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Effects of environmental predictability on life history traits and population dynamics. Insights from a three-year population experiment on the common lizard (*Zootoca vivipara*)

Efectos de la previsibilidad ambiental en las historias de vida y la dinámica de poblaciones. Estudio basado en un experimento poblacional de tres años con la lagartija de turbera (*Zootoca vivípara*)

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TESIS DOCTORAL

Instituto Pirenaico de Ecología (IPE-CSIC)

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"The wonderful things in life are the things you do, not the things you have"

(Reinhold Messner)

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Abstract

A central theme in ecology and evolution is to understand whether and how species respond to environmental changes. During the last few decades, the amount of studies focusing on how species might cope with climate change has been steeply growing, given the importance of the actual climate change. At present, it is widely accepted that changes in mean environmental conditions can affect individual performance, life history strategies and population dynamics. While most climate change scenarios forecast a change in average climatic conditions, they as well predict a decrease in environmental predictability. However, evidence for the effects of environmental predictability is scarce and the few existing studies were mainly theoretical or generated extreme events, which are by themselves negative. Therefore, robust evidence for the predicted negative effects is needed and experiments should test the impact of environmental predictability on life-history traits and population dynamics. For this reason, this doctoral thesis aims at providing robust evidence for the effects of environmental predictability on life-history traits, population dynamics, and species responses.

We experimentally tested whether and how changes in the predictability of precipitation affected life history traits and population dynamics of the common lizard *Zootoca vivipara*, a highly hygrophile species. We simulated more and less predictable precipitation in 12 semi-natural populations. Populations were maintained during one year and the experiment was repeated in two subsequent years. This experimental design allows to understand the generality of the responses and it allows testing whether differences in average climatic conditions may affect differences induced by precipitation predictability. Several parameters were measured to unravel effects of environmental predictability on individual performance (survival, reproduction, growth, body condition and ornamental coloration) and to allow for complex population dynamic models.

Decreased environmental predictability, let to reduced growth of yearlings and reduced body condition of female juveniles, but no effects on body condition, growth and survival of adults. This suggests that different age classes and sexes might exhibit different sensitivities to environmental predictability. Less predictable environments negatively affected ornamental coloration of adult males, which shows that less predictable environments are costly. This also suggests that ornamental coloration may act as an early signal of changes in environmental conditions. The results also show that

individuals exhibit compensatory strategies to prevent detrimental effects on fitness. More specifically, the observed differential investment in adult growth, body condition and male ornamental coloration may have allowed to compensate negative effects of decreased precipitation predictability, since no significant differences in reproductive parameters between environmental predictability treatments were found at the end of the experiment.

Environmental predictability did not significantly affect the individual key life history traits (i.e. survival and reproduction) and suggesting that compensatory strategies may have prevented major loses in fitness and effects on population dynamics. Nevertheless, the here applied stage-structured matrix model showed that less predictable environments led to a significant decrease of the population growth rate. This suggests that in order to assess the potential effect of climate change on species persistence, complex population dynamics modelling is required.

This doctoral thesis is one of the first experimental studies demonstrating whether and how species might respond to changes in environmental predictability. The obtained results underpin predictions from theoretic models, that decreased environmental predictability might negatively affect species responses. The results also suggest that decreased environmental predictability may seriously reduce population persistence and increase species extinction risk. Since species, which are highly susceptible to changes in abiotic conditions, might respond similarly to changes in environmental predictability, the forecasted decrease in environmental predictability might aggravate the actual trends of species decline and extinction. This shows that environmental predictability is a very important non-neglectable determinant of population dynamics, which highlights the necessity to consider its effects in studies forecasting the consequences of climate change.

Resumen

Un tema central en ecología y evolución es entender si y cómo las especies responden a los cambios ambientales. En los últimos años ha crecido considerablemente el número de estudios que investigan cómo las especies pueden enfrentarse al cambio climático. Actualmente, está ampliamente aceptado que los individuos, las historias de vida y la dinámica de poblaciones pueden verse afectados por los cambios en las condiciones ambientales. La mayoría de los escenarios de cambio climático pronostican un cambio en las medias de los parámetros ambientales, pero también predicen una disminución de la previsibilidad ambiental. Sin embargo, hay pocos indicios sobre los efectos de la previsibilidad ambiental y la mayoría de los estudios son teóricos o generan eventos extremos y predicen efectos negativos. Por lo tanto, se requieren evidencias robustas que corroboren los efectos negativos predichos y también son necesarios estudios experimentales que permitan comprobar los efectos de la previsibilidad ambiental. Por esta razón, el objetivo principal de esta tesis doctoral es aportar evidencias robustas sobre como la previsibilidad ambiental afecta a las historias de vida y la dinámica de poblaciones.

Se ha testado experimentalmente si y como afectan los cambios en la previsibilidad ambiental a las historias de vida y la dinámica de poblaciones de la lagartija de turbera (*Zootoca vivípara*), una especie altamente hidrófila. Se han simulado 12 poblaciones semi-naturales con precipitación menos o más previsible. El experimento en las poblaciones tuvo la duración de un año y éste se repitió 3 veces seguidas. Este tipo de diseño experimental permite entender la generalidad de las respuestas y también testar si los cambios en las medias ambientales pueden alterar los efectos de la previsibilidad ambiental. Se midieron varios parámetros a nivel de individuo (supervivencia, reproducción, crecimiento, condición y coloración ornamental) para determinar los efectos de la previsibilidad ambiental y para poder realizar análisis complejos sobre dinámica de poblaciones.

Los resultados obtenidos demostraron que en ambientes menos previsibles los individuos de un año crecieron menos y las hembras juveniles presentaban peor condición. Sin embargo, no se encontraron efectos en los individuos adultos, tanto en crecimiento como en supervivencia. Esto sugiere que diferentes clases de edad y sexos pueden mostrar sensibilidades diferentes frente a la previsibilidad ambiental. También se encontraron efectos negativos sobre la coloración ornamental de los adultos. Esto señala que los ambientes menos previsibles pueden generar costes a los individuos

adultos. Además, sugiere que la coloración ornamental puede actuar como una señal precoz de los cambios ambientales, ya que son los primeros signos de un impacto negativo, antes de afectar negativamente a la condición corporal, al crecimiento y a la reproducción. Estos resultados también muestran que los individuos pueden desarrollar estrategias compensatorias para prevenir efectos perjudiciales en la eficacia biológica ("fitness"). Específicamente, se ha observado que los individuos pueden invertir de forma diferencial en crecimiento, condición y coloración ornamental. Esto les ha permitido compensar los efectos negativos de ambientes menos previsibles y por lo tanto, no se han encontrado diferencias significativas en reproducción al final del experimento entre los tratamientos de predictibilidad ambiental.

En definitiva, no se han encontrado diferencias significativas en parámetros clave cómo la reproducción y supervivencia y además, se han observado estrategias compensatorias. Este resultado sugiere que los individuos pueden haber prevenido efectos drásticos en la eficacia biológica y también en la dinámica de poblaciones. Sin embargo, aplicando un modelo de matrices estacional basado en estructuras de edad, se ha observado un decrecimiento de las poblaciones en los ambientes menos previsibles. Esto indica que es necesario utilizar modelos de dinámica de poblaciones complejos para poder evaluar el efecto potencial del cambio climático en la supervivencia de las especies.

Esta tesis doctoral es uno de los primeros estudios experimentales que demuestra como las especies pueden responder a cambios en la previsibilidad ambiental. Los resultados obtenidos respaldan las predicciones teóricas que apuntan que ambientes menos previsibles podrían afectar de forma negativa a las especies. Estos resultados también indican que la persistencia de las poblaciones se podría ver seriamente afectada en ambientes menos previsibles y pudiendo aumentar así, el riesgo de extinción. Además, la previsibilidad ambiental podría afectar de forma similar a otras especies altamente dependientes de las condiciones ambientales y podría empeorar la actual tendencia de disminución y extinción de especies. Esto demuestra que la previsibilidad ambiental es un factor determinante para la dinámica de poblaciones y que se deberían considerar sus efectos para poder predecir las consecuencias del cambio climático.

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Chapter 1

General introduction and objectives

1.1. Environmental change

Environmental change is present everywhere and change is the norm rather than the exception in natural environments (Córdoba-Aguilar et al. 2018). As described in Johnson et al. (1997) environmental change is defined as a change or disturbance of the environment that might occur through natural processes and/or due to human influences. Furthermore, environments are rarely constant (e.g. Donohue and Schmitt 1999; Sergio et al. 2011) and environmental change can take place at all possible geospheres (Johnson et al. 1997), from the atmosphere to the biosphere (see examples in Table 1.1). Thus, environmental change is ubiquitous and species will have to deal with changes of the inhabited environment.

Table 1.1. Examples of environmental changes at different geospheres. Adapted from Johnson et al. (1997).

Geospheres	Examples of environmental changes
Atmosphere	Changes in precipitation or temperature, changes in atmosphere composition and aerosols.
Hydrosphere	Changes in chemical composition of water, nutrients and fluxes.
Lithosphere	Habitat changes, destruction or fragmentation like dam building or quarrying.
Pedosphere	Erosion, deposition and changes in chemical, physical or biological elements of soil.
Biosphere	Biotic changes of communities, populations or, even, species. I.e. extinctions, changing distributions, etc.

Human activities are an important source of environmental change, since they contribute to climate change, habitat destruction, habitat fragmentation, and since humans introduction invasive species, and overharvest resources (Wong and Candolin 2015). Although environmental changes have been occurring before the arrival of humans, human-induced environmental changes might often put organisms into evolutionarily novel conditions that typically involve more rapid change than organisms have experienced previously (Palumbi 2008; van Baaren and Candolin 2018).

Changes in environmental conditions may potentially affect organisms (e.g. Parmesan and Yohe 2003; Chen et al. 2011; Bestion et al. 2015), destabilize populations (Lindstrom and Kokko 2002) and increase their susceptibility to extinction (Lande 1993; Foden et al. 2008; Melbourne and Hastings 2008; Ashander et al. 2016). Understanding the ecological and evolutionary mechanisms underlying species responses to environmental change is thus essential to predict population dynamics and ecosystem function, and for conservation efforts (Ferrière et al. 2004; Saccheri and Hanski 2006; Kinnison and Hairston 2007; Chevin et al. 2013).

Species can be classified into three categories with respect to their likely response to environmental changes (Fig. 1.1; Williams et al. 2008; Hoffmann and Sgró 2011). Species may:

1. Cope with changing environments.
2. Escape changing conditions by moving to better suitable environments.
3. Not be able to escape or cope and may thus die and go extinct.

The first two categories do not directly affect the overall biodiversity. The second category affects the distribution of biodiversity, and the third one drastically reduces biodiversity (Hughes et al. 2003; Thomas et al. 2004; Botkin et al. 2007). Species might cope with changing environments by means of at least two different mechanisms:

1. Species may exhibit a genetic response and adapt to changing habitats due to the survival of the best-adapted individuals.
2. Species may exhibit a plastic response and adapt to changing environments by adjusting their behavior.

Although there is increasing evidence that genetic responses can be fast (Bell and Gonzalez 2009; Lavergne et al. 2010), genetic responses usually require longer time periods than plastic responses and their evolution may not necessarily match with the timing of the environmental change (Freeman et al. 2007). The nature and the time-scale of the environmental changes are suggested to determine the type and rate of responses (Kokko and López-sepulcre 2018). Behavioral responses may directly affect population dynamics when they affect key demographic parameters such as survival or reproduction (Fig. 1.1). Behavioral responses may be beneficial and prevent individuals from suffering fitness losses in new conditions (Tuomainen and Candolin 2011). If behavioral responses are not sufficient to prevent fitness loss, negative effects on key demographic parameters are predicted, which might decrease population growth rate and increase extinction risk (Badyaev 2005; Chevin et al. 2010).
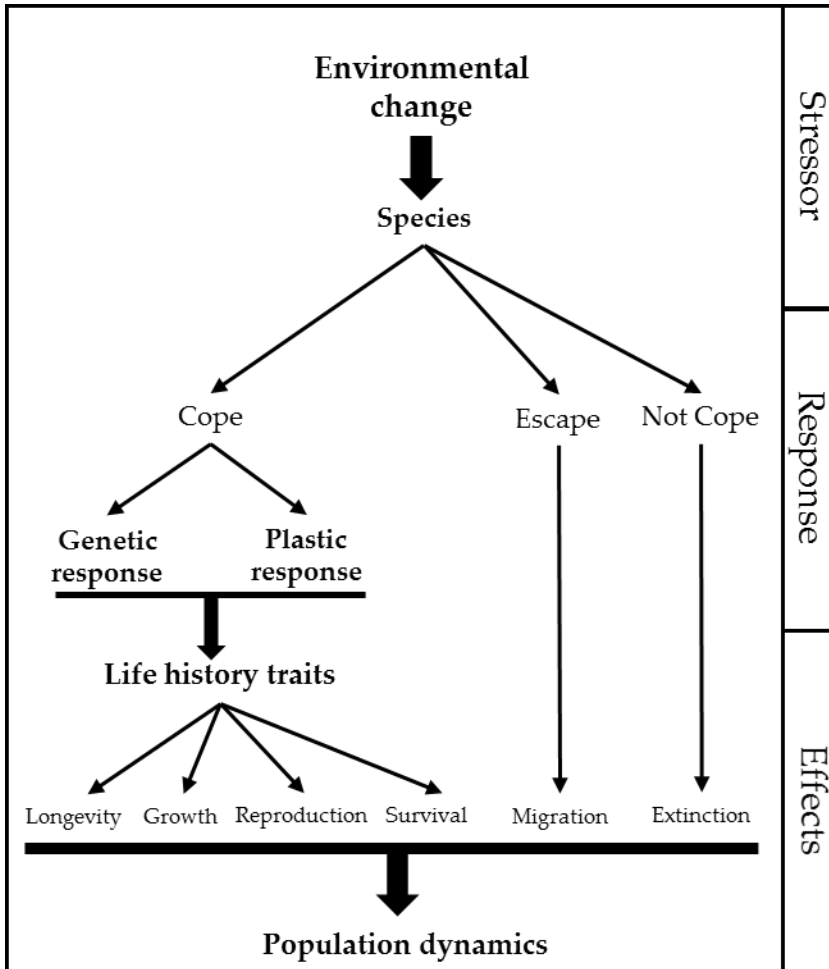
Figure 1.1. Schematic diagram showing how an environmental stressor might affect individuals and the responses that individuals could adopt. Furthermore, these responses might affect life history traits and thereby population dynamics.

Behavioral responses may act trough sexually selection, which can provoke changes in offspring number and quality (Candolin and Heuschele 2008; Heuschele et al. 2012) and thereby affect population growth rate (Kokko et al. 2001). Furthermore, behavioral responses can be innovative, for example, if they allow to exploit novel resources, which may positively affect population growth rates and allow individuals, populations, and species to cope with new environments (Candolin and Wong 2015). In addition, when environmental changes are predictable, maternal effects may evolve, which may increase offspring fitness (Marshall and Uller 2007). Finally, it is important to mention that behavioral responses, that allow species to cope with changing conditions, are

generally not associated with an evolutionary change and associated evolutionary change may take some time (Ghalambor et al. 2007). See some examples of behavior responses due to environmental changes in table 1.2.

Table 1.2. Examples of behaviour responses to environmental changes. Adapted from Tuomainen and Candolin (2011).

Environmental changes	Behavioral response	Species	Reference
Temperature	Adjust reproduction timing Change feeding rate	*Zootoca vivipara* *Nucella ostrina*	Massot et al. 2017 Yamane and Gilman 2009
Humidity	Affect female yearlings growth	*Zootoca vivipara*	Romero-Diaz et al. 2017
Habitat loss	Change ranging behavior	*Tringa totanus*	Burton and Armitage 2008
Pesticides	Affect activity patterns	*Hyla versicolor*	Relyea and Mills 2001
Adult density	Affect inter-class competition	*Zootoca vivipara*	San-Jose et al. 2016
Visibility	Altered mate choice	Cichlids	Seehausen et al. 1997
Change light intensity	Change skin coloration	Crocodiles	Merchant et al. 2018

1.2. The current climate change

The currently observed global climate change is an important driver of environmental change and a major threat to biodiversity (Bellard et al. 2012; Stocker et al. 2013). While some of the past global climate changes were associated with catastrophic events (e.g. meteorite impacts; Brusatte et al. 2015), it has been suggested that anthropogenic activities may be the principal reason of the present global climate change (Stocker et al. 2013). Under climate change, behavioral responses might be beneficial and may allow individuals and species to rapidly cope with changing climate, for example by means of dispersal. However, nowadays opportunities for dispersal and adaptation might be limited by human made habitat fragmentation and barriers (Candolin and Wong 2015)

and thus fast responses allow individuals to cope with the current changing climate conditions might be hindered (Freeman et al. 2007; Chevin et al. 2010; Sinervo et al. 2010).

Genetics
- Natural selection
- Allele diversity
- Mutation rates

Physiology
- Fecundity
- Survival
- Activity rates and rhythms

Behaviour
- Migration departure / arrival
- Growing season length
- Hatching
- Hibernation

Dynamics
- Age structure
- Sex ratio
- Abundance
- Growth rate

Distribution
- Habitat quantity and quality
- Ecological niche
- Range size and localization

Interspecific relationships
- Desynchronization
- Uncoupling
- New interactions

Temperature and precipitation:
Means
Predictability
Extremes
Seasonality

Organisms

Populations

Species

Figure 1.2. Predicted effects global of climate change (left) on different levels of biodiversity (right). Adapted from Bellard et al. (2012).

Global climate change is predicted to increase mean global temperature, affect mean precipitation, increase extreme events and decrease the predictability of these abiotic factors (Easterling et al. 2000; Allan and Soden 2008; Stocker et al. 2013). Other consequences are increased number and increased length of drought periods (Allan and Soden 2008; Dai 2011; Stocker et al. 2013), decreased atmosphere water vapor (Barnett et al. 2005; Wentz et al. 2007) and decreased ice cover (Arnell 1999; Barnett et al. 2005; Stocker et al. 2013). This is in line with many studies showing that the actual species trends are decreasing (Sinervo et al. 2010; Hoffmann and Sgró 2011; Bellard et al. 2012; Stocker et al. 2013; van Baaren and Candolin 2018). Regarding the current and the future projections of global climate change, a central theme is therefore to assess and predict how those changes might affect the levels of diversity (Fig. 1.2).

1.3. Environmental predictability

Most studies focused on whether and how changes in average environmental conditions affect species and individual responses (Chen et al. 2011), and little evidence exists for effects of environmental predictability (Siepielski et al. 2017). Environmental predictability is defined as the probability of correctly predicting environmental fluctuations over time (Zammuto and Millar 1985; Siepielski et al. 2017). For example predicting the daily amount of precipitation or the daily temperature.

Changes in environmental predictability may affect the type, distribution or availability of resources, potentially affecting reproduction and survival of many species (Nevoux et al. 2010). Beside the potential importance of environmental predictability, another understudied parameter is environmental variance and it has been claimed that the key to how species acclimatize and adapt to environmental variability is the degree of environmental predictability (Mora et al. 2013; Botero et al. 2015). While theory on environmental variability suggests that species responses to changes in the variance of environmental conditions are altered or even reversed by differences in mean environmental parameters (Bozinovic et al. 2011; Jenouvrier et al. 2012; Estay et al. 2014; Vasseur et al. 2014), it is fully unclear whether difference in mean environmental parameters also affect environmental predictability.
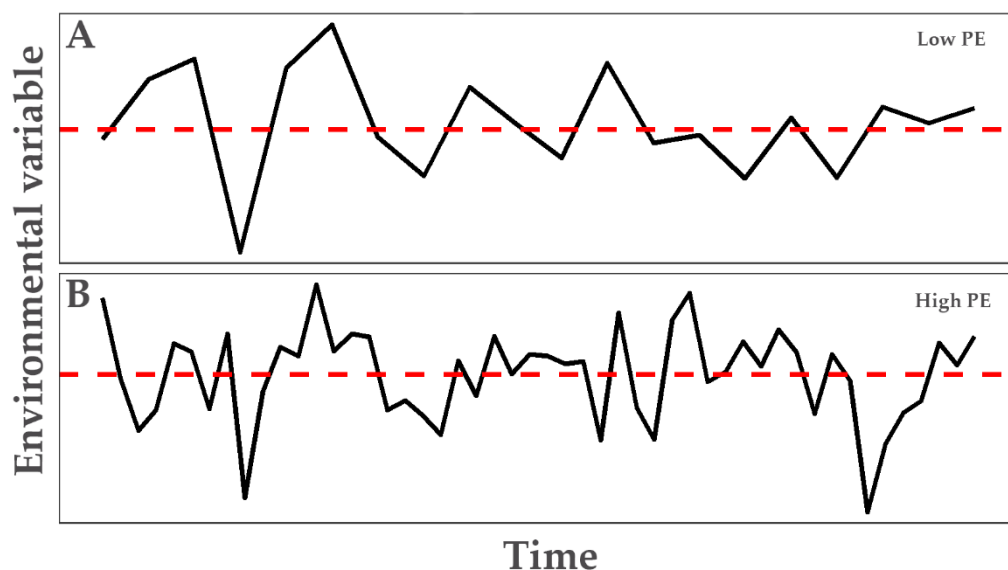
Figure 1.3. Graphical representation of different environmental predictability regimes. Panel "A" represents a more predictable environment and panel "B" a less predictable environment. "PE" corresponds to permutation entropy (for more details see in supporting information "Appendix A") which low PE values correspond to a more predictable environment and high PE values to a less predictable environment.

Precipitation (i.e. condensed water in the atmosphere, that precipitates as rain, snow, or hail) importantly influences habitat, air and soil humidity, and thereby entire food webs and their diversity (Tinkle et al. 1993; Lorenzon et al. 1999; Jordan and Snell 2002; Ferguson 2004; Marquis et al. 2008). Furthermore, precipitation is a vital resource that influences physiology, behavior and life history traits such as body size, body condition, reproduction and survival (Lorenzon et al. 1999; Marquis et al. 2008; Tingley et al. 2012; Moeller et al. 2013; Zylstra et al. 2013; Romero-Diaz et al. 2017). As explained above, most climate change scenarios predict a decrease in precipitation predictability (Karl et al. 1995; Mora et al. 2013). Nevertheless, experimental evidence for the importance of precipitation predictability is scarce and limited to studies generating extreme events (Cherwin and Knapp 2012).

1.4. Effects of environmental predictability on life history traits and population dynamics

It has been suggested that plastic responses to environmental change, such as behavioral responses, are more likely to evolve in predictable than in unpredictable habitats (e.g. Schmitt et al. 1985). However, behavioral responses to changes in environmental

predictability have received little scientific attention. Species may behaviorally adapt to such changes by adapting their life-history strategy (Hazlett 1988; Sorci et al. 1996; Marquis et al. 2008; Lande 2009; Le Galliard et al. 2010; Reed et al. 2010; San-Jose et al. 2016), thereby counterbalancing potential negative effects on life history traits and population growth.

It is well established that changes in environmental means (e.g. mean climatic conditions) can affect life history traits (e.g. survival, growth, and reproduction) and population dynamics (Bjørnstad and Hansen 1994; Lindström 1999) and it is generally thought that less predictable environments may negatively affect life history traits (Tuljapurkar 1990; Dewar and Richard 2007; Marshall and Burgess 2015; Ashander et al. 2016) and thereby population dynamics (Estay et al. 2011). Moreover, environmental predictability may differentially affect the stages of stage-structured populations (e.g. San-Jose et al. 2016; Romero-Diaz et al. 2017), through its effect on inter-stage competition (Leslie 1959; Cooke and Leon 1976; Ebenman 1988; Revilla 2000), or due to inter-stage differences in the sensitivity to environmental predictability (e.g. Rozen-Rechels et al. 2018). However, while environmental predictability may affect population dynamics, frequently no effects on life history traits are found or the direction of the effects are not congruent (Bjørnstad et al. 2004). Thus, sophisticated life history analyses are required to understand whether and how the population dynamics might be affected (Layton-Matthews et al. 2018). In addition, it has been suggested that environmental predictability may be more important than demographic stochasticity, because environmental predictability operates at all population sizes equally (Ashander et al. 2016).

Theory states that in less predictable environments, rapid and more frequent reproduction with minimal investment in offspring is favored (MacArthur 1984) and more recent theory states the contrary, that less predictable environments favor higher investment in individual offspring at the cost of litter size (Einum and Fleming 2004). Both theories suggest that environmental predictability may affect the trade-off between survival and reproduction and/or the trade-off between offspring number and quality (Stearns 1992; Einum and Fleming 2004; Nevoux et al. 2010), but they differ in the direction of the effect. Lack of robust evidence for one or the other hypothesis compromises the understanding of how species will respond to changes in environmental predictability.

Previous studies predicting negative effects of environmental predictability were mainly theoretical (MacArthur 1984; Tuljapurkar 1990; Einum and Fleming 2004; Tuljapurkar et

al. 2009; Ashander et al. 2016), purely empirical (Dewar and Richard 2007; Marshall and Burgess 2015) or generated extreme events, such as severe droughts (Cherwin and Knapp 2012). Thus, experimental tests are needed that provide robust evidence that differences in environmental predictability affect life-history traits and population dynamics (Chevin and Hoffmann 2017).

1.5. Objectives

Climate change scenarios forecast a change in mean environmental conditions and a decrease in environmental predictability (Stocker et al. 2013). While it is widely accepted that changes in average environmental conditions affect individual and species responses (Chen et al. 2011), less evidence exists for effects of environmental predictability. The main objective of this doctoral thesis was to fill this knowledge gap by providing new and robust experimental evidence for whether and how environmental predictability will affect species. We experimentally assessed the effects of different predictability environments on individuals and populations, using the common lizard, *Zootoca vivipara*, as a model species.

Chapter two, describes the methodology used to experimentally assess whether on how environmental predictability could affect common lizard individuals and populations.

Chapters three and four focus on the effects of decreased environmental predictability on individual traits, different age-classes, sexes and in different years.

More specifically, in chapter three, we investigate whether and how differences in environmental predictability affect life-history strategies and life history traits of different age-classes (adults, yearlings, juveniles), by measuring key life history traits such as survival, reproduction, growth and body condition. Furthermore, we assess if those responses depend on average environmental conditions and if the effects were age-dependent.

In chapter four, we examine how environmental predictability affects individual coloration and reproductive traits of male common lizards. Firstly, we assess if male ornamental coloration, which in *Z. vivipara* is related to sexual selection, depends on environmental predictability. Secondly, we assess if male reproductive traits are affected by environmental predictability and if male reproduction is associated with changes in ornamental coloration.

In chapter five we investigate whether and how environmental predictability affects populations. We examine whether environmental predictability affects stage specific vital rates (i.e. survival and reproduction traits) and population dynamics. In this chapter we identify which vital rates are most affected by changes in environmental predictability and, in turn, how these changes influence population dynamics. These results shed light on whether and how environmental predictability affects population dynamics, population trends, and population extinction.

Finally, chapter six consists of a general discussion of the main findings and chapter seven consists of the general conclusions of this doctoral thesis.

Figure 2.1. Female common lizard on a wood pile in the semi-natural populations. By Campo, Benito.

Chapter 2

Study species and experimental procedures

2.1. Study species: the common lizard, *Zootoca vivipara* (Lichtenstein, 1823)

2.1.1. Species description and life history traits

The common lizard, *Zootoca vivipara* (Lichtenstein, 1823), is a small ground-dwelling lizard (adult snout-to-vent length: 45–70 mm). Its geographic distribution ranges from Europe to eastern Asia (Fig. 2.2; Horreo et al. 2018), corresponding to the largest distribution of any terrestrial reptile (Horreo and Fitze 2018). It inhabits humid meadows and grasslands with a predominance of herbs, as well as peat bogs and humid heathlands (Pilorge 1987). Microhabitat choice is linked with humidity (Braña 1996; Peñalver-Alcázar et al. 2016). Six different genetic clades and at least 13 subclades can be differentiated (Horreo et al. 2018). Two clades exhibit oviparous reproduction, and the other four clades are ovoviviparous (Surget-Groba et al. 2006). Only three lizard species, including *Zootoca vivipara*, have been documented to exhibit reproductive bimodality (Qualls and Shine 1995; Smith and Shine 1997). The clade belonging to the study area (Fig. 2.2) corresponds to the subspecies *Zootoca vivipara louislantzi* (Arribas 2009).
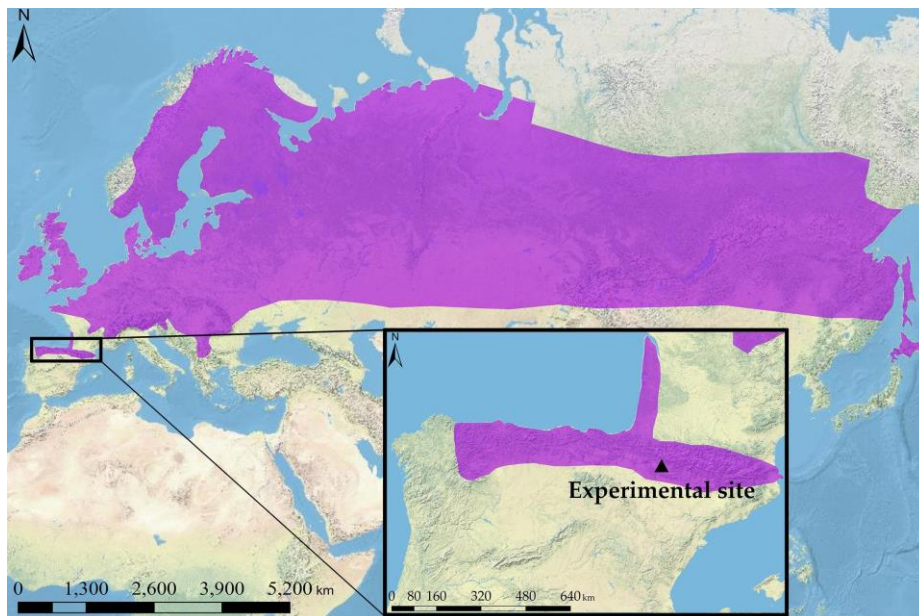
Figure.2.2. Geographic distribution of the common lizard, *Zootoca vivipara*. The zoomed map represents its distribution in Northern Spain and Southern France, corresponding to *Zootoca vivipara louislantzi* (clade B; Arribas 2009), and the black triangle shows the location of the experimental site (▲).

Three age classes can be distinguished based on body size and coloration (Pilorge 1987; Massot et al. 1992; Vercken et al. 2007): juveniles (0-1 years) exhibit an entire black dorsal coloration, and yearlings (1-2 years) and adults (> 2 years) exhibit grey-brown dorsal coloration. While in juveniles sexual dimorphism is less conspicuous, yearlings and adults show a marked sexual dimorphism and sex can be determined by visual secondary sexual traits (e.g. ventral coloration, tail thickness, head shape, etc.). The number of ventral scales remains constant throughout a lizard's life (Bauwens et al. 1987) and allows to determine the sex of juvenile lizards (Lecomte et al. 1994).

In natural populations, survival of adults ranges from 30 to 60 % (Heulin et al. 2011), in immatures it ranges from 16 to 40 % (Heulin et al. 2011), and survival of juvenile lizards is considerably lower (range: 21 – 26 %; Massot et al. 2011). Once survived the first year, life span is 5-6 years in females and 4-5 years in males (Avery 1975). Adults are competitively superior over yearlings and juveniles (San-Jose et al. 2014, 2016; Romero-Diaz et al. 2017), due to size-dependent dominance (Lecomte et al. 1994; San-Jose et al. 2016). Prey size consumed by juveniles and adults largely overlap (Pianka's index 0.62-0.74; Heulin 1986). While adults consume the entire prey size range consumed by yearlings and juveniles, juveniles and yearlings cannot consume the bigger prey eaten by adults (Heulin 1986), because the size of the consumed prey principally depends on the size of their mouth (they swallow the entire prey without cutting it into pieces).

In the Pyrenees, the activity period ranges from March to October. Just after females emerge from hibernation, reproduction begins (Bauwens and Verheyen 1985; Fitze et al. 2010; Breedveld and Fitze 2015). In the Pyrenees, most individuals attain sexual maturity in their second year of life and attaining maturity depends on body size, which is a function of thermoregulatory activity (Sinervo and Adolph 1994) and the length of the activity season (Horváthová et al. 2013). If environmental conditions negatively affect female growth, maturity may be delayed (Dunham 1982; Morrison and Hero 2003; Arribas and Galán 2005). The reproductive system is polygynandrous, and multiple paternity is the norm (Fitze et al. 2005). In oviparous populations, females lay one to three clutches per year (Heulin et al. 1994; Roig et al. 2000; Horváthová et al. 2013) and no parental care is provided once eggs are laid. While, almost all adult females produce eggs, not all reproductively active males fertilize eggs (Fitze et al. 2010). Average clutch size of *Zootoca vivipara louislantzi* is five, and ranges from one to nine eggs (Horváthová et al. 2013).

Zootoca vivipara has a highly permeable skin, which increases the risk of water loss (Grenot et al. 1987). Environmental factors and behavior mainly control the hydric

balance of this species (Grenot and Heulin 1990; Lorenzon et al. 1999; Dupoué et al. 2017). Water availability constrains growth and reproduction (Lorenzon et al. 1999; Le Galliard et al. 2006), litter size (Bleu et al. 2013), juvenile performance (Marquis et al. 2008), and juvenile size at hatching (Lorenzon et al. 2001; Le Galliard et al. 2006; Marquis et al. 2008). Growth mainly depends on food intake (Avery 1994; Le Galliard et al. 2005*b*, 2006; Metcalfe and Alonso-Alvarez 2010), activity time (Sinervo and Adolph 1994; Horváthová et al. 2013), ambient (Liu and Walford 1966; Avery 1994) and body temperature (Sinervo et al. 1990), and thus on food availability and the time available for thermoregulation (Sinervo and Adolph 1994). Growth rate decreases with age and is highest in juveniles, followed by yearlings, and older age-classes (Lorenzon et al. 1999).

2.1.2. Ventral coloration

In this species, ventral coloration shows a marked sexual dimorphism (Fig. 2.3, Bauwens et al. 1987). Adult male common lizards exhibit a conspicuous ventral coloration that consists of carotenoid-based coloration and melanin-based black spots, whereas females exhibit cream to orange belly coloration with few black spots (Bauwens et al. 1987; Sinervo et al. 2007; Vercken et al. 2007; Fitze et al. 2009; San-Jose et al. 2014). Throat and upper belly coloration are highly correlated (Vroonen et al. 2013) and ventral coloration is visible to conspecifics when exhibiting push-ups (Martin et al. 2013). In the South-West European common lizard, *Z. vivipara louislantzi* (clade B: Surget-Groba et al. 2006; Horreo et al. 2018, 2019) males exhibit six discrete color morphs and female bellies are mainly white to cream (Arribas 2009; San-Jose et al. 2013; Fitze et al. 2014). Carotenoid-based coloration of *Z. vivipara* is a condition-dependent trait that reflects the stress response (Cote et al. 2008; Fitze et al. 2009), lipid ingestion (San-Jose et al. 2012) and environmental conditions (San-Jose et al. 2013). Melanin-based coloration is positively correlated with the immune response (Vroonen et al. 2013), body size (Vroonen et al. 2013), head size, and bite force (San-jose et al. 2017) and it is negatively correlated with sprint speed (San-jose et al. 2017).

2.1.3. Population dynamics

Common lizard populations are stage- (age-) structured and age-classes overlap in time. Population dynamics in this species is highly complex and depends on environmental conditions (Pilorge 1981, 1987; Heulin 1985; Grenot and Heulin 1990; Le Galliard et al. 2010; Romero-Diaz et al. 2017). For example, Romero-Diaz et al. (2017) experimentally demonstrated that common lizard responses to changes in average precipitation depend

on a population's color morph frequency, age- and sex-structure. Furthermore, environmental conditions also affect population density (Pilorge 1981, 1987; Heulin 1985; Grenot and Heulin 1990). Population density is higher in humid habitats, suggesting that it might be a function of resource availability (Heulin 1985, 1986). In addition, it has been demonstrated that density-dependent factors, like asymmetric resource competition, play an important role in population dynamics (Massot et al. 1992; Mugabo et al. 2010, 2013; Bleu et al. 2013; San-Jose et al. 2016). Moreover, in most populations the adult sex-ratio is female-biased (Heulin et al. 1997) and male-biased adult sex ratios negatively affect female survival (Pilorge 1987; Le Galliard et al. 2005*a*). Male color morph frequency affects the common lizard's response to environmental change (Romero-Diaz et al. 2017) and exhibits rock-paper-scissors (RPS) dynamics (Sinervo et al. 2007; San-Jose et al. 2014).

Figure 2.3. Example of female (left) and male (right) common lizard's ventral coloration. By Masó, Guillem.

2.1.4. Adequacy of the model species for testing effects of precipitation predictability

Ectotherms largely depend on the environment's abiotic conditions, which increases their vulnerability to the present global climate change. Lizards, and reptiles in general, show high plasticity to environmental conditions (Dunham and Miles 1985; Shine 2005), suggesting that they may adjust life-history strategies in order to cope with changes in environmental conditions. In addition, the low dispersal capacity of the study species (Massot 1992) poses a significant limitation to escape from environmental changes by searching better suited habitats, which promotes the study species' vulnerability to fast environmental changes, as well as the vulnerability of other ectotherms with similar characteristics (Araújo and Guisan 2006; Araújo and Rahbek 2006; Botkin et al. 2007). The high dependence on abiotic factors, the high plasticity to environmental conditions and the low dispersal rates make the study species highly suitable to test whether and how decreased environmental predictability affect individuals, populations, and species. Moreover, since the common lizards habitat choice highly depends on water availability (Peñalver-Alcázar et al. 2016) and hydric conditions affect many aspects of its life history (Grenot and Heulin 1990; Lorenzon et al. 1999; Dupoué et al. 2017), it is an ideal study species to experimentally test the effects of changing precipitation predictability on life-history traits and population dynamics.

2.2. Experimental setup

Figure 2.4. Experimental semi-natural populations when the summer captures take place. By March, Martí.

2.2.1. Enclosures

To test whether and how differences in environmental predictability affect life-history traits, population persistence, and behavioral adaptability of *Zootoca vivipara*, we established 12 semi-natural age-structured common lizard populations at the Research Station 'El Boalar' (Instituto Pirenaico de Ecología, Jaca, Spain, 42°33'N, 0°37'O, 700 m a.s.l.). Populations consisted of escape-proof outdoor enclosures of 100 m² each, delimited by galvanized metal walls that were 1m high and extended 1m below ground. This system allowed conducting population experiments and measuring experimental longer-term consequences. Metal walls prevented predation by terrestrial predators, as well as shrew traps installed outside and inside the enclosures. In addition, nets covered the enclosures to protect lizards from avian predators. Each enclosure contained standardized environment (Fig. 2.4, 2.5) formed by planted natural grassland, two water ponds, logs and stone piles that provided lizards with natural prey, hiding and basking sites (for more details see San-Jose et al. 2014; Romero-Diaz et al. 2017). Common lizards were maintained without the necessity of providing them with extra-food. Finally, a fully automated irrigation system provided the enclosures with precipitation. The sprinkling regime could be programmed individually and each population had 4 sprinklers, one in each corner, which guaranteed homogeneous precipitation.
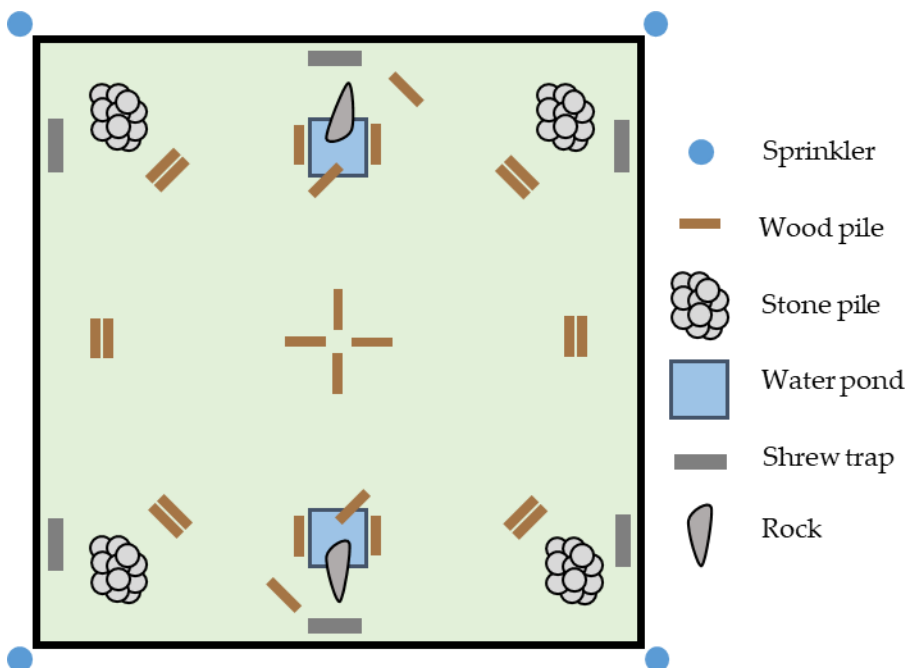
Figure 2.5. Schematic representation of a semi-natural population and its standardized environment.

2.2.2. Predictability treatments

Six enclosures were exposed to more and the other six enclosures to less predictable precipitation, by supplementing precipitation via sprinklers. In the more predictable treatment, one supplemental precipitation event happened every day at 9.00 am and at 6.00 pm (i.e., 14 supplemental precipitation events per 7 days, each providing the same amount of precipitation). In the less predictable treatment, 14 supplemental precipitation events were randomly distributed among 7 days between 9.00 am and 7.00 pm. The natural and the supplemental precipitation together, correspond to more and less predictable precipitation, which was confirmed by weighted permutation entropy (for details see supplementary information section "A"). Permutation entropy was larger in the less (0.86) and smaller in the more predictable treatment (0.77), showing that precipitation was less predictable in the less predictable treatment. Consequently, all enclosures obtained the same amount of precipitation, while the predictability significantly differed among precipitation treatments.

2.2.3. Natural Climate

Environmental predictability was manipulated on the enclosure level over four years (2012-2015). During these four years, average monthly temperatures (from a measurement station located less than 500 meters from the enclosures and shared by AEMET) increased from February (2.96° ± 0.74 SE) to July (19.78° ± 0.74 SE) and thereafter decreased until February (Fig. 2.6). There was a significant quadratic relationship between average monthly temperatures and month (month: $F_{1,42}$ = 18.050, P < 0.001; month^2: $F_{1,42}$ = 177.740, P < 0.001) explaining 80% of the variation, and no significant differences of this relationship existed among years (all interactions with year: P > 0.9). In contrast to temperature, no significant relationship existed between the amount of monthly precipitation and month (all P > 0.8, Fig. 2.6).

2.2.4. Animal release and re-capture protocol

Lizards used for this experiment were originally captured from natural populations located in Aragón and Navarra under license of the relevant authorities, and they belong to the North-East Spain subclade B4, which is oviparous and corresponds to the South-West European common lizard, *Zootoca vivipara louislatzi* (Fig. 2.2; Milá et al. 2013; Horreo et al. 2018).

Semi-natural populations were completely standardized (structure, vegetation, water, sun light, lizard density, etc.), to reduced differences among them and to increase the power of detecting differences among populations induced by the environmental predictability treatments. In each enclosure, the same number of adults and yearlings (Table 2.1), and approximately the same number of juveniles was released.
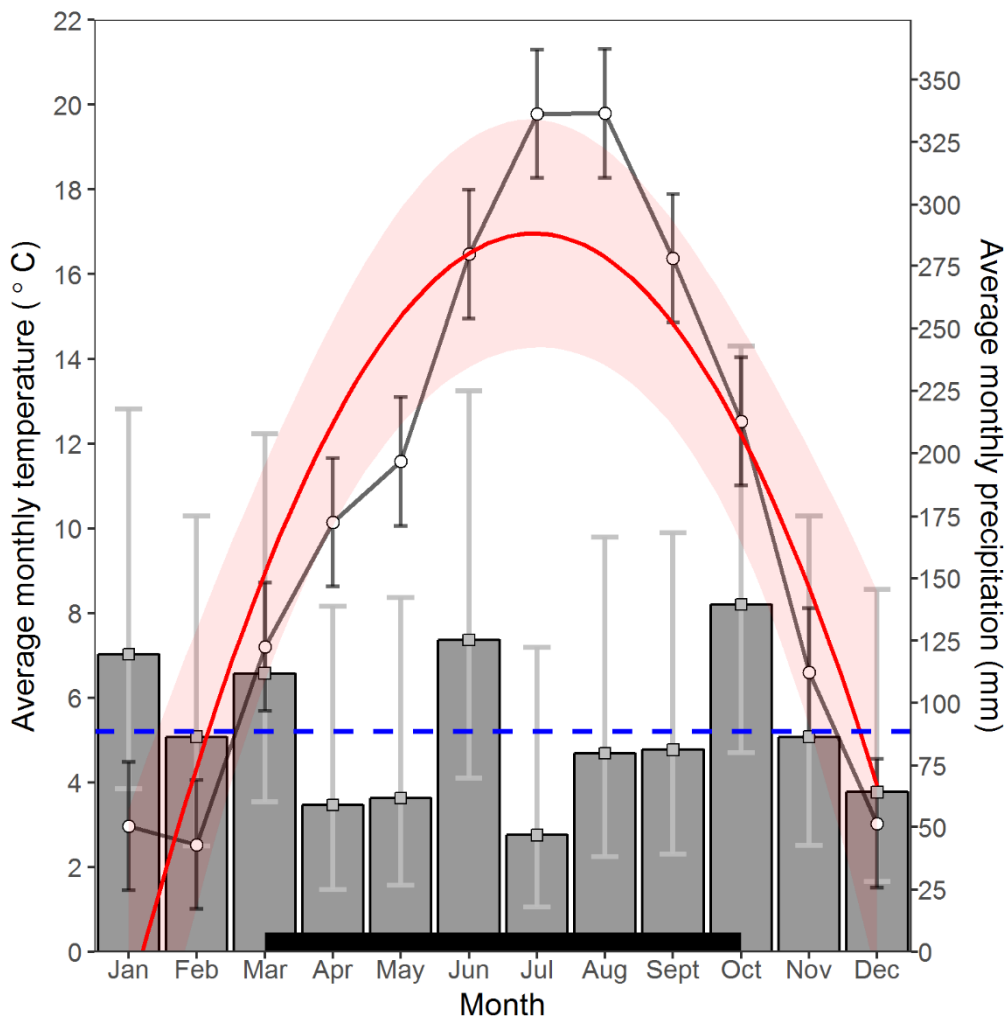
Figure 2.6. Monthly natural precipitation (in mm) and average monthly temperature (in°C) measured at the experimental field site over the duration of the experiment (2012-2015). Shown are average ± standard errors, for precipitation (grey bars) and temperature (white dots). The red line corresponds to the model predictions of average monthly temperature in °C and the blue dashed line corresponds to the predicted monthly precipitation. The black horizontal bar corresponds to the months when lizards are active.

No significant differences existed among treatments in the number ($F_{1,10}$ = 1.033; P = 0.317) and sex-ratio ($F_{1,10}$ = 0.005; P = 0.940) of released juveniles (Table 2.1). Lizards were randomly attributed to enclosures and no significant differences existed among treatment levels in SVL (snout-to-vent length), body condition and adult male color morph frequency (all $P \geq 0.2$). Adult and yearling lizards were released in July, female lizards after parturition, and juvenile lizards were released 2 days after hatching. All adults and all yearlings were released in an unknown enclosure, i.e. not in the enclosure where they have been captured previously. Juveniles belonging to the same clutch were released together in a different enclosure than their mother and not in the enclosure where the mother was recaptured before egg laying to avoid effects of mother-offspring competition (Cote et al. 2007). All used lizards were individually marked by toe-clipping.

Table 2.1. Number of adults, yearlings, and juveniles released per enclosure and year.

	Adults			**Yearlings**			**Juveniles**			**Total**
	Male	*Female*	*Total*	*Male*	*Female*	*Total*	*Male*	*Female*	*Total*	
2012	7	13	20	6	6	12	18.75 ± 1.06	9.67 ± 1.30	28.42 ± 0.79	60.4 ± 0.79
2013	10	17	27	2	2	4	14.83 ± 1.9	5.67 ± 1.67	20.5 ± 1.57	51.5 ± 1.57
2014	9	18	27	2	2	4	15.25 ± 2.14	6.83 ± 2.12	22.08 ± 1.44	53.08 ± 1.44

After release, two recapture sessions were conducted, one at the end of August and the other one at the end of September. Each recapture session consisted of three consecutive days of intensive capture with equal capture effort across time and enclosures. Recaptured lizards were individually identified, SVL measured to the closest millimeter using a transparent ruler, and body mass to the closest 1 milligram. After measurement, lizards were released in the same enclosure and in the same location where they were recaptured. If a lizard was recaptured on several days within the same recapture session, measures of the first recapture were used for analyses. Lizards hibernated in the enclosures and in spring (from mid-April onwards), females were recaptured weekly and gravidity was determined by means of belly palpation. Gravid females were moved to the laboratory where they were kept in individual terrariums under standardized conditions (see below), while non-gravid females were released in the exact recapture location directly after recapture. After the mating season (approximately end of May),

all surviving lizards were recaptured and brought to the laboratory, where spring body size and body condition were measured. Thereafter, all individuals were kept in individual terraria until release (see below). Recapture of all surviving individuals was assured by searching a given enclosure for lizards until five days passed since the last lizard has been recaptured in this enclosure. All spotted lizards were recaptured.

The year before this experiment started, half of the lizards were exposed to less predictable and the other half to more predictable precipitation, i.e. to the same precipitation predictability treatments as during this experiment. In each experimental year, all surviving lizards (recaptured in the enclosures) were released back to the enclosures. At the beginning of the experiment and during the subsequent three years, half of the lizards of each sex and age class were released in the same predictability treatment (but in an unknown enclosure), while the other half was released in the other predictability treatment. The first time a lizard was captured, it was marked by toe clipping and a tissue samples (tail tip) was taken and conserved in 70% ethanol. Genetic analyses were conducted based on five polymorphic microsatellite DNA loci (Lv-3–19, Lv-4–72, Lv-4-alpha, Lv-4X, Lv-4-115; Boudjemadi et al. 1999; Horreo et al. 2017), the genetic profile of each individual was determined, and paternity analyses were performed to determine which male fathered the new-born lizards (for more details see "Methodology" in Chapter 4).
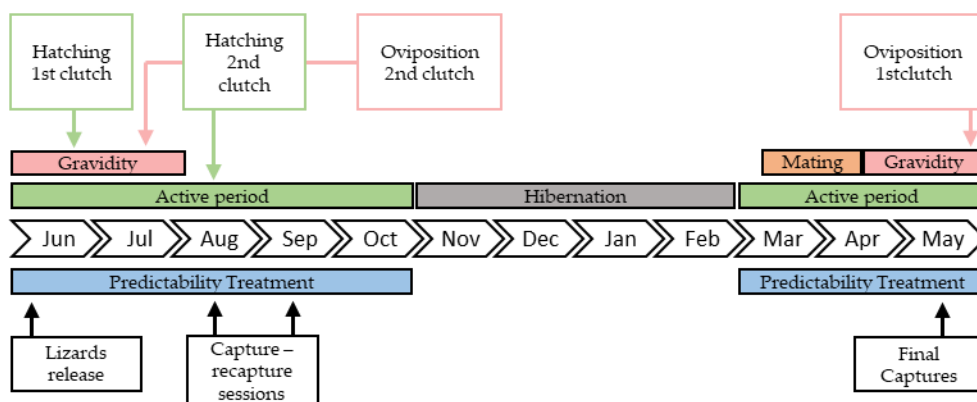
Figure 2.7. General schematic overview of the annual cycle of the oviparous lizards (top) and the time-line of the captures and environmental predictability treatments (bottom).

2.2.5. Laboratory conditions and egg incubation

Lizards brought to the laboratory, were kept in individual terraria under standardized conditions. Each terrarium contained peat substrate, a hide, a water pond, and a heat

source. Terraria were exposed to a standardized light regime consisting of a 10L: 14D photoperiod provided by 40W bulbs and ultraviolet (UV) lamps that provided UVB and UVA for 1.5h per day (San-Jose et al. 2016). Lizards had access to *ad libitum* water and were fed every fourth days, alternatingly with wax moths (*Galleria mellonella*) or house crickets (*Acheta domesticus*). On a weekly basis, body mass of all lizards was measured, individuals were checked for ectoparasites, and terraria were replaced with a new one if necessary. Terraria of gravid females were checked twice a day for laid clutches. On laying, clutch size (i.e., the number of eggs) and laying date were recorded, and laid clutches were thereafter incubated individually in a constantly humid atmosphere at 21ºC during the day (from 9 a.m. to 9 p.m.) and 19ºC during the night (Heulin et al. 1997). Eggs were checked daily and sterile eggs or eggs containing dead embryos were removed. After approximately 40 days of incubation juveniles hatched, and the number of hatched juveniles and the date of hatching were recorded.

Figure 2.8. Detailed photography of a common lizard egg in the incubator just before the juvenile hatches. By Campo, Benito.

2.3. Data analysis

The specific measures and statistical analysis used are detailed in the materials and methods section of each chapter. All the analyses done were conducted with R statistical free software R 3.5.1 (Team 2018) and using the Rstudio platform (version 1.1.463; Team and Others 2015)

"Ignorance more frequently begets confidence than does knowledge: it is those who know little, and not those who know much, who so positively assert that this or that problem will never be solved by science"

(Charles Darwin)

Chapter 3

Age-dependent effects of moderate differences in environmental predictability forecasted by climate change, experimental evidence from a short-lived lizard (*Zootoca vivipara*)

Abstract

Whether and how differences in environmental predictability affect life-history traits is controversial and may depend on mean environmental conditions. Moreover, robust evidence for the effects of differences in environmental predictability is scarce and limited to extreme events. Thus, the consequences of the currently observed and forecasted climate-change induced reduction of precipitation predictability are largely unknown. Here we experimentally tested whether and how changes in the predictability of precipitation affect growth, reproduction, and survival by exposing European common lizard *Zootoca vivipara* populations to more and to less predictable precipitation. Predictability of precipitation affected growth and body condition of adults, and the timing of reproduction in one of the three study years, in line with the idea that effects of environmental predictability depend on mean environmental conditions. While adults were able to compensate the treatment effects, yearlings and juvenile females were not able to compensate negative effects of less predictable precipitation on growth and body condition, respectively. Treatment differences among age-classes cannot be explained by inter-age-class competition, but rather reflect differences among age-classes in the sensitivity to environmental predictability. This indicates that integrating differences in environmental sensitivity, and changes in averages and the predictability of climatic variables will be key for understanding if species may cope with the current climatic change.

Keywords: Climate change, environmental predictability, life-history traits, age-dependent effects, thermoregulation, environmental sensitivity, growth, survival.

3.1. Introduction

It is well established that changes in environmental conditions (e.g. climatic conditions) can affect individual performance (e.g. survival, growth rate, and reproduction), life-history strategies and population dynamics (Bjørnstad and Hansen 1994). Understanding how organisms cope with and adapt to changes in their environment is thus central for conservation, evolution, and ecology (Chevin et al. 2010). While it is widely accepted that changes in average environmental conditions affect species' and individual responses (Chen et al. 2011), less evidence exists for effects of environmental predictability (i.e., environmental fluctuations through time, Siepielski et al. 2017) and it is generally thought that less predictable environments negatively affect life history traits (Tuljapurkar 1990; Dewar and Richard 2007; Marshall and Burgess 2015; Ashander et al. 2016) and thereby population dynamics (Estay et al. 2011).

However, species may behaviorally adapt to such changes in environmental predictability by adapting their life-history strategy (Reed et al. 2010), thereby counterbalancing potential negative effects. While a recent review suggests that the effect of environmental variance may depend on mean environmental conditions (Lawson et al. 2015), no evidence exists that the effects of environmental predictability depends on mean environmental conditions. Moreover, environmental predictability may differentially affect the stages of stage-structured (San-Jose et al. 2016; Romero-Diaz et al. 2017), through its effect on inter-stage competition (Revilla 2000), or due to inter-stage differences in the sensitivity to environmental predictability (Rozen-Rechels et al. 2018). Therefore, differences may exist in population dynamics, but not necessarily in overall population densities (Revilla 2000). Consequently, it is far from being clear that less predictable environmental conditions will be consistently negative.

Previous studies predicting negative effects of environmental predictability were mainly theoretical (Tuljapurkar 1990; Einum and Fleming 2004; Tuljapurkar et al. 2009; Ashander et al. 2016) or generated extreme events, such as severe droughts (Cherwin and Knapp 2012). Thus, studies are needed that experimentally test the effects of differences in environmental predictability on life-history strategies and life-history traits, since only those will be able to provide robust evidence for or against these claims (Chevin et al. 2010).

Robust evidence from experimental work is especially important, since most climate change scenarios predict a long-term increase of rainfall variability, as well as an increase in the frequency of extreme rainfall events (Stocker et al. 2013). These changes

will lead to lower predictability of precipitation and to lower predictability of resources (Karl et al. 1995). Precipitation importantly influences habitat, air and soil humidity and thereby entire food webs and their diversity (Ferguson 2004). Precipitation is a vital resource that influences physiology, behavior, life history traits such as body size, body condition, reproduction and survival (Lorenzon et al. 1999; Romero-Diaz et al. 2017), and that may reinforce differences among age classes and sexes (Grenot et al. 1987). Nevertheless, experimental evidence for the importance of precipitation predictability is scarce and limited to studies generating extreme events (Cherwin and Knapp 2012).

To this end, we experimentally tested in age-structured populations whether and how differences in precipitation predictability affect life-history strategies and life history traits of different age-classes (adults, yearlings, juveniles). We experimentally manipulated the predictability of precipitation in 12 semi-natural European common lizard (*Zootoca vivipara*; Lichtenstein, 1823) populations, while holding the amount of precipitation constant. The predictability of precipitation was manipulated, given the observed and predicted changes in rainfall patterns (Stocker et al. 2013) and given the European common lizard's high dependency on water (Grenot et al. 1987; Lorenzon et al. 1999; Peñalver-Alcázar et al. 2016; Dupoué et al. 2017). Populations were maintained during one year and the experiment repeated in three subsequent years, to test for the generality of the responses and whether differences in mean climatic conditions may affect differences induced by precipitation predictability.

According to theoretic models (Tuljapurkar et al. 2009), we predicted (1) significant negative effects of less predictable precipitation on body size, body condition, survival, and reproductive traits, such as laying date, litter size, offspring traits and early offspring survival. We also tested (2) whether the effect of precipitation predictability may depend on mean climatic conditions. Because different age-classes generally exhibit different competitive abilities and different investment strategies, potentially leading to intense inter-class competition (Grenot et al. 1987; San-Jose et al. 2016; Romero-Diaz et al. 2017), we predicted (3) that effects of precipitation predictability may first manifest in the competitively inferior age-classes, namely in juveniles and yearlings. Alternatively, we predicted (4) that age-class-dependent effects of precipitation predictability may reflect age-dependent sensitivity to precipitation predictability.

3.2. Materials and methods

3.2.1. Species description

The European common lizard, *Zootoca vivipara* is a small ground-dwelling ovoviviparous lizard (adult snout-to-vent length (SVL): 45–70 mm). It is distributed across Europe and northern Asia. It inhabits humid habitats, and microhabitat choice is linked to soil humidity (Peñalver-Alcázar et al. 2016). *Zootoca vivipara* has a highly permeable skin, which increases the risk of hydric loss (Grenot et al. 1987). Environmental factors and behavior, mainly control the hydric balance of this species (Lorenzon et al. 1999; Dupoué et al. 2017). Water availability constrains growth and reproduction, litter size, juvenile performance and size at hatching (Lorenzon et al. 1999; Bleu et al. 2013). Growth mainly depends on food intake (Avery 1994), activity time (Horváthová et al. 2013), ambient (Avery 1994) and body temperature, and thus on food availability and the time available for thermoregulation (Sinervo and Adolph 1994). In most *Zootoca vivipara* populations, three age classes can be distinguished based on body size (Massot et al. 1992) and coloration (San-Jose et al. 2016): juveniles are entire black and yearlings, and adults exhibit grey-brown cryptic dorsal coloration. Growth rate is highest in juveniles, followed by yearlings, and it is lowest in older age-classes (Lorenzon et al. 1999). Mortality of juveniles is high (up to 90%) and once survived the first year, life span is 5-6 years in females and 4-5 years in males (Avery 1994). Adults are competitively superior over yearlings and juveniles (San-Jose et al. 2014, 2016; Romero-Diaz et al. 2017), due to size-dependent dominance (San-Jose et al. 2016). Prey size consumed by juveniles and adults largely overlap (Pianka's index 0.62-0.74, Heulin 1986). While adults consume the entire prey size range consumed by yearlings and juveniles, juveniles and yearlings cannot consume the bigger prey eaten by adults (Heulin 1986), because the size of the consumed prey principally depends on the size of their mouth.

3.2.2. Experimental setup

3.2.2.1. Environmental procedures

To test how differences in environmental predictability affect life-history strategies and reproduction of *Zootoca vivipara*, we established 12 age-structured lizard populations in enclosures with natural vegetation located at the Research Station 'El Boalar' (Jaca, Spain; for details see San-Jose et al. 2014; Romero-Diaz et al. 2017). Environmental predictability was manipulated on the enclosure level over four years (2012-2015).

During these four years, average monthly temperatures (from a measurement station located less than 500 meters from the enclosures and shared by AEMET) increased from February (2.533°C ± 0.736 SE) to July (19.795°C ± 0.736 SE) and thereafter decreased until February (Fig.2.6 in "chapter 2"). There was a significant quadratic relationship between average monthly temperatures and month (month: $F_{1,42}$ = 18.050, P < 0.001; month²: $F_{1,42}$ = 177.740, P < 0.001) explaining 80% of the variation, and no significant differences of this relationship existed among years (all P > 0.9). In contrast to temperature, no significant relationships existed between the amount of monthly precipitation and month, and all monthly standard errors overlapped (all P > 0.8, Fig. 2.6 in "chapter 2"). Six enclosures were exposed to more and another six to less predictable precipitation, by supplementing precipitation with 4 sprinklers per enclosure, one in each corner, ensuring homogeneous precipitation. In the more predictable treatment, one supplemental precipitation event happened every day at 9.00 am and at 6.00 pm (i.e., 14 supplemental precipitation events per 7 days, each providing the same amount of precipitation). In the less predictable treatment, 14 supplemental precipitation events were randomly distributed among 7 days between 9.00 am and 7.00 pm. The natural and the supplemental precipitation together, correspond to more and less predictable precipitation, which was confirmed by weighted permutation entropy (for calculation details see supporting information section "A"). Permutation entropy was larger in the less (0.86) and smaller in the more predictable treatment (0.77), showing that precipitation was less predictable in the less predictable treatment. Consequently, all enclosures obtained the same amount of precipitation, while the predictability significantly differed among precipitation treatments.

3.2.2.2. Animal release and re-capture protocol

Lizards used for this experiment were originally captured from natural populations located in Aragón and Navarra, and they belong to the North-East Spain subclade, B4 (Milá et al. 2013; Horreo et al. 2018). In July of each experimental year, all lizards that have previously been captured in the enclosures were released back to the enclosures. In 2013 and 2014, half of the lizards of each sex and age class were released in the same predictability treatment (but in an unknown enclosure), while the other half was released in the other predictability treatment. In each enclosure, the same number of adults and yearlings, and a similar number of juveniles was released (Table 2.1). No significant differences existed among treatments in the number ($F_{1,10}$ = 1.033; P = 0.317) and sex-ratio ($F_{1,10}$ = 0.005; P = 0.940) of released juveniles. Lizards were randomly attributed to enclosures and no significant differences existed among treatment levels in

SVL, body condition and adult male color morph frequency (all $P \geq 0.2$). Adult and yearling lizards were released in July, females after parturition, and juveniles two days after hatching. All adults and all yearlings were released in an unfamiliar enclosure, i.e. not in the enclosure where they have been captured previously. Juveniles belonging to the same clutch were released together and not in the enclosure where the mother was recaptured before egg laying. Moreover, to avoid effects of mother-offspring competition (Cote et al. 2007), juveniles were released in a different enclosure than their mother. All used lizards were individually marked by toe-clipping. After release, two recapture sessions were conducted, one at the end of August and the other one at the end of September, and each consisted of three consecutive days of capture with equal capture effort across time and enclosures. After measurement, lizards were released in the same enclosure and in the same location where they were recaptured. If a lizard was recaptured on several days within the same recapture session, measures of the first recapture were used for analyses. Lizards hibernated in the enclosures and in spring (from mid-April onwards), females were recaptured weekly and gravidity was determined by means of belly palpation. Gravid females were moved to the laboratory where they were kept in individual terrariums under standardized conditions (for details see San-Jose et al. 2016), while non-gravid females were released in the exact recapture location directly after recapture. Terraria of gravid females were checked twice a day for laid clutches which were thereafter incubated individually under standardized conditions (San-Jose et al. 2016). After the mating season (approximately end of May), all surviving lizards were recaptured and brought to the laboratory. Thereafter, all individuals were kept in individual terrariums until release following the protocol used by San-Jose et al. (2016). Recapture of all surviving individuals was assured by searching a given enclosure for lizards until five days passed since the last lizard has been recaptured in this enclosure. All detected lizards were recaptured.

3.2.3. Measures and statistical analysis

Before release and at each capture, SVL (accuracy: 1 mm) and body mass (accuracy: 1 mg) were measured. For each gravid female, body mass before and after parturition, laying date, clutch size, number of removed eggs (sterile or containing a dead embryo), and the number of hatchlings were measured. For laying date, the 1st of May corresponds to day 0 (2nd of May to day 1, etc.) in each studied year. From this data the following parameters were derived: annual survival (yes/no), probability of egg laying (yes/no), proportion of alive juveniles ($N_{hatchlings}$ /clutch size), and maternal investment,

which corresponds to the difference in body mass before laying minus body mass after laying. Body condition corresponds to the residuals of a linear regression of body mass on SVL. Growth rate and change in body condition were calculated as difference in SVL and body condition between captures divided by the number of days passed between captures ($\frac{trait_{(later\ capture)} - trait_{(earlier\ capture)}}{N_{days\ between\ captures}}$). Both variables were calculated for three different periods: from release to August, from August to September and from September to spring. For the latter period, the days spent hibernating were subtracted (1st of November to 1st of March), following San-Jose et al. (2016).

Mixed models (Bates et al. 2014) were ran using treatment, sex and year as fixed factors and enclosure as random factor. Year refers to the period from the yearly set-up of the experimental populations in July to recapture and egg laying in the following year. For example, individuals released in 2012, recaptured in 2013, and egg laying of females in 2013, were modelled as belonging to 2012. In the case of repeated measures taken on the same animal, "animal ID" was modelled as random factor. Finally, in models on juveniles, "Mother ID" was modelled as a random factor since individuals belonging to the same clutch are not independent. Because individuals living in the same enclosure are not independent, the enclosure / year combination was modelled as a random factor, when the analyzed data included all three years. Linear mixed models with Gaussian error distribution were applied to analyze treatment effects on SVL, body condition and most reproductive traits. Generalized mixed models with binomial error distribution were used to analyze survival, the probability of egg laying and the proportion of alive juveniles. In analyses including data of different periods, period was modelled as fixed factor and its interactions with the other parameters was included.

Natural climatic data (daily precipitation and average daily temperature) was analyzed using general linear mixed models with Gaussian error distribution for average daily temperature and with Poisson error and a log link for daily precipitation. To test for differences among periods, factor "period" was included as a fixed factor. To test if variance in climatic parameters was different among month, periods and years, each month was cut into three equal intervals (from 1.-10., from 11.-20., from 21.-30. or -31.) and variance was calculated for each interval.

Model selection started with the full model that included all parameters and all possible interactions, and the minimum adequate model was determined using backward elimination (see tables 3.1, 3.2., and in Appendix B see tables B.1., B.2. and B.3.). For all tests, the significance level was set at α = 0.05 (two-tailed test). All model assumptions

were tested and if they were not met, transformations were applied. If heteroscedasticity still existed, weighted least square regressions were ran. Overdispersion existed in none of the non-Gaussian models. For significant factors containing more than two levels, post-hoc tukey-tests accounting for multiple testing were run. All analyses were run using R 3.5.1 (Team 2018).

3.3. Results

3.3.1. Climatic differences among years and seasons

Air temperatures significantly differed between periods ($F_{2,941}$ = 512.450, P < 0.001) and no significant differences existed in average daily precipitation (χ^2_2 = 0.291, P = 0.864). Between release and August, average daily air temperature was 19.79°C ± 0.31 SE, between August and September it was 17.04°C ± 0.26 SE, and during the rest of the year it averaged 9.36°C ± 0.22 SE (all pairwise contrasts: P ≤ 0.001). The natural average daily precipitation was 2.77mm ± 0.25 SE.

There was a significant interaction between period (summer: release to August, autumn: August to September) and year in average daily temperatures (interaction: $F_{2,192}$ = 38.826, P < 0.001, Fig. B.1 supporting information). In 2013, the temperature decline between summer and autumn was steepest (contrast: $F_{1,257}$ = 145.178, P < 0.001), shallower in 2012 ($F_{1,257}$ = 23.170, P < 0.001; slope difference 2012 vs 2013: $F_{1,159}$ = 5.985, P = 0.016), and no significant change existed in 2014 ($F_{1,257}$ = 0.465, P = 0.496, Fig. B.1 supporting information). In summer average daily temperatures were significantly lower in 2014 compared to 2012 and 2013 (all P < 0.001), while no significant differences existed between 2012 and 2013 (P = 0.802). In autumn daily temperatures were significantly lower in 2013 than in 2014, and they were intermediate in 2015. There was no significant interaction between period and year in daily precipitation (χ^2_2 = 0.261, P = 0.877), nor significant differences among periods (χ^2_1 = 0.066, P = 0.797). Moreover, there were no significant differences between periods and years in variances of daily precipitation and temperature ($F_{5,19}$ = 0.665, P = 0.537, $F_{5,19}$ = 7.75, P = 0.944).

In Spring there was a significant interaction between year and month in average daily temperatures ($F_{4,267}$ = 5.391, P < 0.001; Fig. B.2 supporting information) and in temperature variance ($F_{4,18}$ = 3.362, P = 0. 032; Fig. B.3 supporting information), but neither in daily precipitation (χ^2_4 = 4.372, P = 0.358), nor in precipitation variance (χ^2_4 = 3.051, P = 0.549). No significant difference among years existed in average monthly temperatures in March (all post-hoc contrasts: P > 0.05), while average April

temperatures in 2013 were lower than in 2014 ($P = 0.015$) and intermediate in 2015 (Fig. B.2 supporting information). In May 2015, temperatures were significantly higher than in the other years, in May 2014 they were intermediate and in May 2013 they were lowest (all differences: $P < 0.001$; Fig. B.2 supporting information). No significant pairwise contrasts existed among and within years in temperature variance in March, April, and May (all $P > 0.05$; Fig. B.3 supporting information), showing that small within-year differences caused the significant interaction.

Table 3.1. Summary of treatment effects on survival, body size, body condition, growth, and change in body condition. Treatment effects (environmental predictability) and interactions including treatment are given. Significant P-values or '-' for non-significant parameters are given. Minimum adequate models and test statistics are shown in supporting information tables B.1, B.2 and B.3. The following abbreviations were used: ΔBC, change in body condition ; BC, body condition; SVL,snout-to-vent lenght; sp, spring ; *trt*, treatment.

Response variable	*Treatment effects*	*df*	Adults		Yearlings		Juveniles	
			$\chi 2$	*P*	$\chi 2$	*P*	$\chi 2$	*P*
survival	*trt*	1	-	-	-	-	-	-
growth	*trt* × period	2	-	-	19.591	< 0.001	-	-
	trt × year × period	4	21.448	< 0.001	-	-	-	-
ΔBC	*trt* × sex × year × period	4	13.917	< 0.001	-	-	-	-
sp SVL	*trt*	1	-	-	4.799	0.028	-	-
sp BC	*trt* × sex	1	-	-	-	-	6.679	< 0.001

3.3.2. Treatment effects on survival, growth, and body condition

There was no significant treatment effect on survival in any of the age classes (Table 3.1). In adults, growth was affected by a significant interaction between treatment, year and period ($\chi^2_4 = 21.448$; $P < 0.001$; Fig. 3.1A). Post-hoc analyses showed significant differences among environmental predictability treatments in 2013. From August to September 2013 growth was significantly faster in the more predictable treatment ($P < 0.001$) and from September to spring it was significantly slower ($P = 0.012$), the latter effect compensating the former effect. As a result, no significant differences existed between treatments in spring SVL ($\chi^2_1 = 0.158$; $P = 0.691$; Fig. 3.1B). In adult lizards, the change in body condition was affected by a significant interaction between treatment, sex, year and period ($\chi^2_4 = 13.917$; $P = 0.007$; Fig. 3.1A). Post-hoc analyses showed that in 2013 and 2014 significant differences among treatment levels existed in males, while no significant differences existed in females (Fig. 3.1A). The change in male body condition

was bigger in the less predictable treatment from release to August 2013 and from September to spring 2014. However, no treatment effects existed in spring body condition (χ^2_1 = 0.231; P = 0.631; Fig. 3.1B), showing that in 2013, this difference was compensated by small differences in subsequent periods and that in 2014, the treatment effect compensated previous small differences.

In yearlings, growth was affected by a significant interaction between predictability treatment and period (χ^2_2 = 19.591; P < 0.001; Fig. 3.2A). In the more predictable treatment, yearlings grew significantly faster before hibernation (i.e. from release to august and from august to September) than in the less predictable treatment and no significant differences existed between September and spring. Consequently, spring SVL was significantly longer in the more predictable treatment (χ^2_1 = 4.799; P = 0.028; Fig. 3.2B). Treatment did not significantly affect the change in body condition or spring body condition of yearlings (P > 0.05; Table 3.1).

In juveniles, treatment did not significantly affect growth nor spring SVL (Table 3.1). Spring body condition was significantly affected by an interaction between predictability treatment and sex (χ^2_1 = 6.679; P = 0.009; Fig. B.4B supporting information). Post-hoc analyses showed that in the less predictable treatment body condition of males was higher than in females, while no significant sex-differences existed in the more predictable treatment (Fig. B.4B supporting information). There was no significant interaction between treatment and sex on the change in body condition (χ^2_1 = 0.526; P = 0.468; Fig. B.4A supporting information), but graphical representation of the interaction unraveled trends that are congruent with the significant treatment x sex interaction on spring body condition (Fig. B.4A supporting information).

3.3.3. Treatment effects on reproduction

Laying date was affected by a significant interaction between treatment and year (χ^2_2 = 8.887; P = 0.012; Fig. 3.3). Post-hoc analyses show that in spring 2015, lizards in the more predictable treatment laid eggs significantly earlier than those exposed to the less predictable treatment. In the other years, no significant treatment effects existed. Treatment did not affect the other reproductive parameters (Table 3.2).

3.4. Discussion

Climate change research predicts a decrease in the predictability of precipitation (Stocker et al. 2013), potentially having negative effects on species viability, population growth, and individual performance (Marshall and Burgess 2015; Ashander et al. 2016).

Most studies on this subject are theoretical (Tuljapurkar 1990; Tuljapurkar et al. 2009; Ashander et al. 2016) or correlate environmental predictability with life-history traits (Dewar and Richard 2007; Marshall and Burgess 2015; Siepielski et al. 2017), and the few experimental studies produced extreme events that severely affected life-history traits (Cherwin and Knapp 2012). Moreover, while it has been predicted that the effect of environmental variance may depend on mean environmental conditions (Lawson et al. 2015), no evidence exists that the effects of environmental predictability depends on mean environmental conditions. Thus, robust experimental proof for the effects of environmental predictability are lacking (Chevin et al. 2010). Here we experimentally test whether life-history strategies and life-history traits are affected by moderate differences in the predictability of precipitation, i.e., without producing extreme events (i.e., droughts or floods), and whether differences in mean climatic conditions alter their effects.

Table 3.2. Minimum adequate models and test statistics for the analysed reproductive traits are given. Significant factors and/or interactions are shown in bold. The following abbreviation was used: *trt*, treatment.

		Clutch size		Laying date		Hatching Success		Nº Juveniles		Laying Success		Maternal Investment	
Parameter	*df*	χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*
trt	1	-	-	0.137	0.712	-	-	-	-	-	-	-	-
age	1	**5.577**	**0.018**	**18.757**	**<0.001**	1.772	0.183	-	-	1.772	0.183	**7.086**	**0.008**
year	2	**18.755**	**<0.001**	**88.206**	**<0.001**	**8.477**	**0.014**	**9.510**	**0.009**	**8.477**	**0.014**	-	-
trt × age	1	-	-	-	-	-	-	-	-	-	-	-	-
trt × year	2	-	-	**8.887**	**0.012**	-	-	-	-	-	-	-	-
age × year	2	-	-	-	-	**6.306**	**0.043**	-	-	**6.306**	**0.043**	-	-
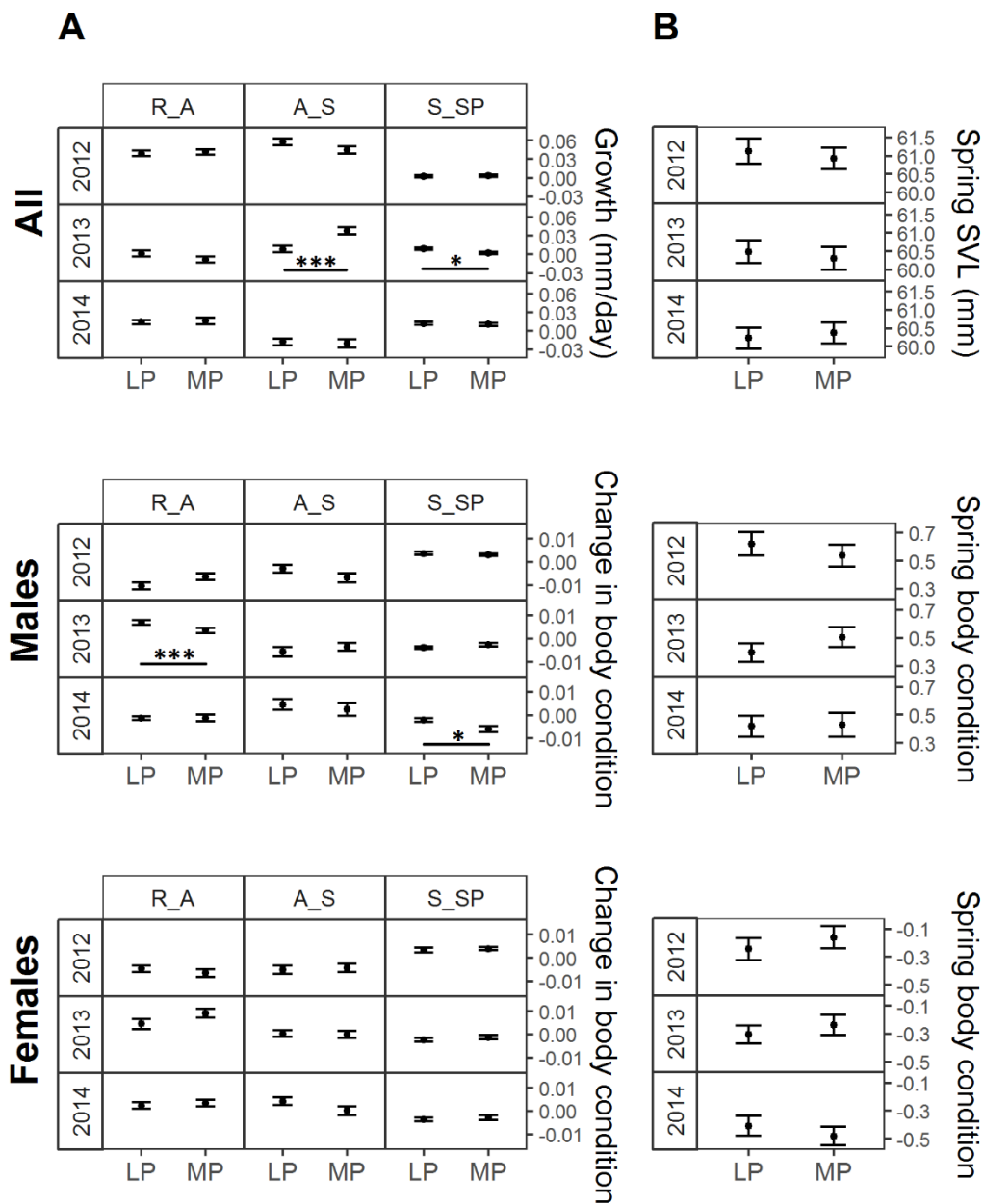
Figure 3.1. Treatment effects on adult body size (above) and adult body condition (below). In (A), changes in SVL and body condition are shown and in (B), spring SVL and spring body condition. Predicted means ± se per treatment, growth period, year and sex (in body condition) are shown in (A) (LP: less predictable; MP: more predictable; R_A: Release to August; A_S: August to September; S_SP: September to spring) and predicted means ± se per treatment, year, and sex in (B). Horizontal lines indicate significant post-hoc contrasts: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Our results show that reduced precipitation predictability negatively affected growth of yearlings, body condition of juvenile females (Table 3.1; Fig. 3.2, B.4 supporting information), and the timing of egg laying (Table 3.2, Fig. 3.3) of common lizards. Precipitation treatment significantly affected adult growth rate and body condition of adult males (Fig. 3.1A), and all effects were compensated over the course of the experiment, leading to no significant differences on adult spring traits (Fig. 3.1B). These findings are in line with theory suggesting that less predictable environments negatively affect life history traits (Dewar and Richard 2007; Marshall and Burgess 2015; Ashander et al. 2016) and especially those of competitively inferior age classes, namely, yearlings and juveniles (San-Jose et al. 2016). The absence of treatment effects on adult spring traits, further points to highly plastic compensatory strategies that mitigate environmentally induced effects on traits relevant to sexual selection (Cote et al. 2008; Fitze and Le Galliard 2008). Moreover, reduced growth in the less predictable treatment in autumn 2013, is congruent with reduced growth of yearlings, potentially pointing to inter-age class competition (San-Jose et al. 2016). However, absence of treatment effects on juvenile growth are not congruent with the predicted cascading effects and thus, with the prediction that effects of precipitation predictability may first manifest in the competitively inferior age-classes, i.e. juveniles followed by yearlings (prediction 3; San-Jose et al. 2016). Consequently, it is unlikely that the differential treatment effects observed in the different age classes are the result of treatment-induced differences in inter-age class competition (for further discussion see in supporting information Appendix B.1).

The inter-annual differences in age-class dependent treatment effects, as well as sex-dependent treatment effects, show that there exist age-class and sex-dependent differences in the sensitivity to differences in precipitation predictability (Rozen-Rechels et al. 2018). Different sensitivities may result from differences in water flux (Grenot et al. 1987) and/or thermoregulatory activity (Christian et al. 2006). In *Zootoca vivipara* water flux positively correlates with growth rates and in summer, gravid females exhibit higher water fluxes than males and non-gravid females, while in autumn no significant differences exist between sexes and age-classes (Grenot et al. 1987). Differences in water fluxes between sexes and age-classes can thus hardly explain the here observed patterns, while differences in thermoregulatory activity are congruent with the observed effects. If precipitation is falling, common lizards hide and are thus not able to thermoregulate, and differences in thermoregulation directly feed back into growth and timing of egg laying (Huey and Slatkin 1976). Moreover, thermoregulatory capacity is known to depend on body size (Christian et al. 2006) and on coloration (Clusella-Trullas et al.

2009). Larger animals (adults) have higher thermal inertia and can keep heat for longer (Christian et al. 2006), thus they might be less affected by precipitation predictability, and similarly, juveniles exhibit darker coloration that leads to faster heating (Clusella-Trullas et al. 2009), what may explain the absence of treatment effects on juvenile growth (for further discussion see in supporting information Appendix B.2).
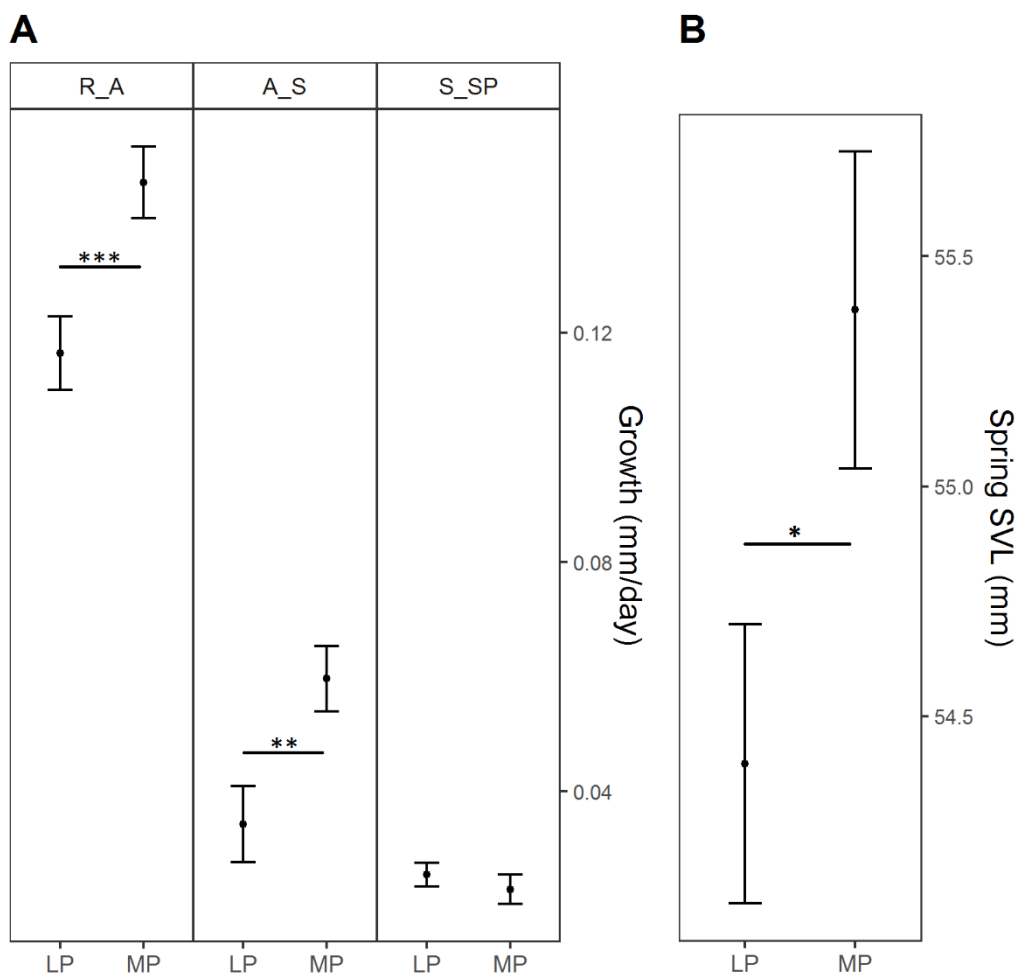
Figure 3.2. Treatment effects on growth (A) and spring SVL (B) of yearlings. For growth, predicted means ± se per treatment and growth period (LP: less predictable; MP: more predictable; growth period: R_A: Release to August; A_S: August to September; S_SP: September to spring) are shown and for spring SVL, predicted means ± se per treatment. Horizontal lines indicate significant post-hoc contrasts: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Theory indicates that reduced predictability negatively affects life history traits (Ashander et al. 2016), but here, the predictability of precipitation did neither affect survival, nor most of the reproductive traits (Table 3.1, 3.2). This suggests that reduced precipitation predictability may not necessarily negatively affect life-history traits and since adults compensate treatment-induced effects, it is also unlikely that it affects sexual selection (Fitze and Le Galliard 2008). However, predictability treatment affected spring body size of yearlings, which may lead to a delay in maturation and to differences in clutch size (Horváthová et al. 2013), both potentially affecting population dynamics.
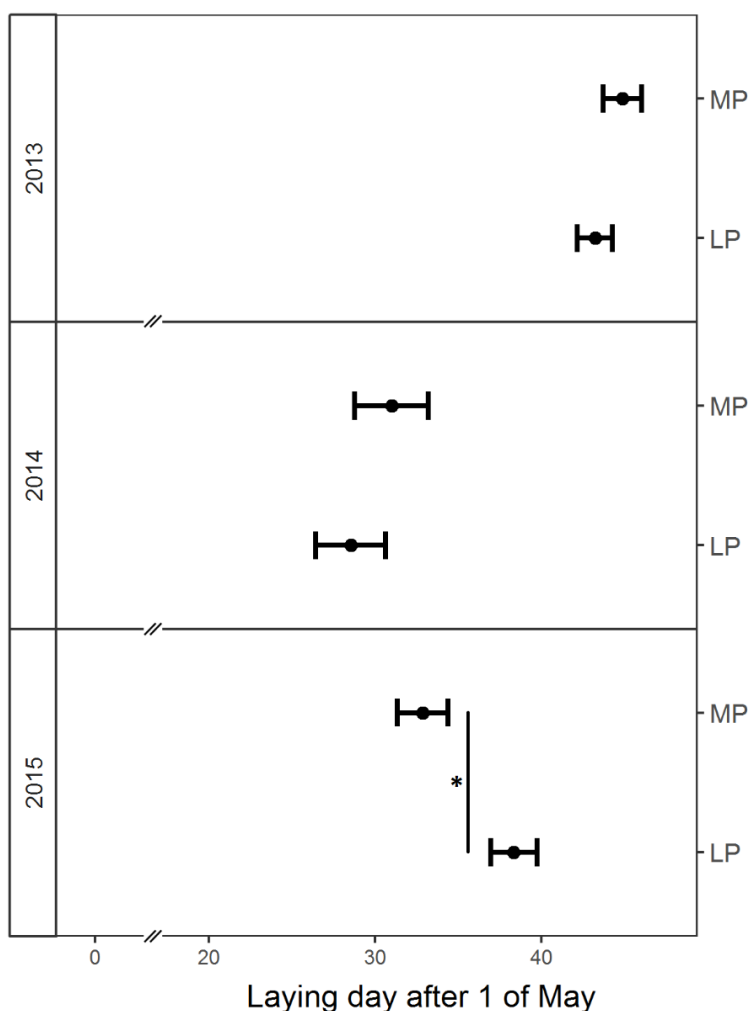
Figure 3.3. Treatment effect on laying date (1st of May corresponds to day 0). Shown are predicted means ± se per treatment (LP: less predictable; MP: more predictable) and the year the experiment started (note: in the 2012 experiment, laying date was measured in spring 2013, in the 2013 experiment it was measured in spring 2014, etc). Vertical lines indicate significant post-hoc contrasts: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Finally, treatment effects on adults (growth, body condition, laying date) were indeed year-specific (Table 3.1), while treatment effects on yearlings and juveniles were independent of year. Adult growth was reduced in the less predictable treatment in 2013, when average autumn temperature was lowest (15.312°C ± 0.400 SE in 2013, 16.988°C ± 0.564 SE in 2012 and 18.833 °C ± 0.360 in 2014, Fig. B.1 supporting information), but not in the other years. Laying date was affected by a significant interaction between year and predictability treatment (Fig. 3.3) and there existed a significant interaction between year and month in average monthly temperatures (Fig. B.2 supporting information) and no significant interaction between year and month in daily precipitation, nor in precipitation variances. In the 2013 experiment, April temperatures were highest (see temperatures during April 2014, Fig. B.2 supporting information) and eggs were laid earliest (average date: give data: 30th of May ± 1.49 SE) and in the 2012 experiment, April temperatures were coolest (see temperatures during April 2013, Fig. B.2 supporting information) and eggs were laid latest (average date: give data: 14th of June ± 0.77, Fig. 3.3), while in the 2014 experiment average daily temperatures and date of egg laying were intermediate (5th of June ± 1, Fig. 3.3, B.2 supporting information). Average April temperatures significantly predicted laying date ($F_{1,1}$ = 157451, P = 0.002), while May temperatures did not ($F_{1,1}$ = 0.501, P = 0.61). This points to reproductive activities being induced by April temperature, which is in line with previous findings showing that emergence of *Zootoca vivipara* females from hibernation mainly depends on maximum daily temperatures (Breedveld and Fitze 2015).

In the 2014 experiment, females laid their eggs on average 5 days earlier in the more predictable (3th of June ± 1.48) compared to the less predictable treatment (8th of June ± 1.36, Fig. 3.3), a result that clearly contrasts to the classic tenet, that lower predictability should favor rapid reproduction (Einum and Fleming 2004). However, no significant treatment effects on laying date existed in the 2012 and 2013 experiments (Fig. 3.3). This suggests that effects on laying date and adult growth, but not those on yearlings and juveniles, might be the consequence of differences in average climatic conditions. The results on adults show for the first time that population responses to differences in environmental predictability depend on mean conditions.

In summary, the results show for the first time that different age classes and sexes exhibit different sensibilities to the predictability of precipitation (Rozen-Rechels et al. 2018). However, the simulated moderate differences in precipitation predictability (Karl et al. 1995) had no lasting effects on life history traits of adults and juveniles (Tuljapurkar

1990; Dewar and Richard 2007; Marshall and Burgess 2015; Ashander et al. 2016) and no effects on parameters being directly related to population growth (Estay et al. 2011). This suggests, that moderate changes in the predictability of precipitation, may not necessarily affect population densities and population persistence, which clearly contrasts to earlier studies, where a decrease of precipitation predictability led to severe droughts and associated strong negative effects on life-history traits and reproduction (Cherwin and Knapp 2012). Consequently, as long as the predicted decrease in rainfall predictability (Stocker et al. 2013) will not lead to an increase in the magnitude and frequency of extreme events, its effect on populations, species and biodiversity may not necessarily be negative.

Acknowledgments

"The evolution of sex is the hardest problem in evolutionary biology"

(John M. Smith)

Chapter 4

Precipitation predictability affects male ornamental coloration. Evidence for compensatory strategies among carotenoid- and melanin-based coloration

Masó, G. and Fitze, P.S. Manuscript submitted.

Abstract

Ornamental coloration is frequently an honest signal of quality that can reflect environmental conditions. While studies show that average conditions importantly affect carotenoid- and melanin-based coloration, no evidence exists that environmental predictability forecasted by climate change scenarios affects coloration and thereby sexual selection. Here we experimentally tested whether and how changes in the predictability of precipitation affect ornamental coloration and reproduction of male common lizards *Zootoca vivipara*. More and less predictable precipitation was simulated in 12 semi-natural *Z. vivipara* populations over 3 years and ornamental and reproductive traits were measured, the latter using molecular paternity analyses. Less predictable precipitation decreased hue of carotenoid-based coloration and the extent of melanin-based coloration, showing that both types of coloration are highly sensitive to changes in environmental predictability. Hue was positively correlated and the extent of melanin-based coloration was negatively correlated with the male's number of confirmed mate partners, indicating that both traits affect sexual selection. This indicates that treatment effects on hue let to a reduction and treatment effects on the extent of melanin-based coloration to an increase of male access to females, in line with differential effects on sexual selection. Neither male survival nor male reproductive success significantly differed among predictability treatments, suggesting that differential investment in ornamentation and its effects on reproduction reflect compensatory strategies. The results also suggest that ornamentation, rather than reproduction and survival, is first affected by less favorable conditions and that it can be used for the early detection of subtle negative effects induced by differences in environmental predictability, and more generally environmental conditions.

Keywords: Climate change, environmental predictability, ornamental coloration, reproduction, sexual selection, compensatory strategies, early signal.

4.1. Introduction

In many animal species, conspicuous ornamental colors are honest signals of individual quality (Johnstone 1995), which are used in intra- and inter- sexual interactions (Galeotti et al. 2003; Sinervo et al. 2007; San-Jose et al. 2014). Honesty originates from the costs of producing or carrying the signal and the production and maintenance of elaborate ornaments may depend on the resolution of the trade-off with other life-history traits (Kokko 1998; Siefferman and Hill 2005). In line with these ideas there are studies showing that the expression of ornamental coloration depends at least partly on environmental conditions (Kodric-Brown 1989; Fitze et al. 2003, 2007; Tschirren et al. 2003; Hill and J.McGraw 2006). For example, in many species stress, resource availability (i.e. ingestion of carotenoids or lipids; San-Jose et al. 2012, 2013), parasite load (Fitze et al. 2008; Megía-Palma et al. 2018), and operational sex ratio (Cote et al. 2008) influence the expression of ornamental coloration (e.g. Fitze et al. 2009; Moore et al. 2016; San-Jose et al. 2016; Lewis et al. 2017). However, less evidence exists about whether and how changes in abiotic conditions lead to changes in ornamental coloration and published studies mainly investigated effects of changing temperature (Bajer et al. 2012; Langkilde and Boronow 2012), changes in ambient color and changes in light conditions on color expression (Merchant et al. 2018). These studies tested whether changes in means provoke changes in ornamental coloration and to our knowledge no single study tested whether differences in environmental variances or environmental predictability affect ornamental coloration. Furthermore, behavioral strategies may have evolve that might mitigate effects of reduced ornamental coloration on fitness-related traits (e.g. best-of-bad-job strategies; Gonzalez-Jimena and Fitze 2012). Thus, more evidence is required to understand if in general, changes in abiotic environmental conditions affect ornamental coloration and whether environmental conditions may thereby affect sexual attractiveness, competitive capacity, thermoregulation and reproductive success (Denardo and Behavior 1993).

Such evidence may not only be important for theory, but as well serve to predict effects of the present climate change (Stocker et al. 2013). Among other parameters, the present climate change alters temperature, precipitation, and environmental predictability (Stocker et al. 2013) and especially little evidence exists about whether and how environmental predictability affects ornamental coloration. Decreased environmental predictability may lead to habitat change (Coulson et al. 2001; Grant and Grant 2002; Stenseth 2002) and thereby to an increase in stress (Pétavy et al. 2004), , which may potentially increase the costs of producing and maintaining elaborate ornaments.

Moreover, less predictable environments are predicted to negatively affect life history traits (Tuljapurkar 1990; Dewar and Richard 2007; Marshall and Burgess 2015; Ashander et al. 2016), potentially feeding back on ornamentation (Kokko 1998; Siefferman and Hill 2005). However, at present no experimental evidence exists for the hypothesis that environmental predictability affects color expression.

Here, we experimentally investigated whether and how precipitation predictability affects carotenoid- and melanin-based ornamental coloration of male common lizards, *Zootoca vivipara* (Lichtenstein, 1823). *Zootoca vivipara* is a highly hydrophilic species (Grenot et al. 1987; Pilorge 1987; Grenot and Heulin 1990; Lorenzon et al. 1999; Peñalver-Alcázar et al. 2016; Dupoué et al. 2017, 2018) and its belly exhibits carotenoid- and melanin-based coloration, both being highly plastic traits (Fitze et al. 2009; San-Jose et al. 2013). Hue of carotenoid-based coloration is linked to reproductive success (Fitze et al. 2009) and melanin-based coloration is linked with bite force (San-jose et al. 2017) and thereby with reproductive success (Huyghe et al. 2013). Female mate choice is important in *Zootoca vivipara* (Fitze et al. 2008, 2010; Gonzalez-Jimena and Fitze 2012; San-Jose et al. 2013) and male ornamental coloration predicts male reproductive success (Fitze et al. 2009; San-Jose et al. 2013).

To assess whether and how decreased precipitation predictability affects ornamental coloration, precipitation predictability was manipulated in 12 semi-natural populations of *Zootoca vivipara* and the yearly color change was assessed over three subsequent years, to investigate the robustness of the treatment effects.

We predicted that precipitation predictability will affect (1) hue of carotenoid-based coloration and (2) melanin-based coloration, given that previous tests repeatedly showed plasticity of these traits (Fitze et al. 2009; San-Jose et al. 2013). If treatment-induced color changes affect individual performance, we predicted (3) that coloration will be significantly correlated to reproductive success (Sinervo et al. 2007; San-Jose et al. 2014). Moreover, if behavioral strategies compensate effects on coloration (e.g. by means of best-of-bad-job strategies: Gonzalez-Jimena and Fitze 2012) we predicted (4) compensatory strategies in order to mitigate effects on reproductive success.

4.2. Methodology

4.2.1. Species description

The common lizard (*Zootoca vivipara*) is a small lacertid widely distributed across Europe and Asia. It inhabits peat- bogs and moist heathlands. Microhabitat selection is positively related to habitat humidity (Braña 1996; Peñalver-Alcázar et al. 2016) and it is a highly hydrophilic species, whose control of the hydric balance is of great importance (Grenot et al. 1987; Lorenzon et al. 1999; Dupoué et al. 2017). Many studies demonstrated negative effects of reduced humidity on life history traits, like growth and reproduction (Lorenzon et al. 1999, 2001, Le Galliard et al. 2006, 2010; Bleu et al. 2013) and humidity is also related to intra- and inter-age variation in vital rates (Romero-Diaz et al. 2017).

In this species, ventral coloration shows a marked sexual dimorphism (Bauwens et al. 1987). Adult male common lizards exhibit a conspicuous ventral coloration that consists of carotenoid-based coloration and melanin-based black spots, whereas females exhibit cream to orange belly coloration with few black spots (Bauwens et al. 1987; Sinervo et al. 2007; Vercken et al. 2007; Fitze et al. 2009; San-Jose et al. 2014). Throat and upper belly coloration are highly correlated (Vroonen et al. 2013) and ventral coloration is visible to conspecifics when exhibiting push-ups (Martin et al. 2013). In the South-West European common lizard, *Z. vivipara louislantzi* (clade B: Surget-Groba et al. 2006; Horreo et al. 2018, 2019) males exhibit six discrete color morphs and female bellies are mainly white to cream (Arribas 2009; San-Jose et al. 2013; Fitze et al. 2014). Carotenoid-based coloration of *Zootoca vivipara* is a condition-dependent trait that reflects the stress response (Cote et al. 2008; Fitze et al. 2009), lipid ingestion (San-Jose et al. 2012) and environmental conditions (San-Jose et al. 2013). Melanin-based coloration is positively correlated with the immune response (Vroonen et al. 2013), body size (Vroonen et al. 2013), head size and bite force (San-jose et al. 2017) and negatively with sprint speed (San-jose et al. 2017). In lizards, coloration is produced by the dermal chromatophore, which consists of at least four independent layers (from outside to inside): epidermis, xanthophores containing carotenoids, iridophores, melanophores, and a reflecting keratin layer (Grether et al. 2004; Haisten et al. 2015).

4.2.2. Experimental setup

4.2.2.1. Environmental procedures

To test how differences in environmental predictability affect male ornamental coloration and reproductive traits of *Zootoca vivipara*, we established 12 age-structured lizard populations in enclosures with natural vegetation located at the Research Station 'El Boalar' (Jaca, Spain; for details see San-Jose et al. 2014; Romero-Diaz et al. 2017). Environmental predictability was manipulated on the enclosure level over four years (2012-2015). Six enclosures were exposed to more and another six to less predictable precipitation, by supplementing precipitation with 4 sprinklers per enclosure, one in each corner, ensuring homogeneous precipitation. In the more predictable treatment, one supplemental precipitation event happened every day at 9.00 am and at 6.00 pm (i.e., 14 supplemental precipitation events per 7 days, each providing the same amount of precipitation). In the less predictable treatment, 14 supplemental precipitation events were randomly distributed among 7 days between 9.00 am and 7.00 pm. The natural and the supplemental precipitation together, correspond to more and less predictable precipitation, which was confirmed by weighted permutation entropy (for calculation details see supporting information section "A"). Permutation entropy was larger in the less (0.86) and smaller in the more predictable treatment (0.77), showing that precipitation was less predictable in the less predictable treatment. In summary, precipitation predictability differed among treatments, and no differences existed in the amount of precipitation among treatments and enclosures.

4.2.2.2. Release and captures

Lizards used for this experiment were originally captured from natural populations located in Aragón and Navarra, and they belong to the North-East Spain subclade, B4 (Milá et al. 2013; Horreo et al. 2018). In July of each experimental year, lizards were released in enclosures. In 2013 and 2014, half of the recaptured lizards of each sex and age class were released in the same predictability treatment (but in an unknown enclosure), while the other half was released in the other predictability treatment. In each enclosure, the same number of adults and yearlings, and a similar number of juveniles was released (Table 2.1). No significant differences existed among treatments in the number ($F_{1,10}$ = 1.033; P = 0.317) and sex-ratio ($F_{1,10}$ = 0.005; P = 0.940) of released juveniles. Lizards were randomly attributed to enclosures and no significant differences existed among treatment levels in SVL, body condition and adult male color morph frequency (all $P \geq 0.2$). All adults and all yearlings were individually marked by toe-

clipping and released in an unfamiliar enclosure in July, i.e. not in the enclosure where they have been captured previously. Lizards hibernated in the enclosures and in spring (from mid-April onwards). After the mating season (approximately end of May), all surviving lizards were recaptured and brought to the laboratory. Thereafter, all individuals were kept in individual terrariums until release following the protocol used by San-Jose et al. 2016. Recapture of all surviving individuals was assured by searching a given enclosure for lizards until five days passed since the last lizard has been recaptured in this enclosure. All detected lizards were recaptured. Each year, at the beginning and at the end of the experiment SVL (accuracy: 1 mm) and body mass (accuracy: 1 mg) were measured and standardized photographs of all adult and yearling males were taken (Fitze 2002).

4.2.3. Color analyses

For taking standardized photos, lizards were gently placed into a dark box filled with foam material and a photographic filter lens (Hoya UV-filter, Kenko Tokina Co., Ltd., Tokyo, Japan) was slid over the lizard to immobilized it and to guarantee that the distance between the object and the objective was exactly the same for all photos. Standard color squares (white, green, red, blue and yellow) were located on each lens side to detect potential failures of the flashes (for more details see San-Jose et al., 2012). The dark box was placed in a fixed position inside a larger opaque camera box. The distance between the box and the digital camera (Nikon D70S, 6.10 megapixels, with a 105mm f/2.8 Nikkor objective, Nikon Corporation, Tokyo, Japan) was set at 40 cm. Illumination was provided by two flashes (Nikon SB-600, Nikon Corporation) positioned on each side of the camera box at an angle of 13° relative to the optical axis. Illumination settings were manually set to ensure that each photo received the exactly same amount of light (Fitze 2002; San-Jose et al. 2012).

Of each photo, coloration was measured with ADOBE PHOTOSHOP CS6 (Adobe Systems, Inc, San Jose, CA, USA). Blackness and the extent of the melanin-based coloration were measured. To this end, the belly (from anal plate to gular scales) was divided into three thirds (anterior, central and posterior third), each of them consisting of the same number of inner longitudinal scales (± 1 scale). The three thirds were divided in the middle of the two inner longitudinal scale lines (right, left side), resulting in six regions. In each lizard, five spots were selected in three regions (left-anterior, right-central and left-posterior third). The selected spots were evenly distributed within regions (2 spots on the exterior and 3 on the interior longitudinal line). Each color photo

was then transformed to grey-scale, an area of 5 × 5 pixels was selected in the center and close to the border of each selected spot, and average brightness (%) of each area was measured using the average filter implemented in Photoshop. Thereafter, average brightness per lizard was calculated (average of the 30 measurements: 3 regions x 5 spots per regions x 2 measures per spot) and blackness (BL) calculated as '100 – mean brightness', where 100% reflects completely black and 0% completely white (San-Jose et al. 2013; San-jose et al. 2017). To measure the extent of the black belly coloration (E; i.e. the proportion of black surface of a lizard's belly), the two inner and exterior longitudinal lines were selected and within this selection the surface of the black spots was determined by selecting all pixels exhibiting a lizard's average spot brightness ± 30%, using the 'Color range' tool implemented in Photoshop. The number of the selected black pixels was divided by the number of pixels of the initially selected belly surface, yielding the proportion of black belly coloration.

Carotenoid-based coloration was measured on the third scale from the collar scales, on the third scale from the anal scale, and on the scale being in the middle of the two measurements on both, the left and right inner longitudinal line. In the middle of each selected scale a square of 8 x 8 pixels was placed that did not include black spots, and average hue (H), saturation (S) and brightness (B) were measured using the average filter implemented in Photoshop. Average hue, saturation and brightness were calculated per lizard (average of the 6 measurements) and used for further analyses. In the range of the coloration exhibited by *Zootoca vivipara*, higher H values indicate lower redness, i.e. yellower coloration, higher S values correspond to purer coloration, and higher B indicates brighter and more intense coloration (Foley and Dam 1982; Fitze 2002; Fitze et al. 2009).

4.2.4. Paternity analyses

Paternity analyses based on five polymorphic microsatellite DNA loci (Lv-3–19, Lv-4–72, Lv-4-alpha, Lv-4X, Lv-4-115; Boudjemadi et al. 1999; Horreo et al. 2017) were run to measure male reproduction. To this end, DNA from tissue samples and eggs was extracted using a BioSprint 96 DNA Blood Kit (Qiagen, Hilden, Germany). The methods used for polymerase chain reaction and determination of allelic size have been previously described (Horreo et al. 2017). The genetic profile of all mothers and of all potential fathers was known. Paternity assessment was performed manually by first assigning the alleles inherited from the mother. Thereafter the father was searched among all putative fathers, by determining which genotype matched with the remaining

alleles. This assignment was then verified using Cervus v.3.0 (Marshall et al. 1998). In cases where the genotype of two fathers matched with the remaining juvenile alleles, the paternity was confirmed by analyzing two additional loci (Lv-1-139, Lv-2–145; Boudjemadi et al. 1999). This procedure let to unique paternity attribution in all offspring, without any mismatch between the fathers and the offspring's genotype. Thereafter, the following multiplicative male reproductive traits were derived per year: reproductive success (juveniles produced: "1"; no juveniles produced: "0"), number of confirmed mate partners (number of females of whose clutch the male fertilized at least one egg), and average number of juveniles sired per mate partner (total number of juveniles produced per male / number of confirmed mate partners).

4.2.5. Measures and statistical analysis

Treatment effects on coloration (H, S, B of carotenoid-based and blackness (BL) and extent of melanin-based coloration (E) and reproductive parameters (reproductive success, number of confirmed mate partners and number of juveniles produced) were analyzed using mixed models (lmer and glmer from the package lme4; Bates et al. 2014). Linear mixed models with Gaussian error distribution were applied to analyze coloration, generalized mixed models with binomial error distribution for reproductive success, and generalized mixed models with Poisson error distribution for number of confirmed mate partners and number of juveniles produced. In all analyses, treatment and year were modelled as fixed factors and enclosure as random factors. Analyses of coloration consisted of two measures per individual: coloration at the beginning of the experiment (initial measures) and coloration at the end of the experiment (final measures), and therefore, the statistical model additionally included time as a fixed factor and "animal ID" as random factor. In these models a significant interaction between treatment and time indicates that treatment affected the color change measured over the course of a year. To consider color changes due to moulting, a factor moult was included in the model (0: moulting; 1: not moulting). Additionally, SVL and body condition were added as covariates. Body condition corresponds to the residuals of a linear regression of body mass on SVL. Analyses on reproductive traits additionally included the color parameters measured during the reproductive period, SVL, and body condition as covariates, the former to test for an association between coloration and reproduction. To account for potential effects of moult on coloration, a linear model with moult as fixed factor was previously run, and the residuals were extracted and used as covariates.

Model selection started with the full model that included all parameters and all possible interactions, and the final model was determined using backward elimination. For all tests, the significance level was set at α = 0.05 (two-tailed test). All assumptions of the applied models (e.g. for linear models: normality and heteroscedasticity of the residuals) were tested and if they were not met, transformations were applied. If after transformation heteroscedasticity still existed, weighted least square regressions were ran. Overdispersion existed in none of the non-Gaussian models. For significant factors containing more than two levels, post-hoc Tukey-tests accounting for multiple testing were run. All analyses were run using R 3.5.0 (Team 2018).

4.3. Results

4.3.1. Carotenoid- and melanin- based ventral coloration

A significant interaction was found on hue of carotenoid-based coloration time (χ^2 = 4.465, P = 0.035; Fig. 4.1A) and the extent of melanin-based coloration time (χ^2 = 4.141, P = 0.042; Fig. 4.1B) between predictability treatment and time (Table 4.1). Post-hoc contrasts showed that, in the less predictable treatment, final H measures were significantly lower than initial H measures (P = 0.029), and no significant differences existed in the more predictable treatment (P = 0.401). There were no significant differences among treatment levels in initial measures (P = 0.403) and there was a tendency in final measures (P = 0.069; Fig. 4.1A). No significant treatment differences existed in initial measures of the extent of melanin-based coloration (P > 0.104, and final measures were significantly bigger in the more predictable than the less predictable treatment (P < 0.001; Fig. 4.1B). All other color parameters (S, B, blackness) were not affected by treatment (Table 4.1).

A significant interaction between year and time (Table 4.1) affected saturation (χ^2 = 11.0006, P = 0.004; Fig. 4.2A) and brightness (χ^2 = 12.467, P = 0.002; Fig. 4.2B) of carotenoid-based coloration and blackness (χ^2 = 32.232, P < 0.001; Fig. 4.2C) of melanin-based. Post-hoc contrasts showed that in 2012 and 2014 S was significantly lower in final, compared to initial measures (P = 0.001 and P < 0.001, respectively) and no significant differences existed in 2013 (P = 0.784, Fig. 4.2A). Consequently, S decreased from initial to final measures in two of the three study years. Brightness of carotenoid-based coloration was significantly higher in final compared to initial measures in 2014 (P < 0.001), and no significance differences existed between initial and final B in 2012 (P = 0.352) and 2013 (P = 0.963; Fig. 4.2B). Blackness of melanin-based coloration was

significantly lower in final, compared to initial measures in 2012 ($P = 0.001$) and 2014 ($P < 0.001$), and it was significantly higher in 2013 ($P = 0.003$; Fig. 4.2C). Thus, blackness of melanin-based coloration decreased in two and increased in one of the study years. Moult negatively affected saturation (Initial = 57.628 ± 1.616; Final = 49.287 ± 2.019), brightness (Initial = 50.676 ± 0.390; Final = 49.061 ± 0.546) and blackness (Initial = 85.205 ± 0.287; Final = 82.577 ± 0.423), and positively affected hue (Initial = 34.231 ± 0.489; Final = 35.932 ± 0.739; Table 4.1).

Hue was significantly and positively correlated with SVL ($P < 0.001$; Table 4.1) and all other color parameters were not significantly correlated with SVL or body condition (all $P > 0.05$; Table 4.1).

Table 4.1. Minimum adequate models of carotenoid- and melanin-based coloration. Shown are test statistics. Significant parameters are bold and parameters removed from the initial model are denoted as "-". The following abbreviations were used: BC, body condition; SVL, snout-to-vent length; *trt*, treatment; H, hue; S, saturation; B, brightness; E, extent of melanin based coloration; BL, blackness of melanin-based coloration.

| | | Carotenoid-based | | | | | | Melanin-based | | | |
| | | H | | S | | B | | BL | | E | |
Parameter	*df*	$\chi2$	*P*	$\chi2$	*P*	$\chi2$	*P*	$\chi2$	*P*	$\chi2$	*P*
Moult	1	**5,540**	**0,019**	**28,126**	**<0.001**	**8,286**	**0,004**	**41,944**	**<0.001**	0,179	0,672
trt	1	0,224	0,322	-	-	-	-	-	-	**5,211**	**0,022**
time	1	0,981	0,322	**28,525**	**<0.001**	**13,112**	**<0.001**	**26,381**	**<0.001**	0,079	0,779
year	2	-	-	**27,990**	**<0.001**	**14,111**	**0,004**	**23,721**	**<0.001**	0,907	0,635
trt × time	1	**4,465**	**0,035**	-	-	-	-	-	-	**4,14**	**0,042**
trt × year	2	-	-	-	-	-	-	-	-	**6,493**	**0,039**
time × year	2	-	-	**11,006**	**0,004**	**12,467**	**0,002**	**32,232**	**<0.001**	-	-
trt × time × year	2			-	-	-	-	-	-	-	-
Covariates	*df*	$\chi2$	*P*	$\chi2$	*P*	$\chi2$	*P*	$\chi2$	*P*	$\chi2$	*P*
SVL	1	**12,249**	**<0.001**	0,183	0,672	2,982	0,084	0,196	0,658	2,395	0,122
BC	1	1,639	0,200	0,319	0,592	0,151	0,698	0,142	0,707	3,673	0,055

4.3.2. Reproductive traits

Precipitation predictability, alone or in interaction with year or the covariates, did not significantly affect reproduction (all $P > 0.05$; Table 4.2). There existed significant differences among years in reproductive success and number of confirmed mate partners ($P < 0.01$; Table 4.2). Post hoc contrasts showed that reproductive success was significantly higher in 2014 compared to 2013 ($P = 0.023$), and in 2012 it was intermediate. The number of confirmed mate partners was significantly higher in 2014 than in 2012 and 2013 (all $P < 0.05$), and no differences existed between 2012 and 2013.

Table 4.2. Treatment effects on male reproductive traits. Minimum adequate models of reproductive success (RS), and number of confirmed mate partners (NM), average number of juveniles sired per mate partner (ϕNJ). Shown are test statistics based on standardized variables after backward elimination. Parameters removed from the initial model are denoted as "-". The following abbreviations were used: *trt*, treatment; BC, body condition; SVL, snout-to-vent length; H, hue; S, saturation; B, brightness; E, extent of melanin based coloration; BL, blackness of melanin-based coloration.

			RS				**NM**				**ϕNJ**			
Parameter		*df*	χ^2	*P*			χ^2	*P*			χ^2	*P*		
trt		1	-	-			-	-			-	-		
time		1	-	-			-	-			-	-		
year		2	**7.173**	**0.028**			**19.137**	**<0.001**			-	-		
Covariates		*df*	χ^2	*P*	*β*	*se*	χ^2	*P*	*β*	*se*	χ^2	*P*	*β*	*se*
SVL		1	1.753	0.185	-	-	**5.073**	**0.024**	**0.259**	**0.115**	0.588	0.443		
BC		1	0.116	0.733	-	-	0.283	0.595	-	-	0.414	0.520		
Carotenoid	S	1	0.199	0.655	-	-	0.001	0.970	-	-	0.318	0.573		
	H	1	0.249	0.134	-	-	**4.851**	**0.028**	**0.231**	**0.105**	0.743	0.389		
	B	1	1.755	0.185	-	-	0.175	0.676	-	-	0.270	0.604		
Melanin	E	1	2.678	0.102	-	-	**6.982**	**0.008**	**-0.305**	**0.115**	0.415	0.520		
	BL	1	1.680	0.195	-	-	0.558	0.455	-	-	**5.501**	**0.019**	**4.051**	**1.727**

The number of confirmed mate partners was significantly and positively correlated with H and SVL ($P < 0.05$; Table 4.2), and it was significantly and negatively correlated with the extent of melanin-based coloration ($P < 0.05$; Table 4.2). The average number of juveniles sired was negatively correlated with blackness (Table 4.2). For both, number of confirmed mate partners and average number of juveniles sired no significant

correlations existed with other color parameters or body condition (all $P > 0.05$; Table 4.2). In contrast, reproductive success was not significantly correlated with any of the covariates ($P > 0.05$; Table 4.2).

4.4. Discussion

Many animal colors are honest signals of individual quality, whose expression depends on biotic (Kodric-Brown 1989; Fitze et al. 2003, 2007; Tschirren et al. 2003; Hill and J.McGraw 2006; Cote et al. 2008; San-Jose et al. 2013) and abiotic environmental conditions (Bajer et al. 2012; Langkilde and Boronow 2012; Stephenson et al. 2017; Merchant et al. 2018). While effects of temperature, ambient color and light conditions on color expression have been demonstrated, it is unclear whether and how predictability of abiotic conditions affect ornamental coloration. The present study experimentally tested whether differences in precipitation predictability affect carotenoid- and melanin-based ornamental coloration of common lizards. Less predictable precipitation let to reduced hue of carotenoid-based coloration and to a reduced extent of melanin-based coloration (Fig. 4.1). Hue of carotenoid-based coloration and SVL were positively, the extent of melanin-based coloration was negatively correlated with the number of confirmed mate partners, and blackness of melanin-based coloration was negatively correlated with the average number of sired juveniles (Table 4.2).

Treatment effects on hue of carotenoid-based coloration and the extent of melanin-based male ventral coloration are in line with the previously observed plasticity of these traits (Fitze et al. 2009; San-Jose and Fitze 2013) and predictions 1 and 2. Moreover, absence of treatment effects on saturation and brightness of carotenoid-based coloration are also in line with previous results (Fitze et al. 2009). Under less predictable precipitation hue of carotenoid-based coloration decreased (Fig. 4.1A). SVL and hue were positively correlated with reproductive traits (Table 4.2), the former being in line with previous studies showing that body size positively predicts reproductive success of males (Fitze and Le Galliard 2008) and the latter being in line with prediction 3, that coloration predicts reproduction. Consequently, the treatment-induced decrease in hue is associated with less mate partners (Table 4.2), which indicates that less predictable environments negatively affect carotenoid-based coloration. These negative effects are in line with negative effects of reduced precipitation predictability on growth and body size of yearlings (Masó et al. 2019, in prep).
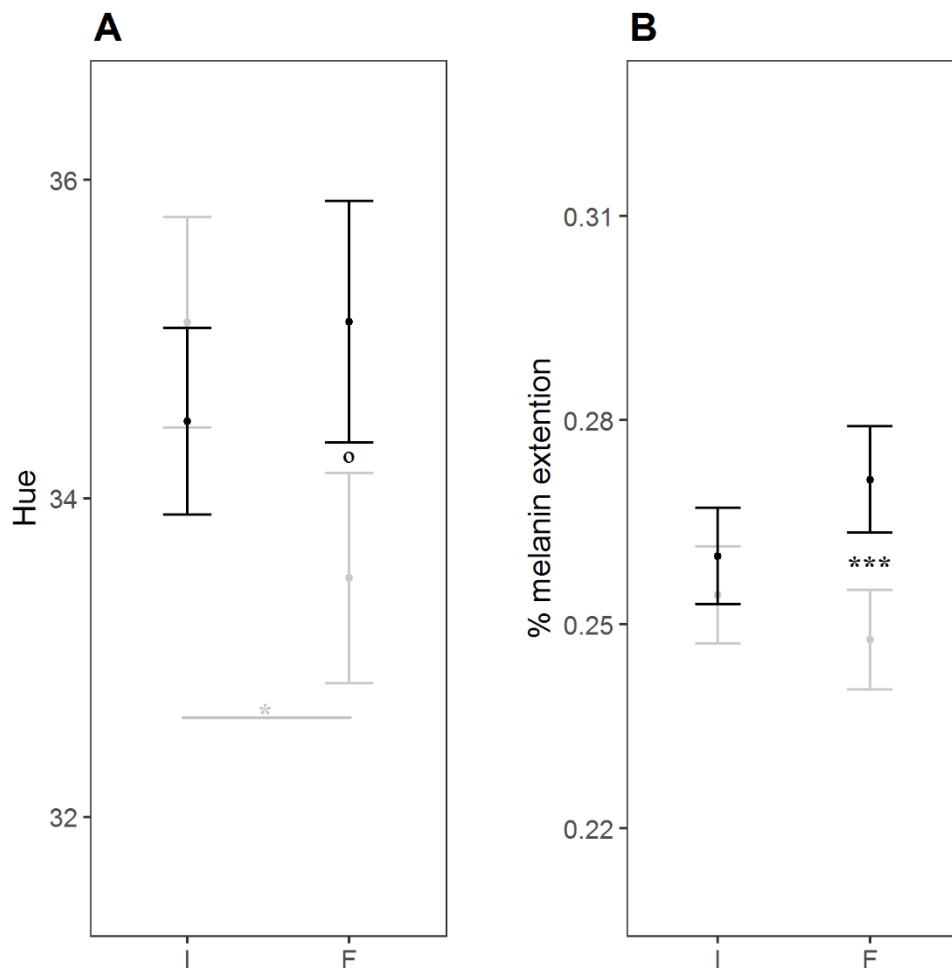
Figure 4.1. Treatment effects (black: more predictable precipitation; grey: less predictable precipitation) on hue of carotenoid-based coloration (A) and the extent of melanin based-coloration (B). Predicted means ± se per treatment and time (I: Initial; F: Final) are shown. Horizontal lines indicate significant post-hoc contrasts: ^{o}P = 0.069; * $P < 0.05$; *** $P < 0.001$.

Less predictable precipitation decreased and more predictable precipitation increased the extent of melanin-based coloration, leading to significant differences during the reproductive season (Fig. 4.1B; Table 4.1). Treatment did not significantly affect blackness (Table 4.1), indicating that the extension, but not the density of melanins, was modified. Consequently, in the more predictable treatment more of the costly melanin-pigments (Lozano 1994; Von Schantz et al. 1999; Blount et al. 2003; Metcalfe and Alonso-Alvarez 2010) were produced and incorporated into coloration, while in the less predictable treatment melanins were removed from ventral coloration. Treatment effects

on hue of carotenoid-based coloration and on the extent of melanin-based coloration both coincide with the idea that less predictable environments impose costs (Pétavy et al. 2004; Ashander et al. 2016) and they show that both traits are condition-dependent honest signals (San-Jose et al. 2013).
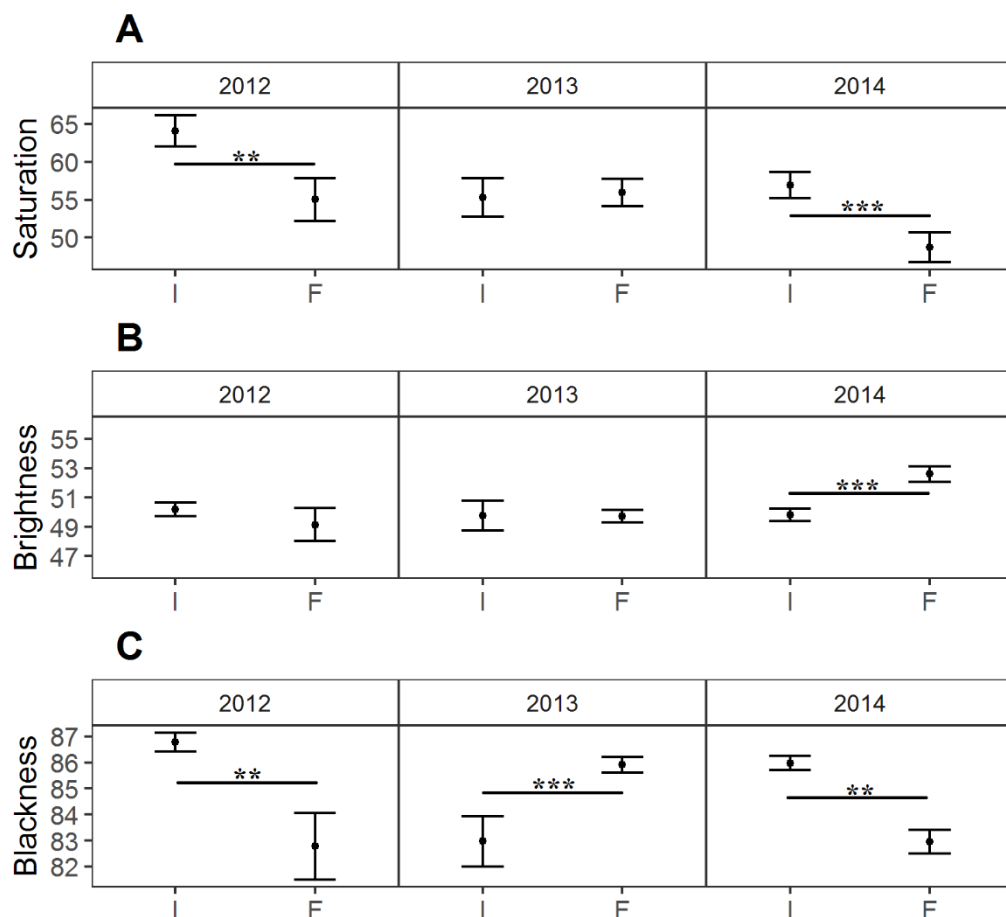
Figure 4.2. Significant year effects on saturation (A) and brightness (B) of carotenoid-based coloration and blackness (C) of melanin-based coloration per year and measurement time (initial versus final measures). Predicted means ± se per year and time are shown. Horizontal lines indicate significant post-hoc contrasts: ** $P < 0.01$; *** $P < 0.001$.

However, while hue of carotenoid-based coloration was positively associated with the number of confirmed mates (Table 4.2), the extent and the blackness of melanin-based coloration were negatively correlated with the number of confirmed mates and the average number of sired juveniles, respectively (Table 4.2). This indicates that in less predictable environments a reduction of hue was associated with reduced reproductive

success, while a reduction in the extent of melanin-based coloration was associated with an increase in mate partners (Table 4.2; for further discussion of this result see next paragraph). Since the estimates were of similar magnitude (Table 4.2), the treatment effect on hue of carotenoid-based coloration and its effect on number of mate partners was cancelled out by the treatment's effect on the extent of melanin-based coloration and its effect on reproduction. This finding is in line with no significant treatment effects on reproductive parameters (Table 4.2; note that in models without covariates, treatment was not significant either) and it suggests that males traded treatment effects on one color trait with effects on another color trait in order to maximize reproduction (Kokko 1998). In other words, this suggests that males compensated treatment effects by differentially investing in carotenoid- and melanin-based coloration, which is in line with prediction 4 and life-history theory predicting a trade-off for self-maintenance (Stearns 1992).

The negative association between the extent of melanin-based coloration and reproduction is at first sight counter-intuitive, since under more predictable precipitation (i.e. better conditions) males increased the extent of melanin-based coloration (Fig. 4.1B). Moreover, the extent of melanin-based coloration is positively associated with the immune response (Vroonen et al. 2013) and bite force capacity (San-jose et al. 2017), suggesting that males exhibiting more melanin-based coloration may be of better quality and thus they should have higher rather than lower reproductive success. While an increased immune response is certainly beneficial (Vroonen et al. 2013), increased bite force capacity can be an advantage for common lizard males, since stronger bites allow to better immobilize and coerce females during sexual selection (Fitze et al. 2010; Huyghe et al. 2013). However, male aggression towards females has fatal consequences, since it increases the risk of injuries on females, weakens female mate choice, reduces a female's reproductive success, and can lead to female death (Fitze et al. 2005; Le Galliard et al. 2005a). Consequently, in order to maximize their reproductive success females should avoid males with strong bites, potentially explaining the here detected and the previously described negative correlation between bite force and reproductive success (Huyghe et al. 2013). The results on melanin-based coloration are thus in line with males of the more predictable treatment optimizing traits unrelated to reproductive success (e.g. immune defense; Vroonen et al. 2013) at the expense of reproductive success, the latter being compensated by differential expression of other sexually selected ornaments (in this study hue of carotenoid-based coloration, Fig. 4.1A).

Contrary to the theory predicting negative effects of decreased environmental predictability on life history traits (prediction 6; Tuljapurkar 1990; Dewar and Richard 2007; Marshall and Burgess 2015; Ashander et al. 2016), our results indicate that differential investment into independent ornamental traits may compensate negative effects manifesting in a particular ornamental trait and its effect on reproduction. The absence of treatment effects on survival (Masó et.al. 2019, in prep), reproduction, and growth of adult males, and the presence of effects on ornamentation and the detected compensatory strategies, suggest that ornamentation is first affected by less favorable conditions and that ornamentation may be used to early detect slight difference in environmental changes.

To our knowledge, this is first study to experimentally demonstrate that individual coloration responds to differences in environmental predictability. In line with theory (Pétavy et al. 2004), our results indicate that less predictable environments are more stressful, that they may impose cost, and that they first manifest in ornamental coloration. Other species exhibiting ornamental coloration could show similar effects to changes in environmental predictability. Results found highlight that ornamental coloration is highly plastic to environmental changes. Thus, the effects observed could also influence conspicuous coloration and it could drive to other effects, such as increasing depredation rates (i.e. due to worse camouflage). This study also shows that it is important to analyze many ornaments at the same time, since at first sight results on carotenoid-based and on melanin-based coloration were opposite and the interpretation of how precipitation predictability affects ornamental coloration would have depended on the choice of the analyzed ornament, potentially leading to erroneous conclusions. Moreover, here we show that common lizard males traded ornaments with a net effect that mitigated effects on reproduction. Our study experimentally demonstrates that ornamental coloration is highly sensitive to environmental changes, which it responds to differences in environmental predictability. This suggests that ornamental coloration most likely reflects the most important sources of environmental constraints (means, predictability, temperature, precipitation, etc.) imposed on lizards and most likely as well on wide range of other animal species.

Acknowledgments

"It is not the strongest of the species that survives, nor the most intelligent that survives. It is the one that is the most adaptable to change"

(Charles Darwin)

Chapter 5

Decreased precipitation predictability negatively affects population growth through differences in adult survival in a short-lived lizard (*Zootoca vivipara*)

Abstract

Global climate change is leading to decreased climatic predictability. Theoretical work indicates that changes in climatic predictability will affect population dynamics and extinction, but experimental evidence is scarce. Here, we experimentally tested whether differences in precipitation predictability affect population dynamics of the European common lizard (*Zootoca vivipara*) by simulating more (MP) and less predictable (LP) precipitation in 12 semi-natural populations over 3 years and measuring different vital rates. A seasonal age-structured matrix model was parametrized to assess treatment effects on vital rates and asymptotic population growth (λ). Survival was consistently, but not significantly higher in MP than LP, and no differences existed in reproductive rates. Small survival differences in adults explained changes in λ and survival differences among age-classes were in line with predictions from cohort resonance. As a result, λ was significantly higher in MP than LP. This experimentally shows that small effects have major consequences on λ, that forecasted decreases in precipitation predictability are likely to exacerbate the current rate of population decline and extinction, and that stage-structured matrix models are required to unravel the aftermath of climate change.

Keywords: Climate change, precipitation predictability, vital rates, demography, elasticity analysis, perturbation analysis, asymptotic growth rate.

5.1. Introduction

The currently observed global climate change affects average environmental conditions (e.g. average temperature) and decreases their temporal predictability (Stocker et al. 2013). Both effects, but especially temporal predictability, may destabilize populations (Lindstrom and Kokko 2002) and increase their susceptibility to extinction (Lande 1993; Foden et al. 2008; Melbourne and Hastings 2008; Ashander et al. 2016). Changes in average environmental conditions have been largely studied and nowadays it is clear that they are responsible for distributional shifts (Parmesan and Yohe 2003), local extinctions (Sinervo et al. 2010), species extinction (Huey et al. 2009; Lunney et al. 2014), and changes in biodiversity (Pounds et al. 2006). Classic theory states that in less predictable environments rapid and more frequent reproduction with minimal investment in offspring is favored (MacArthur 1984) and more recent theory states the contrary, that less predictable environments favor higher investment in individual offspring at the cost of litter size (Einum and Fleming 2004). Both theories suggest that environmental predictability may affect the trade-off between survival and reproduction and/or the trade-off between offspring number and quality (Stearns 1992; Einum and Fleming 2004; Nevoux et al. 2010), but they differ in the direction of the effect. Lack of robust evidence for one or the other hypothesis compromises the understanding of how species respond to changes in environmental predictability, which is essential to predict effects of climate change on population dynamics, ecosystems and biodiversity, and for designing conservation measures (Ferrière et al. 2004; Saccheri and Hanski 2006; Kinnison and Hairston 2007; Chevin et al. 2013).

The few empirical studies (Dewar and Richard 2007; Burgess and Marshall 2014) suggest that decreasing environmental predictability may negatively affect vital rates, such as reproduction or survival. Predictability effects on vital rates can yield substantial information on whether and how species can deal with changes in environmental predictability and they can be indicative for effects on population dynamics (Bjørnstad et al. 2004). However, frequently the direction of effects on different vital rates are not congruent, no significant differences and/or cohort resonance effects exist (Bjornstad et al. 1999) requiring more sophisticated life history analyses to understand whether and how the population dynamic is affected (Bjornstad et al. 1999; Layton-Matthews et al. 2018).

Here we experimentally test over three consecutive years, whether and how differences in precipitation predictability affect population dynamics using 12 independent semi-natural common lizard *Zootoca vivipara* (Lichtenstein, 1823) populations. Half of the

populations were exposed to more predictable and the other half to less predictable precipitation, while holding average precipitation constant. Precipitation predictability was manipulated given the European common lizard's high dependency on water (Grenot et al. 1987; Lorenzon et al. 1999; Peñalver-Alcázar et al. 2016; Dupoué et al. 2017; Romero-Diaz et al. 2017) and given the changes in rainfall patterns observed in the last decades and predicted under climate change (Stocker et al. 2013). Measures of individual vital rates including survival, and different aspects of reproduction were measured and used to parametrize a seasonal age-structured matrix model for each predictability treatment based on the species-specific seasonal life cycle. Treatment effects on age- and season-specific vital rates and asymptotic population growth were tested and retrospective perturbation analysis were used to investigate which treatment effects (treatment effects on which age classes and seasons) mainly let to differences in asymptotic population growth (λ). These analyses thus allowed to identify the key life-history processes that are most affected by changes in precipitation predictability and how they affect population dynamics, shedding light on how species may cope with changes in environmental predictability.

According to theoretic models (Tuljapurkar et al. 2009) and empirical studies (Dewar and Richard 2007; Marshall and Burgess 2015), we predicted (1) significant negative effects of less predictable precipitation on survival (Ashander et al. 2016). In addition, we predicted (2) significant negative effects of less predictable precipitation on reproductive traits, such as laying success, hatching success, litter size, and new-born female ratio (Einum and Fleming 2004; Dewar and Richard 2007; Botero et al. 2015). Given that due to their lower competitive ability, younger age classes are more affected by density-dependent effects and inter-age class competition than adults (San-Jose et al. 2016; Romero-Diaz et al. 2017), we predicted that (3) precipitation predictability may stronger affect the competitively inferior age-classes, namely juveniles and yearlings, e.g. due to cohort resonance (Bjornstad et al. 1999; Bjørnstad et al. 2004). As a result of the anticipated effects on vital rates, we also predicted (4) lower population growth in the less predictable environments.

5.2. Methodology

5.2.1. Study species

The common lizard, *Zootoca vivipara* (Lichtenstein, 1823), is a small ground-dwelling ovoviviparous lizard widely distributed throughout Eurasia. *Zootoca vivipara* inhabits

humid meadows and grasslands, and humidity is a key predictor of habitat choice (Braña 1996; Peñalver-Alcázar et al. 2016). Humidity has been shown to affect individual activity, growth rate (Lorenzon et al. 1999, 2001), and several reproductive parameters (Lorenzon et al. 1999, 2001; Le Galliard et al. 2006; Bleu et al. 2013). Moreover, differences in the quantity of humidity and in its predictability are sources of intra- and inter-age variation in vital rates (Romero-Diaz et al. 2017).

Zootoca vivipara emerges from hibernation in March/April, and reproductive activities start just after the emergence of the females (Bauwens and Verheyen 1985; Fitze et al. 2010; Breedveld and Fitze 2015). The reproductive system is polygynandrous (Fitze et al. 2005) and in the oviparous populations, females lay one, two, and in exceptional cases three clutches per year, and average litter size is five, ranging between one and nine eggs (Heulin et al. 1994; Roig et al. 2000; Horváthová et al. 2013). In most populations, individuals attain sexual maturity in their second or third year of life (Horváthová et al. 2013; Roitberg et al. 2013) and the age of female maturity depends on body size and on the length of the activity season (Horváthová et al. 2013). In many populations, three age classes can be distinguished based on body size and coloration (Pilorge 1987; Massot et al. 1992; Vercken et al. 2007): Juveniles (1st year of life), yearlings (2nd year) and adults (>2 years old). While juveniles and yearlings are generally immature, adults are mature and participate in reproductive activities. Almost all adult females produce eggs and not all reproductively active males fertilize eggs (Fitze et al. 2010). In natural populations, survival of adults ranges from 30 to 60 % (Heulin et al. 2011), in immatures it ranges from 16 to 40 % (Heulin et al. 2011), and survival of juvenile lizards is considerably lower (range: 21 – 26 %; Massot et al. 2011).

5.2.2. Semi-natural populations

All common lizards used for this experiment were originally captured from natural populations located in Aragón and Navarra, corresponding to the South-West European clade B (*Zootoca vivipara louislantzi*; Arribas 2009; and the North-East Spain subclade, B4; Milá et al. 2013; Horreo et al. 2018). Lizards were individually marked by toe-clipping and kept in 12 semi-natural populations located at the Research Station 'El Boalar' (Instituto Pirenaico de Ecología, Jaca, Spain, 42°33'N, 0°37'O, 700 m a.s.l.), consisting of enclosures (100m2) delimited by galvanized metal walls that were 1m high and extended 1m below ground to prevent the escape of lizards and the entrance of predators. Shrew traps were installed inside and outside the enclosures and enclosures were covered by nets, both to avoid predation. Each population contained natural

grassland, two water ponds, logs, and stone piles that provided lizards with naturally occurring prey, hiding and basking sites (for more details see Romero-Diaz et al. 2017)).

In each experimental year, the same number of adults and yearlings, and a similar number of juveniles were released in each enclosure (Table 2.1). No significant differences in the number ($F_{1,10}$ = 1.033; P = 0.317) and sex-ratio ($F_{1,10}$ = 0.005; P = 0.94) of released juveniles existed among precipitation treatments (Table 2.1). Lizards were randomly distributed among enclosures, and no significant differences existed among precipitation treatments in snout-to-vent length (SVL), body condition and adult male color morph frequency (all $P \geq 0.2$). Adults and yearling lizards were released in July, female lizards were released after parturition, and juvenile lizards were released two days after hatching. All lizards were released in unknown enclosures. Juveniles from the same clutch were released together, in a different enclosure than their mother, and not into the enclosure where the mother lived during the previous year. In each experimental year, all surviving lizards were captured in late spring. Half of the captured lizards, i.e. half of each sex and half of each age class, were released in the same predictability treatment (but not in the enclosure in which they have been living before), while the other half was released in the other predictability treatment.

5.2.3. Precipitation predictability treatments

The precipitation predictability was manipulated during three years using an automatic irrigation system. Each year, six populations were exposed to more and another six to less predictable precipitation, by supplementing precipitation with four sprinklers per enclosure, one in each corner, which ensured homogeneous precipitation of the entire enclosure. In the more predictable treatment, two precipitation events happened every day (i.e., 14 supplemental precipitation events per seven days), one at 9:00 and the other one at 18:00. Together with the natural precipitation, this treatment corresponded to more predictable precipitation events. In the less predictable treatment, the 14 supplemental precipitation events were randomly distributed among seven days between 9:00 and 18:00. Weighted permutation entropy was calculated to quantify the predictability of precipitation in each treatment level (for calculation details see supporting information section "A"). Permutation entropy was larger in the less (0.86) and smaller in the more predictable treatment (0.77), showing that precipitation was less predictable in the less predictable treatment. Consequently, all enclosures obtained the same amount of precipitation, while the predictability significantly differed among precipitation treatments.

5.2.4. Data collection

5.2.4.1. Survival

After release, two capture-recapture sessions were conducted, one at the end of August and the other one at the end of September. Each capture session consisted of three consecutive days of intensive capture with equal effort across time and enclosures. Captured lizards were individually identified and released on the same day and in the same enclosure where they were captured. Approximately, at the end of May, all surviving lizards were captured and brought to the laboratory, where they were kept in individual terrariums until release. Recapture of all surviving individuals was assured by searching a given enclosure for lizards until five days passed since the last lizard has been detected and recaptured in this enclosure. Survival was determined per capture session, and corresponds to the recapture of a lizard on at least one of the three capture days (per session), following a robust design (Kendall et al. 1995).

5.2.4.2. Reproduction

From end of April until end of May (for first clutches) and from mid-June onwards until mid-July (for second clutches), females were captured weekly and gravidity was determined by means of belly palpation. Gravid females were moved to the laboratory where they were kept in individual terrariums under standardized conditions (see below), while non-gravid females and females with small eggs were released in the exact capture location directly after capture. All lizards that were brought to the laboratory where they were maintained in individual terraria, that contained peat substrate, a hide, a water pond, and a heat source, and that were exposed to a standardized light regime (see San-Jose et al. 2016; Romero-Diaz et al. 2017). Lizards had access to ad libitum water and were fed every fourth day with wax moths (Galleria mellonella) or house crickets (Acheta domesticus). Every week, body mass was measured, individuals were checked for ectoparasites, and terraria were checked for mould and faeces and replaced with a new one when necessary. Terraria of gravid females were checked twice a day for laid clutches. Litter size (i.e., the number of eggs) and laying date of detected clutches were recorded and detected clutches were individually incubated in a constantly humid atmosphere at 21ºC during the day (from 9:00 to 21:00) and 19ºC during the night (Heulin et al. 1997). Incubating eggs were checked daily, and sterile eggs or eggs containing dead embryos were removed. Once juveniles hatched, the number of juveniles hatched per clutch and the date of hatching were recorded. Juvenile lizards born before the August capture session were classified as "early juveniles" and juveniles

born afterwards were classified as "late juveniles", the former corresponding to first clutches and the latter to second clutches.

5.2.5. Seasonal life cycle

We developed a flexible seasonal life cycle for the South-West European common lizard *Zootoca vivipara louislantzi* (Fig.5.1), which allows testing how differences in age at first reproduction affect asymptotic population growth rate (see below). The life cycle consists of three seasons that correspond to the oviparous common lizard's main life stages and to the time between capture sessions: May – August, August – September and September – May, hereafter referred to as 'spring', 'summer', and 'winter', for simplicity. Five life-history stages: early juveniles (JE), late juveniles (JL), yearlings (Y), first year adults (AD1) and adult lizards (AD) were considered. The life cycle was based on females, because females represent the reproductive segment of the population (Caswell 1989). Survival and reproductive rates were calculated for spring and summer, and survival was calculated for winter. The life cycle valid for most *Zootoca vivipara* populations (Pilorge 1982; Heulin 1985; Massot et al. 1992), included the following stage- and season-specific vital rates:

- Spring (*sp*): survival (*SAD_sp*, *SAD1_sp*, *SY_sp*), reproductive rate *(RAD_sp, RAD1_sp*)
- Summer (*sm*): survival (*SAD_sm*, *SAD1_sm*, *SY_sm*, *SJE_sm*), reproductive rate (*RAD_sm*, *RAD1_sm*)
- Winter (*wt*): survival (*SAD_wt*, *SAD1_wt*, *SY_wt*, *SJE_wt*, *SJL_wt*).

The transition between age-classes took place during winter: first year adults (AD1), yearlings (Y), and juveniles (early and late juveniles) changed to the AD, AD1, and Y stage, respectively. Since in most populations lizards are not mature in the year following birth (Bauwens and Verheyen 1985), reproductive rates for adults and first-year adults (RAD, RAD1), but not for yearlings, were calculated using several multiplicative fitness proxies:

$$Ra = La*Na*Ha*Fa$$

These proxies consisted of laying success (*L*: 0 = no eggs laid, 1 = eggs laid), litter size (number of eggs: *N*), hatching success (*H: Nhatched offspring/N*) and the female ratio of a clutch (*F: Nfemales/N*). a represents the age class and in the here described basic life-cycle (Fig. 5.1) it has two levels: *AD and AD1*.
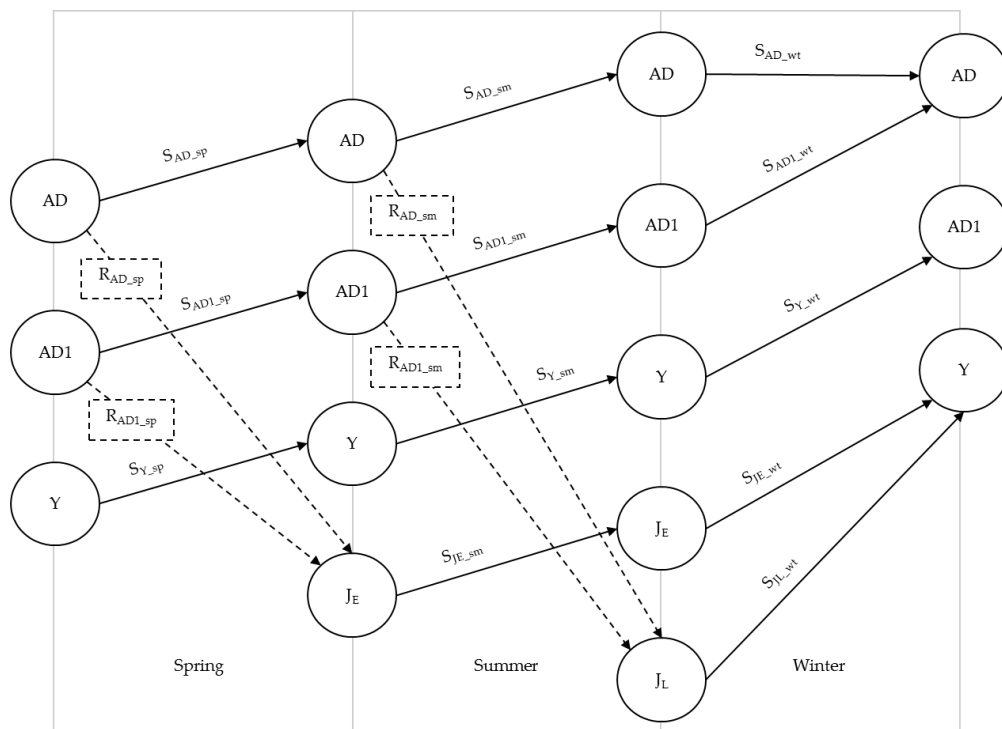
Figure 5.1. Life cycle of the oviparous South-West European common lizard *Zootoca vivipara louislantzi* (clade B; Horreo et al. 2018). *Sx* is the probability that an individual in stage x survives until the next census. The reproductive rate, *Rx*, is the probability of producing at least one juvenile. Abbreviations for life-history stages correspond to: adults (*AD*), first-year adults (*AD1*), yearlings (*Y*), early juveniles (*J*E), and late juveniles (*J*L). Seasons are abbreviated as spring (*sp*), summer (*sm*) and winter (*wt*).

5.2.5.1. Estimation of vital rates

All vital rates (survival and reproductive parameters) shown in Figure 5.1 and those used for calculating *Ra* were estimated for each precipitation predictability treatment, age class, and season, using generalized linear mixed models (glmer or lmer from package lme4, (Bates et al. 2014). Age class, treatment, and season were modelled as fixed factors and enclosure, year, and individual ID (when appropriate) as random factors. For survival, laying success, hatching success and female ratio glmer's with binomial error distribution and a logit link were used (Bolker et al. 2009), for litter size glmer's with Poisson error distribution and a log link, and for the other variables lmer's with Gaussian error distribution. To predict the mean and standard error of each vital rate from the fitted generalized linear mixed model, the function "predictSE" included in the package AICcmodavg (Mazerolle and Mazerolle 2017) was used. To test if significant differences between precipitation predictability treatments existed in the

vital rates, a permutation test was run at the enclosure level. To this end, all permutations for six enclosures with less predictable precipitation (LP) and six enclosures with more predictable precipitation (MP) were generated (924 permutations in total). For each permutation each vital rate was calculated for the LP and the MP treatment, and the difference between predictability treatments ("x_{LP} - x_{MP}") was calculated, rendering the exact distribution of treatment differences. Based on this distribution, we then determined for each vital rate whether the observed treatment difference was significantly different from the expected treatment differences, assuming a two-tailed test with a significance level of $P < 0.05$. All analyses were run using R 3.5.0 (Team 2018).

5.2.6. Population dynamics

To compare the population dynamics among the two precipitation predictability treatments, a periodic, stage-structured, female-based matrix model was parameterized for each predictability treatment (Caswell 2001). This model included a matrix for each season.

The spring matrix M_{sp} projected the population from three spring stages (AD, AD1 and Y) to four summer stages (AD, AD1, Y and J_E):

$$
\begin{array}{c}
\\
J_E \\
Y \\
AD_1 \\
AD
\end{array}
\begin{array}{ccc}
Y & AD1 & AD \\
\left[\begin{array}{ccc}
0 & R_{AD1\_sp} & R_{AD\_sp} \\
S_{Y\_sp} & 0 & 0 \\
0 & S_{AD1\_sp} & 0 \\
0 & 0 & S_{AD\_sp}
\end{array}\right]
\end{array}
$$

The summer matrix M_{sm} projected the population from four summer stages (AD, AD1, Y and J_E) to five winter stages (AD, AD1, Y, J_E and J_L):

	Je	Y	AD1	AD
J_L	0	0	R_{AD1_sm}	R_{AD_sm}
J_E	S_{JE_sm}	0	0	0
Y	0	S_{Y_sm}	0	0
AD1	0	0	S_{AD1_sm}	0
AD	0	0	0	S_{AD_sm}

And the winter matrix M_{wt} projected the population from five winter stages (AD, AD1, Y, J_E and J_L) to three spring stages (AD AD1 and Y):

	J_L	J_E	Y	AD1	AD
Y	S_{JL_wt}	S_{JE_wt}	0	0	0
AD1	0	0	S_{Y_wt}	0	0
AD	0	0	0	S_{AD1_wt}	S_{AD_wt}

The asymptotic population growth rate λ was estimated as the dominant eigenvalue of the population projection matrix. Means and 95% confidence intervals were estimated for λ using a parametric bootstrapping approach (Wisdom et al. 2000). The annual population projection matrix was calculated as:

$$A = Mwt \cdot Msm \cdot Msp$$

Elasticity analysis, a widely used prospective perturbation analysis, was used to measure the sensitivity of λ to a change in a given vital rate, based on the annual projection matrix (Caswell and Trevisan 1994). Lower-level elasticities for common lizard vital rates were calculated analytically using the chain rule (Caswell 2001):

$$\frac{x}{\lambda}\frac{\delta\lambda}{\delta x} = \frac{x}{\lambda}\sum_{ij}\frac{\delta\lambda}{\delta aij}\frac{\delta aij}{\delta x}$$

where a_{ij} is the matrix element in row i and column j, and x is a lower-level parameter of survival or reproductive rate. $\delta\lambda/\delta aij$ is the matrix element sensitivity, whereas $\delta aij/\delta x$ is the partial derivative of a given matrix element with respect to the lower-level parameter x.

Using a fixed one-way life table response experiment (LTRE), a commonly used retrospective perturbation analysis (Caswell 1989), we identified the demographic causes of differences in λ between the two predictability treatments. Using the matrix of the more predictable precipitation regime as a reference, the observed difference in asymptotic population growth rate between the MP and the LP precipitation regime ($\Delta\lambda$) was decomposed into contributions from each vital rate, according to:

$$\Delta\Lambda = \Lambda_{LP} - \Lambda_{MP} \approx \sum_{ij} (x_{LP} - x_{MP}) \frac{\delta\Lambda}{\delta x_{MP}}$$

(subscripts LP and MP indicate the matrices of less and the more predictable precipitation regime, respectively). "$x_{LP} - x_{MP}$" represents the difference between treatments of the lower level-parameters and "$\frac{\delta\Lambda}{\delta x_{MP}}$" represents the sensitivity of the lower-level parameters, estimated using the reference matrix.

5.2.7. Effects of delayed and advanced maturity

Differences in environmental conditions may lead to differences in growth rate (e.g. San-Jose et al. 2016; Romero-Diaz et al. 2017) and thus differences in the age at first reproduction. To assess the influence of delayed and advanced maturity on asymptotic population growth rate (λ), the basic life cycle (Fig. 5.1) was re-parametrized. To simulate a delay of maturity by one year in the LP treatment (Masó et. al. 2019, in prep), that means that the first reproduction happens in the third instead of the second spring, we set R_{AD1_sp} and R_{AD1_SM} to zero in the matrix model for LP (Fig.5.1). To simulate an advance of maturity by one year, i.e. first reproduction in the first instead of the second spring, we assumed that already yearlings reproduce by parametrizing R_{Y_sp} and R_{Y_SM} with the reproductive rates of the first-year adults of the basic model (Fig. 5.1, R_{AD1_sp} and R_{AD1_SM}) and likewise, R_{AD1_sp} and R_{AD1_SM} were equal to those of R_{AD_sp} and R_{AD_SM} of the basic model. All the rest remained equal. For each model, we estimated the asymptotic population growth rate λ for LP, compared it to the previously derived λ for MP and performed a prospective perturbation analysis.
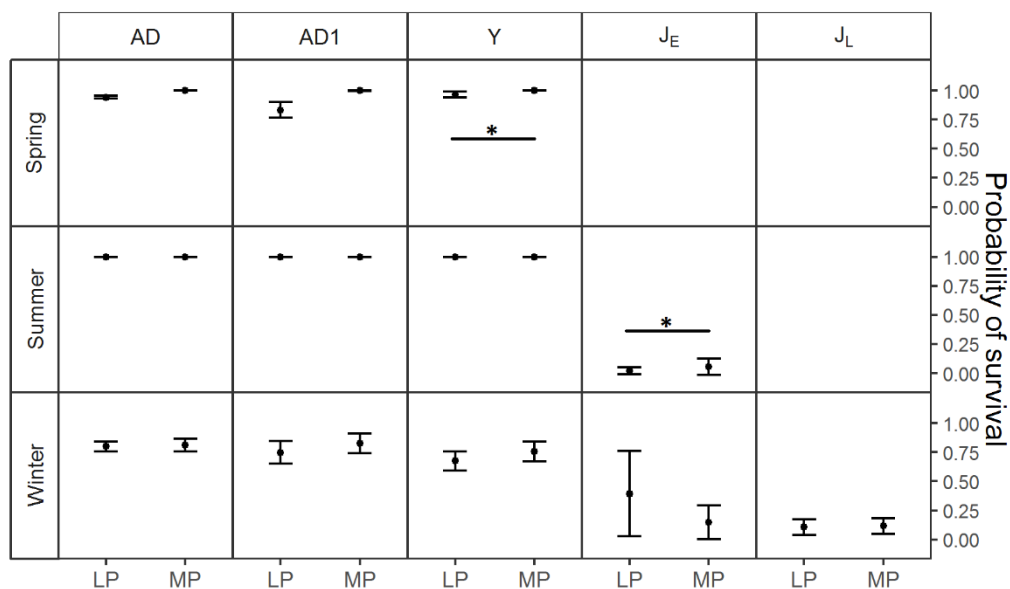
Figure 5.2. Survival probability per season and age class, predicted by the matrix model for the less (*LP*) and the more (*MP*) predictable precipitation treatment. Age classes are abbreviated as follows: adults (*AD*), first-year adults (*AD1*), yearlings (*Y*), early juveniles (*JE*) and late juveniles (*JL*), and means ± SE are given. Significant differences in average survival among treatments are indicated with horizontal lines and significance is abbreviated as * *P*<0.05.

5.3. Results

Spring survival of yearlings and summer survival of early juveniles were significantly higher in the more compared to the less predictable treatment (Fig. 5.2). In all other survival vital rates differences among treatment levels were not significant (Figs. 5.2, 5.3; all *P* > 0.05). Survival was estimated for three seasons, five age classes, and a total of 12 combinations (Fig. 5.2). In eight of the twelve combinations, lizards exposed to the MP treatment exhibited higher survival (in the three spring measures; in four of five winter measures, and in one summer measure; note: in six of them the differences was not significant). In contrast, winter survival of early juveniles exposed to LP was slightly higher than that of early juveniles exposed to MP, and no visible differences existed in summer survival of adults, first-year adults, and yearlings (Fig. 5.2 – see also differences in Fig. 5.3). Thus, there existed significantly more combinations where survival was slightly higher in the more predictable treatment (t_{11} = 3.023, *P* = 0.012). Four reproductive traits were estimated for two seasons, two age classes, and 16 combinations (Fig. 5.4). In seven combinations, reproductive parameters were higher in the less

predictable treatment, in another five combinations reproductive parameters were higher in the more predictable treatment, no visible differences existed in the remaining four combinations (Fig. 5.4, and differences in Fig. 5.5), and no significant differences existed (t_{15} = -0.565, P =0.581, Fig. 5.4).
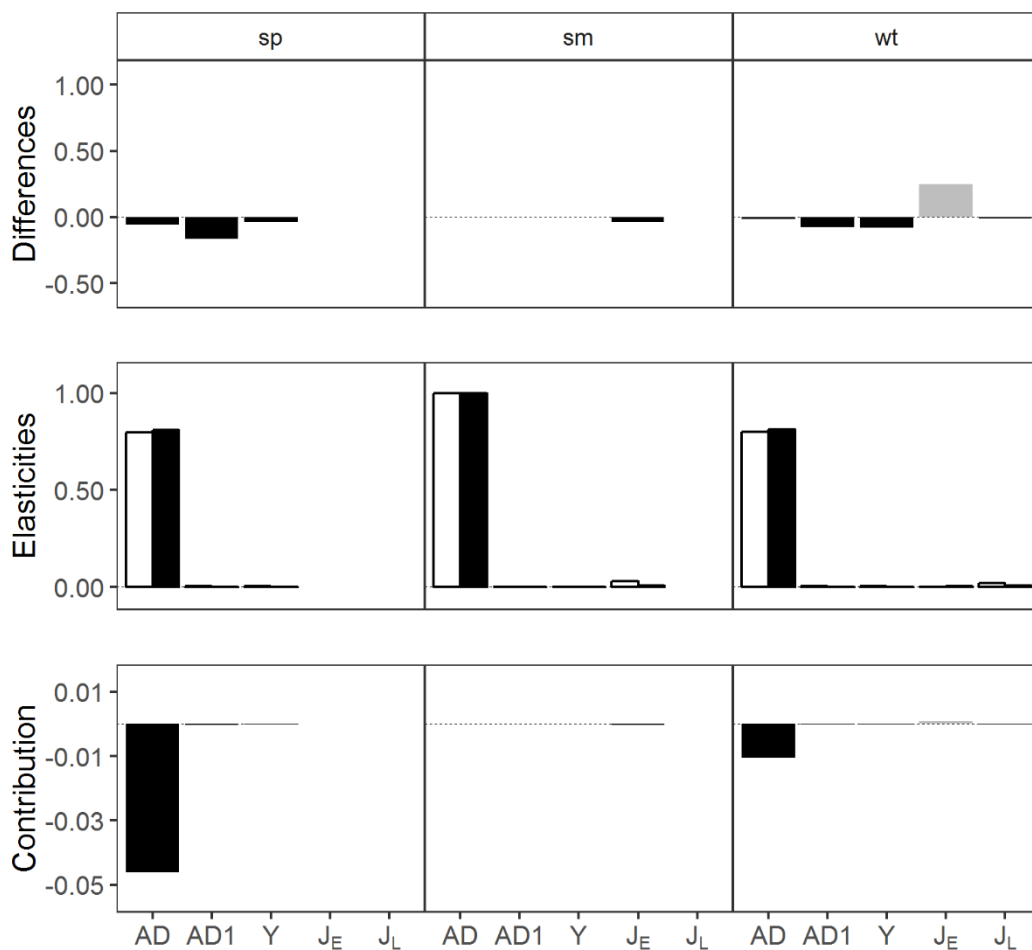
Figure 5.3. Differences in survival probability (row 1), elasticity of λ to survival (row 2), and the contribution of survival difference to the difference in λ (row 3) between less and more predictable precipitation. For differences and contributions, black bars depict situations where survival in the less predictable treatment (*LP*) is smaller than in the more predictable treatment (*MP*) and grey bars where *LP* > *MP*. For elasticity of λ white depicts *LP* and black *MP*. Seasons and age classes are abbreviated as spring (*sp*), summer (*sm*), winter (*wt*), and adults (*AD*), first-year adults (*AD1*), yearlings (*Y*), early juveniles (*J_E*), and late juveniles (*J_L*).
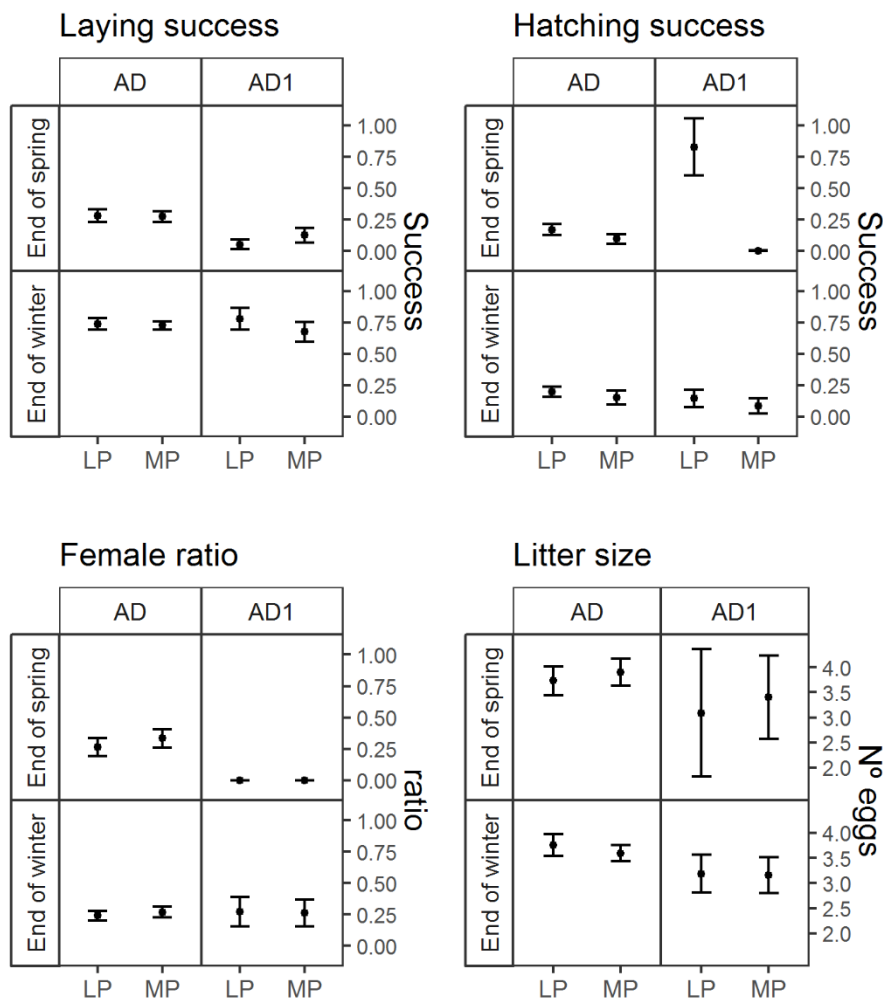
Figure 5.4. Reproductive rates for adult (*AD*) and first-year adult (*AD1*) females per season, predicted by the matrix model for the less (*LP*) and the more (*MP*) predictable precipitation treatment. Means ± SE are given.

The asymptotic population growth rate ($\lambda < 1$) was significantly higher in the MP than in LP treatment (Fig. 5.6). The elasticity of λ to vital rates was most affected by changes in adult survival, while changes in first-year yearling and juvenile survival exhibited small elasticities (Fig. 5.3). Elasticities were almost identical between precipitation predictability treatments and only in summer survival of early juveniles they were higher in the LP treatment (Fig. 5.3). The contribution of survival differences to differences in λ was highest for adult survival in spring, followed by adult survival in winter, and they were neglectable small for the other survival differences (Fig. 5.3). Elasticities of λ to reproductive rates were small (Fig. 5.5). In adults, hatching success

(*H*) at the end of spring and female ratio (*F*) at the end of spring exhibited the highest elasticities and they were higher in the LP treatment (Fig. 5.5). The contribution of differences in vital rates to differences in λ were neglectable small for most reproductive rates (Fig. 5.5).
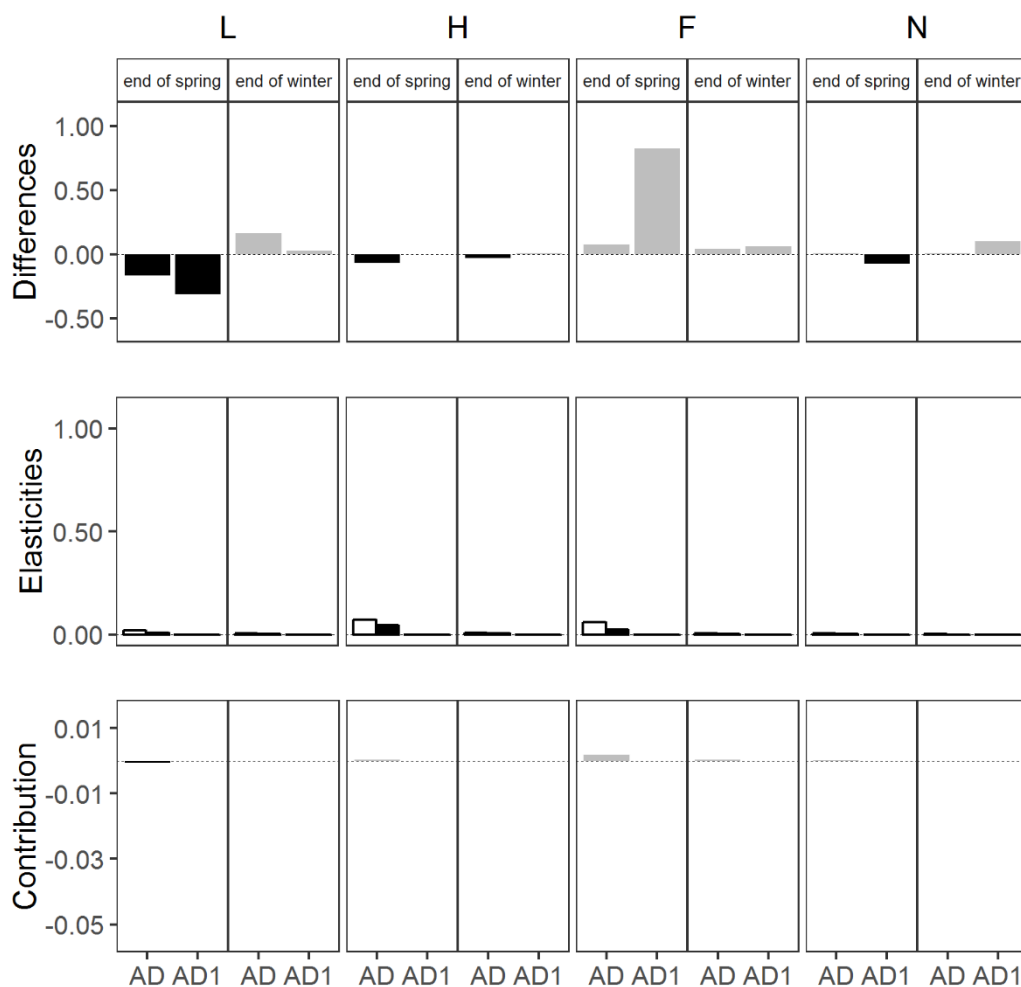
Figure 5.5. Differences in reproductive rates (row 1), elasticity of λ to vital rates (row 2), and contribution of the difference observed in vital rates to the difference in λ between more (*MP*) and less predictable (*LP*) precipitation (row 3). For differences and contributions, black bars depict situations where vital rates in the LP treatment are smaller than in the MP treatment and grey bars where LP > MP. For elasticity of λ white depicts LP and black MP. Seasons, age classes and reproductive rates are abbreviated as end of winter (wt), end of spring (sp), adults (*AD*), first-year adults (*AD1*), laying success (*L*), hatching success (*H*), number of eggs (*N*), and female ratio (*F*).

Delaying or advancing maturity by one year did not substantially affect population dynamics. In both models, asymptotic population growth rates were identical to those of the main model (Fig. 5.6). In addition, in both model types perturbation analysis showed that the main contributors to λ were adult survival rates in spring and winter, as found in the basic model (Fig. 5.3).

5.4. Discussion

Climate change scenarios forecast a reduction in the predictability of precipitation (Stocker et al. 2013) and analyses over the last decades showed that the predictability of precipitation decreased over time, while the probability of extreme precipitation events increased (Stocker et al. 2013). Understanding whether and how such changes affect organisms is central for conservation, evolution, and ecology (Chevin et al. 2010). However, population responses to a decrease in environmental predictability remain poorly investigated (e.g. Bjørnstad et al. 2004; Ashander et al. 2016), and to our knowledge, experimental proof is lacking. Here, we experimentally manipulated precipitation predictability and tested its effect on the population dynamics of a short-lived lizard, the European common lizard *Zootoca vivipara*, using a seasonal stage-structured matrix model.

Experimental manipulation of precipitation predictability demonstrated that the simulated moderate decrease in precipitation predictability reduced the asymptotic population growth rate λ (Fig. 5.6), in line with prediction four. This result was robust with respect to treatment-induced differences in the age of first reproduction (Masó et al., unpublished results.), since delayed and advanced maturity in LP let to the same treatment differences in λ as those of the standard life cycles (Fig. 5.1, 5.6). Significant treatment-differences in spring survival of yearlings and summer survival of early juveniles, and the significant amount of small non-significant survival differences (Fig. 5.2) between treatment levels were in line with the observed decline in population growth rate (Fig. 5.6). The elasticity and the prospective perturbation analyses showed that treatment differences in spring and winter survival of adults (Fig. 5.4, 3rd row) mainly contributed to the decrease in population growth observed in the less predictable treatment (Fig. 5.6). Although other survival probabilities varied between precipitation predictability treatments, their effect on population growth rate was almost null (Fig. 5.2, 5.3). For example, yearling spring survival and summer survival of early juveniles were significantly higher in the more predictable treatment (Fig. 5.2). The elasticity of λ to these parameters was low and differences in elasticity among treatments were only

visible in early juveniles (Fig. 5.3, 2nd row) and their contribution to λ was negligible (Fig. 5.3, 3rd row).

These results are in line with prediction one, that survival may be negatively affected by decreased environmental predictability (Durant et al. 2003; Jenouvrier et al. 2003; Sandvik et al. 2005; Ashander et al. 2016). In our study, most treatment-effects on survival were non-significant and existed mainly in spring and during winter. However, the direction of the treatment effect was consistent (Fig. 5.3) and the prospective perturbation analyses underpin the hypothesis that climatic predictability affects the survival rate of adults (Durant et al. 2003; Jenouvrier et al. 2003; Sandvik et al. 2005). Furthermore, significant negative effects found in juvenile and yearling survival in the LP treatment, but not in the hierarchically superior age classes (in juveniles: yearlings, AD1, and AD and in yearlings: AD1 and AD), are in line with prediction three, that precipitation predictability may stronger affect the competitively inferior age-classes (Grenot et al. 1987; San-Jose et al. 2016; Romero-Diaz et al. 2017), potentially due to inter age-class resource competition previous to hibernation (San-Jose et al. 2016). Similarly, the higher survival of adults and yearlings during the winter period (i.e. during early spring) in the MP treatment may have let to stronger inter-age-class competition during sexual selection (San-Jose et al. 2016), potentially explaining the reduced survival of early juveniles (Fig. 5.2). Thus, these effects on survival are in line with predictions from cohort resonance (Bjornstad et al. 1999; Bjørnstad et al. 2004).

In contrast, reproductive rates were not affected by treatment, non-significant differences among treatments that may explain the observed decline in population growth rate were not consistent (Fig. 5.4, differences in Fig. 5.5), and their contribution to differences in population growth were insignificant (Fig. 5.5). These results contrast to prediction two, that environmental predictability affects reproduction (Einum and Fleming 2004; Dewar and Richard 2007; Botero et al. 2015). Given that summer survival did not differ among treatments (Fig. 5.2), these results also suggest that the here simulated differences in precipitation predictability did not affect the trade-off between investing in reproduction and subsequent survival (under the trade-off we would predict increased investment into reproduction during spring leading to reduced survival during summer; Stearns 1992). This suggests that surviving individuals can cope with decreased environmental predictability (Ashander et al. 2016), and that only the non-significant treatment differences in survival affected λ.

The difference in λ was in the range of 5.7 % (Fig. 5.6), showing that over less than twelve years, populations exposed to the here simulated less predictable precipitation will

decline by 50%. Moreover, life history theory states that individuals should reduce reproductive investment and increase survival to reduce the deleterious effects of reduced predictability (Roff et al. 2002; Nevoux et al. 2010). However, *Zootoca vivipara* did not adjust reproduction, suggesting that changes in life-history strategy with respect to environmental predictability may be slow or absent (Ashander et al. 2016).

The precipitation predictability effect on λ is particularly dramatic since in our population experiment adult survival, the main contributor to the difference in λ, is almost twice as high as in the natural populations (average annual adult survival: 0.45 ± 0.15SE in the Pyrenees, Heulin et al. 2011; 0.42 ± 0.06 SE in the Cévennes, Massot et al. 2011; 0.81 ± 0.06 SE in populations exposed to MP precipitation). Because higher survival rates are indicative for less stressful environments (Romero et al. 2000), our results suggest that in natural populations, *i.e.* in more stressful environments, the same differences in precipitation predictability may have even stronger effects on λ. This finding experimentally underpins the results of theoretic studies predicting that less predictable environments will increase the risk of population extinction (Chevin et al. 2010; Ashander et al. 2016).
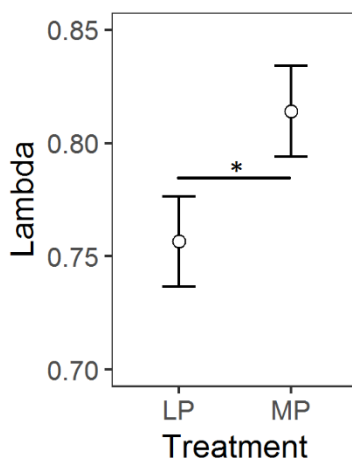
Figure 5.6. Asymptotic population growth rate, λ, in less (*LP*) and more (*MP*) predictable environments. Shown are predicted means ± SE, and an asterisk indicates $P < 0.05$.

In summary, our results experimentally show that the predicted decrease in environmental predictability (Stocker et al. 2013) is likely to exacerbate the rate of currently observed population decline and extinction (e.g. 12% of extinction since 1975 in lizards; 48 % of rapidly declining amphibian species; 21% of bird species are extinction prone and 6.5% functionally extinct; Sekercioglu et al. 2004; Sinervo et al. 2010). The

important effects of the non-significant survival differences on λ show that even non-significant and small effects can have major consequences (Bjørnstad et al. 2004), and that those may not be anticipated by studies of short duration and studies analyzing a few parameters. On the contrary, only the here applied stage-structured matrix model allowed to understand the consequences of differences in precipitation predictability on population dynamics, while a few selected parameters measured in one or two years on the individual level, would not have let to the same conclusions (see Appendix C.1 supporting information). Consequently, assessment of how changes in environmental predictability affect populations, species' persistence, and biodiversity requires solid and difficult to get data that allows testing effects on the population dynamics using stage-structured matrix models, since only those models may allow to understand the ultimate effects of changes in environmental predictability.

Acknowledgments

Figure 6.1. Juvenile lizard basking on a rock in the semi-natural populations. By Campo, Benito.

Chapter 6

General discussion

Current climate change is predicted to increase mean global temperature, affect mean precipitation and decrease the predictability of these abiotic factors (Easterling et al. 2000; Allan and Soden 2008; Stocker et al. 2013). While there is a growing body of work on how change in average conditions might affect individuals and species responses, little evidence exists about whether and how changes in the predictability will affect species and populations (Chen et al. 2011).

The broad objective of this doctoral thesis was to provide robust evidence on whether and how species respond to changes in environmental predictability. The results will shed light on the importance, the direction, and the strength of decreased environmental predictability on species persistence. Based on previous studies (Tuljapurkar 1990; Dewar and Richard 2007; Marshall and Burgess 2015; Ashander et al. 2016), the main hypothesis of this thesis was that decreased environmental predictability might negatively affect life history traits and, thereby, populations dynamics. In particular, we experimentally tested whether and how decreased environmental predictability affects individual growth, body condition, survival and female reproduction (Chapter 3); whether it affects male ventral ornamental coloration and male reproduction (Chapter 4); and, finally, whether it affects population dynamics, including vital rates and asymptotic population growth rate (Chapter 5).

The obtained results support the hypothesis that less predictable environments negatively affect life-history traits (Tuljapurkar 1990; Dewar and Richard 2007; Marshall and Burgess 2015; Ashander et al. 2016). Less predictable precipitation negatively affected growth of yearlings (Chapter 3), body condition of female juveniles (Chapter 3), and male ornamental coloration (Chapter 4).

First, reduced yearling growth and body condition of juvenile females (Chapter 3) are in line with theory predicting that environmental conditions first affect the competitively inferior age-classes (Grenot et al. 1987; San-Jose et al. 2016; Romero-Diaz et al. 2017) and with stage-dependent effects due to inter-stage competition (e.g. San-Jose et al. 2016; Romero-Diaz et al. 2017). However, inter-annual differences in age-class-dependent treatment effects, as well as sex-dependent treatment effects found on growth were not consistent with this hypothesis. In contrast, the results provide for the first time experimental evidence for age- and sex-dependent sensitivities to precipitation predictability (Rozen-Rechels et al. 2018), for example, due to differences in thermoregulatory activity (Christian et al. 2006).

Second, less predictable environments negatively affected the ornamental coloration of male lizard (Chapter 4). Treatment effects observed on hue of carotenoid-based coloration and on the extent of melanin-based male ventral coloration are in line with the previously observed plasticity of these traits (Fitze et al. 2009; San-Jose and Fitze 2013). While under less predictable precipitation, hue values and the extension of melanin-based coloration got smaller over the course of a year, and no changes in hue and an increase of the extent of melanin-based coloration were found in the more predictable treatment. Treatment-induced changes found in both coloration parameters were congruent with the hypothesis that less predictable environments impose costs (Pétavy et al. 2004; Ashander et al. 2016), showing that these ornamental coloration traits are condition-dependent honest signals (San-Jose et al. 2013).

Third, compensatory strategies that mitigated negative effects on life history traits were found in the less predictable treatment. In different seasons, precipitation predictability affected adult growth and body condition change in different directions, and therefore no significant differences existed in spring SVL and body condition (Chapter 3). Furthermore, treatment effects on different types of ornamental coloration represented compensatory strategies that let to no significant treatment effects on male reproductive traits (Chapter 4).

Fourth, the absence of significant treatment effects on survival (Chapter 3), reproduction, and growth of adults (Chapter 3), and treatment-effects on ornamentation and the detected compensatory strategies (Chapter 3 and 4), suggest that ornamentation, rather than growth, reproduction, and survival, is first affected by less favorable environmental conditions. Thus, environmental predictability seem to first affect parameters being less important for individual fitness, increasing the chance for individuals to cope with different environmental predictability (Stearns 1992).

Fifth, while it has been suggested that species responses to changes in the environmental variance might be altered or even reversed by differences in mean environmental conditions (Lawson et al. 2015), no evidence for similar effects exist in environmental predictability. In Chapter 3 and 4, we therefore assessed if effects due to changes in environmental predictability may also depend on average environmental conditions. Treatment effects on growth, body condition and laying date of adult lizards (Chapter 3) were year-specific, while treatment effects on yearling growth (Chapter 3), juvenile body condition (Chapter 3) and male reproductive traits (Chapter 4) were consistent among years. Analyses of average yearly climatic conditions showed that effects on

laying date, adult growth, and body condition might indeed be the consequence of differences in average climatic conditions.

Sixth, most of the key life history traits (e.g. reproduction and survival) were not significantly affected by precipitation predictability over the duration of a year. However, several of the non-significant treatment effects exhibited the same direction and the more sophisticated stage-structured matrix models unraveled that the simulated decrease in environmental predictability importantly reduced the asymptotic population growth rate (Chapter 5). Theory predicts that survival may be negatively affected by decreased environmental predictability (Durant et al. 2003; Jenouvrier et al. 2003; Sandvik et al. 2005; Ashander et al. 2016), and the results of the stage-structured population models on survival vital rates (Chapter 5) are in line with these predictions. The elasticity and the prospective perturbation analyses showed that slightly treatment differences in survival of adults mainly contributed to the decrease in population growth rate observed in the less predictable treatment. Because treatment effects of environmental predictability on life-history parameters were not significant, the results of the population model show that even non-significant and small effects can have major consequences (Bjørnstad et al. 2004). Consequently, only complex stage-structured population models may unravel the true action of environmental predictability on population dynamics and population extinction.

Seventh, decreased environmental predictability affected spring body size of yearlings (Chapter 3), which may lead to a delay in maturation (Horváthová et al. 2013). Consequently, additional population models were run that simulated a delay or an advancement of the maturation of juveniles. However, both, the delay or the advancement of the maturation did not affect treatment effects on population growth rate, showing that the treatment-induced reduction of the asymptotic growth rate was robust, which is in line with the perturbation analyses showing that survival differences of adults mainly contributed to the decrease in population growth rate.

Finally, the absence of environmental predictability effects on reproduction and summer survival (Chapter 5) suggest that environmental predictability did not affect the trade-off between investing in reproduction and subsequent survival (Stearns 1992). This indicates that surviving individuals can indeed cope with decreased environmental predictability (Ashander et al. 2016), which is in line with the idea that changes in life history strategies evolved to compensate deleterious effects of reduced environmental predictability (Roff et al. 2002; Nevoux et al. 2010).

To our knowledge, this doctoral thesis is one of the first experimentally studies demonstrating whether and how species might respond to changes in environmental predictability. The results mainly support the theory that less predictable environments might negatively affect individual life history traits and, thereby, population dynamics (Tuljapurkar 1990; Dewar and Richard 2007; Marshall and Burgess 2015; Ashander et al. 2016). In addition, they show that a huge amount of data and stage-structured matrix models are required to unravel strategic investment, differences among age-classes and sexes, and effects on growth, body condition, coloration, and population dynamics. The analyses also show that studies that only incorporate average environmental conditions, that analyze a single life-history trait, or a single age class or sex, or a small sample size, may miss the major effects imposed by environmental predictability and climate change *per se*. Consequently, they may not be sufficiently accurate when predicting the impact of climate change on species persistence, potentially explaining why in many cases the causes of species extinctions or population declines remain unknown.

The results presented in this doctoral thesis suggest that species being highly dependent on abiotic conditions, may show similar responses under decreased environmental predictability. This suggests that the rate of the currently observed population decline and extinction (e.g. 12% of extinction since 1975 in lizards; 48 % of rapidly declining amphibian species; 21% of bird species are extinction prone and 6.5% functionally extinct; Sekercioglu et al. 2004; Sinervo et al. 2010) may importantly increase given the projected decrease in environmental predictability. The study also shows, that a better understanding of the current effects of climate change and successful development of conservation measures, requires considering changes in environmental predictability and studies on other taxa might unravel the generality of the presented findings.

Figure. 7.1. Immature lizard basking on a rock in the semi-natural populations. By Campo, Benito.

Chapter 7

General conclusions

The main conclusions of this thesis are listed by chapter below and including the general conclusions at the end:

Chapter 3

♦ Different age classes and sexes exhibit different sensibilities to the predictability of precipitation.

♦ Decreased precipitation predictability had no lasting effects on survival, growth, and body condition of adults and juveniles, pointing to compensatory strategies

♦ Negative effects of decreased environmental predictability on yearling growth and spring SVL may lead to a delay in maturation and to differences in clutch size.

♦ Decreased precipitation predictability did not significantly affect survival or reproduction, which suggests that environmental predictability may not necessarily affect population dynamics.

♦ Responses to changes in average environmental conditions could be altered or even reversed under different environmental predictability.

Chapter 4

♦ Male ornamental coloration is negatively affected by decreased environmental predictability. More specifically, lower precipitation predictability negatively affected hue of carotenoid-based coloration and the extent of melanin-based coloration.

♦ Hue of carotenoid-based coloration and SVL were positively and the extent of melanin-based coloration was negatively correlated with the number of mate partners and no significant correlation existed with the proportion of fertilized eggs.

♦ Differential investment into independent ornamental traits was in line with compensatory strategies. While both traits are under sexual selection, the strategies led to equal attractiveness, and no significant differences in male reproductive success.

♦ Less favorable environmental conditions, may first affect ornamentation, rather than growth, reproduction and survival, and thus it might be used to early detect slight difference in environmental changes.

Chapter 5

♦ Decreased environmental predictability negatively affected asymptotic population growth rate, leading to a 50% population decline in less than 11 years.

♦ Non-significant survival differences in adults explained treatment differences in population growth rates, showing that even small effects can have major consequences.

♦ Only complex population dynamic analyses, such as stage-structured matrix models, might allow to test and predict the effects of changes in environmental predictability on population or species persistence.

General conclusions

♦ In line with theoretic predictions, less predictable environments negatively affected life history traits and population growth rate.

♦ Ornamentation may act as an early signal allowing to detect slightly differences in environmental conditions.

♦ Species exhibit compensatory strategies that prevent major effects on fitness and these strategies also exist with respect to environmental predictability.

♦ Species whose performance importantly depends on abiotic factors may exhibit similar responses to changes in environmental predictability.

♦ Considering environmental predictability in models forecasting changes in population growth rates might exacerbate the rate of currently observed and predicted population decline and extinction.

♦ This study provides the first evidence that response to changes in environmental predictability might be altered or even reversed by average conditions, similarly to the effects predicted for environmental variance.

♦ This study emphasizes that changes in environmental predictability should be considered when predicting and analyzing individual and species responses to climate change.

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Supporting information

This section comprises supporting information for chapters 2, 3 and 5.

Appendix A. Supplementary information of chapter 2: Study species and field design.

Appendix B. Supplementary information of chapter 3: Age-dependent effects of moderate differences in environmental predictability forecasted by climate change, experimental evidence from a short-lived lizard (*Zootoca vivipara*).

Appendix C. Supplementary information of chapter 5: Decreased precipitation predictability negatively affects population growth through differences in adult survival in a short lived lizard (*Zootoca vivipara*).

Appendix A. Supplementary information of chapter 2: Study species and field design.

Appendix A.1. Weighted Permutation Entropy

Weighted permutation entropy was calculated to quantify the predictability of precipitation in each treatment level. Permutation entropy is a measure of time series complexity that is inversely related to intrinsic predictability. Time series with high permutation entropy have low redundancy and low intrinsic predictability (Garland and Bradley 2015). Weighted permutation entropy was calculated for each environmental predictability treatment and year based on the obtained daily amount of precipitation (natural precipitation plus supplemental precipitation) during the lizards' active season (from March to October). To calculate the permutation entropy, time series were translated into permutation patterns of length n (Fig. A.1 supporting information; Riedl et al. 2013).

Weighted permutation entropy was then calculated according to:

$$H_n = -\sum_{j=1}^{n!} p_j \, log_2(p_j) \, / \, log_2(n!)$$

where *pj* represents the relative frequencies of the observed permutation patterns (Bandt and Pompe 2002). The number of successive measures (*n*) included in a permutation pattern depends on the time-series length (for more details see Pennekamp et al. 2019), and in our case, the optimal n of the sequence used to encode permutation patterns was four (Fig. A.2 supporting information).
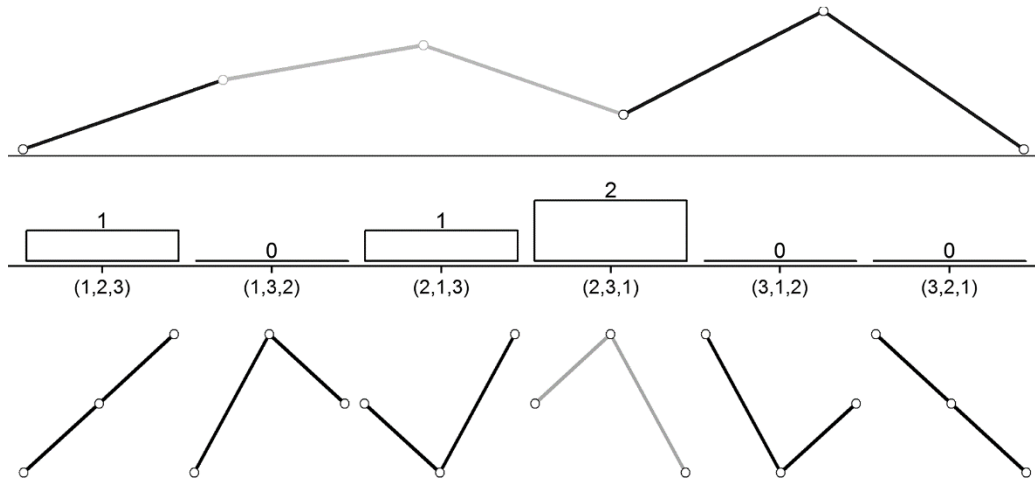
Figure A.1. Example of the encoding for the calculation of the permutation entropy adapted from Riedl et al. 2013. Time series (top) are encoded into permutation patterns of length n; labelled in grey is a random sequence of three successive values (n = 3). For each permutation pattern the rank of the n observations is established and the pattern coded as the sequence of the ranks, for the grey example permutation pattern: 2,3,1 (bottom). The frequency of all possible permutation patterns is calculated (middle); for this example time series with n = 3.
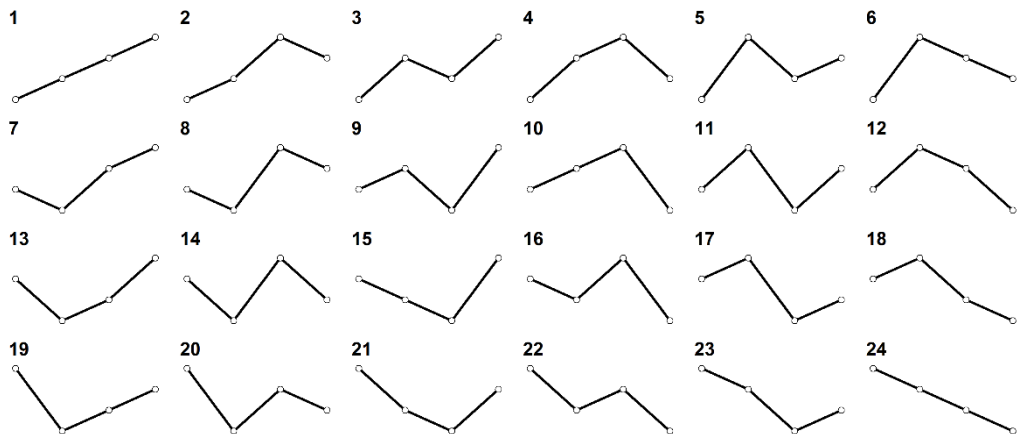
Figure A.2. All possible permutation patterns of length n = 4.

Appendix B. Supplementary information of chapter 3. Age-dependent effects of moderate differences in environmental predictability forecasted by climate change, experimental evidence from a short-lived lizard (*Zootoca vivipara*).

Appendix B.1. Absence of evidence that treatment affected inter-age class competition.

If inter-age class competition explains differences between age-classes in the treatment's effect, we predicted cascading effects and thus, that effects of precipitation predictability may first manifest in the competitively inferior age-classes (prediction 3). Such hierarchic treatment effects, would predict immediate cascading effects on inferior age-classes (San-Jose et al. 2016). For example, if a given treatment induces food shortage, adults may be able to cope with this situation by eating all size classes of prey consumed by inferior age-classes (in *Zootoca vivipara* adults eat Collembola, prey eaten by juveniles; San-Jose et al. 2016; and by excluding inferior age-classes from food; Heulin 1986). As a consequence, treatments may affect traits of inferior age classes, but not those of adults (e.g. San-Jose et al. 2016). Alternatively, adult traits may also be affected by treatment, but less than those of inferior age classes. In this study, the observed differences among age-classes in the treatment's effect (i.e. between adults and the inferior age classes) were not congruent with predictions from inter-age class competition. First, adult males of the more predictable treatment exhibited a significantly smaller positive change in body condition between release and august 2013 than those of the less predictable treatment (Fig. 3.1A). This suggests that inter-age class competition may have been higher in the more predictable treatment, which should lead to negative effects on yearlings and/or juveniles. Nevertheless, in the more predictable treatment growth of yearlings and the body condition change of female juveniles was bigger compared to the less predictable treatment (Fig. 3.2A, B.4 supporting information) and thus inter-age class competition, e.g. by means of food competition, cannot explain these patterns. Second, in 2014 the body condition change of adult males from September to spring was more negative in the more predictable treatment (Fig. 3.1A). This suggests that inter-age class competition may have been higher in the more predictable treatment, but yearling traits (growth and change in body condition) were not affected by treatment (Fig. 3.2A, Table 3.1), and the body condition change of female juveniles was more positive in the more predictable treatment (Fig. B.4 supporting information). Third, in 2013 adults grew less in the more

predictable treatment from September to spring, suggesting that inter-age class competition may have been higher. Nevertheless, no treatment effects existed on yearlings from September to spring, and the body condition change of female juveniles was positive in the more predictable treatment (Fig. B.4 supporting information), i.e. opposite to the direction predicted by the suggested inter-age class competition. Fourth, there was a consistent negative effect of less predictable precipitation on yearling growth during summer and autumn (Fig. 3.2A), that let to reduced spring body size (Fig. 3.2B), suggesting that inter-class competition among yearlings and juveniles may have been highest in the less predictable treatment. Nevertheless, only the change in body condition of female juveniles was in line with inter-age class competition, while the change in body condition of juvenile males was positive in less predictable conditions and negative in more predictable conditions (Fig. B.4 supporting information). Most importantly, while treatment effects existed on growth of yearlings, no treatment effects existed on growth of juveniles (Table 3.1), a trait known to rapidly respond to inter-age class competition, at least in *Zootoca vivipara* (San-Jose et al., 2016). Fifth, if adult growth between September and spring would reflect a pure life-history strategy, that responded to previous but not to the prevailing environmental conditions, one would predict that reduced growth of individuals exposed to more predictable conditions would lead to reduced competition among age-classes. Nevertheless, no significant treatment effects existed on yearling traits (Fig. 3.2A) and only body condition of juvenile females would have been positively affected (Fig. B.4 supporting information), but neither juvenile males, nor juvenile growth. Sixth, there was indeed only one effect that might be in line with differences in inter-age class competition due to environmental predictability: adults and yearlings were growing less in the less predictable compared to the more predictable treatment from August to September 2013 (estimate ± SE for adults: -0.029 mm/day ±SE, yearlings: -0.025 ± 0.001 SE). However, the magnitude of the effect was similar (see estimates) and no effects existed on juvenile growth (Table 3.1). Consequently, it is unlikely that the differential treatment effects observed in the different age classes are the result of treatment-induced differences in inter-age class competition (prediction 3).

Appendix B.2. Potential causes of differences between age-classes in the sensitivity to precipitation predictability.

Differences among treatment levels and age classes in the sensitivity to precipitation predictability may have arisen due to differences in thermal inertia and heating up by

means of thermoregulation. If precipitation is falling, common lizards hide and are thus not able to thermoregulate, and differences in thermoregulation directly feed back into growth and timing of egg laying (Huey and Slatkin 1976). Moreover, thermoregulatory capacity is known to depend on body size (Christian et al. 2006) and on coloration (Clusella-Trullas et al. 2009). Larger animals (adults) have higher thermal inertia and can keep heat for longer (Christian et al. 2006). Thus, if the precipitation event is not too long adults may keep heat, while smaller individuals may rapidly cool down, but note, smaller individuals also heat up more rapidly than larger animals (Herczeg et al. 2007). Moreover, darker coloration (e.g. black color exhibited by juveniles), leads to faster heating (Clusella-Trullas et al. 2009). Only in 2013, the year with the coolest autumn temperatures (Fig. B.1 supporting information), less predictable precipitation let to reduced adult growth during autumn (Fig. 3.1A), which is in line with predictability treatment-induced less regular thermoregulatory possibilities. Moreover, no significant treatment differences on adult growth existed in autumn 2012 and 2014 (Fig. 3.1A), which is in line with higher autumn temperatures in 2012 and 2014 (Fig. B.1 supporting information) leading to a minor effect of less regular precipitation. In yearlings, growth was significantly lower in summer and autumn in the less predictable treatment, suggesting that given their small body size, they may have suffered more from less predictable thermoregulation due to reduced thermal inertia and the grey-brown dorsal coloration that may not have allowed to heat up as fast as juveniles. In contrast, growth of the black juveniles was not affected in any year, which is in line with fast heating-up of small-sized lizards and the thermoregulatory advantages of black coloration (Herczeg et al. 2007; Clusella-Trullas et al. 2009). Similar to the growth patterns, treatment effects on laying date may as well have arisen due to treatment-induced differences in thermoregulation. April temperatures in 2015 were intermediate to those in 2013 and 2014 (Fig. B.2 supporting information), and significant treatment effects on laying date only existed in 2015. While April temperatures in 2013 may have been too low for reproductive activity (even after an increase in body temperature due to thermoregulation), those in 2014 were already high and thus slight treatment effects on thermoregulation may not have been important enough to affect growth, leading to no significant treatment effects. In contrast, in presence of intermediate temperatures, thermoregulating more regularly may have been an advantage allowing to lay the eggs 5 days ± 1.42 SE earlier. Our results are in line with prediction 4, that age-dependent effects of environmental predictability reflect differential sensitivities (Rozen-Rechels et al. 2018), rather than inter-age class competition, and they suggest that the observed

effects may have arisen through differences in thermal inertia and heating up due to thermoregulatory activity.

Table B.1. Minimum adequate models and test statistics for growth and change in body condition per age class. Significant factors and/or interactions are plotted in bold. The following abbreviations were used: BC, body condition; *trt*, treatment.

| Parameter | df | Adults | | | | Yearlings | | | | Juveniles | | | |
| | | Growth | | Change in BC | | Growth | | Change in BC | | Growth | | Change in BC | |
		χ^2	P	χ^2	P	χ^2	P	χ^2	P	χ^2	P	χ^2	P
trt	1	1.309	0.253	0.006	0.940	1.925	0.165	-	-	-	-	-	-
sex	1	**4.871**	**0.027**	**12.223**	**<0.001**	**40.906**	**<0.001**	**19.553**	**<0.001**	-	-	-	-
year	2	**12.919**	**0.002**	**39.837**	**<0.001**	0.885	0.643	**6.943**	**0.031**	-	-	**10.053**	**0.040**
period	2	**58.112**	**<0.001**	**11.110**	**0.004**	**596.062**	**<0.001**	**14.232**	**0.001**	-	-	**8.954**	**0.011**
trt × sex	1	-	-	2.001	0.157	-	-	-	-	-	-	-	-
trt × year	2	1.480	0.477	3.738	0.154	-	-	-	-	-	-	-	-
sex × year	2	-	-	2.945	0.229	**14.337**	**0.001**	0.055	0.973	-	-	-	-
trt × period	2	1.717	0.424	1.817	0.403	**19.591**	**<0.001**	-	-	-	-	-	-
sex × period	2	**13.764**	**0.001**	**6.559**	**0.038**	**16.324**	**<0.001**	**6.205**	**0.045**	-	-	-	-
year × period	4	**253.954**	**<0.001**	**371.035**	**<0.001**	**38.801**	**<0.001**	**112.938**	**<0.001**	-	-	**10.053**	**0.040**
trt × sex × year	2	-	-	1.776	0.412	-	-	-	-	-	-	-	-
trt × sex × period	2	-	-	0.467	0.792	-	-	-	-	-	-	-	-
trt × year × period	4	**21.448**	**<0.001**	6.833	0.145	-	-	-	-	-	-	-	-
sex × year × period	4	-	-	6.055	0.195	-	-	**14.524**	**0.006**	-	-	-	-
trt × sex × year × period	4	-	-	**13.917**	**0.008**	-	-	-	-	-	-	-	-

Table B.2. Minimum adequate models and test statistics for final SVL and final body condition per age class. Significant factors and/or interactions are shown in bold. "-". The following abbreviations were used: SVL, snout-to-vent length; BC, body condition; *trt*, treatment.

		Adults				Yearlings				Juveniles			
		Final SVL		Final BC		Final SVL		Final BC		Final SVL		Final BC	
Parameter	*df*	χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*
trt	1	-	-	-	-	**4.799**	**0.028**	-	-	-	-	1.012	0.315
sex	1	**189.922**	**<0.001**	**406.399**	**<0.001**	**24.923**	**<0.001**	**139.553**	**<0.001**	-	-	0.940	0.332
year	2	**9.455**	**0.009**	**12.952**	**0.002**	**14.545**	**0.001**	**12.110**	**0.002**	**36.531**	**<0.001**	-	-
trt x sex	1	-	-	-	-	-	-	-	-	-	-	**6.679**	**0.010**

Table B.3. Minimum adequate models and test statistics for survival per age class. Significant factors and/or interactions are shown in bold. The following abbreviations were used: *trt*, treatment.

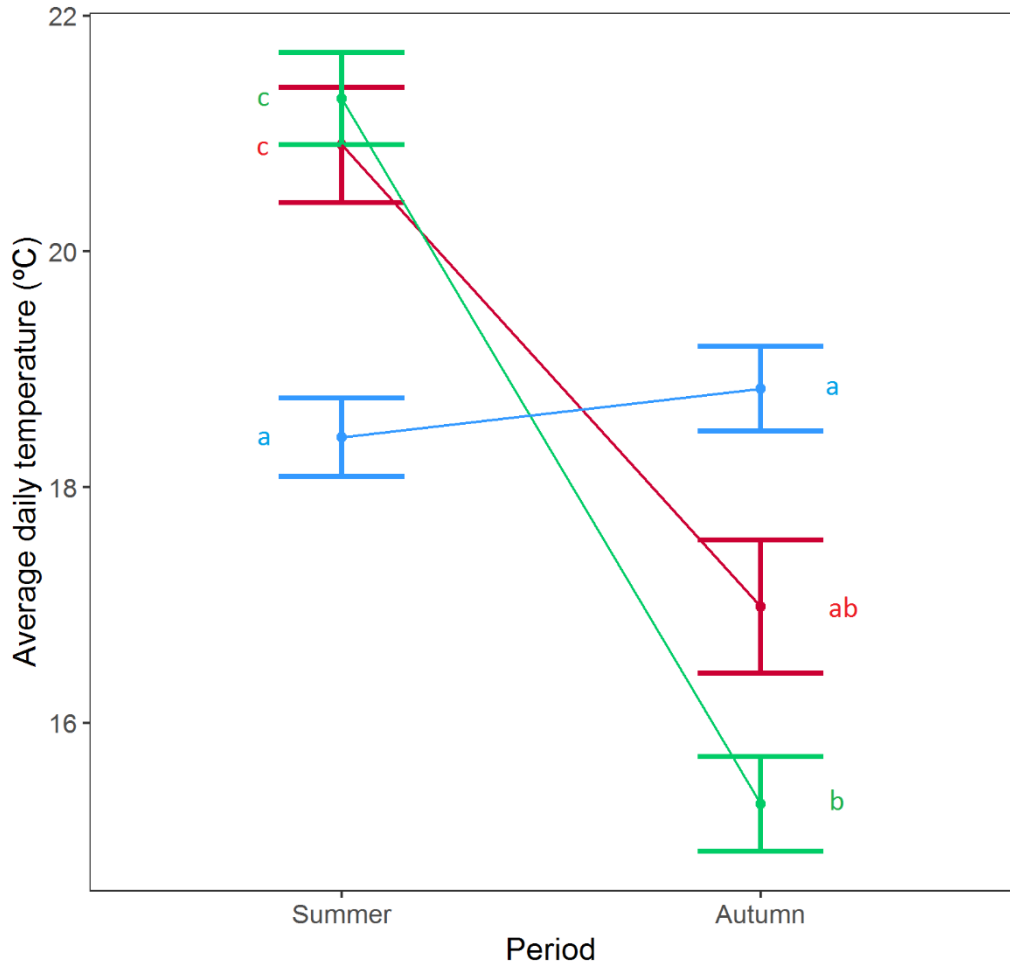|		Adults		Yearlings		Juveniles	
Parameters	*df*	χ^2	*P*	χ^2	*P*	χ^2	*P*
trt	1	-	-	-	-	-	-
sex	1	-	-	-	-	-	-
year	2	**13.500**	**0.001**	-	-	**2.6E6**	**<0.001**

Figure B.1. Differences between growth periods, summer (release - August) and autumn (August - September), and years in average daily temperature (°C). Red: 2012, green: 2013, blue: 2014. Given are means ± standard errors. Significant pairwise post-hoc comparisons are indicated with different letters.
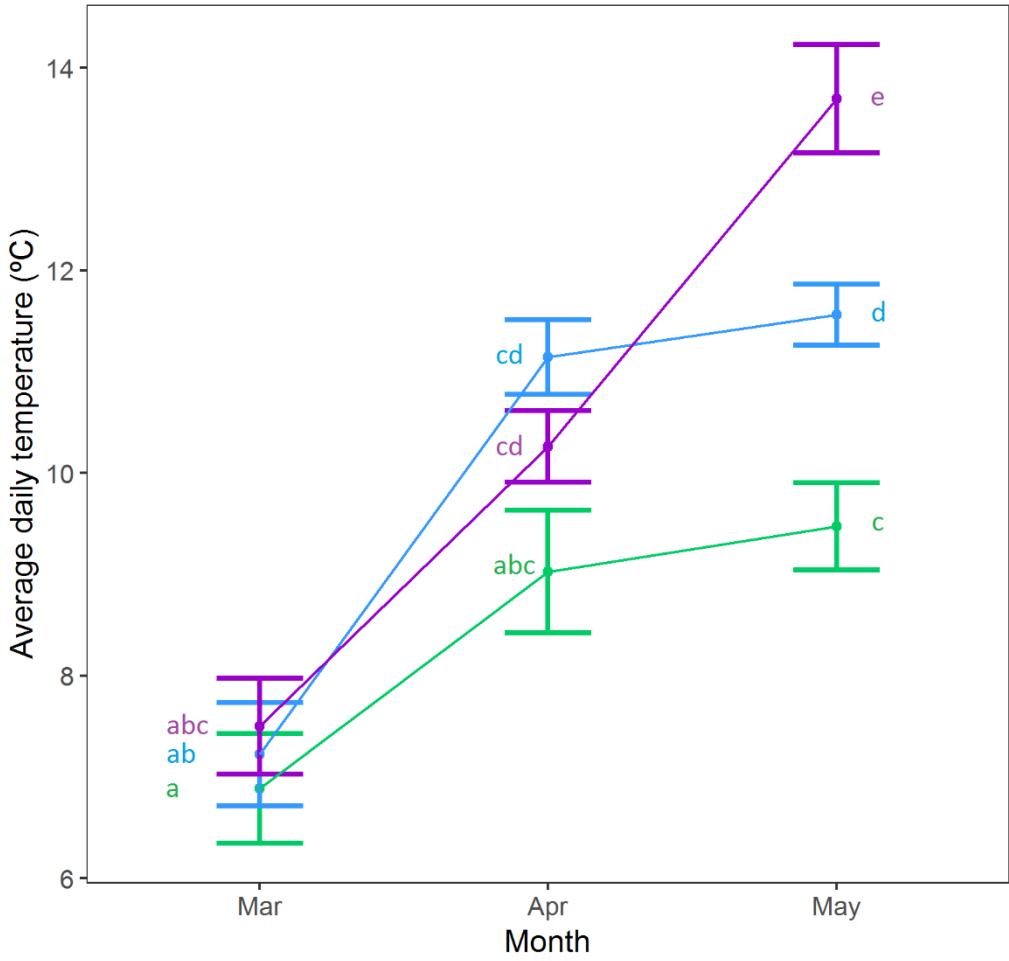
Figure B.2. Differences between month and years in average daily temperatures (°C) during spring (March-May). Green: 2013, blue: 2014, violet: 2015. Given are means ± standard errors. Note, individuals of the 2012 experiment were exposed to spring temperatures in 2013, those of the 2013 to spring temperatures in 2014, etc. Significant pairwise post hoc comparisons are indicated with different letters.

Figure B.3. Differences between month and years in daily temperature variance (°C) during spring (March-May). Green: 2013, blue: 2014, violet: 2015. Given are variance means ± standard errors. Note, individuals of the 2012 experiment were exposed to spring temperatures in 2013, those of the 2013 to spring temperatures in 2014, etc. Significant pairwise post hoc comparisons are indicated with different letters.
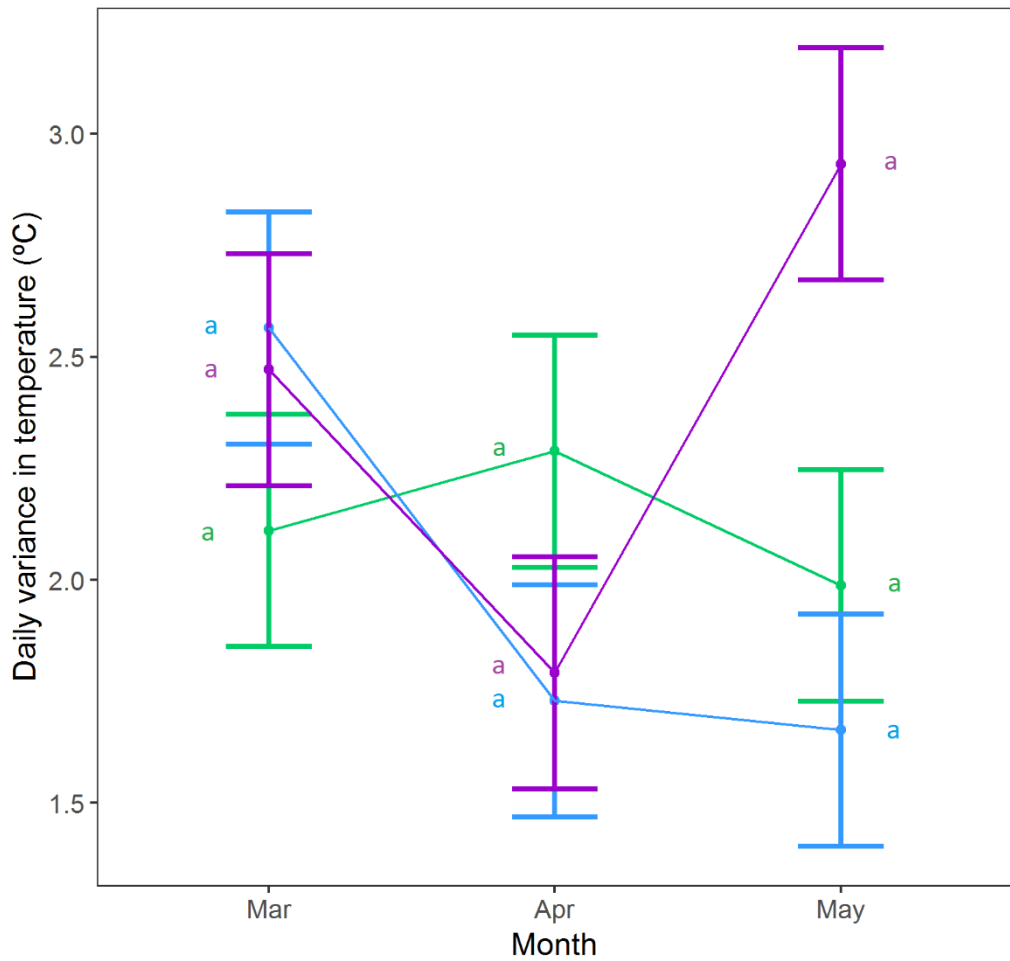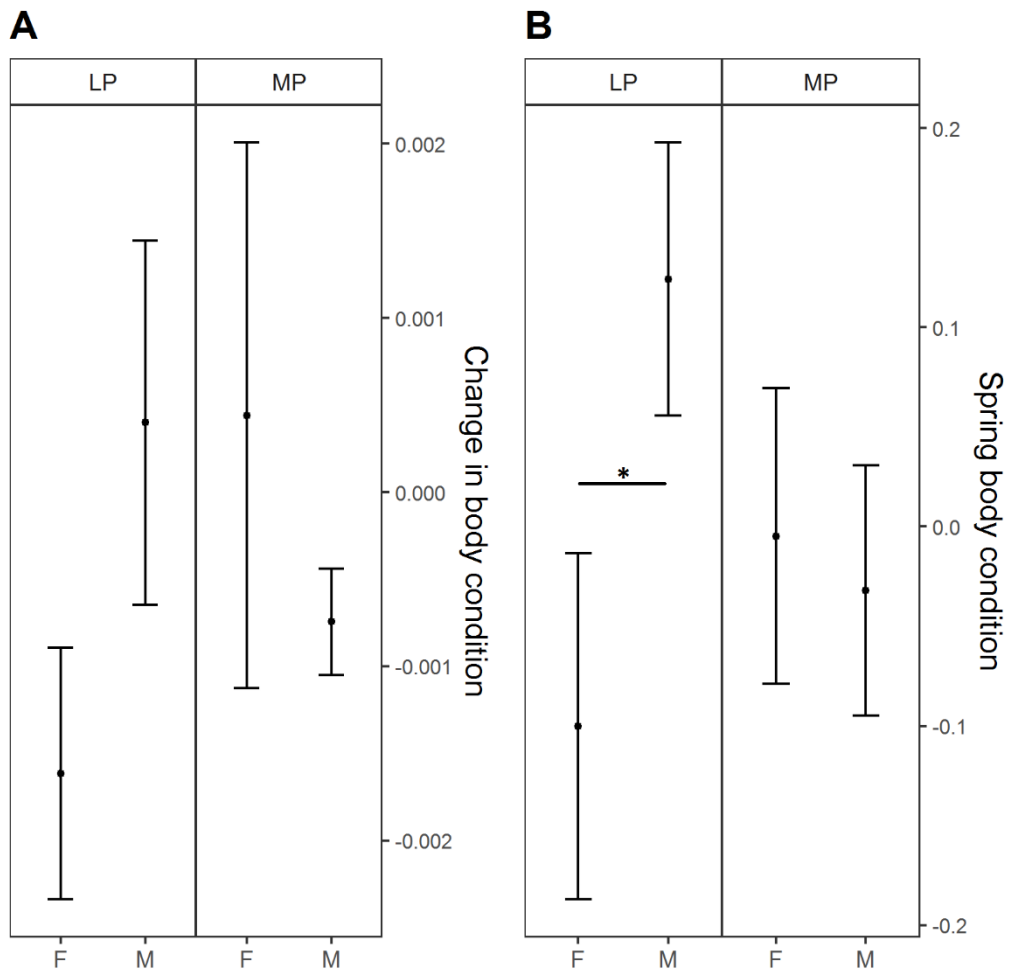
A

B

Figure B.4. Treatment effects on the change in body condition (A) and on spring body condition (B) of juveniles. Shown are predicted means ± se per treatment and sex (LP: less predictable; MP: more predictable; sex: M: Males; F: Females). Horizontal lines indicate significant post-hoc contrasts: * *P* < 0.05; ** *P* < 0.01; *** *P* < 0.001.

Appendix C. Supplementary information of chapter 5. Decrease precipitation predictability negatively affects population growth through differences in adult survival in a short-lived lizard (*Zootoca vivipara*).

Appendix C.1. Treatment effects on survival of different age classes and during different time periods using generalized linear mixed models.

To test effects of precipitation predictability on survival, we conducted general (for all individuals) and age-specific (for a particular age class) generalized linear mixed models (GLMM; (Bates et al. 2014) on annual and season-specific survival probabilities. GLMMs were performed with precipitation predictability treatment as a fixed factor, enclosure/year combination as random factor and using a binomial error distribution. The enclosure / year combination was modelled as a random factor, since individuals living in the same population are not independent and since individuals surviving a given year were thereafter distributed into another, unknown enclosure together with many unknown lizards. Survival between predictability treatments was analyzed per age class (age-specific models) for each period (spring, summer and winter; season-specific models), for annual survival (from spring to end of winter), and for annual survival and for all individuals, irrespective of their age (general models). For all tests, the significance level was set at $\alpha = 0.05$ (two-tailed test). Overdispersion was tested and existed in none of the models. All analyses were run using R 3.5.1 (Team 2018).

The results of these analyses showed, that neither in annual, age-specific, season-specific, nor in general models did significant precipitation predictability effects on survival exist (all $P > 0.2$; table C.1 supporting information). This shows that measuring a given parameter in one or another season, or measuring it in a given age class or over all age classes, does not unravel the population dynamics (Fig. 5.6). Thus, it is necessary to use stage-structured matrix models to understand how differences in predictability affect population dynamics. The results further suggest, that conventional methods (table C.1 supporting information), may only unravel huge differences on population dynamics, while the here detected population decline (50% over 12 years in the less predictable treatment), would be missed. Consequently, important effects on population dynamics might be missed and thus the main effects of differences in environmental predictability underestimated. On the other hand, considering significant effects on vital rates does not allow to discriminate if those effects will indeed affect asymptotic

population growth rate, given that their effect depends on the contribution to λ (Caswell 1989).

Table C.1. Treatment effects on survival rates in general (for all individuals), age-specific (for a particular age class), annual and season-specific models. Shown are test statistics and significance (P- values). "-". The following abbreviations were used: AD, adults; AD1, first year adults; Y, yearlings; J_E, early juveniles; J_L, late juveniles.

Model type	Age class	Annual survival		Season-specific survival					
				Spring		Summer		Winter	
		χ^2_1	P	χ^2_1	P	χ^2_1	P	χ^2_1	P
Age-specific	AD	0.050	0.824	0.229	0.632	0.337	0.562	0.044	0.834
	AD1	0.010	0.919	0.193	0.661	0.184	0.668	0.400	0.527
	Y	0.627	0.429	1.285	0.257	1.489	0.222	0.769	0.381
	J_E	0.007	0.933	-	-	0.139	0.709	1.482	0.224
	J_L	0.000	1.000	-	-	-	-	0.000	1.000
general	all	0.025	0.876	-	-	-	-	-	-

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