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Ecological Effects of Climate Change on Snakes
Vliv klimatických změn na ekologii hadů

Bachelor's thesis

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Čestné prohlášení

Prohlašuji, že jsem závěrečnou práci zpracovala samostatně a že jsem uvedla všechny použité informační zdroje a literaturu. Tato práce ani její podstatná část nebyla předložena k získání jiného nebo stejného akademického titulu.

V Praze ……………………………………………………..

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Abstract

Climate change is currently one of the biggest threats that animal species must face. Increasing temperatures cause declines in wildlife populations all around the world. Ectothermic animals might be amongst the most threatened organisms by climate change due to their ecology that makes them dependent on ambient temperature. As ectotherms, snakes will most likely need to adapt to new climatic conditions, or they become extinct. To escape raising temperatures and decreasing precipitation, snakes might shift their ranges and move into more suitable areas. However, snakes have a low dispersal ability, which might lead to range reduction and in some populations even extinction. Climatic changes might affect health and behaviour of snake species as well. Increased temperatures can alter incubation period and embryonic development. Alterations in embryonic development and reduction of incubation period can cause different kinds of malformations, especially in oviparous snakes. These malformations can negatively impact fitness, depending on their severity. Some snake species might also benefit from climate change. Elevated temperatures allow snakes to be more active and, in some cases, even shorten hibernation duration. Snakes are also able to better escape predators in high temperatures than in low temperatures. Even though climate change is mostly seen as a threat to wildlife, it may actually benefit snakes in certain ways.

Keywords: climate change, snakes, ecology, behavioural changes, distribution, health, temperature, precipitation

Abstrakt

Klimatické změny momentálně představují jednu z největších hrozeb, se kterými se živočišné druhy musí potýkat. Zvyšující se teploty ohrožují spoustu populací po celém světě. Ektotermní živočichové by mohli díky své ekologii, která je dělá závislými na okolní teplotě, patřit mezi organismy nejvíce ohrožené klimatickými změnami. Hadi se jako ektotermní živočichové pravděpodobně budou muset přizpůsobit měnícím se klimatickým podmínkám, nebo vyhynou. Aby hadi unikli vzrůstajícím teplotám a klesajícím srážkám, mohou se přesunout do míst s vhodnějšími klimatickými podmínkami. Hadi však mají omezenou schopnost disperze, což by mohlo vést k redukci areálu výskytu a u některých populací až k extinkci. Klimatické změny také s největší pravděpodobností ovlivní kondici a chování hadů. Zvýšená teplota může ovlivnit dobu inkubace a embryonální vývoj. Hlavně u vejcorodých druhů pak mohou změny v embryonálním vývoji a zkrácení doby inkubace způsobit různé malformace. Tyto malformace mohou v závislosti na jejich závažnosti negativně ovlivnit fitness jedince. Některé druhy hadů mohou však využít klimatické změny ve svůj prospěch. Zvýšená teplota prostředí dovoluje hadům být více či déle aktivní a v některých případech dokonce zkrátit dobu hibernace. Hadi dokážou při vyšších teplotách také lépe uniknout predátorům. Přestože jsou klimatické změny obecně považovány za hrozbu, některé druhy hadů je mohou využít ve svůj prospěch.

Klíčová slova: změny klimatu, hadi, ekologie, behaviorální změny, rozšíření, kondice, teplota, srážky

Contents

1. Introduction

Raising temperatures and decreasing precipitation associated with climate change are currently threatening many species. Ectotherms are more sensitive to climate change variables than endotherms (Aragón *et al.,* 2010), because of their ecology. Performance of ectothermic animals depends on ambient temperatures (Kearney *et al.,* 2009), which makes them especially prone to changes of climatic conditions. Ectothermic species might be amongst the most vulnerable to climate change not only because their dependence on temperature, but also due to their inability to migrate over long distances.

In this thesis, I will be dealing with snakes, because from the conservation perspective, they have been overlooked in comparison to the flagship organisms such as mammals or birds (Guedes *et al*., 2018; Lourenço-de-Moraes *et al.,* 2019). Snakes are highly vulnerable to climate change due to their specialised habitat requirements and slow life histories (Araújo *et al.,* 2006; Reading *et al.,* 2010). However, snakes are known to prefer warm areas, hence they might be less severely affected by increasing temperatures and might even benefit from them. On the other hand, water availability might decrease under future climatic conditions and thus negatively impact snake species.

Climate change will most likely benefit snakes from temperate zones the most, because they should spend less time thermoregulating under future climatic conditions (Weatherhead and Madsen, 2009). Conversely, snakes from the tropical zones or regions where water and shade availability is already low, will most likely experience the most negative consequences (e.g. Brito *et al*., 2011; Penman *et al.,* 2010). Dispersal ability will probably determine the survival of species from areas that will become unsuitable under future climate conditions (Araújo *et al.,* 2006).

Elevated temperatures and decreased precipitation will most likely alter many life history traits of snakes, such as size of offspring, growth pattern etc., and distribution (e.g. Idrisova and Khairutdinov, 2018; O'Donnell and Arnold, 2005; Zacarias and Loyola, 2019). Elevated temperatures might allow snakes to be more active and alter their predatory and antipredatory behaviour as well (e.g. Capula *et al.,* 2016; Mori and Burghardt, 2001). This thesis aims to find out how those traits will change and whether snakes will be able to adapt to future climatic conditions, based on what we currently know about snakes and future predictions. I would also like to determine the benefits that climate change brings to snakes and whether or not they are insignificant compared to the threats that snakes will have to face under future climatic conditions.

In the last chapter, I would like to compare snake vulnerability to climate change to other ectothermic vertebrates to find out, whether snakes are more prone to climate change than others. I assume that amphibians will be more inclined to extinction than snakes and other reptiles, due to their high dependence on water.

2. Impacts of climate change on distribution

One of the effects that climate change may have on snakes are changes in geographic distribution of species (Zacarias and Loyola, 2019). Climate changes could significantly change distribution of natural habitats and biodiversity patterns. (Malcolm *et al.,* 2006; Thomas *et al.,* 2019). Although climate cooling would probably cause more harm to snakes than climate warming, their ability to cope with the warming climate might be affected by associated decrease in water availability (Araújo *et al.,* 2006). As many areas of current distribution might become unsuitable for snakes under future climate change (e.g. Araújo *et al.,* 2006; Penman *et al.*, 2010; Lourenço-de-Moraes *et al.,* 2019), species survival will mostly depend on their dispersal ability and range shifts (Araújo *et al.,* 2006). The direction of range shifts in snakes seems to tend towards poles and higher elevations. Snake populations in the northern hemisphere are predicted to shift northwards and populations in the southern hemisphere, southwards. However, continentality of climate or topography play also an important role in range shifts, contractions or expansions. (e.g. Bombi, Akani, *et al.,* 2011; Needleman *et al.,* 2018).

To be able to determine future changes in species distribution, scientists often use Ecological Niche Models (ENMs) (e.g. Sahlean *et al.,* 2014; Vasconcelos, 2014; Zacarias and Loyola, 2019). ENMs use known distribution of species and environmental conditions (mainly precipitation and temperature) to predict future species response to climate change (Márquez *et al.,* 2011). Distribution modelling is a good alternative to other experiments and field research, however, combination of both approaches should be favoured (Bombi, Capula, *et al., 2011)*. Knowing how species shifted their distribution as a response to past climate change can play an important role in predicting possible future range shifts (Wu, 2016). Studies on the effects of climate change should also consider other influential factors (e.g. habitat destruction and changes in vegetation cover) to be able to better predict changes in species distribution (Márquez *et al.,* 2011; Winter *et al.,* 2016).

Even though Ecological Niche Models are widely used by researchers, we need to keep in mind that these algorithms work at a probability level and have many limitations. For instance, studies that only investigate effects of climatic variables might be biased, because they do not consider other variables such as anthropogenic impact on habitats (Winter *et al.,* 2016) and therefore predicted outcomes might differ from actual possible impacts (Wu, 2016). However, Winter *et al.* (2016) also stated that similar results of climate change effects on species distribution occurred in their study, no matter if other causes of change were examined. This implies that reporting bias might be minimal even in studies that examine climate change as the only influential factor. Climate envelope models (they define climatic niche of species - envelope) might be even more reliable than conclusions based solely on field research. Current studies based on field research have only gathered data over short periods of time and thus climate change effects might not have been strong enough to be detectable yet (Winter *et al.,* 2016). Ecological Niche Models can additionally be used to predict future effectiveness of conservation function of protected areas as they might lose it due to species distribution changes and emigration (Lourenço-de-Moraes *et al*., 2019).

The chapters that follow break down how snake distributions change on different continents. Snakes from different climatic conditions will most likely react differently to climatic changes, which is indicated in the following chapters.

2.1 Europe

European species of snakes are generally predicted to lose suitable habitats in areas with high annual temperature and decreases in annual precipitation. Increase in suitable habitats for most of the species is expected in cooler regions that are anticipated to become warmer in the future. Losses in species richness are therefore predicted for instance in southern France, Italy, and the Iberian Peninsula. Habitat expansion is, on the other hand, anticipated in the southern and eastern rims of Central Europe, however habitat fragmentation and degradation might make it harder for snake species to disperse (Araújo *et al.,* 2006).

Research from Spain (Moreno-Rueda *et al.,* 2012) found out that between the years 1940 and 2005 some European species have already shifted their range northwards, which indicates that extinction driven by climate change might not be as bad as previously anticipated. However, many European snake species are predicted not only to shift their range northwards, but also to lose significant parts or even almost all of their current ranges (e.g. isolated island and montane species and populations) under future climatic conditions (e.g. Santos *et al.*, 2009; Sahlean *et al.*, 2014; Ahmadi *et al.*, 2019).

Isolated populations of snakes might be more prone to habitat loss and local extinctions (e.g. Santos *et al.*, 2009; Bombi, Capula, *et al.*, 2011). For example, suitable habitats of Sardinian populations of *Hemorrhois hippocrepis* are predicted to reduce from the original 1391 km^2 to 11 km^2 by 2050 (Fig. 1), out of which only 1 km^2 falls into the protected areas (Bombi, Capula, *et al.* 2011). Similar fate is anticipated for *Vipera graeca*, which is a cold-adapted snake inhabiting the highest and coldest areas of Pindos Mountains in Greece and Albania (Mizsei *et al*., 2016; 2020). Mizsei *et al.* (2020) expect an 81-90% reduction of its suitable habitat by the end of the 2080s. Moreover, their limitation to highest and coldest areas makes it impossible for long-distance dispersal to other suitable high-elevation mountains.

Some European snake species are anticipated to gain suitable habitat north of their current ranges (e.g. Popescu *et al.*, 2013; Sahlean *et al.*, 2014). According to Popescu *et al.* (2013), three (*Coluber/Dolichophis caspius, Elaphe quatrolineata* and *Vipera ammodytes*) out of eight snake species they studied in Romania are predicted to gain new suitable habitat by the 2050s. Findings of a different independent study on *Dolichophis caspius* predict slight loss of habitat in southern range limit but also gaining new climatically suitable areas north of its current range (Sahlean *et al.,* 2014), which agrees with the findings of Popescu *et al.* (2013).

In summary, distributions of European species will most likely shift northwards, although isolated species or populations might experience major losses in suitable habitats under future climate conditions. In my opinion, raising habitat fragmentation and anthropogenic habitat degradation, which the studies mentioned above did not consider, might make it even harder for certain species to disperse and thus lead them to extinction.

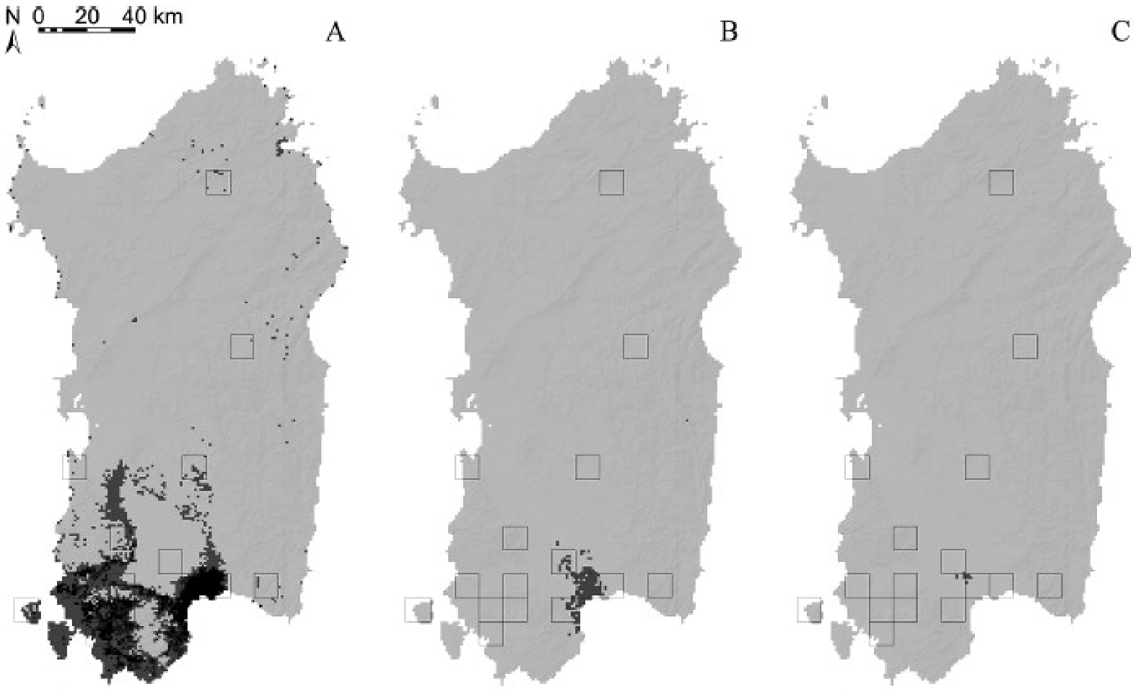

Figure 1 Models of suitable habitat of *Hemorrhois hippocrepis* in Sardinia, a – climatic conditions in 2011, b – climatic scenario for 2020, c – climatic scenario for 2050. The light grey colour represents unsuitable areas, dark grey and black colour represent suitable areas. The squares represent the known distribution of *H. hippocrepis* in Sardinia in 2011. Source - Bombi, Capula, *et al.* (2011)

2.2 Africa

Distribution changes of snake species in Africa are driven by temperature and especially precipitation (e.g. Bombi, Akani, *et al.*, 2011; Brito *et al.*, 2011; Sow *et al.*, 2014). Unlike European snakes, African snakes are expected to shift ranges not only northwards but in some cases also southwards (e.g. Bombi, Akani, *et al.*, 2011; Zacarias and Loyola, 2019). African snake species will most likely face similar distribution changes to those in Europe, with many species losing a fair portion of their current suitable habitat, especially those in north Africa (e.g. Brito *et al.*, 2011; El-Gabbas *et al.*, 2016). Some species might also be expanding to new areas under future climatic conditions (e.g. Bombi, Akani, *et al.*, 2011; Zacarias and Loyola, 2019).

Among the species that are predicted to lose suitable habitat are African populations of *Vipera latastei* in Morocco (Brito *et al.,* 2011). Brito *et al.* (2011) found out that precipitation was the most important variable for occurrence of the species. Future projections predicted a major habitat loss by 2080 and no new suitable areas to occur for *Vipera latastei* under future climate conditions. The current range of the species in Morocco is severely fragmented. The habitat fragmentation, and the Sahara Desert being an ecological barrier, might be the reason for the improbability of gaining new suitable habitats. Other African species projected to lose range are *Thelotornis capensis* and *Causus rhombeatus*, both losing more than a half of their current range. (Zacarias and Loyola, 2019).

A study of iconic vipers *Bitis gabonica* and *Bitis nasicornis* in southern Nigeria (Bombi, Akani, *et al.,* 2011) determined temperature and precipitation to be an important climatic variable for distribution of both species. Both of the species have similar ecology and inhabit rainforest habitats (Luiselli, 2006b), but *Bitis gabonica* preys solely on mammals and *Bitis nasicornis* also preys on amphibians (Luiselli, 2006a). They imply that the distribution of the high-abundance species of *Bitis gabonica* will expand to southern Nigeria and neighbouring areas of Cameroon under future climatic conditions. They also believe that interspecific competition between the two species will increase with possible negative impacts on demography and population density of *Bitis nasicornis*. Additionally, the dispersal of *Bitis nasicornis* into new suitable habitats seems unlikely as those future suitable areas are densely populated, fragmented, and degraded. Their findings agree with those of Zacarias and Loyola (2019), who also predict *Bitis gabonica* to gain new suitable areas in the future. Besides *Bitis gabonica*, Zacarias and Loyola (2019) also expect *Naja melanoleuca* to gain new suitable habitats of almost the same area size it currently occupies.

Future expansion of venomous snakes' habitats mentioned above can increase the risk of snakebite. Zacarias and Loyola (2019) state that snakebite risk might increase e.g., in the southern part of Mozambique due to changes in distribution of venomous snakes. Most species mentioned in their study are connected to human settlements and their range shifts might cause more areas to become risky. This could raise the numbers of both human and snake fatalities.

2.3 The Americas

Predictions for South American snake species are quite alarming, with many species being anticipated to lose significant parts of their distribution ranges rather than gain new suitable areas (Lourenço-de-Moraes *et al.,* 2019; Nori *et al.,* 2016; Vasconcelos, 2014). Compared to those in South America, North American species seem to have a better future ahead of them. Some species are predicted to be able to disperse and shift their range into more suitable areas (Archis *et al.,* 2018; Yañez-Arenas *et al.,* 2016) and some will possibly lose suitable habitat with low probability of dispersal (Davis *et al.,* 2015).

Studies conducted in South America seem to show similar outcomes for snake species, for most of them, decrease in suitable habitat is predicted. For example, Mesquita *et al.* (2013) carried out a study on future climate conditions effects on *Liophis reginae,* which is a species widespread in South America. Their models predicted 30% loss of suitable habitat and 40% increase of its habitat fragmentation under future conditions. According to their findings, populations most affected by habitat reduction will be those in the northern coastal areas and especially those in Brazil, where isolated populations might also occur. However, they also imply that southern limits of the species habitat might become more suitable and even expand in the future. Other South American species that are predicted to lose their range are for example *Bothrops diporus* and *Bothrops ammodytoides* (Nori *et al.,* 2016) and *Phalotris lativittatus* (Vasconcelos, 2014).

Lourenço-de-Moraes *et al.*, (2019) assessed distribution changes of viviparous and oviparous species in the Atlantic Forest under future climate change. They predict range contraction as well, however, oviparous snakes appear to be more inclined to range loss than viviparous species, although they currently inhabit a broader area in the Atlantic Forest. The cause behind it might be the fact that viviparous snakes can regulate the temperature of their body and of their offspring by moving and therefore adapt better to changes in their distribution (Shine, 2004). According to their findings, only two out of 110 oviparous species inhabiting the Atlantic Forest are anticipated to gain new suitable areas (*Xenodon merremii* by 37% and *Drymachron corais* by 14%) and *Clelia Hussami* was found to be most endangered by climate change and might even become completely extinct in the future. Their results agree with those of Mesquita *et al.* (2013), that major losses in suitable habitat should occur in the coastal areas. Lourenço-de-Moraes *et al.* (2019) also suggest expanding the protected areas network as the effectiveness of protected areas in the Atlantic Forest is insufficient and its insufficiency will most likely keep rising in the future.

Species in North America will probably tend to shift northwards (Whiting and Fox, 2020; Yañez-Arenas *et al.,* 2016) with some range-restricted endemic species predicted to lose most of their suitable habitats (Davis *et al.,* 2015). A study of *Micrurus fulvius* (Archis *et al.,* 2018) forecasts northern increase in suitable habitat and northward shifts in current range with minimal contractions by 2050. Unlike for South American species, coastal areas of North America are anticipated to become more suitable in the future, at least for *Micrurus fulvius.* However, Archis *et al.* (2018) point out that their fossorial nature and activity patterns of the species might mean that their thermal optimum could be surpassed in the future in some areas of their distribution. This and the fact that the south-eastern part of their habitat is highly fragmented, could limit their ability to disperse in the future (Archis *et al.*, 2018).

Range-restricted endemic species like *Crotalus willardi obscurus* might face extinction under future climate conditions. Models predict its range to shift northwards, however, the species displays restricted dispersal ability and therefore the only possibility is to shift into higher elevation within its current range. This area of possible suitable habitat is very small, which could drive this species to extinction (Davis *et al.,* 2015).

The Americas might face an increase in numbers of snakebite under future climate change (Needleman *et al.,* 2018; Nori *et al.,* 2014; Yañez-Arenas *et al.,* 2016). In South America, snakebite numbers might increase due to the tendency of species to shift ranges from north to south (Nori *et al.,* 2014). Snakes might expand to areas where people are not used to venomous snakes. According to Yañez-Arenas *et al.* (2016), snakebite risk might increase in Argentina and Chile. Another example, Nori *et al.* (2014) predict Bothrops ammodytoides to expand southwards to places where there have never been venomous snakes. Nori *et al.* (2014) also imply that this range expansion could cause snakebites in human populations with no proper personnel and health care available. In North America, Yañez-Arenas *et al.* (2016) anticipate snakebite risk to expand northwards. They estimate a future increase of people being at risk of snakebite to be 5.5 to 6.7 million in the Americas alone.

2.4 Asia and Australia

The number of studies dedicated to the effects of climate change on distribution of snakes in Asia and Australia is low compared to the rest of the world, even though both regions have a very high abundance of snake species. In Asia, dispersal ability of snakes might be affected by habitat loss and fragmentation associated with deforestation, and population isolation (on both mainland and islands). As for Australian snakes, populations along the east coast and temperate regions seem to be most inclined to habitat loss, most likely because of their high habitat specialisation (Cabrelli *et al.*, 2014).

Asian snake species are predicted to gain more suitable areas than they are expected to lose (Huang *et al.,* 2013; Wu, 2016), however, with increasing drought, fossorial taxa, such as *Calamaria* spp. might need to burrow deeper into the soil in order to find sufficient moisture (Bickford *et al.,* 2010). Some species have already exhibited range shifts as a response to climatic changes. Wu (2016) found out that seven out of nine species in China that he studied, had not only shifted ranges, but gained new suitable habitat as well. His data indicate that ranges of studied species had shifted in all directions, but mostly northwards or westwards. He associated those changes with temperature, precipitation, and potential evapotranspiration rate. Even some high-elevation species might be able to gain new suitable habitat under future climatic conditions (Huang *et al.,* 2013). As Huang *et al.* (2007) imply, neither critical thermal maximum nor critical thermal minimum are a limiting factor for altitudinal distribution of some species. In my opinion, this might indicate that these species will be able to disperse more easily to escape the changing climate in the future.

In Australia, predictions are a lot more pessimistic compared to Asia. Many species are anticipated to lose suitable habitat under future climatic conditions rather than gain new suitable areas (Cabrelli *et al.,* 2014; Penman *et al.,* 2010). Most elapid snake species are predicted to lose suitable habitat by 2050, with some populations losing more than 50% of its current habitat. Range loss will probably affect populations in coastal and temperate areas the most. However, thirteen elapid snake species might experience range expansion (Cabrelli *et al.,* 2014). Among the elapid snakes that will lose range is *Holocephalus bungaroides.* This species will probably lose nearly all of its current range under future climatic conditions (Fig. 2) and Penman *et al.* (2010) suggest that other actions such as translocation of snakes might be needed as current protection areas might become inefficient in the future.

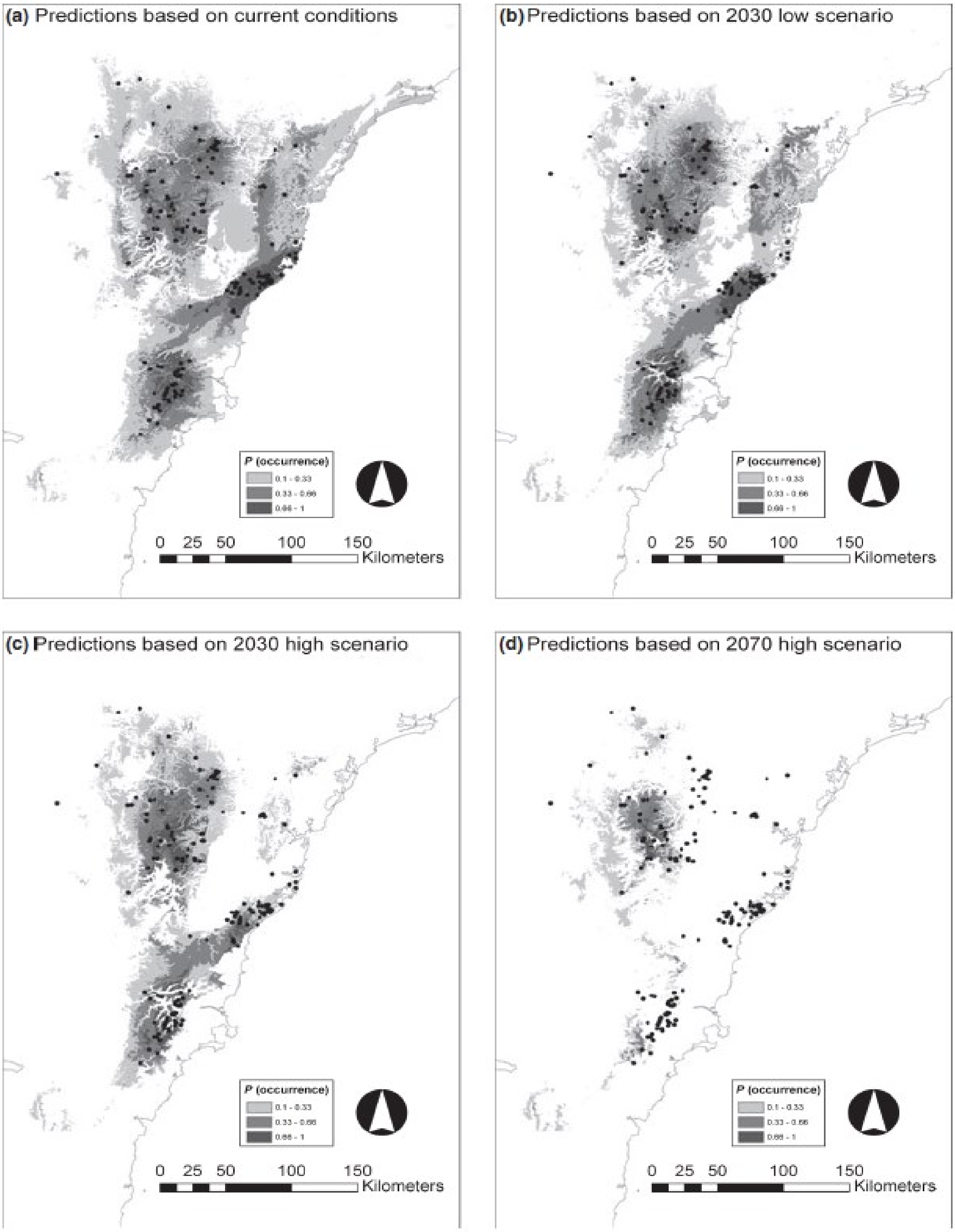

Figure 2 Models of possible future distributions of *Holocephalus bungaroides* using Maxent (ENM), a – climatic conditions in 2010, b – low warming scenario for 2030 (temperature increased by 0.5 ˚C, rainfall reduced by 5%), c – high warming scenario for 2030 = low warming scenario for 2070 (temperature increased by 1.5 ˚C, rainfall reduced by 5%), d – high warming scenario for 2070 (temperature increased by 4 ˚C, rainfall reduced by 5%), (n = 159). Source - Penman *et al*. (2010)

2.5 Sea snakes

Effects of climate change on distribution of sea snakes have not been thoroughly studied yet. Although Dunson and Ehlert (1971) conducted a study of *Pelamis platurus* and its response to high and low temperatures. *Pelamis platurus* is a cosmopolitan species and its range is the broadest range of all sea snakes. Their findings indicate that temperature might be one of the factors limiting the species from colonizing cooler southwest coasts of South America and Africa in present times. Their upper limit of temperature tolerance seems to slightly differ in water and air. The upper lethal temperature level of these snakes seems to be higher in air (over 34 ˚C) than in water (between 33.2 and 33.6 ˚C). Dunson and Ehlert (1971) also suppose that this species uses a behavioural thermoregulation by diving into colder waters to escape deadly temperatures, because some individuals they caught were close to their upper lethal level. In conclusion, sea snake species are most likely sensitive to too high or too low temperatures, however, thorough research on how the temperatures alter their dispersal has yet to be conducted.

3. Effects of climate change on health

Changes in temperature and precipitation linked to climate change will most likely affect health and overall fitness of snake species. As ectotherms, snakes rely on external temperatures and thus too high temperatures might have a serious impact on their health. Scientists imply that climate change will probably affect development of snakes, embryo mortality, phenotype, and more (e.g. O'Donnell and Arnold, 2005; Brown and Shine, 2006; Pincheira-Donoso and Meiri, 2013). Inbreeding and genetic isolation combined with changes in climatic conditions might also cause declines in snake populations (e.g. isolated population of *Crotalus horridus* in New Hampshire) (Clark *et al.*, 2011). Combrink *et al.* (2021) suggest innate immunity to be affected by climatic variables as well. Annual spring precipitation was associated with innate immunity of *Thamnophis elegans* and *Thamnophis sirtalis*, therefore decrease in precipitation might decrease immune function in some species.

3.1 Embryonic development

Incubation temperature, and in some cases also moisture, have a significant impact on embryonic development of snakes. High temperatures cause a number of alterations in development, which can cause elevated mortality rates in embryos and neonatal snakes (Idrisova and Khairutdinov, 2018; O'Donnell and Arnold, 2005) or affect vitality and fitness later in life (Lin *et al.,* 2005).

Viviparous and ovoviviparous species. In *Vipera aspis* (viviparous), high temperatures during summer caused faster embryonic development and early birth. Mean temperature in early stages of embryogenesis affected ventral scalation of neonatal snakes, with higher temperatures causing an increase in the number of ventral scales (Lourdais *et al.*, 2004). O'Donnell and Arnold (2005) found out that temperature affected sex ratio of stillborn offspring in the viviparous snake *Thamnophis elegans*. Higher temperatures caused more of the stillborn offspring to be male, which was probably caused by maladaptation induced by sexual selection. Preferred body temperature (PBT) in ovoviviparous neonates can be affected by temperature, which was not found in oviparous species. PBT was affected by incubation temperature in *Nerodia sipedon* (ovoviviparous) but not in *Elaphe obsoleta* (oviparous). The reason behind this difference might be the fact that females of *Nerodia sipedon* are able to alter the effects of ambient temperature on offspring development by thermoregulation, whereas eggs of *Elaphe obsoleta* are completely dependent upon the nest temperature (Blouin-Demers *et al*., 2000).

Oviparous species. Effects of climate change on oviparous species slightly differ from effects on viviparous or ovoviviparous species. According to Brown and Shine (2006), nest temperature and moisture affect mass of the eggs and phenotypic traits of hatchlings of *Tropidonophis mairii*. However, soil moisture had a more significant impact on phenotypes of the hatchlings than temperature. High temperatures reduce the incubation period length and hatched snakes are less developed and smaller (Idrisova and Khairutdinov, 2018; Lin *et al.,* 2005). The cause behind it might be higher basal metabolic demands caused by high-temperature incubation, which may reduce growth efficiency (Souchet *et al.*, 2021). Snakes incubated in high temperatures can also develop malformations like scale deviations (similar to those in viviparous snakes), kyphosis (tail curvature) or scoliosis (spine curvature) (Fig. 3). These malformations are often shared by siblings or mother and her offspring (Idrisova and

Khairutdinov, 2018). However, Burger (1998b) states that hatchlings of *Pituophis melanoleucus* incubated in high temperatures were more likely to survive in the wild than those from low temperatures. A study of *Natrix maura* incubated in high temperatures and hypoxia implies that even though chances of survival are lowered, majority of embryos were able to develop into viable snakes nevertheless (Souchet *et al.,* 2021). Females of viviparous snake species might be able to decrease the impact of high temperatures on embryos by choosing nest-sites with lower temperatures and higher moisture (Brown and Shine, 2006).

Figure 3 Malformations in hatchlings of *Natrix natrix* incubated in high temperatures: a - kyphosis; b - scoliosis; c - tail curvature; d - head deformation; e - microphthalmia; f - ventral scales deviations (green colour) in an individual with spine curvature; g - stripe pattern of an individual with spine curvature. Source - Idrisova and Khairutdinov (2018)

3.2 Growth

As mentioned above, climate change might alter embryonic growth in snakes. When it comes to embryonic growth changes, results mostly correspond across studies. That is not the case with growth after hatching. There is just a small number of studies and their results vary. Accelerated growth might negatively impact lifespan of snakes.

According to Pincheira-Donoso and Meiri (2013), temperature and precipitation do have an impact on snake growth, but only in some species they studied. Temperature and precipitation also seem to have opposite effects on snakes. Body size of some snakes increases with higher temperature (e.g. *Cerastes cerastes*), whereas with increasing precipitation, body size of some snakes decreases (e.g. *Natrix tesselata*) (Pincheira-Donoso and Meiri, 2013). However, climate change trends show raising temperatures and decreasing precipitation, which implies that species mentioned above should both experience an increase in growth rates. High temperatures also increase metabolic rates and lead to high energy expenditure (Michel and Bonnet, 2010), which might cause reduction in lifespan. Some studies found growth rates to be linked to food availability rather than climatic conditions (Madsen and Shine, 2000; Michel and Bonnet, 2010), which implies that some snakes might not experience any changes in growth associated directly to climate change. However, food availability might decrease under future climatic conditions, which could affect growth.

4. Effects of climate change on behaviour

Ambient temperature greatly affects behaviour of ectotherms. Their activity levels are linked to body temperature and body temperature is dependent on ambient temperature. Elevated temperatures can affect a wide range of behavioural traits in snakes, such as antipredatory and predatory behaviour, which are crucial for survival or diurnal activity and reproductive behaviour. Climate change and elevated temperatures that are associated with it will therefore most likely affect behaviour of many snake species.

4.1 Antipredatory behaviour

Antipredatory behaviour is an important behavioural trait, which allows organisms to avoid being killed by a predator. All animals that are exposed to predators need to recognize a threat and respond accordingly. Antipredatory behaviour is crucial for survival of individuals and elevated temperatures associated with climate change will most likely alter it.

Snakes seem to be most at risk of predation when their body temperatures are low (e.g. Brodie and Russell, 1999; Mori and Burghardt, 2001). Multiple studies observed that snakes tend to choose static responses at low temperatures and dynamic responses at higher temperatures to avoid a predator (e.g. Mori and Burghardt, 2001; Schieffelin and Queiroz, 2017). Snakes at higher temperatures generally seem to be more aggressive (Burger, 1998a; Schieffelin and Queiroz, 2017) but also choose to flee from a predator rather than use crypsis. Higher temperatures allow snakes to move faster, which is most likely the reason why snakes preferred dynamic responses when exposed to higher temperatures (Brodie and Russell, 1999; Mori and Burghardt, 2001). Incubation temperature plays a role in antipredatory behaviour as well. Hatchlings incubated at higher temperatures respond faster and more defensively than snakes incubated at low temperatures (Burger, 1998a; 1998b). Size of an individual also affects antipredatory behaviour. Increased temperatures can increase growth in snakes (Pincheira-Donoso and Meiri, 2013) and larger snake species tend to be more aggressive towards predators. Crypsis is, on the other hand, more effective for smaller individuals because they are harder to detect. Crypsis also requires less energy, but snakes might need to use a risky behaviour such as biting when detected in order to protect themselves (Delaney, 2019). Larger individuals of *Haldea striatula* were for instance found to have more scarring than smaller individuals, which indicates that increased body size increases a risk of predation (Taylor and Cox, 2019).

In conclusion, elevated temperatures associated with climate change might cause snakes to be more aggressive towards predators and use more dynamic responses to predation in general. Therefore, increased temperatures might increase survival, because they allow snakes to escape faster and use a wider range of antipredatory responses. However, increased body size caused by increased temperatures might cause snakes to be more at risk by predation and decrease chances of survival.

4.2 Predatory behaviour

The frequency and speed at which snakes hunt for food is most likely dependent on ambient temperature. Increased temperatures might affect locomotion and the ways snakes hunt and therefore alter their chances of survival.

Snakes usually tend to hunt more at higher temperatures (e.g. Santos *et al.*, 2007; Capula *et al.*, 2016). However, a study of *Crotalus oreganus* in California (Putman and Clark, 2017) came to a different result. Individuals of this species spent less time hunting with increasing temperatures. Studied individuals preferred to hunt at lower temperatures (16 - 31 ˚C) and usually retreated to shelter before their body temperature reached 31 ˚C. These findings indicate that elevated temperatures associated with climate change might limit the time this species spends on hunting. Putman and Clark (2017) also imply that increased temperatures might force the species to hunt during the night rather than during the day or earlier or later in the season when daily temperatures drop.

Ambient temperatures affect predatory behaviour in both amphibious and terrestrial snake species. Higher temperatures increase swimming speed in amphibious snakes but decrease apnoea (suspension of breathing) time. Therefore, active foraging might be advantageous in warmer waters, but decrease in apnoea time might decrease capture success rate due to the higher frequency of swimming to the surface to take a breath (Aubret *et al.*, 2015). Some snakes might additionally hunt more frequently in arboreal environments with increased temperatures (Cox *et al.*, 2013; Gerald *et al.*, 2008), because increased temperatures cause snakes to fall less frequently (Gerald *et al.,* 2008).

Prey diversity might also be affected by temperature alterations. Snakes are gape-limited predators and increased body size induced by climate change might allow them to prey on a wider spectrum of prey. The findings of Santos *et al.* (2007) imply that larger individuals of *Vipera latastei* fed on larger and different species of prey (mammals and birds) than smaller individuals (centipedes and lizards). Additionally, Capula *et al.* (2016) found out that higher annual temperatures increase prey diversity of *Hierophis viridiflavus*. This might be caused by increased foraging activity, which allows snakes to encounter a wider spectrum of potential prey species. Higher temperatures also caused snakes to feed more, which agrees with the findings of other studies, such as those of Santos *et al.* (2007). However, Capula *et al.* (2016) also found links between rainfall and hunting. During heavy rainfall the number of fed snakes decreased.

Higher temperatures seem to be in favour of most species; however, it is obvious that some species such as *Crotalus oreganus* might need to alter their hunting methods to survive under future climatic conditions. For many species, climate change might bring benefits in the form of more frequent feedings or a wider variety of prey.

4.3 Activity

Activity period and locomotion is dependent on ambient temperatures in snakes (e.g. Moreno-Rueda *et al.*, 2009). Generally, the activity period of snakes increases with increasing temperatures (e.g. Moreno-Rueda and Pleguezuelos, 2007; Capula *et al.*, 2014). Snakes from temperate regions might especially benefit from climate warming by extending their activity period (Moreno-Rueda *et al.,* 2009).

Although increased daily activity has its benefits, it also has its downsides. Not only does increased activity elevate metabolic rates (Dupoué *et al.*, 2017), but also causes more snakes to be killed on the road (Capula *et al.,* 2014). The findings of Capula *et al.* (2014) indicate that the number of individuals of *Hierophis viridiflavus* killed on the road was negatively influenced by temperature during summer (less killed snakes), but positively influenced in spring and winter (more killed snakes, Fig. 4). This indicates a delayed hibernation and early emergence from hibernation caused by increased temperatures. However, higher temperatures and dry air can also cause snakes to urinate more during hibernation and force them to search for water due to dehydration (Lutterschmidt *et al.*, 2006). Snakes might avoid dehydration during hibernation by submerging in water (Costanzo, 1989).

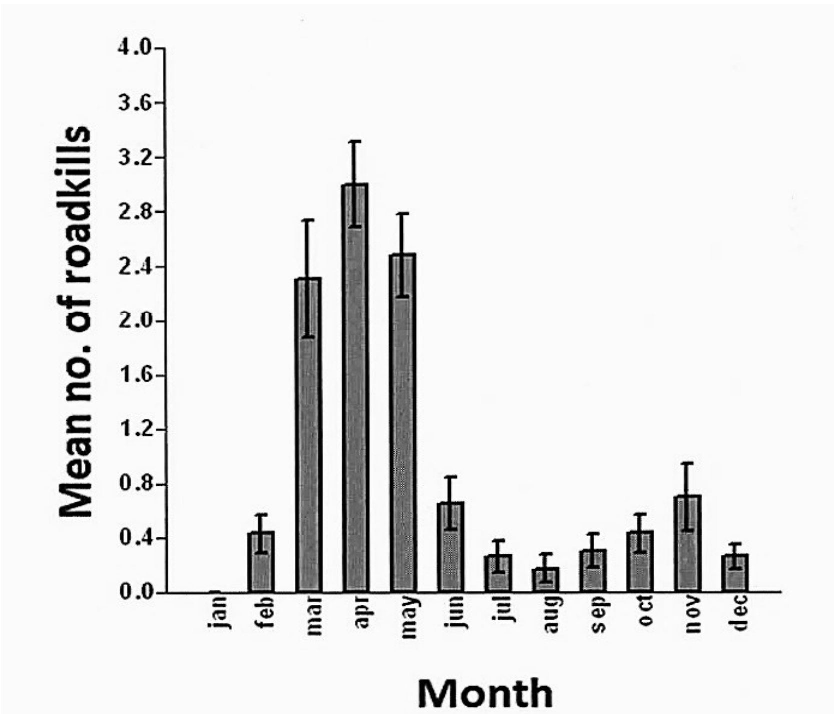

Figure 4 Mean number of individuals of *Hierophis viridiflavus* killed on the road. Source - Capula *et al.* (2014)

Semi-arboreal snakes will most likely benefit from increased temperatures, as they tend to fall less from branches and move faster at higher temperatures. This will allow them to climb and bask in vegetation more frequently (Gerald *et al.,* 2008). Nevertheless, increased daily activity as a response to elevated temperatures does not apply to all snakes. Some aquatic snakes, such as *Nerodia cyclopion*, are most active during the cooler months in order to gain heat and are mostly aquatic and nocturnal during the hottest months to escape the heat (Mushinsky *et al.,* 1980). These findings indicate that species like *Nerodia cyclopion* might become less active during the cooler months in the future under elevated temperatures.

4.4 Reproductive behaviour

The number of studies dealing with the links between temperature and reproductive behaviour of snakes is very low. It is therefore impossible to deduce a general conclusion. However, it has been observed that reproductive behaviour of some species is indeed temperature-dependent (Hawley, 1975; Lutterschmidt and Mason, 2009). It has been proved that elevated hibernation temperatures delay onset of mating behaviour in males of *Thamnophis sirtalis parietalis* (Lutterschmidt and Mason, 2009). Ambient temperatures after hibernation also affect sexual activity in *Thamnophis sirtalis parietalis.* Generally, the higher the temperature, the higher the number of sexually active snakes. Additionally, mating behaviour was more influenced by temperature than other types of behaviour such as antipredatory behaviour (Hawley, 1975). In intertropical regions with a dry season, females reproduce during the rainy season and a longer rainy season means a longer mating season (Girons, 1982), which might indicate that decreased precipitation might shorten mating periods of some species.

5. Comparison with other ectothermic vertebrates (excluding fish)

In this chapter, I am comparing the impacts of climate change on snakes with impacts on other ectothermic vertebrates. I would like to find out whether snakes evince any effects that are not found in other ectotherms and whether they are more vulnerable to changing climatic conditions than other taxa. Generally, thermoregulation and above-ground activity of ectothermic vertebrates is dependent on shade (Kearney *et al.,* 2009). This might be especially troubling in regions where vegetation cover is insufficient, such as north Africa, or conversely in regions where there is way too much vegetation cover, such as Europe (Fig. 5).

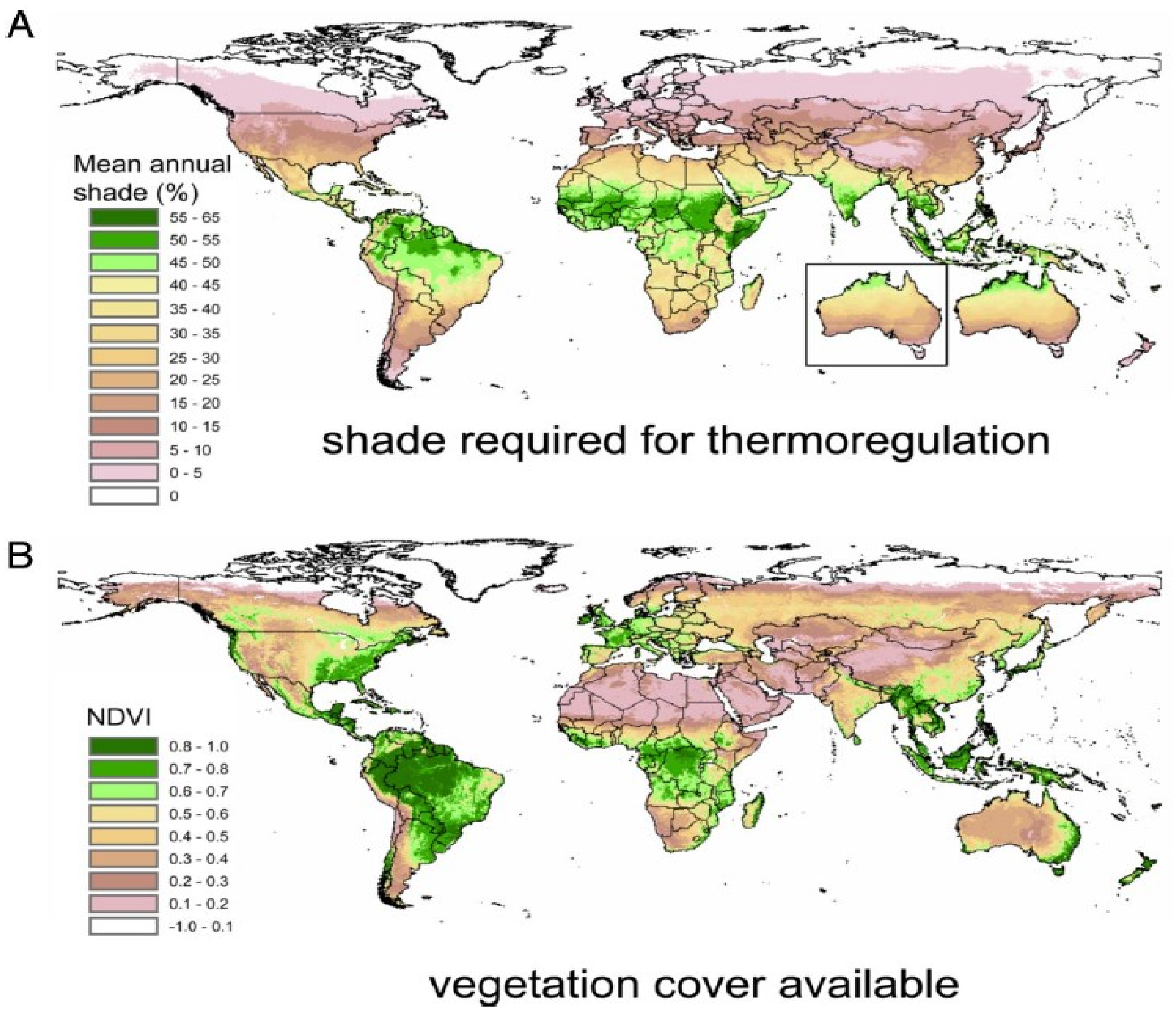

Figure 5 A - Global shade requirements of a small terrestrial ectotherm thermoregulating between core body temperature of 20 and 40 ˚C, targeting a temperature of 33 ˚C; B- mean annual vegetation cover available, represented by the normalized difference vegetation index (NDVI). Source - Kearney *et al.* (2009)

5.1 Reptiles

Lizards. Snakes are generally less threatened than lizards (Böhm et al., 2013), however, effects of climate change on snakes are very similar to those on lizards. Species of the northern hemisphere such as *Zootoca vivipara* are, similarly to snakes, expected to shift ranges northwards under future climatic scenarios. By the end of the century, this species is also predicted to move into higher elevations (Feldmeier *et al.,* 2020). There is insufficient data on fossorial snake species, but a study of two North American fossorial lizards (Lara-res *et al*., 2021) shows that fossorial species might be at a high risk under future climatic conditions.

Both fossorial species in this study are predicted to lose suitable habitat and mobility limitations restrict them from seeking new suitable areas in the future. This study also implies, that *Anniella geronimensis* might be threatened by raising sea level due to its low elevation habitat. Although there is not enough data on fossorial snake species, we could expect fossorial snakes to be in a similar situation since climate change affects snakes and lizards similarly. Growth rates were proved to increase in the lizard *Tropidurus torquatus*. However, increased growth rates were also proved to reduce the number of reproductive years in this lizard, which I was not able to prove in snakes. This tropical lizard is also predicted to reduce its activity (Piantoni *et al*., 2019). Conversely, an Australian crepuscular lizard is predicted to increase its activity and extend its active season (summer) (Moore *et al.*, 2018).

Turtles. Turtles seem to react a bit differently to climatic changes compared to snakes. Sea turtles, like *Chelonia mydas*, are (contrary to snakes) most likely directly more influenced by food availability than ambient temperatures. This means that if temperatures increase and food availability does not change, neither will growth, reproduction and egg quality (Stubbs *et al.,* 2020). However, if temperatures exceed thermal limits, turtles can move into cooler waters, as found in *Macrochelys temminckii* (Fitzgerald and Nelson, 2011). This behaviour was also found in a sea snake, which indicates that other sea snake species might be able to escape heat by moving into cooler waters as well. Even though some turtles have the ability to escape heat by moving, some turtles will probably lose suitable habitat, nevertheless. *Glyptemis insculpta*, a North American species, is predicted to lose habitat in the southern part of its range and the southern populations will most likely need to shift northwards into more suitable habitats (Mothes *et al.*, 2020). This pattern is similar to the patterns seen in snakes.

Crocodiles. Snakes generally seem to be more vulnerable to climate change than crocodiles. Rodgers and Franklin (2021) imply that aerobically fuelled activities of *Crocodylus porosus* will likely not be restricted by climate, however, growth and antipredatory behaviour might be if thermoregulation is not used. Similarly to snakes, crocodiles kept at higher temperatures eat more and have an increased metabolic rate. However, crocodiles kept constantly at the temperature of 25 ˚C became shorter (Kanui *et al.,* 1991), which was not found in snakes. Cooper-preston (1989) also found out that higher temperature shortens the incubation period and causes deformities in embryos with high mortality rates. Deformities and elevated mortality linked to high temperatures were found in snakes as well (e.g. Idrisova and Khairutdinov, 2018).

5.2 Amphibians

Generally, aquatic habitats provide greater opportunity for ectotherms to behaviourally thermoregulate than terrestrial habitats (Rodgers and Franklin, 2021). However, Böhm *et al*. (2013) state, that amphibians (42% threatened) are generally more threatened than reptiles (20% threatened). This implies that further pressure from climatic conditions might cause even more amphibians to become endangered. Increased temperatures will most likely restrict activity of amphibians (Lertzman-lepofsky *et al.,* 2020; Rohr *et al.,* 2013), especially during critical periods for migration and breeding (Lertzman-lepofsky *et al.,* 2020). Furthermore, decreased water levels in breeding ponds cause reproductive failure and severe reduction of population size (Araújo *et al.,* 2006). Increasing temperatures and reduction in precipitation might therefore drive many amphibian species to extinction. Snake species are not dependent on water to breed successfully, which makes them less vulnerable to climate change compared to amphibians. According to Araújo *et al.* (2006), amphibians are also less likely to disperse than other ectotherms. However, Tiberti *et al.* (2021) found out that two amphibian species (*Bufo bufo* and *Triturus carnifex*) have shifted ranges into higher elevations over the past 15 years in association with climate change. Feldmeier *et al.* (2020) came to similar results when projecting future response of *Salamandra atra* to climate change. This species is predicted to shift into higher elevations, but also northwards under future climatic conditions. This indicates that colonization by amphibians is indeed possible when colonizable habitats are available.

In comparison to other ectothermic vertebrates, responses of snakes to climate change are the closest to those of lizards. Both taxa seem to be affected and respond in similar ways. This indicates that we might be able to predict effects of climate change on some snake species that are data deficient (especially fossorial snake species - Böhm *et al.,* 2013) by looking into effects on fossorial lizards species. It is important to note, that some reptile species have temperature-dependent sex determination (TSD), which was not found in snakes. This implies that those species might be more vulnerable to increased temperature than others.

Overall, snakes do not evince any traits that cannot be found in other ectothermic vertebrates. After comparing snakes to other ectotherms, we can tell that snakes are amongst the more vulnerable, but not the most vulnerable of ectotherms. Amphibians and their high dependency on water most likely makes them the most vulnerable to climate change of the ectothermic taxa. However, snakes are usually hard to sample and sample sizes are therefore low, which might cause biases when comparing snakes to species that are easier to sample (Böhm *et al.*, 2013).

6. Conclusion

Snake species are indeed under a threat by changing climatic conditions. 12% of snakes are currently threatened with extinction (Böhm *et al.,* 2013) and climate change will most likely cause more snake species to become endangered or, as an ultimate consequence, drive species to extinction.

Distribution of snake species will greatly change by the end of the 21st century. Both temperature and precipitation are important drivers of snake species range shifts. To escape the raising temperatures associated with climate change, many species will have to move into more suitable areas to survive. The pattern of poleward range shifts as well as the pattern of shifts into higher elevations were proved to be true. Species from temperate regions, such as North America and Europe, will most likely gain the most and lose the least of their current range under future climatic conditions compared to species from other climate zones. This is because the areas that are currently too cold will become suitable under future climatic conditions and snakes will be able to move into those areas.

Conversely, species from hot regions will lose a lot, in some cases even all, of their current suitable habitat. This applies for example to snakes in Australia, Africa, and South America. Asian snake species have not been thoroughly studied, but it seems like they are mostly going to gain suitable habitat under future climatic conditions. In regions like Africa and South America, shifts in distribution of snake species will put more people at risk of snakebite. Areas where snakes are not found today might become suitable habitats for snakes in the future, which could be a problem as people in those areas are not used to or adequately prepared for snakebites.

There is not enough data to make a general conclusion about distribution of sea snakes, but based on the findings of Dunson and Ehlert (1971), I assume that other sea snake species will be able to thermoregulate by diving into cooler waters as well.

Climate change will greatly impact health of snakes, especially in oviparous species. Females of viviparous and ovoviviparous species are to a certain level able to control the temperature of their offspring by thermoregulating behaviourally. Although eggs of oviparous species depend on the nest temperature, females might be able to abate the impacts of high temperatures by choosing cooler nest-sites with higher moisture. High temperatures cause a decrease in incubation period length and elevated mortality of embryos. The embryos that survive are often born smaller and with malformations that greatly decrease life quality and fitness. When it comes to growth after hatching, results of studies vary. I think it is safe to say that temperature and precipitation does affect growth in some species. Those species whose growth is affected by temperature and precipitation tend to grow faster under higher temperatures and decreased precipitation. To summarize it, climate change will most likely have a very negative impact on health of snake species if they do not somehow manage to adapt in time.

Increased temperatures have generally a very positive impact on snake behaviour and activity. Antipredatory behaviour of snakes significantly changes from static to more dynamic when exposed to higher temperatures. This means that snakes might be able to escape predators more successfully under future climate change. However, if growth rates of snakes increase under future climatic conditions, it might cause snakes to be more at risk of predation, because larger individuals were proved to be more predated.

Snakes also tend to spend more time hunting at higher temperatures; however, some species prefer to hunt at lower temperatures. Those species (such as *Crotalus oreganus*) will most likely need to alter their predatory strategies under future climatic conditions, like hunt during the day or later or sooner during the season. For amphibian snake species, elevated temperatures mean faster swimming but also decreased apnoea time, which causes more frequent swimming to the surface to take a breath. This could lead to less successful hunting, because the prey is more likely to notice the snake. However, prey variability and feeding frequency will most likely increase in association with elevated levels of foraging activity under future climatic conditions.

At higher temperatures, snakes generally spend more time being active. Increased activity in association with higher temperatures also mean delayed hibernation and early emergency from it. This however also means more roadkills during spring and winter.

Reproductive behaviour is affected by climatic variables in some species, however, there is not enough data to make any general conclusion. Temperature can delay onset of reproductive behaviour, the number of sexually active individuals, and in regions with dry seasons, reduced precipitation can shorten the mating period.

Compared to other ectothermic vertebrates, snakes are affected similarly to lizards by climate change. We might be able to estimate effects of climate change on data-deficient snake species by what we know about lizards. Snakes (and reptiles in general) are less vulnerable to climate change than amphibians, whose breeding and many other activities are strictly water dependent. Finally, I did not find any effect of climate change on snakes that cannot be found in other ectotherms.

Even though snakes are not the most vulnerable of ectotherms, steps towards their conservation should be made. Snakes will benefit from climate change in the form of increased activity and some species will also gain new suitable habitat. However, many snake species are not able to disperse on their own and many protected areas are not efficient or will become inefficient under future climatic conditions. According to Cabrelli *et al*. (2014), only highly endangered species have benefited from practical conservation programmes, which is alarming and a change needs to be made. Many snake species will lose suitable habitat and experience health issues. There is also a very low data availability on fossorial and sea snake species, which should be brought to attention. Conservation of snakes has been overlooked compared to more charismatic taxa such as mammals or even sea turtles. This needs to change or we will lose many snake species to extinction under future climate. I believe that we also need to educate the general public on the importance of snakes in ecosystems in order to stop them from killing snakes and help us conserve them.

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