

# 9

## **Ecological Effects of Climate Change on European Reptiles**

Jean François Le Galliard, Manuel Massot,  
Jean-Pierre Baron, and Jean Clobert

The destruction and fragmentation of habitats, overexploitation of natural resources, and invasion of pest species have resulted in worldwide declines of many animal and plant species (Morris and Doak 2002). It is increasingly apparent that the effects of this deadly cocktail will be reinforced by global warming, which might disrupt and eventually push towards extinction entire ecosystems and an increasing number of species (e.g., Walther et al. 2002, Thomas et al. 2004, Parmesan 2006). As a consequence, there is a pressing need for data and predictions on wildlife responses to global warming, and for an agenda of conservation strategies to mitigate its deleterious impacts (Hannah et al. 2005).

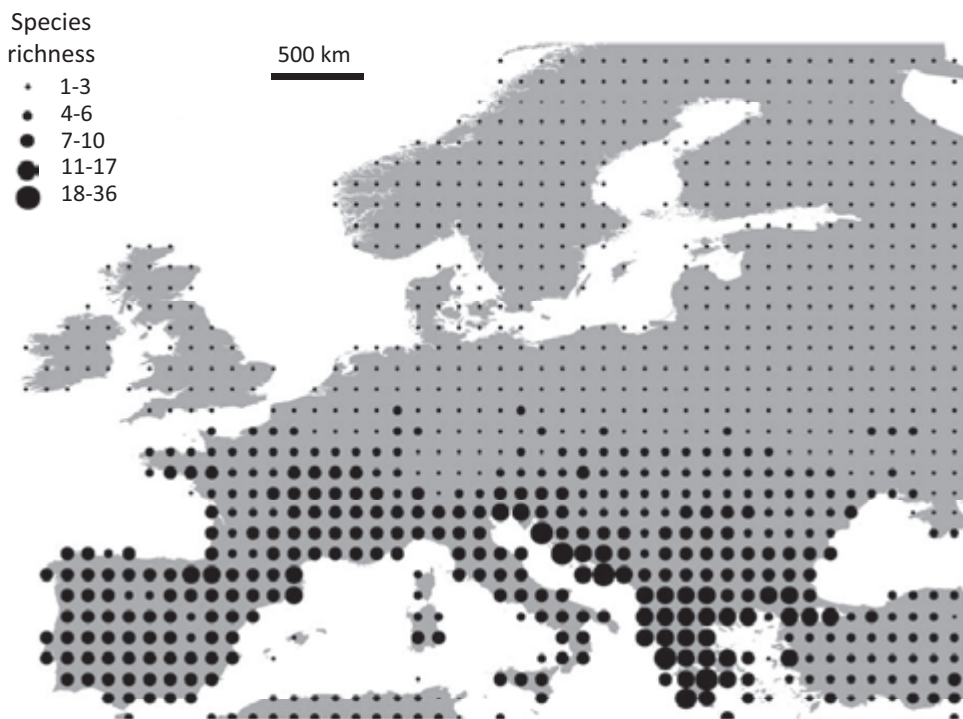
Responses to climate change have been summarized for plants, passerine birds, butterflies, mammals, and some amphibians (Parmesan 2006, Rosenzweig et al. 2007, and references therein). Until now, however, they have not been reviewed for reptiles, despite the fact that these animals are often at the forefront of conservation priorities (Pounds et al. 1999, Gibbons et al. 2000, Thomas et al. 2004). Reptiles constitute an assemblage of terrestrial and aquatic vertebrates broadly defined as a paraphyletic group (i.e., excluding birds; Pough et al. 2001, Pianka and Vitt 2003). Squamates, or “scaled reptiles,” include snakes and lizards and make up the most diverse order of reptiles, distributed almost worldwide (e.g., Tinkle and Ballinger 1972, Huey et al. 1983, Pianka and Vitt 2003). Key characteristics of squamates include ectothermy (reliance on external means to control body temperature); continuous growth through repeated molting, resulting in great size variation within a single population; intermediate levels of mobility; and the presence of two major reproductive modes, viviparity and oviparity, associated with an absence of parental care in most species (Pough et al. 2001). Ectothermy is a fundamental characteristic of squamates, and it has generated the evolution of physiological and behavioral tactics that enable partial control of body temperatures (Huey 1982, Adolph and Porter 1993, Kearney et al. 2009). The demographic effects of climate change in reptiles should be mediated by interactions between the direct effects of warming on behavior

and physiology and the indirect ecological effects that result from trophic interactions and habitat changes (Matthews et al. this volume).

Climate warming has begun to be considered as a major extinction threat for these animals, especially in tropical environments, in species with restricted spatial ranges, and in species with temperature-dependent sex determination (Janzen 1994, Gibbons et al. 2000, Cox and Temple 2009, Sinervo et al. 2010). In this chapter we assess ecological consequences and challenges posed by global warming in Europe for conservation biology of reptiles. We focus our attention on field data, model predictions, and conservation problems in the European geographic area, defined to include all species north of the Mediterranean Sea and west of Russia (see figure 9.1 and Gasc et al. 1997). We discuss only data for squamate reptiles (lizards and snakes) for which long-term demographic studies are available.

Historical reconstructions of species distributions in Europe have improved our understanding of the factors that shaped their spatial ranges during the Quaternary ages. These studies all point out that major range shifts were driven by change in climatic conditions and were constrained by geographic barriers and life-history adaptations (e.g., Surget-Groba et al. 2001, Ursenbacher et al. 2006, Pinho et al. 2007, Ursenbacher et al. 2008). Areas of endemism and high species richness occur now in southern refugia to which reptiles retreated during the ice ages. Range expansions to the north during interglacial ages have been more complex than a simple uniform expansion wave. Different species have followed distinct expansion routes constrained by the presence of mountainous barriers (Pyrenees, Alps and Balkan, and Carpathian) and also by characteristics that provide the physiological capacity to live in colder climates, such as viviparity or the ability to perform critical performances at low temperatures. Altogether, these data suggest that some species of reptiles may be able to expand their range into northern habitats with future warming.

During the last decades, however, European reptiles have suffered great numeric declines (Corbett 1989, Gasc et al. 1997, Hickling et al. 2006, IUCN 2008, Cox and Temple 2009). Major factors of these declines include habitat loss and fragmentation, change in land use, and invasion by pest species (Cox and Temple 2009). Some species also suffer from persecution and can be threatened by illegal captures for the trade market. Major threats to the 31 species listed in table 9.1, obtained from IUCN 2008 (Cox and Temple 2009), were considered to be changes in habitat, collection of live specimens, persecution, and negative effects of invasive species. Climate change was also considered as a potential threat to a significant number of species. Unfortunately, quantitative data for



**Figure 9.1.** Spatial distribution of species richness for European squamate reptiles (snakes and lizards). A map of species richness (number of species per half-degree of latitude indicated by diameter of circles around points spaced one degree apart) was calculated from spatial data downloaded in August 2010 from the IUCN website ([www.iucnredlist.org/technical-documents/spatial-data](http://www.iucnredlist.org/technical-documents/spatial-data)). Spatial data were corrected for numerous taxonomic and biogeographic errors. The diversity of European squamate amounts to approximately 90 species of lizards belonging to 6 families, 1 amphisbaenian species, and about 40 species of snakes belonging to 4 families (Arnold et al. 2002, 2007). Figure kindly drawn by B. Decencière Ferrandière.

climate change effects are missing in these evaluations (IUCN 2008, Cox and Temple 2009). For most reptiles, a link between demography and climatic conditions therefore remains to be established. Below we use field data and predictive models to describe the effects of climate change for European squamates.

### **The Significance of Climate Change for Reptiles in Europe**

In Europe, the average climate warming was on the order of more than 0.4 °C per decade during the last century, with stronger warming at high altitudes and in central and northeastern Europe, stronger average

**Table 9.1.** List of critically endangered (CR), endangered (EN), vulnerable (VU), and near threatened (NT) squamates in Europe according to the IUCN 2008 Red List, downloaded on August 12, 2009 (IUCN 2008, Cox and Temple 2009). The total number of native squamate reptiles amounts to approximately 90 species of lizards from six families (Agamidae, Anguillidae, Chamaeleonidae, Gekkonidae, Lacertidae, Scincidae), as well as one amphisbenian and approximately 40 species of snakes from four families (Boidae, Colubridae, Typhlopidae, Viperidae). Species from the Canary Islands and from northern Africa were excluded from the list. Assessment criteria: (1) restricted and fragmented range, (2) decline in size and quality of habitat, and (3) decline in abundance.

Assessment	Family	Species	Geographic distribution	Major threats
CR (1, 3)	Lacertidae	<i>Iberolacerta martinezical*</i>	Sierra de Francia (Spain)	Collection, habitat loss, and future climate change
CR (1, 3)	Lacertidae	<i>Podarcis raffonei</i>	Aeolian Islands (Italy)	Collection and invasive species, intrinsic factors
EN (1, 2)	Lacertidae	<i>Iberolacerta aranica*</i>	Pyrenees Mountains (France and Spain)	Land use, habitat loss, collection, and future climate change
EN (1, 2)	Lacertidae	<i>Iberolacerta aurelioi*</i>	Pyrenees Mountains (France and Spain)	Land use, habitat loss, collection, and future climate change
EN (1, 2)	Lacertidae	<i>Iberolacerta cyreni</i>	Central Spain	Habitat loss and future climate change
EN (1, 2)	Lacertidae	<i>Podarcis cretensis*</i>	Crete and satellite islands	Habitat loss and degradation
EN (1, 2, 3)	Lacertidae	<i>Algyroides marchi</i>	Southeast Spain	Habitat loss, land use, and invasive species
EN (1, 2, 3)	Viperidae	<i>Macrovipera schweizeri</i>	Western Cyclade Islands (Greece)	Collection, persecution, and habitat loss
EN (1, 2, 3)	Lacertidae	<i>Podarcis carbonelli*</i>	Western and central Portugal	Habitat loss and future climate change
VU (1)	Lacertidae	<i>Podarcis gaigeae*</i>	Aegean Islands (Greece)	No major threat at present
VU (1)	Lacertidae	<i>Podarcis levendis</i>	Greekislets	No major threat at present
VU (1)	Lacertidae	<i>Podarcis milensis</i>	Aegean Islands (Greece)	No major threat at present
VU (1, 2)	Lacertidae	<i>Dinarolacerta mosorensis†</i>	Balkans (Bosnia and Montenegro)	Habitat loss, land use, and collection

VU (1, 2)	Lacertidae	<i>Iberolacerta monticola</i>	Northern Spain and Portugal	Habitat loss and land use
VU (1, 2)	Viperidae	<i>Vipera ursinii</i>	Southeast and central Europe	Habitat loss, land use, collection, and climate change
VU (2)	Viperidae	<i>Vipera latastei</i>	Portugal and Spain	Persecution, habitat loss, and natural mortality
NT (1)	Anguillidae	<i>Anguis cephalonnica</i>	Greece	Persecution
NT (1)	Gekkonidae	<i>Euleptes europaea</i>	Corsica and Sardinia (France and Italy)	Habitat loss and invasive species
NT (1)	Lacertidae	<i>Iberolacerta bonnali</i> *	Pyrenees Mountains (France and Spain)	Land use, habitat loss, collection, and future climate change
NT (1)	Lacertidae	<i>Iberolacerta galani</i> *	Montes de León (Spain)	Habitat loss and land use
NT (1)	Lacertidae	<i>Iberolacerta horvathi</i>	Austria, Italy, and Balkans	Intrinsic factors but no major threat at present
NT (1)	Lacertidae	<i>Podarcis pityusensis</i>	Balearic Islands (Spain)	No major threat at present
NT (1, 2)	Lacertidae	<i>Algyroides moreoticus</i>	Greece	Habitat loss, land use, and persecution
NT (1, 2)	Lacertidae	<i>Archaolacerta bedriagae</i>	Corsica and Sardinia (France and Italy)	Habitat loss, land use, and intrinsic factors
NT (1, 2)	Lacertidae	<i>Heilanolacerta graeca</i>	Southern Greece	Land use
NT (2)	Scincidae	<i>Chalcides bebrigi</i>	Spain and Portugal	Habitat loss and natural predation
NT (2)	Lacertidae	<i>Darevskia praticola</i> *	Eastern Europe (Serbia, Romania, Bulgaria)	Habitat loss and land use
NT (2)	Colubridae	<i>Elaphe quatuorlineata</i>	Italy, Balkans, and Greece	Habitat loss and persecution
NT (2)	Lacertidae	<i>Lacerta schreiberi</i>	Spain and Portugal	Habitat loss and land use
NT (2)	Colubridae	<i>Macroprotodon brevis</i> *	Southern Spain	Habitat loss, land use, and natural mortality
NT (2)	Lacertidae	<i>Timon lepidus</i>	Portugal, Spain, France, and Italy	Habitat loss, pollution, and land use

\* Recently described species. † Recently proposed species.

warming during the winter, and an increase in the occurrence of warm extremes (IPCC 2007). Less obvious and spatially variable trends in precipitation were also observed with a pattern of wetter climates in oceanic and northern Europe, and drier climates around the Mediterranean basin. Climate scientists now forecast further changes in climatic conditions for the next century, even under the most optimistic scenarios of reduced emission of greenhouse gases (Alcamo et al. 2007). Annual mean temperatures in Europe should increase by 0.2 to 0.5° C per decade, with mean summer levels as high as 0.6° C per decade in parts of France or the Iberian Peninsula. Precipitation should also decrease in the south, but will most likely increase as much as 15% to 30% in the north and west, with significant seasonal and regional contrasts. Summer precipitation may strongly decrease by as much as 70% in southern and central Europe, as well as by as much as 30% in western Europe. Daily precipitation is likely to become increasingly variable, and dry summer spells may increase by as much as 50% in southern Europe, France, and central Europe.

These changes in climate conditions are significant for squamates because heat and water availability are direct determinants of their whole-organism performances (e.g., Huey 1982, Nagy et al. 1991, Angilletta 2001). Thermal performance curves for locomotor or behavioral activities typically exhibit a bell shape: optimal performance values are observed within a mode or narrow range of temperatures, called the thermal mode (Huey 1982, Huey and Kingsolver 1989). Reptiles can control their body temperatures by means of behavioral tactics, and preferred body temperatures usually match the thermal mode. The thermal plasticity of life-history strategies suggests several potential effects of climate changes on the population demography of lizards and snakes. In thermally constrained environments (upland or northern habitats), warming should increase growth rates and result in earlier maturation because of direct, positive effects on body temperatures, because warmer environments enable longer activity periods, and because of potential indirect effects of warmer environments on prey abundance (Sinervo and Adolph 1989, Adolph and Porter 1993). Growth and reproduction are tightly linked since body size has a positive effect on fecundity (Clobert et al. 1998). Thus, warming may also have positive effects on reproductive effort. Also, thermal conditions are known to be important for the development of embryos in utero or ex utero. Embryonic development usually requires heat but temperature extremes may cause deaths or injury among embryos. In addition, abiotic conditions during embryonic development can influence the physiology, morphology, and behavior of neonate reptiles (Shine and Harlow 1993, Shine and Downes 1999, Massot et al. 2002, Brown and Shine 2005).

Although less often studied than thermal conditions, water availability may constrain reptiles' physiology even more severely through water balance (e.g. Nagy et al. 1991, Peterson 1996). Reptiles can control their evaporative water balance by reductions in water loss from activity, exposure to wind, and temperature control, or by increases in water gain from habitat and food selection, but water limitation during embryonic development may have lethal or deleterious effects. Variation in rainfall may induce further direct change in growth rates (Lorenzon et al. 1999), and it is also likely to have indirect effects through habitat quality and prey abundance (Marquis et al. 2008). In reality, temperature and humidity conditions may have interactive effects on reptiles' life history, resulting in a subtle balance between positive effects of warming and negative effects of drought.

### **Modeling Reptile Responses to Changing European Climates**

As described above, future climate changes in Europe should directly affect the conditions for physiological processes and therefore the distribution of physiological niches. Physiological data can be used to forecast the dynamics and spatial range of each species in response to global warming (Grant and Porter 1992). A typical physiological niche model predicts mass-energy balance, water budget, and body growth and translates these predictions into demographic data in a specific area. These models have been used to map the niche of various physiological processes (Kearney and Porter 2004), to predict the spatial range and abundance of reptiles (Buckley 2008, Deutsch et al. 2008), or to test the effects of behavioral flexibility on responses to climate warming (Kearney et al. 2009).

In Europe, a physiological niche model based on thermal performance curves for sprint speed suggests positive effects of warming on lizards (Deutsch et al. 2008). Another model, which includes more complex assumptions, predicts further that species around the Mediterranean basin will be at greater risk of heat stress (Kearney et al. 2009). These predictions must, however, be interpreted with caution. Indeed, forecasts from Deutsch et al. (2008) depend on the questionable assumption that sprint speed is tightly linked to fitness. Also, the physiological model by Kearney et al. (2009) was built up to predict the physiology and behavior of a "standard" small ectotherm. In reality, species have physiological and behavioral adaptations to abiotic conditions, such as summer quiescence in some Mediterranean species (Arnold et al. 2002), or low-temperature digestion in cold-temperate vipers (Naulleau 1983). Future models should try to account explicitly for these differences, because they may represent adaptive buffers against the ecological consequences of warming (Grant and Porter 1992).



Climate niche models offer an alternative approach to forecasting a species' response to global warming. These models rely on distribution data and statistical tools to predict the range of a species. Araùjo et al. (2006) used this approach to forecast potential range shifts of European reptiles in response to global warming and predicted dramatic changes. Range contractions for 5% to 35% of species predominated in southern areas subject to important reductions in annual precipitation (the Iberian, Italian, and Anatolian peninsula). Many species (44% to 65%) should expand in cooler areas if they have unlimited dispersal capacity. However, the ranges of most species (97% to 100%) should contract if the species lack dispersal capacity. Species whose ranges are predicted to consistently retract are endemic lizards with restricted ranges (*Iberolacerta spp*, *Podarcis tiligertus*), species distributed in humid and cold habitats (the common lizard *Zootoca vivipara*, the adder *Vipera berus*, and the sand lizard *Lacerta agilis*), the Seoane's viper (*Vipera seoanei*) from temperate humid habitats in southwestern Europe, and the Schreiber's green lizard (*Lacerta schreiberi*) in Spain. Again, these predictions must be interpreted with caution, since we lack information on dispersal capacity (see below). Furthermore, these models ignore the ecological diversity of reptiles. For example, the northern or upper altitudinal ranges of several squamate species may be subject to clear thermal constraints, but the southern and lower altitudinal ranges of those same species and the distribution limits of Mediterranean species are much more complex and could involve constraints due not only to temperature but also to water limitations, interspecific interactions, and historical factors (e.g., Gasc et al. 1997).

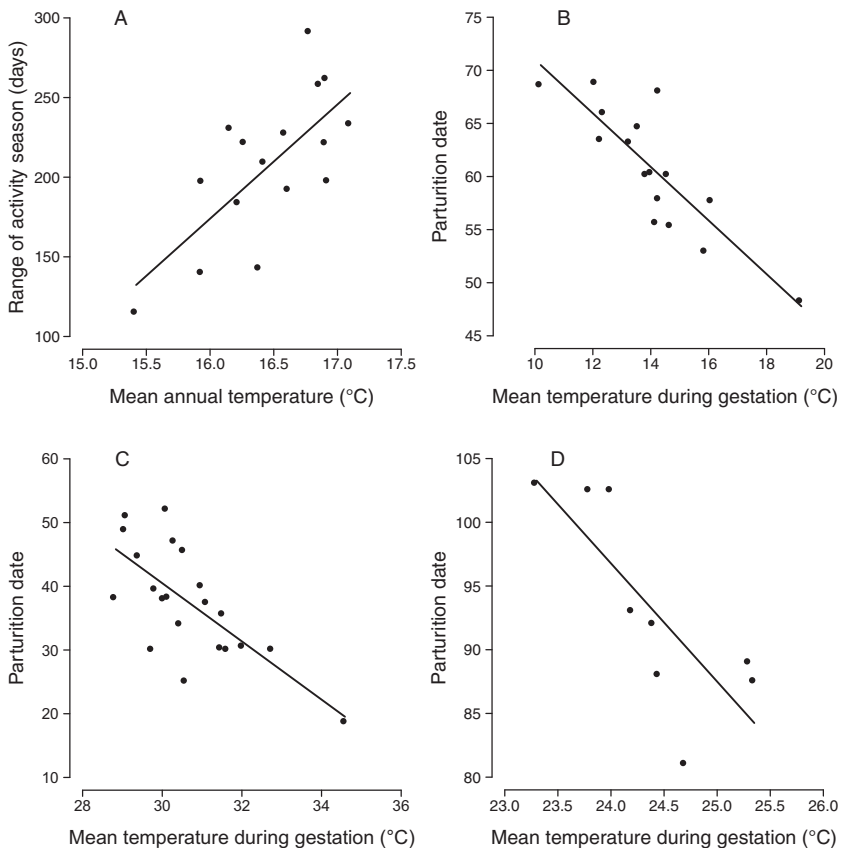
### **Observed Ecological Effects of Climate Change**

Niche models indicate that the effects of global warming may be substantial, but these predictions may suffer from not considering species-specific demographic and evolutionary mechanisms. Here, we review the links between climatic variation and phenology, life history, spatial dynamics, and evolutionary dynamics.

### **Phenological Changes**

Changes in the annual timing of life-history events have been linked with climate warming in many species (Parmesan 2006) and are also expected for squamates (Saint Girons 1985, Adolph and Porter 1993, and references therein). Timing of the breeding cycles is controlled by external cues, such as light and temperature, and by internal cues, such as age, sex, and body condition (reviewed in Licht 1972). All else being





**Figure 9.2.** Phenological changes associated with climate warming in squamate reptiles from Europe. In response to local warming, increase in the length of the activity season was observed in (a) the Montpellier snake (after Moreno-Rueda et al. 2009), and advancement of breeding dates was found in (b) the common lizard (after Le Galliard et al. 2010), in (c) the meadow viper (after Baron and Le Galliard, unpub. data), and in (d) the asp viper (after Lourdaï et al. 2002). Parturition date is calculated from June 1 in b, from August 1 in c, and from June 10 in d.

equal, warmer climates should result in longer activity periods and earlier breeding times. Some of the best evidence available so far comes from a study of the Montpellier snake (*Malpolon monspessulanus*), in which the annual activity period has increased in concert with climate warming (Moreno-Rueda et al. 2009; see figure 9.2A). Anecdotal observations also suggest that warmer climates are associated with earlier winter emergence in northern species, prolonged activity into the autumn and winter, and increased winter activity (Henle et al. 2008). In most species investigated so far, during the activity season the gestation length

is shorter in a warmer climate (figure 9.2B to 9.2D). For example, a detailed investigation of thermal constraints on reproductive timing in the asp viper concluded that temperature was most critical in mid-gestation, and this explained up to half of the temporal variation in gestation length (Lourdais et al. 2004).

The match-mismatch hypothesis for consumer-resource systems predicts that the ecological consequences of global warming depend critically on the temporal concordance between the phenology of a species and the availability of the resources it needs (Post et al. 2001, Stenseth and Mysterud 2002). Unfortunately, it remains unclear whether this hypothesis provides a useful scenario for ectothermic consumers such as reptiles. We suspect that major differences in demographic response to phenological changes may exist between insectivorous species (most lizards and some snakes) and other carnivorous species (most snakes), as well as between short- and long-lived species. Insectivorous species prey on a highly sensitive resource that responds quickly to climate variation, while the availability of prey for carnivorous species (e.g., mammals, lizards, or amphibians) may be less sensitive to climate. Also, earlier breeding may be beneficial in short-lived, fast-growing species because it creates an extended growth period for the offspring prior to wintering, or because offspring born earlier suffer less from competition with their congeners (Olsson and Shine 1997, Sinervo 1999). In long-lived, slow-growing species, the fitness effects of an earlier breeding may be weaker or even potentially negative (Baron et al. 2010a).

### **Sex Ratio at Birth**

Temperature-dependent sex determination (TSD) implies that changes in incubation temperatures could lead to imbalanced sex ratios at birth (Janzen 1994). However, TSD systems based on heteromorphic sex chromosomes are absent in snakes, and reports of TSD in lizards from Europe are equivocal (Viets et al. 1994, Ciofi and Swingland 1997, Andrews 2005, Janzen and Phillips 2006). More work is needed to clarify the phylogenetic distribution of TSD systems in squamates, but we suspect that climate-induced change in sex ratio at birth is unlikely to be a major threat to these species in Europe (Baron et al. 2010b).

### **Growth, Survival, and Reproduction**

Results on life-history sensitivity to climatic conditions in European reptiles come primarily from long-term studies of the common lizard (*Zootoca vivipara*) and the meadow viper (*Vipera ursinii ursinii*) in France, as well from two field studies of the asp viper (*Vipera aspis*). Common liz-

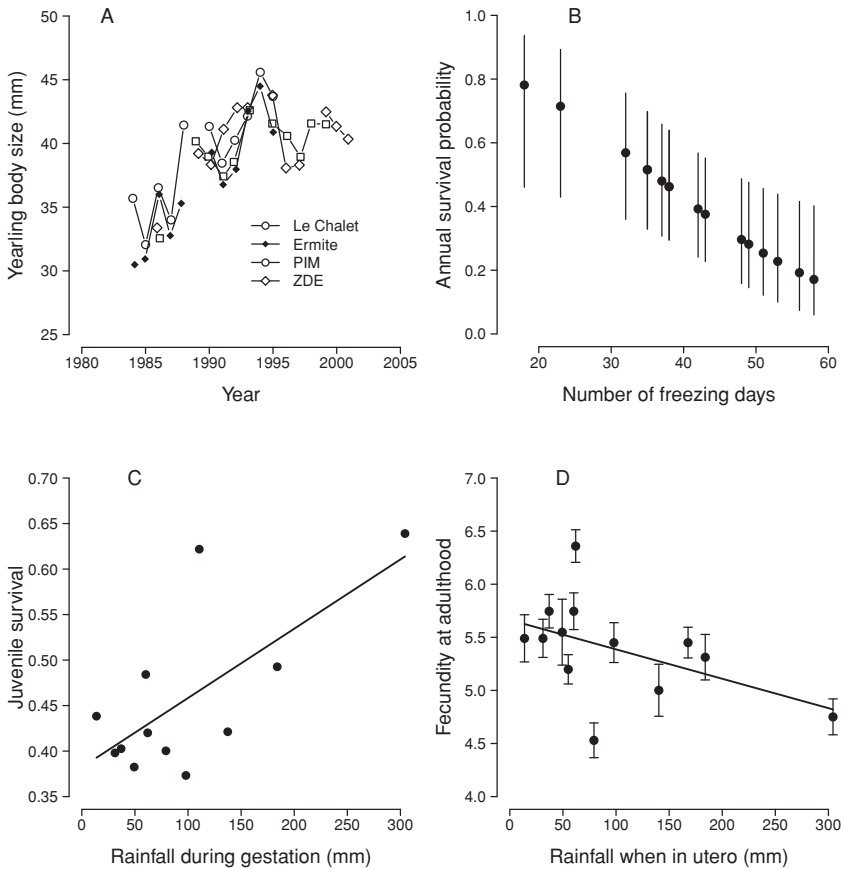
ard populations have been monitored in mountains from central France (ca. 1400 m above sea level) since the mid-1980s. This species is very widespread and is not considered at risk in Europe, though its populations are located in endangered habitats such as peat bogs and wetlands (Clobert et al. 1994). The asp viper has been monitored in a high-density population located around sea level in western France (Lourdais et al. 2004), as well as in marginal low-density populations in Switzerland (ca. 400–1,100 m above sea level) where the species is critically endangered (Altwegg et al. 2005). The meadow viper has been monitored intensively in one study population located in southeast France (ca. 1400 m above sea level) at the most western part of its distribution (Baron et al. 1996). This snake is listed as vulnerable across Europe and as critically endangered in France.

In general, climate warming has positive effects on most life-history traits (see table 9.2). In the common lizard this includes a clear trend towards larger body sizes and litters (figure 9.3A; Chamaillé-Jammes et al. 2006), faster growth at the yearling stage (Le Galliard et al. 2010), weak positive effects on adult survival (Chamaillé-Jammes et al. 2006), and strong positive effects on maternal body condition after parturition (Le Galliard et al. 2010). The increased body size and fecundity at the population level come primarily from increased growth opportunities due to earlier birth dates (see figure 9.2B) and longer activity seasons (Le Galliard et al. 2010). In vipers, warmer environments are associated with faster growth during nonreproductive years (Forsman 1993, Lourdais et al. 2002), increased maternal condition after parturition (Baron and Le Galliard, unpub. data), and fewer late embryonic failures (Lourdais et al. 2004, Baron and Le Galliard, unpub. data). However, temperatures negatively affect the mass gain during reproduction in the asp viper, thus suggesting metabolic costs of gestation at high temperatures in this species (Lourdais et al. 2002, Ladyman et al. 2003). In general, thermal effects are important during gestation and the juvenile stage (table 9.2). However, Altwegg et al. (2005) also discovered negative effects of winter freezing on juvenile survival, which points to the importance of thermal conditions during the inactivity season (figure 9.3B).

Limitation of growth and reproduction by availability of water has been quantified in the common lizard, in which complex patterns of positive and negative effects have been revealed (Marquis et al. 2008, Le Galliard et al. 2010; also see table 9.2 and figure 9.3C). This complexity could be explained by a combination of positive, indirect effects of rainfall on the summer availability of food and direct, negative effects of rainfall on insolation and therefore on growth opportunities (Marquis et al. 2008, Le

**Table 9.2.** Summary of observed climate effects on life-history traits (growth, survival, and reproduction) in natural populations of squamate reptiles subject to long-term demographic studies in Europe. Source references are provided in the main text.

Climate factor	Season	Study species	Life stage	Demographic trait	Climate effect
Temperature	Summer	<i>Vipera aspis</i>	Adult, gestation	Litter success	Positive
			Adult, gestation	Offspring size at birth	Positive
			Adult, gestation	Maternal condition	Negative
Temperature	Summer	<i>Vipera ursinii</i>	Mean annual conditions	Nonreproductive adult body growth	Positive
			Adult, gestation	Litter success	Positive
Temperature and cloud cover	Summer	<i>Vipera berus</i>	Adult, gestation	Maternal condition	Positive
			Mean annual conditions	Adult growth	Positive
Number of freezing days	Winter	<i>Vipera aspis</i>	Juvenile	Survival	Negative
	Spring	<i>Zootoca vivipara</i>	Adult, emergence	Survival	Positive
Temperature	Summer	<i>Zootoca vivipara</i>	Mean annual conditions	Yearling and adult size	Positive
			Mean annual conditions	Fecundity	Positive
Rainfall	Summer	<i>Zootoca vivipara</i>	Juvenile	Yearling body growth	Positive
			Adult, gestation	Maternal condition	Positive
			Adult, gestation	Litter success	Negative
			Adult, gestation	Offspring growth and survival	Positive
			Adult, gestation	Fecundity at adulthood	Negative
			Adult, gestation	Size of F1 offspring at adulthood	Positive
			Juvenile	Juvenile growth	Negative
			Juvenile	Juvenile survival	Positive



**Figure 9.3.** Effects of climatic conditions on life-history traits in squamate reptiles from Europe. In the common lizard, long-term field studies have shown positive effects of global warming on (a) body size (after Chamailé-Jammes et al. 2006), positive effects of rainfall on (c) juvenile survival (after Le Galliard et al. 2010), and negative delayed effects of rainfall on (d) female fecundity (after Marquis et al. 2008). Juvenile survival shrinks during the coldest winters in (b) the asp viper (after Altwegg et al. 2005).

Galliard et al. 2010). Altogether, these studies suggest that the total demographic effects of climate change will depend on a balance between positive thermal effects and the potentially negative effects of water limitation. For example, in the common lizard, warming has little effect on juvenile survival and positive effects on size and fecundity, but drier environments are associated with a lower juvenile survival (figure 9.3D). A matrix population model that includes temporal variation in all demographic traits shows that this species is most sensitive to changes in juve-

nile survival, and that the observed variation in juvenile survival contributes most to the variation in population growth (Le Galliard et al. 2010). Thus, even though positive fitness effects of local warming have been found (Chamaillé-Jammes et al. 2006), a trend towards lower juvenile survival in drier environments could contribute to population decrease in this species. In sharp contrast, the population dynamics of vipers are most sensitive to variation in adult survival, and then to variations in juvenile survival and reproduction (Altwegg et al. 2005). Thus, the positive effects of warming on reproduction are unlikely to cause major changes in the dynamics of viper populations, while warming during the winter may be beneficial for the persistence of endangered populations of asp vipers from Switzerland.

### **Range Shifts and Dispersal Behavior**

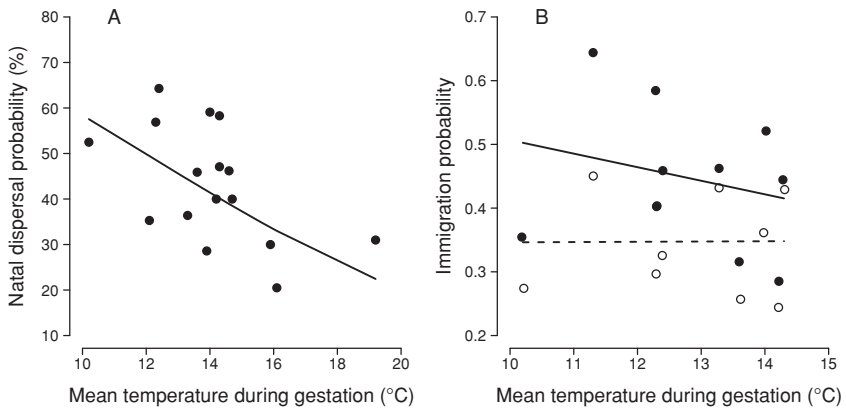
Recent latitudinal or elevational expansions have been observed in mobile animals and in plants (Parmesan 2006). Range expansion in European squamates has been described for two southern species, *Vipera aspis* and *Hierophis viridiflavus*, that have shifted 60 km north in 40 years (Naulleau 2003). Such limited evidence in reptiles may be due to their intermediate mobility, a lack of data, or confounding effects of habitat loss and shifting land use (Hickling et al. 2006). Many reptiles are also predicted to retreat from their southern or lowland margins (Sinervo et al. 2010). For example, the adder (*Vipera berus*) has retreated from southern habitats in some parts of France (Naulleau 2003). Field studies on numerous populations across the distribution area of the common lizard illustrate another case of range retraction. Monitoring the southern margin of the species range has shown that several lowland populations went extinct in 10 years' time, or that their density was reduced by more than 50% after a warm spell (Sinervo, Massot, and Clobert, unpub. data).

The ability of a species to expand its range or to persist after range contraction is critically dependent on its dispersal potential, which is a key parameter in the processes of colonization and invasion (Thomas et al. 2001, Clobert et al. 2004, Parmesan 2006). Unfortunately, relatively little is known about dispersal in reptiles. For example, Bowne and Bowers (2004) only found three suitable studies from two reptiles in their review of interpatch movements. Also, rates of colonization are poorly known, with the best data coming from two European species introduced in North America. The Mediterranean gecko *Hemidactylus turcicus*, introduced some decades ago in Texas, increased its range at a rate of about 20m per year (Locry and Stone 2008). The wall lizard *Podarcis mura-*

*lis*, introduced in Canada, expanded its range more rapidly (400 m per year, after Bertram 2004). These examples illustrate colonization ability in introduced populations, but say little about responses in dispersal behavior to climate change in the native range. Future studies should focus on understanding the effects of global warming on dispersal, and on distinguishing processes at work at the southern and northern margins of a species' range. At the northern margins, new habitats become available, and the major process driving range shift is colonization. It is now recognized that colonizers are not a random sample of individuals (Clobert et al. 2009). For example, in the common lizard, individuals that disperse to avoid mother-offspring competition are asocial, are prepared to take important risks, and prefer empty habitats where they achieve higher fitness (Le Galliard et al. 2003, Cote and Clobert 2007, Cote et al. 2007, Cote and Clobert 2010). Thus, avoidance of kin competition may be the main process by which colonization is achieved at the northern margin (Clobert et al. 2009). In contrast, processes at work at the southern margins are characterized mainly by the loss of suitable habitats (Thomas et al. 2004, Massot et al. 2008). As suitable habitats deteriorate, the distance between hospitable patches increases, and therefore the costs of dispersal should increase. Moreover, in a southern mountainous population of the common lizard, ongoing climate warming clearly inhibits dispersal (Massot et al. 2008, Lepetz et al. 2009a; also see figure 9.4). This plastic response of dispersal should further increase the speed of extinction at the southern margin by decreasing colonization and rescue effects.

A species that cannot track environmental changes in space could still adapt to new environmental conditions. Adaptation may involve phenotypic plasticity or evolutionary changes driven by selection. The dominant view is that life-history adaptations to climate change in animals are mainly caused by phenotypic plasticity (Parmesan 2006, Charman-tier et al. 2008). Unfortunately, there are very few examples of adaptive phenotypic plasticity in response to global warming in squamates (Telemeco et al. 2009). Selection on preexisting genetic polymorphism has also been implicated in birds and mammals (Réale et al. 2003, Nussey et al. 2005). In squamates, substantial genetic variation exists for traits ranging from morphology to physiology and life history (reviewed in Shine 2005), but no study has yet documented evolutionary responses to warming. Color morphs in lizards can be determined by genetic and environmental cues (Sinervo et al. 2001, Cote et al. 2008), and may be good markers for studying the interplay between genetic and plastic responses to global warming. In Europe, Lepetz et al. (2009a) reported on





**Figure 9.4.** Dispersal inhibition in response to climate warming in a natural population of the common lizard (*Zootoca vivipara*). Natal dispersal inside a natural population (movement probability out of the natal home range) and immigration into this natural population (proportion of immigrants) decreased concurrently with local warming. Data are (a) dispersal frequencies from Massot et al. (2008), and (b) immigration frequencies for linear morphs (filled circles) and reticulated morphs (empty circles) from Lepetz et al. (2009a).

a correlation between mean temperature and the population frequency of dorsal, melanin-based coloration in the common lizard. As expected, it was observed that common lizards with less melanin on their backs were more numerous in more recent and warmer years. However, this change was due not to phenotypic plasticity or to differential selection, but to a temporal trend towards a lower immigration rate of lizards with more melanin. This result provides the first evidence of the impact of climate warming on population composition due to migration.

### Interspecific Interactions

The effects of climate change may involve interspecific interactions (Walther et al. 2002). For example, studies of squamates in deserts from North America indicate that rainfall determines the abundance of plants, insects, and small mammals that are prey for a whole community of lizards and snakes (e.g., Tinkle et al. 1993). In Europe, similar trophic interactions have yet to be quantified but are expected in water-limited environments and for squamates specialized for fluctuating resources (e.g., the asp viper; Lourdaux et al. 2002). In addition, warming may lead to community reassembly and may promote coexistence with novel competitors, predators, or invasive species. For example, ophiophagous snakes have

started to colonize habitats occupied by meadow vipers (Baron, personal observation) and the green lizard has been recently seen in high-altitude habitats occupied by the common lizard (Clobert, personal observation). However, the link between these extinction factors and climate change remains to be more thoroughly examined.

### **Promoting Climate Change Resilience in European Reptiles Synthesis and Knowledge Gaps**

Our review shows clearly that some climate change effects are already occurring. Some of the observed demographic effects are positive (enhanced growth and fecundity, earlier maturation and higher reproductive success, enhanced survival) but others are negative (lower survival, increased water and heat stress, reduced dispersal). Demographic growth or declines caused by climate change are not yet apparent, except in data collected in southern populations of the common lizard. On the other hand, niche models predict that future projected changes in climate should result in substantial range shifts for most reptiles in Europe. Several reptiles may benefit from climate warming if they can expand their range northward or upward, but cool-adapted, water-limited endemic species around the Mediterranean basin are predicted to decline. The relative effects of temperature and water availability are difficult to tease apart in most studies, and it is premature to compare the results of field studies with those of niche models.

Our ability to understand the ecological consequences of global warming is still limited by gaps in our knowledge of European squamates. Four major shortcomings can be recognized. First, current evidence for the impact of climate change comes only from three model species out of about 130. Demographic data are surprisingly rare for the most threatened species that attract considerable attention and funding (Cox and Temple 2009). Second, even the best studies are focused on only a few target populations, rather than across the entire geographic range, with the notable exception of data collected along the southern limit of the common lizard's range (Sinervo, Massot and Clobert, unpub. data). Third, even the best available studies do not allow us to distinguish between the direct and indirect effects of climatic conditions. Fourth, basic information on dispersal is lacking for most species. Only the common lizard has been investigated in sufficient detail for us to make predictions concerning spatial population dynamics (Massot et al. 2008). This critical gap is not specific to squamates, since we lack information on the dispersal potential of other animals (Kokko and Lopez-Sepulcre 2006).

## Implications for Conservation

Environmental agencies and stakeholders point out the need to conserve European biodiversity, including squamates, in the face of climate change (see table 9.1), but no clear recommendation has been made for the management of squamates potentially threatened by climate change. Extinction risk from climate change has been investigated across a wide range of species on the basis of climate niche models (Araújo et al. 2006), and in the common lizard on the basis of field census (Sinervo, Massot, and Clobert, unpub. data). These studies suggest that several species will be threatened in the future, especially common and cold-adapted species at their southern margins, water-limited species, and range-restricted endemics of the Mediterranean basin. Yet it remains difficult to quantify the risks posed by global warming relative to other extinction threats. Monitoring programs aimed at tracking the spatial and temporal changes of reptiles are rare (see [eumon.ckff.si](http://eumon.ckff.si)), and funding such programs should be considered a research priority (Lengyel et al. 2008, Lepetz et al. 2009b). Collaboration and consensus over monitoring schemes and monitored species will be needed to achieve these aims. Compared to birds and mammals, many species of reptiles are easily amenable to experiments at the individual or population level. Experiments on climate change effects should also be conducted to gain insights into mechanisms, causal pathways involved, and nonlinear responses to warmer climates expected in the future. These new data should stimulate the development of predictive models, such as population viability analyses, that would help in predicting the future of reptile populations in Europe.

Firm measures to promote climate change resilience in European reptiles will also be needed (Brodie et al., this volume; Popescu and Hunter, this volume). First, we must promote action against existing threats to improve conditions so that species can respond to future climate changes. Squamates are highly sensitive to their landscape, and securing the size, quality, and connectivity of their natural habitat should be treated as a top conservation priority (Cox and Temple 2009, Silva et al. 2009). In the most common species potentially threatened by climate change (e.g., widespread, cool-adapted species), the preservation of natural habitat should help maintain large populations within a connected network of habitat patches, which in turn will facilitate ecological and evolutionary responses to global warming. As a general rule, we recommend three major conservation priorities for these species: (1) restraints on existing protected areas to secure the size and evolutionary potential of existing populations, even if they are not currently threatened; (2) definition and

protection of suitable habitats in the future, such as those at the northern margin and in higher altitudinal ranges; and (3) definition and protection of denser networks of protected areas, including habitat corridors, to enable dispersal movement.

In addition, species at risk of extinction from climate change (e.g., island endemics or range-restricted species) and species that are already threatened (see table 9.1) should be the focus of further studies to test on-the-ground management strategies to mitigate the effects of climate in local populations. For example, Kearney et al. (2009) have noted that the availability of shade and moisture will be crucial for the persistence of small lizards in semiarid regions. In these areas, conservation action to promote shade and moisture and facilitate movement may include changes in land use practices and effective restoration of natural corridors (i.e., maintenance of mixed structures in open and shaded areas). Similarly, information on the reproductive biology and its sensitivity to climate conditions can be used for field management (Shine and Bonnet 2009). For snakes, ponds and artificial shelters will probably prove useful to create sites for resting, basking, and nesting and to mitigate some impacts of climate change. Hence, knowledge of the natural history of squamates will provide “best of the bad job” management options. Because climate change effects on ectothermic vertebrates are unavoidable, and because these animals’ dispersal capacity may be limited, proactive measures to assist their movement might be needed. Unfortunately, we lack information on the success of *ex situ* conservation and assisted dispersal (Silva et al. 2009). Furthermore, assisted migration of a given species may interfere with evolutionary responses or unassisted range shifts in other species. More studies are needed to evaluate the feasibility and potential negative impacts of assisted colonization strategies in European reptiles before we decide to implement such measures.

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