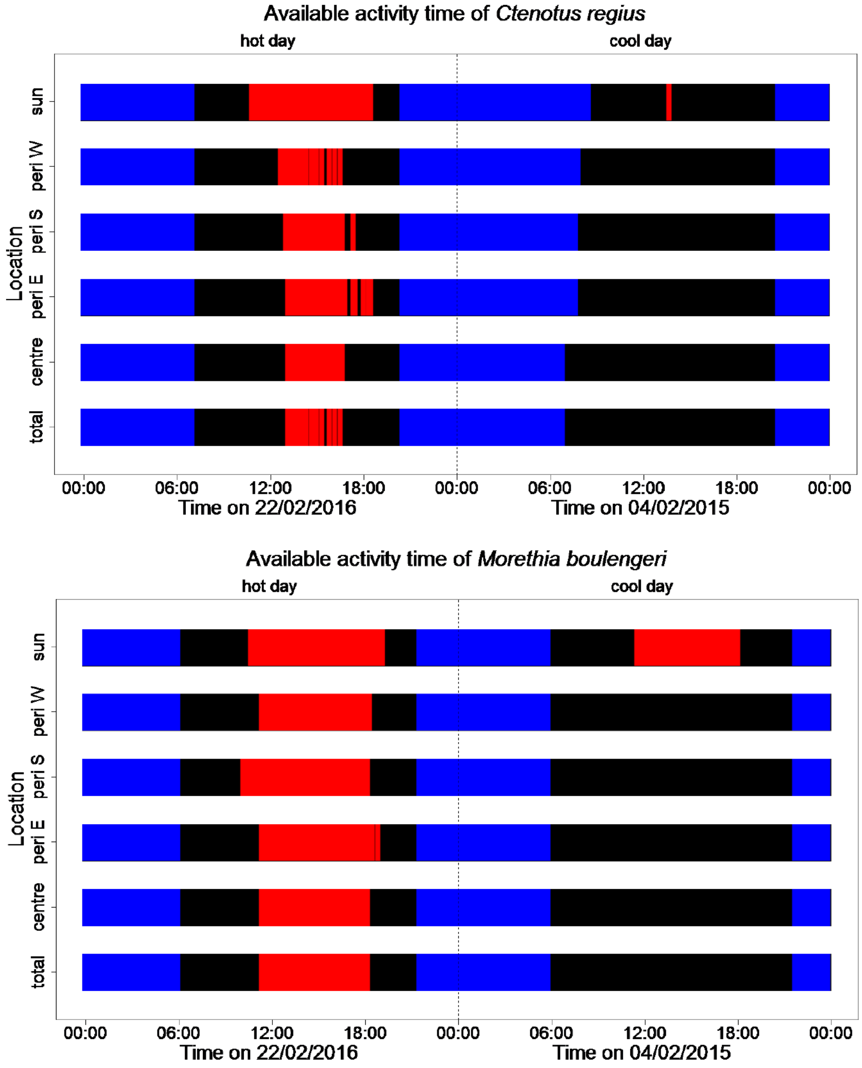

Figure 4: Comparison of available activity time on a very hot (22/2/2016) and a very cool (04/02/2015) summer day for *C. regius* (above) and *M. boulengeri* (below) across five locations. "Total" means the species can be active if it can be active at any location. Red areas symbolise inactivity due to temperatures above CTmax, blue areas symbolise inactivity due to night or temperatures below CTmin, black areas symbolise activity.

When considered all year round (Fig. 5), RelAT under large bushes was always higher than under small bushes or in the sun. In summer, both species were found to be fully active if large bushes were available

(RelAT≈100%), whereas they showed a restricted diurnal activity budget if only small bushes were available (RelAT=80-90%) or if no bush was present at all (RelAT=60-70%). The annual activity of *C. regius* still peaked in summer if only small bushes were available, but showed an annual bimodal activity without the presence of bushes. In comparison, *M. boulengeri* already showed an annual bimodal activity if only small bushes were available (Fig. 5). In winter, the activity budgets of *C. regius* dropped to 20% or less irrespective of the presence of bushes with several days showing no activity at all. Winter activity budgets of *M. boulengeri* also dropped below 60% but were above 20% all year round. Notably, its activity budget without the presence of bushes was identical between mid-winter (July) and mid-summer (January), implying strong restrictions due to the heat in summer and due to the cold in winter (Fig. 5).

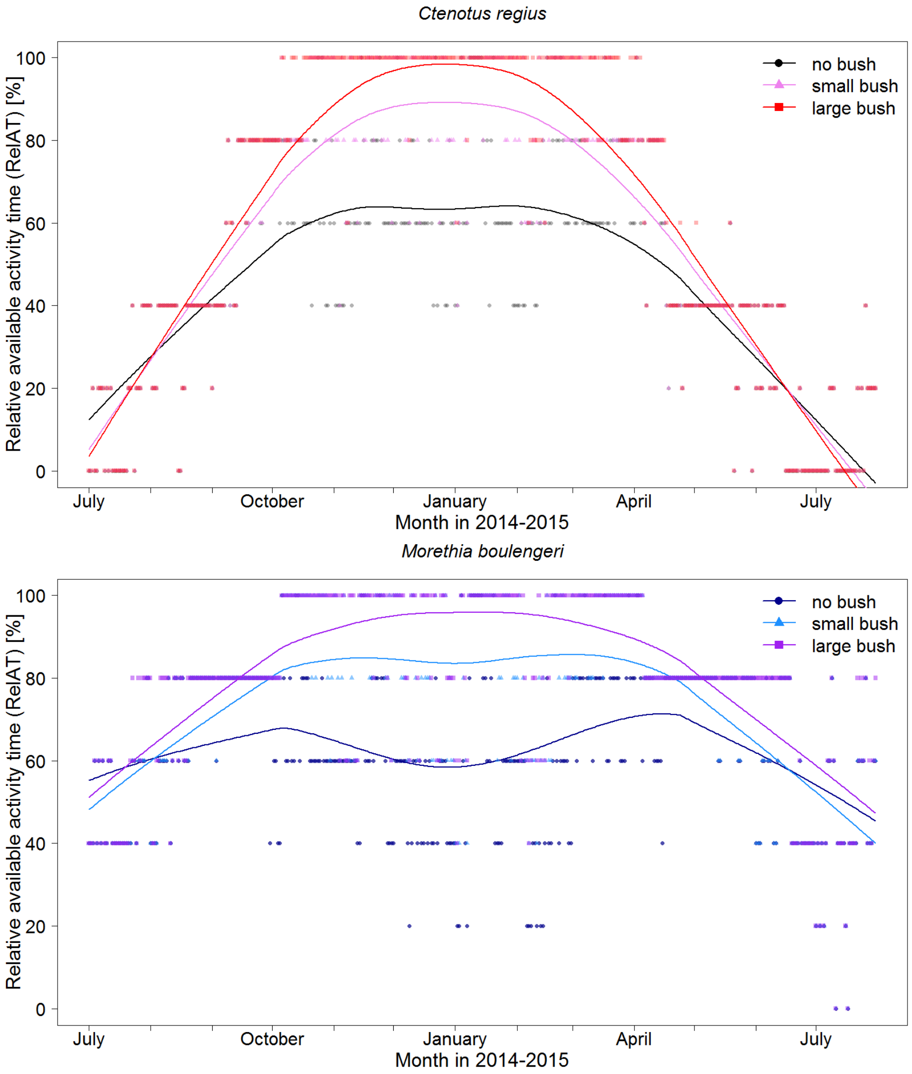

Figure 5: Relative available activity time (RelAT) preditions for *C. regius* (above) and *M. boulengeri* (below) across three bush types for one year. Symbols are calculated values, lines represent moving averages (smoother span factor 0.3).

4.4.3 AVAILABLE ACTIVITY TIME UNDER PAST AND FUTURE CONDITIONS

Activity budgets for *C. regius* were found to increase significantly for both time spans from the past to the present ($0.003 \leq p \leq 0.007$) and from the past to future conditions ($p << 0.001$; Table 1; Fig. 6) irrespective of the presence of bushes and for both seasons: summer and winter. On the contrary, activity budgets for *M. boulengeri* were found to decrease in the summer for both time spans from the past to the present ($0.009 \leq p \leq 0.064$) and from past to future conditions ($0.001 \leq p \leq 0.047$). They were only found to increase in the winter from past to recent conditions under large bushes (p = 0.033), but irrespective of bush presence from past to future conditions (p << 0.001; Table 1; Fig. 6). RelAT in winter always remained below the RelAT in summer for *C. regius* and increased by approximately 30% between 1985 and 2090 (Appendix S3, Figs S3.1, S3.3). On the contrary, the RelAT of *M. boulengeri* in winter was lower than in summer in the past. Nowadays, both winter and summer RelAT are almost equal but might be higher in the winter than in the summer by 2090, while still showing annual bimodal activity peaking in spring and autumn (Appendix S3, Figs S3.2, S3.3). Mean $T_{air.max}$ and $T_{air.min}$ as well as averaged RelAT separated by species, bush type, and season are summarised in Table S3.1 (Appendix S3).

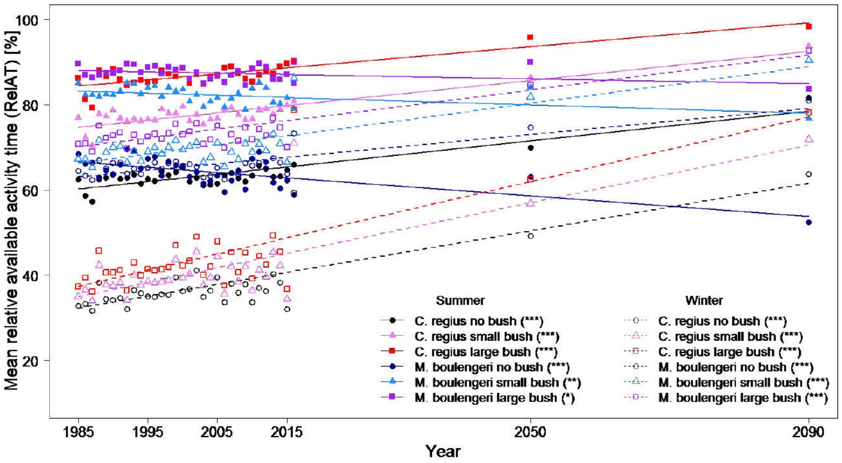

Figure 6: Mean relative available activity time (RelAT) across seasons for both skink species and three bush types. Symbols represent predicted values, lines are lines of best fit (filled and solid: summer, open and dashed: winter). Significance levels are shown in brackets in the legend.

Table 1: Estimates and p-values for the fixed effect of year of an LMM investigating the temporal change of relative available activity time per day in Kinchega National Park.

		Time period	**1985-2016**		**1985-2090**	
Season	**Bush type**	**Species**	***Ctenotus regius***	***Morethia boulengeri***	***Ctenotus regius***	***Morethia boulengeri***
Summer	**no**	estimate	0.077	-0.133	0.170	-0.116
		p-value	0.007	0.009	<0.001	<0.001
	small	estimate	0.091	-0.074	0.165	-0.047
		p-value	0.003	0.024	<0.001	0.004
	large	estimate	0.099	-0.050	0.135	-0.027
		p-value	0.003	0.064	<0.001	0.047
Winter	**no**	estimate	0.137	0.026	0.266	0.149
		p-value	0.005	0.360	<0.001	<0.001
	small	estimate	0.176	0.072	0.322	0.207
		p-value	0.007	0.078	<0.001	<0.001
	large	estimate	0.195	0.083	0.359	0.196
		p-value	0.009	0.033	<0.001	<0.001

As the strongest differences in activity budgets between species occurred in summer, we will describe these changes in more detail (Appendix S3). In cooler years (i.e. in the 1980s and 1990s, Appendix S3Table S3.1), *C. regius* showed an average daily activity budget of 80-85%, while nowadays it has increased to 90% and is predicted to be above 95% in the future, when the presence of large bushes is assumed. Moreover, the number of days with RelAT of 100% in summer increased over time (Appendix S3, Figs S3.1, S3.3). Although *C. regius* always showed a unimodal annual activity distribution with one peak in summer, it might become bimodal in the future if no or only small bushes will be available (Appendix S3, Fig. S3.1). On the contrary, *M. boulengeri* always showed a slight bimodal activity distribution throughout the year with the strongest bimodality in areas without bushes (Appendix S3, Fig. S3.2). Activity budgets with up to 100% RelAT were found around April and November. When comparing past and future conditions, however, average summer activity decreased slightly from ≈90% and ≈80% for large and small bushes to ≈85% and ≈80% for now and ≈83% and 75% for the future, respectively (Appendix S3, Figs S3.2, S3.3).

We also found that the number of days within a year on which individuals could be active at least 80% of the day (Grimm et al. in prep.) was increasing for both species – irrespective of bush type (Appendix S3, Fig. S3.4). This increase continued until 2090 for *C. regius* but levelled off for *M. boulengeri* between 2050 and 2090 for areas with small or large bushes.

4.5 Discussion

We found that the microhabitat (vegetation shading gradient and bush size) had a strong influence on the operative temperatures and the activity budgets of both species. At high temperatures, individuals of the two species benefited from shaded locations which decreased the operative temperatures and increased the activity budgets, especially for locations at the centre of the bush and for large bushes. The shade of eucalypt trees additionally enhanced this cooling effect for *M. boulengeri*. However, bushes also enabled the two skink species to save heat when the temperature was cold with temperatures at central locations and large bushes cooling down more slowly than locations on the periphery of the bush gradient and smaller bushes. Thus, microhabitat conditions considerably increased the activity time for both species by balancing either warm or cold temperatures, confirming the critical influence of heterogeneous vegetation structures on both body temperature and activity (Kearney 2013). Our results also showed fluctuations in the buffering effect of temperature along the vegetation gradient within the day which allowed behavioural thermoregulation in reptiles by providing alternative options while selecting optimal thermal places. Such active microhabitat selection behaviour is important for the survival of lizards in hot deserts (Clusella-Trullas et al. 2011, Vickers et al. 2011) and was frequently observed for both species in the field. Especially during summer individuals were observed hunting in bushes and not in open areas in the early afternoon (Henle 1989b; own observations).

In a detailed study of the reptile community of Kinchega National Park between 1985 to 1987, Henle (1989b) investigated the activity of both species through direct observations every second month. He found that *M. boulengeri* was active throughout the year with decreased activity in winter and hot summer months, while *C. regius* was only active from September to May with a peak of activity in hot summer months. Furthermore, he observed bimodal diurnal activity for *M. boulengeri* in November and January and for *C. regius* in January (there were no observations in December and February). Both observations are in line with our model predictions, strengthening the advantages of our approach that extrapolates fine-scale experimental data to broad-scale time series and that uses T_e to test whether the activity budget is an appropriate fit with the individual activity observed in the field.

The thermal preferences of the two species are also reflected by the location of Kinchega with respect to their distribution range: in our study area the activity of *C. regius*, a species inhabiting Australia's hot central deserts (Fig. 1), was most likely to be restricted by cold temperatures. Consequently, T_e in *C. regius* was certainly below CTmax most of the time, corroborating that hot periods enhance the activity time of this species in the study area. However, the restriction of activity on cold days even in summer or between autumn and spring was still very strong and *C. regius* had to shift its activity towards the warmer part of the day, i.e. during early afternoon hours (Henle 1989b; this study). Importantly, without large bushes saving heat in cold morning hours but cooling during hot early afternoon hours, *C. regius* was only able to be active on hot summer days until it became too hot and average summer activity would decrease by 20% per day (Appendix S3 Table S3.1). On the contrary, *M. boulengeri* inhabits cooler habitats towards Eastern Australia with Kinchega on the warm edge of its distribution area (Fig. 1). Thus, T_e exceeded CTmax quite often, leading to frequent activity restrictions throughout summer months and bimodal activity. Although bimodal diurnal activity is a commonly observed behavioural strategy in desert lizards in summer (Adolph and Porter 1993), the species' activity in Kinchega would be restricted for an average of 40-50% of the day throughout almost the entire summer without the presence of large bushes under which they would be only restricted for an average of 10-15% per day (Appendix S3 Table S3.1). Our findings suggest that in addition to temperature as the most important driver (Cahill et al. 2014), the availability of vegetation and heterogeneity are highly important factors in determining the warm-edge range limits for ectotherms. Likewise, Walker, Stuart-Fox & Kearney (2015) observed a warm-edge range restriction in an Australian desert agama which was potentially driven by reduced mid-summer activity budgets, not only depending on temperature but water and shelter availability. In addition, Clusella-Trullas et al. (2011) found that precipitation rather than temperature is driving lizard performance, especially in arid areas. Although our study only examined the thermoregulatory options available to two lizard species, these two species represent the sympatric presence of warm-adapted and cold-adapted lizards in relation to the thermal habitat. Our predictions rely on thermal processes in ectotherms which do not differ fundamentally between species or regions. Differences would only occur if species were able to use a broader range of thermal habitats by either becoming nocturnal (Henle et al. 2010, Grimm et al. 2014b) or living in a subterranean environment where small changes in height can change the entire thermal conditions (Henle 1989c, Henle et al. 2010, Clusella-Trullas et al. 2011). Since both species are diurnal and terrestrial, differences in their responses can only be explained by their adaptation to warm or cold habitats.

In the future, cooler microhabitats might become more favourable for *C. regius* which has already benefitted from a prolonged annual activity time, from which it might benefit even more in the future. In contrast, warmer microhabitat temperatures could well be above the thermal preferences of *M. boulengeri*, possibly restricting its activity completely during mid-summers in the future. Hence, we could postulate that with climate warming warm-adapted species might profit at their cold distribution edge while cold-adapted species might suffer at their warm distribution edge. Generally, climate warming will have less influence in shaded regions and a loss of shade in the future would be a more critical driver of reptile life histories and distributions than warming itself (Kearney 2013; this study). Since every type of vegetation might provide cooling effects (Kearney et al. 2009, Huang et al. 2014), future reptile distribution patterns would certainly be strongly affected by vegetation patterns (Sears et al. 2016). Modelling attempts to forecast future distributions of reptiles therefore critically need to consider more mechanistic processes to offer reliable and accurate predictions (Urban et al. 2016), for instance by integrating future vegetation patterns to reflect thermoregulation potential.

Thermoregulatory behaviour might not shape the response to climate warming alone and could even limit a species' potential for physiological adaptation (Buckley et al. 2015). Instead of physiological adaptation, these species might shift their seasonal timing of activity. In line with that, we showed that with a warming climate, the total activity budget across the year was increasing for the two species investigated as it is the case for other desert species (Walker et al. 2015). However, the days of high activity budgets shifted to spring and autumn and the species might aestivate in hot summer months in the future. Since we showed that temperature in retreats (i.e. in burrows) were always below both species' CTmax, aestivation would not pose any risk of overheating at times of inactivity. In addition to seasonal shifts, Henle (1989b) observed a few individuals of *M. boulengeri* active at night suggesting some flexibility in the timing of activity in that species. Likewise, Treilibs et al. (2016) observed nocturnal activity of the desert skink *Liopholis slateri* during the hottest months. Nevertheless, it remains unclear how successful desert lizards would be able to change their diurnal or seasonal timing of activity. Generally, reptile species seem to have a large phenotypic plasticity and an earlier spring and later fall provide a great opportunity for many species to increase their overall activity season (Bradshaw and Holzapfel 2006, 2008, Walker et al. 2015) albeit this will depend on species-specific genetic adaptation in photoperiodic responses (Bradshaw and Holzapfel 2007). Comparably, widespread lizard species already show huge variability between phenological periods across latitudes with species with a shorter hibernation period often producing more and / or larger clutches (Grimm et al. 2014b). In contrast, warmer hibernation periods in turtles led to greater energy losses during hibernation and in turn poorer body conditions during reproduction (Muir et al. 2013).

Together, not only the thermal preferences of the species but also the availability of vegetation and the seasonal timing of activity will determine whether a species can persist in a specific habitat (Kearney et al. 2009; Hacking, Abom & Schwarzkopf 2014; this study). While we cannot influence species' adaptation mechanisms, we should preserve vegetation as refuges for small reptiles to increase the probability of persistence. In Australia, this means avoiding grazing and trampling by livestock or feral herbivores and preventing wildfires (Pavey et al. 2017) as well as preserving native vegetation and managing alien plants since their thermal microhabitats can differ substantially making alien plants unsuitable for small lizards (Valentine et al. 2007, Hacking et al. 2014).

4.6 Conclusion

Extrapolating short-term, high-resolution experimental data to longer and less accurate time-series is a promising approach to fill gaps in past records. Reconstructing past ecological conditions creates important challenges but is also imperative to address the long-term responses of species to environmental changes. Here, we could stress that thermoregulatory behaviour and the activity budgets of diurnal, terrestrial desert skinks were strongly impacted by the amount of vegetation and its heterogeneity, which provided both cooling spots and heat reservoirs. Although climate change is likely to lead to a species-specific reduction in activity budgets in mid-summer, it might also provide novel temporal niches that could even contribute to an increasing annual activity budget. Moreover, the cascading effects of vegetation rather than climatic envelopes alone should be addressed in future conservation strategies to prevent desert lizards from extinction.

4.7 Authors' Contributions

All authors conceived the ideas, designed the general methodology and collected field data. AG analysed the data, performed the modelling and led the writing of the manuscript. All authors contributed critically to the drafts and gave their final approval for publication.

4.8 Acknowledgements

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4.9 Supporting Information

Appendix S1: Climatic parameter space measured in 2014-2016

Appendix S2: Calibrating high-resolution experimental data to longer thermal time-series with different temporal resolutions

Appendix S3: Additional data and figures of relative available activity time from the past to the future

Figure 7: *Ctenotus regius* in front of a blue bush. Photo by Annegret Grimm-Seyfarth.

Figure 8: Copper pipe model of *C. regius*. Photo by Annegret Grimm-Seyfarth.

5 Individual and population responses to trophic species interactions under climatic fluctuations

In addition to the described non-trophic interactions between reptiles and vegetation, reptiles are affected by trophic interactions. This is particularly important in deserts where reptiles strongly depend on scattered food availability and their communities are largely shaped by predation. While direct relations among climatic conditions, invertebrates, vegetation, or reptiles have been frequently explored, to my knowledge, species' responses to direct and indirect pathways of multiple climatic and biotic factors and their interactions have rarely been examined comprehensively. However, effects from multiple pathway investigations may differ fundamentally from effects of isolated climatic or biotic factors since single factors could be enhanced by synergistic pathways or diminished by opposing pathways. Therefore, I investigated the direct and indirect effects of both climatic and biotic parameters on the individual condition and occupancy of the eight most abundant lizard species occurring in my study area throughout the 30-year monitoring period. I used structural equation modelling to disentangle single and interactive effects of climatic and biotic parameters, and further assessed whether species could be grouped in functional groups according to their responses to climatic and biotic parameters. This chapter gives an indication of how to identify relevant functional groups at different ecological levels. This could be important for both field work targeted at determining relevant mechanistic processes that facilitate the response of species or functional groups to global change stressors, and targeted conservation. Moreover, it stresses the importance of indirect pathways and species interactions when analysing the effects of climate change.

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Eat or be eaten: Desert reptiles between prey, predators and climatic extremes

5.1 Abstract

While direct relations among climatic conditions, invertebrates, vegetation, or reptiles have been frequently explored, to our knowledge, species' responses to direct and indirect pathways of multiple climatic and biotic factors and their interactions have rarely been examined comprehensively. We investigated these effects on body condition and occupancy of the eight most abundant lizard species in an Australian hot desert lizard community using a 30-year multi-trophic monitoring study. We used structural equation modelling to disentangle single and interactive effects and assessed whether species could be grouped into functional groups according to their responses. Lizard species differed strongly in how they responded to climatic and biotic factors. The factor to which they responded seemed to be closely related to their functional traits. While body conditions were determined by their habitat, activity time and prey, occupancy responses were mainly determined by habitat specialisation, body size and longevity. Our findings highlighted key actions necessary for predicting impacts of climate change and for conservation planning: (1) Inclusion of indirect pathways in predictive models to increase accuracy when predicting future species presence; (2) consideration of species functional groups for modelling since one might never obtain all mechanistic pathways on the species level, and (3) conservation of natural floodplains even in hot deserts to secure a natural turn-over of community composition. With these key actions, the effects of climate change in a desert reptile community may be buffered to a large extent.

5.2 Introduction

In a world driven by ongoing global changes (IPCC 2014b), it is an urgent need to understand how species might respond to climate change. Ectotherms are assumed to be particularly vulnerable (Kearney et al. 2009, Gunderson and Leal 2016) and especially terrestrial reptiles are of high concern (Gunderson and Stillman 2015). Among the highest reptile density and diversity on earth can be found in hot drylands (Pianka and Schall 1981, Powney et al. 2010) making the conservation of dryland reptiles particularly important (Webb et al. 2015). Hot drylands are characterised by extremely high temperatures and low precipitation and cover over 40% of the global terrestrial area (Millennium Ecosystem Assessment 2005).

Deserts reptile communities will likely react asynchronously to fluctuations of local climatic conditions (Read 1995, Dickman et al. 1999, Letnic et al. 2004, Read et al. 2012). Individual conditions and life-history parameters of single reptile species can be either enhanced or diminished in reaction to temperature (Adolph and Porter 1993, Sarre et al. 1995, Chamaillé-Jammes et al. 2006, Massot et al. 2008, Monasterio et al. 2013), rainfall (Dickman et al. 1999, Letnic et al. 2004, Holmgren et al. 2006, Marquis et al. 2008, Ryan et al. 2016), or a combination of both (Smith et al. 1995, Barrows 2011, Read et al. 2012, Grimm-Seyfarth et al. 2017a). However, no climatic factor will affect reptiles only directly but rather through multiple pathways (Ockendon et al. 2014, Deguines et al. 2017). Exemplarily, effects of rainfall on lizards were frequently interpreted as indirect through resource availability (Barrows 2011, Read et al. 2012, Grimm-Seyfarth et al. 2017a). Indeed, lizards are strongly dependent on food availability (Ballinger 1977, Pianka 1986, Barrows 2011) and vegetation cover (Letnic et al. 2004, Kearney et al. 2009, Read et al. 2012, Grimm-Seyfarth et al. 2017b). In turn, desert invertebrates themselves, which are both the most common food of arid-zone lizards (Pianka 1986) and potential predators (Henle 1990a), depend on water, temperature, and vegetation abundance and composition (Denlinger 1980, Read 1995, Kwok et al. 2016), with the latter being also related to rainfall (Shmida et al. 1986, Robertson 1987, 1988, Morton et al. 2011) or to standing water in flooded anabranches (Shmida et al. 1986, Robertson et al. 1987, Roberts and Marston 2011).

While direct relations among climatic conditions, invertebrates, vegetation, or reptiles have been frequently explored, to our knowledge, the multiple pathways along which the climatic and biotic relations interact directly or indirectly affecting reptiles in a changing climate have rarely been examined. Results of studies simultaneously considering the effects from multiple pathways may differ fundamentally from those analysing isolated climatic or biotic factors since single factors could be enhanced by synergistic or diminished by antagonistic pathways (Werner and Peacor 2003, Deguines et al. 2017). Therefore, Ockendon et al. (2014) recently advocated monitoring of multiple trophic levels to understand the overall effects of drivers of global change on single species, which is essential for designing optimal future conservation strategies.

A limitation for such integrative investigations is that they are only possible through long-term multi-species monitoring. Taking advantage of a unique 30-years monitoring study of a community of 20 lizard species in arid Australia, we investigated the direct and indirect effects of climatic and biotic parameters on body condition and occupancy of the eight most abundant lizard species using structural equation modelling.

Following Ockendon et al. (2014), we hypothesized that biotic factors are at least as important as climatic factors, but that the effects differ between the individual and the population level (Grimm-Seyfarth et al. 2017a). The eight lizard species we focussed on differed in their functional traits (Table 1). Since different functional traits could potentially explain different reactions among species (Read et al. 2012), we tested whether individual and population responses were related to species' functional traits. Based on the results, we identified key actions for both fundamental ecology and future conservation strategies.

5.3 Materials and methods

5.3.1 STUDY SITE AND STUDY SPECIES

The study was conducted in Kinchega National Park, New South Wales, Australia (32°28' S, 142°20' E). Kinchega is situated at the eastern margin of Australia's arid zone and characterized by high and increasing summer temperatures and low but highly variable rainfall without seasonal patterns. Additionally, Kinchega contains floodplains with flooding being related to rainfall in inland Queensland due to La Niña events (Grimm-Seyfarth et al. 2017a). We monitored three study plots: Two riverine woodlands and the Kinchega field station as described in Henle (1989a, 1990a). The first riverine woodland (RWI) was characterised by cracking clay, widely dispersed black box eucalypts (*Eucalyptus* *largiflorens*) and highly varying vegetation cover. The second riverine woodland (RWII) was characterised by sandy clay with only slightly dispersed black box eucalypts. The herb layer coverage varied strongly among years and the shrub layer was dominated to varying extends by black blue bush (*Maireana pyramidata*), black rolypoly (*Sclerolaena muricata*), cannonball burr (*Dissocarpus paradoxus*), and ruby saltbush (*Enchylaena tomentosa*). The Kinchega field station (hereafter station) consisted of seven huts in 1986/7 and eight huts since 1991 made of corrugated iron and surrounded by sandy soil occasionally covered by single shrubs and low and patchy herbs. During the 30 years, park rangers and individual researchers have used the huts to a varying extend and it is likely that the frequency and intensity of the station usage impact on lizards species living in this plot.

Monitoring took place on an almost annual basis at the end of the reproductive season in February or March from 1986 to 2016 except for 1988-1991, 1993, 1995, and 2008-2011. Each species was caught during its active time of the day during at least five days per plot per season (see Appendix S1.1 for capture methods). Every individual caught was measured, weighted, sexed and aged (if possible), and individually identified (Appendix S1.1).

Body condition was calculated for each captured individual using the scaled mass index (SMI) which accounts for individual growth (Peig and Green 2009; Appendix S1.2). We conducted multi-season occupancy modelling (MacKenzie et al. 2006) by means of the *colext* function of the R-package *unmarked* (Fiske and Chandler 2011). For details see Appendix S1.2.

The functional traits of the eight most abundant lizard species used in this study are summarised in Table 1. We divided species into four functional groups based on two functional traits (activity time and habitat use) that we assumed most important for hot desert reptiles: two diurnal, terrestrial skinks (*Morethia boulengeri*, *Ctenotus regius*), two nocturnal, terrestrial geckos (*Heteronotia binoei*, *Diplodactylus tessellatus*), three nocturnal, subterranean skinks (*Lerista punctatovittata*, *Lerista xanthura*, *Eremiascincus richardsonii*), and the nocturnal, arboreal gecko *Gehyra variegata*. Species names follow Cogger (2014), except for following Greer (1990) who showed that *L. aericeps* is a synonym of *L. xanthura*.

During each monitoring season, we recorded specific proxies for vegetation, prey, and predation for each study plot. The obtained biotic parameters and their measurements and calculations were summarised in Tables 2 and S2.1.1, respectively. The different methodologies for quantifying the proxies for vegetation, prey, and predation per plot did not affect our statistical methodology because all network analyses were based on data originating from the same plot. Specifically, in the RWII plot a clear difference between herb and shrub layer was present in almost all years and we therefore measured the herb-layer biomass (in kg/ha) and the shrub coverage (%) separately. In the other two plots, the RWI and the station, we estimated the overall non-tree vegetation coverage (%). Additionally, since the RWI was dominated by black box, we estimated eucalypt foliage (Table S2.1.1).

Table 1: Overview on the eight most abundant lizard species. The main study plot used for analyses are shown in bold. All data stem from own analyses and Henle (1989a-c, 1990a-b) except CTmax (see Table S1.1). SVL – mean adult snout-vent-lengths; CTmax – critical thermal maximum (i.e., when righting reflexes cease); N – sample size across all years; a.f. cannibal. – apart from cannibalistic. Longevity refers to minimal longevity as individuals can only be aged when they were captured before adulthood.

Species	Study plot	Activity	Habitat	Prey	Foraging mode	Predators	SVL [cm]	Longevity [years]	CTmax [°C]	N
Morethia boulengeri	**RWII**	diurnal	terrestrial	arthropods	widely-foraging	diurnal	4.2	4	41.6	704
Ctenotus regius	**RWII**	diurnal	terrestrial	arthropods/ vertebrates	widely-foraging	diurnal a.f. cannibal.	6.0	1	45.1	116
Heteronotia binoei	RWI, RWII, **Station**	nocturnal	terrestrial	arthropods	widely-foraging	nocturnal	4.35	3	40.6	135
Diplodactylus tessellatus	**RWI**	nocturnal	terrestrial	arthropods	sit-and-wait	nocturnal	4.7	3	43.5	316
Lerista punctatovittata	**RWII**	nocturnal	subterranean	fossorial arthropods	widely-foraging	nocturnal, *Varanus*	8.2	2	43.1	88
Lerista xanthura	**RWII**	nocturnal	subterranean	fossorial arthropods	widely-foraging	nocturnal, *Varanus*	4.5	1	40.9	47
Eremiascincus richardsonii	RWI, **RWII**, Station	nocturnal	subterranean	arthropods/ vertebrates	widely-foraging	nocturnal a.f. cannibal.	8.2	3	42.0	71
Gehyra variegata	**RWI**, **Station**	nocturnal	arboreal	arthropods	sit-and-wait	nocturnal	5.15	28	45.6	1676 3740

We estimated the prey index as the amount of flying and ground dwelling potential prey arthropods observed (Table S2.1.1) except for three species: both *Lerista* species for which we did not measure densities of their main prey species, termites and ants (Henle 1989c), and *E. richardsonii* which mainly predates on small vertebrates (Henle 1989c) for which we calculated a prey index as the number of potential prey vertebrates observed per day (Table S2.1.1). Potential predatory species (Table S1.3) were recorded and (if possible) determined to species level during each diurnal and nocturnal capture occasion. Additionally, smaller predatory arthropods, reptiles, and marsupial mice were captured in pitfall traps. We calculated a species-specific (Table 1) predator index as the number of daily sightings of potential predators (Henle 1989a; Table S2.1.1).

5.3.2 CLIMATE DATA

Climatic data from the weather station closest to Kinchega (station 047019 Menindee Post Office; Bureau of Meteorology, Australian Government http://www.bom.gov.au/climate/data/stations) matched the local conditions very well (Grimm-Seyfarth et al. 2017a). We chose climatic parameters that likely affect the biotic conditions in late summer (Tables 2, see Table S2.1.1 for details). We chose summer mean maximum temperature and the number of days warmer than 45°C reflecting the number of days exceeding all species' critical thermal maxima (Table 1). We further chose the summed summer and the summed previous winter rainfall, both known to affect vegetation in summer (Robertson 1987, 1988). Moreover, since both vegetation (Robertson et al. 1987) and lizard species (Grimm-Seyfarth et al. 2017a) are likely affected by floodplain dynamics, we further considered the averaged summer and winter river heights of the adjacent Darling River at the closest weir (weir 32; Department of Primary Industries, Office of Water, New South Wales Government; http://realtimedata.water.nsw.gov.au/water.stm?ppbm=DAILY_REPORTS&dr&3&drkd_url). Previous analyses indicated that the Darling River heights were strongly related to the ENSO phenomenon (Simpson et al. 1993, Grimm-Seyfarth et al. 2017a) and thus represent indirect distant climatic factors acting on the local ecosystem. As flooding effects might appear with delay, we also considered the number of years after the last flooding of the study area (Table S2.1.1). Finally, we also considered an interaction between each water parameters (summer and winter precipitation and Darling River height) and summer temperature in all analyses since temperature and water availability could potentially interact in the effect they have on plants and animals (Kwok et al. 2016).

Table 2: Summary of all climatic and biotic factors and factor groups (following Fig. 1) influencing lizards at the individual and population level, their description and the study plot for which they apply. See methods and Table S2.1.1 for details and calculations.

Factor group	Factor	Description	Study plot
Temperature	summer temperature	mean maximum summer temperature [°C]	all
	number of days > 45°C	number of days above 45°C	all, but plot-specific
Precipitation	summer rain	total rainfall in summer [mm]	all
	previous winter rain	total rainfall in the previous winter [mm]	all
Flood	summer Darling River height	average Darling River height in summer [m]	all
	winter Darling River height	average Darling River height in previous winter [m]	all
	number of years post flood	number of years since the study area was flooded last time	all
Vegetation	vegetation coverage	estimated non-tree vegetation coverage (%)	RWI, Station
	herb layer biomass	biomass of the herb layer [kg/ha]	RWII
	shrub coverage	estimated shrub and bush vegetation coverage (%)	RWII
	eucalypt foliage	black box eucalypt foliage (5 categories)	RWI
Station usage	station usage intensity	classification (4 categories) of the number of people that stayed longer	Station
Prey	prey index	either arthropod abundance (3 categories), or calculated small-vertebrate index	all, but species-specific
Predation	predator index	calculated predator index	all, but species-specific

5.3.3 STRUCTURAL EQUATION MODELLING

Based on previous studies (see introduction) and our own expertise, we developed a conceptual network between the climatic (temperature, precipitation, flooding) and biotic factor groups (vegetation, prey, predation) that could potentially influence the eight focal lizard species at either individual or population level (Fig. 1, Table 2, see Appendix S1.3 for a detailed description). We applied this conceptual network at individual (body condition) and population level (occupancy) for each focal lizard species through separate analyses.

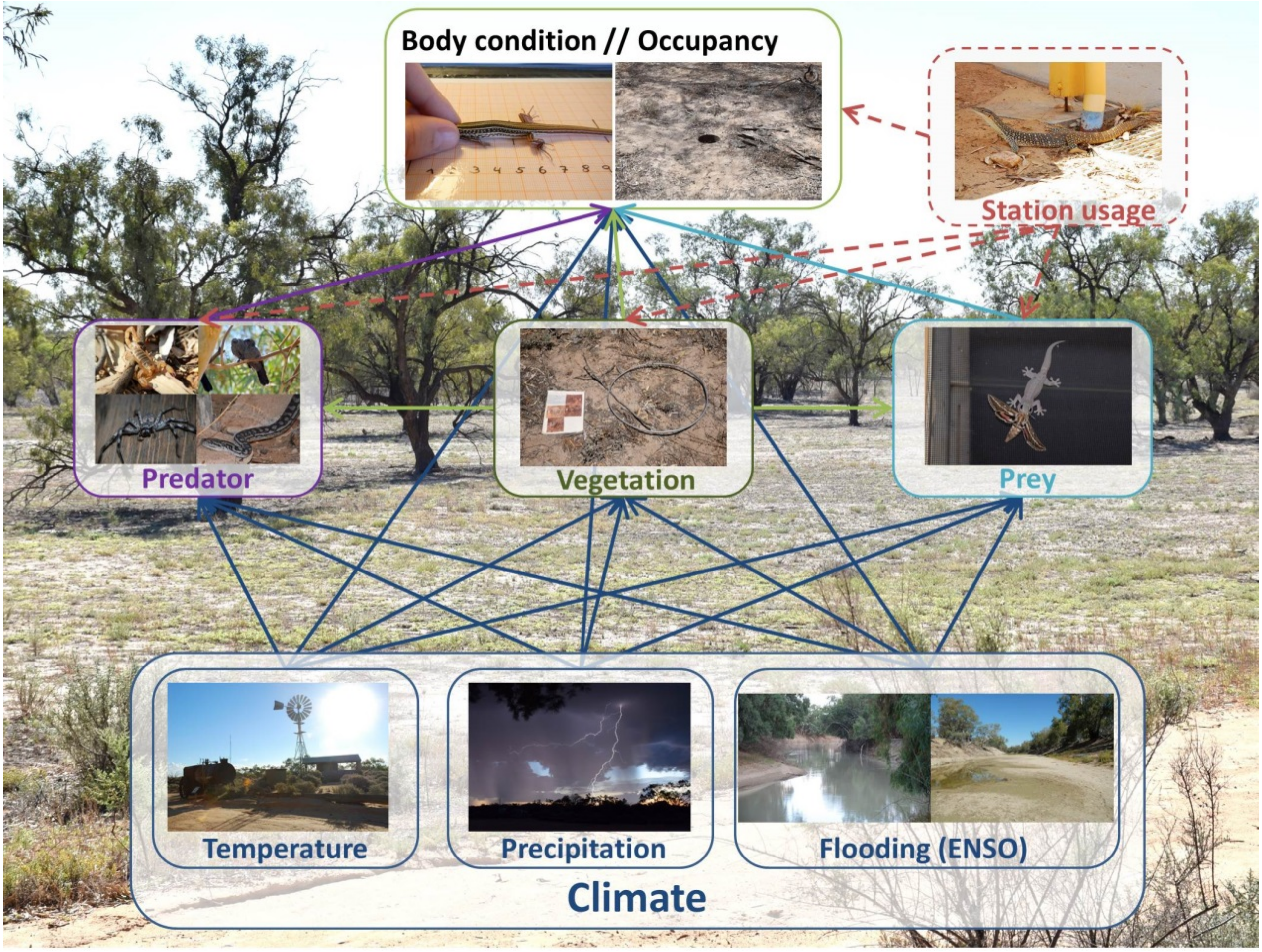

Figure 1: Conceptual network between climatic and biotic factors influencing body condition or occupancy in eight lizard species in Kinchega National Park. The background shows the RWI study site in 2015, a year with high winter rain and high vegetation coverage. Arrows represent the potential direct effects of one factor group (predictor) on another (response). The exact factors behind each factor group are described in Table 2.

Both species-specific body condition measures and annual occupancy rates were used as overall response variable in the piecewise structural equation modelling (SEM) (Shipley 2009) using the R-package *piecewiseSEM* with year as the grouping variable (Lefcheck 2016). It has the advantage that multiple generalized linear mixed models (GLMMs) with various random effects and variance structures can be joined into a single SEM. Specifically, we built five different GLMMs within each SEM based on our conceptual network (Fig. 1): responses of (1) and (2) two specific vegetation measures per plot (i.e., herb-layer biomass, shrub coverage, vegetation coverage, or eucalypt foliage); (3) the species-specific prey index; and (4) the species-specific predator index to climatic factors; and (5) species-specific body condition or occupancy in response to climatic and biotic factors (and additionally to station usage in all analyses at the station). Details on error distributions, control variables, and random structures are described in Appendix S2.

To reduce the number of initial paths in the SEM, we performed a pre-selection on the single GLMMs (Appendix S2.1). We kept all climatic factors that turned out to be potentially important for a biotic factor (within ΔAIC < 2) in SEMs to make sure that we did not miss potentially important paths. We then used Shipley's test of d-separation to assess the overall fit of the SEMs and to control for potential missing paths (Shipley 2009). We included missing paths when the test was significant and a plausible ecological connection could exist. An overview on all final paths can be found in Tables S2.2.2 and S2.2.3 for individual and population analyses, respectively.

For comparisons among predictors, we obtained scaled standardised path coefficients. We corrected the factors that were part of an interaction by summing the estimate of the factor itself and the product of the interaction estimate and the estimate of the factor in the interaction (Whisman and McClelland 2005). We calculated the total effect of each (corrected) climatic and biotic factor by multiplying all coefficients along each path and summing all paths per predicting factor (Fig. 1), and the overall indirect effect by subtracting the direct effect from the total effect.

To assess the relative importance of each climatic and biotic factor group (Table 2) for individual or population response per species, we set the sum of all absolute scaled estimates to 100% and calculated the percentage taken by each factor group. Last, we analysed which functional traits could influence to which factor group species were responding by means of permutational multivariate analyses of variance (pMANOVA) (Mcardle and Anderson 2001) using Gower dissimilarity (Gower 1971) and the R-package *vegan* (Oksanen et al. 2017). We tested different functional traits and their combinations based on eight hypotheses: study design, foraging, morphometrics, habitat and activity, physiology, and all hypotheses together with habitat and activity since we assumed initially that habitat and activity influence desert reptiles most.

All statistical analyses were performed in R 3.1.1 (R Core Team 2016).

5.4 Results

5.4.1 GENERAL RESULTS

Both body condition (Fig. S1.2.1) and occupancy (Fig. S1.2.2) were highly variable among years. The scale of body condition measures strongly varied among but less within species. *G. variegata* showed the highest (usually > 0.7) and least varying occupancy across time. Occupancy of *M. boulengeri* was around 0.5 and did not vary much, whereas occupancy of all remaining species spanned the whole range between 0 and 1. Confidence intervals of occupancy were highly variable across time, with high intervals being typically associated to extremely low capture rates.

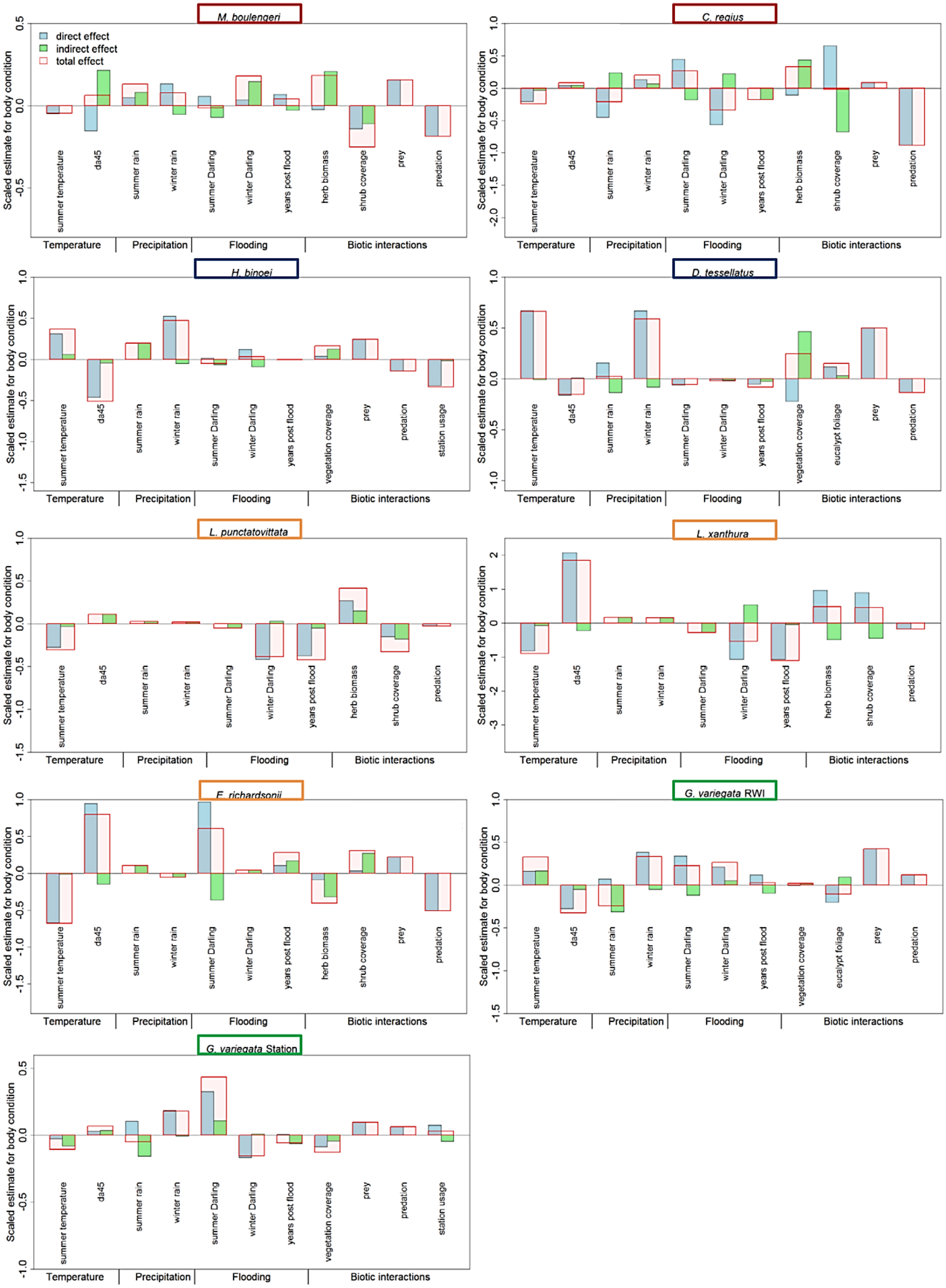

Figure 2: Direct, indirect, and total scaled estimates of SEMs for body condition. Species names are colour-coded according to their functional groups: red – terrestrial, diurnal; blue – terrestrial, nocturnal; orange – subterranean, nocturnal; green – arboreal, nocturnal.

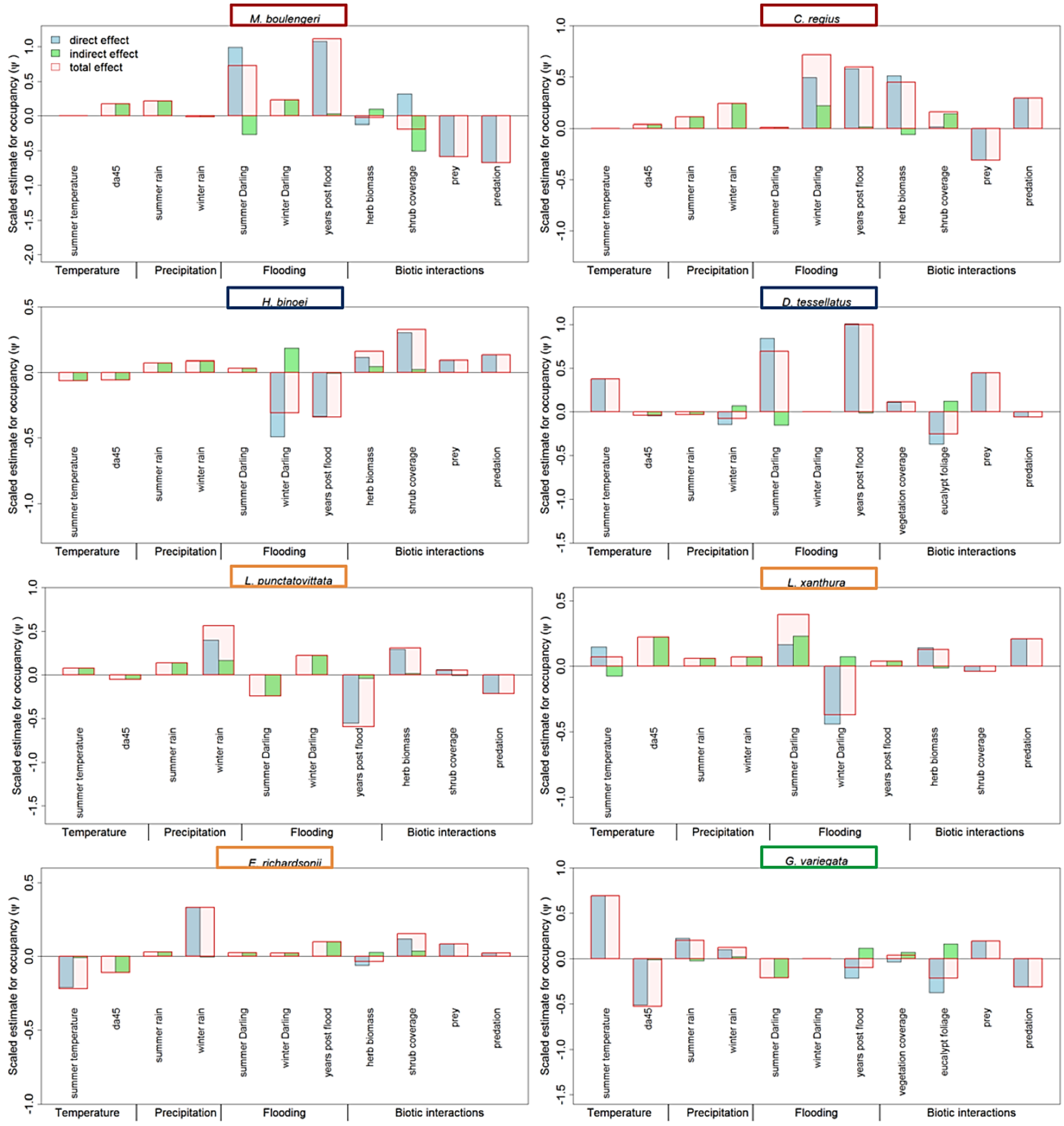

Figure 3: Direct, indirect, and total scaled estimates of SEMs for occupancy. Species names are colour-coded according to their functional groups: red – terrestrial, diurnal; blue – terrestrial, nocturnal; orange – subterranean, nocturnal; green – arboreal, nocturnal.

Vegetation measurements differed among years but showed a strong synchrony in temporal variations among plots (Fig. S1.3.1). In the RWI, vegetation overage and eucalypt foliage were positively correlated, while herb biomass and shrub coverage in the RWII were negatively correlated (Table S2.2.2). Vegetation coverage at the station increased with station usage (Table S2.2.2). Both prey and predator abundance varied strongly over time (Figs S1.3.2, S1.3.3). Except eucalypt foliage, increasing vegetation cover/biomass usually facilitated arthropod abundance, while vegetation biomass at the RWII decreased abundance of prey lizard species of *E. richardsonii*. Vegetation coverage facilitated all predatory species except at the station. Eucalypt foliage decreased predator abundance at the RWI and herb-layer biomass facilitated nocturnal predators but supressed diurnal predators (Tables S2.2.2, S2.2.3).

Individual and population responses were highly variable among species, but two common response patterns could be identified. Body condition profited from higher prey availability in all species but decreased when predators increased, except *G. variegata* where predator abundance was positively correlated with body condition (Table S2.2.2, Fig. 2). Likewise, occupancy of all species increased with prey abundance except for diurnal terrestrial skinks where occupancy decreased (Table S2.2.3, Fig. 3).

All final SEMs showed a good fit (Fisher's C test, p > 0.9) and completeness without missing paths (Shipley's test of d-separation, p > 0.1). All models fulfilled the requirements that the ratio of the total sample size to the number of paths was larger than five (Grace et al. 2015).

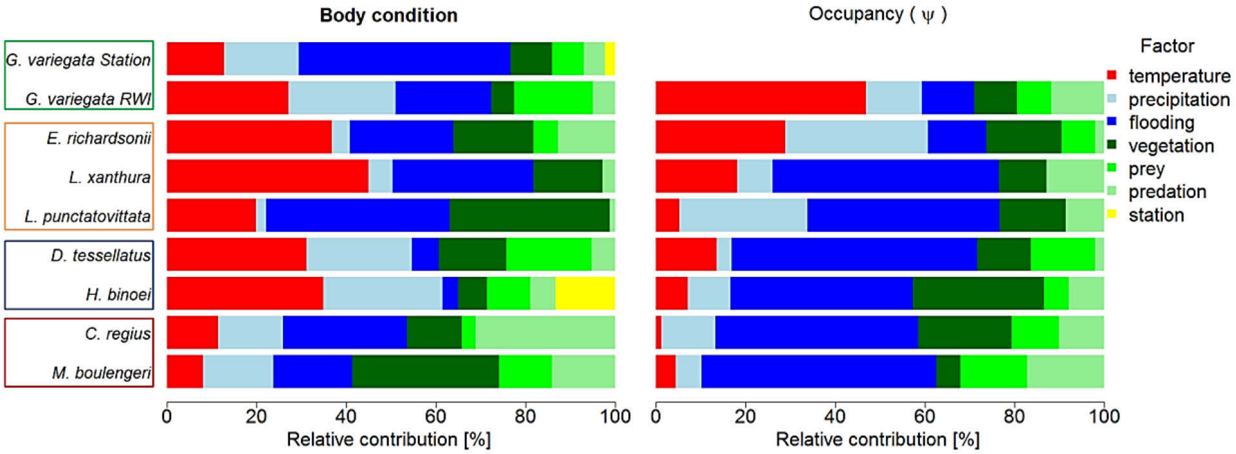

Figure 4: Relative contribution of each factor group (see Table 2) to the influence on body condition (left) and occupancy (right). Species names are colour-coded according to their functional groups: red – terrestrial, diurnal; blue – terrestrial, nocturnal; orange – subterranean, nocturnal; green – arboreal, nocturnal.

5.4.2 DIURNAL, TERRESTRIAL LIZARDS

Body condition of the two skink species was mainly driven by biotic factors, followed by flood parameters (Fig. 4). Specifically, herb-layer biomass was overall positive through reducing predators. The effect of shrub coverage was entirely negative for *M. boulengeri*, whereas positive direct and negative indirect (through facilitating predators) effects compensated each other in *C. regius*. Winter Darling River height increased body condition of *M. boulengeri* but decreased it in *C. regius*, while summer Darling River height only facilitated the latter. Additionally, summer rain slightly decreased body condition in *C. regius* (Fig. 2, Tables S3.1.1, S3.1.2).

Both species' occupancy was most impacted by flood parameters (Fig. 4) showing an increase mainly with the number of years post flooding. Additionally, winter and summer Darling River heights increased occupancy of *C. regius* and *M. boulengeri*, respectively. Increasing herb-layer biomass directly increased occupancy of *C. regius*. Despite its direct positive affect, increasing shrub coverage overall decreased occupancy of *M. boulengeri* mainly through predator facilitation. Occupancy of *C. regius* was positively correlated with predator abundance (Fig. 3, Tables S3.2.1, S3.2.2).

5.4.3 NOCTURNAL, TERRESTRIAL LIZARDS

Temperature and rainfall contributed most to both gecko species' body condition (Fig. 4). It directly increased with increasing summer temperature, decreased with too many days above 45°C, and increased with winter rain. Increasing summer rain favoured only *H. binoei* indirectly through both increasing vegetation coverage, which in turn increased prey abundance, and decreasing predator abundance. In contrast, despite increasing summer rain having had a slight direct positive effect for *D. tessellatus*, it was indirectly negative through decreasing prey abundance. Additionally, the direct effect of vegetation coverage was negative for *D. tessellatus* but was balanced by stronger indirect positive effect through increasing prey and decreasing predator abundance. Two site-specific factors were also relevant. While *H. binoei* was negatively affected by the intensity of the station usage, *D. tessellatus* was slightly positively influenced by increasing eucalypt foliage (Fig. 2, Tables S3.1.3, S3.1.4).

Flood parameters were most important for both species' occupancy, followed by vegetation parameters (Fig. 4). While occupancy of *H. binoei* was highest in flooded years and decreased subsequently, occupancy of *D. tessellatus* increased the longer the study site was not flooded. Whereas winter Darling River heights decreased occupancy of *H. binoei*, summer river heights increased occupancy of *D. tessellatus*. Vegetation coverage increased occupancy of both species, but herb-layer biomass only that of *H. binoei*, whereas eucalypt foliage decreased occupancy of *D. tessellatus*. Predation pressure was positively correlated with occupancy of *H. binoei* but slightly decreased occupancy of *D. tessellatus* (Fig. 3, Tables S3.2.3, 3.2.4).

5.4.4 NOCTURNAL, SUBTERRANEAN LIZARDS

Body condition of the three skink species was most affected by temperature and flood parameters (Fig. 4). It decreased with summer temperature but increased with a higher number of days above 45°C. Both *Lerista* species suffered from high Darling River heights in winter and with increasing number of years after flooding. Contrarily, *E. richardsonii* strongly profited from high summer Darling River heights. Responses to vegetation were highly species-specific. Both *Lerista* species directly profited from increasing herb-layer biomass, while *L. punctatovittata* suffered but *L. xanthura* profited from increasing shrub coverage. Vegetation only indirectly affected *E. richardsonii* since increasing herb-layer biomass decreased prey abundance but favoured predators whereas increasing shrub coverage facilitated prey abundance (Fig. 2; Tables S3.1.5, S3.1.6, S3.1.7).

Responses of species' occupancy differed among species with flood being the most important for both *Lerista* species (Fig. 4). Occupancy of *L. punctatovittata* decreased with time after the study area adjacent to the study plot had been flooded. In *L. xanthura*, occupancy increased with summer but decreased with winter river heights. All species increased in occupancy with increasing winter rain. In *E. richardsonii*, it additionally decreased with increasing summer temperature. Occupancy of both *Lerista* species further increased with increasing herb-layer biomass and in *E. richardsonii* with increasing shrub coverage. Last, predator abundance decreased occupancy of *L. punctatovittata* but increased occupancy of *L. xanthura* (Fig. 3, Tables S3.2.5, S3.2.6, S3.2.7).

5.4.5 NOCTURNAL, ARBOREAL LIZARDS

In contrast to the previous functional groups, we focus here on among study plot comparisons within a single species. While at the station body condition of *G. variegata* was mostly driven by flood parameters, in RWI temperature, rain and flood parameters were similarly important (Fig. 4). Body condition increased with summer Darling River height and winter rain at both sites. We further found a positive direct influence of summer rain, which was suppressed by a strong indirect negative effect through reduction of prey abundance. Actually, in both study plots, the interaction between summer temperature and summer rain drove the prey index most strongly (Table S2.1.2). Differences were found for winter Darling River heights, which increased body condition at the RWI site but decreased it at the station, and for temperature, which was more important at the RWI site with higher temperatures increasing but a high number of days above 45°C decreasing body condition. Vegetation coverage and eucalypt foliage negatively affected the species (Fig. 2, Tables S3.1.8, S3.1.9).

We could only examine occupancy in RWI with temperature being the most important factor (Fig. 4). *G. variegata* occupied more area the warmer the summer, but too many days above 45°C decreased occupancy. Further, it increased with summer and winter rainfall but decreased after the area was flooded as well as with increasing eucalypt foliage and predator presence (Fig. 3, Table S3.2.8).

5.4.6 FUNCTIONAL TRAITS IN RELATION TO SPECIES RESPONSES

Functional traits significantly determined the factor group to which species responded (Table 3). Mainly the interaction of activity and habitat determined to which factor group body condition responded (pMANOVA, p = 0.003, Fig. 5a), as summarised above. To a lower extent, the species-specific prey also contributed (pMANOVA , p = 0.07) with arthropod feeding species responding to prey and rainfall but species feeding on fossorial arthropods to vegetation and flood (Fig. 5b). In all other model combinations, the interaction between habitat and activity remained the only significant functional trait (Table 3).

Responses of species' occupancy were mainly driven by the mean adult snout-vent-length, minimal longevity, and habitat specialisation (pMANOVA, p = 0.01; Table 3). Specifically, species responded more to rainfall but less to flooding with increasing size, semelparous species responded most to predation, and habitat specialists responded more to flooding but habitat generalists to temperature and vegetation (Fig. 5c-f). The foraging mode and CTmax did not determine any responses, nor did the study plot.

Table 3: Functional traits that determined the relative contribution of all factor groups on body condition and occupancy (see Fig. 4) based on eight different hypotheses. Functional trait values can be found in Table 1. Notably, *habitat specialisation* refers to the number of study plots where a species occurred with specialists having occurred in one and generalists in several plots. We obtained p-values of the pMANOVAs for each functional trait present in an analysis ($p_{marginal}$) and overall p-values (p_{model}). Significant overall p-values are highlighted in yellow.

Hypothesis	**Functional trait(s)**	**Body condition**		**Occupancy**	
		$p_{marginal}$	p_{model}	$p_{marginal}$	p_{model}
design	study plot	0.23	0.23	0.36	0.36
foraging	foraging mode	0.58	0.58	0.82	0.82
	prey	0.07	0.07	0.84	0.84
	foraging mode * prey	0.21	0.21	0.88	0.88
morphometrics&longevity	snout vent length	0.21	0.21	0.06	0.06
	longevity	0.76	0.76	0.24	0.24
	snout vent length + longevity	0.29 0.82	0.50	0.03 0.04	0.02
habitat&activity	activity	0.16	0.16	0.25	0.25
	habitat	0.21	0.21	0.28	0.28
	habitat * activity	0.003	0.003	0.47	0.47
	habitat specialisation	0.29	0.29	0.05	0.05
	habitat specialisation + habitat * activity	0.06 0.003	0.003	0.04 0.18	0.08
physiology	CTmax	0.66	0.66	0.87	0.87
foraging+ habitat&activity	foraging mode + habitat * activity	0.3 0.005	0.01	0.36 0.35	0.43
	prey + habitat * activity	0.6 0.05	0.06	0.38 0.48	0.40
	foraging mode * prey + habitat * activity	0.54 0.1	0.10	0.30 0.23	0.32
morphometrics+ habitat&activity	snout vent length + longevity + habitat * activity	0.97 0.62 0.1	0.20	0.27 0.96 0.75	0.59
	snout vent length + longevity + habitat specialisation	0.08 0.55 0.09	0.21	0.03 0.11 0.08	0.01
physiology+ habitat&activity	CTmax + habitat * activity	0.64 0.05	0.04	0.85 0.66	0.70

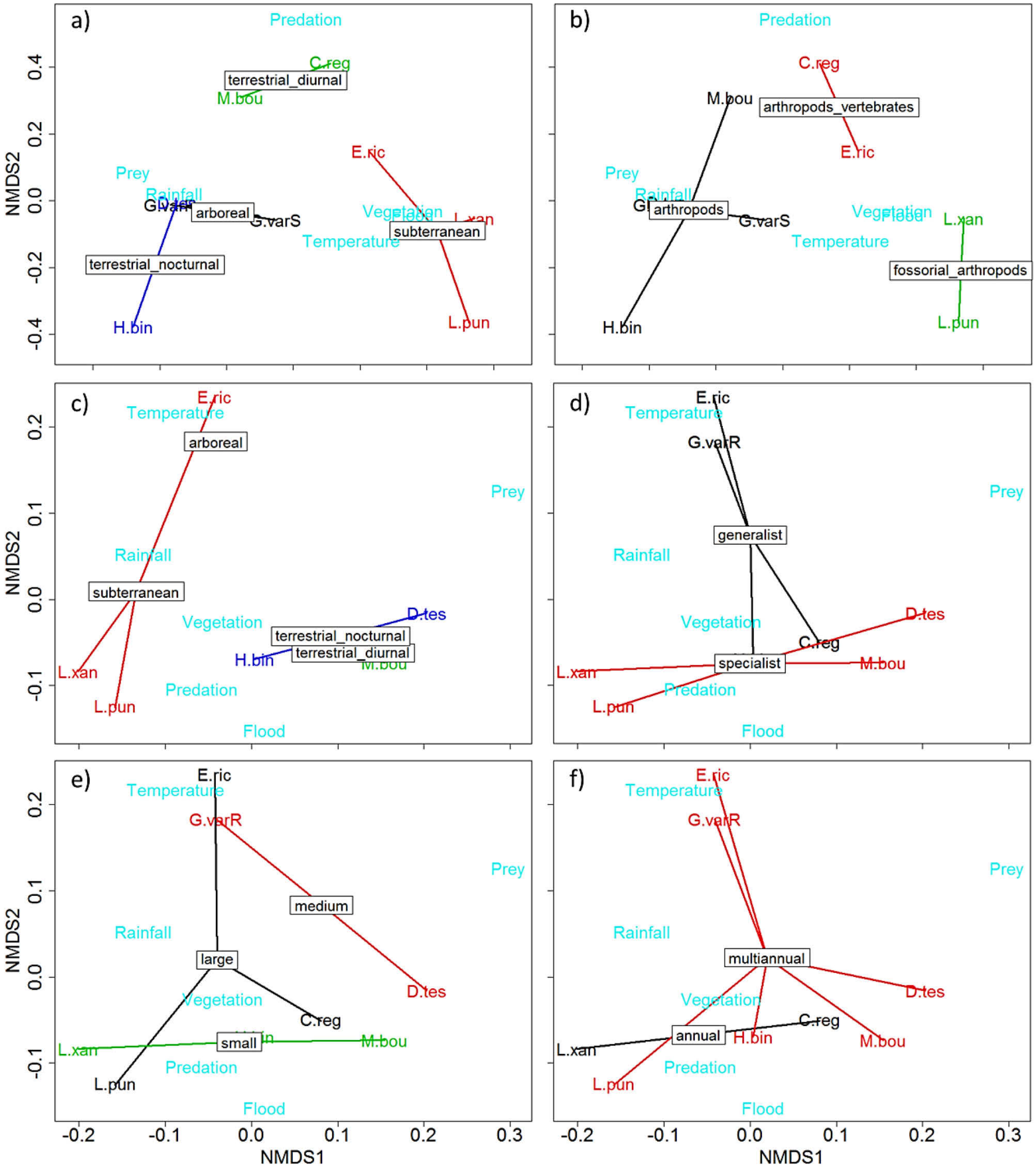

Figure 5: Significant species functional traits determining species responses in body condition (a-b) and occupancy (c-f) to factors groups: habitat and activity (a) and prey (b); habitat and activity (c), habitat specialisation (d), snout-vent-length (e), and longevity (f). Nonmetric multidimensional scaling was used for visualisation (Oksanen et al. 2017). Species names (sometimes hidden behind labels) are abbreviated using the capital letter of the genus and the first three letters of the species and coloured according to their functional group. Factor groups are highlighted in light-blue.

5.5 Discussion

Responses to biotic and climatic factors at both individual and population level were often highly species specific or even demonstrated opposite responses. Despite those species-specific responses, some consistent patterns in terms of factor groups to which species responded could be identified based on species' functional traits. Responses of body condition were mainly determined by their activity period and habitat. Body condition of diurnal, terrestrial species was most influenced by biotic factors followed by flood parameters, whereas body condition of nocturnal, terrestrial species was most influenced by temperature and rainfall while flood parameters were rather unimportant. However, both nocturnal subterranean and arboreal species were highly influenced by flood parameters. Additionally, rainfall was important for arboreal species and vegetation for species feeding on fossorial arthropods.

Responses of occupancy to certain factor groups were less clearly separated by functional traits, with subterranean and arboreal species together being different from terrestrial species independent of their activity period. Occupancy of all but arboreal species and *E. richardsonii* was mainly driven by flood parameters. For the latter it was mainly influenced by temperature and rainfall. Lizard size determined responses to rainfall and flooding, longevity to predation, and habitat specialisation to flooding, temperature, and vegetation.

Notably, there was no single overarching factor group influencing all species or functional groups contradicting the general assumption that precipitation is the overall driver framing the ecology of species in arid ecosystems (Morton et al. 2011, McCluney et al. 2012, Deguines et al. 2017). Nevertheless, our study supports previous findings identifying prey availability as an important driver for desert lizards (Letnic et al. 2004, Flesch et al. 2017) , with increasing prey abundance always increasing body condition corroborating that food availability and food intake are positively correlated (Henle 1989a, 1990b). The two *Lerista* species feeding on fossorial arthropods, which we could not measure directly, responded strongest to vegetation (Fig. 5), potentially serving as a proxy for termite and ant abundance (Rissing 1988, Read 1995). Increasing prey abundance further increased occupancy in all nocturnal species, presumably through increasing abundance, as shown for *G. variegata* (Henle 1990a). The opposite response pattern to prey in occupancy was observed for diurnal lizards, despite diurnal desert lizards increased in abundance elsewhere (Flesch et al. 2017). This may result from differences in habitat selection behaviours that shape distribution in space rather than from variations in abundance since high prey abundance was highly associated with shrub coverage, which could lead to aggregations of diurnal lizards around bushes (Shmida et al. 1986).

Pianka (1986) stated that desert lizard community compositions, particularly in Australia, are to a large extent shaped by predation. We found that increasing predation pressure diminished body condition of most of the species presumably due to increasing energetic costs with predator avoidance strategies (Pianka 1986) since lizards face trade-offs between feeding and fleeing (Vitt 1983, Cooper and Peréz-Mellado 2004) or even hiding (Amo et al. 2007b). The only species which showed a positive correlation of body condition with predator abundance was *G. variegata* independent of the habitat. While this effect was relatively low in comparison to those of others, this is in line with previous findings showing that adult mortality increased with decreasing body condition (Henle 1990a). Thus, predators presumably have primarily caught individuals with lower body condition which increased the average body condition among surviving individuals.

Predator abundance further decreased occupancy of iteroparous species but increased occupancy of semelparous species (*C. regius*, *L. xanthura*). A decreased occupancy in relation to predation pressure could be explained by decreasing abundance through increased mortality, as known for the iteroparous species *G. variegata* (Henle 1990a), *M. boulengeri* (Henle 1989a), and nocturnal, terrestrial geckos (Henle 1990b), but also through decreased reproductive success. In an experiment with fish species, Magnhagen (1990) could show that under predation pressure, semelparous species, which have a pressure to reproduce in their first season, reproduced equally well while long-living species did not reproduce as they might benefit more from delaying reproduction by one year. We assume a similar behaviour in lizard species. Especially since they have adjustable reproductive strategies in relation to mortality risks such as predation pressure (Amat 2008), semelparous lizards might even increase their reproduction rate resulting in slightly increased occupancy.

Besides direct effects of climatic factors, we also observed some unexpected results through indirect interdependencies. Exemplarily, summer rain had a direct positive effect on body condition of *D. tessellatus* and *G. variegata*. However, increasing summer rain decreased prey, possibly due to an earlier abundance peak in early summer triggered through rain (Shmida et al. 1986), while simultaneously increasing predator abundance, together cancelling or even reversing the direct effect in both species. In deserts, species of the same habitat were often found to show revers responses to rainfall. Exemplarily, Dickman et al. (1999) found that the agama *Ctenophorus nuchalis* was most abundant in dry years with little vegetation cover while *C. isolepis* was most abundant in wet years with high vegetation cover. Other observations showed differences among functional groups with some nocturnal gecko species being most abundant in wet years but the diurnal, terrestrial *Ctenotus leonhardii* being most abundant in dry years (Read et al. 2012). In this study, rainfall was most important for larger species and more important for subterranean and arboreal species than for terrestrial species, with increasing rainfall facilitating occupancy.

Fluctuations in lizard occupancies in Kinchega were mainly related to the flooding regime of the bordering Darling River. With the number of years post flooding as measure of the flooding regime, occupancy strongly increased in some species (*M. boulengeri, C. regius, D. tessellatus*), but decreased in others (*H. binoei, L. punctatovittata*). Despite we also detected effects of the flooding regime on vegetation, prey, and predators, occupancy of the species was mainly directly affected. *D. tessellatus* occurred in the site that got almost entirely flooded during each flood, which destroyed arthropod burrows and condensed the soil making the habitat unsuitable (own observations) and recolonization necessary. The two diurnal skinks, *M. bouleneri* and *C. regius*, probably avoid high soil moisture during or immediately after floods as they have never been found inside periodically flooded lakes (Briggs et al. 2000). In the other species the “direct” effects presumably were due to unmeasured pathways, for example changing soil texture and composition. With flooding, the edges of the sandy clay at the RWII, the site that remained just above flood level in all floods that occurred throughout our study, become sandier and with more leave litter (photo comparison) and thus more favourable for *L. punctatovittata* and *H. binoei*. Overall, periodic flooding was among the strongest drivers of lizards' occupancy. Rivers of highly variable flow regimes, such as the Darling River, are components of many desert systems and may transport the effects of climate change taking place at distant regions over considerable distances. However, despite river heights themselves being strongly related to La Niña events (Grimm-Seyfarth et al. 2017a), the subsequent flooding is regulated for water supply and irrigation (Murray–Darling Basin Authority 2015). If flooding of the area would be decreased in duration or even prevented in the future, it would prevent the lizard community from natural fluctuations and also affect the well-adapted vegetation (Roberts and Marston 2000), changing important habitat requirements (Grimm-Seyfarth et al. 2017b). Flooding might be a disturbance on the first look (McCluney et al. 2012), but it is an important component of the unique arid-zone lizard community.

With advancing climate change, hot deserts will become hotter and dryer (Noble and Gitay 1998, Stahlschmidt et al. 2011). Even under small changes in temperature or precipitation, desert species composition could change (Sala et al. 2000). In Kinchega, local occupancy of *E. richardsonii* and *L. punctatovittata* is likely to decrease with decreasing winter rain and for *G. variegata*, fewer trees may remain suitable for occupancy with an increasing number of days above 45°C. Likewise, body condition of most species studied by us was negatively affected by increasing temperature, which in turn may reduce reproductive success (Ballinger 1977). Importantly, distant climatic factors had strong impacts on the local desert reptile community. Thus, climate change in a particular region may have important effects on species communities at far distances, even if they are only indirectly exposed through changes in adjacent ecosystems such as periodic floodplains. Such natural floodplains must not be prevented from flooding and a management of the area should secure flood duration to be long enough to secure a natural turn-over of the community composition.

Because of the species-specific differences in the trophic and climatic interrelationships, we will be able to predict future changes only if these interdependencies are understood and accounted for. The structural equation modelling of the desert lizard community allowed us to analyse pathways that would have otherwise remained overlooked. Our results thus support the recommendations of Walther (2010) that robust predictions of the future distribution of species under climate change require consideration of mechanistic processes. While this is in important approach, we often lack the relevant information for many species (Urban et al. 2016). Since one might never get all necessary information to accurately calibrate mechanistic models for all species, modelling species and community response through "functional groups" instead of "true species" might offer a solution. This study gives an indication how to identify relevant functional groups at different ecological levels, which could be important for both field work targeted at determining relevant mechanistic processes and targeted conservation. We believe that long-term empirical studies need to be appreciated and rewarded much more again to advance our understanding of future biodiversity change (Ferreira et al. 2016). With those key actions, we believe that it is possible that the effects of climate change in desert reptile communities could be buffered to a large extent.

5.6 Authors' Contributions

All authors conceived the ideas, designed the general methodology and collected field data. AG analysed the data, performed the modelling and led the writing of the manuscript. All authors contributed critically to the drafts and gave their final approval for publication.

5.7 Acknowledgements

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5.8 Supporting Information

Appendix S1: Overview on underlying field and analytical methods of the conceptual framework

Appendix S2: Structural equation modelling: pre-analyses and paths selection

Appendix S3: Summary results of structural equation models (SEMs)

Figure 6: *Varanus gouldii*, a top predator in the desert ecosystem. Photo by Annegret Grimm-Seyfarth.

6 General discussion

In the three articles that comprise this dissertation, I investigated how lizard species in Kinchega National Park, which is situated within the eastern margin of arid Australia, responded to fluctuations in various climatic parameters at different spatial scales. I found that the responses were often species-specific, with different species responding to different climatic parameters or to the same climatic parameters but in different directions. I focussed on responses at both the individual and the population level and found that they often differed substantially and occasionally even demonstrated opposite responses. These findings emphasise the importance of considering the response of different ecological processes along various climatic scales in order to better understand the complexity of climate change effects on biodiversity. I further analysed two main underlying mechanisms underpinning how desert reptile species responded to different climatic parameters: thermoregulatory behaviour and interactions of species with their biotic environment. I was able to show that thermoregulatory behaviour and activity time were strongly impacted by climatic conditions, but also by the amount of vegetation available in the area and its heterogeneity that provided both cooling spots and heat reservoirs. The ecological network formed by prey and predators of the lizards also emerged as an important driving factor of the reptile community. The diversity in all these mechanisms needs to be accounted for if we want to understand potential impacts of on-going climate change. These general findings together with implications for conservation and future research are discussed in detail hereafter.

6.1 Individual and population responses to climatic fluctuations

I focussed on three different groups of factors describing climatic fluctuations: temperature, rainfall, and flooding. While temperature and rainfall are describing local climatic conditions, the flooding regime of the bordering Darling River was strongly related to ENSO (Simpson et al. 1993, Chapter 3 Appendix S1.1) and thus, can be considered as a distant climatic factor acting locally on the ecosystem. Since rivers with highly variable flow regimes are components of many desert systems, they may dissipate the effects of climate change that take place at distant regions over considerable distances. I considered effects of rainfall and river heights both in the summer, when monitoring took place, and in the previous winter since both could potentially influence local vegetation (Shmida et al. 1986, Robertson 1987, 1988, Robertson et al. 1987, Morton et al. 2011, Roberts and Marston 2011). Different groups of climatic factor were important for different species or ecological levels (individual or population level; Chapters 3 and 5) and there was no single overarching climatic factor influencing all species or ecological levels, which contradicts the general assumption that precipitation is the overall driver framing the ecology of species in arid ecosystems (Morton et al. 2011, McCluney et al. 2012).

Nevertheless, I found that precipitation was an important factor for body condition of nocturnal terrestrial and arboreal gecko species and, to a lesser extent, for diurnal terrestrial skink species. Precipitation was further found to be particularly important for large bodied species' occupancy (Chapter 5). Generally, higher amounts of rain increased body condition and occupancy except for *C. regius* whose body condition decreased, presumably due to decreased summer activity time under high summer rain

(Chapter 4). For *G. variegata*, the arboreal gecko, rainfall further facilitated body growth rates, total population sizes and presumably accelerated sexual maturity (Chapter 3). Positive effects of rainfall on body condition or body growth have also been described in the desert Gila Monster *Heloderma suspectum* (Davis and DeNardo 2010), in the tropical lizard *Anolis aeneus* (Stamps and Tanaka 1981), and in the temperate lizard *Podarcis lilfordi* (Rotger et al. 2016) suggesting that this is a general pattern rather than a pattern specific for desert species, presumably due to higher food abundance under high precipitations (Masters et al. 1998, Kwok et al. 2016; see Chapter 6.3).

In deserts, species of the same habitat were often found to show reverse responses to rainfall. Exemplarily, Dickman et al. (1999) found that the agama *Ctenophorus nuchalis* was most abundant in dry years while *C. isolepis* was most abundant in wet years, presumably related to vegetation cover. Other studies showed differences between functional groups with some nocturnal gecko species being most abundant in wet years but the diurnal, terrestrial *Ctenotus leonhardii* being most abundant in dry years (Read et al. 2012). Likewise, the abundance of the diurnal, terrestrial *Uta stansburiana* decreased with increasing precipitation in a semi-arid grassland (Deguines et al. 2017). I did not observe such patterns in Kinchega as increasing rainfall always increased both occupancy and abundance. Possibly, increasing rainfall increased survival or reproduction, as shown in other long-term studies for *Sceloporus virgatus* (Smith et al. 1995) and *Zootoca vivipara* (Marquis et al. 2008, Bleu et al. 2013), or enabled lizards to occupy marginal habitats due to an induced growing season (Whitford and Creusere 1977).

In Kinchega, fluctuations in lizard occupancies were mainly related to the flooding regime of the Darling River. With an increasing number of years post flooding, occupancy strongly increased in some species (*M. boulengeri, C. regius, D. tessellatus*), but decreased in others (*H. binoei, L. punctatovittata*). Those fluctuations are likely dependent on alternating habitat conditions, such as changing soil or vegetation textures and compositions (see Discussion in Chapter 5), which has already been suggested for *M. boulengeri* (Henle 1989a) and *D. tessellatus* (Henle 1990b). Likewise, Masters (1996) and Letnic et al. (2004) suggested that reptiles leave areas when they become unsuitable but recolonise them when they become suitable again. Such micro-successions due to changing soil and vegetation structure could generally be triggered through many factors, such as the aforementioned drought-wet-cycles (Dickman et al. 1999, Read et al. 2012), but also after fire (Letnic et al. 2004, Pianka and Goodyear 2012, Smith et al. 2012) or flooding (this thesis). To my knowledge, fluctuations in a hot desert reptile community due to the flooding regime have never been shown before. Apart from the flooding and subsequent micro-successions, fluctuating Darling River heights themselves influenced all species but terrestrial, nocturnal geckos at individual levels, usually increasing body condition and body growth. Only in three species (*C. regius*, *L. punctatovittata*, and *L. xanthura*) did increasing winter river heights decrease body condition, presumably due to increasing ground water which might disturb their hibernation and in turn decrease body condition (Muir et al. 2013). Increasing river heights also facilitated occupancy of most terrestrial species and increased abundance and reproductive success (measured as subadult population size in the following year) in *G. variegata*. Overall, it is likely that water availability in general, through either rainfall or standing water in the Darling River and its anabranches, enhances individual and population conditions. Thus, bad climatic conditions at one scale could potentially be balanced by good conditions at another climatic scale, as most species showed high body condition and body growth in years with low rainfall but comparably high river heights (e.g., 1999 and 2012, Chapter 3 Figs. 2, S3.4, Chapter 5 Fig. S1.2.1). This suggests that in such arid systems with temporary floodplains, bad conditions at one climatic scale (low amount of local rainfall) could be compensated at another scale by floods through La Niña events (see also Chapter 3 Appendix S1.3 for a relation between flooding and La Niña).

Additional to water availability, temperature was recently called the limiting factor for terrestrial ectotherms (Cahill et al. 2014, Gunderson and Stillman 2015). Specifically at the individual level, I found that temperature was affecting nocturnal but not diurnal lizard species. While body condition of nocturnal, subterranean skinks declined with increasing summer temperatures, an increasing number of excessive hot days above 45°C increased their body condition. The reverse case was observed for terrestrial and arboreal geckos with rising summer temperatures increasing both body condition and body growth rate, whereas body condition but not body growth declined with the number of days above 45°C. High temperatures are a prerequisite for body growth (Greer 1989) and often enhance both body mass and body growth (Autumn and De Nardo 1995). However, geckos may grow very fast during hot periods while body mass might not increase in the same intensity (Autumn and De Nardo 1995) leading to lower body condition. Obviously, the relationship between temperature and body condition or growth differes between geckos and skinks, presumably due to different evolution of nocturnality and thermoregulatory behaviour (Huey and Bennett 1987, Huey et al. 1989, Autumn et al. 1999).

At the population level, the effects of temperature were weaker and evident only for four of the six nocturnal species, while there was no effect on diurnal lizard species. Higher summer temperatures decreased occupancy of *E. richardsonii* but increased occupancy of *D. tessellatus*, *L. xanthura*, and *G. variegata*. The latter also increased in survival and abundance, while at the same time fewer trees remained suitable for occupancy with an increasing number of days above 45°C. Likewise, previous studies demonstrated that survival and fecundity of arid-zone lizards was temperature dependent (Read et al. 2012) and that high temperatures were essential for egg development in *G. variegata* (Bustard 1969), whereas excessive heat in microhabitats can also cause egg mortality (Henle 1990a). In addition, summer temperature was found to be particularly important when interacting with water availability through rainfall or river heights in both summer and winter. Such interactions became extraordinary remarkable in years with extreme climatic conditions like simultaneously hot and dry years (2003, 2013). While all species responded with decreasing body condition to such adverse climatic conditions, no such changes were observed in occupancy. Under these adverse climatic conditions, *G. variegata* even delayed sexual maturity by one year while maintaining survival and population sizes. This suggests that plasticity in individual traits could act as a resilience strategy off-setting effects of adverse environmental conditions at the population level. Likewise, Adolph and Porter (1993) predicted that effects of temperature on life-history traits might be compensatory with populations showing a trade-off between survival, age at sexual maturity, and fecundity, at least as long as food is available.

Effects of multiple climatic factors on lizards have been remarkably well studied in temperate zone lizards. Exemplarily, reproduction of *Zootoca vivipara* was affected by rain (Bleu et al. 2013) whereas survival was positively related to temperature (Chamaillé-Jammes et al. 2006). In two other lacertid lizards, *Algyroides marchi* and *Podarcis hispanica*, species occurrence was driven by water loss rather than temperature (García-Muñoz and Carretero 2013). On a global scale, Clusella-Trullas et al. (2011) found that both temperature and rainfall determined lizards' individual performance, however, in arid ecosystems precipitation was claimed to be the more important driver. In deserts, only two long-term lizard monitoring studies have analysed effects of rainfall and temperature on local population dynamics. While in arid Australia precipitation was affecting survival of most species and temperature was affecting survival and fecundity of selected species (Read et al. 2012), in arid Arizona effects of precipitation on abundance were much stronger than those of temperature (Flesch et al. 2017)

6.2 Behavioural thermoregulation and non-trophic interactions with vegetation

Desert reptiles have evolved different kinds of behaviour enabling them to offset the impacts of hot temperatures (Bartholomew 1964). Behavioural thermoregulation might be among the most important mechanisms and can buffer climatic variations to some extent (Angilletta 2009). I analysed behavioural thermoregulation in one nocturnal and two diurnal species in relation to environmental temperature, which was recently suspected to be the main limiting factor for reptiles (Cahill et al. 2014, Gunderson and Stillman 2015), even though this thesis rises some doubts about this (see above). In my analyses, I always considered the whole day instead of the species' active period only.

Gehyra variegata is a nocturnal, arboreal gecko (Chapter 3). During the night when geckos were hunting, geckos' body temperatures strongly followed surface temperatures and were slightly adjusted towards air temperatures. Additionally, strong differences occurred between the surface materials geckos were sitting on, with materials of high heat storage capacity (stone, metal) increasing but materials of low heat storage capacity (wood, corrugated iron with thorough air circulation below the grooves) decreasing body temperatures. This suggests that during night-time, geckos are strong thermoconformers but can easily change microhabitats to heat up or cool down (Kearney and Predavec 2000). Moreover, I observed geckos voluntarily tracking heat in the late afternoon exposed on stones of 45-48°C surface temperature with 43°C air temperature and Henle (1990) even observed high activity during a night with 45°C air temperature. Hot temperatures further allow geckos to extend their activity further into the night than under cooler temperatures and Tan and Schwanz (2015) found evidence that warm nights lower the costs of finding ideal substrates. Together, there was no indication that hot temperatures could be a limiting factor during night-time activities, and this finding is in line with Greer's (1989) assumption that geckos have an extremely wide physiological range.

I measured much higher body temperatures during daytime than during night-time (Chapter 3 Table 3). Remarkably, no differences in CTmax, the critical maximum temperature when righting abilities cease, between diurnal and nocturnal species were found (Chapter 5 Table 1). Huey et al. (1989) argued that nocturnal geckos need similar or higher CTmax comparable to that of diurnal species as they have to survive hot days. By observing diurnal thermoregulation behaviour, I found that geckos did not only stand the heat but rather voluntarily tracked high body temperatures up to more than 40°C during the day. While thermoregulation in retreats have been described frequently for nocturnal geckos (Bustard 1967, Autumn and De Nardo 1995, Angilletta et al. 1999, Hitchcock and Mcbrayer 2006), I specifically observed movements to higher, smaller, dead, and more exposed branches or even outside trees in the sun in cool days, allowing the geckos to warm up. This suggests that under cool, but not warm, temperatures, diurnal behavioural thermoregulation is necessary to enhance digestion, egg development, and growth (Autumn and De Nardo 1995, Angilletta et al. 1999, Angilletta 2009), an observation underpinned by the detected increase in body condition and body growth of nocturnal geckos under increasing summer temperatures (Chapters 3 and 5).

Findings for nocturnal geckos could differ substantially from those of diurnal skinks with diurnal reptiles likely being more affected by hot temperatures than nocturnal ones (Kearney et al. 2009). Indeed, I observed that summer daytime operative temperatures (i.e., the potential body temperature in a non-thermoregulating individual) in the sun exceeded species' CTmax for an average of six and eight hours for the terrestrial, diurnal skinks *C. regius* and *M. boulengeri*, respectively. Interestingly, while operative temperatures of the latter strongly followed soil surface temperature in the sun, operative temperatures of the former heated up much slower and to a lower level (Chapter 4 Fig. 2). This probably reflects different sizes (6 cm vs. 4.2 cm average adult snout-vent-length) and surface colours (bright ivory vs. darker grey) of *C. regius* and *M. boulengeri*, respectively, possibly resulting in different heat capacities and conductivities and showing stronger morphological adaptation to solar radiation (Porter 1967) in deserts for *C. regius*. What has often been overlooked is that diurnal lizards also show microhabitat selection behaviour to thermoregulate, which is a prerequisite for the survival of lizards in hot deserts (Bradshaw 1986, Huey et al. 2009, Clusella-Trullas et al. 2011, Vickers et al. 2011) and was frequently observed for both species in the field. Especially during summer, diurnal lizards in Kinchega were observed hunting in bushes and not in open areas in the early afternoon (Henle 1989b; own observations). Hence, it is not surprising that the activity budgets of both lizards strongly depended on available microhabitat conditions, such as vegetation heterogeneity and bush sizes with larger bushes increasingly providing both cooling spots and heat reservoirs and thus securing activity throughout the whole day in most summer days.

Differences in species' physiological traits and the fact that *M. boulengeri* prefers slightly colder temperatures than *C. regius* likely influenced the individual responses to temperature fluctuations of both species. *C. regius* can be active under hot temperatures (Henle 1989b) and a series of days above 45°C did not impact its body condition (Chapter 5). Conversely, *M. boulengeri* is restricted in its activity if too many days in summer are above 45°C (Chapter 4) and thus an increasing number of days above 45°C directly declined its body condition (Chapter 5). Notably, those effects did not dissipate to the population level with occupancy of both species not being affected by temperature at all. Comparable to these findings, decreasing body condition was usually not correlated with mortality in *M. boulengeri* (Henle 1989a). Together, these findings show that even if climate warming might affect individuals of a species, it will not necessarily affect the species' distribution. Nevertheless, a decline in species' distributions with climate warming could theoretically also be due to a tremendous reduction in activity budgets, which could restrain metabolic functions and result in reduced reproductive success (Sinervo et al. 2010). My predictions showed that activity budgets of both species are likely to decline in mid-summers with climate warming by the end of the century. However, I also detected novel temporal niches in both spring and autumn that would even contribute to an increasing annual activity budget. Generally, reptile species seem to have a large phenotypic plasticity and an earlier spring and later fall could increase their overall activity season (Bradshaw and Holzapfel 2006, 2008, Walker et al. 2015). Other species adjust their activity by becoming nocturnal in hot summers (Henle 1980, Stahlschmidt et al. 2011, Carretero et al. 2012, Grimm et al. 2014b). Importantly, my analyses on both nocturnal and diurnal species stressed the critical influence of heterogeneous vegetation structures on both body temperature and activity budgets (Kearney 2013; this thesis), which should not be confounded with vegetation density (Coops et al. 2017). Future reptile distribution patterns will thus certainly be strongly affected by vegetation patterns (Sears et al. 2016; this thesis) stressing the importance of considering non-trophic species interactions for predicting reptile persistence or extinctions. Future climate change will strongly change plant composition and abundance (Fordham et al. 2012) and plant extinction was recently found to be more likely than animal extinction and could even drive coextinctions (Schleuning et al. 2016). Hence, future conservation strategies should address the cascading effects of vegetation rather than climatic envelopes alone to prevent desert lizards from extinction.

6.3 Trophic species interactions

Climatic factors will likely not affect reptiles only directly, but will also act through multiple pathways (Ockendon et al. 2014, Deguines et al. 2017). Such indirect pathways include the described non-trophic interactions between reptiles and vegetation, but also trophic interactions among reptiles, prey, and predators. I found that the influence of biotic factors was almost as high as the influence of climatic factors on both the individual and population levels (Chapter 5 Fig. 4). Specifically, body condition of arthropod-feeding species was mainly influenced by prey abundance, reflecting the fact that for those species the prey index used (arthropods) was closest to their true prey. In line with that, the two *Lerista* species feeding on fossorial arthropods (not measured) responded strongest to vegetation (Chapter 5 Fig. 5). This may serve as a proxy for termite and ant abundance (Rissing 1988, Read 1995) and suggests that those species might be as dependent on prey abundance. Overall, body condition of all lizard species (Chapter 5), and presumably also body growth of *G. variegata* (Chapter 3), profited from increasing prey abundance corroborating that food availability and food intake are positively correlated (Henle 1989a, 1990b). While prey abundance supported body condition, increasing predation pressure diminished it, a relationship that could reflect predator avoidance behaviours. Most of the lizard species studied in this thesis are widely-foraging species that use running as an escape strategy (Vitt 1983, Henle 1991) and thus regularly face a trade-off between fleeing and feeding (Cooper and Peréz-Mellado 2004). Likewise, increasing predation pressure increases the use of refuges for hiding, which leaves less time to the individuals for feeding (Amo et al. 2007b). In any case, predator avoidance behaviours reduce fat reserves (Pianka 1986) and thus body condition.

Responses of lizard species' occupancy to prey and predation could be based on two patterns: A change in space or in abundance. Taking the example of the two diurnal, terrestrial skinks, they rely on different predator escape strategies (Henle 1991), with *M. boulengeri* taking refuge primarily within denser bushes, digging into soft soil and taking cover underneath leaf litter, whereas *C. regius* escapes through rapid long distance sprints. An increase in predation pressure would then result in a clumped distribution around dense bushes for the former species thus reducing its occupancy. In contrast, the rapid long distance sprints of *C. regius* expose it more to being caught in pitfall traps including in areas that are less permanently occupied, thus possibly resulting in larger occupancy. Secondly, a decreased occupancy in relation to predation pressure could also be explained by decreasing abundance through increased mortality, which are linked in the iteroparous species *G. variegata* (Henle 1990a), *M. boulengeri* (Henle 1989a), and nocturnal, terrestrial geckos (Henle 1990b). However, abundance changes could also be due to varying reproductive success, which might explain why semelparous lizard species profited from increasing predation pressure. Since semelparous species have a pressure to reproduce in their first season despite high predation pressure, they might even increase their reproduction rate resulting in higher overall abundance and slightly increased occupancy. Similar relationships have been found in fish species (Magnhagen 1990) and are further corroborated by the fact that lizards have adjustable reproductive strategies in relation to mortality risks such as predation pressure (Amat 2008). On the other hand, iteroparous species are more likely to show a decreased reproductive success with increasing predation pressure (Downes 2001) or might even benefit from delaying reproduction by one year (Bull and Shine 1979, Magnhagen 1990).

The findings of this thesis underpin the importance of trophic species interactions among lizards, prey, and predation. Importantly, predator-prey interactions are assumed to occur only when activity times overlap (Porter et al. 1973, Parmesan 2006, but see Chapter 5 Table 1). Activity times of species on various trophic levels could respond differently to a changing climate, a mismatch that would change encounter rates and thus, energy intake and mortality of the lizards (Adolph and Porter 1993). Durant et al. (2007) summarised many such examples for birds but stated that lizards as typical food generalists are less likely to be affected. While the eight species studied in this dissertation are indeed food generalists that do not depend on the abundance of one prey species, other reptiles in this community are food specialists such as *Ctenophorus pictus* (Henle 1989b), *Rhamphotyphlops bituberclatus*, *R. proximus* (Henle 1989c), and *Rhynchoedura ornata* (Pianka and Pianka 1976). I thus hypothesise that those species are more prone to mismatches with advancing climate change, likely resulting in reduced reproductive success (Durant et al. 2007). Nevertheless, shifts in diet of food generalist lizards with respect to changing climatic conditions could also result in a different distribution of the species in space (Goodyear and Pianka 2011). On the other hand, lizards make the main prey for three co-occurring nocturnal snakes, *Furina diadema*, *Suta suta*, and smaller individuals of (occasionally also diurnal) *Pseudonaja textilis*, with the former taking mainly diurnal skinks but the two latter showing a broader diet also taking other lizards, small mammals and amphibians (Shine 1981, 1988, 1989). If predators pursue their prey primarily while they are inactive in refuges, mismatches in timing with advancing climate change are very unlikely, even if the predatory species are food specialists.

6.4 Evolutionary potential

Observations from the reptile community in Kinchega strongly support the assumption that species show very different physiological response to climate change, suggesting a certain adaptive capacity. In this case, I refer to adaptive capacity as the ability of a species to persist in changing environments through changes in phenotype (i.e., physiological tolerances or phenotypic plasticity) or in genotype (i.e., evolutionary adaptation) (Catullo et al. 2015). Phenotypic adaptation [e.g., the existing capacity to change thermal limits, often referred to as existing thermal tolerance (ETT), warming tolerance, or thermal safety margin] is then defined as the difference between the current physiological limit (i.e., the fundamental niche) and the realised limit (i.e., the observed (realised) niche), while evolutionary adaptation is defined as the rate at which the current physiological limit can evolve towards the evolutionary physiological limit (i.e., the maximal physiological limit a species can reach through time) (Catullo et al. 2015; Fig. 6.1). In turn, the evolutionary potential of a species is the ability that evolutionary adaption occurs fast enough to track environmental changes resulting in deviations of the phenotype from the current optimum (Chevin et al. 2010).

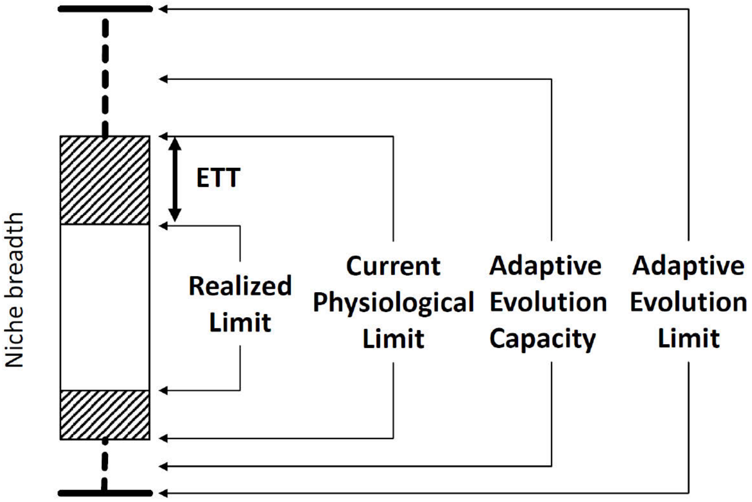

Figure 6.1: The parameters of the adaptive capacity through changes in phenotype (difference between the current physiological and realised limit) and genotype (current physiological limit can evolve towards the evolutionary physiological limit). Adapted from Catullo et al. (2015) with kind support from A. Bush. ETT: existing thermal tolerance as example for phenotypic adaptation.

The rate of evolutionary adaptation can only be directly assessed if the heritability of key traits is known. However, direct measurements of heritability in reptiles are rare and differ strongly among species. For example, in a laboratory experiment with the arid-zone lizard *Uta stansburiana,* preferred body temperatures (T_p) of hatchlings were strongly positively influenced by mothers' T_p (Paranjpe et al. 2013) whereas T_p in the temperate-zone *Zootoca vivipara* was much less heritable (Bestion et al. 2015). Phylogenetically, some lizard lineages such as Lacertidae show a highly conserved T_p (e.g., Bauwens et al. 1990, Van Damme et al. 1990), whereas other lineages such as *Liolaemus* species exhibit remarkable potential for evolutionary adaption in T_p (Labra 1998). Apart from T_p, evaporative water loss (EWL) could be an important key trait in reptiles. In the lizard *Podarcis erhardii*, EWL showed about the same heritability (Belasen et al. 2016) as T_p in *Z. vivipara* (Bauwens et al. 1990, Van Damme et al. 1990). Belasen et al. (2016) further observed that T_p and CTmax did not differ among sites when measured under laboratory conditions, whereas EWL differed strongly and was related to soil moisture suggesting higher evolutionary potential in EWL than in T_p and CTmax. Generally, CTmax seems to be rather conserved across individuals and related species and showed much lower evolutionary potential than CTmin (Grigg and Buckley 2013, Hoffmann et al. 2013). More studies about heritability, including in life-history traits, are necessary to understand how species might be able to adapt genetically to climate change (Visser 2008).

To assess the evolutionary potential, other indirect methods could be applied through assessing genetic changes in space (Bonebrake and Mastrandrea 2010, Hoffmann and Sgró 2011). In reptiles, variation of both phenological traits and T_p with altitude and latitude have commonly been observed, suggesting that natural selections have fine-tuned the level of adaptation on these traits (Angilletta 2009, Grimm et al. 2014b). In a literature review, Urban et al. (2014) could not detect any direct evidence for evolutionary adaptation but several indirect indications through variations along spatial gradients. Likewise, Llewelyn et al. (2016) observed substantial variation in thermal traits (CTmax, CTmin, T_p) in time and space in the widespread tropical skink *Lampropholis coggeri* and concluded that such species might have a much higher evolutionary potential than previously assumed, implying that they might not be as vulnerable to climate change as formerly thought. Similar results were found in invasion biology studies, which suggests that evolutionary adaptation can happen quite fast even in thermal traits (Eckstut et al. 2009, Rödder and Lötters 2009, Hoffmann and Sgró 2011, Leal and Gunderson 2012). If the evolutionary potential of species in relation to predicted future changes can be obtained, threatened species or populations could be identified much easier (Hoffmann and Sgró 2011), which would represent a great advantage for targeted conservation.

6.5 Predicting the responses to climate change

As shown above, reptiles show a remarkable diversity of life-history traits and adaptations to a range of different climatic regimes and are noticeably well adapted to extreme conditions in hot deserts (Bradshaw 1986, Stahlschmidt et al. 2011, this thesis). Most current models predicting reptiles' distribution in response to climate change scenarios only account for a limited subset of reptile's life-history and ecological diversity. Moreover, a strong limitation in the reliability of predictions arising from distribution models is the assumption of niche conservatism (Pearman et al. 2008, Dormann et al. 2010) and frequently the assumption that all species show similar physiological and demographic response to climatic changes. As a consequence, a huge proportion of global reptile diversity is predicted to decline rapidly or even go extinct, especially in arid regions (Araújo et al. 2006, Wake 2007, Deutsch et al. 2008, Sinervo et al. 2010), but these predictions might be too pessimistic (Pearman et al. 2008). Reptiles might have strategies to cope with climate change, e.g. through alternations of their timing of activity and adjustment of their reproductive effort or growth (e.g., Chamaillé-Jammes et al. 2006, Doody et al. 2006, Aubret and Shine 2010, Dubey and Shine 2011, this thesis). Integrating such strategies, processes, and mechanisms should greatly improve predictions of future reptile distributions (Pagel and Schurr 2012).

Recent attempts have been made towards a more mechanistic modelling of reptiles' response to climate change. For example, predictions for future reptile distributions included demographic variations (Keith et al. 2008, Pagel and Schurr 2012, Thompson et al. 2016), biophysical and thermal ecology (Kearney and Porter 2009, Kearney 2012, Ceia-Hasse et al. 2014), species-specific thermal adaptive dispersal decisions (Bestion et al. 2015), or even physiological and demographic traits simultaneously (Buckley 2008). Other authors used a combination of correlative and process-based approaches into one semi-correlative approach to allow for the inclusion of ecological processes into known methods under the limits of current knowledge (Mokany and Ferrier 2011). I myself am working on an approach to include the adaptive capacity of diurnal desert lizards into SDMs based on and in close collaboration with Bush et al. (2016).

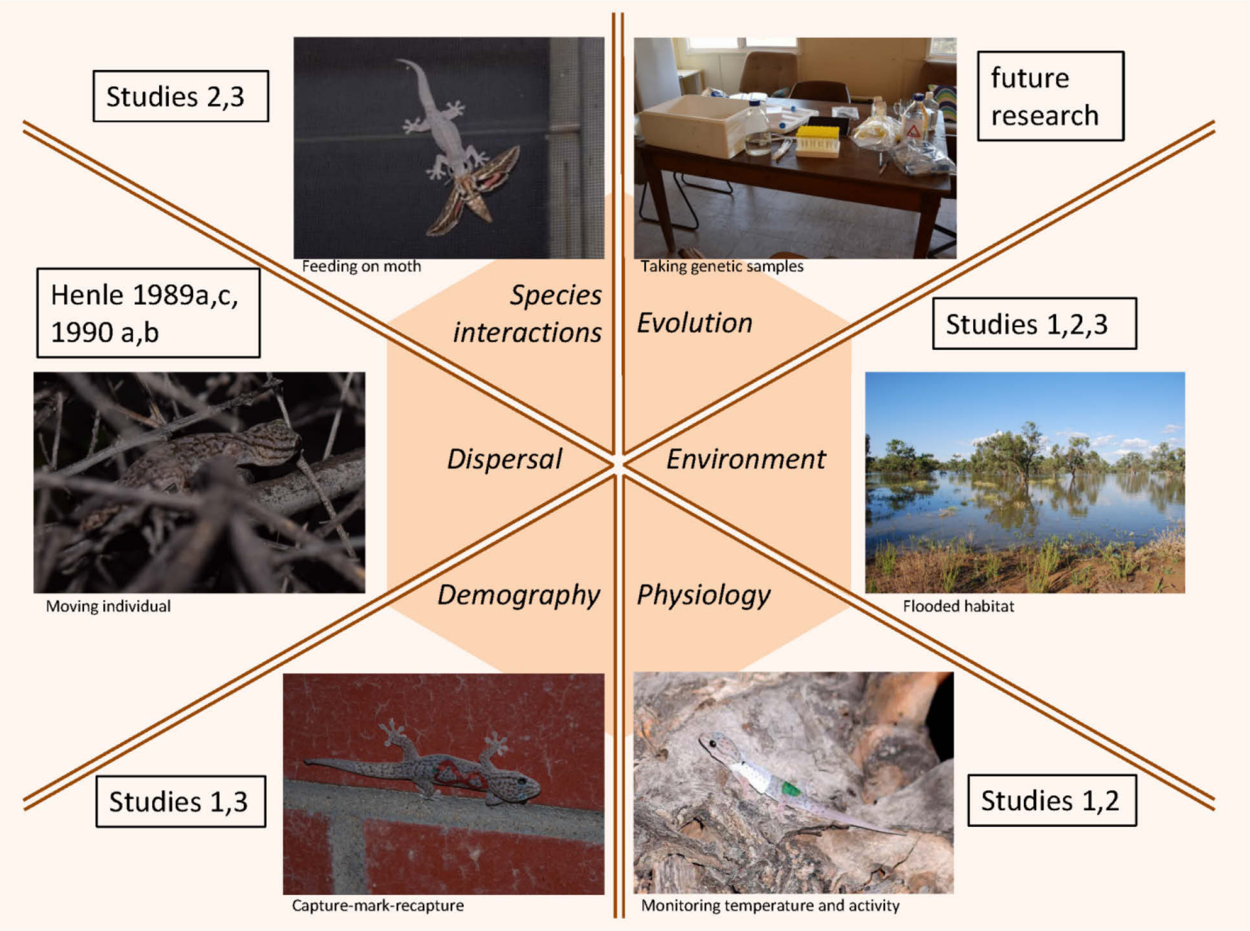

Figure 6.2: Overview of the key biological mechanisms that can improve fundamental understanding and predictions of species responses to climate change taking the example of an arboreal arid-zone gecko, *Gehyra variegata*. Boxes summarise the contribution provided by studies 1, 2, and 3 (that refer to Chapters 3, 4, and 5, respectively) to advancing knowledge on these mechanisms, or, in the case of *dispersal* and *evolution*, indicate that they have been or will be investigated. Photos by Annegret Grimm-Seyfarth. Scheme adapted from Urban et al. 2016.

Urban et al. (2016) stressed that any added mechanistic process to SDMs will improve both our fundamental understanding and more realistic predictions. They summarised such processes into the aforementioned categories: (1) *Physiology*; (2) *Demography*, life history, and phenology; (3) *Dispersal*, colonisation, and range dynamics; (4) *Species interactions*; (5) *Evolutionary* potential; and (6) Responses to *environmental* variation, and argued that even for the most well-studied species remarkable data gaps exist. With this thesis I aimed to fill in such data gaps for some arid-zone lizards, as shown schematically for the best studied species in Kinchega, *G. variegata* (Fig. 6.2). In general, I obtained substantial knowledge for eight lizard species on their responses to *environmental* variation (Chapters 3-5), their individual and *demographic* variability (Chapters 3, 5), and regarding both trophic and non-trophic *species interactions* (Chapters 4, 5). For three lizard species, I additionally obtained data to understand thermal *physiology* (Chapters 3, 4) although other physiological processes such as EWL remain unstudied. Moreover, dispersal data are available for several of the species in Kinchega (Table 6.1) although they probably do not reflect the total dispersal ability of the species. Lastly, genetic samples have been taken for *G. variegata* and occasionally for other species during field studies and first attempts have been made to analyse those data (Hoehn and Sarre 2006). For *G. variegata*, a previous study has further shown that if 55 adult individuals are present, which reflects the average adult population size quite well (Chapter 3), the effective population size is approximately 30 (Grimm et al. 2016) suggesting that only 55% of the overall population is actually breeding. All this knowledge can now be used to predict potential future changes in the community of arid-zone lizards.

Table 6.1: Summary of dispersal and movement observations of lizard species in Kinchega National Park.

Species	Movement	Distance	Reference
G. variegata	dispersing individuals	50 – 150 m	Henle 1990a
G. variegata	dispersal between RWI/Station (10 individuals)	80 – 200 m	own observation, unpublished data
G. variegata	within-year movement	200 m	Moritz 1987
M. boulengeri	dispersal following drying of bushes	25 – 100 m	Henle 1989a
E. richardsonii	foraging movement / dispersing individual	ca. 200 m	Henle 1989c
H. binoei	home range movement / dispersing individual	ca. 80 m	Henle 1990b
H. binoei	home range movement	23 – 48 m	Bustard 1968b
D. tessellatus	dispersing individuals	> 60 m	Henle 1990b
D. tessellatus	home range / foraging movement	ca. 100 m	Henle 1990b
L. damaeum	dispersing individual	ca. 175 m	Henle 1990b

Importantly, these mechanisms can also interact (Urban et al. 2016). In this study, for example, *physiological* processes (thermoregulation) strongly depended on non-trophic *species interactions* (vegetation cover and heterogeneity). Similarly, trophic *species interactions* such as responses to prey and predator abundances depended on species' *demographic* and life-history traits (longevity, reproduction). Another known example is the trade-off between thermoregulation and predator exposure where, in turn, predation constrained thermoregulation and thus lowered species' physiological performance and survival rates, which has been shown for garden skinks (*Lampropholis guichenoti*) (Downes 2001), several snake species (Webb and Whiting 2005, Lelièvre et al. 2013), and juvenile gopher tortoises (*Gopherus polyphemus*) (Radzio and O'Connor 2017). Furthermore, responses of certain species might have a cascading effect on other species and thus affect the whole community. For example, Zarnetske et al. (2012) suggested that the strongest effects come through top consumers and modelling them would ultimately lead to top-down effects through local food webs. Moreover, presence of predators in fragmented habitat patches could create ecological traps for lizards and thus lead to local extinctions (Hawlena et al. 2010).

Despite all observed species-specific differences, species' responses strongly depended on their functional traits. Since one might never get all the necessary information to accurately calibrate mechanistic models for all species, modelling species and community response through "functional groups" instead of "true species" might offer a much more effective path. Recent models have been developed that combine species traits, energy budgets, or biophysical processes with population modelling and environmental variations (Kearney and Porter 2006, Kearney et al. 2010b) that could be the basis for identifying the relevant functional groups to model. Thakur and Wright (2017) recently suggested a combined approach between environmental filtering (e.g., temperature, precipitation) and niche construction by species (through their functional traits) to understand trait-environment relationships. Another model considering functional groups in savanna birds showed promising results to accurately predict future species distributions (Scherer et al. 2016), an approach that might be also adaptable to desert lizards. Notably, the biggest challenge for using functional groups instead of true species is to identify the relevant functional traits across many species (Angert et al. 2011), which is needed to define meaningful functional groups and assess how these respond to various global stressors.

6.6 Conclusion and perspective for conservation

With advancing climate change, hot deserts like Kinchega are predicted to become hotter and drier (Noble and Gitay 1998, Stahlschmidt et al. 2011, Settele et al. 2014) while ENSO is likely to intensify (Cai et al. 2014, but see Wang et al. 2017). All studied species showed remarkable adaption potential; however, my results indicate that a series of extremely dry and simultaneously hot years is likely to have negative effects on all species' individual and population responses. Notably, in this system, it could be possible that improved conditions on one climatic scale (extended standing water due to higher frequencies of high Darling River heights with intensified ENSO) could compensate deteriorating conditions on another climatic scale (decreasing rainfall). Results of this thesis indicate that water availability rather than temperature will be the limiting factor for most desert reptiles. For example, even if I predicted a decreasing diurnal activity budget in diurnal species in summer, temperature was almost unimportant in comparison to precipitation and biotic interactions, which suggests that their thermoregulatory behaviour and activity might be flexible enough to adjust to increasing temperatures at a large extent. However, since climate change will likely lead to more extreme temperature and thus, species will face novel thermal stress (Buckley and Huey 2016), it remains unclear if the detected relationships will hold in the future. Nevertheless, the flexible responses of all species at the individual level in response to adverse climatic conditions partly buffered consequences at the population level (e.g., maintaining population size, survival, or occupancy). Hence, I conclude that a lizard population has the potential for resilience (Williams et al. 2008) before adaptation is required, a process that seems to be widely overlooked.

A detailed mechanistic understanding and implementation in SDMs is necessary to identify target species and regions for future conservation. However, this thesis also shows the complexity of such an attempt. Therefore, I argue for approaches that are based on species' functional traits and include a variety of parameters. If detailed responses are unknown, a broad range of scenarios to identify robust estimations of possible future changes are required. When comparing those different models, the most important regions or vulnerable species should become visible and can be targeted in conservation. In addition, field work targeted at determining relevant mechanistic processes that facilitate the response of species or functional groups to global change stressors will be a most promising approach for the conservation of (reptile) species and to fill in important knowledge gaps. This knowledge will help improving our fundamental understanding of the consequences of global change and thereby prevent biodiversity loss in vulnerable ecosystems, like hot arid deserts, but certainly also all around the globe.

7 Summary

Accumulating evidence has demonstrated considerable impact of climate change on biodiversity, with terrestrial reptiles being of particularly high concern. Previous studies frequently predicted reptile populations to decline or even go extinct. While climate-induced range shifts and extinction risks of reptiles are often addressed in literature, little is known about the underlying individual and population responses as well as involved ecological processes. In fact, reptiles show a remarkable plasticity to climatic fluctuations and can also adapt locally through phenotypic and genetic adaptation. Another highly important mechanism allowing reptiles to respond to thermal variations is behavioural thermoregulation. Its efficiency might become crucial for securing activity budgets under future climate change and might be highly dependent on the thermal microhabitat variability. Furthermore, reptile species are not isolated systems but part of a large species assemblage with many trophic dependencies. Thus, investigations of responses of reptile species to climate change should consider multiple trophic levels to understand the overall effects of drivers of global change on single species, which is essential for designing optimal future conservation strategies.

Climate change will likely cause particularly severe modifications in dryland ecosystems, which are already characterised by strong water stress and hot temperatures each year and thus, pose a challenge to biodiversity. Importantly, the major part of vertebrate density and diversity in deserts is represented by reptiles and the worldwide highest lizard diversity can be found in arid Australia, where the density and diversity of other vertebrates is particularly low. Thus, hot desert ecosystems are of high conservation importance. Regrettably, while several studies investigated climatic sensitivity of reptiles and potential involved mechanisms in (sub-)tropical and temperate regions, very few studies have focused on such adaptation mechanisms in hot deserts. However, ecological processes in hot deserts strongly differ from those of tropical and temperate regions. It is therefore of paramount importance to assess reptile species response to climate change in arid regions and to forecast future trends of a unique biodiversity component on Earth.

The main limitation for such investigations integrating both individual and population response to climatic fluctuations while keeping track of underlying mechanisms is that they are only possible through long-term multi-species monitoring. In this dissertation, I took advantage of the unique opportunity provided by a detailed 30-year long-term reptile monitoring scheme that started in 1985 and which I continued from 2012 to 2016. This monitoring scheme was located at the eastern margin of Australia's arid zone in Kinchega National Park, New South Wales, which is characterised by high and increasing summer temperatures and low but highly variable rainfall without seasonal patterns. It additionally contains floodplains with flooding being related to rainfall in inland Queensland due to La Niña events as part of the El Niño Southern Oscillation (ENSO) and thus, can be considered as distant climatic factor acting locally on the ecosystem. The complexity of different local and distant climatic drivers, together with the high species richness, makes Kinchega a very suitable location for studying the effects of climate change on reptiles. Throughout the 30 years, a total of 23 reptile species belonging to seven families were caught or observed. Eight of these species, five scincids and four gekkonids, were particularly abundant and build the basis for this dissertation. My main objective was to investigate how reptile species in arid Australia responded to various climatic parameters at different spatial scales and to analyse the two potential main underlying mechanisms: thermoregulatory behaviour and interactions of species with their biotic environment. Therefore, this dissertation combines extensive individual-based field data across trophic levels, selected field experiments, statistical analyses, and predictive modelling.

I used the most abundant species, an arboreal, nocturnal gecko species (*Gehyra variegata*), to determine the relative contribution of climatic factors acting locally (temperature, rainfall) or distantly (La Niña induced flooding) on ecological processes from traits at individual level (body condition, body growth) to demography at population level (survival, sexual maturity, population sizes). I then investigated whether thermoregulatory behaviour and activity during both active (night) and resting (daytime) periods of the day can explain these responses. This species is of particular interest to such investigations as it is a long-living species (up to 28 years in the study area) and responses of long-living species to climate have rarely been studied. I found that relative effects of various local and distant climatic parameters differed depending on the ecological level considered. Generally, both high temperatures and high water availability enhanced individual and demographic parameters. The impact of water availability was scale-independent as local rainfall and La Niña induced flooding compensated each other. Importantly, plasticity in life-history traits at the individual level in response to adverse climatic conditions, like extremely hot and dry years, could partly buffer consequences on the population level by maintaining survival rates. Furthermore, only cool temperatures induced diurnal thermoregulatory behaviour with individuals moving to exposed hollow branches and even outside tree hollows for sun-basking during the day. Since diurnal behavioural thermoregulation likely induced costs on fitness (e.g., greater predation risk), it could decrease performance under cool temperatures at both individual and population level. Together, I conclude that dryer rather than warmer conditions will be detrimental for nocturnal desert reptiles.

Findings for nocturnal geckos could differ substantially from those of diurnal skinks with diurnal reptiles likely being more affected by hot temperatures than nocturnal ones. Therefore, I investigated the mechanism of thermoregulatory behaviour in two diurnal, terrestrial skink species, *Morethia boulengeri* and *Ctenotus regius*, and the interacting effects of vegetation on body temperatures and activity budgets. I combined different data sets by calibrating high-resolution experimental data to longer but less accurate time series with different temporal resolutions to determine the activity budgets under past (1985 to now) and future (until 2090) climatic conditions. With this approach, I could identify that both the thermoregulatory behaviour and the activity budgets of diurnal, terrestrial desert skinks were strongly impacted by the amount of vegetation and its heterogeneity, which provided both cooling spots and heat reservoirs. According to future climate change scenarios, cooler microhabitats might become beneficial to warm-adapted species, such as *C. regius,* by increasing the duration of daily activity. Contrarily, warmer microhabitats might become unsuitable for less warm-adapted species such as *M. boulengeri* for which mid-summers might result in a complete restriction of activity irrespective of vegetation. However, despite climate change likely leading to a species-specific reduction in activity budgets in mid-summer, it might also create novel temporal niches at the annual scale. Provided that individuals would be able to shift their seasonal timing towards spring and autumn, climate change could even contribute to an increasing annual activity budget. Overall, this thesis highlights the critical importance of thermoregulatory behaviour to buffer temperatures and its dependence on vegetation heterogeneity. Hence, the loss of shaded microhabitats is likely having a stronger impact on diurnal reptiles than rising temperature itself. In future conservation strategies, I argue that the cascading effects of vegetation rather than climatic envelopes alone should be considered to prevent desert lizards from extinction.

In addition to the described non-trophic interactions between reptiles and vegetation, reptiles are affected by trophic interactions. To my knowledge, species' responses to direct and indirect pathways of multiple climatic and biotic factors and their interactions have rarely been examined comprehensively. Therefore, I investigated the direct and indirect effects of both climatic and biotic parameters on the individual condition and occupancy of the eight most abundant lizard species occurring in my study area throughout the 30-year monitoring period. I used structural equation modelling to disentangle single and interactive effects of climatic and biotic parameters, and further assessed whether species could be grouped in functional groups according to their responses to climatic and biotic parameters. Overall, lizard species differed strongly in how they reacted to climatic and biotic factors, but the factor to which they responded seemed to be closely related to their functional traits and suggest options for functional grouping of species. At the individual level, functional groups were determined by activity (nocturnal versus diurnal) and habitat (terrestrial, subterranean or arboreal), while at the population level, functional groups were more determined by species' average adult snout-vent-lengths, longevity, and habitat specialisation (generalists versus specialists). This thesis gives an indication how to identify relevant functional groups at different ecological levels, which could be important for both field work targeted at determining relevant mechanistic processes that facilitate the response of species or functional groups to global change stressors, and targeted conservation. Moreover, it stresses the importance of indirect pathways and species interactions when analysing the effects of climate change.

In summary, both local and distant climatic factors had strong impacts on the local desert reptile community. Thus, climate change in a particular region may have important effects on species communities at far distances, even on communities that are only indirectly exposed via changes in adjacent ecosystems such as periodic floodplains through La Niña, which were found to play a key role for the reptile community segregation. Hence, such natural floodplains must not be prevented from flooding and a management of the area should ensure long enough flood duration to allow a natural turn-over of the community composition. In general, results of this thesis indicate that water availability rather than temperature will be the limiting factor for desert reptiles and that biotic interactions through vegetation (shade, refuge) and prey or predation largely determine species' responses. Identifying the actual limiting climatic factors at different scales and their interactions at different ecological levels is crucial to reliably predict future population dynamics and support conservation planning in arid ecosystems. Lastly, the flexible responses of all species on an individual level in response to adverse climatic conditions partly buffered consequences on the population level, indicating the potential for resilience before adaptation is needed, a process which seems to be widely overlooked.

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9 Selbstständigkeitserklärung

Hiermit erkläre ich, Annegret Grimm-Seyfarth, geboren am 08.08.1988, dass mir die Promotionsordnung der Mathematisch-Naturwissenschaftlichen Fakultät der Universität Potsdam vom 18.09.2013 bekannt ist und ich diese anerkenne.

Insbesondere versichere ich, dass ich die vorliegende Arbeit selbst angefertigt habe, ohne unzulässige Hilfe und ohne Benutzung anderer als der angegebenen Hilfsmittel und dass die aus fremden Quellen direkt oder indirekt übernommenen Gedanken in der Arbeit als solche kenntlich gemacht worden sind.

Ich versichere, dass alle Personen, die mich bei der Durchführung der Analysen und Anfertigung der Manuskripte (Kapitel 3-5) unterstützt haben, als Co-Autoren genannt sind und dass Dritte weder unmittelbar noch mittelbar geldwerte Leistungen von mir für Arbeiten erhalten haben, die im Zusammenhang mit dem Inhalt der vorgelegten Dissertation stehen.

Ich versichere weiterhin, dass ich die vorgelegte Arbeit nicht bereits zuvor in gleicher oder in wesentlichen Teilen ähnlicher Form einer anderen staatlichen oder wissenschaftlichen Einrichtung zum Zwecke einer Promotion oder eines anderen Prüfungsverfahrens vorgelegt habe.

Potsdam, 18.12.2017

Annegret Grimm-Seyfarth

Erklärung zum Eigenanteil an den Publikationen

Die vorliegende Dissertation umfasst drei wissenschaftliche Studien (Kapitel 3-5), die als unabhängige Manuskripte vorbereitet wurden. Kapitel 3 ist derzeit in überarbeiteter Version wieder eingereicht im Journal *Ecological Monographs* und wird dort nun erneut überprüft. Kapitel 4 wurde bereits im Journal *Ecology and Evolution* publiziert. Kapitel 5 ist bereit zur Einreichung in eine internationale Fachzeitschrift. Meine Ko-Autoren umfassen jeweils meinen Hauptbetreuer Prof. Dr. Klaus Henle vom Department Naturschutzforschung am Helmholtz-Zentrum für Umweltforschung, Leipzig, meinen Mentor Dr. Jean-Baptiste Mihoub von der Sorbonne Universités, Paris/Frankreich, sowie für Kapitel 3 meinen Kooperationspartner Associate Prof. Dr. Bernd Gruber vom Institute for Applied Ecology der University of Canberra, Australia. Als Erstautorin der Manuskripte habe ich die Studien unter üblicher Unterstützung meines Betreuers konzipiert, die Untersuchungen sowie Analysen der Daten und Modellierungen in Kapitel 4 ausschließlich selbstständig durchgeführt und die Manuskripte geschrieben. Alle Manuskripte erhalten Vorschläge der Ko-Autoren, sowie in Kapitel 3 und 4 auch von unabhängigen GutachterInnen der Fachzeitschriften. Die Felddaten vor 2012 stammen von Klaus Henle mit Unterstützung von Bernd Gruber. Bei der Erhebung der Felddaten von 2012 bis 2016 haben mich Klaus Henle und gelegentlich auch Bernd Gruber und Jean-Baptiste Mihoub unterstützt. Experimente aus den Kapiteln 3 und 4 (Thermoregulation) habe ich selbstständig konzipiert und durchgeführt.

Leipzig, 29.11.2017

Annegret Grimm-Seyfarth

Prof. Dr. Klaus Henle
(Betreuer)

Prof. Dr. Florian Jeltsch
(Betreuer)

10 Supporting Information

10.1 Appendix to Chapter 3

10.1.1 APPENDIX S1: FURTHER CLIMATIC INVESTIGATIONS

S1.1: Dependencies of Darling River heights on the ENSO phenomenon

The Darling River has its spring in Queensland about 1000 km NE of Kinchega National Park. While the Darling usually has low water level, water level increases enormously during La Niña events that cause extremely high rainfall in Queensland. Depending on the location of the rainfall, it can take more than half a year until the water reaches Kinchega. We considered the monthly river height data from the closest weir to our study area (weir 32, available from the Department of Primary Industries, Office of Water, New South Wales Government; http://realtimedata.water.nsw.gov.au/water.stm?ppbm=DAILY_REPORTS&dr&3&drkd_url).

To investigate whether river heights are related to the ENSO phenomenon, we downloaded the monthly Southern Oscillation Index (SOI) as an index to track ENSO from the Bureau of Meteorology, Australian Government (http://www.bom.gov.au/climate/current/soi2.shtml) and calculated summer (October-March) and winter (April-September) mean indices. Averaged indices over longer intervals are known to reflect the actual ENSO better than over short intervals (http://www.bom.gov.au/climate/current/soi2.shtml) and the chosen periods reflect the seasonal activity of *Gehyra variegata* (Henle 1990). We used Pearson's correlation tests to determine whether the average summer Darling River height (October-March) is correlated to the current summer SOI, the previous winter SOI, or the previous summer SOI. Likewise, we determined whether the average winter Darling River height (April-September) is correlated to the current winter SOI, the previous summer SOI, or the previous winter SOI. We found that summer Darling River height at weir 32 in Kinchega National Park was correlated to current summer SOI ($t = 3.01$, $p = 0.005$, $R^2 = 0.48$) and previous winter SOI ($t = 3.34$, $p = 0.002$, $R^2 = 0.52$), but not to the previous summer SOI ($t = -0.09$, $p = 0.92$, $R^2 = -0.02$). In contrast, winter Darling River height was only weakly correlated to current winter SOI ($t = 1.78$, $p = 0.08$, $R^2 = 0.31$), but marginally significant to previous summer SOI ($t = 1.93$, $p = 0.06$, $R^2 = 0.33$) and highly significant to previous winter SOI ($t = 2.74$, $p = 0.01$, $R^2 = 0.45$). All significant correlations showed that higher SOI indices (i.e., La Niña events) led to higher Darling River levels. Exemplarily, this correlation can be seen in Figure S1.1.1 for summer Darling River heights in relation to summer SOI indices.

The difference in the correlations of Darling River heights to the respective La Niña event between summer and winter can be explained by both evaporation and discharge rates (Simpson et al. 1993). Evaporation data clearly showed a three-fold increase during summer in comparison to winter (Fig. S1.1.2). Faster evaporation dampened the increase in river height during summer. For that reason, summer La Niña events cannot be seen (in terms of increased river height) in Kinchega after one year in contrast to winter La Niña. Furthermore discharge rates of the Darling River for anthropogenic use (irrigation and drinking water, Murray–Darling Basin Authority 2015) were twice as high in summer than in winter (Fig. S1.1.2). Thus, the Darling River flowed faster in summer than in winter. For these reasons, Darling River height in Kinchega in summer was directly correlated to recent SOI indices, whereas river height in winter was correlated to SOI events one or two seasons ago.

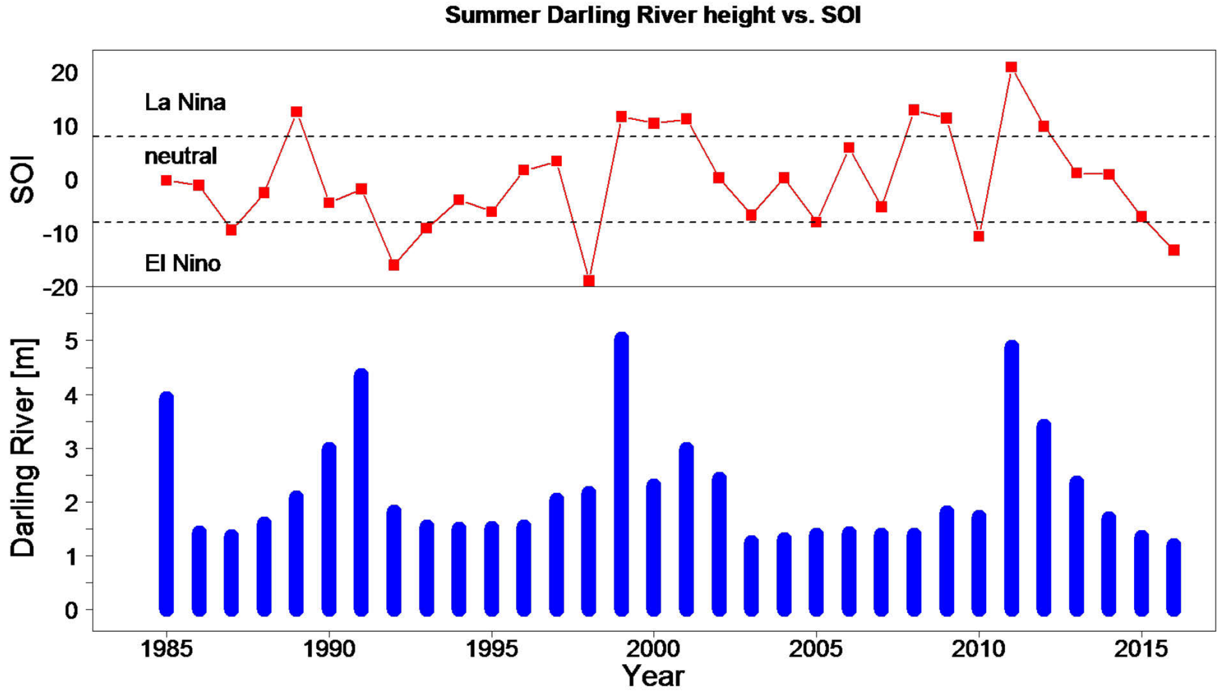

Figure S1.1.1: Darling River heights in summer in relation to summer SOI indices.

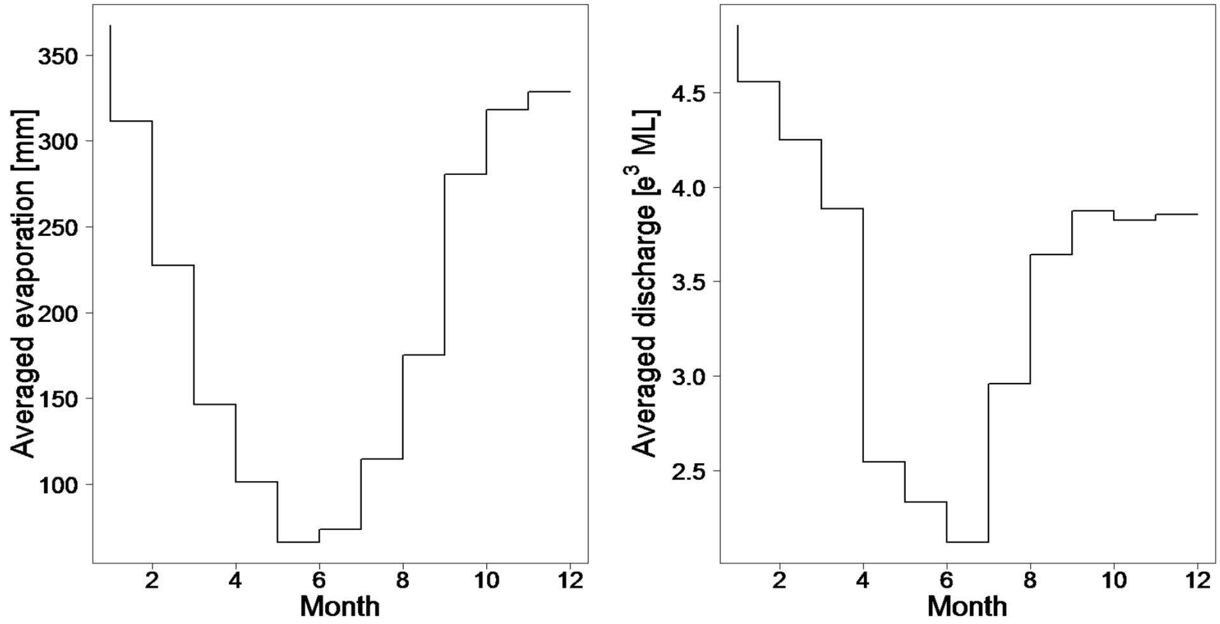

Figure S1.1.2: Averaged evaporation (2011-2016) and discharge rates (1984-2016) of the Darling River. Data from the Department of Primary Industries, Office of Water, New South Wales Government; http://realtimedata.water.nsw.gov.au/water.stm?ppbm=DAILY_REPORTS&dr&3&drkd_url.

S1.2: Calibration of weather parameters from Menindee to Kinchega

Although it was already known that weather parameters obtained from Menindee Post Office (station number 047019, http://www.bom.gov.au/climate/data/stations) strongly correlated with weather data in Kinchega National Park between 1985 and 1987 (Henle 1990), we also calibrated them for recent weather parameters. For these calibrations, microhabitat temperatures and humidity were recorded every three hours for two years from March 2014 to February 2016 (with a gap between October 2016 and January 2016 because the data logger dropped down) using iButton® temperature/humidity loggers (DS1923). These data loggers were covered with bright carton and hang up on a non-leaved eucalypt branch in 1.5 m height. Mean maximum daily temperatures during that year were highly correlated (Pearson's correlation test, $t = 71.42$, $p << 0.001$, $R^2 = 0.95$) between Menindee and Kinchega although Kinchega was slightly warmer than Menindee (paired t-test, two-sided, $t = 14.04$, $p << 0.001$, mean difference = 1.52°C). Thus, temperatures from Menindee can be used as precise predictors for Kinchega (Fig. S1.2.1). To obtain the number of days above 45°C per month we added 1.52°C to the daily maximum temperatures registered in Menindee. Likewise, both monthly relative humidity in Kinchega and Menindee (Pearson's correlation test, $t = 6.73$, $p=0.001$, $R^2 = 0.95$) and daily relative humidity in Kinchega and rainfall in Menindee (Pearson's correlation test, $t = 8.05$, $p << 0.001$, $R^2 = 0.32$) were highly correlated (Fig. S1.2.2). Hence, also rainfall data from Menindee could be used as predictor for precipitation in Kinchega.

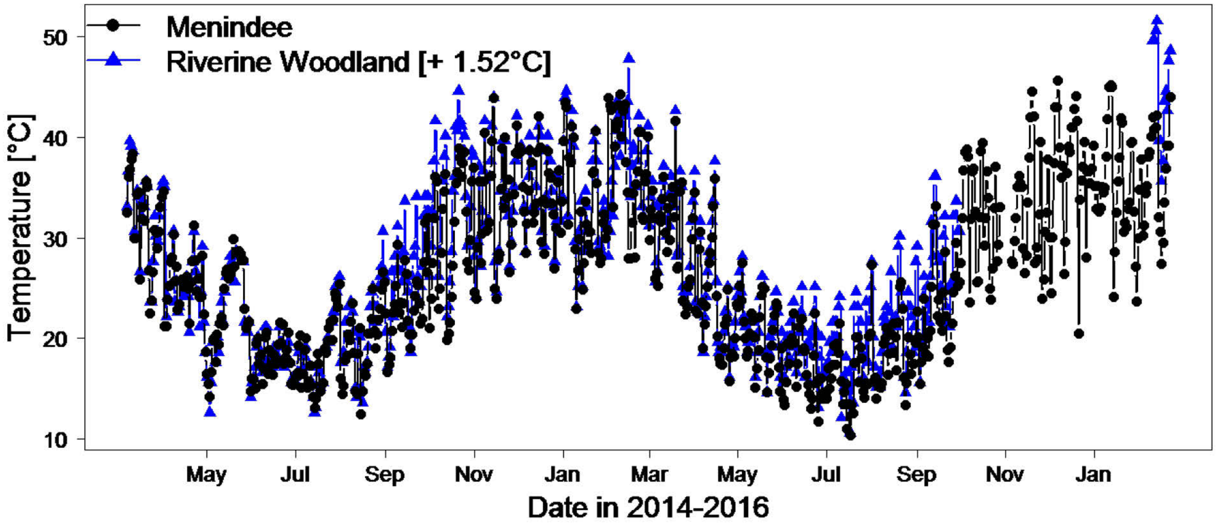

Figure S1.2.1. Comparison between daily temperatures in Menindee and Kinchega National Park. Riverine Woodland refers to the study area in Kinchega. [+ 1.52°C] indicates that temperatures in Kinchega were on average 1.52°C higher than in Menindee.

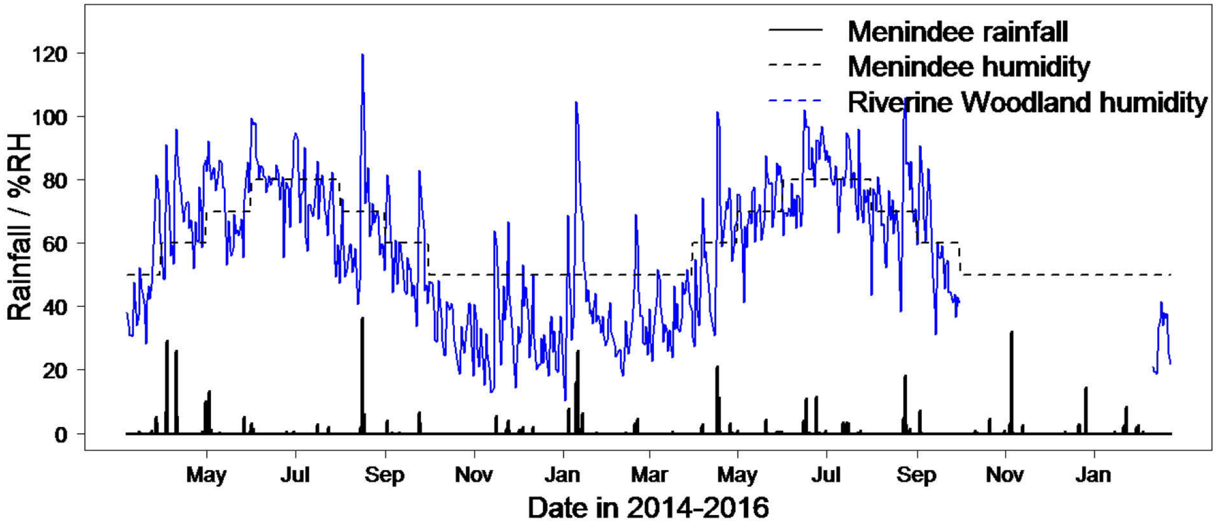

Figure S1.2.2. Comparison between monthly averaged humidity in Menindee and dailty humidity in Kinchega. Rainfall in Menindee is also indicated.

S1.3: Climatic parameter space

The relation between the most important parameters, average summer temperature and winter rain, during our study period can be seen in Figure S1.3.1. In most years, average summer temperature laid between 30 and 34°C and winter rainfall between 70 and 170 mm without any concordant pattern between both. However, in 2003 and 2013 we had exceptionally high average summer temperatures above 34°C paired with extremely low winter rainfall below 50 mm.

The smoothed relation between summer temperatures, winter rainfall, and the Darling River height in summer is shown in Figure S1.3.2. No clear pattern between the three parameters emerged from that. There are only a few years where high temperatures occurred together with both extremely low winter rainfall and a low Darling River height.

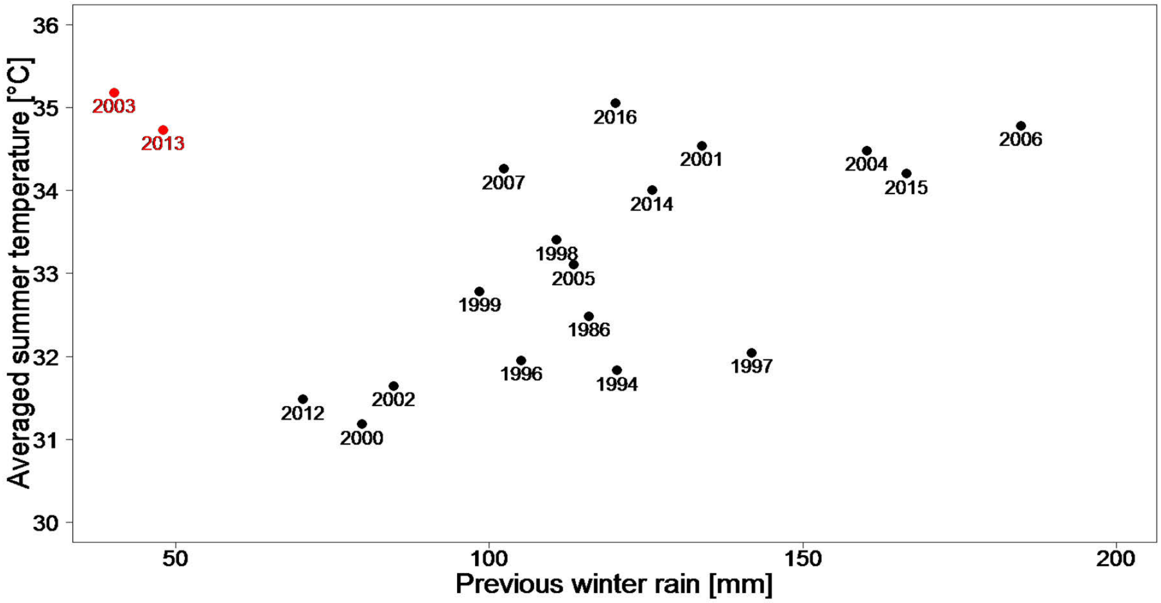

Figure S1.3.1: Relation between average summer temperatures and previous winter rainfall during our study period in Kinchega National Park.

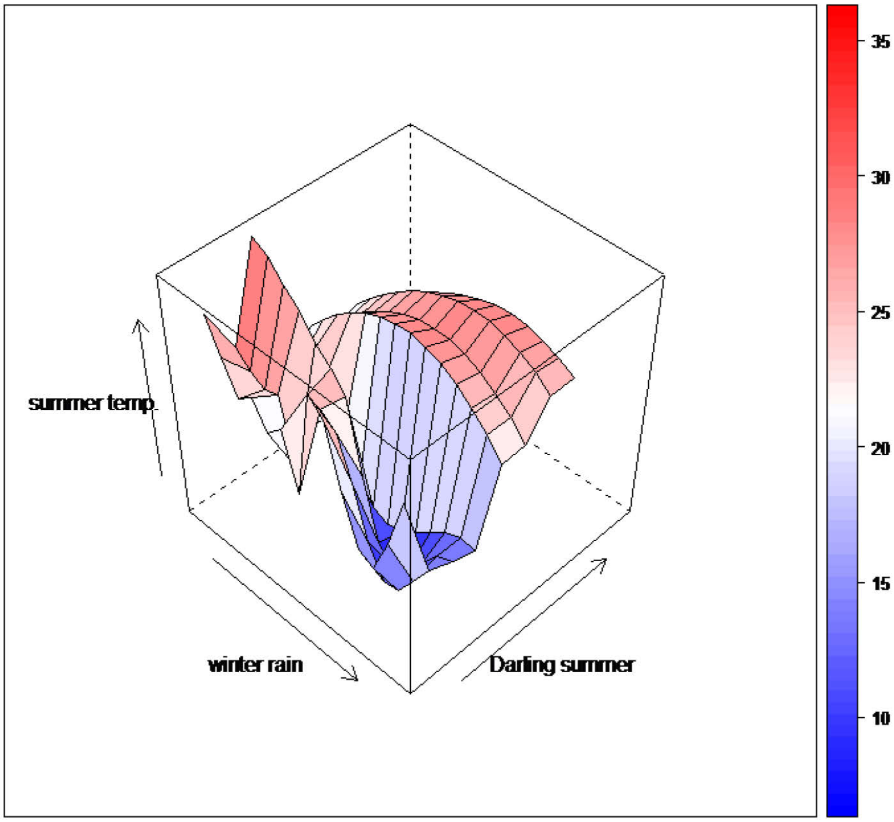

Figure S1.3.2: Smoothed relation between summer temperature, winter rain, and Darling River height (named Darling summer in the graph) in summer during our study period. The color key refers to the smoothed temperature in °C at a specific parameter combination of winter rain and Darling River height.

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10.1.2 APPENDIX S2: DEPENDENCE OF BODY TEMPERATURES ON AMBIENT TEMPERATURES DURING NOCTURNAL ACTIVITY

Beside thermoregulatory investigations during the day, we investigated which ambient temperatures determined geckos' body temperatures during their nocturnal activity. We measured body temperatures of individual adult geckos using an infrared thermometer (Raytek MX2 TD 60:1, 0.75K accuracy) by following the individuals on 5 nights in February 2013, 2014, and 2015. In total, we measured 63 different individuals. We conducted these temperature measures at the Kinchega Station, a habitat adjacent to the riverine woodland. This station comprises seven huts that are also inhabited by *Gehyra variegata* (Henle 1990). We chose this habitat for direct measures of body temperatures to avoid inferences with any branches.

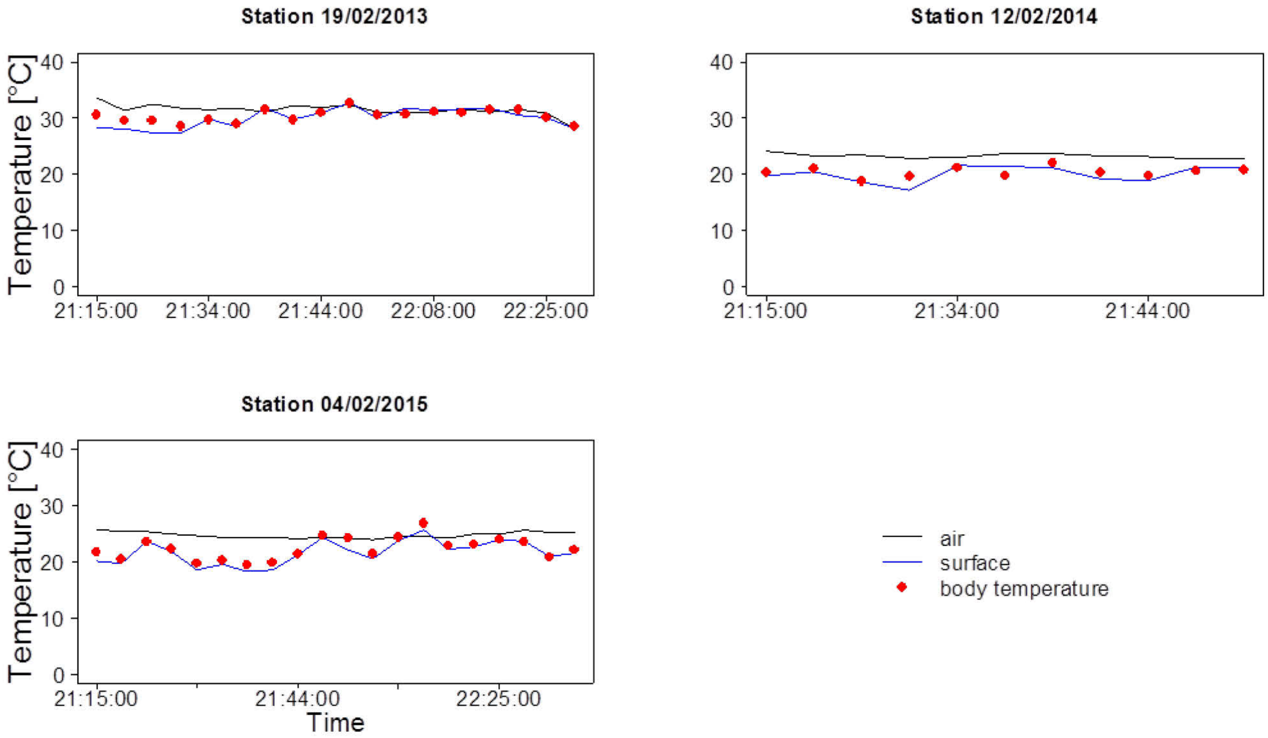
Additional to body temperatures, we always recorded surface temperatures on the exact location where the gecko sat, air temperatures using a hand thermometer (TFA Dorstmann, No. 30.1012), the hut, and the microhabitat (surface material). To determine which factors affect body temperatures, we built a GLMM using body temperature as response variable and air and surface temperatures as well as the microhabitat as test predictors. We included both air and surface temperatures as they can differ substantially on a small scale and as geckos are directly exposed to both. Additionally, we included the random intercept of the gecko's ID, of the day of measurement, and the hut as well as the random slope of hut per day as control predictors to account for pseudoreplications. Model procedures followed the descriptions of GLMMs in the main text.

The full model was significantly different from the null model (ANOVA, $p<<0.001$) and no obvious deviations from model assumptions could be found. We found that all three test predictors (air and surface temperature, microhabitat) had a significant influence on body temperature and were highly important ($\omega AIC \geq 0.93$, Table S2.1). It can be seen in Table S2.1 and Figure S2.1 that geckos' body temperatures strongly followed surface temperatures (slope: 0.80±0.04°C) but were adjusted towards air temperatures (slope: 0.26±0.05°C). Moreover, microhabitats that were expected to have a high heat storage capacity (iron, stone, metal) positively affected body temperature while microhabitats with a presumed low heat storage capacity (wooden doors, corrugated iron with thorough air circulation below the grooves) negatively affected body temperatures (Table S2.1).

In comparison, temperature measurements conducted across a year, and thus covering a much higher temperature span, the correlation between cloacal body temperature (measured within 45s after sighting) and substrate temperature measured with a digitron thermal probe (accuracy ± 0.1°C) was even *r* = 0.98 (Henle 1990).

Table S2.1: Overview of the estimates, standard errors, significance (p-value) and importance (ωAIC) of the test predictors for nocturnal body temperatures. Estimates and standard error for microhabitat cover the span across all microhabitat types.

Test predictor	Estimate	Standard error	p-value	Σ(ωAIC)
T(surface)	0.80	0.04	<0.001	1
T(air)	0.26	0.05	0.008	0.93
microhabitat	[-0.92; 1.38]	[0.50; 0.71]	0.004	0.97


Station 19/02/2013

Station 12/02/2014

Station 04/02/2015

Figure S2.1: Individual body temperatures (red dots) of G. variegata on three exemplary days in February 2013, 2014, and 2015 in relation to surface (blue line) and air temperature (black line).

References

Henle, K., 1990. Population ecology and life history of the arboreal gecko *Gehyra variegata* in arid Australia. Herpetological Monographs 4:30–60.

10.1.3 Appendix S3: Parameter estimates for all LMMs and correlation graphs of the main individual traits

We calculated individual traits and demographic parameters according to Fig. S3.1. Of them, relations of body condition, body growth rates and population sizes to climatic parameters were obtained using LMMs as described in the main text. The following full (i.e. all test and control predictors) and null models (i.e. only control predictors) were examined:

Body condition

Y = μ + MeasurementDate + SVL.TL + AgeSex + T(summer) + P(summer) + T:P(summer) + #days>45°C + P(winter) + T:P(winter) + Darling(summer) + T:D(summer) + Darling(winter) + T:D(winter) + #years.post.flood + [ID] + [Year] + [Tree] + [Person] + [MeasurementDate|Year] + ε

Body growth rates

Y = μ + AgeSex + T(summer) + P(summer) + T:P(summer) + #days>45°C + P(winter) + T:P(winter) + Darling(summer) + T:D(summer) + Darling(winter) + T:D(winter) + #years.post.flood + [ID] + ε

Population size

Y = μ + CV + prev.N + T(summer) + P(summer) + T:P(summer) + #days>45°C + P(winter) + Darling(summer) + Darling(winter) + #years.post.flood + ε

In our annotation, μ represents the intercept, ε the error term, MeasurementDate the day of individual measurements within a capture period, SVL.TL the quotient tail length divided by snout-vent-length, AgeSex the combined age and sex variable (juveniles, subadults, adult females or adult males), ID the gecko's ID, Year the year of capture, Tree the tree of capture, Person the person who measured the individual, MeasurementDate|Year the random slope of the day of measurements per year, CV the coefficient of variation (i.e., individual heterogeneity of capture probabilities), and prev.N the population size of the previous year. Abbreviations of climatic test predictors can be found in Table S3.2.

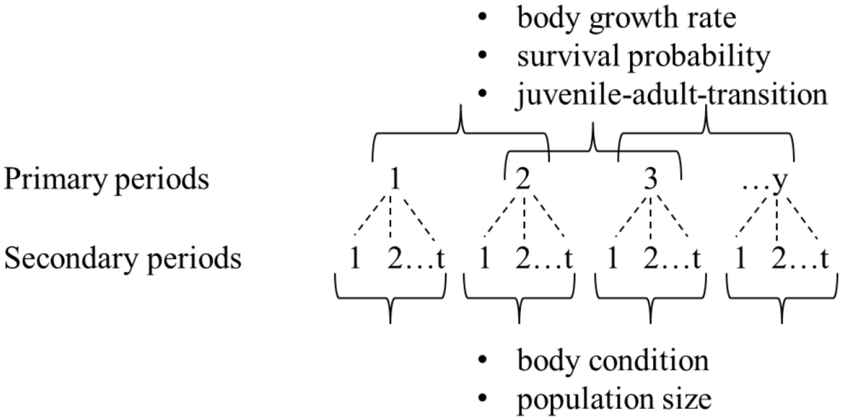


Figure S3.1: Overview on the arrangement of primary (i.e. years) and secondary periods (i.e. survey within a year) which are used to calculate different individual and demographic traits. Body condition and population size are calculated within years, while body growth rates, survival probabilities and juvenile-adult-transitions are calculated between years.

Table S3.2: Untransformed estimates, standard errors, scaled estimates (Scale.est) and their standard errors (Scale.SE) of the full model and estimates and standard errors of the best model (Sc.est.b and Sc.SE.b, respectively), significance (p-value), importance (ωAIC), and the percentage of independent variance explained (VE) of all test predictors affecting various response variables. juv.: juveniles, sub.: subadults, ad.: adults, T: temperature, P: precipitation, D: Darling; ":" symbolises interaction, Darling refers to Darling River heights. "-" indicates that this predictor was not included in the L(M)M. See Methods for details.

Response		T(summer)	P(summer)	T:P(summer)	# days > 45°C	P(winter)	T:P(winter)	Darling (summer)	T:D(summer)	Darling (winter)	T:D(winter)	# years post flood
Body condition	Estimate	0.183	0.027	-0.001	-0.010	0.027	-0.001	0.707	-0.018	-0.359	0.012	0.010
	SE	0.125	0.013	0.0005	0.013	0.022	0.0005	1.543	0.047	1.424	0.042	0.016
	Scale.est	0.010	-0.023	-0.057	-0.036	0.192	-0.048	0.124	-0.028	0.053	0.019	0.032
	Scale.SE	0.033	0.029	0.024	0.030	0.038	0.031	0.026	0.050	0.041	0.044	0.039
	Sc.est.b	-	-	-	-	0.140	-	0.110	-	0.052	-	-
	Sc.SE.b	-	-	-	-	0.033	-	0.028	-	0.035	-	-
	p-value	[1]	[1]	0.02	0.26	[1]	0.14	[1]	0.57	[1]	0.67	0.42
	Σ(ωAIC)	0.74	0.63	0.36	0.32	1.00	0.38	1.00	0.22	0.63	0.14	0.29
	VE	3.84	4.33	6.80	9.34	12.67	9.05	30.08	2.33	5.60	3.86	12.07
Body growth rate	Estimate	0.032	0.001	-1.1e-5	0.001	0.004	-1.1e-4	-0.200	0.007	-0.593	0.017	0.009
	SE	0.020	0.003	7.8e-5	0.002	0.003	7.3e-5	0.140	0.004	0.214	0.006	0.002
	Scale.est	0.001	0.010	-0.001	0.003	0.027	-0.008	0.022	0.011	-0.026	0.027	0.032
	Scale.SE	0.006	0.004	0.005	0.005	0.006	0.005	0.005	0.007	0.011	0.010	0.008
	Sc.est.b	0.004	0.009	-	-	0.026	-0.007	0.020	0.011	-0.027	0.029	0.031
	Sc.SE.b	0.004	0.003	-	-	0.006	0.005	0.004	0.007	-0.010	0.009	0.007
	p-value	[1]	[1]	0.88	0.58	[1]	0.12	[1]	0.11	[1]	0.005	<<0.001
	Σ(ωAIC)	1.00	0.94	0.27	0.31	1.00	0.61	1.00	0.68	0.97	0.97	1.00
	VE juv.	14.99	8.03	3.79	5.51	24.07	12.02	6.50	13.15	3.66	5.44	2.83
	VE sub.	2.60	2.07	2.61	5.96	37.04	19.05	3.25	5.90	7.13	2.72	11.68
	VE ad.	6.52	5.22	4.46	5.16	14.90	5.77	6.06	15.72	11.23	11.94	13.02

Population size sub.+ad. (*t*)	Estimate	12.770	4.549	-0.142	0.212	0.005	-	0.809	-	13.263	-	1.260
	SE	5.434	1.612	0.050	1.298	0.077	-	4.246	-	4.225	-	2.182
	Scale.est	-0.750	-6.541	-9.130	0.735	0.232	-	0.873	-	13.595	-	4.296
	Scale.SE	3.379	4.497	3.248	4.507	3.492	-	4.578	-	4.331	-	7.442
	Sc.est.b	1.116	-7.071	-8.682	-	-	-	-	-	12.597	-	-
	Sc.SE.b	2.068	2.981	2.098	-	-	-	-	-	2.795	-	-
	p-value	[1]	[1]	<0.001	0.77	0.91	-	0.73	-	<0.001	-	0.31
	Σ(ωAIC)	0.99	0.62	0.61	0.04	0.02	-	0.02	-	0.90	-	0.02
	VE	31.31	7.66	34.84	3.12	1.60	-	0.48	-	19.72	-	1.27
Population size sub. (*t-1*)	Estimate	2.472	0.833	-0.028	-0.436	-0.137	-	4.254	-	3.992	-	2.851
	SE	6.900	1.530	0.048	1.074	0.068	-	3.160	-	3.738	-	2.509
	Scale.est	-2.298	-6.229	-4.657	-1.515	-6.226	-	4.587	-	4.092	-	9.722
	Scale.SE	6.009	8.491	8.157	3.730	3.061	-	3.407	-	3.832	-	8.558
	Sc.est.b	-	-	-	-	-5.331	-	-	-	-	-	-
	Sc.SE.b	-	-	-	-	2.001	-	-	-	-	-	-
	p-value	[1]	[1]	0.34	0.49	0.003	-	0.03	-	0.08	-	0.07
	Σ(ωAIC)	0.09	0.13	0.00	0.08	0.80	-	0.33	-	0.11	-	0.09
	VE	17.58	24.87	24.48	4.08	5.67	-	9.71	-	1.52	-	12.09

[1] p-value not indicated because it is conditional on another predictor and thus does not have a meaningful interpretation (Aiken & West 1991, Schielzeth 2010)

Table S3.3: Explained variances of random effects control predictors for LMMs of body condition, annual growth, and nocturnal body temperature. Std. Dev. refers to "Standard Deviation". "-" indicates that this predictor was not included in the LMM. See Methods for details.

Random effect	**Body condition**		**Body growth rate**		**Body temperature**	
	Variance	**Std. Dev.**	**Variance**	**Std. Dev.**	**Variance**	**Std. Dev.**
Gecko's ID (intercept)	0.013	0.11	0.00	0.00	2.74	1.66
Tree (intercept)	0.001	0.023	-	-	-	-
Person (intercept)	0.004	0.063	-	-	-	-
Year (intercept)	0.003	0.057	-	-	-	-
Day in year (slope)	0.0002	0.017	-	-	-	-
Day (intercept)	-	-	-	-	0.06	0.24

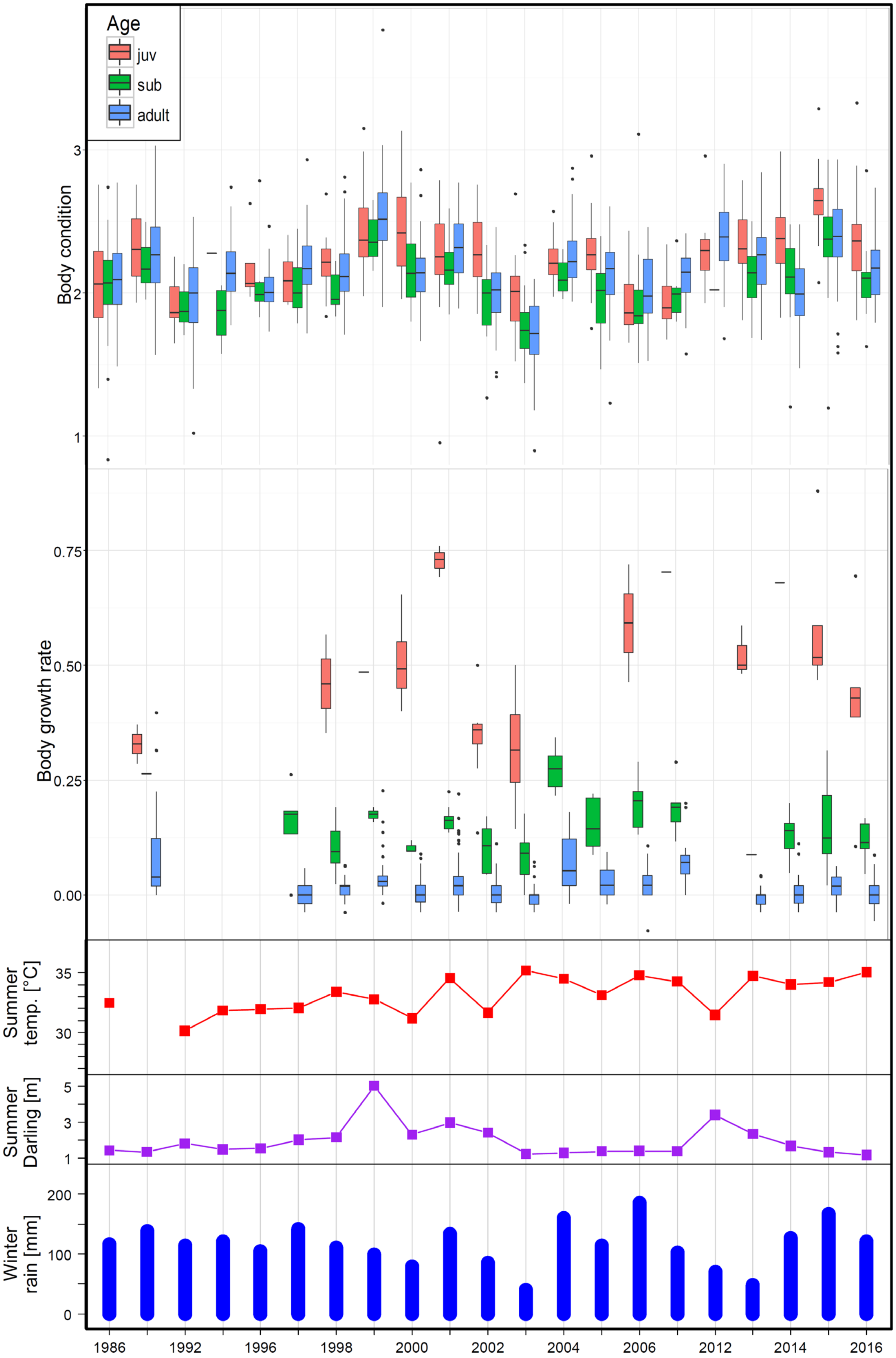


Figure S3.4: Body condition and body growth rates in annual comparison with the most important climatic parameters for three age classes. juv: juveniles; sub: subadults; adult: adults.

Table S3.5: Untransformed estimates, standard errors, scaled estimates (Scale.est) and their standard errors (Scale.SE) of the full model and estimates and standard errors of the best model (Sc.est.b and Sc.SE.b, respectively), significance (p-value), and importance (ωAIC) of ENSO test predictors affecting various response variables. sub.: subadults, ad.: adults. "-" indicates that this predictor was not included in the L(M)M. See Methods for details.

Response		**SOI(summer)**		**SOI(prev.winter)**		**SOI(prev.summer)**	
		linear	**quadratic**	**linear**	**quadratic**	**linear**	**quadratic**
Body condition	**Estimate**	-0.007	0.0004	0.131	-0.0003	-0.006	0.0005
	SE	0.007	0.0005	0.008	0.0007	0.004	0.0005
	Scale.est	-0.066	0.043	0.120	-0.024	-0.050	0.053
	Scale.SE	0.054	0.037	0.050	0.041	0.029	0.028
	Sc.est.b	-	-	0.072	0.016	-0.047	0.038
	Sc.SE.b	-	-	0.048	0.041	0.034	0.026
	p-value	0.14		0.04		0.06	
	Σ(ωAIC)	0.35		0.49		0.62	
Body growth rate	**Estimate**	0.001	0.0004	-0.001	-0.001	-0.002	-0.0002
	SE	0.001	0.0001	0.001	0.0001	0.0004	0.0001
	Scale.est	0.008	0.038	0.009	-0.041	-0.015	-0.019
	Scale.SE	0.007	0.005	0.006	0.006	0.003	0.005
	Sc.est.b	0.008	0.038	0.009	-0.041	-0.015	-0.019
	Sc.SE.b	0.007	0.005	0.006	0.006	0.003	0.005
	p-value	<<0.001		<<0.001		<<0.001	
	Σ(ωAIC)	1.00		1.00		1.00	
Population size sub.+ad. (*t*)	**Estimate**	-0.041	-0.080	-0.317	-0.045	0.066	0.058
	SE	1.150	0.085	1.295	0.117	0.566	0.083
	Scale.est	-3.435	-7.089	-1.181	-3.127	0.730	4.950
	Scale.SE	10.669	7.546	9.615	8.097	5.301	7.100
	Sc.est.b	-	-	-	-	-	-
	Sc.SE.b	-	-	-	-	-	-
	p-value	0.41		0.85		0.59	
	Σ(ωAIC)	0.09		0.04		0.01	
Population size sub. (*t-1*)	**Estimate**	-0.539	0.011	-0.137	-0.067	0.383	0.061
	SE	0.473	0.041	0.045	0.059	0.202	0.020
	Scale.est	-5.129	0.933	1.023	-4.641	3.674	5.257
	Scale.SE	4.509	3.601	4.080	4.078	1.863	1.754
	Sc.est.b	-	-	-	-	0.401	0.016
	Sc.SE.b	-	-	-	-	0.299	0.027
	p-value	0.28		0.27		<0.001	
	Σ(ωAIC)	0.01		0.12		0.87	

Table S3.6: Summary of coefficient estimates, standard errors, significance levels (p-value) and relative importance (ωAIC) of the test predictors for diurnal body temperatures in Gehyra variegata in **2015**. T(hollow): tree hollow temperature. [x;y]: signifies the lowest and highest value obtained for this categorical variable.

Test predictor	Estimate	Standard error	p-value	Σ(ωAIC)
T(hollow)	0.81	0.05	<<0.001	1
Height above ground	-2.03	1.00	0.34	0.32
Branch diameter	-0.09	0.04	0.11	0.51
Exposure	[-2.07; 2.01]	[0.96; 2.99]	0.34	0.04

Table S3.7: Summary of coefficient estimates, standard errors, significance levels (p-value) and relative importance (ωAIC) of the test predictors for diurnal body temperatures in Gehyra variegata in **2016**. T(hollow): tree hollow temperature. [x;y]: signifies the lowest and highest value obtained for this categorical variable.

Test predictor	Estimate	Standard error	p-value	Σ(ωAIC)
T(hollow)	0.68	0.06	<<0.001	1
Height above ground	1.55	0.58	0.02	0.92
Branch diameter	-0.05	0.09	0.05	0.33
Exposure	[-1.80; 5.50]	[0.89; 1.39]	0.002	0.98

References

Aiken, L.S. and S.G. West. 1991. Multiple regression: testing and interpreting interactions. Sage. Newbury Park.

Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. Methods in Ecology and Evolution 1:103-113.

10.2 Appendix to Chapter 4

10.2.1 APPENDIX S1: CLIMATIC PARAMETER SPACE MEASURED IN 2014-2016

Temperature and humidity were measured every three hours from February 2014 to February 2016 using iButton® temperature/humidity loggers (DS1923). Maximum temperature was lowest in the air, followed by temperature on the soil surface in the shadow and temperature on the soil surface in the sun. While this difference was up to more than 30°C in summer, it almost vanished in winter (Figure S1.1, exemplarily for 2015). Minimum temperature was lowest in the air but almost identical between the soil surface temperature in the shadow and in the sun. There was no seasonal difference in this order (Figure S1.2, exemplarily for 2015).

The temperatures measured in the air were between -3.9°C and 48.6°C. Soil surface temperature in the shadow laid between 1.6°C and 63.4°C, while in the sun they rang was 0.12°C to 78.8°C.

Humidity varied between 0.2% and 100% in all locations. Temperature and humidity were strongly correlated across all locations (Pearson correlation test, p<<0.001). The hotter a day was, the less humid it was. Due to this strong correlation we excluded humidity as explanatory variable from all analyses.

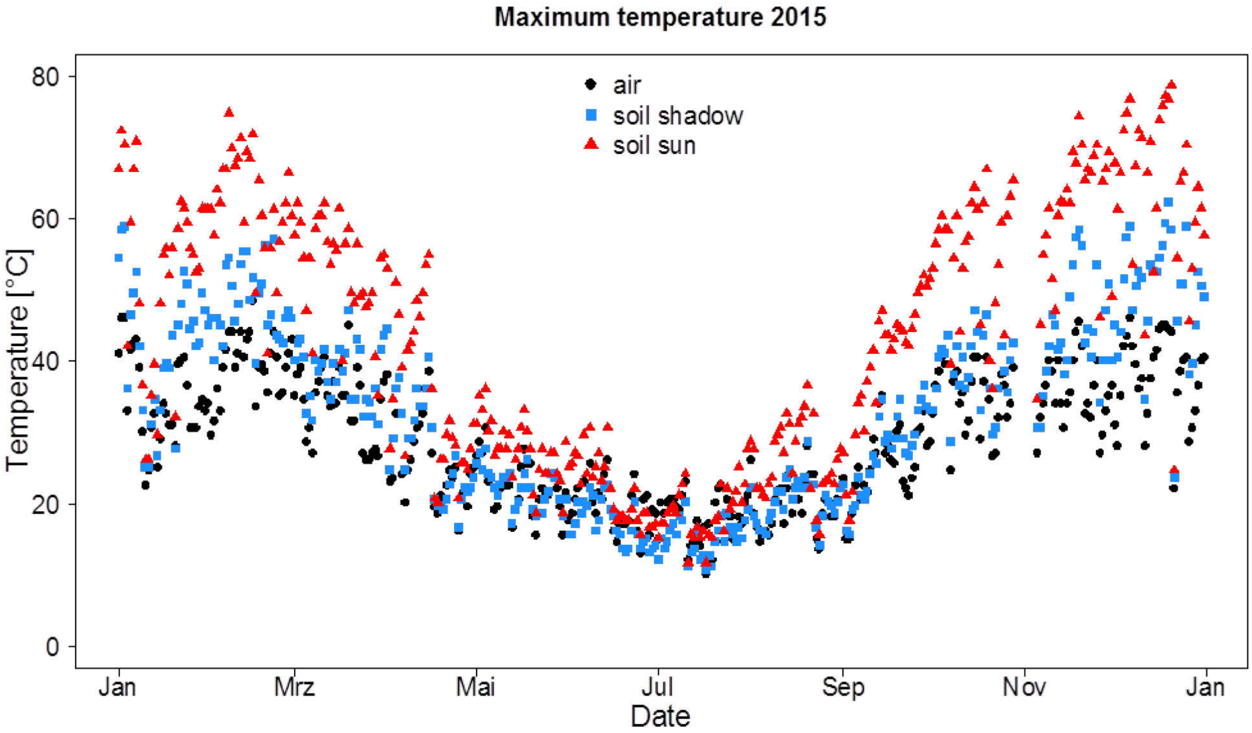


Figure S1.1: Maximum daily temperature measured throughout the year 2015 in the air, on soil surface in the shadow and in the sun.

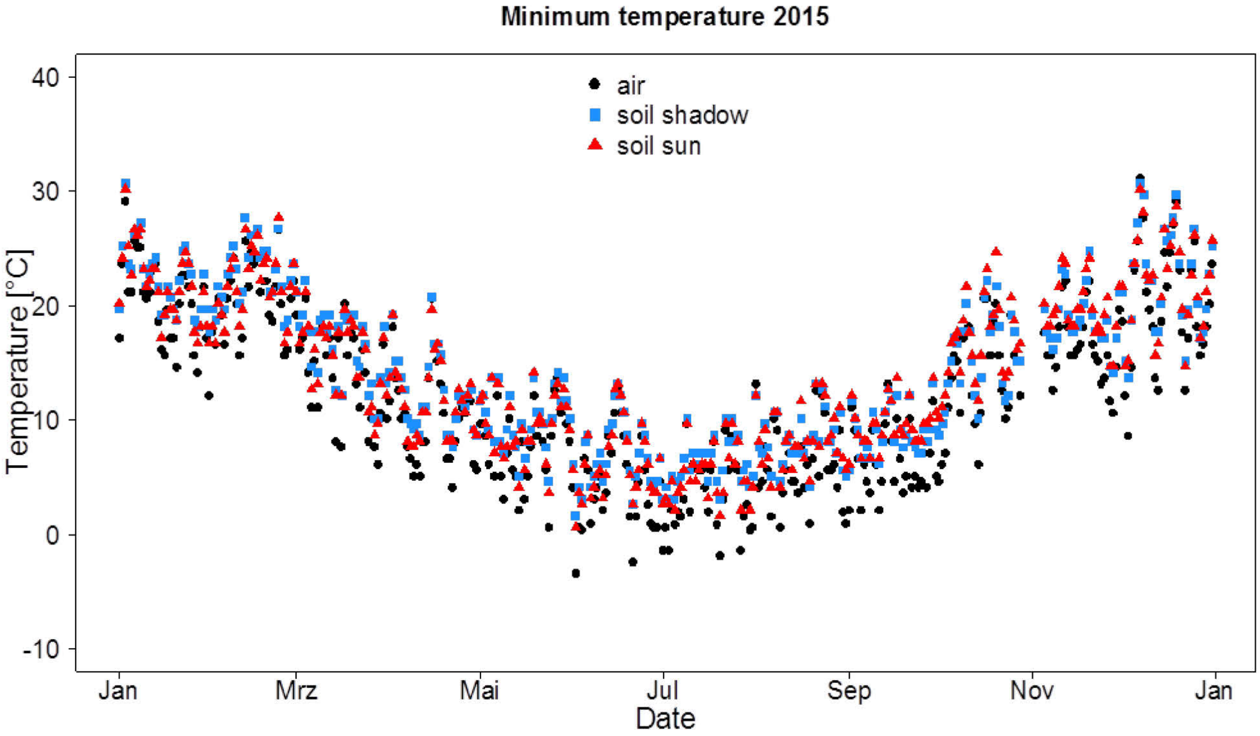


Figure S1.2: Minimum daily temperature measured throughout the year 2015 in the air, on soil surface in the shadow and in the sun.

10.2.2 APPENDIX S2: CALIBRATING HIGH-RESOLUTION EXPERIMENTAL DATA TO LONGER THERMAL TIME-SERIES WITH DIFFERENT TEMPORAL RESOLUTIONS

S2.1: Extrapolation of T_e to environmental measures 2014-2016

In order to extend the species specific T_e measured by copper models in February 2015 and February 2016 to all days for which we only measured environmental temperatures (February 2014-February 2016), we build a linear model (LM) using the measures of February 2015 and validated the model using the measures from February 2016. After successful validation, we projected T_e at any other day and time between February 2014 and February 2016. In doing so, we increased our dataset for which we could determine activity budgets from two month to two years in order to get more robust models for activity budget predictions (see S2.2).

Specifically, $T_{e.sun}$ (T_e in sun) was determined by an LM depending on soil surface temperature in the sun (T_{sun}). At all other locations in the bush gradients, we used T_e as response variable and explained it with the LM

$T_e \sim T_{sun}$*bush.area + T_{sun}*$TAVE_{sun}$*AMP_{sun} + location

with bush.area being the calculated bush area (N-S length · E-W length) where T_e was measured, $TAVE_{sun}$ being the temperature average of that day calculated as $(T_{sun.max}+T_{sun.min})/2$, AMP_{sun} being the temperature amplitude of that day calculated as ($T_{sun.max}$-$T_{sun.min}$)/2, location being the location category where T_e was measured (periphery East, West, South, or centre of the bush), and * symbolising interaction. The interaction T_{sun}*bush.area emerged from the fact that on a cool day the cooling power determined by the bush area was smaller and thus had less impact than on a hot day (see Appendix 1 and results in the main text). The relationship between T_e and T_{sun} further depended on the temperature behaviour throughout the day which is well described through TAVE and AMP (Reicosky et al. 1989). We assumed that the relationship of T_{sun} to TAVE and AMP reflected whether the bush was cooling or saving heat. For *M. boulengeri*, LM additionally contained a binary factor indicating whether the bush could be shaded by a eucalypt or not. We did not include the bush species as this was strongly correlated with bush.area (e.g., *D. attenuata* being larger than *M. pyramidata*).

As our data showed extremely strong temporal autocorrelation, which could not be solved by any autocorrelation term (results not shown), we randomly sampled half of the data to remove autocorrelation resulting in 4,718 data points. We ensured that this sampling procedure result in comparable sample size regarding the amount of data per day (270-321) and per location (923-960). After this sampling procedure, no deviation from any other model assumption could be detected. We performed two model validation steps. First, we checked how accurate the LM could predict T_e measurements in 2015 by checking the overall fit and deviance. For that we plotted the measured T_e in relation to T_{sun} and added the predicted T_e based on the LM separately for each skink species (Figure S2.1.1). We found that the predicted values mimic the variation in the measured values extremely well. Even extreme temperatures were accurately predicted.

Second, we predicted T_e based on the environmental data in February 2016 and checked whether predicted and measured T_e were comparable. For that we plotted predicted against measured T_e (Figure S2.1.2). We found that higher predicted values are in line with higher measured values. However, precision was higher for lower values of T_e. Therefore, we compared the amount of T_e values above the species' CTmax to ensure that we do not underestimate temperature extremes. For *C. regius*, we found that 614 measured and 700 predicted values of T_e were above the CTmax of 45°C. Likewise, for *M. boulengeri* 1345 measured and 1217 predicted values of T_e were above the CTmax of 42°C. As there was little difference between the measured and predicted values of T_e above CTmax, we expect that we cover extreme values well.

Parameter estimates and p-values can be found in Table S.1. We then used this LM to predict T_e according to the environmental temperatures (T_{sun}) in 2014-2016. We predicted T_e at each location along the gradient in the bush assuming three different bush types: no bush (i.e., T_e in sun), small bushes, and large bushes. The size of the bushes emerged from average bush sizes measured in the field (*C. regius*: small = 4 m², large = 20 m²; *M. boulengeri*: small = 3 m², large = 10 m²).

Table S2.1: Parameter estimates and p-values of the LM to predict Te at any location in the bush based on field measurements in 2015. The last line represents the results of the LM Te.sun depending only on Tsun.

Test parameter	***C. regius***		***M. boulengeri***	
	Estimate	**p-value**	**Estimate**	**p-value**
T_{sun}	2.37	<0.001	2.11	<0.001
bush.area	0.47	0.031	1.30	<0.001
T_{sun} * bush.area	-0.01	<0.001	-0.03	<0.001
location	-0.60 – -0.52	<0.001	-1.10 – -0.39	<0.001
shade by Eucalypt	NA	NA	-0.82	<0.001
$TAVE_{sun}$	1.71	<0.001	1.49	<0.001
AMP_{sun}	1.38	<0.001	2.32	0.004
$TAVE_{sun}$ * AMP_{sun}	-0.06	<0.001	-0.07	<0.001
T_{sun} * $TAVE_{sun}$	-0.05	<0.001	-0.04	<0.001
T_{sun} * AMP_{sun}	-0.08	<0.001	-0.09	<0.001
T_{sun} * $TAVE_{sun}$ * AMP_{sun}	0.002	<0.001	0.003	<0.001
T_{sun}	0.83	<0.001	0.90	<0.001

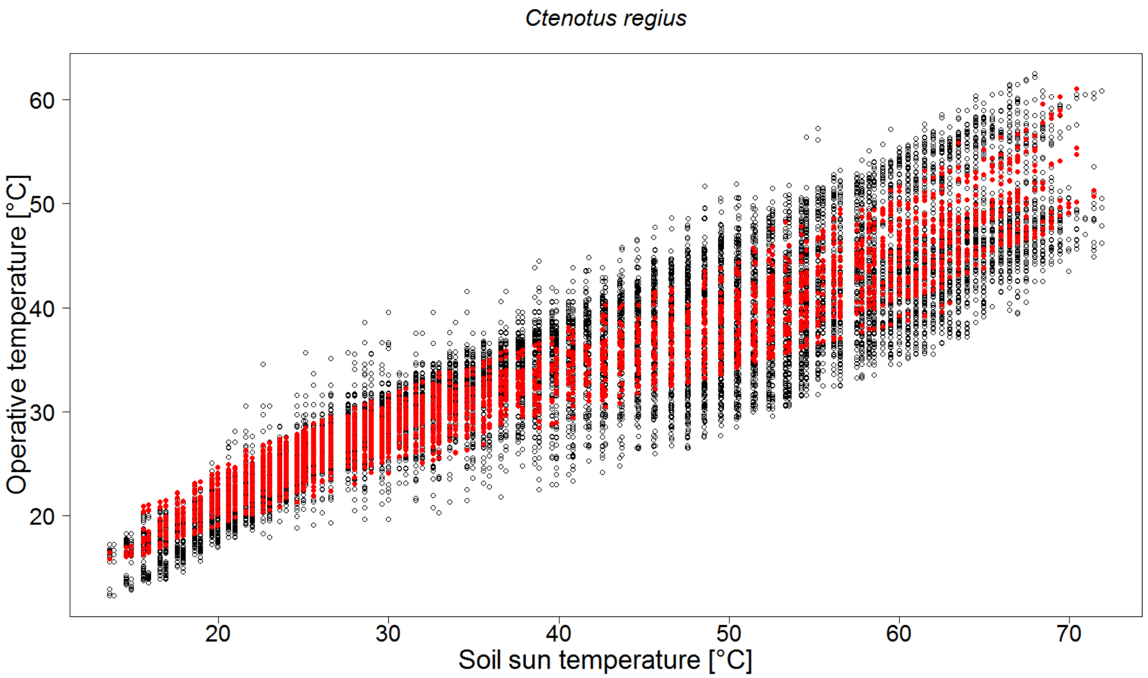


Figure S2.1.1a: Operative temperatures T_e for *Ctenotus regius* in relation to soil surface temperature in the sun. Black dots represent measured values in 2015, red dots represent predicted values for 2015.

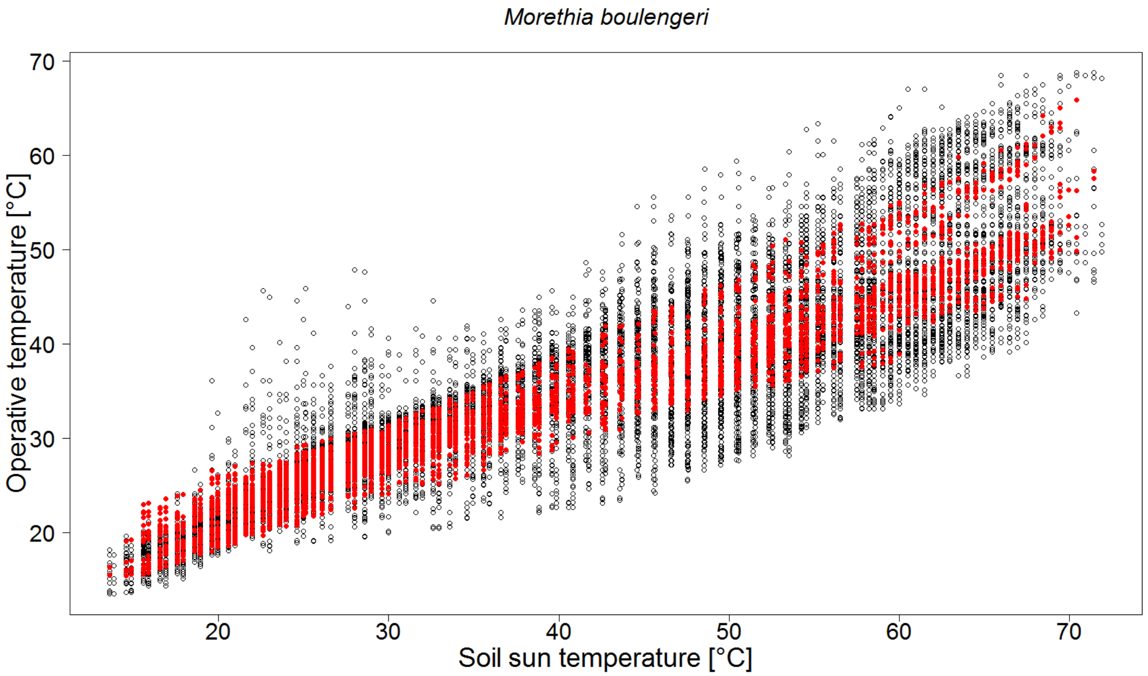


Figure S2.1.1b: Operative temperatures T_e for *Morethia boulengeri* in relation to soil surface temperature in the sun. Black dots represent measured values in 2015, red dots represent predicted values for 2015.

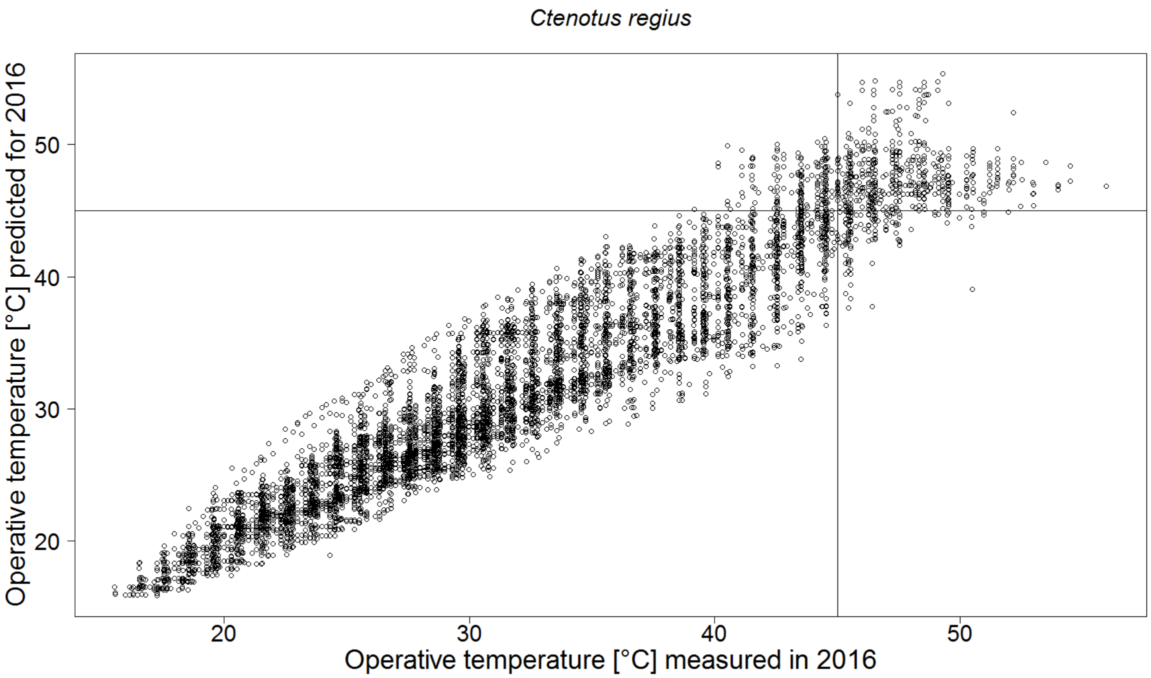


Figure S2.1.2a: Predicted operative temperatures in relation to measured operative temperatures for *Ctenotus regius* in 2016.

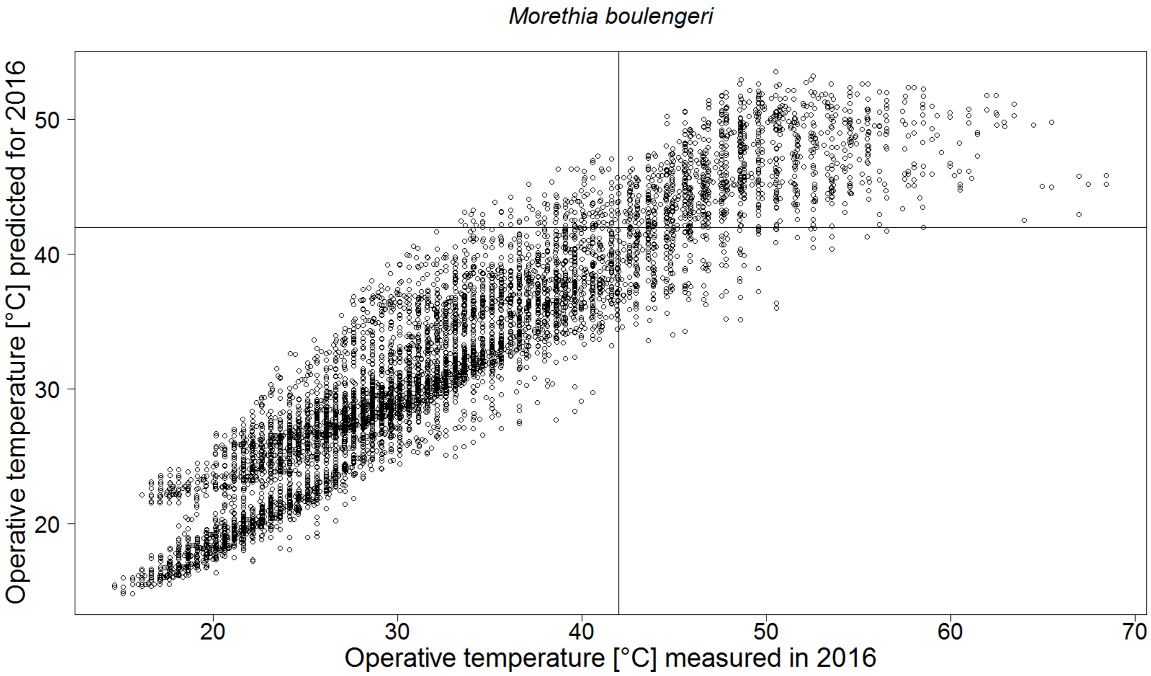


Figure S2.1.2b: Predicted operative temperatures in relation to measured operative temperatures *Morethia boulengeri* in 2016.

S2.2: Temporal extrapolation of relative available activity time (RelAT)

As we were interested in how the relative activity time (RelAT, see main text for calculation and definition) changed from 1985 until now and how it might change until 2050 and 2090, we first had to predict RelAT at any other day that we did not measure. The only environmental temperature available for decades and with at least a maximum and minimum value per day was air temperature (T_{air}) (see Climate data section of the main text). Thus, we constructed an LM with RelAT per day (from February 2014 – February 2016) as response variable in relation to T_{air}. We built separate LMs per species and per bush type (no bush, small, large). We did AIC comparisons of all model combinations with $T_{air.max}$, $T_{air.min}$, $TAVE_{air}$, and AMP_{air} (Table S2.2) and found that the only model that always was among the most parsimonious models with the lowest AIC was

$$RelAT \sim TAVE_{air}{}^{2} * AMP_{air}{}^{2}$$

with TAVE and AMP being the average and the amplitude of air temperature a given day, respectively (Reicosky et al. 1989). These models were significantly different from the respective intercept models ($p < 0.001$) and did not show temporal autocorrelation or any deviation from model assumptions. This relation was then used to predict daily RelAT throughout the last 30 years and towards the future.

While maximum and minimum T_{air} values were available between 1985 and 2016, we had to predict them under climate warming assumptions for 2050 and 2090. We used the worst case IPCC emission scenario RCP 8.5. which predicts +2°C [+1°C; +3°C] for 2050 and +4.5°C [+3°C; +6°C] for 2090 relative to the temperature mean in 1986-2005 for this region (Reisinger et al. 2014). To predict the climate warming on a daily basis in 2050 and 2090, we simulated a set of daily temperature increases by creating a random normal distribution with 365 values per year with a mean ± standard deviation of 2 ± 0.5 and 4.5 ± 1, respectively, as the uncertainty is higher for 2090 (Reisinger et al. 2014). We then added these daily temperature increases to the daily $T_{air.max}$ and $T_{air.min}$ values averaged across 1986-2005. These predictions resulted in a mean $T_{air.max}$ of 30.10°C in 2050 and 32.51°C in 2090. We did not consider a more benign emission scenario because our predictions of $T_{air.max}$ were still below a continuation of the current linear trend in warming in Kinchega which would result in a mean $T_{air.max}$ of 32.42°C and 35.81°C in 2050 and 2090, respectively.

Table S2.2: Model comparisons specific for each species and bush type. "+" indicate the explanatory variables used in an LM, "*" symbolises interaction with the previous parameter. The two models with the lowest AIC values are always highlighted.

Species	bush type	$T_{air.max}$	$T_{air.min}$	$TAVE_{air}^2$	AMP_{air}^2	AIC
C. regius	none	+	+			6128.3
		+	*			6123.1
				+		6216.9
					+	6714.0
		+		+		6128.8
		+		*		6111.5
				+	+	6207.5
				+	*	6112.0
	small	+				6226.4
		+	+			6138.2
		+	*			6109.4
				+		6205.6
					+	6951.2
				+	+	6188.8
				+	*	6133.8
	large	+				6152.0
		+	+			6052.5
		+	*			6000.7
				+		6093.6
					+	7053.0
				+	+	6065.9
				+	*	6030.6
M. boulengeri	none	+				5981.7
		+	+			5927.9
		+	*			5807.8
				+		5958.5
					+	6204.4
				+	+	5885.2
				+	*	5865.5
	small	+				5978.5
		+	+			5903.7
		+	*			5831.1
				+		5875.6
					+	6307.7
				+	+	5846.1
				+	*	5845.9
	large	+				5915.3
		+	+			5859.6
		+	*			5818.6
				+		5839.0
					+	6280.9
				+	+	5825.3
				+	*	5822.1

References

Reicosky, D.C., Winkelman, L.J., Baker, J.M. & Baker, D.G. (1989) Accuracy of hourly air temperatures calculated from daily minima and maxima. Agricultural and Forest Meteorology, 46, 193–209.

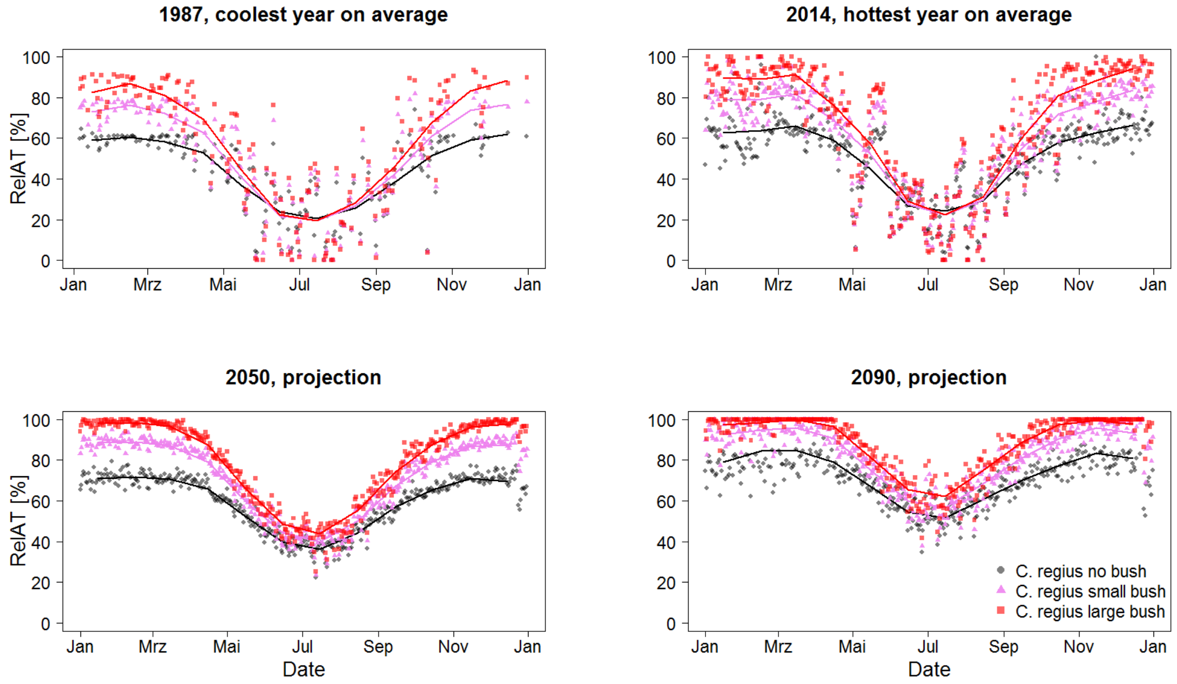
Reisinger, A., Kitching, R.L., F., C., Hughes, L., Newton, P.C.D., Schuster, S.S., Tait, A. & Whetton, P. (2014) Chap 25: Australasia. Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (eds V.R. Barros, C.B. Field, D.J. Dokken, M.D. Mastrandrea, K.J. Mach, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, B. Girma, E.S. Kissel, A.N. Levy, S. MacCracken, P.R. Mastrandrea & L.L. White), pp. 1371–1438. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

10.2.3 APPENDIX S3: ADDITIONAL DATA AND FIGURES OF RELATIVE AVAILABLE ACTIVITY TIME THROUGHOUT THE PAST AND THE FUTURE

Table S3.1: Summary of mean annual air temperatures and averaged relative available activity time (RelAT) separated by species, bush type, and season.

Year	T_{max}	T_{min}	Summer						Winter					
			C. regius			*M. boulengeri*			*C. regius*			*M. boulengeri*		
			none	small	large	none	small	large	none	small	large	none	small	large
1985	26.83	10.41	62.50	76.97	86.32	68.54	85.12	89.75	32.80	34.98	37.43	64.56	67.31	70.85
1986	26.78	9.49	58.61	72.37	81.38	66.21	82.38	87.03	33.30	36.60	39.44	63.44	67.18	70.94
1987	26.13	7.98	57.28	70.55	79.35	66.55	82.31	86.47	31.70	33.93	36.20	62.35	65.30	69.06
1988	28.89	11.46	62.47	77.85	88.02	63.05	81.98	87.02	38.24	42.31	45.73	67.01	71.69	75.15
1989	28.12	11.35	62.90	77.29	86.71	64.61	82.50	87.51	34.49	37.75	40.64	65.13	68.83	72.29
1990	28.06	12.33	63.60	78.78	88.47	63.81	82.29	87.58	34.22	37.50	40.68	66.40	70.04	72.88
1991	28.30	11.81	62.66	76.86	85.97	65.97	83.18	88.06	34.73	38.16	41.21	66.50	70.21	73.53
1992	26.26	11.02	62.87	76.11	84.51	69.60	85.14	89.72	32.04	34.10	36.40	63.85	66.50	69.88
1993	27.33	11.29	63.62	76.80	85.16	69.23	84.95	89.50	36.58	40.00	43.00	65.03	69.11	72.93
1994	28.13	10.12	61.52	76.24	85.81	65.09	82.55	87.73	35.77	37.73	39.87	63.71	66.77	71.41
1995	27.40	11.29	62.64	76.56	85.37	67.35	84.06	88.76	35.01	38.43	41.44	65.20	69.02	72.54
1996	27.06	11.09	62.19	76.39	85.56	67.87	84.44	89.21	34.92	38.15	41.15	66.54	69.95	73.19
1997	28.59	12.26	64.37	79.04	88.03	63.36	81.98	87.44	35.56	38.47	41.40	65.04	68.47	72.12
1998	27.64	11.86	63.52	77.97	87.26	66.76	84.04	88.95	35.47	38.79	41.91	66.33	70.03	73.37
1999	28.46	11.94	64.20	77.98	86.64	65.83	83.20	88.15	39.58	43.68	47.03	66.79	71.62	75.60
2000	27.78	11.76	65.32	79.64	88.67	65.79	83.65	88.74	36.27	39.40	42.26	65.75	69.45	73.10
2001	28.00	11.75	62.05	76.18	85.05	63.19	80.77	86.19	36.74	40.27	43.37	66.09	70.24	73.77
2002	29.34	11.45	62.91	77.70	87.20	64.32	82.46	87.65	41.10	45.58	49.05	65.55	71.19	75.69

Year	T_{max}	T_{min}	Summer						Winter					
			C. regius			*M. boulengeri*			*C. regius*			*M. boulengeri*		
			none	small	large	none	small	large	none	small	large	none	small	large
2003	28.43	10.96	61.16	75.51	84.95	61.50	79.59	85.07	34.94	37.62	40.03	63.04	66.57	70.84
2004	28.91	10.72	61.24	76.55	86.62	62.18	80.76	86.24	36.42	39.37	42.03	63.44	67.65	71.93
2005	29.36	11.50	61.56	76.83	87.06	63.40	81.63	86.86	39.49	44.34	47.98	65.29	71.09	75.12
2006	29.38	11.42	63.51	78.85	88.64	59.52	79.50	85.34	33.73	35.62	37.61	62.53	65.48	69.96
2007	29.28	11.67	64.04	79.28	89.02	62.25	81.48	87.02	37.98	42.10	45.43	63.99	68.92	73.10
2008	28.56	10.88	62.79	77.68	87.39	64.62	82.70	87.91	35.93	38.44	40.69	63.55	67.16	71.61
2009	29.01	12.20	62.01	76.52	86.18	60.21	78.90	84.62	37.97	42.01	45.32	66.37	70.87	74.71
2010	27.03	11.97	63.33	76.76	85.43	67.37	83.87	88.59	33.70	36.39	39.22	65.76	68.89	71.97
2011	27.72	12.39	65.80	78.89	87.11	68.92	85.27	89.77	37.07	41.19	44.57	66.31	70.79	74.34
2012	27.93	11.84	65.03	79.10	87.82	66.58	83.99	88.94	36.24	39.60	42.51	65.16	69.24	72.89
2013	29.29	12.30	63.20	77.93	87.30	61.84	80.57	86.09	40.22	45.36	49.34	67.53	73.22	76.86
2014	29.36	12.33	63.21	78.89	89.03	60.46	80.20	86.01	38.34	42.26	45.53	66.53	70.91	74.67
2015	28.17	11.76	64.71	79.95	89.76	62.29	81.67	87.17	32.12	34.41	36.81	63.75	66.50	70.08
2016	34.22	17.28	65.95	80.85	90.35	58.87	79.08	85.08	59.42	71.02	78.78	73.39	86.34	90.12
2050	30.10	15.28	70.00	86.36	95.84	63.18	84.11	90.06	49.18	56.74	62.55	74.72	81.83	84.69
2090	32.51	20.19	81.68	93.82	98.37	52.42	76.80	83.68	63.81	71.91	78.19	80.99	90.45	92.65


1987, coolest year on average

2014, hottest year on average

2050, projection

2090, projection

Figure S3.1: Relative available activity time (RelAT) in comparison between the coolest (1987) and hottest (2014) year in the past and the projected years in 2050 and 2090 for *C. regius*. Symbols represent daily RelAT, lines are connections between monthly mean values.

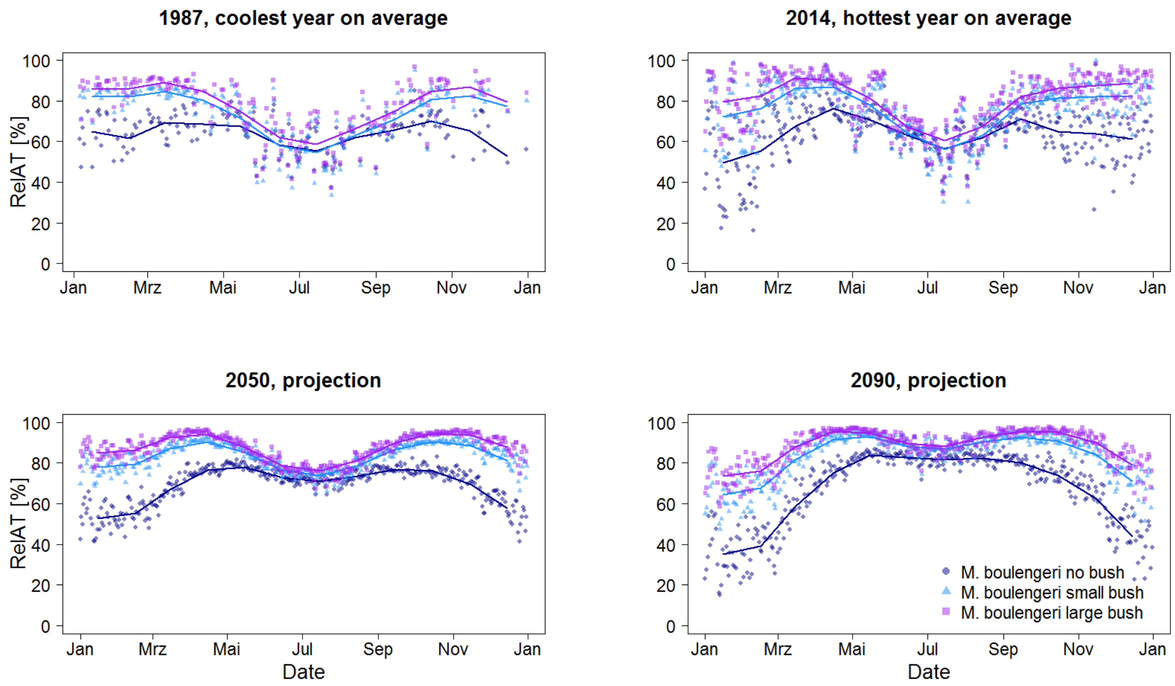


Figure S3.2: Relative available activity time (RelAT) in comparison between the coolest (1987) and hottest (2014) year in the past and the projected years in 2050 and 2090 for *M. boulengeri*. Symbols represent daily RelAT, lines are connections between monthly mean values.

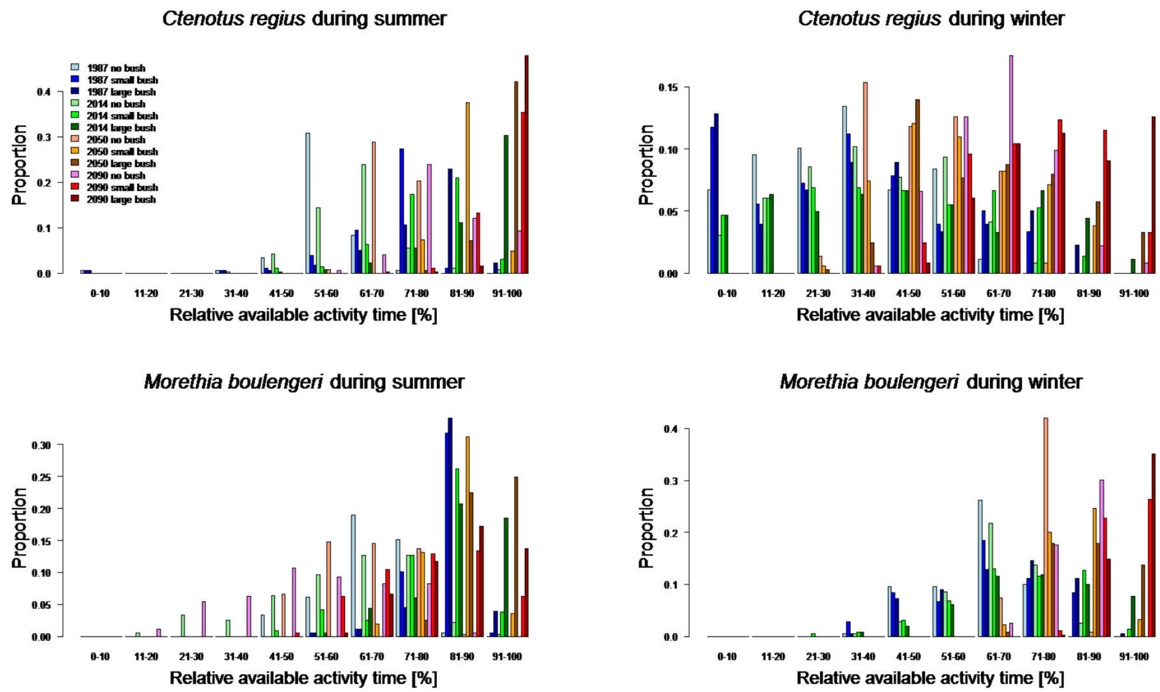


Figure S3.3: Proportion per season spent in relative available activity time (RelAT) categories for *C. regius* (upper) and *M. boulengeri* (lower) in comparison between the coolest (1987) and hottest (2014) year in the past and the projected years in 2050 and 2090.

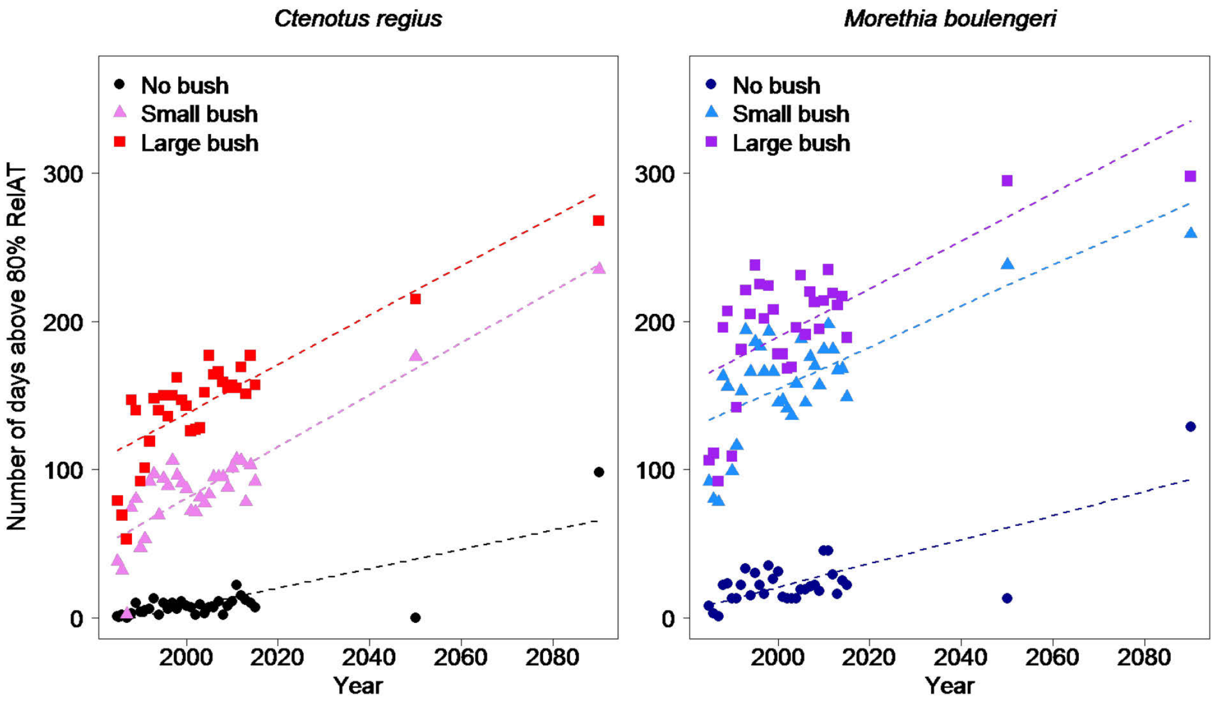


Figure S3.4: Total number of days above 80% relative available activity time (RelAT) per year for *C. regius* (left) and *M. boulengeri* (right). Symbols represent true values, dashed lines represent lines of best fit.

10.3 Appendix to Chapter 5

10.3.1 APPENDIX S1: OVERVIEW ON UNDERLYING FIELD AND ANALYTICAL METHODS OF THE CONCEPTUAL FRAMEWORK

S1.1 Capture methods of the lizard species

Each lizard species was caught during its active time of the day. Capture methods were adapted to the species known to occur in each study plot and therefore differed between them. We caught nocturnal geckos and *Eremiascincus richardsonii* by spotlighting for at least five days per plot per season (9.8 and 6.8 days on average at RWI and station, respectively). In the RWII plot, we buried 24 11l-icecream-containers as pitfall traps. Traps were checked at least once daily over at least ten days (20 days on average) and were removed between capture seasons. Additionally, *Morethia boulengeri* was caught by hand in the RWII plot by transect searching across at least five days (10 days on average). Every individual caught was measured, weighted, sexed and aged (if possible), photographed for long-term identification, and marked with a dorsal colour mark for short-term identification. Additionally, *M. boulengeri* and *Gehyra variegata* were individually marked through toe-clipping which had no negative effect on either species (Hoehn et al. 2015). To obtain the species specific CTmax (critical thermal maximum, i.e., when righting reflexes cease), we either used literature values or maximum extrapolated field body temperature (Tb) (Table S1.1).

Table S1.1: Sources for CTmax (critical thermal maximum, i.e., when righting reflexes cease) values or maximum extrapolated field body temperature (Tb) used in Table 1 of the main text and in analyses of functional traits. Species: the eight target species; Reference: the source of the CTmax values; Measured species: the species measured in the source, which differ from the target species if no data were available for the latter; CTmax: values measured in the source; CTmax used: values used in this study, usually identical to CTmax except for *D. tessellatus*, which is an average of *D. conspicillatus, D. vittatus*, and *D. steindachneri*, and *M. boulengeri*, which is an average of the two values from the source populations. For both *Lerista* species, we used values from conspecific species of similar size.

Species	Reference	Measured species	CTmax	CTmax used
Gehyra variegata	Grimm-Seyfarth et al. 2017a	*G. variegata*	45.6 (Tb)	45.6
Heteronotia binoei	Spellerberg 1972	*H. binoei*	40.6	40.6
Diplodactylus tessellatus	Greer 1989	*D. conspicillatus* *D. vittatus* *D. steindachneri*	43.8 43.4 43.5	43.5
Eremiascincus richardsonii	Bennett and John-Alder 1986	*E. richardsonii*	42.0	42.0
Ctenotus regius	Bennett and John-Alder 1986	*C. regius*	45.1	45.1
Lerista punctatovittata	Greer 1989	*L. neander*	43.1	43.1
Lerista xanthura	Greer 1989	*L. orientalis*	40.9	40.9
Morethia boulengeri	Henle 1989a,b	*M. boulengeri*	41.3 (Tb); 42 (Tb)	41.6

S1.2 Calculating body condition and occupancy

Body condition (Fig. S1.2.1) was calculated for each captured individual using the scaled mass index (SMI) which accounts for individual growth (Peig and Green 2009; Table S2.1.1). First, we calculated the SMI calibration curve between mass and snout-vent-length by means of major axis regressions (Legendre 2014) from the measurements of a subset of individuals that had a complete tail (original or regenerated, with complete tail being defined as at least as long as the average relation of the tail length divided by snout-vent-length). Then, we obtained the SMI for all individuals by fitting the individual measurements to the calibration curve (Peig and Green 2009).

We conducted multi-season occupancy modelling (MacKenzie et al. 2006) by means of the *colext* function of the R-package *unmarked* (Fiske and Chandler 2011). To account for false-negative detections in years when monitoring was conducted only for a short time and no individual of a certain species was observed (Wintle et al. 2012), we created a species-specific capture history across all 30 years representing whether the species was observed on a specific day at a specific site, not observed, or no monitoring took place. We assumed year-dependent colonisation, extinction, and detection and considered the years from 1986 to 2016 as yearly site covariates. We performed 1000 non-parametric bootstraps to obtain smoothed annual occupancy rates (ψ), standard errors and confidence intervals for each species (Fig. S1.2.2).

Figure S1.2.1: Annual body condition per lizard species, measured as scaled mass index (SMI). Points represent annual averages and bars represent the minimal and maximal value per species per year.

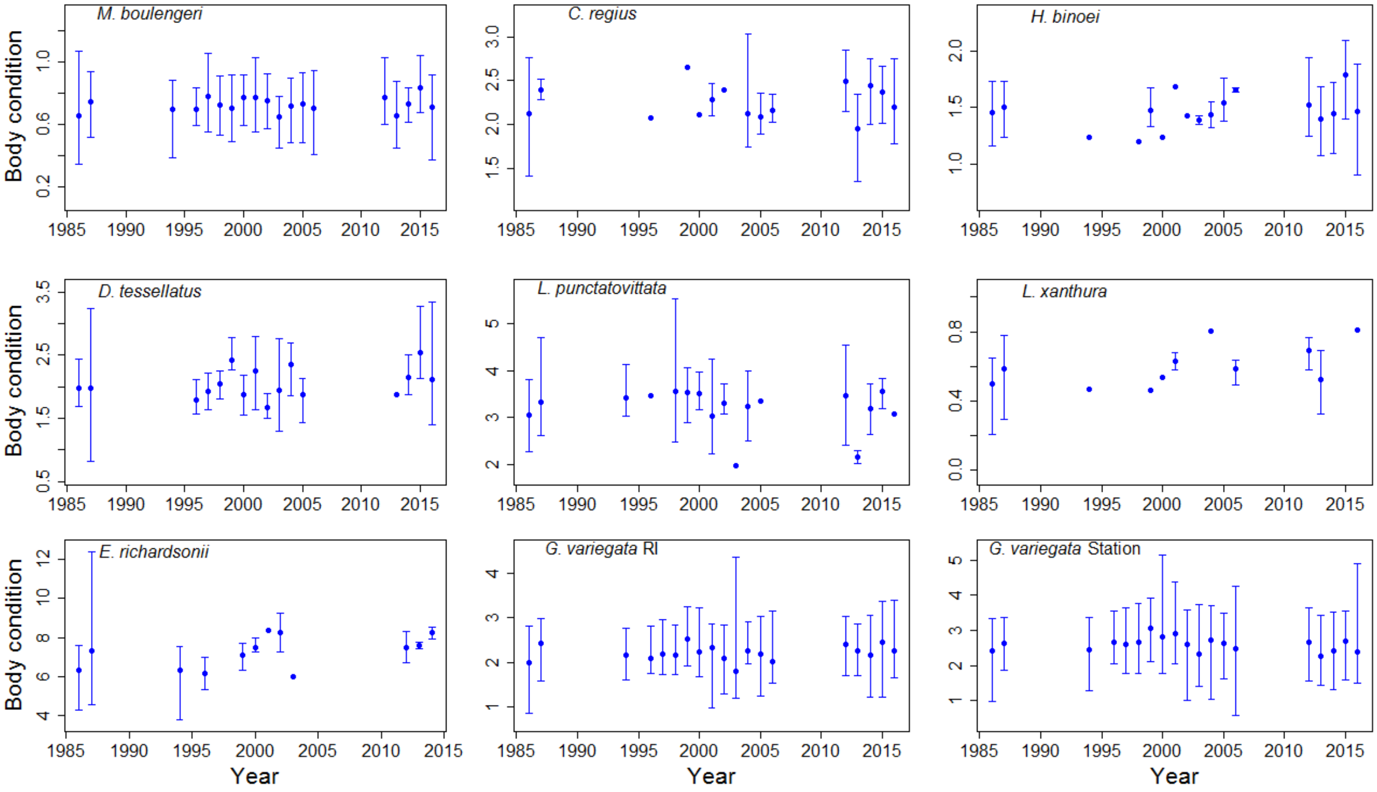
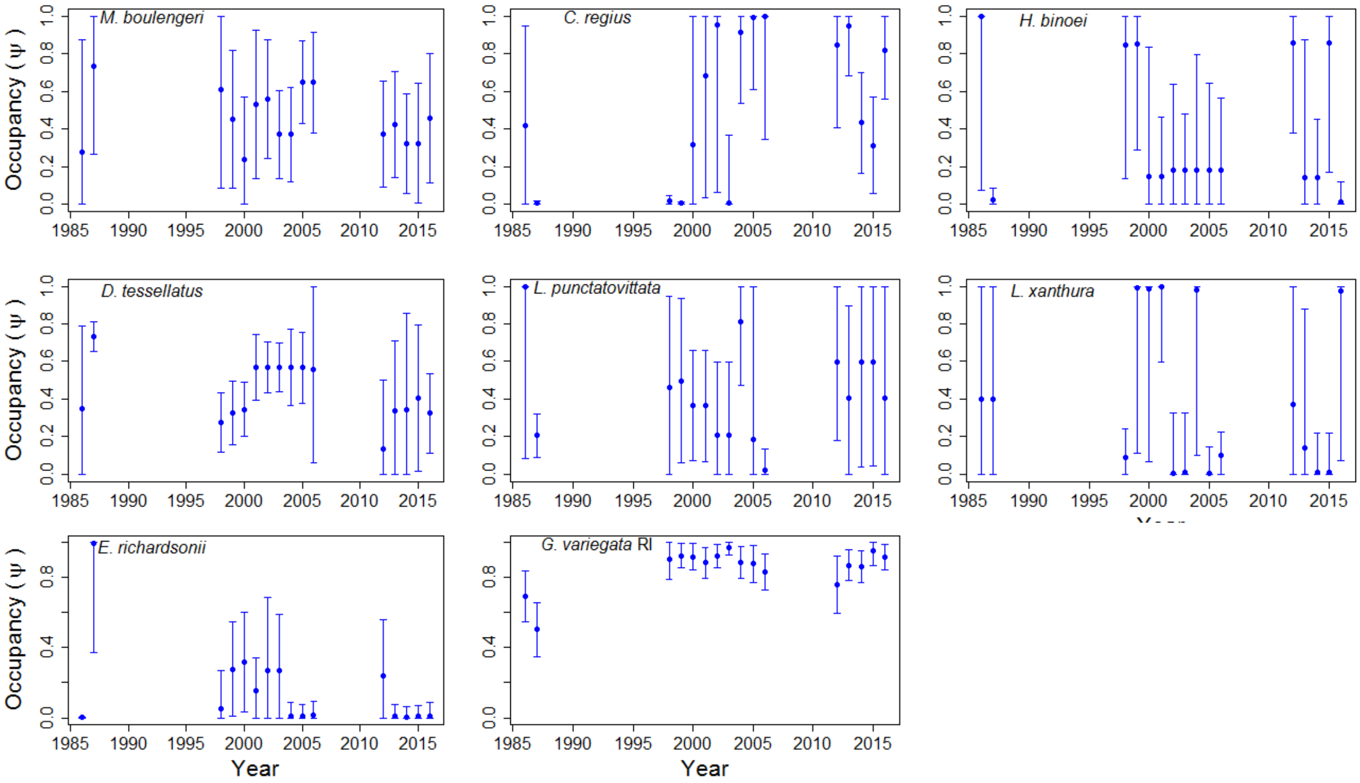


Figure S1.2.2: Annual occupancy per lizard species. Points represent annual estimated smoothed occupancy values and bars represent the estimated confidence interval by means of non-parametric bootstrapping.



S1.3 The conceptual framework

Based on previous studies and our own expertise, we developed a conceptual network between the climatic (temperature, precipitation, flooding) and biotic factor groups (vegetation, prey, predation) that could potentially influence the eight focal lizard species at either individual or population level (main text Fig. 1, Table 2). Within this conceptual workflow, we assumed that (1) each climatic factor could potentially affect vegetation (Robertson 1987, 1988, Robertson et al. 1987), arthropods (Denlinger 1980, Kwok et al. 2016) and small mammals (marsupials and rodents) (Letnic et al. 2004, Greenville et al. 2012) as either prey or predators, predatory birds (Cook 1997), and reptiles at all trophic levels (prey, predators, focal lizards) (Barrows 2011, Read et al. 2012, Grimm-Seyfarth et al. 2017a); (2) vegetation could affect all animal species through either shelter or food availability (Read 1995, Masters et al. 1998, Filazzola et al. 2017, Grimm-Seyfarth et al. 2017b); (3) various vegetation features (e.g., herb-layer biomass, shrub/vegetation coverage, eucalypt foliage) could interact with each other through facilitation and inference (Knoop and Walker 1985, Scholes and Archer 1997, Maestre et al. 2003); and (4) prey and predators could affect focal lizard species directly (Ballinger 1977, Cooper and Peréz-Mellado 2004, Amo et al. 2007). We did not include competition among our focal lizard species since no two species of similar activity, habitat, or size occurred together in a plot (main text Table 1) making competition unlikely (Pianka 1986). A list of observed potential predator species and body condition, occupancy and biotic factors across time are shown hereafter.

Table S1.3: List of observed potential predator species. [1] main study plot (only a few individuals in the other plots). * not recorded but present; goannas, snakes, cats, foxes, and birds were assigned to all study plots due to their high mobility.

Group	Latin name	English name	Station	RWI	RWII	Activity
Arthropods	*Aranae*	unidentified large spider	yes	yes	yes	diurnal
	Chilopoda	Centipedes	yes	yes	yes	nocturnal
	Isopoda immanis	Huntsman spider	yes	yes[1]	yes	nocturnal
	Latrodectus hasseltii	Redback spider	yes	yes	no	cathemeral
	Lycosidae	Wolf spiders	no*	no*	yes	nocturnal
	Mantodea	Mantis	yes[1]	yes	yes	nocturnal
	Urodachnus sp.	Scorpions	yes	yes	yes[1]	nocturnal
Reptiles	*Ctenotus regius*	Royal ctenotus	yes	yes	yes[1]	diurnal
	Eremiascincus richardsonii	Sandswimmer	yes	no	yes	nocturnal
	Furina diadema	Red-naped snake	yes	yes	yes	nocturnal
	Morelia spilota	Carpet python	yes	yes	yes	cathemeral
	Pseudonaja textilis	Brown snake	yes	yes	yes	cathemeral
	Suta suta	Curl snake	yes	yes	yes	nocturnal
	Varanus gouldii	Sand goanna	yes	yes	yes	diurnal
	Varanus varius	Lace monitor	yes	yes	yes	diurnal
Birds	*Accipiter sp.*	Hawk	yes	yes	yes	diurnal
	Aegotheles cristatus	Australian owlet-nightjar	yes	yes	yes	nocturnal
	Aquila audax	Wedge-tailed eagle	yes	yes	yes	diurnal
	Corcorax melanorhamphos	White-winged chough	yes	yes	yes	diurnal
	Corvus coronoides	Australian raven	yes	yes	yes	diurnal
	Corvus mellori	Little raven	yes	yes	yes	diurnal
	Cracticus nigrogularis	Pied butcherbird	yes	yes	yes	diurnal
	Cracticus torquatus	Grey butcherbird	yes	yes	yes	diurnal
	Dacelo gigas	Kookaburra	yes	yes	yes	diurnal
	Elanus sp.	Kite	yes	yes	yes	diurnal
	Eurostopodus argus	Spotted nightjar	yes	yes	yes	nocturnal
	Falco berigora	Brown falcon	yes	yes	yes	diurnal
	Grallina cyanoleuca	Magpie lark	yes	yes	yes	diurnal
	Gymnorhina tibicen	Australian magpie	yes	yes	yes	diurnal
	Halcyon sancta	Sacred kingfisher	yes	yes	yes	diurnal
	Haliastur sphenurus	Whistling kite	yes	yes	yes	diurnal
	Hieraaetus morphnoides	Little eagle	yes	yes	yes	diurnal
	Milvus migrans	Black kite	yes	yes	yes	diurnal
	Ninox boobook	Boobook	yes	yes	yes	nocturnal
	Petroica goodenovii	Red-capped robin	yes	yes	yes	diurnal
	Podargus strigoides	Tawny frogmouth	yes	yes	yes	nocturnal
	Struthidea cinerea	Apostlebird	yes	yes	yes	diurnal
	Tyto alba	Barn owl	yes	yes	yes	nocturnal

Group	Latin name	English name	Station	RWI	RWII	Activity
Marsupials	*Planigale gilesi*	Giles' planigale	no	yes	yes	nocturnal
	Planigale tenuirostris	Narrow-nosed planigale	no	no	yes	nocturnal
	Sminthopsis crassicauda	Fat-tailed dunnart	no	yes	no	nocturnal
Placentals	*Felis cato*	Cat	yes	yes	yes	cathemeral
	Mus musculus	House mouse	yes	no	no	cathemeral
	Vulpes vulpes	Fox	yes	yes	yes	cathemeral

Figure S1.3.1: Scaled vegetation measurements across time.

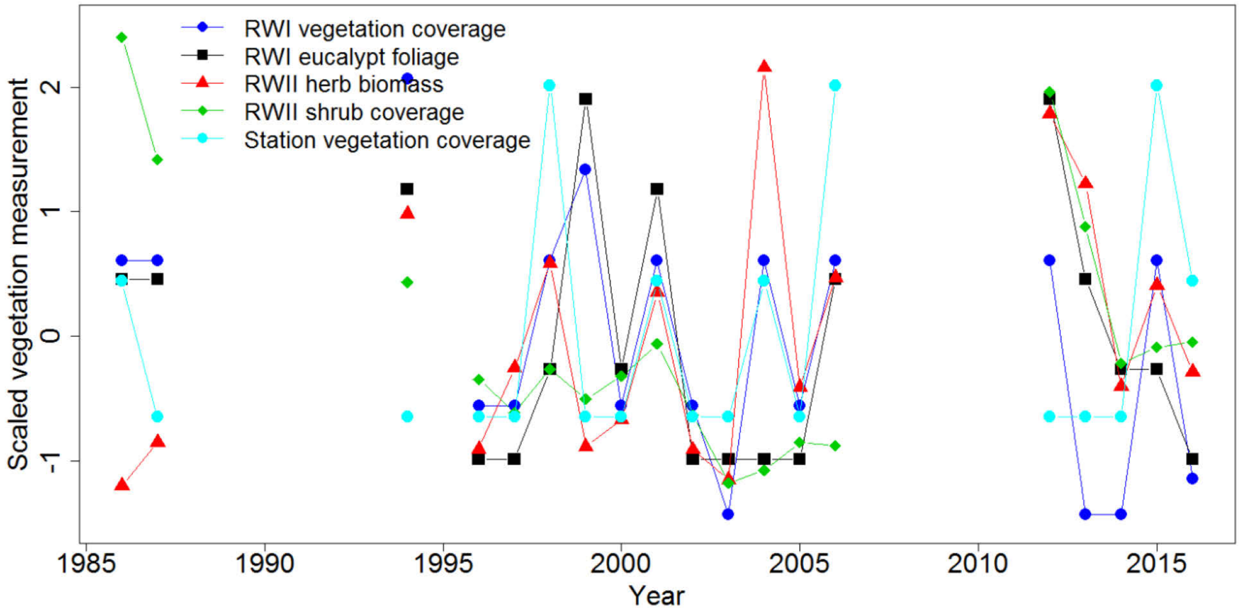


Figure S1.3.2: Insect abundance and the prey index for small vertebrates across time.

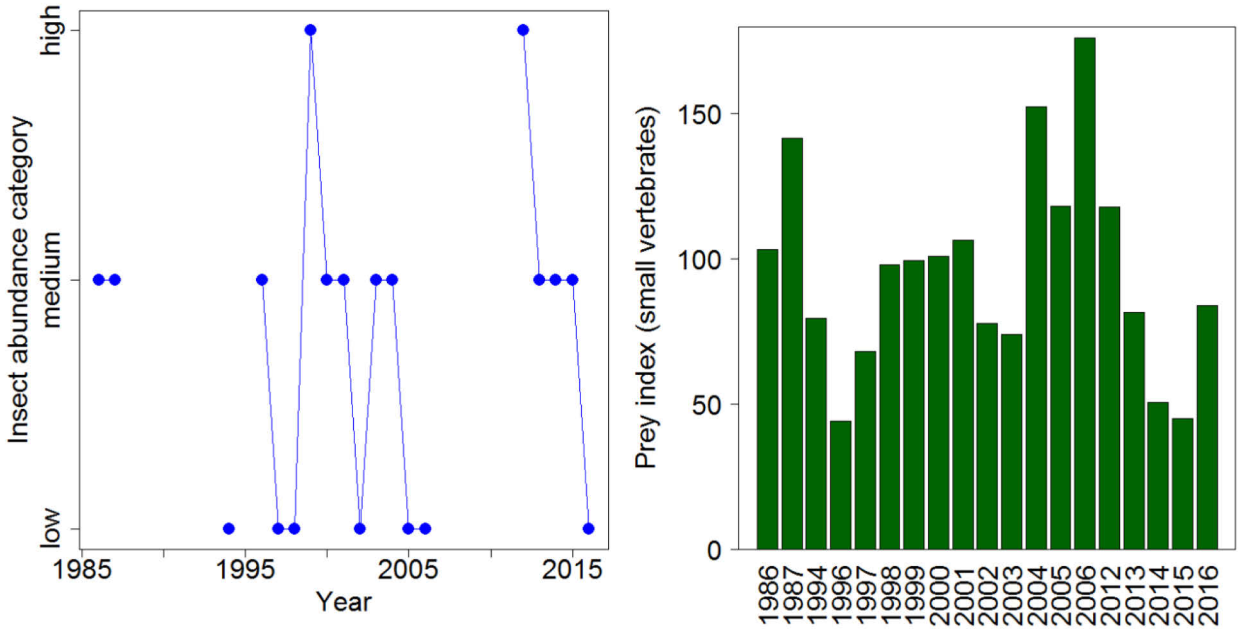
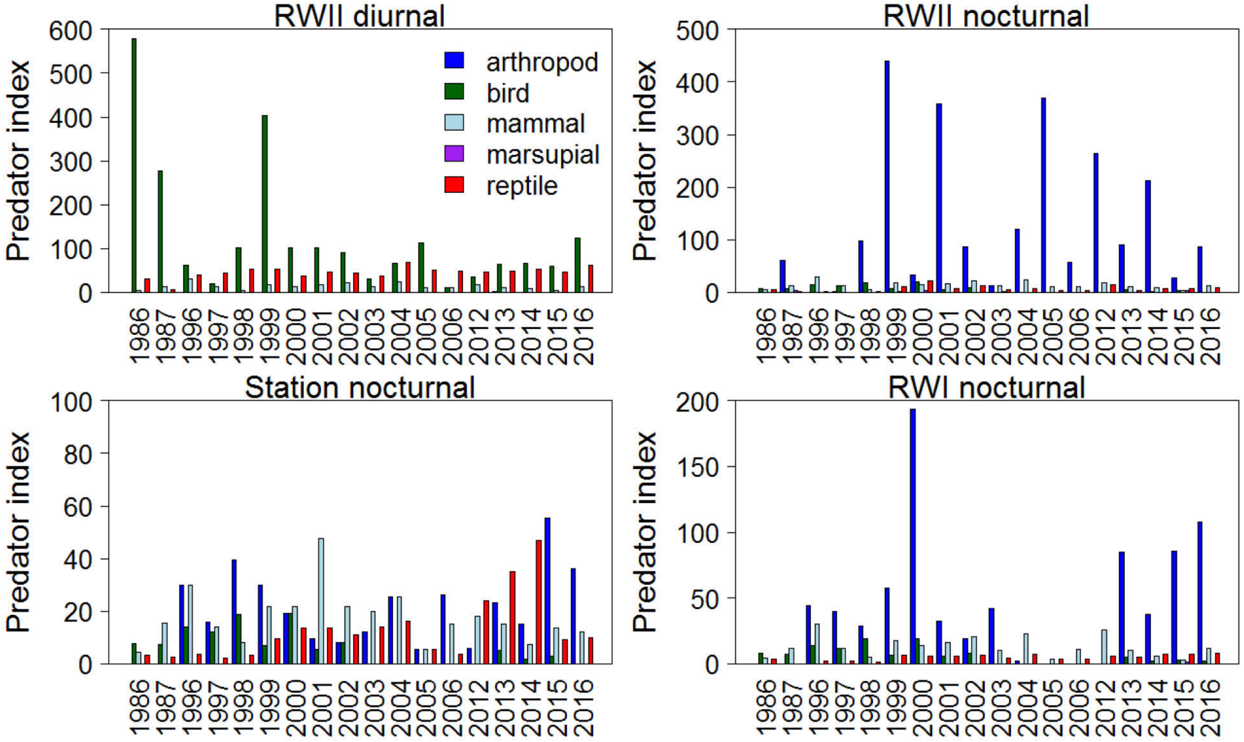


Figure S1.3.3: Predator index separated by taxonomic group across time per activity and study plot. Please note that we used additional predator indices in our analyses (Tables 1 and 2 of the main text) that are combinations of the four main groups displayed in this graph.



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10.3.2 APPENDIX S2: STRUCTURAL EQUATION MODELLING: PRE-ANALYSES AND PATHS SELECTION

S2.1 GLMM pre-analyses

We built five different generalized linear mixed models (GLMMs) (McCullagh and Nelder 1989, Baayen 2008, Bolker et al. 2009) within each structural equation model (SEM) based on our conceptual network (Fig. 1 of the main text): (1) and (2) responses of two specific vegetation measures per plot (i.e., herb-layer biomass, shrub coverage, vegetation coverage, or eucalypt foliage; Table 2); (3) the species-specific prey index; and (4) the species-specific predator index to climatic factors; and (5) species-specific body condition or occupancy in response to climatic and biotic factors (and in relation to station usage in all analyses at the station). We used a Gaussian error distribution except for the ranked insect class as prey index where we used a Poisson error distribution. If body condition was the response variable, we additionally controlled for the quotient tail length divided by snout-vent-length (to account for energy channeled into tail regeneration), a categorical variable combining age and sex (juveniles, subadults, adult females or adult males), and random intercepts of the individual's ID (if individuals were measured several times in different years), the plot (if individuals were frequently caught in different study plots), and the year to account for pseudoreplications within individuals, study plots and years. If occupancy was the response variable, we controlled for the standard error of the smoothed occupancy rate. All test and control factors and their measurements and calculations are described in Table S2.1.1.

10 Supporting Information

Table S2.1.1: Summary of all factors included in SEMs and GLMMs, the factor group (following Fig. 1 of the main text), their abbreviation and calculation. See method descriptions of the main text for study plot descriptions and Table 1 of the main text for an overview on which species belonged to which study plot.

Factor group	Abbreviation	Factor	Calculation
Temperature	summer_temperature	summer temperature	mean maximum temperature from the first month when all species were fully active during each day or night (November, Henle 1989a-c, 1990a,b) to the month of capture (February/March)
	RWI_da45	number of days > 45°C in RWI	the number of days with a corrected daily maximum temperature for RWI ≥ 45°C (Grimm-Seyfarth et al. 2017a)
	RWII_da45	number of days > 45°C in RWII	the number of days with a corrected daily maximum temperature for RWII ≥ 45°C (Grimm-Seyfarth et al. 2017b)
Precipitation	summer_rain	summer rain	summed monthly precipitation from the first month when all species were fully active during each day or night (November, Henle 1989a-c, 1990a,b) to the month of capture (February/March)
	prev.winter_rain	previous winter rain	summed rainfall of the precipitation during the hibernation period for most species from previous April to October
Flood	summer_Darling	summer Darling River height	monthly mean Darling River height averaged across all summer month (October to March)
	prev.Winter_Darling	winter Darling River height	monthly mean Darling River height averaged across all previous winter month (April to September)
	years.post.flood	number of years post flood	counted number of years since the study area was flooded last time; 0 for a year with flooding
Vegetation	ln(herb.biomass)	herb-layer biomass in the RWII	measured total herb layer biomass using the dry-weight rank method (Mannetje and Haydock 1963) of the RWII standardised to kg/ha; ln-transformed for some analyses
	veg.coverage.RWI	vegetation coverage in the RWI	estimated coverage of non-tree vegetation of the RWI in %: <5; 5-10; 10-25; 25-50; 50-75; 75-100; estimations were standardised among persons; additional standardised pictures were taken for later confirmations and comparisons among years
	shrub.coverage.RWII	shrub coverage in the RWII	estimated coverage of all shrubs and bushes of the RWII in %: <5; 5-10; 10-25; 25-50; 50-75; 75-100; estimations were standardised among persons; additional standardised pictures were taken for later confirmations and comparisons among years
	veg.coverage.Station	vegetation coverage at the station	estimated coverage of non-tree vegetation at the station in %: <5; 5-10; 10-50; 50-75; 75-100; estimations were standardised among persons; additional standardised pictures were taken for later confirmations and comparisons among years
	eucalypt.foliage.RWI	eucalypt foliage in the RWI	estimated intensity of black box eucalypt foliage between -2 and 2 with 0 being average, -2: very little, -1: rather little, +1: rather dense, +2: very dense; estimations were standardised among persons; additional standardised pictures were taken for later confirmations and comparisons among years

Factor group	Abbreviation	Factor	Calculation
Station usage	station_usage	station usage intensity	usage category of Kinchega station (mimicking light intensity): 0: no longer stay of people; 1: few longer stays (few nights); 2: occasionally longer stays (several times few nights); 3: long-term stay (more than one month) of at least one person
Prey	prey.index	prey index	either abundance of flying and ground dwelling potential prey arthropods in three categories (1: few amount observed during capture; 2: medium amount; 3: high amount) (as insect.index in GLMMs), or, for *E. richardsonii*, calculated small-vertebrate index as number of observed small vertebrates (lizards and planigales) per day across 30 days (as prey.index.ER in GLMMs)
Predation	predator.index	predator index	number of observed potential predators (Table S1.1) per day across 30 days; separated per lizard species (Table 1 of the main text); observed and caught predatory arthropods, lizards, marsupial mice, and house mice (*Mus musculus*) were assigned to the study plot where they were observed, while each observed individual of goannas, snakes, cats, foxes, and birds were assigned to all study plots due to their high mobility (Table S1.1); here this general abbreviation comprised all predators.diurnal and predators.nocturnal of the GLMMs
Individual response	SMI	body condition (scaled mass index)	scaled mass index (SMI) (Peig and Green 2009, 2010); within each species, individuals that had a complete tail (original or regenerated, with complete tail being defined as at least as long as the average relation of the tail length divided by snout-vent-length) were used for calibration; SMIs for all individuals were obtained by fitting the individual measurements to the calibration curve (S1.2)
	TL.SVL	control factor: relation between tail and snout-vent-lengths	the quotient tail length divided by snout-vent-length of every individual
	Age2	control factor: age-sex-combination	combined category of sex and age per individual: juveniles, subadults, adult females or adult males (if sex-determination was possible, otherwise adults)
Population response	psi.smoothed	ψ as occupancy	estimated smoothed annual occupancy (see Weir et al. (2009) for a description) per species per study plot
	psi.SE	control factor: standard error of ψ	estimated standard errors of the smoothed annual occupancy per species per study plot

To reduce the number of paths in the subsequent structural equation models (SEMs), we performed a pre-selection of the direct relations of climatic factors on each biotic factors (prey, predators, vegetation) as well as on lizard variables at both individual and population level by applying GLMMs using the R-package lme4 (Bates et al. 2015). After visual inspection of 1:1 correlations to examine whether the relations where true linear relations, we ln-transformed the herb-layer biomass measured at the RWII in relations to body condition. Despite slight indications that shrub coverage at the RWII was in quadratic relations to body condition, we kept it linear since SEMs currently do not allow polynomial effects. Additionally, we z-transformed all explanatory parameters to a mean of zero and a standard deviation of one for comparability among predictors. Since predictors on different hierarchical levels that interact with each other cannot be compared by means of single GLMMs, we concentrated on selecting the appropriate climatic factors that likely influence the prey index, predator index, vegetation measurements, and body condition or occupancy.

We performed whole model selections of all potential model combinations using AIC (Burnham and Anderson 2002). Results of the best models (ΔAIC < 2) are shown in the subsequent tables. For each response parameters, we present two model selection tables, one including interactions in the model selection (Table S2.1.2) and one without interactions (Table S2.1.3). This is due to the fact that for some species we did not catch enough individuals per year to include interactions in all subsequent analyses (Table S2.2.1).

For analyses of body condition per species, we used the climatic and biotic factors of the study plot where the species occurred. If the species occurred in more than one study plot, we used the data from the main plot where the species was most abundant and the study plot as control variable except for G. variegata, which was overly abundant in both RWI and the station and therefore body condition was analysed separately per habitat (Table 1 of the main text). For occupancy analyses, we only used observations from RWI and RWII. The spatial unit “site” for calculating occupancy was adjusted to the sampling design of each plot. For occupancy of G. variegata in RWI, we used each of the 60 trees as single site. For D. tessellatus in RWI, we divided the soil surface area in 56 sites of 25x20 m each. For all remaining species in RWII, we used the 24 traps as separate sites.

All statistical analyses were performed in R 3.1.1 (R Core Team 2016).

Table S2.1.2: GLMM selections of biotic factors as response parameters including all possible interactions (summer temperature and all water parameters, i.e. summer and winter rainfall and Darling River height) in the model selection procedure. For clarity reasons, we only show the best models with a ΔAIC < 2. K represents the number of parameters; ":" symbolizes interactions.

Study plot	Response	Models	K	AIC	ΔAIC
all	insect.index	1	1	52.59	0.00
		1+z.summer_Darling	2	53.35	0.75
		1+z.years.post.flood	2	53.44	0.84
		1+z.prev.winter_rain	2	54.16	1.57
		1+z.prev.winter_Darling	2	54.41	1.82
		1+z.RWII_da45	2	54.47	1.88
		1+z.summer_rain	2	54.50	1.91
		1+z.summer_temp	2	54.54	1.95
RWII	prey.index.ER	1+z.summer_rain+z.summer_Darling+z.years.post.flood	5	180.87	0.00
		1+z.summer_rain+z.prev.winter_rain+z.summer_Darling+z.years.post.flood	6	181.41	0.55
		1+z.summer_rain+z.summer_Darling+z.prev.winter_Darling+z.years.post.flood	6	182.81	1.94
		1+z.summer_temp+z.summer_rain+z.summer_Darling+z.years.post.flood	6	182.81	1.94
		1+z.summer_rain+z.RWII_da45+z.summer_Darling+z.years.post.flood	6	182.84	1.97
RWI	veg.coverage.RWI	1+z.RWI_da45+z.prev.winter_rain+z.summer_Darling+z.years.post.flood	6	156.72	0.00
		1+z.RWI_da45+z.prev.winter_rain+z.summer_Darling	5	157.20	0.48
		1+z.RWI_da45+z.prev.winter_rain	4	157.81	1.09
		1+z.RWI_da45+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling	6	157.91	1.19
		1+z.summer_rain+z.RWI_da45+z.prev.winter_rain+z.summer_Darling+z.years.post.flood	7	157.91	1.19
		1+z.RWI_da45+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling+z.years.post.flood	7	158.14	1.42
		1+z.summer_temp+z.RWI_da45+z.prev.winter_rain+z.summer_Darling+z.years.post.flood	7	158.35	1.63
RWI	eucalypt.foliage.RWI	1+z.summer_Darling	3	60.67	0.00
		1+z.summer_rain+z.summer_Darling	4	61.84	1.17
		1+z.prev.winter_rain+z.summer_Darling	4	61.87	1.20
		1+z.RWI_da45+z.summer_Darling	4	62.20	1.53
		1+z.summer_Darling+z.years.post.flood	4	62.29	1.63
		1+z.summer_temp+z.summer_Darling	4	62.58	1.91
		1+z.summer_Darling+z.prev.winter_Darling	4	62.65	1.98
RWII	herb.biomass	1+z.summer_rain+z.RWII_da45+z.prev.winter_rain+z.prev.winter_Darling	6	219.97	0.00

Study plot	Response	Models	K	AIC	ΔAIC
		1+z.summer_temp+z.summer_rain+z.prev.winter_rain+z.prev.winter_Darling	6	220.59	0.61
		1+z.summer_temp+z.summer_rain+z.prev.winter_rain+z.prev.winter_Darling+z.summer_temp:z.prev.winter_Darling	7	221.33	1.35
		1+z.summer_temp+z.summer_rain+z.prev.winter_rain+z.prev.winter_Darling+z.summer_temp:z.prev.winter_rain	7	221.47	1.49
		1+z.summer_rain+z.RWII_da45+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling	7	221.64	1.66
		1+z.summer_temp+z.summer_rain+z.RWII_da45+z.prev.winter_rain+z.prev.winter_Darling	7	221.83	1.85
		1+z.summer_rain+z.RWII_da45+z.prev.winter_rain+z.prev.winter_Darling+z.years.post.flood	7	221.87	1.90
		1+z.summer_temp+z.summer_rain+z.prev.winter_rain+z.prev.winter_Darling+z.years.post.flood	7	221.89	1.91
RWII	shrub.coverage.RWII	1+z.RWII_da45	3	115.20	0.00
		1+z.RWII_da45+z.prev.winter_Darling	4	115.36	0.16
		1+z.RWII_da45+z.summer_Darling+z.prev.winter_Darling	5	116.02	0.82
		1+z.RWII_da45+z.summer_Darling	4	116.84	1.64
		1+z.summer_rain+z.RWII_da45	4	117.01	1.81
		1+z.summer_temp+z.RWII_da45	4	117.07	1.87
		1+z.RWII_da45+z.years.post.flood	4	117.09	1.89
		1+z.RWII_da45+z.prev.winter_rain	4	117.12	1.92
		1+z.RWII_da45+z.prev.winter_rain+z.prev.winter_Darling	5	117.13	1.93
Station	veg.coverage.Station	1+z.summer_temp+z.summer_rain+z.RWI_da45+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling+z.summer_temp:z.summer_rain+z.summer_temp:z.prev.winter_rain	10	137.28	0.00
		1+z.summer_temp+z.summer_rain+z.RWI_da45+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling+z.summer_temp:z.summer_rain+z.summer_temp:z.prev.winter_rain+z.summer_temp:z.summer_Darling	11	138.00	0.73
		1+z.summer_temp+z.summer_rain+z.RWI_da45+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling+z.years.post.flood+z.summer_temp:z.summer_rain+z.summer_temp:z.prev.winter_rain	11	138.34	1.06
		1+z.summer_temp+z.summer_rain+z.RWI_da45+z.prev.winter_rain+z.summer_Darling+z.summer_temp:z.summer_rain+z.summer_temp:z.prev.winter_rain	9	138.52	1.24
		1+z.summer_temp+z.summer_rain+z.RWI_da45+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling+z.summer_temp:z.summer_rain+z.summer_temp:z.prev.winter_rain+z.summer_temp:z.summer_Darling+z.summer_temp:z.prev.winter_Darling	12	138.57	1.30
		1+z.summer_temp+z.summer_rain+z.RWI_da45+z.prev.winter_rain+z.summer_Darling+z.summer_temp:z.summer_rain+z.summer_temp:z.prev.winter_rain+z.summer_temp:z.summer_Darling	10	138.59	1.31
		1+z.summer_temp+z.summer_rain+z.RWI_da45+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling+z.years.post.flood+z.summer_temp:z.summer_rain+z.summer_temp:z.prev.winter_rain+z.summer_temp:z.summer_Darling	12	138.65	1.37
		1+z.summer_temp+z.summer_rain+z.RWI_da45+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling+z.years.post.flood+z.summer_temp:z.summer_rain+z.summer_temp:z.prev.winter_rain+z.summer_temp:z.summer_Darling+z.summer_temp:z.prev.winter_Darling	13	138.69	1.41
		1+z.summer_temp+z.summer_rain+z.RWI_da45+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling+z.summer_temp:z.summer_rain+z.summer_temp:z.prev.winter_rain+z.summer_temp:z.prev.winter_Darling	11	139.28	2.00
RWII	predators.diurnal	1+z.summer_temp+z.summer_rain+z.RWII_da45+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling+z.years.post.flood+z.summer_temp:z.summer_rain+z.summer_temp:z.prev.winter_rain+z.summer_temp:z.summer_Darling+z.summer_temp:z.prev.winter_Darling	13	8439.29	0.00

Study plot	Response	Models	K	AIC	ΔAIC
		1+z.summer_temp+z.summer_rain+z.RWII_da45+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling+z.years.post.flood+ z.summer_temp:z.summer_rain+z.summer_temp:z.summer_Darling+z.summer_temp:z.prev.winter_Darling	12	8439.61	0.32
		1+z.summer_temp+z.summer_rain+z.RWII_da45+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling+ z.summer_temp:z.summer_rain+z.summer_temp:z.summer_Darling+z.summer_temp:z.prev.winter_Darling	11	8440.69	1.40
RWII	predators.diurnal without *C. regius*	1+z.summer_temp+z.summer_rain+z.prev.winter_rain+z.prev.winter_Darling+z.years.post.flood+z.summer_temp:z.summer_rain+ z.summer_temp:z.prev.winter_Darling	9	1351.59	0.00
		1+z.summer_temp+z.summer_rain+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling+z.years.post.flood+ z.summer_temp:z.summer_rain+z.summer_temp:z.prev.winter_Darling	10	1351.62	0.03
		1+z.summer_temp+z.summer_rain+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling+z.years.post.flood+ z.summer_temp:z.summer_rain+z.summer_temp:z.summer_Darling+z.summer_temp:z.prev.winter_Darling	11	1353.01	1.42
		1+z.summer_temp+z.summer_rain+z.RWII_da45+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling+z.years.post.flood+ z.summer_temp:z.summer_rain+z.summer_temp:z.prev.winter_Darling	11	1353.33	1.74
		1+z.summer_temp+z.summer_rain+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling+z.years.post.flood+ z.summer_temp:z.summer_rain+z.summer_temp:z.prev.winter_rain+z.summer_temp:z.prev.winter_Darling	11	1353.53	1.94
		1+z.summer_temp+z.summer_rain+z.prev.winter_rain+z.prev.winter_Darling+z.years.post.flood+z.summer_temp:z.summer_rain+ z.summer_temp:z.prev.winter_rain+z.summer_temp:z.prev.winter_Darling	10	1353.58	2.00
		1+z.summer_temp+z.summer_rain+z.RWII_da45+z.prev.winter_rain+z.prev.winter_Darling+z.years.post.flood+ z.summer_temp:z.summer_rain+z.summer_temp:z.prev.winter_Darling	10	1353.59	2.00
RWI	predators.nocturnal	1+z.summer_temp+z.summer_rain+z.RWI_da45+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling+z.years.post.flood+ z.summer_temp:z.summer_rain+z.summer_temp:z.prev.winter_rain+z.summer_temp:z.summer_Darling	12	2631.14	0.00
		1+z.summer_temp+z.summer_rain+z.RWI_da45+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling+z.years.post.flood+ z.summer_temp:z.summer_rain+z.summer_temp:z.prev.winter_rain+z.summer_temp:z.summer_Darling+ z.summer_temp:z.prev.winter_Darling	13	2632.55	1.42
RWII	predators.nocturnal	1+z.summer_temp+z.RWII_da45+z.summer_Darling+z.prev.winter_Darling+z.summer_temp:z.summer_Darling+ z.summer_temp:z.prev.winter_Darling	8	858.19	0.00
		1+z.summer_temp+z.RWII_da45+z.summer_Darling+z.prev.winter_Darling+z.years.post.flood+z.summer_temp:z.summer_Darling+ z.summer_temp:z.prev.winter_Darling	9	858.32	0.13
		1+z.summer_temp+z.RWII_da45+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling+z.summer_temp:z.summer_Darling+ z.summer_temp:z.prev.winter_Darling	9	860.08	1.89
		1+z.summer_temp+z.summer_rain+z.RWII_da45+z.summer_Darling+z.prev.winter_Darling+z.years.post.flood+ z.summer_temp:z.summer_Darling+z.summer_temp:z.prev.winter_Darling	10	860.12	1.93
		1+z.summer_temp+z.summer_rain+z.RWII_da45+z.summer_Darling+z.prev.winter_Darling+z.summer_temp:z.summer_Darling+ z.summer_temp:z.prev.winter_Darling	9	860.15	1.97
RWII	predators.nocturnal without *E. richardsonii*	1+z.summer_temp+z.summer_rain+z.RWII_da45+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling+z.years.post.flood+ z.summer_temp:z.summer_rain+z.summer_temp:z.prev.winter_rain+z.summer_temp:z.summer_Darling+ z.summer_temp:z.prev.winter_Darling	13	-3986.93	0.00
Station	predators.nocturnal	1+z.summer_temp+z.summer_rain+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling+z.years.post.flood+z.summer_temp: z.summer_rain+z.summer_temp:z.prev.winter_rain+z.summer_temp:z.summer_Darling+z.summer_temp:z.prev.winter_Darling	12	30287.45	0.00
		1+z.summer_temp+z.summer_rain+z.RWI_da45+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling+z.years.post.flood+ z.summer_temp:z.summer_rain+z.summer_temp:z.prev.winter_rain+z.summer_temp:z.summer_Darling+ z.summer_temp:z.prev.winter_Darling	13	30287.60	0.14

Table S2.1.3: GLMM selections of biotic factors as response parameters without any interaction in the model selection procedure. For clarity reasons, we only show the best models with a ΔAIC < 2. K represents the number of parameters; “:” symbolizes interactions.

study plot	response	models	K	AIC	ΔAIC
all	insect.index	1	1	52.59	0.00
		1+z.summer_Darling	2	53.35	0.75
		1+z.years.post.flood	2	53.44	0.84
		1+z.prev.winter_rain	2	54.16	1.57
		1+z.prev.winter_Darling	2	54.41	1.82
		1+z.RWII_da45	2	54.47	1.88
		1+z.summer_rain	2	54.50	1.91
		1+z.summer_temp	2	54.54	1.95
RWII	prey.index.ER	1+z.summer_rain+z.summer_Darling+z.years.post.flood	5	180.87	0.00
		1+z.summer_rain+z.prev.winter_rain+z.summer_Darling+z.years.post.flood	6	181.41	0.55
		1+z.summer_rain+z.summer_Darling+z.prev.winter_Darling+z.years.post.flood	6	182.81	1.94
		1+z.summer_temp+z.summer_rain+z.summer_Darling+z.years.post.flood	6	182.81	1.94
		1+z.summer_rain+z.RWII_da45+z.summer_Darling+z.years.post.flood	6	182.84	1.97
RWI	veg.coverage.RWI	1+z.RWI_da45+z.prev.winter_rain+z.summer_Darling+z.years.post.flood	6	156.72	0.00
		1+z.RWI_da45+z.prev.winter_rain+z.summer_Darling	5	157.20	0.48
		1+z.RWI_da45+z.prev.winter_rain	4	157.81	1.09
		1+z.RWI_da45+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling	6	157.91	1.19
		1+z.summer_rain+z.RWI_da45+z.prev.winter_rain+z.summer_Darling+z.years.post.flood	7	157.91	1.19
		1+z.RWI_da45+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling+z.years.post.flood	7	158.14	1.42
		1+z.summer_temp+z.RWI_da45+z.prev.winter_rain+z.summer_Darling+z.years.post.flood	7	158.35	1.63
RWI	eucalypt.foliage.RWI	1+z.summer_Darling	3	60.67	0.00
		1+z.summer_rain+z.summer_Darling	4	61.84	1.17
		1+z.prev.winter_rain+z.summer_Darling	4	61.87	1.20
		1+z.RWI_da45+z.summer_Darling	4	62.20	1.53
		1+z.summer_Darling+z.years.post.flood	4	62.29	1.63
		1+z.summer_temp+z.summer_Darling	4	62.58	1.91
		1+z.summer_Darling+z.prev.winter_Darling	4	62.65	1.98
RWII	herb.biomass	1+z.summer_rain+z.RWII_da45+z.prev.winter_rain+z.prev.winter_Darling	6	219.97	0.00
		1+z.summer_temp+z.summer_rain+z.prev.winter_rain+z.prev.winter_Darling	6	220.59	0.61

study plot	response	models	K	AIC	ΔAIC
		1+z.summer_rain+z.RWII_da45+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling	7	221.64	1.66
		1+z.summer_temp+z.summer_rain+z.RWII_da45+z.prev.winter_rain+z.prev.winter_Darling	7	221.83	1.85
		1+z.summer_rain+z.RWII_da45+z.prev.winter_rain+z.prev.winter_Darling+z.years.post.flood	7	221.87	1.90
		1+z.summer_temp+z.summer_rain+z.prev.winter_rain+z.prev.winter_Darling+z.years.post.flood	7	221.89	1.91
RWII	shrub.coverage.RWII	1+z.RWII_da45	3	115.20	0.00
		1+z.RWII_da45+z.prev.winter_Darling	4	115.36	0.16
		1+z.RWII_da45+z.summer_Darling+z.prev.winter_Darling	5	116.02	0.82
		1+z.RWII_da45+z.summer_Darling	4	116.84	1.64
		1+z.summer_rain+z.RWII_da45	4	117.01	1.81
		1+z.summer_temp+z.RWII_da45	4	117.07	1.87
		1+z.RWII_da45+z.years.post.flood	4	117.09	1.89
		1+z.RWII_da45+z.prev.winter_rain	4	117.12	1.92
		1+z.RWII_da45+z.prev.winter_rain+z.prev.winter_Darling	5	117.13	1.93
RWII	predators.diurnal	1+z.summer_rain+z.RWII_da45	4	243.12	0.00
		1+z.summer_rain+z.RWII_da45+z.prev.winter_Darling	5	244.04	0.91
		1+z.RWII_da45	3	244.11	0.99
		1+z.summer_Darling+z.prev.winter_Darling	4	244.49	1.36
		1	2	244.49	1.36
		1+z.summer_rain+z.RWII_da45+z.summer_Darling+z.prev.winter_Darling	6	244.50	1.38
		1+z.summer_rain+z.RWII_da45+z.summer_Darling	5	244.51	1.39
		1+z.RWII_da45+z.prev.winter_Darling	4	244.54	1.41
		1+z.summer_temp+z.summer_rain+z.RWII_da45	5	244.77	1.65
		1+z.summer_Darling	3	245.01	1.88
		1+z.RWII_da45+z.summer_Darling+z.prev.winter_Darling	5	245.01	1.89
		1+z.prev.winter_Darling+z.years.post.flood	4	245.07	1.95
		1+z.summer_rain+z.RWII_da45+z.prev.winter_rain	5	245.09	1.97
		1+z.summer_rain+z.RWII_da45+z.years.post.flood	5	245.09	1.97
RWII	predators.diurnal without *C. regius*	1+z.summer_rain+z.RWII_da45	4	242.33	0.00
		1+z.summer_rain+z.RWII_da45+z.prev.winter_Darling	5	243.06	0.73
		1+z.summer_rain+z.RWII_da45+z.summer_Darling+z.prev.winter_Darling	6	243.26	0.92

study plot	response	models	K	AIC	ΔAIC
		1+z.RWII_da45	3	243.56	1.23
		1+z.summer_rain+z.RWII_da45+z.summer_Darling	5	243.62	1.29
		1+z.RWII_da45+z.prev.winter_Darling	4	243.77	1.44
		1+z.summer_temp+z.summer_rain+z.RWII_da45	5	243.98	1.65
		1+z.RWII_da45+z.summer_Darling+z.prev.winter_Darling	5	244.00	1.67
		1+z.summer_Darling+z.prev.winter_Darling	4	244.07	1.74
		1+z.summer_rain+z.RWII_da45+z.years.post.flood	5	244.30	1.97
		1+z.summer_rain+z.RWII_da45+z.prev.winter_rain	5	244.31	1.98
RWI	predators.nocturnal	1	2	231.39	0.00
		1+z.RWI_da45	3	231.92	0.53
		1+z.summer_temp	3	232.40	1.02
		1+z.summer_rain	3	232.76	1.37
		1+z.prev.winter_rain	3	233.11	1.72
		1+z.years.post.flood	3	233.34	1.95
		1+z.summer_Darling	3	233.38	1.99
		1+z.prev.winter_Darling	3	233.39	2.00
RWII	predators.nocturnal	1+z.RWII_da45+z.summer_Darling	4	232.06	0.00
		1+z.summer_Darling+z.years.post.flood	4	233.03	0.98
		1+z.summer_temp+z.RWII_da45+z.summer_Darling	5	233.08	1.03
		1+z.RWII_da45+z.summer_Darling+z.prev.winter_Darling	5	233.20	1.14
		1+z.RWII_da45+z.summer_Darling+z.years.post.flood	5	233.88	1.83
RWII	predators.nocturnal without *E. richardsonii*	1+z.summer_temp+z.RWII_da45+z.summer_Darling+z.prev.winter_Darling	6	228.94	0.00
		1+z.summer_temp+z.RWII_da45+z.summer_Darling	5	228.97	0.03
		1+z.RWII_da45+z.summer_Darling+z.prev.winter_Darling	5	229.41	0.47
		1+z.RWII_da45+z.summer_Darling	4	229.56	0.63
		1+z.RWII_da45+z.summer_Darling+z.years.post.flood	5	229.78	0.84
		1+z.summer_temp+z.RWII_da45+z.summer_Darling+z.years.post.flood	6	229.82	0.88
		1+z.summer_temp+z.summer_rain+z.RWII_da45+z.summer_Darling	6	230.35	1.41
		1+z.summer_temp+z.RWII_da45+z.prev.winter_rain+z.summer_Darling	6	230.35	1.42
		1+z.summer_temp+z.RWII_da45+z.summer_Darling+z.prev.winter_Darling+z.years.post.flood	7	230.57	1.63

study plot	response	models	K	AIC	ΔAIC
		1+z.summer_temp+z.summer_rain+z.RWII_da45+z.summer_Darling+z.prev.winter_Darling	7	230.64	1.70
		1+z.RWII_da45+z.summer_Darling+z.prev.winter_Darling+z.years.post.flood	6	230.65	1.71
		1+z.summer_Darling+z.years.post.flood	4	230.80	1.86
		1+z.summer_temp+z.RWII_da45+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling	7	230.91	1.97
		1+z.RWII_da45+z.prev.winter_rain+z.summer_Darling	5	230.91	1.97

Table S2.1.4: GLMM selections of body condition (scaled mass index) as response parameters including all possible interactions (summer temperature and all water parameters, i.e. summer and winter rainfall and Darling River height) in the model selection procedure. For clarity reasons, we only show the best models with a ΔAIC < 2. K represents the number of parameters; ":" symbolizes interactions.

Species	models	K	AIC	ΔAIC
M. boulengeri	1+z.summer_temp+z.prev.winter_rain+z.prev.winter_Darling+z.summer_temp:z.prev.winter_Darling	9	-1307.75	0.00
	1+z.summer_temp+z.prev.winter_Darling+z.summer_temp:z.prev.winter_Darling	8	-1306.38	1.37
	1+z.summer_temp+z.prev.winter_rain+z.prev.winter_Darling+z.summer_temp:z.prev.winter_rain+z.summer_temp:z.prev.winter_Darling	10	-1306.25	1.50
	1+z.summer_temp+z.summer_rain+z.prev.winter_rain+z.prev.winter_Darling+z.summer_temp:z.prev.winter_Darling	10	-1306.19	1.56
	1+z.summer_temp+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling+z.summer_temp:z.prev.winter_Darling	10	-1305.98	1.77
	1+z.summer_temp+z.prev.winter_rain+z.prev.winter_Darling+z.years.post.flood+z.summer_temp:z.prev.winter_Darling	10	-1305.76	1.99
	1+z.summer_temp+z.summer_rain+z.prev.winter_rain+z.prev.winter_Darling+z.summer_temp:z.summer_rain+z.summer_temp:z.prev.winter_Darling	11	-1305.76	1.99
	1+z.summer_temp+z.RWII_da45+z.prev.winter_rain+z.prev.winter_Darling+z.summer_temp:z.prev.winter_Darling	10	-1305.76	1.99
C. regius	1+z.summer_temp+z.summer_rain+z.RWII_da45+z.prev.winter_rain+z.summer_Darling+z.summer_temp:z.summer_rain	11	39.57	0.00
	1+z.summer_temp+z.summer_rain+z.prev.winter_rain+z.summer_Darling+z.summer_temp:z.summer_rain	10	39.62	0.05
	1+z.summer_temp+z.summer_rain+z.RWII_da45+z.prev.winter_rain+z.prev.winter_Darling+z.summer_temp:z.summer_rain+ z.summer_temp:z.prev.winter_Darling	12	40.05	0.48
	1+z.summer_temp+z.summer_rain+z.RWII_da45+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling+z.summer_temp:z.summer_rain+ z.summer_temp:z.prev.winter_Darling	13	40.08	0.51
	1+z.summer_temp+z.summer_rain+z.prev.winter_rain+z.summer_Darling+z.summer_temp:z.summer_rain+z.summer_temp:z.summer_Darling	11	40.41	0.84
	1+z.summer_temp+z.summer_rain+z.RWII_da45+z.prev.winter_rain+z.summer_Darling+z.summer_temp:z.summer_rain+ z.summer_temp:z.summer_Darling	12	40.57	1.01
	1+z.summer_temp+z.summer_rain+z.RWII_da45+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling+z.years.post.flood+ z.summer_temp:z.summer_rain+z.summer_temp:z.prev.winter_Darling	14	40.68	1.11
	1+z.summer_temp+z.summer_rain+z.RWII_da45+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling+z.summer_temp:z.summer_rain+ z.summer_temp:z.summer_Darling	13	40.73	1.16
	1+z.summer_temp+z.summer_rain+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling+z.summer_temp:z.summer_rain+ z.summer_temp:z.prev.winter_Darling	12	41.05	1.48

Species	models	K	AIC	ΔAIC
	1+z.summer_temp+z.summer_rain+z.prev.winter_rain+z.summer_Darling+z.years.post.flood+z.summer_temp:z.summer_rain	11	41.08	1.51
	1+z.summer_temp+z.summer_rain+z.prev.winter_rain+z.prev.winter_Darling+z.years.post.flood+z.summer_temp:z.prev.winter_Darling	11	41.12	1.55
	1+z.summer_temp+z.summer_rain+z.RWII_da45+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling+z.summer_temp:z.summer_rain	12	41.15	1.58
	1+z.summer_temp+z.summer_rain+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling+z.summer_temp:z.summer_rain+z.summer_temp:z.summer_Darling	12	41.29	1.72
	1+z.summer_temp+z.summer_rain+z.RWII_da45+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling+z.summer_temp:z.summer_rain+z.summer_temp:z.prev.winter_rain+z.summer_temp:z.prev.winter_Darling	14	41.31	1.74
	1+z.summer_temp+z.summer_rain+z.prev.winter_rain+z.summer_Darling+z.years.post.flood+z.summer_temp:z.summer_rain+z.summer_temp:z.summer_Darling	12	41.33	1.76
	1+z.summer_temp+z.summer_rain+z.prev.winter_rain+z.summer_Darling+z.summer_temp:z.summer_rain+z.summer_temp:z.prev.winter_rain+z.summer_temp:z.summer_Darling	12	41.35	1.79
	1+z.summer_temp+z.summer_rain+z.RWII_da45+z.prev.winter_rain+z.summer_Darling+z.years.post.flood+z.summer_temp:z.summer_rain	12	41.39	1.82
	1+z.summer_temp+z.summer_rain+z.prev.winter_rain+z.prev.winter_Darling+z.summer_temp:z.summer_rain+z.summer_temp:z.prev.winter_Darling	11	41.41	1.84
	1+z.summer_temp+z.summer_rain+z.RWII_da45+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling+z.years.post.flood+z.summer_temp:z.summer_rain+z.summer_temp:z.summer_Darling	14	41.43	1.86
	1+z.summer_temp+z.summer_rain+z.RWII_da45+z.prev.winter_rain+z.summer_Darling+z.summer_temp:z.summer_rain+z.summer_temp:z.prev.winter_rain	12	41.47	1.90
	1+z.summer_temp+z.summer_rain+z.RWII_da45+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling+z.years.post.flood+z.summer_temp:z.summer_rain	13	41.50	1.93
	1+z.summer_temp+z.summer_rain+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling+z.summer_temp:z.summer_rain	11	41.51	1.94
	1+z.summer_temp+z.summer_rain+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling+z.summer_temp:z.prev.winter_rain+z.summer_temp:z.prev.winter_Darling	12	41.54	1.97
H. binoei	1+z.summer_temp+z.RWI_da45+z.prev.winter_rain+z.prev.winter_Darling+z.years.post.flood+z.summer_temp:z.prev.winter_rain+z.summer_temp:z.prev.winter_Darling	13	-79.34	0.00
	1+z.summer_temp+z.RWI_da45+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling+z.years.post.flood+z.summer_temp:z.prev.winter_rain+z.summer_temp:z.prev.winter_Darling	14	-79.00	0.34
	1+z.summer_temp+z.summer_rain+z.RWI_da45+z.prev.winter_rain+z.prev.winter_Darling+z.years.post.flood+z.summer_temp:z.prev.winter_rain+z.summer_temp:z.prev.winter_Darling	14	-77.70	1.64
	1+z.summer_temp+z.RWI_da45+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling+z.years.post.flood+z.summer_temp:z.prev.winter_rain+z.summer_temp:z.summer_Darling+z.summer_temp:z.prev.winter_Darling	15	-77.45	1.89
	1+z.summer_temp+z.RWI_da45+z.prev.winter_rain+z.prev.winter_Darling+z.summer_temp:z.prev.winter_rain+z.summer_temp:z.prev.winter_Darling	12	-77.35	1.99
D. tessellatus	1+z.summer_temp+z.prev.winter_rain+z.summer_Darling+z.years.post.flood+z.summer_temp:z.prev.winter_rain+z.summer_temp:z.summer_Darling	12	97.97	0.00
	1+z.summer_temp+z.prev.winter_rain+z.summer_Darling+z.summer_temp:z.prev.winter_rain+z.summer_temp:z.summer_Darling	11	98.88	0.92
	1+z.summer_temp+z.RWI_da45+z.prev.winter_rain+z.summer_Darling+z.summer_temp:z.prev.winter_rain+z.summer_temp:z.summer_Darling	12	99.40	1.43
	1+z.summer_temp+z.summer_rain+z.prev.winter_rain+z.summer_Darling+z.years.post.flood+z.summer_temp:z.summer_rain+z.summer_temp:z.prev.winter_rain+z.summer_temp:z.summer_Darling	14	99.58	1.61
	1+z.summer_temp+z.RWI_da45+z.prev.winter_rain+z.summer_Darling+z.years.post.flood+z.summer_temp:z.prev.winter_rain+z.summer_temp:z.summer_Darling	13	99.60	1.63
	1+z.summer_temp+z.summer_rain+z.prev.winter_rain+z.summer_Darling+z.years.post.flood+z.summer_temp:z.prev.winter_rain+z.summer_temp:z.summer_Darling	13	99.61	1.64

Species	models	K	AIC	ΔAIC
	1+z.summer_temp+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling+z.years.post.flood+z.summer_temp:z.prev.winter_rain+ z.summer_temp:z.summer_Darling	13	99.80	1.83
L. punctatovittata	1+z.summer_temp+z.prev.winter_rain+z.years.post.flood+z.summer_temp:z.prev.winter_rain	9	131.43	0.00
	1+z.summer_temp+z.prev.winter_rain+z.prev.winter_Darling+z.years.post.flood+z.summer_temp:z.prev.winter_rain	10	132.32	0.89
	1+z.summer_temp+z.prev.winter_rain+z.summer_Darling+z.summer_temp:z.prev.winter_rain	9	132.53	1.10
	1+z.summer_temp+z.prev.winter_rain+z.summer_Darling+z.years.post.flood+z.summer_temp:z.summer_Darling	10	132.69	1.27
	1+z.summer_temp+z.prev.winter_rain+z.summer_Darling+z.years.post.flood+z.summer_temp:z.prev.winter_rain	10	132.82	1.39
	1+z.summer_temp+z.prev.winter_rain+z.summer_Darling+z.summer_temp:z.summer_Darling	9	132.92	1.50
	1+z.summer_temp+z.RWII_da45+z.prev.winter_rain+z.years.post.flood+z.summer_temp:z.prev.winter_rain	10	133.27	1.85
	1+z.summer_temp+z.prev.winter_rain+z.summer_Darling	8	133.35	1.93
	1+z.summer_temp+z.summer_rain+z.prev.winter_rain+z.years.post.flood+z.summer_temp:z.prev.winter_rain	10	133.39	1.97
L. xanthura	1+z.summer_temp+z.RWII_da45+z.prev.winter_Darling+z.years.post.flood	9	-56.00	0.00
	1+z.summer_rain+z.RWII_da45	7	-55.17	0.83
	1+z.summer_temp+z.RWII_da45+z.years.post.flood	8	-54.98	1.02
	1+z.summer_temp+z.RWII_da45+z.summer_Darling+z.prev.winter_Darling+z.years.post.flood	10	-54.81	1.18
	1+z.summer_temp+z.RWII_da45	7	-54.48	1.52
	1+z.summer_temp+z.summer_rain+z.RWII_da45+z.prev.winter_Darling+z.years.post.flood	10	-54.28	1.72
	1+z.summer_temp+z.RWII_da45+z.prev.winter_rain+z.years.post.flood	9	-54.20	1.79
	1+z.summer_rain+z.RWII_da45+z.prev.winter_Darling	8	-54.12	1.88
	1+z.summer_temp+z.RWII_da45+z.prev.winter_rain+z.prev.winter_Darling+z.years.post.flood	10	-54.06	1.93
E. richardsonii	1+z.summer_temp+z.RWII_da45+z.summer_Darling	9	221.85	0.00
	1+z.summer_temp+z.RWII_da45+z.summer_Darling+z.years.post.flood	10	223.40	1.54
	1+z.summer_temp+z.RWII_da45+z.prev.winter_rain+z.summer_Darling	10	223.58	1.72
	1+z.summer_temp+z.summer_rain+z.RWII_da45+z.summer_Darling	10	223.69	1.84
	1+z.summer_temp+z.RWII_da45+z.summer_Darling+z.prev.winter_Darling	10	223.82	1.96
	1	6	223.84	1.98
***G. variegata* RWI**	1+z.prev.winter_rain+z.summer_Darling	8	207.90	0.00
	1+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling	9	208.29	0.39
	1+z.summer_rain+z.prev.winter_rain+z.summer_Darling	9	208.55	0.65
	1+z.RWI_da45+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling	10	208.92	1.01
	1+z.RWI_da45+z.prev.winter_rain+z.summer_Darling	9	209.02	1.11

Species	models	K	AIC	ΔAIC
	1+z.summer_rain+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling	10	209.15	1.25
	1+z.prev.winter_rain+z.summer_Darling+z.years.post.flood	9	209.18	1.28
	1+z.summer_temp+z.prev.winter_rain+z.summer_Darling	9	209.23	1.33
	1+z.summer_temp+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling	10	209.27	1.37
	1+z.summer_temp+z.summer_rain+z.RWI_da45+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling+z.summer_temp:z.summer_rain	13	209.85	1.95
	1+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling+z.years.post.flood	10	209.88	1.98
***G. variegata* Station**	1+z.summer_rain+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling	10	2566.94	0.00
	1+z.summer_rain+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling+z.years.post.flood	11	2568.25	1.31
	1+z.summer_temp+z.summer_rain+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling	11	2568.51	1.57
	1+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling	9	2568.60	1.66
	1+z.summer_rain+z.RWI_da45+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling	11	2568.90	1.96
	1+z.summer_temp+z.prev.winter_rain+z.summer_Darling+z.prev.winter_Darling	10	2568.92	1.99

Table S2.1.5: GLMM selections of smoothed annual occupancy values as response parameters including all possible interactions (summer temperature and all water parameters, i.e. summer and winter rainfall and Darling River height) in the model selection procedure. For clarity reasons, we only show the best models with a ΔAIC < 2. K represents the number of parameters; ":" symbolizes interactions.

Species	models	K	AIC	ΔAIC
M. boulengeri	1	3	-8.85	0.00
	1+z.years.post.flood	4	-8.56	0.29
C. regius	1+z.prev.winter_Darling+z.years.post.flood	5	10.34	0.00
H. binoei	1	3	11.46	0.00
	1+z.RWII_da45	4	11.70	0.24
	1+z.years.post.flood	4	12.40	0.94
	1+z.prev.winter_Darling+z.years.post.flood	5	12.46	1.00
	1+z.summer_Darling	4	12.75	1.29
D. tessellatus	1+z.years.post.flood	4	-14.27	0.00
	1+z.summer_temp+z.summer_Darling+z.years.post.flood+z.summer_temp:z.summer_Darling	7	-13.54	0.72
L. punctatovittata	1	3	3.19	0.00
	1+z.prev.winter_rain+z.years.post.flood	5	3.55	0.36

Species	models	K	AIC	ΔAIC
	1+z.years.post.flood	4	3.87	0.68
L. xanthura	1+z.prev.winter_Darling	4	9.28	0.00
	1+z.summer_Darling+z.prev.winter_Darling	5	9.37	0.09
	1+z.prev.winter_rain	4	10.66	1.38
	1+z.summer_temp+z.summer_Darling+z.prev.winter_Darling	6	10.81	1.53
	1	3	10.89	1.62
	1+z.RWII_da45+z.summer_Darling+z.prev.winter_Darling	6	11.04	1.76
E. richardsonii	1+z.summer_temp+z.prev.winter_rain+z.summer_temp:z.prev.winter_rain	6	-31.60	0.00
	1+z.summer_temp+z.summer_rain+z.prev.winter_rain+z.summer_temp:z.prev.winter_rain	7	-31.04	0.57
	1+z.summer_temp+z.RWII_da45+z.prev.winter_rain+z.summer_temp:z.prev.winter_rain	7	-30.26	1.35
	1+z.summer_temp+z.summer_rain+z.RWII_da45+z.prev.winter_rain+z.summer_temp:z.prev.winter_rain	8	-29.99	1.61
	1+z.summer_temp+z.prev.winter_rain+z.prev.winter_Darling+z.summer_temp:z.prev.winter_rain	7	-29.94	1.66
	1+z.summer_temp+z.prev.winter_rain+z.summer_Darling+z.summer_temp:z.prev.winter_rain	7	-29.71	1.89
	1+z.summer_temp+z.prev.winter_rain+z.years.post.flood+z.summer_temp:z.prev.winter_rain	7	-29.61	1.99
***G. variegata* RWI**	1+z.summer_temp+z.prev.winter_rain+z.summer_temp:z.prev.winter_rain	5	-23.30	0.00
	1+z.summer_temp	3	-21.58	1.72

S2.2 Summary of factors and paths used in structural equation models (SEMs)

Table S2.2.1: Overview on model compositions for body condition and occupancy analyses per species. Interactions represent which interactions were possible to be tested in GLMMs and transferred to SEMs: all – all potential interactions simultaneously [summer temperature and each water parameter (summer and winter precipitation and Darling River height)]; one-by-one – all potential interactions after each other but not together; none – too few data to include interactions. ID and Site symbolise whether the random intercept of individual's ID (individual measured multiple times across time) or of the site of capture (several sites with many individuals) was included in both GLMMs and SEMs of body condition.

Species	Response	Interactions	ID	Site
M. boulengeri	body condition occupancy	all one-by-one	yes not applicable	no not applicable
C. regius	body condition occupancy	none one-by-one	no not applicable	no not applicable
H. binoei	body condition occupancy	all one-by-one	no not applicable	yes not applicable
D. tessellatus	body condition occupancy	all one-by-one	no not applicable	no not applicable
L. punctatovittata	body condition occupancy	none one-by-one	no not applicable	no not applicable
L. xanthura	body condition occupancy	none one-by-one	no not applicable	no not applicable
E. richardsonii	body condition occupancy	none one-by-one	no not applicable	no not applicable
***G. variegata* RWI**	body condition occupancy	all one-by-one	yes not applicable	no not applicable
***G. variegata* station**	body condition occupancy	all one-by-one	yes not applicable	no not applicable

Table S2.2.2: Scaled estimates, standard errors and p-values of each path per species for analyses of body condition. All predictors are abbreviated; see Table S2.1.1 for explanations and calculations. ":" symbolises interactions. Importantly, interaction paths in mixed models cannot be displayed by the R-function in the package piecewiseSEM but are part of the model, despite they do not appear in this table. All paths were selected using GLMMs (see Appendix S2.1) except the bold paths, which were added due to suggestions of Shipley's test of d-separation (Shipley 2009) when the test was significant and a plausible ecological connection could exist.

Species	Response	Predictor	Estimate	SE	p-value
M. boulengeri	ln(herb.biomass)	shrub.coverage.RWII	-0.491	0.026	0.000
		prev.winter_Darling	0.605	0.033	0.000
		summer_rain	0.370	0.023	0.000
		prev.winter_rain	0.445	0.031	0.000
		RWII_da45	0.241	0.043	0.000
		summer_temperature	-0.127	0.040	0.002
		summer_temperature:prev.winter_rain	0.037	0.023	0.097
		summer_temperature:prev.winter_Darling	-0.035	0.027	0.191
	shrub.coverage.RWII	ln(herb.biomass)	-0.468	0.040	0.000
		RWII_da45	-0.938	0.087	0.000
		prev.winter_rain	0.401	0.038	0.000
		prev.winter_Darling	0.391	0.043	0.000
		summer_temperature:summer_rain	-0.369	0.041	0.000
		summer_temperature	0.413	0.064	0.000

Species	Response	Predictor	Estimate	SE	p-value
		summer_Darling	-0.221	0.038	0.000
		summer_temperature:prev.winter_Darling	0.124	0.029	0.000
		years.post.flood	0.138	0.049	0.005
		summer_temperature:prev.winter_rain	0.015	0.027	0.584
		summer_rain	0.009	0.045	0.843
	prey.index	summer_temperature:summer_rain	-0.310	0.050	0.000
		shrub.coverage.RWII	0.169	0.044	0.000
		summer_rain	-0.213	0.058	0.000
		summer_Darling	0.152	0.042	0.000
		years.post.flood	-0.119	0.059	0.044
		summer_temperature	0.042	0.038	0.275
		prev.winter_Darling	-0.040	0.052	0.451
		summer_temperature:summer_Darling	0.019	0.047	0.683
		prev.winter_rain	0.018	0.053	0.733
		ln(herb.biomass)	0.010	0.057	0.861
	predator.index	summer_Darling	0.566	0.016	0.000
		shrub.coverage.RWII	0.508	0.016	0.000
		ln(herb.biomass)	-0.574	0.019	0.000
		prev.winter_Darling	-0.551	0.021	0.000
		summer_temperature:prev.winter_Darling	0.403	0.016	0.000
		summer_temperature:summer_Darling	-0.355	0.025	0.000
		prev.winter_rain	0.199	0.019	0.000
		summer_temperature:summer_rain	0.167	0.018	0.000
		summer_temperature	-0.251	0.028	0.000
		RWII_da45	0.353	0.040	0.000
		years.post.flood	-0.133	0.021	0.000
		summer_rain	0.050	0.019	0.009
		summer_temperature:prev.winter_rain	0.019	0.012	0.108
	SMI	TL.SVL	0.391	0.032	0.000
		Age2	-0.223	0.032	0.000
		prev.winter_rain	0.132	0.051	0.009
		predator.index	-0.188	0.087	0.032
		shrub.coverage.RWII	-0.141	0.089	0.113
		prey.index	0.157	0.111	0.159
		summer_rain	0.049	0.045	0.277
		RWII_da45	-0.153	0.160	0.341
		years.post.flood	0.069	0.080	0.394
		summer_Darling	0.057	0.089	0.526
		prev.winter_Darling	0.034	0.057	0.553
		summer_temperature	-0.047	0.103	0.651
		ln(herb.biomass)	-0.023	0.084	0.785
C. regius	ln(herb.biomass)	summer_rain	0.600	0.038	0.000
		shrub.coverage.RWII	-0.669	0.058	0.000
		prev.winter_Darling	0.458	0.055	0.000
		prev.winter_rain	0.185	0.058	0.002
		summer_temperature	0.170	0.053	0.002
		RWII_da45	0.126	0.070	0.074
	shrub.coverage.RWII	ln(herb.biomass)	-0.802	0.067	0.000

Species	Response	Predictor	Estimate	SE	p-value
		summer_rain	0.507	0.056	0.000
		years.post.flood	-0.338	0.055	0.000
		prev.winter_Darling	0.270	0.063	0.000
		summer_temperature	0.154	0.054	0.005
		summer_Darling	-0.132	0.055	0.017
		RWII_da45	-0.107	0.072	0.141
		prev.winter_rain	0.061	0.059	0.310
	prey.index	prev.winter_rain	0.319	0.169	0.059
		years.post.flood	-0.218	0.163	0.182
		prev.winter_Darling	0.193	0.193	0.319
		summer_temperature	-0.129	0.141	0.362
		summer_Darling	0.074	0.127	0.559
		shrub.coverage.RWII	0.051	0.236	0.827
		ln(herb.biomass)	0.042	0.245	0.864
		summer_rain	-0.026	0.182	0.888
	predator.index	ln(herb.biomass)	-0.886	0.082	0.000
		summer_Darling	0.213	0.047	0.000
		years.post.flood	0.183	0.052	0.001
		shrub.coverage.RWII	0.249	0.081	0.003
		summer_temperature	0.085	0.044	0.058
		prev.winter_Darling	-0.066	0.058	0.256
		summer_rain	-0.058	0.060	0.334
		prev.winter_rain	0.024	0.049	0.624
	SMI	prev.winter_Darling	-0.563	0.233	0.018
		predator.index	-0.885	0.374	0.020
		summer_Darling	0.449	0.190	0.020
		shrub.coverage.RWII	0.655	0.313	0.039
		summer_rain	-0.450	0.219	0.043
		TL.SVL	0.147	0.090	0.106
		summer_temperature	-0.207	0.223	0.355
		prev.winter_rain	0.134	0.242	0.580
		prey.index	0.090	0.355	0.800
		Age2	0.019	0.089	0.833
		ln(herb.biomass)	-0.106	0.525	0.841
		RWII_da45	0.040	0.222	0.857
H. binoei	veg.coverage.Station	summer_temperature	0.949	0.041	0.000
		prev.winter_rain	0.604	0.038	0.000
		RWI_da45	-0.605	0.039	0.000
		summer_rain	0.725	0.055	0.000
		summer_temperature:summer_rain	0.470	0.048	0.000
		summer_Darling	-0.335	0.035	0.000
		years.post.flood	-0.188	0.040	0.000
		summer_temperature:summer_Darling	-0.166	0.061	0.007
		summer_temperature:prev.winter_rain	0.053	0.034	0.121
		summer_temperature:prev.winter_Darling	-0.074	0.071	0.298
		Station_usage	0.035	0.047	0.452
		prev.winter_Darling	-0.007	0.086	0.937
	prey.index	summer_temperature	-0.371	0.228	0.104

Species	Response	Predictor	Estimate	SE	p-value
		summer_Darling	0.320	0.226	0.157
		veg.coverage.Station	0.432	0.309	0.162
		summer_rain	-0.546	0.475	0.250
		summer_temperature:summer_rain	-0.412	0.362	0.255
		summer_temperature:summer_Darling	0.283	0.278	0.309
		prev.winter_rain	-0.278	0.284	0.328
		Station_usage	-0.149	0.260	0.568
		years.post.flood	-0.049	0.257	0.847
		prev.winter_Darling	0.001	0.401	0.998
	predator.index	prev.winter_rain	0.917	0.157	0.000
		summer_temperature	1.183	0.301	0.000
		prev.winter_Darling	0.509	0.156	0.001
		summer_Darling	0.332	0.103	0.002
		summer_temperature:prev.winter_rain	-0.222	0.089	0.014
		summer_temperature:summer_rain	-0.452	0.209	0.033
		years.post.flood	-0.262	0.134	0.053
		RWI_da45	-0.375	0.206	0.071
		Station_usage	-0.103	0.109	0.345
		summer_rain	-0.218	0.280	0.436
		veg.coverage.Station	-0.144	0.282	0.611
	SMI	prev.winter_rain	0.525	0.203	0.016
		TL.SVL	0.167	0.073	0.026
		Station_usage	-0.319	0.116	0.033
		Age2	-0.151	0.074	0.047
		RWI_da45	-0.465	0.297	0.169
		prey.index	0.243	0.220	0.277
		predator.index	-0.141	0.143	0.348
		prev.winter_Darling	0.120	0.146	0.419
		summer_temperature	0.310	0.329	0.424
		veg.coverage.Station	0.037	0.239	0.889
		summer_Darling	0.013	0.130	0.922
D. tessellatus	veg.coverage.RWI	summer_temperature:summer_rain	0.554	0.048	0.000
		summer_rain	0.255	0.024	0.000
		eucalypt.foliage.RWI	0.510	0.064	0.000
		prev.winter_rain	0.370	0.057	0.000
		prev.winter_Darling	-0.186	0.033	0.000
		summer_Darling	0.150	0.038	0.000
		years.post.flood	0.083	0.021	0.000
		summer_temperature:summer_Darling	-0.209	0.057	0.000
		summer_temperature:prev.winter_rain	-0.102	0.042	0.015
		summer_temperature:prev.winter_Darling	0.072	0.034	0.035
		RWI_da45	-0.081	0.065	0.217
		summer_temperature	0.051	0.045	0.263
	eucalypt.foliage.RWI	summer_temperature:summer_rain	-0.572	0.034	0.000
		summer_Darling	0.338	0.025	0.000
		RWI_da45	-0.544	0.044	0.000
		summer_temperature:summer_Darling	0.405	0.042	0.000
		summer_temperature:prev.winter_rain	-0.269	0.031	0.000

Species	Response	Predictor	Estimate	SE	p-value
		summer_temperature:prev.winter_Darling	0.218	0.025	0.000
		veg.coverage.RWI	0.343	0.043	0.000
		prev.winter_Darling	-0.181	0.026	0.000
		prev.winter_rain	0.307	0.047	0.000
		summer_rain	-0.141	0.022	0.000
		summer_temperature	0.044	0.037	0.239
		years.post.flood	-0.005	0.018	0.799
	prey.index	veg.coverage.RWI	0.680	0.203	0.001
		summer_temperature:summer_rain	-0.618	0.187	0.001
		prev.winter_rain	-0.264	0.085	0.002
		summer_rain	-0.304	0.106	0.004
		years.post.flood	-0.157	0.071	0.028
		eucalypt.foliage.RWI	-0.263	0.170	0.123
		summer_Darling	-0.101	0.070	0.151
		summer_temperature:summer_Darling	0.218	0.156	0.164
		summer_temperature	-0.143	0.119	0.231
		prev.winter_Darling	0.059	0.058	0.315
	predator.index	summer_temperature	0.969	0.050	0.000
		veg.coverage.RWI	-0.835	0.063	0.000
		summer_rain	0.414	0.031	0.000
		summer_Darling	0.536	0.043	0.000
		RWI_da45	-0.793	0.072	0.000
		years.post.flood	-0.230	0.024	0.000
		summer_temperature:summer_rain	-0.550	0.063	0.000
		summer_temperature:summer_Darling	-0.514	0.064	0.000
		prev.winter_Darling	-0.296	0.038	0.000
		summer_temperature:prev.winter_Darling	0.246	0.038	0.000
		prev.winter_rain	0.428	0.067	0.000
		summer_temperature:prev.winter_rain	0.262	0.046	0.000
		eucalypt.foliage.RWI	-0.319	0.077	0.000
	SMI	TL.SVL	0.391	0.049	0.000
		summer_temperature	0.906	0.255	0.000
		prev.winter_rain	0.751	0.218	0.001
		summer_temperature:summer_Darling	-0.509	0.205	0.013
		Age2	-0.113	0.047	0.018
		summer_Darling	0.280	0.126	0.027
		prey.index	0.499	0.247	0.044
		summer_rain	0.157	0.136	0.248
		predator.index	-0.136	0.175	0.438
		summer_temperature:prev.winter_rain	-0.124	0.161	0.443
		veg.coverage.RWI	-0.220	0.304	0.470
		eucalypt.foliage.RWI	0.119	0.171	0.486
		RWI_da45	-0.162	0.253	0.524
		years.post.flood	-0.053	0.090	0.558
		prev.winter_Darling	-0.008	0.064	0.904
L. punctatovittata	ln(herb.biomass)	shrub.coverage.RWII	-0.661	0.057	0.000
		prev.winter_Darling	0.790	0.071	0.000
		summer_rain	0.507	0.051	0.000

Species	Response	Predictor	Estimate	SE	p-value
		prev.winter_rain	0.663	0.076	0.000
		summer_temperature	-0.117	0.079	0.141
		RWII_da45	0.128	0.092	0.169
	shrub.coverage.RWII	ln(herb.biomass)	-1.001	0.110	0.000
		prev.winter_Darling	0.927	0.105	0.000
		prev.winter_rain	0.778	0.107	0.000
		summer_rain	0.567	0.093	0.000
		RWII_da45	-0.209	0.134	0.121
		years.post.flood	0.140	0.120	0.250
		summer_Darling	0.069	0.099	0.486
		summer_temperature	-0.056	0.111	0.615
	predator.index	summer_Darling	1.102	0.057	0.000
		RWII_da45	0.423	0.090	0.000
		ln(herb.biomass)	0.144	0.062	0.023
		shrub.coverage.RWII	0.137	0.062	0.029
		prev.winter_Darling	-0.140	0.081	0.089
		years.post.flood	0.081	0.067	0.230
		prev.winter_rain	0.079	0.077	0.309
		summer_temperature	-0.058	0.073	0.429
	SMI	TL.SVL	0.470	0.088	0.000
		prev.winter_Darling	-0.414	0.128	0.002
		summer_temperature	-0.275	0.107	0.012
		years.post.flood	-0.373	0.148	0.013
		Age2	0.247	0.100	0.015
		ln(herb.biomass)	0.267	0.130	0.044
		shrub.coverage.RWII	-0.149	0.145	0.306
		predator.index	-0.025	0.123	0.841
L. xanthura	ln(herb.biomass)	shrub.coverage.RWII	-0.534	0.100	0.000
		prev.winter_Darling	0.496	0.131	0.001
		summer_rain	0.209	0.086	0.019
		summer_temperature	-0.472	0.204	0.026
		RWII_da45	0.406	0.259	0.125
		prev.winter_rain	0.102	0.156	0.517
	shrub.coverage.RWII	prev.winter_Darling	0.566	0.143	0.000
		summer_Darling	-0.411	0.119	0.001
		RWII_da45	-1.011	0.350	0.006
		prev.winter_rain	0.538	0.222	0.020
		ln(herb.biomass)	-0.383	0.180	0.040
		years.post.flood	-0.432	0.226	0.064
		summer_temperature	0.540	0.296	0.076
		summer_rain	0.151	0.101	0.144
	predator.index	ln(herb.biomass)	0.821	0.025	0.000
		years.post.flood	-0.939	0.031	0.000
		summer_Darling	0.489	0.017	0.000
		prev.winter_rain	0.804	0.029	0.000
		summer_temperature	0.531	0.035	0.000
		prev.winter_Darling	-0.230	0.022	0.000
		RWII_da45	-0.251	0.048	0.000

Species	Response	Predictor	Estimate	SE	p-value
		shrub.coverage.RWII	0.034	0.021	0.113
	SMI	prev.winter_Darling	-1.068	0.434	0.019
		shrub.coverage.RWII	0.906	0.383	0.024
		RWII_da45	2.067	0.946	0.035
		years.post.flood	-1.071	0.493	0.036
		ln(herb.biomass)	0.968	0.647	0.143
		summer_temperature	-0.820	0.711	0.256
		Age2	0.096	0.153	0.532
		TL.SVL	-0.082	0.141	0.562
		predator.index	-0.173	0.386	0.657
E. richardsonii	ln(herb.biomass)	prev.winter_Darling	0.788	0.075	0.000
		shrub.coverage.RWII	-0.675	0.070	0.000
		prev.winter_rain	0.543	0.103	0.000
		summer_rain	0.276	0.084	0.002
		summer_temperature	-0.196	0.133	0.147
		RWII_da45	0.044	0.108	0.684
	shrub.coverage.RWII	prev.winter_Darling	0.820	0.087	0.000
		prev.winter_rain	0.769	0.092	0.000
		ln(herb.biomass)	-0.700	0.118	0.000
		RWII_da45	-0.590	0.135	0.000
		summer_rain	0.361	0.087	0.000
		summer_temperature	0.456	0.167	0.008
		summer_Darling	-0.174	0.093	0.066
		years.post.flood	0.073	0.075	0.335
	predator.index	summer_Darling	0.964	0.037	0.000
		prev.winter_rain	0.390	0.059	0.000
		summer_temperature	0.243	0.045	0.000
		ln(herb.biomass)	0.238	0.072	0.002
		summer_rain	0.045	0.047	0.347
		years.post.flood	-0.022	0.037	0.565
		shrub.coverage.RWII	0.026	0.055	0.638
		prev.winter_Darling	0.007	0.066	0.916
	prey.index	summer_Darling	0.822	0.081	0.000
		years.post.flood	0.625	0.064	0.000
		summer_rain	0.580	0.084	0.000
		ln(herb.biomass)	-0.685	0.126	0.000
		prev.winter_rain	0.576	0.114	0.000
		prev.winter_Darling	0.499	0.115	0.000
		summer_temperature	-0.474	0.150	0.003
		shrub.coverage.RWII	0.199	0.108	0.070
		RWII_da45	0.222	0.131	0.094
	SMI	TL.SVL	0.459	0.114	0.000
		RWII_da45	0.945	0.454	0.042
		summer_temperature	-0.667	0.419	0.117
		summer_Darling	0.967	0.676	0.158
		predator.index	-0.510	0.497	0.309
		prey.index	0.222	0.229	0.335
		years.post.flood	0.108	0.198	0.587

Species	Response	Predictor	Estimate	SE	p-value
		Age2	0.062	0.114	0.588
		ln(herb.biomass)	-0.087	0.197	0.661
		shrub.coverage.RWII	0.033	0.242	0.893
***G. variegata* RI**	veg.coverage.RWI	eucalypt.foliage.RWI	0.649	0.015	0.000
		summer_rain	0.557	0.016	0.000
		summer_temperature:summer_rain	0.465	0.014	0.000
		prev.winter_Darling	-0.458	0.015	0.000
		prev.winter_rain	0.292	0.016	0.000
		summer_temperature:summer_Darling	-0.191	0.020	0.000
		summer_temperature	-0.174	0.020	0.000
		summer_temperature:prev.winter_Darling	0.106	0.016	0.000
		years.post.flood	0.098	0.015	0.000
		summer_temperature:prev.winter_rain	-0.086	0.013	0.000
		RWI_da45	-0.113	0.023	0.000
		summer_Darling	-0.004	0.018	0.812
	eucalypt.foliage.RWI	veg.coverage.RWI	0.837	0.019	0.000
		summer_temperature:summer_rain	-0.513	0.016	0.000
		prev.winter_Darling	0.465	0.018	0.000
		summer_Darling	0.419	0.018	0.000
		summer_rain	-0.456	0.021	0.000
		summer_temperature	0.351	0.022	0.000
		summer_temperature:summer_Darling	0.275	0.022	0.000
		prev.winter_rain	-0.095	0.020	0.000
		RWI_da45	-0.111	0.026	0.000
		summer_temperature:prev.winter_Darling	-0.070	0.018	0.000
		years.post.flood	0.064	0.017	0.000
		summer_temperature:prev.winter_rain	0.016	0.015	0.276
	prey.index	summer_temperature:summer_rain	-0.398	0.044	0.000
		summer_rain	-0.451	0.052	0.000
		years.post.flood	-0.216	0.036	0.000
		veg.coverage.RWI	0.300	0.057	0.000
		summer_temperature	0.122	0.028	0.000
		prev.winter_Darling	0.104	0.035	0.003
		prev.winter_rain	-0.080	0.028	0.005
		summer_Darling	-0.030	0.038	0.427
		eucalypt.foliage.RWI	-0.020	0.051	0.689
		summer_temperature:summer_Darling	-0.007	0.032	0.840
	predator.index	summer_temperature:summer_rain	-0.795	0.041	0.000
		veg.coverage.RWI	0.897	0.055	0.000
		summer_rain	-0.672	0.048	0.000
		summer_temperature:prev.winter_Darling	0.406	0.037	0.000
		prev.winter_rain	-0.434	0.039	0.000
		RWI_da45	-0.500	0.051	0.000
		summer_temperature	0.396	0.047	0.000
		summer_Darling	-0.342	0.042	0.000
		eucalypt.foliage.RWI	-0.374	0.049	0.000
		summer_temperature:prev.winter_rain	0.194	0.030	0.000
		prev.winter_Darling	0.135	0.043	0.002

Species	Response	Predictor	Estimate	SE	p-value
		summer_temperature:summer_Darling	0.014	0.046	0.763
		years.post.flood	0.002	0.034	0.942
	SMI	TL.SVL	0.317	0.021	0.000
		prev.winter_rain	0.384	0.032	0.000
		summer_Darling	0.340	0.039	0.000
		prey.index	0.422	0.052	0.000
		prev.winter_Darling	0.213	0.030	0.000
		predator.index	0.119	0.023	0.000
		RWI_da45	-0.275	0.056	0.000
		eucalypt.foliage.RWI	-0.200	0.047	0.000
		summer_temperature	0.163	0.045	0.000
		years.post.flood	0.122	0.039	0.002
		summer_rain	0.072	0.024	0.002
		Age2	0.007	0.023	0.749
		veg.coverage.RWI	-0.004	0.045	0.931
***G. variegate* Station**	veg.coverage.Station	summer_temperature	1.086	0.007	0.000
		summer_rain	0.717	0.006	0.000
		RWI_da45	-0.592	0.008	0.000
		prev.winter_rain	0.327	0.006	0.000
		summer_Darling	-0.397	0.005	0.000
		summer_temperature:summer_rain	0.495	0.005	0.000
		summer_temperature:prev.winter_rain	0.212	0.004	0.000
		summer_temperature:summer_Darling	-0.477	0.008	0.000
		Station_usage	0.229	0.006	0.000
		summer_temperature:prev.winter_Darling	0.111	0.004	0.000
		years.post.flood	-0.110	0.005	0.000
		prev.winter_Darling	-0.101	0.005	0.000
	prey.index	summer_temperature:summer_rain	-0.393	0.032	0.000
		summer_Darling	0.256	0.023	0.000
		summer_rain	-0.395	0.043	0.000
		Station_usage	-0.238	0.031	0.000
		years.post.flood	-0.171	0.023	0.000
		veg.coverage.Station	0.250	0.042	0.000
		summer_temperature:summer_Darling	0.219	0.037	0.000
		prev.winter_rain	-0.139	0.029	0.000
		prev.winter_Darling	-0.077	0.020	0.000
		summer_temperature	-0.116	0.031	0.000
	predator.index	years.post.flood	-0.906	0.020	0.000
		summer_temperature:prev.winter_rain	0.657	0.021	0.000
		summer_temperature:prev.winter_Darling	0.403	0.018	0.000
		summer_temperature	1.595	0.073	0.000
		veg.coverage.Station	-1.027	0.062	0.000
		prev.winter_Darling	-0.327	0.021	0.000
		summer_Darling	-0.451	0.031	0.000
		summer_rain	0.620	0.050	0.000
		RWI_da45	-0.590	0.048	0.000
		summer_temperature:summer_rain	0.345	0.036	0.000
		summer_temperature:summer_Darling	-0.327	0.043	0.000

Species	Response	Predictor	Estimate	SE	p-value
		prev.winter_rain	0.204	0.030	0.000
		Station_usage	0.131	0.028	0.000
	SMI	TL.SVL	0.223	0.015	0.000
		summer_Darling	0.326	0.025	0.000
		prev.winter_Darling	-0.166	0.019	0.000
		prev.winter_rain	0.184	0.023	0.000
		summer_rain	0.106	0.020	0.000
		predator.index	0.065	0.018	0.000
		Station_usage	0.075	0.025	0.002
		Age2	-0.047	0.016	0.004
		veg.coverage.Station	-0.085	0.030	0.005
		prey.index	0.097	0.035	0.005
		RWI_da45	0.032	0.043	0.455
		summer_temperature	-0.026	0.047	0.571
		years.post.flood	0.005	0.029	0.875

Table S2.2.3: Scaled estimates, standard errors and p-values of each path per species for analyses of occupancy. All predictors are abbreviated; see Table S2.1.1 for explanations and calculations. ":" symbolises interactions. All paths were selected using GLMMs (Appendix S2.1) except the bold paths, which were added due to suggestions of Shipley's test of d-separation (Shipley 2009) when the test was significant and a plausible ecological connection could exist.

Species	Response	Predictor	Estimate	SE	p-value
M. boulengeri	herb.biomass.RWII	winter_Darling	0.666	0.267	0.032
		prev.winter_rain	0.538	0.256	0.062
		summer_rain	0.455	0.222	0.068
		RWII_da45	0.410	0.274	0.164
		shrub.coverage.RWII	-0.017	0.262	0.949
	shrub.coverage.RWII	RWII_da45	-0.726	0.260	0.018
		summer_Darling	-0.359	0.255	0.187
		winter_Darling	0.332	0.248	0.209
		herb.biomass.RWII	0.129	0.251	0.617
	prey.index	summer_Darling	0.146	0.255	0.567
		shrub.coverage.RWII	0.100	0.223	0.655
		years.post.flood	-0.058	0.324	0.858
		herb.biomass.RWII	0.031	0.188	0.870
	predator.index	shrub.coverage.RWII	0.664	0.253	0.027
		winter_Darling	-0.456	0.221	0.070
		summer_Darling	0.368	0.236	0.153
		summer_rain	-0.337	0.235	0.186
		herb.biomass.RWII	-0.208	0.244	0.416
		RWII_da45	-0.071	0.338	0.839
	psi.smoothed	summer_Darling	0.991	0.389	0.034
		years.post.flood	1.081	0.474	0.052
		psi.SE	0.743	0.487	0.166
		predator.index	-0.677	0.465	0.183
		prey.index	-0.591	0.589	0.346
		shrub.coverage.RWII	0.319	0.344	0.381
		herb.biomass.RWII	-0.122	0.281	0.675
C. regius	herb.biomass.RWII	winter_Darling	0.666	0.267	0.032

Species	Response	Predictor	Estimate	SE	p-value
		prev.winter_rain	0.538	0.256	0.062
		summer_rain	0.455	0.222	0.068
		RWII_da45	0.410	0.274	0.164
		shrub.coverage.RWII	-0.017	0.262	0.949
	shrub.coverage.RWII	RWII_da45	-0.726	0.260	0.018
		summer_Darling	-0.359	0.255	0.187
		winter_Darling	0.332	0.248	0.209
		herb.biomass.RWII	0.129	0.251	0.617
	prey.index	summer_Darling	0.146	0.255	0.567
		shrub.coverage.RWII	0.100	0.223	0.655
		years.post.flood	-0.058	0.324	0.858
		herb.biomass.RWII	0.031	0.188	0.870
	predator.index	shrub.coverage.RWII	0.613	0.246	0.035
		winter_Darling	-0.440	0.216	0.072
		summer_Darling	0.375	0.230	0.137
		summer_rain	-0.317	0.229	0.200
		herb.biomass.RWII	-0.244	0.238	0.333
		RWII_da45	-0.110	0.330	0.746
	psi.smoothed	psi.SE	0.427	0.161	0.029
		years.post.flood	0.580	0.222	0.031
		herb.biomass.RWII	0.512	0.201	0.034
		winter_Darling	0.494	0.216	0.051
		predator.index	0.297	0.243	0.256
		prey.index	-0.311	0.300	0.331
		shrub.coverage.RWII	0.016	0.210	0.942
H. binoei	herb.biomass.RWII	winter_Darling	0.666	0.267	0.032
		prev.winter_rain	0.538	0.256	0.062
		summer_rain	0.455	0.222	0.068
		RWII_da45	0.410	0.274	0.164
		shrub.coverage.RWII	-0.017	0.262	0.949
	shrub.coverage.RWII	RWII_da45	-0.726	0.260	0.018
		summer_Darling	-0.359	0.255	0.187
		winter_Darling	0.332	0.248	0.209
		herb.biomass.RWII	0.129	0.251	0.617
	prey.index	summer_Darling	0.146	0.255	0.567
		shrub.coverage.RWII	0.100	0.223	0.655
		years.post.flood	-0.058	0.324	0.858
		herb.biomass.RWII	0.031	0.188	0.870
	predator.index	summer_Darling	1.038	0.236	0.002
		RWII_da45	0.884	0.420	0.065
		summer_temperature	-0.466	0.336	0.199
		winter_Darling	-0.235	0.225	0.323
		shrub.coverage.RWII	0.134	0.254	0.611
		herb.biomass.RWII	0.002	0.213	0.994
	psi.smoothed	psi.SE	0.565	0.217	0.032
		winter_Darling	-0.493	0.247	0.081
		shrub.coverage.RWII	0.304	0.239	0.239
		years.post.flood	-0.334	0.291	0.285

Species	Response	Predictor	Estimate	SE	p-value
		predator.index	0.132	0.225	0.573
		herb.biomass.RWII	0.115	0.223	0.621
		prey.index	0.091	0.392	0.822
D. tessellatus	veg.coverage.RWI	prev.winter_rain	0.638	0.201	0.010
		RWI_da45	-0.374	0.203	0.095
		eucalypt.foliage.RWI	0.297	0.260	0.280
		summer_Darling	0.269	0.277	0.355
		years.post.flood	0.102	0.267	0.711
	eucalypt.foliage.RWI	summer_Darling	0.605	0.183	0.006
		veg.coverage.RWI	0.313	0.184	0.115
		summer_rain	0.117	0.172	0.510
	prey.index	eucalypt.foliage.RWI	0.212	0.334	0.526
		years.post.flood	-0.109	0.279	0.697
		veg.coverage.RWI	-0.025	0.244	0.918
		summer_Darling	-0.025	0.308	0.935
	predator.index	years.post.flood	-0.432	0.346	0.237
		eucalypt.foliage.RWI	-0.395	0.429	0.378
		veg.coverage.RWI	-0.247	0.313	0.446
		summer_Darling	0.280	0.421	0.519
	psi.smoothed	summer_temperature:summer_Darling	0.933	0.323	0.045
		years.post.flood	1.010	0.370	0.052
		summer_Darling	0.491	0.381	0.267
		prey.index	0.445	0.490	0.416
		eucalypt.foliage.RWI	-0.372	0.428	0.434
		psi.SE	-0.178	0.228	0.479
		prev.winter_rain	-0.146	0.399	0.734
		predator.index	-0.060	0.254	0.824
		veg.coverage.RWI	0.107	0.469	0.830
		summer_temperature	-0.082	0.392	0.846
		RWI_da45	0.001	0.516	0.998
L. punctatovittata	herb.biomass.RWII	winter_Darling	0.666	0.267	0.032
		prev.winter_rain	0.538	0.256	0.062
		summer_rain	0.455	0.222	0.068
		RWII_da45	0.410	0.274	0.164
		shrub.coverage.RWII	-0.017	0.262	0.949
	shrub.coverage.RWII	RWII_da45	-0.726	0.260	0.018
		summer_Darling	-0.359	0.255	0.187
		winter_Darling	0.332	0.248	0.209
		herb.biomass.RWII	0.129	0.251	0.617
	predator.index	summer_Darling	1.035	0.271	0.004
		RWII_da45	0.662	0.468	0.191
		summer_temperature	-0.373	0.358	0.325
		years.post.flood	0.186	0.322	0.578
		herb.biomass.RWII	-0.043	0.207	0.841
		shrub.coverage.RWII	0.008	0.252	0.975
	psi.smoothed	psi.SE	0.594	0.207	0.019
		years.post.flood	-0.555	0.273	0.072
		prev.winter_rain	0.396	0.232	0.123

Species	Response	Predictor	Estimate	SE	p-value
		herb.biomass.RWII	0.294	0.202	0.180
		predator.index	-0.211	0.214	0.350
		shrub.coverage.RWII	0.061	0.245	0.808
L. xanthura	herb.biomass.RWII	winter_Darling	0.666	0.267	0.032
		prev.winter_rain	0.538	0.256	0.062
		summer_rain	0.455	0.222	0.068
		RWII_da45	0.410	0.274	0.164
		shrub.coverage.RWII	-0.017	0.262	0.949
	shrub.coverage.RWII	RWII_da45	-0.726	0.260	0.018
		summer_Darling	-0.359	0.255	0.187
		winter_Darling	0.332	0.248	0.209
		herb.biomass.RWII	0.129	0.251	0.617
	predator.index	summer_Darling	1.035	0.271	0.004
		RWII_da45	0.662	0.468	0.191
		summer_temperature	-0.373	0.358	0.325
		years.post.flood	0.186	0.322	0.578
		herb.biomass.RWII	-0.043	0.207	0.841
		shrub.coverage.RWII	0.008	0.252	0.975
	psi.smoothed	psi.SE	0.831	0.151	0.001
		winter_Darling	-0.443	0.170	0.031
		predator.index	0.205	0.214	0.367
		herb.biomass.RWII	0.142	0.153	0.379
		summer_temperature	0.147	0.166	0.403
		summer_Darling	0.166	0.239	0.506
		shrub.coverage.RWII	-0.041	0.171	0.816
E. richardsonii	herb.biomass.RWII	winter_Darling	0.666	0.267	0.032
		prev.winter_rain	0.538	0.256	0.062
		summer_rain	0.455	0.222	0.068
		RWII_da45	0.410	0.274	0.164
		shrub.coverage.RWII	-0.017	0.262	0.949
	shrub.coverage.RWII	RWII_da45	-0.726	0.260	0.018
		summer_Darling	-0.359	0.255	0.187
		winter_Darling	0.332	0.248	0.209
		herb.biomass.RWII	0.129	0.251	0.617
	prey.index	years.post.flood	1.163	0.333	0.007
		summer_Darling	0.664	0.262	0.032
		summer_rain	0.539	0.213	0.032
		shrub.coverage.RWII	0.369	0.221	0.129
		prev.winter_rain	0.168	0.218	0.460
		herb.biomass.RWII	0.093	0.198	0.649
	predator.index	summer_Darling	1.036	0.240	0.002
		RWII_da45	0.889	0.428	0.068
		summer_temperature	-0.445	0.342	0.226
		winter_Darling	-0.241	0.229	0.322
		shrub.coverage.RWII	0.145	0.258	0.589
		herb.biomass.RWII	0.002	0.217	0.994
	psi.smoothed	psi.SE	0.815	0.143	0.001
		prev.winter_rain	0.277	0.120	0.054

Species	Response	Predictor	Estimate	SE	p-value
		summer_temperature:prev.winter_rain	-0.276	0.143	0.094
		shrub.coverage.RWII	0.120	0.119	0.347
		prey.index	0.086	0.105	0.440
		summer_temperature	-0.133	0.186	0.497
		herb.biomass.RWII	-0.063	0.114	0.598
		predator.index	0.022	0.090	0.812
***G. variegata* RI**	veg.coverage.RWI	prev.winter_rain	0.638	0.201	0.010
		RWI_da45	-0.374	0.203	0.095
		eucalypt.foliage.RWI	0.297	0.260	0.280
		summer_Darling	0.269	0.277	0.355
		years.post.flood	0.102	0.267	0.711
	eucalypt.foliage.RWI	summer_Darling	0.605	0.183	0.006
		veg.coverage.RWI	0.313	0.184	0.115
		summer_rain	0.117	0.172	0.510
	prey.index	eucalypt.foliage.RWI	0.212	0.334	0.526
		years.post.flood	-0.109	0.279	0.697
		veg.coverage.RWI	-0.025	0.244	0.918
		summer_Darling	-0.025	0.308	0.935
	predator.index	years.post.flood	-0.432	0.346	0.237
		eucalypt.foliage.RWI	-0.395	0.429	0.378
		veg.coverage.RWI	-0.247	0.313	0.446
		summer_Darling	0.280	0.421	0.519
	psi.smoothed	summer_temperature:prev.winter_rain	0.538	0.164	0.030
		summer_temperature	0.840	0.304	0.051
		psi.SE	-0.761	0.298	0.063
		eucalypt.foliage.RWI	-0.375	0.223	0.169
		RWI_da45	-0.513	0.377	0.245
		predator.index	-0.309	0.304	0.367
		years.post.flood	-0.213	0.227	0.401
		prev.winter_rain	-0.272	0.302	0.419
		summer_rain	0.227	0.261	0.434
		prey.index	0.197	0.324	0.576
		veg.coverage.RWI	-0.034	0.316	0.918

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10.3.3 Appendix S3: Summary results of structural equation models (SEMs)

S3.1. Body condition SEMs

Tables S3.1.1-S3.1.9 show corrected direct effects (scaled standardised path coefficients) of each climatic and biotic factor on individual body condition, all indirect effects (scaled standardised path coefficients) on biotic parameters, the total effect on body condition as the sum of all potential paths (Fig. 1 main text), and the overall indirect effects as sum of all indirect paths on body condition equaling the total effect minus the direct effect (i.e., ensuring to consider also interactions along paths with several biotic factors). Significant effects are highlighted in yellow, almost significant effects (p ≈ 0.1) are highlighted in green. Factor names follow Table S2.1.1. Crossed cells symbolise that those paths were not considered.

Table S3.1.1: *Morethia boulengeri*

factor	direct effect	indirect on herb-layer biomass	indirect on shrub coverage	indirect on prey	indirect on predators	total effect	indirect effect
summer temperature	-0.05	-0.13	0.46	0.11	-0.66	-0.05	0.00
da45	-0.15	0.24	-0.94	0.00	0.35	0.06	0.22
summer rain	0.05	0.37	-0.16	-0.25	-0.06	0.13	0.08
winter rain	0.13	0.44	0.41	0.02	0.19	0.08	-0.05
summer Darling	0.06	0.00	-0.22	0.15	0.80	-0.01	-0.07
winter Darling	0.03	0.61	0.45	-0.04	-0.82	0.18	0.15
years post flood	0.07	0.00	0.14	-0.12	-0.13	0.04	-0.03
herb-layer biomass	-0.02		-0.47	0.01	-0.57	0.18	0.21
shrub coverage	-0.14	-0.49		0.17	0.51	-0.25	-0.11
prey	0.16					0.16	0.00
predation	-0.19					-0.19	0.00

Table S3.1.2: *Ctenotus regius*

factor	direct effect	indirect on herb-layer biomass	indirect on shrub coverage	indirect on prey	indirect on predators	total effect	indirect effect
summer temperature	-0.21	0.17	0.15	-0.13	0.09	-0.24	-0.03
da45	0.04	0.13	-0.11	0.00	0.00	0.08	0.04
summer rain	-0.45	0.60	0.51	-0.03	-0.06	-0.21	0.24
winter rain	0.13	0.19	0.06	0.32	0.02	0.20	0.07
summer Darling	0.45	0.00	-0.13	0.07	0.21	0.27	-0.18
winter Darling	-0.56	0.46	0.27	0.19	-0.07	-0.34	0.22
years post flood	0.00	0.00	-0.34	-0.22	0.18	-0.18	-0.18
herb-layer biomass	-0.11		-0.80	0.04	-0.89	0.33	0.44
shrub coverage	0.65	-0.67		0.05	0.25	-0.02	-0.67
prey	0.09					0.09	0.00
predation	-0.88					-0.88	0.00

Table S3.1.3: *Heteronotia binoei*

factor	direct effect	indirect on vegetation coverage	indirect on station usage	indirect on prey	indirect on predators	total effect	indirect effect
summer temperature	0.31	1.38		-0.05	1.08	0.37	0.06
da45	-0.47	-0.61		0.00	-0.37	-0.51	-0.05
summer rain	0.00	1.37		-0.52	-0.71	0.19	0.19
winter rain	0.52	0.68		-0.28	0.68	0.47	-0.05
summer Darling	0.01	-0.56		0.30	0.33	-0.05	-0.06
winter Darling	0.12	-0.11		0.00	0.51	0.03	-0.09
years post flood	0.00	-0.19		-0.05	-0.26	-0.01	-0.01
vegetation coverage	0.04			0.43	-0.14	0.16	0.13
prey	0.24					0.24	0.00
predation	-0.14					-0.14	0.00
station usage	-0.32	0.04		-0.15	-0.10	-0.33	-0.02

Table S3.1.4: *Diplodactylus tessellatus*

factor	direct effect	indirect on vegetation coverage	indirect on eucalypt foliage	indirect on prey	indirect on predators	total effect	indirect effect
summer temperature	0.67	0.11	0.14	0.02	0.51	0.66	-0.01
da45	-0.16	-0.08	-0.54	0.00	-0.79	-0.16	0.01
summer rain	0.16	0.32	-0.22	-0.32	0.14	0.02	-0.13
winter rain	0.67	0.36	0.27	-0.26	0.56	0.59	-0.08
summer Darling	-0.06	0.13	0.39	-0.10	0.28	-0.06	0.00
winter Darling	-0.01	-0.18	-0.15	0.06	-0.17	-0.02	-0.01
years post flood	-0.05	0.08	0.00	-0.16	-0.23	-0.08	-0.03
vegetation coverage	-0.22		0.34	0.68	-0.83	0.24	0.46
eucalypt foliage	0.12	0.51		-0.26	-0.32	0.15	0.03
prey	0.50					0.50	0.00
predation	-0.14					-0.14	0.00

Table S3.1.5: *Lerista punctatovittata*

factor	direct effect	indirect on herb-layer biomass	indirect on shrub coverage	indirect on predators	total effect	indirect effect
summer temperature	-0.27	-0.12	-0.06	-0.06	-0.30	-0.03
da45	0.00	0.13	-0.21	0.42	0.11	0.11
summer rain	0.00	0.51	0.57	0.00	0.03	0.03
winter rain	0.00	0.66	0.78	0.08	0.02	0.02
summer Darling	0.00	0.00	0.07	1.10	-0.05	-0.05
winter Darling	-0.41	0.79	0.93	-0.14	-0.38	0.03
years post flood	-0.37	0.00	0.14	0.08	-0.42	-0.05
herb-layer biomass	0.27		-1.00	0.14	0.42	0.15
shrub coverage	-0.15	-0.66		0.14	-0.33	-0.18
predation	-0.02				-0.02	0.00

Table S3.1.6: *Lerista xanthura*

factor	direct effect	indirect on herb-layer biomass	indirect on shrub coverage	indirect on predators	total effect	indirect effect
summer temperature	-0.82	-0.47	0.54	0.53	-0.89	-0.07
da45	2.07	0.41	-1.01	-0.25	1.84	-0.22
summer rain	0.00	0.21	0.15	0.00	0.17	0.17
winter rain	0.00	0.10	0.54	0.80	0.16	0.16
summer Darling	0.00	0.00	-0.41	0.49	-0.27	-0.27
winter Darling	-1.07	0.50	0.57	-0.23	-0.53	0.54
years post flood	-1.07	0.00	-0.43	-0.94	-1.11	-0.04
herb-layer biomass	0.97		-0.38	0.82	0.48	-0.49
shrub coverage	0.91	-0.53		0.03	0.46	-0.45
predation	-0.17				-0.17	0.00

Table S3.1.7: *Eremiascincus richardsonii*

factor	direct effect	indirect on herb-layer biomass	indirect on shrub coverage	indirect on prey	indirect on predators	total effect	indirect effect
summer temperature	-0.67	-0.20	0.46	-0.47	0.24	-0.68	-0.01
da45	0.95	0.04	-0.59	0.22	0.00	0.80	-0.15
summer rain	0.00	0.28	0.36	0.58	0.04	0.10	0.10
winter rain	0.00	0.54	0.77	0.58	0.39	-0.05	-0.05
summer Darling	0.97	0.00	-0.17	0.82	0.96	0.60	-0.36
winter Darling	0.00	0.79	0.82	0.50	0.01	0.04	0.04
years post flood	0.11	0.00	0.07	0.62	-0.02	0.28	0.17
herb-layer biomass	-0.09		-0.70	-0.68	0.24	-0.40	-0.32
shrub coverage	0.03	-0.67		0.20	0.03	0.31	0.27
prey	0.22					0.22	0.00
predation	-0.51					-0.51	0.00

Table S3.1.8: *Gehyra variegata* RWI

factor	direct effect	indirect on vegetation coverage	indirect on eucalypt foliage	indirect on prey	indirect on predators	total effect	indirect effect
summer temperature	0.16	0.01	0.67	0.30	0.90	0.33	0.16
da45	-0.27	-0.11	-0.11	0.00	-0.50	-0.32	-0.05
summer rain	0.07	0.56	-0.80	-0.57	-1.38	-0.24	-0.31
winter rain	0.38	0.29	-0.08	-0.08	-0.26	0.33	-0.05
summer Darling	0.34	-0.01	0.60	-0.03	-0.33	0.22	-0.12
winter Darling	0.21	-0.46	0.42	0.10	0.50	0.26	0.05
years post flood	0.12	0.10	0.06	-0.22	0.00	0.03	-0.10
vegetation coverage	0.00		0.84	0.30	0.90	0.02	0.02
eucalypt foliage	-0.20	0.65		-0.02	-0.37	-0.10	0.10
prey	0.42					0.42	0.00
predation	0.12					0.12	0.00

Table S3.1.9: *Gehyra variegata* station

factor	direct effect	indirect on vegetation coverage	indirect on station useage	indirect on prey	indirect on predators	total effect	indirect effect
summer temperature	-0.03	1.69		0.10	1.96	-0.11	-0.08
da45	0.03	-0.59		0.00	-0.59	0.07	0.04
summer rain	0.11	1.55		-0.43	1.30	-0.05	-0.16
winter rain	0.18	0.69		-0.14	1.49	0.18	0.00
summer Darling	0.33	-1.20		0.28	-1.09	0.44	0.11
winter Darling	-0.17	0.09		-0.08	0.46	-0.15	0.01
years post flood	0.00	-0.11		-0.17	-0.91	-0.06	-0.06
vegetation coverage	-0.09			0.25	-1.03	-0.13	-0.04
prey	0.10					0.10	0.00
predation	0.06					0.06	0.00
station usage	0.08	0.23		-0.24	0.13	0.03	-0.04

S3.2. Occupancy SEMs.

Tables S3.2.1-S3.2.8 show corrected direct effects (scaled standardised path coefficients) of each climatic and biotic factor on smoothed annual occupancy, all indirect effects (scaled standardised path coefficients) on biotic parameters, the total effect on body condition as the sum of all potential paths (Fig. 1 of the main text), and the overall indirect effects as sum of all indirect paths on body condition equaling the total effect minus the direct effect (i.e., ensuring to consider also interactions along paths with several biotic factors). Significant effects are highlighted in yellow, almost significant effects (p ≈ 0.1) are highlighted in green. Factor names follow Table S2.1.1. Crossed cells symbolise that those paths were not considered.

Table S3.2.1: *Morethia boulengeri*

factor	direct effect	indirect on herb-layer biomass	indirect on shrub coverage	indirect on prey	indirect on predators	total effect	indirect effect
summer temperature	0.00	0.00	0.00	0.00	0.00	0.00	0.00
da45	0.00	0.41	-0.73	0.00	-0.07	0.18	0.18
summer rain	0.00	0.45	0.00	0.00	-0.34	0.22	0.22
winter rain	0.00	0.54	0.00	0.00	0.00	-0.01	-0.01
summer Darling	0.99	0.00	-0.36	0.15	0.37	0.72	-0.27
winter Darling	0.00	0.67	0.33	0.00	-0.46	0.23	0.23
years post flood	1.08	0.00	0.00	-0.06	0.00	1.12	0.03
herb-layer biomass	-0.12		0.13	0.03	-0.21	-0.02	0.10
shrub coverage	0.32	-0.02		0.10	0.66	-0.19	-0.51
prey	-0.59					-0.59	0.00
predation	-0.68					-0.68	0.00

Table S3.2.2: *Ctenotus regius*

factor	direct effect	indirect on herb-layer biomass	indirect on shrub coverage	indirect on prey	indirect on predators	total effect	indirect effect
summer temperature	0.00	0.00	0.00	0.00	0.00	0.00	0.00
da45	0.00	0.41	-0.73	0.00	-0.11	0.04	0.04
summer rain	0.00	0.45	0.00	0.00	-0.32	0.11	0.11
winter rain	0.00	0.54	0.00	0.00	0.00	0.24	0.24
summer Darling	0.00	0.00	-0.36	0.15	0.38	0.01	0.01
winter Darling	0.49	0.67	0.33	0.00	-0.44	0.72	0.22
years post flood	0.58	0.00	0.00	-0.06	0.00	0.60	0.02
herb-layer biomass	0.51		0.13	0.03	-0.24	0.45	-0.06
shrub coverage	0.02	-0.02		0.10	0.61	0.16	0.14
prey	-0.31					-0.31	0.00
predation	0.30					0.30	0.00

Table S3.2.3: *Heteronotia binoei*

factor	direct effect	indirect on herb-layer biomass	indirect on shrub coverage	indirect on prey	indirect on predators	total effect	indirect effect
summer temperature	0.00	0.00	0.00	0.00	-0.47	-0.06	-0.06
da45	0.00	0.41	-0.73	0.00	0.88	-0.06	-0.06
summer rain	0.00	0.45	0.00	0.00	0.00	0.07	0.07
winter rain	0.00	0.54	0.00	0.00	0.00	0.09	0.09
summer Darling	0.00	0.00	-0.36	0.15	1.04	0.03	0.03
winter Darling	-0.49	0.67	0.33	0.00	-0.24	-0.31	0.18
years post flood	-0.33	0.00	0.00	-0.06	0.00	-0.34	-0.01
herb-layer biomass	0.11		0.13	0.03	0.00	0.16	0.05
shrub coverage	0.30	-0.02		0.10	0.13	0.33	0.02
prey	0.09					0.09	0.00
predation	0.13					0.13	0.00

Table S3.2.4: *Diplodactylus tessellatus*

factor	direct effect	indirect on vegetation coverage	indirect on eucalypt foliage	indirect on prey	indirect on predators	total effect	indirect effect
summer temperature	0.38	0.00	0.00	0.00	0.00	0.38	0.00
da45	0.00	-0.37	0.00	0.00	0.00	-0.04	-0.04
summer rain	0.00	0.00	0.12	0.00	0.00	-0.03	-0.03
winter rain	-0.15	0.64	0.00	0.00	0.00	-0.07	0.07
summer Darling	0.84	0.27	0.61	-0.03	0.28	0.69	-0.15
winter Darling	0.00	0.00	0.00	0.00	0.00	0.00	0.00
years post flood	1.01	0.10	0.00	-0.11	-0.43	1.00	-0.01
vegetation coverage	0.11		0.31	-0.03	-0.25	0.11	0.00
eucalypt foliage	-0.37	0.30		0.21	-0.39	-0.25	0.12
prey	0.44					0.44	0.00
predation	-0.06					-0.06	0.00

Table S3.2.5: *Lerista punctatovittata*

factor	direct effect	indirect on herb-layer biomass	indirect on shrub coverage	indirect on predators	total effect	indirect effect
summer temperature	0.00	0.00	0.00	-0.37	0.08	0.08
da45	0.00	0.41	-0.73	0.66	-0.05	-0.05
summer rain	0.00	0.45	0.00	0.00	0.14	0.14
winter rain	0.40	0.54	0.00	0.00	0.56	0.17
summer Darling	0.00	0.00	-0.36	1.03	-0.24	-0.24
winter Darling	0.00	0.67	0.33	0.00	0.22	0.22
years post flood	-0.55	0.00	0.00	0.19	-0.59	-0.04
herb-layer biomass	0.29		0.13	-0.04	0.31	0.02
shrub coverage	0.06	-0.02		0.01	0.05	-0.01
predation	-0.21				-0.21	0.00

Table S3.2.6: *Lerista xanthura*

factor	direct effect	indirect on herb-layer biomass	indirect on shrub coverage	indirect on predators	total effect	indirect effect
summer temperature	0.15	0.00	0.00	-0.37	0.07	-0.08
da45	0.00	0.41	-0.73	0.66	0.22	0.22
summer rain	0.00	0.45	0.00	0.00	0.06	0.06
winter rain	0.00	0.54	0.00	0.00	0.07	0.07
summer Darling	0.17	0.00	-0.36	1.03	0.39	0.23
winter Darling	-0.44	0.67	0.33	0.00	-0.37	0.07
years post flood	0.00	0.00	0.00	0.19	0.04	0.04
herb-layer biomass	0.14		0.13	-0.04	0.13	-0.01
shrub coverage	-0.04	-0.02		0.01	-0.04	0.00
predation	0.20				0.20	0.00

Table S3.2.7: *Eremiascincus richardsonii*

factor	direct effect	indirect on herb-layer biomass	indirect on shrub coverage	indirect on prey	indirect on predators	total effect	indirect effect
summer temperature	-0.21	0.00	0.00	0.00	-0.44	-0.22	-0.01
da45	0.00	0.41	-0.73	0.00	0.89	-0.11	-0.11
summer rain	0.00	0.45	0.00	0.54	0.00	0.03	0.03
winter rain	0.33	0.54	0.00	0.17	0.00	0.33	0.00
summer Darling	0.00	0.00	-0.36	0.66	1.04	0.02	0.02
winter Darling	0.00	0.67	0.33	0.00	-0.24	0.02	0.02
years post flood	0.00	0.00	0.00	1.16	0.00	0.10	0.10
herb-layer biomass	-0.06		0.13	0.09	0.00	-0.03	0.03
shrub coverage	0.12	-0.02		0.37	0.14	0.16	0.04
prey	0.09					0.09	0.00
predation	0.02					0.02	0.00

Table S3.2.8: *Gehyra variegata* RWI

factor	direct effect	indirect on vegetation coverage	indirect on eucalypt foliage	indirect on prey	indirect on predators	total effect	indirect effect
summer temperature	0.69	0.00	0.00	0.00	0.00	0.69	0.00
da45	-0.51	-0.37	0.00	0.00	0.00	-0.53	-0.01
summer rain	0.23	0.00	0.12	0.00	0.00	0.20	-0.02
winter rain	0.10	0.64	0.00	0.00	0.00	0.12	0.02
summer Darling	0.00	0.27	0.61	-0.03	0.28	-0.21	-0.21
winter Darling	0.00	0.00	0.00	0.00	0.00	0.00	0.00
years post flood	-0.21	0.10	0.00	-0.11	-0.43	-0.10	0.12
vegetation coverage	-0.03		0.31	-0.03	-0.25	0.04	0.07
eucalypt foliage	-0.37	0.30		0.21	-0.39	-0.21	0.16
prey	0.20					0.20	0.00
predation	-0.31					-0.31	0.00

Photo by Annegret Grimm-Seyfarth.