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Effects of Climate Change on the Breeding Phenology of Newts

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"On climate change, we often don't fully appreciate that it is a problem. We think it is a problem waiting to happen"

Kofi Annan

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Abstract

Phenological advancements have been documented in a variety of taxa in response to climate change. Amphibians have mostly been studied in the northern hemisphere with the majority of responses suggesting an advancement in breeding dates in line with increasingly warmer spring temperatures. This study looked at various aspects of the breeding phenology of palmate, smooth and great crested newts at two neighbouring metapopulations in Canterbury, Kent, UK over a period of 20 years. Median date (seasonality), duration of aquatic period and individual body condition were analysed to identify any changes over time and then again to identify any relationships with climatic factors. The responses varied between pond and species: great crested newts showed a delay in median capture date and a lengthening in duration of aquatic period at two out of five ponds, plus an increase in body condition; palmate newts showed a delay in median capture and lengthening of duration at one pond; and smooth newts showed a lengthening in duration at two of the five ponds. There does appear to be a relationship with climate, but as the changes in phenology were not observed at all ponds within the same local climatic region, it suggests that the effects of climate change may be indirect, and local conditions may compensate or override any potential climate-related effects. This study is the first to document delayed breeding activity in great crested and palmate newts, and the first for urodeles in Europe. These contrasting results show that amphibians are responding to environmental changes at a population level and therefore climate change mitigation measures may need to be population-specific.

Key words: great crested newt; climate change; metapopulation; phenology

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CHAPTER ONE: General Introduction

Global Climate Change

Since pre-industrialisation, humans have been increasing the quantities of carbon dioxide in the atmosphere, creating a greenhouse effect on the planet (IPCC, 2014). As emissions continue to increase, global temperature has followed suit, with sea and land surface temperatures having risen more in the last 30 years than in any other time period since 1850 (IPCC, 2014). Since 1900 the mean global surface temperature of the earth has increased by 0.4 - 0.8°C (Gitay et al., 2002; Lovejoy and Hannah 2005). This change has not been consistent and periods of intense warming have been noted between 1910 and 1940 and later from 1970 to the present day. Warming during these two periods is recorded at 0.1°C per decade, with a greater proportion of this warming occurring over land masses, particularly the inner regions of America and Europe (Lovejoy and Hannah, 2005). The warmest year on record for global surface temperatures was 2016; temperatures were an average of 0.77 +/- 1°C greater than those recorded prior to industrialisation. Along with 2015, these two years are the warmest on record since 1850 (Met Office, 2017).

From the 1950s onwards, it has been observed that daily night time minimum temperatures are increasing at a greater rate than those during the day; 0.2°C per decade compared to 0.1°C (Gitay et al. 2002; Lovejoy and Hannah, 2005). This discrepancy between temperatures has resulted in a shortening of frost periods and their frequency (Lovejoy and Hannah, 2005) and a decline in sea ice extent and glacier mass, which has consequently increased sea level by 0.91 m between the years 1901 and 2010 (IPCC, 2014). Daily minimum temperature extremes have thus decreased in frequency, more so than daily maximum temperature extremes have increased (Lovejoy and Hannah, 2005).

Precipitation has been found to show weaker trends than temperature, though this is partly due to equipment; instruments are generally inferior compared to those used to measure temperature and there is an inability to obtain quality measurements over water bodies. Reliable data only span the last 100 years, however it does show strong latitudinal variation in precipitation levels. Subtropical bands show a decrease in rainfall by up to 30% whereas latitudes above 45 degrees show a yearly increase of 5-10% rain (Gitay et al., 2002), effective in the form of more winter precipitation and less during the summer (Lovejoy and Hannah, 2005).

Future precipitation patterns are likely to vary depending on latitude and biome (IPCC, 2014). Using climate modelling, the IPCC (IPCC, 2014) found that in every potential scenario of climate change severity, temperatures and extreme weather events, particularly heat waves and heavy precipitation, will continue to rise or increase in frequency and duration during the rest of this century and onwards. Periods of extreme cold temperatures, on the other hand, are forecast to decrease at both a daily and seasonal scale (IPCC, 2014).

The Northern Atlantic Oscillation (NAO) refers to large scale changes in pressure over the North Atlantic; low pressure typically exists in the north (Iceland) and high pressure in the south (Azores), and the oscillation refers to fluctuations in pressure between these two areas. Changes in the pressure has an impact on weather and climate systems of the surrounding continents (Met Office, 2016a, b), particularly air temperature and precipitation patterns in Northern Europe (Otterson et al., 2001). The effects of the NAO are strongest during winter and can determine the strength and frequency of storms. A negative NAO phase sees cold and dry winters whilst a positive NAO phase brings mild, wet and windy winters. Since the 1970s the NAO has displayed a multi-decade tendency towards positive phases, explaining the wet and mild winters we have seen in recent years (Lovejoy and Hannah, 2005).

As well as assessing global changes in climate, regional differences in climate are much more variable and can be hidden under global figures (Lovejoy and Hannah, 2005). Global air surface temperature refers to 1.5 m from the surface of both land and oceans. Oceans cover two thirds of the planet, and although oceanic temperatures are predicted to experience greater changes in temperature, land warms faster than oceans in general. Factors such as these need to be taken into account when using global mean surface temperature as regional changes are likely to be underestimated (Lovejoy and Hannah, 2005).

In terms of extreme weather events, assessing any change is difficult as records are limited, so it is not possible to determine certainty and causality on a global scale. However, it has been noted that certain events, such as hurricanes, occurred at greater than average frequency in North America in the 1990s. Changes in daily temperature extremes have been noted worldwide, with a reduction in daily minima and an increase in daily maxima (Frich et al., 2002). It is likely that heatwaves have increased in Asia, Australia and Europe, with the probability of occurrence doubling in some regions due to human impacts. It is also likely that in North America and Europe heavy precipitation events have increased in frequency and intensity in the last 50 years, again as a result of anthropogenic forcing (IPCC, 2014).

Climate Change in the UK

In Europe, extreme high temperatures have become more frequent whilst cold ones less so since 1950. Average temperatures in the UK have risen by 1 °C in the last century and half of this increase has occurred since 1970 (Gov UK, 2014). National records document that since 1766 rainfall in England and Wales has decreased during the summer months yet increased in winter (Alexander and Jones, 2001).

In all predictive models, the strongest warming is predicted to occur in southern Europe during summer and northern Europe during winter. Similarly, rainfall is likely to decrease in southern Europe and increase in the north. As suggested above, in Europe there is a projected increase in extreme weather, such as droughts, heat waves and heavy precipitation (Kovats et al., 2014).

Models predict that temperatures in the UK will rise over 2 °C by 2040 and potentially an additional 2 °C by 2080. As a result, the UK Environment Agency believe that the UK is to expect an increase in flooding events through a rise in winter rainfall of up to 40% (Environment Agency, 2009), a higher frequency and intensity of heatwaves and higher sea levels, especially during storm events (Gov UK, 2014).

Effects of Climate Change on Biodiversity

Natural fluctuations in climate are known to have caused significant changes to ecosystems including complete shifts and species extinctions millions of years ago. Given that natural climate change occurs at a rate much slower than the currently observed anthropogenic climate change, it is thus irrefutable that such changes are likely to occur and on a larger scale in the present and foreseeable future (IPCC, 2014). The variability of the climate, i.e. changes in extreme weather events, has been found to have a much greater impact on biodiversity than average annual climate (Lovejoy and Hannah, 2005). Should warming continue to occur and to an increasing extent, such changes to species and ecosystems are likely to be irreversible (IPCC, 2014).

In order to survive a shifting environment in the face of climate change, species need to either adapt to the new climatic conditions forced upon their current habitat through genetic adaptation or phenotypic plasticity, move to find a suitable niche or face extinction (Coope, 2004; Fuller et al., 2010). It has already been observed that the impacts of climate change on biodiversity are diverse, both direct and indirect, and may affect habitats (vegetation, soil, hydrology), food availability, predator-prey relationships, community structure, pathogen-host dynamics, survival, growth, reproduction and dispersal (Blaustein et al., 2010). Of the impacts already observed, it is thought that ectothermic vertebrates are more sensitive to changes in the climate than endotherms (Aragón et al., 2010). The following have been identified as occurring at an increasing rate due to climate change: habitat loss (through fire, drought, rising sea levels, acidification, melting), range shifts (typically poleward in latitude and increasing in elevation), changes and mismatches in phenology (affecting trophic webs), ecosystem change, disease and invasive species (as a result of range shifts or increase in climatic optima) and coral bleaching. If climate change continues at the current rate many species face a great risk of extinction (IPCC, 2014).

Impacts of climate change have been detected in a broad spectrum of taxa, from terrestrial to marine to freshwater to migratory, showcasing that climate change is a global issue. As there has been such a wide range of documented responses, only those relevant to this study are discussed in further detail below.

Range Shifts and Habitat Loss

Some species will thrive in the changing environment and as a result their ranges will expand, but others are set to lose range as the climate reduces their ability to disperse (Araújo et al., 2006). Historical records exist for many species, particularly birds and invertebrates, allowing for detailed studies into range shifts over time. Climate-mediated shifts in range, poleward or altitudinal, of up to 240 km have been documented in dragonflies, butterflies, birds, mammals, amphibians, lichens, alpine plants and tree lines in a variety of countries (Hannah, 2011).

Barriers, either physical or geographical, are limiting factors in the ability of some species to adjust their range into suitable climate, and as a result are experiencing a loss of habitat through climate change (Parmesan, 2006; Parmesan et al., 1999). Thomas et al (2004) estimated that up to 37% of species assessed (approximately one million species (Hannah, 2012)) face extinction due to climate-mediated range restrictions.

In some instances, the historic ranges and natural history of a species is so well understood as to identify a lag in range shifts and consequently, be able to respond with assisted colonisation using species-climate models. A successful recolonization and range expansion from both the marbled white (*Melanargia galathea*) and small skipper (*Thymelicus sylvestris*) demonstrate that novel conservation measures can be effective alongside climate change. However, in order to enact such models and measures it is vital to have an understanding of a species' habitat requirements and natural response (Willis et al., 2009).

Ecosystem Change

The projected effects of climate change to European ecosystems are vast: river habitats are expected to become increasingly fragmented; breeding bird habitat is looking to shift almost 550 km to the northeast; montane plants have shown shifts to higher latitudes; it is expected that species diversity is likely to trend towards homogenisation as species diversification is not likely to occur within the same rapid timescale; range contraction is noted in several species of pine while range expansion is predicted for other species (such as holm oak in the Mediterranean); birds have shown declines, range shifts and changes in phenology; mammals and herpetofauna are predicted to be at risk of extinction should there be a lack of sufficient migration, changes in phenology or trophic mismatches; and all of these threats are also replicated in marine habitats (Kovats et al., 2014). Aquatic organisms are just as subject to climate effects; since 1850 there have been widespread changes in species and reorganisations in community structure of algae and invertebrates in Arctic lakes (Smol et al., 2005) while variations in sea temperature due to NAO have been linked to fluctuations in cod recruitment in the North Atlantic (Stenseth et al., 2002).

Invasive Species

The effects of climate change can be indirect; the range of the keel-billed toucan (*Ramphastos sulfuratus*) is increasing in altitude as a result of a changing climate. This is having a negative impact on the quetzal (*Pharomachrus*) a prey species for the toucan. As the toucans move upslope the predation pressure on quetzals increases, forcing the quetzal population to recede even further upslope, reducing their range and impacting on population numbers (Hannah, 2011).

In aquatic systems, effects of climate change on invasive species could be mixed. Coldwater species are likely to perish in increasingly warmer conditions yet these same conditions are likely to provide an optimum environment for the dispersal and survival of other species which would otherwise be killed off during colder periods. Pathways of dispersal may also be affected by a decrease in ice-cover longevity, changes in stream patterns and by human-induced modifications to waterways and land use (Rahel and Olden, 2008).

Disease and Extinction

Bosch et al. (2007) found that rising temperatures in Spain are significantly linked to occurrences of chytridiomycosis. This fungus is also connected to the climate-driven extinction of amphibians in Latin America. First the golden toad (*Incilius periglenes*) disappeared in 1987 and since then 74 species of *Atelopus* have also gone extinct. Most of the species were last seen prior to years of unusually high temperatures, which creates thermal optimums for fungal growth (Hannah, 2011), however there is debate as to whether or not climate change was the driving force behind the decline (Pounds et al., 2006; Rohr et al., 2008). Nevertheless, up to 200 species of frog have since declined or become extinct as a result of the chytrid fungus (Skerratt et al., 2007), making it a real threat indeed.

Growth, Survival and Reproduction

Warmer waters may result in increased growth rates and earlier maturation of aquatic invertebrates (Poff et al., 2002) whilst a population of great crested newts (*Triturus cristatus*) was found to have a lower survival rate due to warmer winter temperatures and higher rainfall outside of the aquatic phase (Griffiths et al., 2010). On the other hand, Benard (2015) found that precipitation during winter was positively associated with female fecundity in the wood frog (*Rana sylvatica*).

Galloy and Denoel (2010) carried out a lab study on palmate newts (*Lissotriton helveticus*) in France and found that female fecundity was negatively impacted by higher water temperatures. As male courtship is reliant on female responsiveness, which is also temperature dependent (Galloy et al., 2008), these studies suggest a potential outcome of changes in population dynamics, recruitment and size. Gibbs and Karraker (2006) found that warming temperatures even affect the morphology of a salamander species, the red-backed salamander (*Plethodon cinereus*), in North America; the frequency of striped morphs decreased over time in line with an increase in ambient temperature.

Mismatches in Phenology

Mismatches occur when established relationships between species become asynchronous due to changes in the phenology of one species but not necessarily the other, or when shifts occur at different rates. Phenological alterations are usually due to changes in temperature or other climatic factors. Due to a 1.4 °C rise in temperature in the Rocky Mountains in the late 20th century, yellow-bellied marmots (*Marmota flaviventris*) emerged from hibernation 23 days earlier but this did not coincide with snow melt and plant flowering, which is a key food source (Inouye et al., 2000). Mismatches have been documented in freshwater lake populations of phytoplankton blooms and zooplankton (Winder and Schindler, 2004) and in the relationship between oak bud burst, caterpillar emergence and great tit (*Parus major*) egg laying date (Visser et al., 2006). Some species may be adapting sufficiently; the orange tip butterfly (*Anthocharis cardamines*) has successfully managed to maintain a matched phenology with its host plants (Brassicaceae), despite the plants budding up to three weeks early (Sparks and Yates, 1997). It is unclear however, as to whether or not these adaptations will be able to keep pace with the continuing rate of climate change (Walls et al., 2013).

Changes in phenology could even alter population dynamics and sex ratios. Van Nouhuys & Lei (2004) found that in a butterfly species, the Glanville fritillary (*Meliaea cinxia*), males emerge before females. With warmer temperatures, the host parasitoid wasp is emerging earlier and more in synchrony with the male butterflies, thus potentially altering the sex ratio.

Phenological Changes

As well as shrinking or expanding in range, some species also appear to be altering their population dynamics. Long-term monitoring and data sets have allowed for analysis with climatic variables to look for any changes over time outside of natural population fluctuations. In recent decades, studies have focussed on a variety of taxa, mainly from the USA, Canada, Europe and Japan (Ficetola and Maiorano, 2016) and some surprising trends in phenology have emerged.

Although there seems to be strong evidence for correlations between breeding phenology and climatic factors, examples of asynchrony among species at the same location suggests that temperature and rainfall alone are not the sole influences on reproductive timing in amphibians (Vitt and Caldwell, 2013). Forecasts of responses to climate change often assume that species will respond homogeneously across their ranges (Smith et al., 2017). It is important to note that reproductive biology varies between species so each is likely to respond uniquely to changes in the climate and that such changes may therefore also affect community structure (Beebee, 2002). As the effects of climate change will vary depending on location, latitude, altitude and ecosystem, it may not be evident at all sites that have been the focus of such studies. Given that climate change is an ongoing process, species that have been found to show non-statistically significant trends towards changes in breeding date may indeed become significant in the future if trends continue (Beebee 2002).

Precipitation and Temperature

Precipitation has been found to have little or no effect on the breeding phenology of amphibians (Beebee 1995; Arnfield et al. 2012), however, given that newts only emerge to migrate during suitably damp periods, this could be suggested to be evidence for a link between precipitation and breeding phenology, although the association may be complex. Precipitation does appear to have a link with survival and population dynamics (Ficetola and Maiorano, 2016; Griffiths et al., 2010) as outlined above in Growth, Survival and Reproduction.

Air temperature seems to be the most influential factor with regards to changes in phenology in populations (Ficetola and Maiorano, 2016); studies cover a wide range of taxa showing significant correlations, typically, though not exclusively, between warming temperatures and phenological advancement. The first date of appearance in butterflies has advanced in the UK, Spain and the USA with warmer temperatures explaining the majority of this observed change (Forister and Shapiro, 2003; Roy and Sparks, 2000; Stefanescu et al., 2003).

Cherry blossoms in Japan are perhaps one of the longest studies into phenology. With records dating back to 1400, blooming has become significantly earlier since 1900, after the start of industrialisation and thus intensive fossil fuel use (Parmesan 2006; Hannah 2011). The grape harvest in Europe has also advanced and to coincide with this is a lengthening of the growing season of up to 4.9 days per decade in the northern hemisphere (Menzel et al., 2003). In the USA, lilac and honeysuckle have shown advances in first flowering by up to 3.8 days per decade (Cayan et al., 2001).

A vast array of bird species have been found to be breeding and laying eggs up to nine days earlier in response to warmer spring temperatures; dippers, blue tit, great tit, tree swallows, Canada geese, snow geese, Mexican jays, nuthatch and reed warblers (Dunn and Winkler, 1999; Goodenough et al., 2010; McCleery and Perrins, 1998; Sæther et al., 2000). Bird migration dates are also affected; in the USA various studies have found that many bird species are arriving later in spring and in Europe autumn migrations are starting later (Bezzel and Jetz, 1995; Bradley et al., 1999; Gatter, 1992; Oglesby and Smith, 1995). Further south, penguins are suffering due to reductions in ice cover, sooty shearwaters have shown a 90% decline in abundance (Veit et al., 1997, 1996; Hannah, 2011) and are also altering their migration routes in accordance with changing sea temperature (Spear and Ainley, 1999).

Although there appears to be a trend towards phenological advancement, it is clear that not all taxa are responding to changes in temperature to the same extent. Ge et al. (2015) analysed data for 112 species of a variety of taxa in China and found that of the significant advancements in phenology, the greatest changes were in herbs and amphibians compared to trees, shrubs and insects. Amphibians have shown an advancement of 6.11 days per decade since 1980. Those species showing significantly earlier spring/summer phenology were found in sites experiencing stronger trends in increasing temperatures.

Amphibians

The most widely documented response to climate change in amphibians is a change in phenology (Table 1). Although there have been some observed changes in fecundity and survival in both larvae and adults (Benard, 2015; Denoël et al., 2005; Galloy and Denoël, 2010; Griffiths et al., 2010), these findings will not be discussed in detail (see Precipitation above).

***Table 1**: A summary of research documenting changes in amphibian phenology, building on that produced by Beebee and Griffiths (2005)*

Species	Study period	Country	Breeding
Ambystoma opacum[13]	1978-2008	USA	later
Ambystoma talpoideum[13]	1978-2008	USA	no change
Ambystoma tigrinum[13]	1978-2008	USA	earlier
Bombus terrestris[13]	1978-2008	USA	no change
Bufo americanus[6]	1900-1999	USA	no change
Bufo americanus[7]	1930-2010	Canada	earlier
Bufo boreas[4]	1982-1998	USA	earlier
Bufo bufo[1]	1998-2010	UK	later
Bufo bufo[14]	1978-2002	Poland	earlier
Bufo bufo[11]	1978-2005	UK	earlier
Bufo bufo[9]	1980-1998	UK	no change
Bufo bufo[10]	1980-2001	UK	no change
Bufo calamita[2]	1978-1994	UK	earlier
Bufo fowleri[4]	1988-1994	Canada	later
Eurycea quadridigitata[13]	1978-2008	USA	later
Gastrophyne carolinensis[13]	1978-2008	USA	no change
Hyla versicolor[6]	1900-1999	USA	earlier
Hyla versicolor[7]	1930-2010	Canada	no change
Pseudacris crucifer[4]	1967-1994	USA	no change
Pseudacris crucifer[13]	1978-2008	USA	no change
Pseudacris crucifer[6]	1900-1999	USA	earlier
Pseudacris crucifer[7]	1930-2010	Canada	no change
Pseudacris ornata[13]	1978-2008	USA	earlier
Pseudacris sp[7]	1930-2010	Canada	no change
Rana cascadae[4]	1982-1999	USA	no change
Rana catesbeiana[6]	1900-1999	USA	earlier
Rana catesbeiana[7]	1930-2010	Canada	no change
Rana clamitans[6]	1900-1999	USA	no change

Rana clamitans[7]	1930-2010	Canada	no change
Rana kl. *esculenta*[2]	1978-1994	UK	earlier
Rana pipiens[7]	1930-2010	Canada	earlier
Rana sphenocephala[13]	1978-2008	USA	no change
Rana sylvatica[3]	2006-2012	USA	earlier
Rana sylvatica[6]	1900-1999	USA	earlier
Rana sylvatica[7]	1930-2010	Canada	earlier
Rana temporaria[8]	1984-2007	France	earlier
Rana temporaria[14]	1978-2002	Poland	earlier
Rana temporaria[12]	1846-1986	Finland	earlier
Rana temporaria[11]	1978-2005	UK	no change
Rana temporaria[2]	1978-1994	UK	no change
Scaphiopus holbrookii[13]	1978-2008	USA	no change
Triturus cristatus[2]	1978-1994	UK	earlier
Triturus helveticus[2]	1978-1994	UK	earlier
Triturus helveticus[5]	1981-2005	UK	earlier
Triturus vulgaris[2]	1978-1994	UK	earlier
Triturus vulgaris[5]	1981-2005	UK	earlier

Data from: Arnfield et al., 2012; Beebee, 1995; Benard, 2015; Blaustein et al., 2001; Chadwick et al., 2006; Gibbs and Breisch, 2001; Klaus and Lougheed, 2013; Neveu, 2009; Reading, 2003, 1998; Sparks et al., 2007; Terhivuo, 1988; Todd et al., 2011; Tryjanowski et al., 2003.

Most studies into the effects of climate change on amphibians have focussed on anurans (Table 1). It appears that there have been no studies with caecilians, although very little is known about their life histories and ecology in general, and only a handful have analysed phenological changes with urodeles. One of these studies however has become a baseline for further analyses, as it identified changes in both anurans and urodeles in the early 1990's, the trends of which have been replicated in other sites and species since. Beebee (1995) studied breeding trends of amphibians in the UK from 1978 to 1982 and compared them with trends in 1990 to 1994, the key findings of which are described in Table 1. For the natterjack toad (*Bufo calamita*), the trends towards earlier breeding correlated with the increase in mean seasonal temperatures and toads were found to be breeding two weeks earlier in the early 1990s than in the 1970-80s. The edible frog (*Rana* kl. *esculenta*) was found to be breeding an average of three weeks earlier whilst all three newt species were breeding an average of 5-7 weeks earlier. This is one of the few studies to look at all British newt species so is an interesting comparison for this research.

In anurans, correlations with phenology have mostly been found with mean air temperatures in either the 40 days preceding arrival or egg laying (Neveu, 2009; Reading, 2003, 1998) or maximum temperatures up to three months preceding (Blaustein et al., 2001). In temperate spring breeders, this time scale usually corresponds to the winter months, during which warmer temperatures have been found to correlate with an earlier breeding season (Arnfield et al., 2012; Benard, 2015). This in turn relates to the effects of the NAO, whereby high positive phases between 1970 and 1994 brought warmer winters, which correlate with the earlier breeding in amphibians (Forchhammer et al., 1998) as documented by Beebee (1995).

Changes in temperature do not only affect the initiation of breeding in amphibians. Benard (2015) found that higher temperatures in winter reduce female fecundity. He also found that there was no association between earlier breeding and larval mass or survival rate at metamorphosis, however it did correlate with delayed larval development. Variation was found between the thermal thresholds in conspecific populations of *Alytes* and *Hyla,* however, suggesting that factors other than just temperature may be required to trigger the onset of reproduction in anurans (Llusia et al., 2013).

These studies all show that amphibians do appear to be altering their breeding phenology and certainly, links with climate do seem to exist. But identifying specific causal factors and their consequences is very difficult (Rudolf and Singh, 2013) as our understanding of the roles of specific climate factors and their impacts is lacking (Münzbergová et al., 2017) and there are likely many other interacting factors, which are difficult to separate (Winter et al., 2016). This much is evident when the variation in responses of conspecific populations is considered (Table 1).

Phenology of Temperate Amphibians

Temperate amphibians tend to breed only once a year (Vitt and Caldwell, 2013) and can generally be classed into two categories: autumn or spring breeders. In the UK, all native amphibians share a similar biphasic lifestyle; as spring breeders, they emerge from terrestrial brumation at the end of winter and migrate to freshwater bodies to breed in early spring (Griffiths, 1996). Given the secretive nature of their terrestrial phase (Jehle et al., 2011), it is during the aquatic breeding phase that British amphibians can be best observed and most research to date has been carried out during this time.

Once night time temperatures begin to remain above 4 °C (Jehle et al., 2011) at the end of winter, newts begin to emerge from brumation on damp evenings and can begin to be found in freshwater ponds. Little is truly known about the triggers of this spring migration (Beebee, 1996) but due to their ectothermic nature we can extrapolate that environmental cues such as rainfall and temperature affect the cycle either directly or indirectly (Vitt and Caldwell, 2013). Ficetola and Maiorano (2016) have found that across five continents, temperature appears to have a greater relationship with breeding patterns than rainfall. They found that precipitation has a large impact on population dynamics and abundance and Benard (2015) found a positive relationship between winter precipitation and female fecundity.

After the breeding period, newts enter a phase of feeding and gonad development ready for the following season. In amphibians in the UK, the gonads mature over late summer and autumn, preceding breeding and winter dormancy (Verrell et al., 1986). This pattern of development separate from the actual breeding season is known as the dissociated pattern (Whittier and Crews, 1987). It has been found that ambient temperatures relate to the rates of maturation and so it follows that climate change could have a direct effect at this physiological level (Beebee, 1996). It is worth bearing in mind that the success of any breeding season is thus dependent on feeding and climatic conditions in the previous year (Griffiths, 1996). Average low water temperatures (<11 °C) reduce the relative weight of the testes of male great crested newts and therefore potentially impact negatively on the following breeding season (Steinborn, 1977). Lower water temperatures also delay metamorphosis and thus could affect larval survival (Jehle et al., 2011).

Amphibian behaviour appears to be not only dictated by climate. Grant et al. (2009) found that first sightings and peak arrivals of newts (*Lissotriton vulgaris* and *L. helveticus*) to the breeding pond occurred in greater numbers around the time of a new and full moon, suggesting that newts appear to be affected by the gravitational pull and/or geomagnetism of the moon. Deeming (2008) reported that the greatest time of great crested newt activity was just prior to a new moon, and for smooth newts it was either side of the new moon.

The State of Amphibians

There are currently 7,628 described species of amphibian, including 695 species (9%) of urodeles (AmphibiaWeb, 2017) though this number appears to be increasing. As ectotherms with often complex life histories (Crump 2009), they are particularly dependent on temperature and moisture levels in their local environment, though the degree of sensitivity varies from species to species (Galloy and Denoël, 2010).

Noticeable declines and extinctions of amphibian populations worldwide during the 1980s brought attention to the plight of this taxon (Gascon et al., 2007). It is now known that of the vertebrate classes assessed, amphibians are the most threatened on earth, with 32.4% of 6,260 assessed species currently classed as threatened and 42.5% of populations in decline (IUCN 2017). They face a multitude of threats, including habitat loss, invasive species, disease, overcollection and climate change, however it was the declines of populations even within protected areas (which typically eliminate many of the anthropogenic threats) that were cause for concern. As a result of these discoveries, the Declining Amphibian Populations Task Force was created within the Species Survival Commission of IUCN to further investigate the causes behind these enigmatic declines, with a goal to create mitigation measures to halt or reverse such trends (Gascon et al., 2007). Since 1980 it is thought that up to 122 amphibian species have gone extinct in the wild, surpassing the mean extinction rate of the last 350 million years by at least 200 times (Roelants et al., 2007).

Conservation efforts are being carried out globally: captive breeding programmes attempt to understand habitat and nutritional requirements, and produce healthy individuals for reintroductions; habitat protection and restoration aims to create safe havens for threatened species and research is being carried out to further our understanding of natural history, population dynamics, impacts of and resistance to disease, overcollection, invasive species and climate change (Wren et al., 2015).

Newts in the UK

The UK is home to three native species of newt in the family Salamandridae; palmate newt (*Lissotriton helveticus*), smooth newt (*Lissotriton vulgaris*) and great crested newt (*Triturus cristatus*) (Figure 2). All three share a similar semi-aquatic life history, with an aquatic spring breeding phase interrupting an otherwise terrestrial life style. Although they have different requirements with respect to water quality, it is not unusual to find all three-species coexisting in the same lentic water bodies, especially in the south (Griffiths, 1986) (Figure 1). All are sexually dimorphic, with males developing secondary sexual characters, such as crests, swollen cloaca and other ornaments, during the breeding season (Beebee, 1996). During the terrestrial phase sexes look similar. Newts within these genera do not exhibit amplexus, making them unusual amongst urodeles (Duellman and Trueb, 1986; Griffiths and Mylotte, 1987; Halliday, 1977).

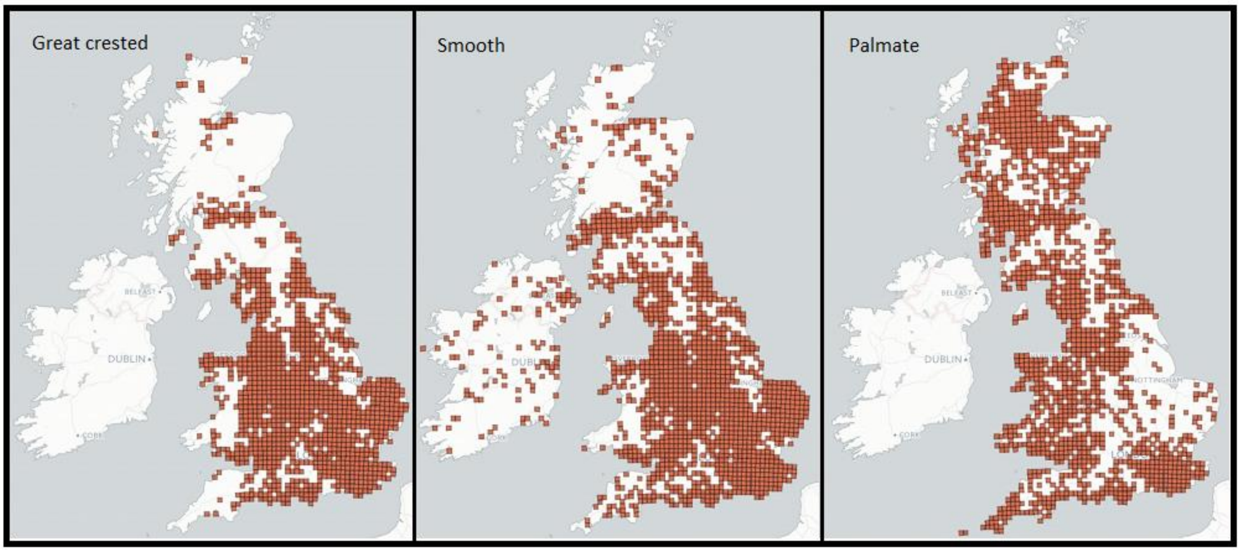

Figure 1*: Distribution of great crested, smooth and palmate newts in the UK (NBN Atlas Partnership, 2017).*

Breeding takes place in ponds during spring and summer after winter brumation. Males are typically the first to arrive in February and perform a mating display, which is variable among species, to the females who arrive shortly after. Mate choice comes down to female preference which is based on a combination of male morphology and display (Cornuau et al., 2012; Green, 1991; Malmgren and Enghag, 2008). Courtship terminates when the male deposits a spermatophore on the pond floor which he then leads the female over to allow for uptake via her cloaca. Fertilisation is internal and there is no parental care. Female newts deposit eggs singly, wrapped in the submerged leaves of plants (AmphibiaWeb, 2012, 2006, 1999). The aquatic breeding phase varies in duration depending on altitude, but typically lasts from February to June-July (Sparreboom 2014). In more recent years, newts have been present in ponds increasingly earlier (Beebee, 1996), suggesting that the breeding pattern is responsive to environmental changes.

Little is known about any of the species during their terrestrial phases (Jehle, Thiesmeier, and Foster 2011); they live secretive lives often hidden below ground in burrows or beneath logs, stones etc. (Sparreboom, 2014). Most research is carried out during spring and summer when newts congregate in ponds, increasing detection rates. As a result, the reproductive biology of each species is quite well understood, with studies identifying the process of courtship displays and mate choice. (Cornuau et al., 2012; Green, 1991; Jehle et al., 2011; Verrell et al., 1986; Zuiderwijk, 1990).

Newt presence and survival is greater in ponds without fish, as eggs and larvae are frequently preyed upon. Insect larvae such as dragonflies, are another major predator. Newt survival increases substantially when water bodies dry out temporarily as this removes invertebrate predators (McDiarmid and Altig, 1999).

Within a pond, the newts demonstrate differences in spatial niche occupancy. Great crested newts are found in the bottom of the water column and in the middle of the pond, preferring the deeper and cooler parts of the pond compared to the small newts (Griffiths and Mylotte, 1987; Jehle et al., 2011). Only once the small newts leave the pond at the end of the breeding season do great crested newts tend to occupy the shallower periphery (Griffiths and Mylotte, 1987).

Figure 2: *Palmate, smooth and great crested newt males with breeding ornaments, photographed at the Field Site, Canterbury, Kent.*

Smooth Newt

The smooth newt, *Lissotriton (*formally *Triturus) vulgaris*, is a small newt, superficially similar to the palmate newt, particularly during the terrestrial phase. Widespread across most of Europe, the smooth newt inhabits the temperate forest belt from the UK in the west over to Russia in the east (Figure 3). It is the most widespread newt in Britain and Ireland (FSC, 2009) (Figure 1) and Europe (Sparreboom 2014). Whilst terrestrial, the smooth newt is nocturnal, however this behaviour changes once aquatic and both adults and larvae can be seen to be active during the day and night in ponds (AmphibiaWeb, 1999), though activity peaks are crepuscular (Sparreboom 2014). Life span varies from 6 to 14 years and sexual maturity is reached after two to three years (Sparreboom 2014). Females lay up to 300 eggs in a season (AmphibiaWeb, 1999) and juveniles will not return to water until they are ready to breed.

Palmate Newt

The palmate newt, *Lissotriton (*formerly *Triturus) helveticus*, is only found in western Europe (Figure 3) and occupies soft water ponds more readily than other urodele species (Buckley and Cole, 2004; FSC, 2009). In the UK, it is the most widespread and abundant newt in Scotland and is mostly absent from the East Midlands and East Anglia (FSC, 2009) (Figure 1). It is found in a variety of habitats including gardens, moorland, woodland and heathland (IUCN, 2008a; Sparreboom, 2014). The species is a typical newt of woodland ponds with high organic matter

(Kent Reptile Amphibian Group, 2017). Their activity pattern is similar to that of the smooth newt. Females lay up to 440 eggs in a season (AmphibiaWeb, 2012) and juveniles only return to ponds to breed at around two years of age (Beebee and Griffiths, 2000). Larvae are often found overwintering in ponds (Sparreboom 2014). Although the habitats of smooth and palmate newts often overlap, hybridisation between the two species is very rare (Arntzen et al., 1998).

Great Crested Newt

The great crested newt, *Triturus cristatus*, is the largest urodele found in the UK (FSC, 2009; JNCC, 2017). It is found in all of Europe apart from the south, extending from the UK over to western Siberia (Figure 3). In the UK it is widely distributed, although more sparsely so in south west England, mid-Wales and Scotland, and is absent from Northern Ireland (JNCC, 2017) (Figure 1). Its preferred terrestrial habitat is forest and forest steppe of deciduous, conifer or mixed tree species, and, although not thought to be very adaptable, it is also found in meadows, parks and gardens (IUCN, 2008b). It prefers ponds with little shading (<40%) (Jehle, Thiesmeier, and Foster 2011) with fecundity found to decrease as shading increases (Cooke et al., 1994). The great crested newt will migrate to permanent stagnant and semi-flowing freshwater bodies such as ponds, quarries and ditches to breed (IUCN 2008b). Females lay up to 600 eggs in a season (AmphibiaWeb, 2006), although half of these abort at the tailbud stage due to lethal homozygosity (Horner and Macggregor, 1985). Unlike the small newts, immature great crested newts can be found in ponds during the breeding season (Jehle, Thiesmeier, and Foster 2011; Sparreboom 2014). Sexual maturity occurs at two to four years of age and wild adults have been documented to live for up to 18 years (Arntzen, 2003).

Figure 3: Global distribution of great crested, smooth and palmate newts (IUCN, 2008a, 2008b, 2008c)

Legislation in England

All three native newt species are listed as Least Concern on the IUCN Red List due to their wide distribution and presumed large populations which are not believed to be declining rapidly (IUCN, 2008a, b, c). The great crested newt is threatened in some subpopulations however, and does appear to be more susceptible to population declines than other European newt species due to its requirements for higher water quality and aquatic behaviours which mean it is more vulnerable to fish predation (AmphibiaWeb, 2006). As a result, they are legally protected from death, injury, possession, sale, disturbance and habitat damage, destruction or obstruction under both UK and EU legislation: Bern Convention (Appendix 2), Wildlife and Countryside Act, 1981 (Schedule 5), EU Natural Habitats Directive (Annex 2 and 4), The Conservation of Habitats and Species Regulations, 2010, Countryside and Rights of Way Act, 2000 (Schedule 12), Natural Environment and Rural Communities Act, 2006 (Section 41) and the Environmental Damage (Prevention and Remediation) Regulations, 2015.

Accordingly, any activity carried out on great crested newt habitat requires a licence from Natural England in order to minimise disturbance and damage to individuals, habitat and populations. Regarding construction and development, this often results in translocation and mitigation measures, the outcomes of which are debatably sustainable (Edgar et al., 2005). Contrastingly, smooth and palmate newts are protected in the UK only from sale in the Wildlife and Countryside Act 1981 (Schedule 5, Section 9). Due to recent changes regarding the UK's position within the European Union, the above-named legal instruments could be altered in the near future.

Climate change is an accepted issue in the UK and phenological events, mostly those responding to changes in temperature, are accepted by the UK government as climate change indicators (Cannell et a 1999; Sparks and Smithers 2002). Given this, we would expect current legislation to reflect the need to manage and mitigate an ongoing threat to species.

Despite this, there is no reference to climate change in the following legislation: Bern Convention, Countryside and Rights of Way Act 2000, Natural Environment and Rural Communities Act 2006, Conservation of Habitats and Species Regulations 2010, Wildlife and Countryside Act 1981 and the Environmental Damage (prevention and remediation) Regulations 2015.

The JNCC UK priority species pages (Document 619) discounts climate change as a threat to great crested newts, however it has been listed as 'false' for causes contributing to changes in population, range and habitat trends. It is worth noting that trends in and original surface area of habitat are listed as unknown. The Biodiversity Strategy 2020 acknowledges the threat of climate change to biodiversity and habitats within the UK, stating that England's wildlife areas in their present condition are not likely to be capable of withstanding the pressures of climate change. Natural England state that they will "consider the impact of climate change and other long-term processes on the existing SSSI network". The Great Crested Newt Species Action Plan (Amphibian and Reptile Conservation, 2009) refers to climate change under objective 2.2(iii), "Ensure understanding of habitat use and distribution, and the extent and impacts of fragmentation and possible changes due to climate change, and that information is available to incorporate these into planning and policy decisions.” It is vital that climate change is not only considered by authorities but findings of research into the effects of climate change on biodiversity must be implemented into current legislation in order to produce effective conservation outcomes.

Study Aims

Effects of climate change previously recorded are highly heterogeneous, even within species and within countries (Ficetola and Maiorano, 2016). Research suggests that individual populations are responding uniquely based on their localised climate and ecosystem/community structure, therefore findings cannot always be extrapolated to cover an entire species' range (Lovejoy and Hannah, 2005).

Numerous studies have looked at changes in amphibian phenology in relation to climate change. Few however, have investigated the effects of climate change on newt phenology and fewer still have analysed for varying responses between neighbouring metapopulations which would be affected by the same climatic patterns.

The focus of this study is to assess whether two neighbouring metapopulations supporting all three British newt species, great crested, palmate and smooth, are responding to changes in the climate by way of altered breeding phenology. As well as assessing any changes between species, it will investigate whether the two metapopulations - and the individual ponds contained within - are responding in the same way.

This study aims to investigate the following questions:

Q: Has there been any change in the breeding phenology of British newts in Canterbury over the past 20 years?

Q: Can any observed changes be attributed to changes in climate?

Q: Are the three species of native newt responding differently?

Q: Are males and females responding in different ways?

Q: Are two neighbouring metapopulations responding in the same way?

CHAPTER TWO: Timing and Duration of Aquatic Period at Two Neighbouring Metapopulations

Abstract

Using two neighbouring metapopulations for comparison, the breeding patterns of three species of newt were analysed over two decades. Smooth, palmate and great crested newts were studied at Well Court between 1996 and 2013, and at the Field Site from 1999 until 2016. Median date of capture each year was used as a measure of the timing of the breeding period. Differences were found between each species and between each pond studied. At Well Court, just one of the ponds (the Snake Pond) showed consistent changes in phenology over time. Palmate and great crested newts arrived up to 5.61 weeks later in 2013 than in 1996. Smooth newts arrived 3.25 weeks later, though this trend was not significant. Relationships between the observed trends and climate variables were different for each species and encompassed autumn rainfall, spring and summer temperatures and winter frost. Duration of the aquatic period was calculated as the number of weeks between the dates when 5% and 95% of the newts were captured each year. At the Snake Pond, smooth newts stayed 6.4 weeks longer and palmate newts 7.6 weeks longer in 2013 than in 1996. At the Field Site populations, there were no trends over time in terms of timing of breeding in any of the species, but great crested newts stayed 10 weeks longer at the Field Site in 2016 than in 1999. Again, the trends for each species showed different relationships to climate.

Over the study period, capture rates varied for each species and each pond. The population of great crested newts at the Field Site increased from 14 to over 85 individuals in twenty years. Predictably, capture rates of great crested newts during the survey season also increased at this site, however they decreased at all other ponds. Captures of smooth newts decreased at both the Snake Pond and the Swimming Pool, and palmate newt captures decreased at the Snake Pond.

Introduction

The response of amphibians to climate change may vary not only between populations occupying different habitat types, but also in part on location; each country or region will experience a slightly different climate and therefore different rates of change. This possibly explains the variation in responses of well-studied species such as the common toad (*Bufo bufo*) and common frog (*Rana temporaria*) (Table 1). Studies have approached the issue of climate-affected phenology by analysing a variety of climatic variables and time scales as well as a variety of species, though none appear to have analysed neighbouring populations simultaneously.

Chadwick et al. (2006) studied smooth (*Lissotriton vulgaris*) and palmate newts (*L. helveticus*) in Wales in 1981-87 and 1997-2005. With every 1° C increase in spring temperature they noted a significant advance of 2-5 days in median arrival date and the dates were also highly correlated with mean temperature in January-February. These spring temperatures explained up to 74% of variability between years in median arrival date. Similar trends were recorded by Beebee (1995) as great crested, smooth and palmate newts were observed to breed an average of 5-7 weeks later in the latter half of the study period, correlated with increases in mean seasonal temperatures. Changes were found to be greater for males than females (in both small newt species) and for *L. helveticus* than *L. vulgaris* (Chadwick et al. 2006). Chadwick et al. (2006) also found the duration of the aquatic phase was 3-4 weeks longer in 1997-2005 than in 1981-97, with a greater increase for *L. helveticus*, but there was no significant difference between gender or species. These studies suggest that newts in the UK are responding to climate change by advancing their timing of breeding, and that these responses vary between species.

This chapter analyses the median date and duration of aquatic period in great crested, smooth and palmate newts at two neighbouring metapopulations in Canterbury, Kent, to identify any changes over time in response to climate change. The use of two study sites within the same area allows for comparison between populations to see whether newts are responding to climate change at a species or population level. It will also look to see whether or not there is significant variation between gender and between species, and how any observed changes might be related to different aspects of the climate.

Methods

Study Site

This study focussed on two amphibian metapopulations in Canterbury, Kent, UK (Figure 4) containing all three British native newt species; *Triturus cristatus, Lissotriton helveticus* and *Lissotriton vulgaris.*

Figure 4: *The location of the research ponds in Canterbury, Kent, where "X" indicates the study ponds.*

Field Site

The Field Site is located at the north-western end of the University of Kent, Canterbury (TR 12982 59668) and consists of eight identical ponds. Four ponds of 2 m x 1 m spaced 2 m apart were constructed in 1998 and an extra four were added later in 2009 following the same dimensions (Figure 5). The ponds are each lined with a PVC sheet and are wedge shaped with a benthic gradient ranging from the shoreline to around 0.7 m deep (Lewis, 2012). The original 1998 ponds were drained and relined in 2006. The pond surfaces are occasionally cleared of overgrown vegetation and filamentous algae during winter. The immediate area between and surrounding the ponds is rough grassland which is lightly managed in order to keep the ponds clear and accessible. Vegetation includes species such as bramble (*Rubus fruticosus*), nettle (*Urtica dioica*), ragwort (*Senecio jacobaea*), bracken (*Pteridium aquilinum*) and grass (Poaceae).

Surrounding the Field Site are university grounds, urban housing areas, grassland, hedgerows and small stands of trees.

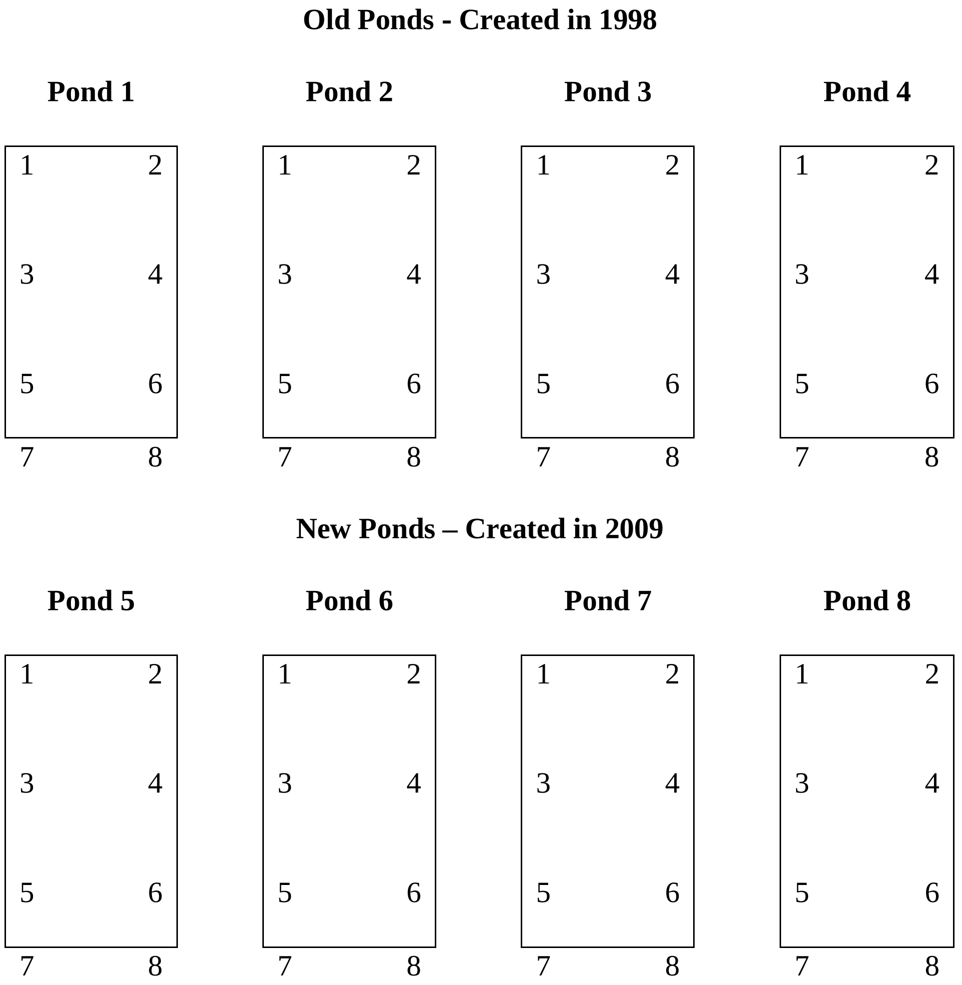

Figure 5: *(from Lewis, 2012) The lay-out of ponds at the Field Site. Numbers 1-8 represent the placement of bottle traps within the ponds. Traps 7 and 8 are placed below traps 5 and 6 in the water (not to scale).*

Once created, the ponds were left to colonise naturally and now support four known species of amphibian: great crested newt (*Triturus cristatus*), smooth newt (*Lissotriton vulgaris*), palmate newt (*Lissotriton helveticus*) and alpine newt (*Ichthyosaura alpestris*). Annual monitoring began in 1999 when the first male great crested newts were recorded. Females were first noted in the ponds the following year. Great crested newts are known to occasionally overwinter in these ponds (Gamboni, 2005).

There is little diversity in vegetation within the ponds, with duckweed (*Lemna minuta*) and filamentous algae being the predominant species. Artificial egg strips, comprising of strips of plastic, are provided in all ponds due to a lack of suitable vegetation for newt oviposition sites.

A range of invertebrate species have been sampled in the ponds, including Mollusca, Copepoda, Ostracoda, Diptera, Arachnida, Annelida, Cladocera, Coleoptera, Odonata, Hemiptera, Ephemeroptera and Trichoptera (Lewis, 2012).

Given the close proximity of the ponds, their similar ecology and high levels of newt movement between ponds, the Field Site will be treated as one site for the purpose of this study, as opposed to eight individual ponds.

Well Court

Located 3.5 km north of Canterbury lies Well Court (TR134619); this site is a farm containing four ponds (Figure 6). The wider landscape consists of a mixture of arable land, orchards, hedgerows, poplar rows and semi-natural woodland, with the village of Tyler Hill to the south. The distances between the ponds varies between 200 and 800 m. Collectively, the ponds are more than 1 km from any other ponds; greater than the migration distance travelled by newts (Beebee, 1996; Kupfer and Kneitz, 2000; Oldham and Swan, 1997; Jehle and Arntzen 2000, but see Haubrock and Altrichter, 2016) so are considered to be an isolated metapopulation. Fertilisers and pesticides are used on fields adjacent to the ponds at the farm but they are otherwise sympathetic to wildlife.

Figure 6: The location of ponds at Well Court in relation to each other and surrounding habitat features

The first pond is an old concrete Swimming Pool (TR 137617) located in a small patch of woodland surrounded by arable fields. The pool was abandoned shortly after its construction in 1970. The pool is 45 m² in surface area and has a depth ranging from 1.5 m to 2 m. Griffiths et al. (2010) caught no *T. cristatus* larvae in this pond during a 12-year survey period. All populations of newts were greatly diminished in 2004, probably due to the unsuitability of the pool for breeding and a wider decline within the metapopulation. Small populations of smooth and palmate newts were caught thereafter but great crested newts were no longer found at the Swimming Pool.

The Garden Pond (TR 134618) consists of three small ponds in very close proximity to one another (within 2 m) and are therefore classed as one pond site, as movement between ponds by newts is very high (Griffiths et al., 2010). The ponds are lined with butyl and vary in size from 4.5 to 32 m² with a maximum depth of 1 m. The ponds were constructed in 1970 and lie in the garden of the farmhouse. Ornamental plants surround the ponds and the lawn is regularly mown. The Garden ponds are located 230 m from both the Snake pond and Swimming pool. Larvae of all species were found annually in the Garden Pond (Griffiths et al., 2010). The dominant species of newt at the Garden Pond fluctuated between great crested and palmate newt.

Snake Pond (TR 135620) is a semi-natural pond which is variable in size and shape; depending on water levels the surface area is usually between 160 and 270 m². This pond is susceptible to diminishing water levels during the summer, with a maximum depth of 2 m falling to about 20 cm in exceptionally dry periods. *T. cristatus* larvae have been caught intermittently since monitoring started in 1996 (Griffiths et al., 2010). The pond lies within a small copse of trees, roughly triangular in shape, with arable fields on two sides and an apple orchard on the other. Of the three species, palmate newts represented the vast majority of captures at the Snake Pond. The smooth newt population at this pond was small, and great crested newts fluctuated in numbers.

Pylon Pond (TR 137623) is a semi-natural pond of around 185 m² with a maximum depth of 1.5 m and is rectangular in shape. The water is often abundant in vegetation. The pond is located on the edge of a large patch of woodland, with an arable field surrounding it on three sides. The Snake Pond is the closest to the Pylon Pond, 350 m to the south (Griffiths et al., 2010). *T. cristatus* larvae were only found at this pond intermittently (Griffiths et al., 2010). Palmate newts were the dominant species at this pond. Great crested newts were rarely and intermittently captured at Pylon Pond, and the smooth newt population was small.

Data Collection

The Field Site has been monitored since 1999 and surveys are ongoing. Well Court was monitored between 1996 and 2013. Data were collected once weekly, generally from the last week of

February and usually continued until no more newts were captured or the ponds desiccated. This end of season date has varied across the years from mid-July until October. Survey seasons have varied from 8 to 36 weeks long. For the purposes of analysis, the last week of February has been standardised as Week 1.

All surveys were carried out under licence from Natural England and used funnel traps as described by Griffiths (1985). Two-litre plastic bottles with the top cut off and inverted were submerged around the periphery of the ponds. Traps were either tied to canes, rocks or vegetation on the shoreline to ensure their placement, or secured to the substrate via a garden cane pierced through the trap at an angle to maintain a sufficient air pocket for any captured animals.

At the Field Site eight traps were set in each pond (Figure 7). Traps 7 and 8 were fully submerged so that they lay on the bottom at 0.7 m depth. However, from Week 9 onwards this practice ceased as the warmer water increased the risk of asphyxiation in the deep traps.

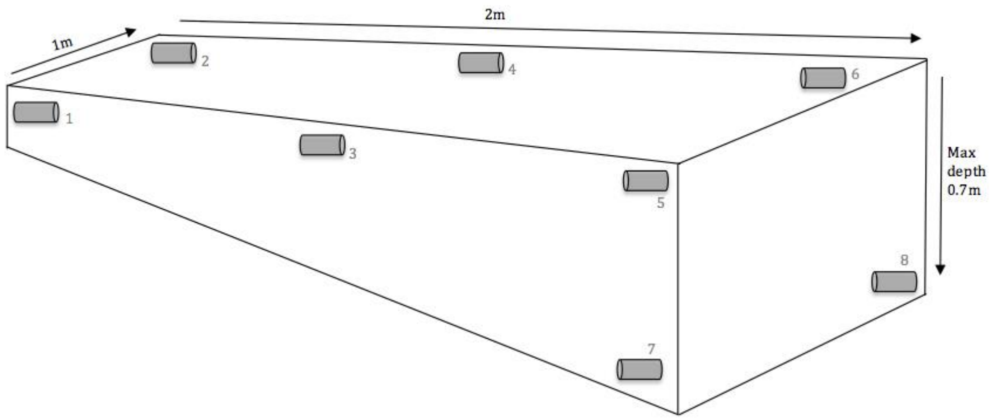

***Figure 7**: The placement of traps in the ponds at the Field Site. Traps 7 and 8 are fully submerged only during the colder months (not to scale) (from Lewis, 2012).*

At Well Court traps were placed around the perimeter of the ponds at 1 m intervals. A set number of traps was allocated to each pond but this was sometimes reduced if the water levels dropped considerably.

Traps were set on Thursday evenings at 19:30. On Friday mornings at 07:30, traps were checked and any captured great crested newts were emptied into labelled buckets, one for each pond, with pond water. Smooth and palmate newts were immediately released back into the ponds, with records taken as to quantity, gender and life stage. Numbers of larvae were also recorded if present.

Morphometric data were collected for metamorphosed great crested newts. They were weighed (g), measured (SVL and TL to nearest mm) and their bellies were photographed as they can be identified to an individual level based on unique ventral patterns. They were then returned to the pond from which they came. Researchers wore nitrile gloves to avoid spread of disease or contaminants to the newts, and any footwear was disinfected with Virkon, especially if surveyors had visited other wetland sites.

Climate Data

Climate data were gathered from the Hadley Centre, Met Office. The Central England Temperature (CET) dataset (Parker et al., 1992) comprises an area from London to Bristol to Lancashire. This dataset encompasses maximum, minimum and mean monthly air temperatures and allows for comparison with other studies (Chadwick et al., 2006; Roy and Sparks, 2000; Sparks and Smithers, 2002).

Datasets from more localised weather stations (Manston and South East/Central South) were disregarded for this analysis as they only provided monthly temperatures which would not allow for detailed analyses. Pearson's correlation was carried out to assess similarity between the three datasets and consistently significant positive correlations ($p<0.0001$) were found, therefore CET data is applicable to Canterbury and will still provide a reliable picture of the relationship between temperature and phenology. SE/CS data were used to analyse air frost, rain days >1 mm and sunshine hours (Met Office, 2015) as a more comprehensive data set was collected at this station than for Manston. UKCP09 gridded datasets, detailing climate data for the UK in 5 km^2 plots, were considered but only provided data up to 2011 and were therefore disregarded.

Precipitation data came from HadUKP (Alexander and Jones, 2001) and consists of daily and monthly total precipitation (mm) recorded as an average from sites across the South East of England, allowing for analysis of monthly totals and daily patterns.

Water temperature was gathered from thermometers and dataloggers placed in the water bodies. Maximum, minimum and mean temperatures were taken on Thursday evening and Friday morning. In analysis, only Thursday temperatures (max, min and mean) were examined as they encompass a greater time span (seven days) and therefore describe the water temperature for the whole breeding season. There has not been a standardised methodology for collecting water temperature data and the thermometers used have proven unreliable, occasionally yielding erratic readings over the years. Anomalous data have therefore been omitted and treated as missing data. However, the data are still useful in identifying an overview of trends in water temperature over time. Where data were obtained for both deep and shallow temperatures, shallow was chosen for analysis as these are likely to be more variable than deep temperatures and thus reflect climatic changes.

Statistical Analysis

Data were compiled in Excel and all statistical analysis was carried out in R (R Core Team, 2016).

At Well Court, ponds that yielded less than a total of six captures per year for each species and/or gender were omitted from further analysis to exclude anomalies, in order for the data to remain representative and reliable. Great crested newts were excluded from analysis at the Swimming Pool as evidence of breeding was never found, numbers were relatively low and no newts were captured after 2003.

In all analyses, year and climatic factors were the independent variables. The response variable was either median capture date, duration of aquatic period, week of first arrival or body condition. The following five stages of statistical analysis were used for each of the response variables. Further detail specific to each response variable is discussed below.

Stage 1 - Exploratory univariate regression analysis was performed between the response variable and year to identify any relationships indicating significant changes over time. Those showing statistical significance ($p<0.05$) were selected for further analysis.

Stage 2 - Those variables showing trends over time in Stage 1 were then plotted against climatic data, and regression analysis was carried out to assess whether there were any significant relationships with climate over the same period. As the climate in certain time periods cannot affect the current year's migration, i.e. because summer temperatures follow spring emergence, analysis of these variables used the previous year's climate data to identify any potential lagged effects. The climate between June and December was treated this way.

Previous studies have used climate data in the three months prior to first arrival (Beebee, 1995; Blaustein et al., 2001). However, due to the truncation previously mentioned (see Data Collection), this was not feasible for this study; climate was analysed on both a monthly and seasonal basis.

Climatic variables included: days of air frost, air temperature (maximum, minimum and/or mean), monthly rain and number of rain days >1 mm. Sunshine and water temperature were excluded from analysis due to inconsistencies in data and/or a lack of significant relationships with response variables.

Stage 3 - From those climatic variables which showed significance in Stage 2, a selection of up to four variables was made for each species. These were selected based on which climatic factors showed the most significant relationships with the response variables and which could be explained biologically. Four independent variables allowed for both individual and paired analyses and encompassed each type of climatic variable as detailed above.

Stage 4 - Response variables were visualised with scatterplots, histograms, Q-Q plots, the Shapiro test, and transformed using natural logs when appropriate, to ensure that they satisfied assumptions of parametric testing, such as normal distribution and homoscedasticity (McGuinness, 2002).

Independent variables were visualised to identify multicollinearity between them (Field et al., 2012). If any were detected, these pairings were omitted from further analysis.

Multivariate analysis was then performed using forced-entry multiple linear regression (Field et al., 2012) to explore the relationships between climatic variables and the response variables. Only those species and models which showed significance were analysed further.

Stage 5 - Models that did not show statistical significance ($p>0.05$) at Stage 4 were omitted. Those that did show statistical significance ($p<0.05$) were subject to model averaging. The package MuMIn (Barton, 2016) was utilised to select the best fitting models from the significant combinations of climatic factors provided. Those models with a delta AIC (ΔAIC) score of <7 were considered along with weighting (w) of individual parameters (Burnham et al., 2011) to infer which climatic factors may be having the greatest effect on the response variables.

Median and Modal Capture Dates

'Median arrival' has often been the chosen percentile in other studies for analysis into phenology (Arnfield et al., 2012; Chadwick et al., 2006). It provides a larger picture of change and is thought to be a more robust measure (Chadwick et al., 2006) as it overcomes the effects of nonmigratory movement and outliers, which could skew the data. Due to the survey methods used, *arrival* could not be accurately determined so median *capture* date was chosen for this analysis. Using the median date also helps to overcome the truncation of a standardised survey start date (see Data Collection). From the capture data, the week when 50% of captures had been made was identified for each species and sex. This was done separately for each pond and will hereon be referred to as median capture date.

Two-way analysis of variance was carried out separately for each species to look for significant main effects on median capture date using year and pond as factors. Three-way analysis of variance was then performed to add species as a third factor. The five-stage analysis was carried out using the climate variables detailed in Table 2.

As the start date for surveying and thus median capture date is truncated at Week 1 (last week of February), modal week was also analysed. This is defined as the week when most newts were captured (or 'peak' week within the season). Modal week for each species and gender were regressed against year and were then correlated against median arrival week to identify any similarities between the two variables.

As only the Snake Pond showed a significant change over time in median capture date, regression was used to quantify the rate of change in each species. The change was assessed as the difference between the mean median date in 1996 and in 2013. No other ponds showed significance in median capture date so were not analysed further.

***Table 2**: Climatic variables chosen for Stage 4 analysis with median capture date, as derived from regression analysis with the response variables*

Species	Climatic Variables			
Great crested	Air frost - December (P)	Maximum temperature - August (P)	Maximum temperature - Annual	Days of rain - Autumn (P)
Smooth	Air frost - Winter	Minimum temperature - February	Minimum temperature - Annual	Monthly rain - March
Palmate	Air frost - Winter	Minimum temperature - Winter	Minimum temperature -Spring	

"P" indicates that the data are from the previous year to account for lag between climate event and newt breeding season

Duration of Aquatic Period

Duration of the aquatic phase was calculated as the number of weeks between the dates when 5% and 95% of each species was captured at each pond. The percentile of 5% was chosen to represent 'first arrival' so as to eliminate any outliers such as non-migratory individuals or newts which overwintered in the ponds (Arnfield et al., 2012; Chadwick et al., 2006).

Analysis of variance was carried out to identify any variation between sexes, year, pond and species. The five-stage analysis was then carried out using the climatic variables in Table 3.

Table 3: *Climatic variables chosen for Stage 4 analysis with duration, as derived from regression analysis with the response variables*

Species	Climatic Variables		
Great crested	Air frost - December (P)	Maximum temperature - Annual (P)	Monthly rain - September (P)
Smooth		Maximum temperature - August (P)	Monthly rain - September (P)
Palmate	Air frost - March	Maximum temperature - July	Monthly rain - September (P)

"P" indicates that the data are from the previous year to account for lag between climate event and newt breeding season

Results

Changes in Median Date of Activity over Time

Median date of newt capture varied between ponds, species and year (Tables 4 and 5). The most significant changes in median date occurred at the Snake Pond, where progressively later arrival was observed for both great crested ($R^2 = 0.45$, F (1,15) = 12.39, $p = 0.003$) and palmate newts ($R^2 = 0.44$, F (1,16) = 12.65, $p = 0.003$). Smooth newts showed a similar trend at the Snake Pond but this was not significant. Median date at all other ponds fluctuated but was not consistently delayed or advanced over time (Figure 7).

From the regressions, at the Snake Pond seasonal activity of great crested newts was an average of 5.61 weeks later in 2013 than in 1999; palmate newts an average 5.47 weeks later; and smooth newts (non-significantly) an average 3.25 weeks later. None of the other ponds within the Well Court metapopulation or at the Field Site showed notable trends.

When the data were analysed using modal date (i.e. the seasonal peak) rather than median date, similar results were obtained for palmate newts at the Snake Pond ($R^2 = 0.46$, F (1,16) =13.68, $p = 0.002$) (Figure 9). However, there were no significant patterns for smooth or great crested newts at the Snake Pond, and no trends were observed for modal arrival week for either of the species or other ponds (data not shown).

Table 4: *2-way ANOVA analysing variation in the median date of activity of each species across ponds and years*

		Df	Sum Sq	Mean Sq	F value	P
Great crested	Pond	4	200.42	50.11	12.19	<0.001
	Year	14	124.21	8.87	2.16	0.03
	Residuals	33	135.6	4.11		
Smooth	Pond	4	97.64	24.41	6.17	<0.001
	Year	14	107.85	7.7	1.95	0.05
	Residuals	44	174.16	3.96		
Palmate	Pond	4	259.92	64.98	21.06	<0.001
	Year	14	95.9	6.85	2.22	0.02
	Residuals	54	166.63	3.09		

Table 5: *3-way ANOVA analysing variation in the median date of activity across ponds, years and species*

	Df	Sum Sq	Mean Sq	F value	P
Pond	4	469.52	117.38	29.62	<0.001
Year	14	213.52	15.25	3.85	<0.001
Species	2	81.95	40.98	10.34	<0.001
Residuals	167	661.92	3.96		

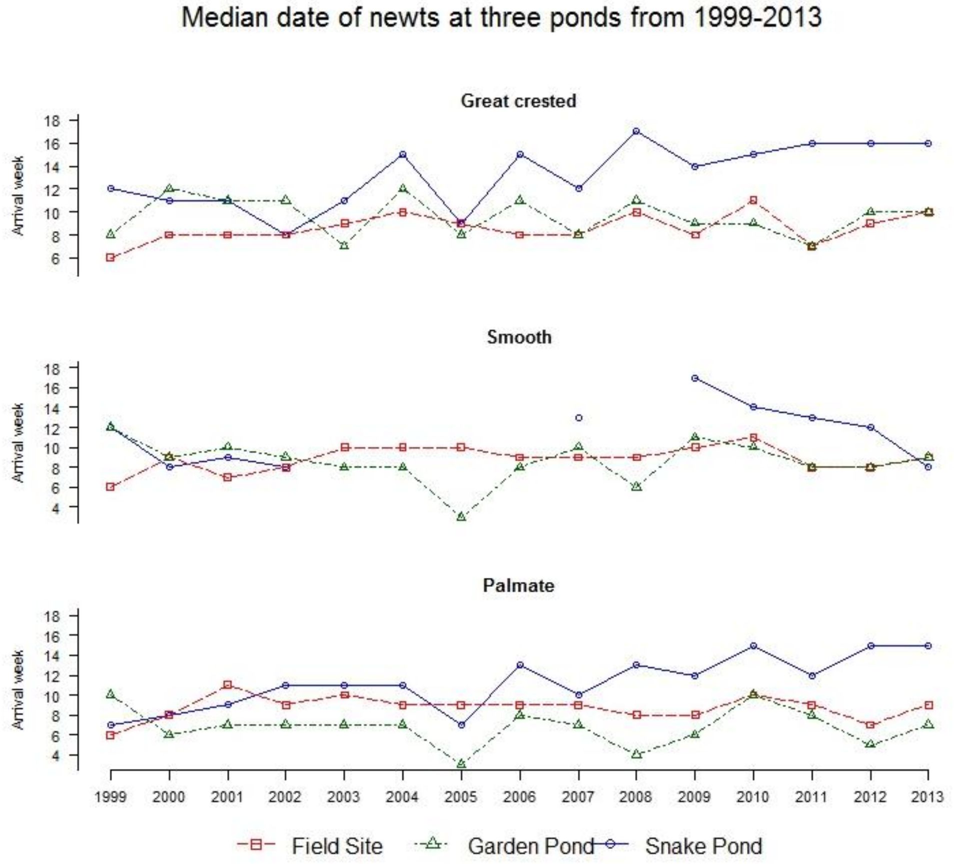

Figure 8: *Changes in median date over the study period for all three species of newt at three ponds across two neighbouring metapopulations*

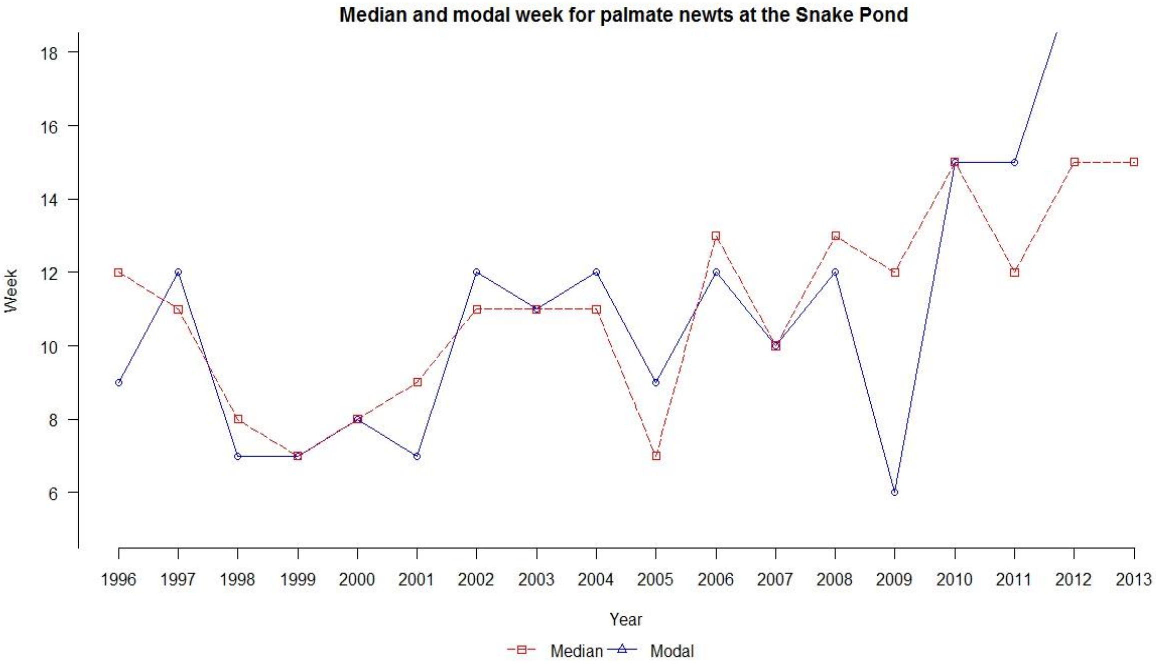

Figure 9*: Comparison of median and modal date for palmate newts at the Snake Pond over the study period.*

Effects of Climate on Median Date of Great Crested Newts at the Snake Pond

As the number of 'rain days in previous autumn' and 'maximum temperature in previous August' decreased, great crested newt breeding activity began later at the Snake Pond in 2013 than in 1996 (regression estimate -0.665 and -0.194 respectively).

The evidence ratio between the top two models (Table 6) was low (1.711) suggesting uncertainty between the two models. Although the ΔAIC of the top model suggests that the variables it contains are most likely to explain variation in median date, the weight is low (w=0.4) therefore it cannot be claimed that these two climatic variables have a large effect on the median date of great crested newts at the Snake Pond (Burnham and Anderson 2002). The relative importance of these two variables independently shows that 'rain days in previous autumn' (w=0.76) is of greater importance than 'maximum temperature in previous August' (w=0.55) and all other variables analysed (Figure 10).

Table 6: *Best fit models for the median date of great crested newts at the Snake Pond when regressed with climate*

Model	df	AICc	ΔAIC	w
Maximum temperature in previous August + rain days in previous autumn	4	82.8	0	0.4
Rain days in previous autumn	3	83.9	1.07	0.23
Maximum temperature in previous August	3	85.7	2.93	0.09
Maximum annual temperature + rain days in previous autumn	4	86.1	3.32	0.08
Maximum temperature in previous August + maximum annual temperature	4	86.6	3.84	0.06
Frost in previous December + rain days in previous autumn	4	86.8	3.99	0.05
Maximum annual temperature	3	87.3	4.5	0.04
Frost in previous December	3	88.4	5.6	0.02
Frost in previous December + maximum temperature in previous August	4	88.9	6.16	0.02

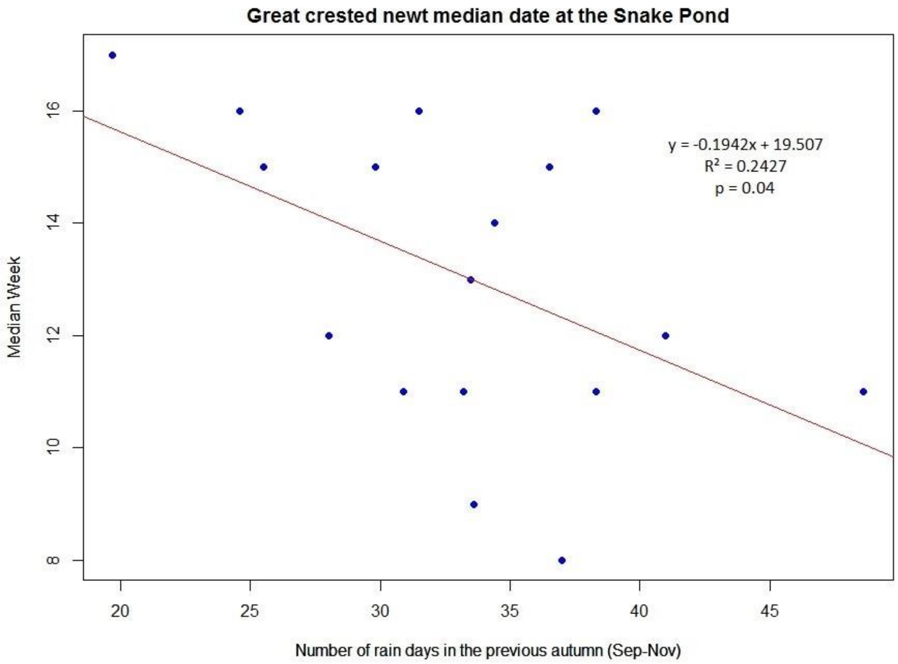

Figure 10*: Fewer rain days in the previous autumn suggests a later median date for great crested newts at the Snake Pond.*

Effects of Climate on Median Date of Male Great Crested Newts at the Snake Pond

Male great crested newts were arriving later at the Snake Pond in 2013 than in 1996. This delay in median date was found as both ‘maximum temperature in the previous August’ and ‘maximum annual temperature’ decreased (regression estimate -1.304 and -1.757 respectively).

The frequent occurrence of ‘maximum temperature in previous August’ in the best-fitting models (Table 7) suggests this is the most important climatic variable irrespective of gender (Table 6). Median date for female great crested newts showed no significant trends at any of the ponds so no further analysis for females was performed.

***Table 7**: Best fit models for the median date of male great crested newts at the Snake Pond regressed with climate*

Model	df	AICc	ΔAIC	w
Maximum temperature in previous August + maximum annual temperature	4	75.5	0	0.43
Maximum temperature in previous August	3	76.3	0.87	0.28
Maximum temperature in previous August + rain days in previous autumn	4	76.9	1.46	0.21
Frost in previous December + maximum temperature in previous August	4	79.1	3.61	0.07

Effects of Climate on Median Date of Palmate Newts at the Snake Pond

Although palmate newts at the Snake Pond responded similarly to great crested newts in terms of seasonality, their breeding behaviour is influenced by the climate at different times of year.

Multiple regression for median date of palmate newts at the Snake Pond with climatic factors showed a range of statistically significant linear models for median date. Within these significant models however, none of the individual climatic factors showed significance. Model averaging found the three most probable models to consist of ‘air frost in winter’ and ‘minimum temperature in spring’, however weighting was low for these models (Table 8). Palmate seasonality was delayed as minimum spring temperature decreased (regression estimate -1.367) and winter frost increased (regression estimate 0.135) over the study period.

Table 8: *Best fit models for the median date of palmate newts at the Snake Pond when regressed with climate*

Model	df	AICc	ΔAIC	w
Frost in winter + minimum temperature in spring	4	83.1	0	0.26
Minimum temperature in spring	3	83.1	0	0.26
Frost in winter	3	83.4	0.34	0.22
Minimum temperature in spring + minimum temperature in winter	4	84.1	1	0.16
Minimum temperature in winter	3	85	1.94	0.1

Effects of Climate on Median Date of Male Palmate Newts at the Snake Pond

Despite having the most significant delay in median date ($p<0.001$), male palmate newts did not show clear significant relationships with climatic variables during regression analysis. Model averaging, however, found that as winter frost increased and minimum temperature in spring decreased, male palmate newts began breeding later at the Snake Pond (Table 9). This supports the findings above for palmate newts irrespective of gender.

Table 9: *Best fit models for median date of male palmate newts at the Snake Pond when regressed with climate*

Model	df	AICc	ΔAIC	w
Frost in winter	3	82.4	0	0.3
Minimum temperature in spring	3	82.6	0.15	0.28
Frost in winter + minimum temperature in spring	4	83.6	1.22	0.16
Minimum temperature in winter	3	83.9	1.44	0.15
Minimum temperature in spring + minimum temperature in winter	4	84.5	2.11	0.11

Effects of Climate on Median Date of Female Palmate Newts at the Snake Pond

Female palmate newts displayed a somewhat stronger relationship with climatic variables than males above (Table 10), however the two key variables remain the same as for the males and species as a whole; as air frost in winter increased and minimum temperature in spring decreased, female palmate newts showed delayed seasonality at the Snake Pond. Female palmate newts show a slightly stronger relationship with ‘minimum temperature in spring’ than with winter frost (evidence ratio between top two models = 2.77).

***Table 10**: Best fit models for median date of female palmate newts at the Snake Pond when regressed with climate*

Model	df	AICc	ΔAIC	w
Minimum temperature in spring	3	91.5	0	0.56
Frost in winter + minimum temperature in spring	4	93.5	2.05	0.2
Minimum temperature in spring + minimum temperature in winter	4	93.9	2.41	0.17
Frost in winter	3	96.6	5.14	0.04
Minimum temperature in winter	3	97.5	6.03	0.03

Variation in Median Date between Genders

Although not all genders appear to respond in the same way (Tables 7, 9 and 10), there was no significant difference between the median date of males and females across all ponds and species, (F (1, 404) = 0.11, p = 0.74) (Figure 11). Two-way ANOVA was carried out with sex and year as factors to see if there was any difference between genders for each species.

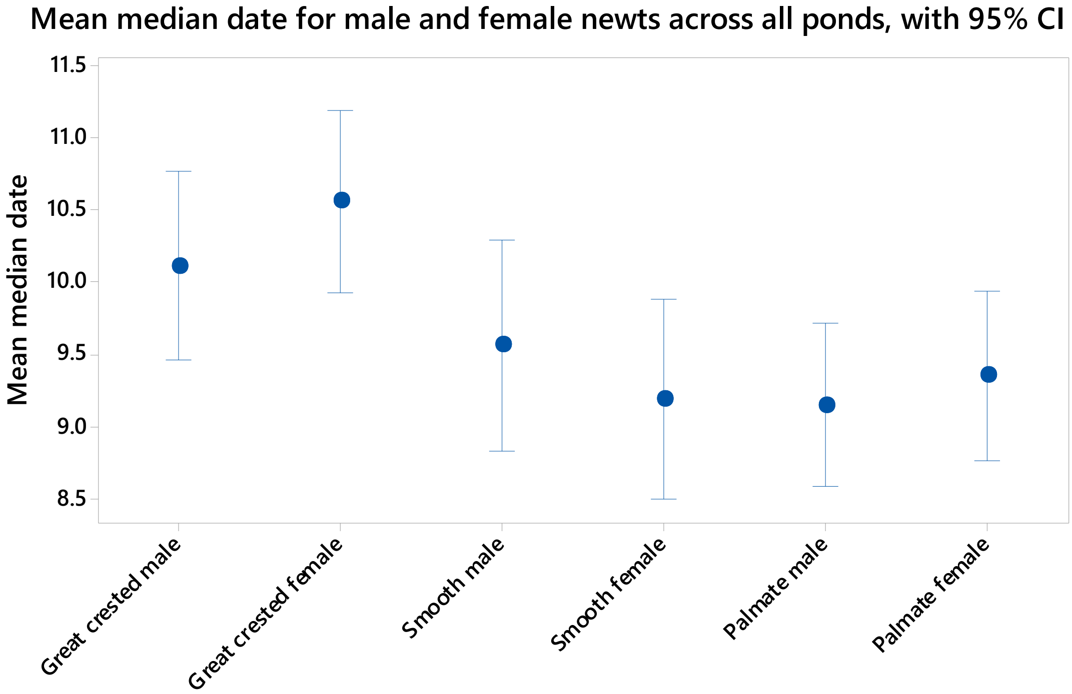

***Figure 11**: Results of two-way ANOVA on mean 'median date' between genders for all species of newt across all ponds; showing the mean median date with 95% CI. Individual standard deviations were used to calculate the intervals.*

Duration of Aquatic Period

Between 1999 and 2016, aquatic period, i.e. breeding season, became progressively longer for great crested and smooth newts at the Field Site, and smooth and palmate newts at the Snake Pond (Figure 12). Changes in duration over the study period were calculated using regression. The greatest change in duration was found at the Field Site for great crested newts (Table 11). Only those species and ponds for which a change in duration was significant (Figure 12) were analysed further with climatic data (see section below). Males and females did not differ significantly in duration (F(1) = 0.07, p=0.08).

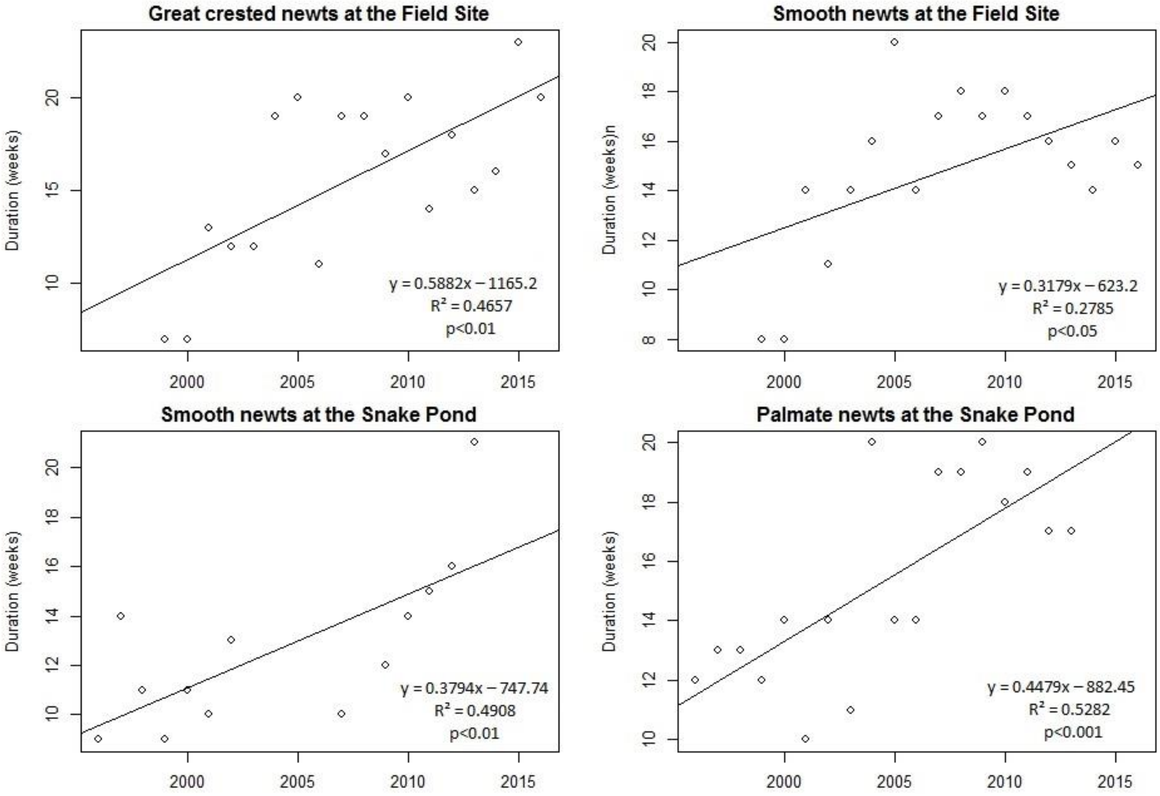

***Figure 12**: Changes in the duration of the aquatic period between 1999 and 2016*

***Table 11**: Changes in duration of aquatic period (weeks) over the study period as calculated via regression*

Species/Pond	Start (1996 or 1999)	End (2013 or 2016)	**Difference (weeks)**
Great crested newt at the Field Site	10.61	20.61	**10.0**
Smooth newt at the Field Site	12.28	17.69	**5.4**
Smooth newt at the Snake Pond	9.54	15.99	**6.4**
Palmate newt at the Snake Pond	11.56	19.17	**7.6**

Effects of Climate on Great Crested Newt Duration at the Field Site

Multiple regression and model averaging found that as rain in the previous September decreased, duration of great crested newts at the Field Site the following year became longer. This variable had a cumulative weighting of w=0.99 across the top three models (Table 12). The top model includes this variable only, with a weighting of w=0.63, suggesting that this factor has an important influence on great crested newt duration at the Field Site.

***Table 12**: Best fit models for great crested newt duration at the Field Site when regressed with climate*

Model	df	AICc	ΔAIC	w
Monthly rain in previous September	3	96.7	0	0.63
Frost in previous December + monthly rain in previous September	4	98.6	1.9	0.25
Monthly rain in previous September + maximum temperature in previous year	4	100	3.3	0.12

Effects of Climate on Smooth Newt Duration at the Field Site

Similarly to great crested newts, the duration of smooth newts at the Field Site showed a significant negative relationship with ‘rain in the previous September’ ($p<0.001$). This variable alone had a high weighting, (w=0.68) but combined with ‘maximum temperature in the previous August’, there was a cumulative weight of w=1.00 for the top two models (Table 13).

Table 13: *Best fit models for smooth newt duration at the Field Site when regressed with climate*

Model	df	AICc	ΔAIC	w
Monthly rain in previous September	3	83.7	0	0.68
Maximum temperature in previous August + monthly rain in previous September	4	85.2	1.5	0.32

Effects of Climate on Smooth Newt Duration at the Snake Pond

The top three models for smooth newt duration at the Snake Pond are similar to those found at the Field Site, with both ‘rain in the previous September’ and ‘maximum temperature in the previous August’ showing significant negative relationships with duration (Table 14). ‘Rain in previous September’ alone holds the largest weighting of w=0.63.

Table 14: *Best fit models for smooth newt duration at the Snake Pond when regressed with climate*

Model	df	AICc	ΔAIC	w
Monthly rain in previous September	3	72	0	0.63
Maximum temperature in previous August	3	74	2.07	0.23
Maximum temperature in previous August + monthly rain in previous September	4	74.9	2.97	0.14

Effects of Climate on Palmate Newt Duration at the Snake Pond

Palmate newt duration at the Snake Pond demonstrated a significant relationship with ‘air frost in March’ and ‘maximum temperature in July’. Model averaging showed that the strongest model was when these two factors were combined (w=0.75) (Table 15).

Table 15*: Best fit models for palmate newt duration at the Snake Pond when regressed with climate*

Model	df	AICc	ΔAIC	w
Frost in March + maximum temperature in July	4	95.3	0	0.75
Maximum temperature in July	3	98	2.7	0.19
Frost in March	3	100.3	5	0.06

Discussion

Median Capture Date

The only pond where there was a delay in more than one species of newt was the Snake Pond, where both great crested and palmate newts showed later seasonal activity over time. Great crested newts did not show a clear relationship between seasonality and climate at this site. There was a (nonsignificant) increase in the number of days of winter frost, and the minimum spring temperature decreased throughout the study period. Together, these factors would delay emergence from terrestrial refuges, and this relationship was identified in palmate newts at the Snake Pond. Palmate newts also showed an extension in their breeding period.

In comparison to the other ponds where these two species occur, the habitat of the Snake Pond is quite different; Garden Pond and Field Site are both open with lawn or rough grassland immediately surrounding the ponds (Appendix 2). The Snake Pond on the other hand, is within a small patch of woodland, potentially becoming increasingly shaded over the years. Although great crested newts prefer minimal shading (Jehle et al., 2011) there was no significant change in the quantity of newts captured throughout the study period at the Snake Pond, suggesting that there was little change in population size which could have influenced median date.

Contrastingly, despite the Snake Pond being a more suitable habitat for palmate newts than the other ponds within the system, the number of newts caught declined throughout the study period (Appendix 3). Larval survival of newts is low, likely due to a combination of predators and interspecific competition (Griffiths et al., 1994). In a mesocosm experiment with larvae, Van Buskirk (2007) found that presence of great crested newts negatively affects palmate newts. Griffiths et al. (1994) performed experiments in the field and laboratory at Well Court and found a similar result; once great crested newt larvae reached a certain size they were a significant predator of both smooth and palmate newt larvae. They also found evidence of interspecific competition between smooth and palmate newts during larval development.

As the Snake Pond is within a small copse of trees surrounded by farmland, it is possible that terrestrial refuges could be closer to the pond, therefore the newts can afford to wait until conditions are optimum before emergence and migration. Newts orientate themselves partially via olfaction (Jehle et al., 2011), so a closer refuge may permit the newts to smell when the pond is suitable and/or when other newts are also migrating (Hayward et al., 2000) which may trigger their own emergence. Newts at the other ponds however, may have a further distance to travel and so leave their terrestrial refuges earlier to ensure that they have the best chance at reproduction. Shaded woodland is likely to remain cooler for longer, so optimal temperatures may not be realised until later in the season. Given that the Pylon Pond is also situated within woodland we might expect to see significant changes there also, but none were observed in either of the species at this pond. This may be due to the difference in size of the ponds (see paragraph below in Duration) but also the surrounding habitat; the Pylon Pond is adjacent to a large continuous tract of woodland, allowing newts to potentially disperse further.

Smooth and palmate newts are frequently found to coexist across their range with a high degree of niche overlap, in both habitat and feeding (Griffiths, 1987, 1986) . Although they show slight macrohabitat partitioning with selection of breeding sites (Cooke and Frazer, 1976), there is no temporal separation in their breeding migrations. Such coexistence is likely dependent on an abundant food source, removing competition (Griffiths, 1987). More recently, Van Buskirk (2007) found that when smooth and palmate newts coexist in the same ponds, the result is a (non-significant) delayed emergence of smooth newts. The present study found all three species of newt naturally coexisting together in the study ponds, with little obvious impact on one another. Although no significant change in median date was noted for smooth newts at any of the ponds, it was not possible to assess whether or not their phenology had changed due to the presence of other species, as all three species were present throughout the entire study period. The delay in palmate newts but not smooth newts suggests that the niche overlap between the two species may also begin to shift. It has been suggested that asynchronous responses between species may reduce interspecific competition, however this is not likely to have a major impact on smooth and palmate newts which show little competition despite high niche overlap (Griffiths, 1987).

Given that newts do not begin to migrate during suitably mild spells in the middle of winter, it could be suggested that perhaps photoperiod plays a role in triggering migration, as it does so in birds (Canavero and Arim, 2009; Gwinner, 2012). However, if this was the case then we are not likely to observe any significant changes in arrival date as day length does not vary between years (Sparks and Smithers, 2002). This strategy would also pose a risk to amphibians as photoperiodism may force them into activity during periods of hot or dry weather which would be detrimental.

Duration of the Aquatic Period

The Field Site ponds are more actively managed than those at Well Court, with researchers maintaining water levels to avoid complete desiccation during the summer months. The Field Site has been consistently managed since its creation in 1999, meaning that the observed changes in duration of aquatic period are due to shifts in smooth and great crested newt behaviour, rather than changes in pond water level. Ponds within the Well Court metapopulation on the other hand, are more likely to suffer from varying levels of desiccation due to the climate and thus affect the duration of the aquatic period.

A pond within shaded woodland will be slower to desiccate than those which are open and exposed to increasingly higher temperatures through direct insolation. Although water levels were observed to fluctuate throughout the seasons, the Snake Pond is both the largest and deepest of the five ponds analysed, making it more likely to retain water towards the end of the season when the smaller ponds within the metapopulation may have dried up. Maximum temperatures for August decreased over the study period, reducing the likelihood of desiccation. This could in part explain the longer breeding duration observed at the Snake Pond for smooth and palmate newts. It does not however, account for why the breeding duration for great crested newts did not increase at this pond. It is also difficult to explain the relationships between duration and rainfall in the previous September.

Conclusion

There was notable variation in responses at each pond, even within the same metapopulation, showing that the unique habitat and management regime of ponds can affect how amphibian populations will respond and adapt to climate change. The increase in duration of aquatic period by great crested newts at the Field Site suggests that newts are indeed shifting their breeding patterns. This emphasises the importance of pond management in order to accommodate those shifts and maintain amphibian populations.

CHAPTER THREE: Variation in Individual Arrival times and Body Condition of Great Crested Newts at the Field Site

Abstract

Advancement in spring phenological events are well documented as an indicator of climate change. Few studies have analysed long-term data sets of great crested newts, *Triturus cristatus*, in response to climate change, but a trend towards earlier breeding is suggested. As an indicator of fitness, body condition is an important parameter in identifying how changes in climate may affect the viability of a population. Using regression analysis, this study looked at long-term trends in (1) the arrival time of 16 male and female great crested newts, determined by the date of first capture in funnel traps; and (2) body condition of the same newts using the Scaled Mass Index, between 1999 and 2016 at a site in Canterbury, Kent. Both factors were then regressed with climatic variables to identify any relationships. There was no consistency or trends in the arrival times of individual newts over the years, but significant relationships were found with monthly precipitation totals and climate during the winter months. This may be due to the need for moist conditions for migration. As winter precedes the breeding period, climate during this time could influence the onset of migration. Both sexes showed an increase in body condition over the study period and changes were greater in females than males. Significant relationships were found between climate and body condition during the winter months, particularly so for females, and during the previous summer months. Both of these time periods can affect body condition; summer is important for resource acquisition and changes in brumation during winter, such as disruption, can alter the metabolism of the newts. The predicted mild winters and hotter summers could lead to changes in body condition, and thus fitness, of great crested newt populations requiring conservation management to take climatic changes into account.

Introduction

Population trends may mask important trends within individuals if they are doing different things (Mendonça et al., 1985). For example, the age-related increase in fecundity found in a population of blackbirds was due to intrinsic individual variation rather than an overarching trend caused by environmental pressures (Desrochers and Magrath, 1993). Changes in the breeding trends of populations could either be as a result of individuals progressively shifting their migration patterns or due to a general shift in the population as a whole, but with no consistency within individuals. Studies looking at changes in the timing of breeding of amphibians have shown a tendency to focus on populations (Table 1), however great crested newts are an ideal species for non-invasive capture-recapture studies due to their unique ventral patterns, allowing for analysis into individual movement patterns.

Body condition is a measure of an animal's fitness and energy reserves, which reflects their ability to reproduce, survive, feed and to cope with environmental pressures. Body condition can be measured as relative 'fatness' based on ratios between their mass and body size (Green, 2001; Jakob et al., 1996; Jarvis, 2015; MacCracken and Stebbings, 2012; Schulte-Hostedde et al., 2005). In newts, body condition fluctuates throughout the breeding season (Arntzen et al., 1999a; Bonetti, 1996; Jarvis, 2015) and is correlated with changes in body size, such as seasonal crest development in males, age, food acquisition, and female fecundity (Beebee, 1996; Green, 1991; Jarvis, 2015; Jehle et al., 2011). It is at its highest in spring, for both adults and juveniles, at its lowest in summer and is generally higher in males than females (Arntzen et al., 1999a; Jarvis, 2016). For brumation, amphibians rely on accumulated fat reserves, and during mild winters, metabolism can increase throughout this period thereby using more energy (Griffiths et al., 2010; Reading, 2007). Survival throughout this winter period is thus dependent on high body condition prior to brumation (Reading, 2007).

Little is known about changes in body condition between years. One study of great crested newts found female body condition to decline over the study period while that of males fluctuated (Jarvis, 2015). In common toads (*Bufo bufo*), female body condition declined over the study period in relation to warmer than average years, and a reduction in body size was found during mild winters which in turn reduced female fecundity (Reading, 2007b). Great crested newts are ideal for such studies as their unique ventral patterns allow for non-invasive capture-mark-recapture.

Body condition is expressed as an index combining body size and body mass; in newts this is snout-vent length (mm) and mass (g). A range of indices exist based on variations in calculations between these two factors, often involving the residuals from regression. These indices have been compared and developed to improve reliability (Băncilă et al., 2010; Jakob et al., 1996; Peig and Green, 2010). The relatively new scaled-mass index (SMI) (Peig and Green, 2009) was found to account for ontogenetic variation, sexual dimorphism in size and avoided bias towards larger individuals, which other indices failed to do (Peig and Green, 2010). This novel index is already being explored and adopted by ecologists and biologists worldwide (MacCracken and Stebbings, 2012; Maceda-Veiga et al., 2014).

Using a selection of individual great crested newts at the Field Site, this chapter addresses whether arrival time varies between individual newts over twenty years, whether there is any difference in arrival time between genders and if any observed changes are related to climate change. The body condition of the same individuals will also be assessed for trends over time, differences between gender and in response to climate.

Methods

Individual First Arrival

To see how the first arrival week of individual great crested newts varied over time, first-capture data was collated for males and females at the Field Site. The eight most frequently recaptured newts of each sex were chosen as a sample. Capture period ranged from 6 to 17 years.

The first-capture week for each year was plotted for each newt and a regression line applied, to identify any obvious trends in first arrival week over time. The five-stage analysis as described in Chapter Two was then applied to identify any significant trends and relationships with climate.

Individual Body Condition

Using the scaled mass index (SMI) (Peig and Green, 2009) the body condition of the same 16 great crested newts during peak season (Weeks 6-12; typically, April-May) was calculated. If newts were captured more than once during this time period, the mean was taken to provide a single value for each year.

The scaled mass index was calculated using the following equation (Peig and Green, 2009):

Scaled mass index: $M_i = M_i \left[\frac{L_0}{L_i}\right]^{bSMA}$

Where:

M_i = the body mass of individual *i*

L_i = the linear body measurement of individual *i*

L_0 = an arbitrary value of L (e.g. the arithmetic mean value for the study population)

^{bSMA} = the scaling exponent estimated by the standardised major axis regression of lnM on lnL

With an SMI value for each year, these were then plotted to visualise any obvious trends over time for each newt independently. The five-stage analysis as described in Chapter Two was applied to these data to identify significant trends and relationships with climate. Due to repeated analysis on the same sixteen individuals, Bonferroni corrections were applied. Three-way ANOVA was used to look for any significant variation between gender, year and individuals.

Body condition was analysed for great crested newts at the Field Site only due to the availability of morphological data.

Results

Arrival of Individual Newts in Relation to Climate

Regression analysis revealed no obvious delays or advancements in first arrival week for individual great crested newts and there was no statistically significant relationship between first arrival week and year (Table 16).

Table 16: Results from regression analysis with the arrival week of individual newts against year

Females	P value	Males	P value
Audrey	0.57	Bruce	0.72
Gwyneth	0.16	Clint	0.26
Halle	0.43	Dustin	0.46
Kiera	0.56	Hugh	0.56
Marilyn	0.96	Kiefer	0.72
Renee	0.53	Mr.T	0.63
Terri	0.06	Richard	0.43
Whoopie	0.68	Sean	0.15

Trends in Individual Body Condition

All newts except two males were found to show an increase in body condition (SMI) over the study period (Figure 13). These trends were statistically significant, highly so in most cases (Table 17). Mr. T displayed a slight non-statistically significant decrease in SMI over time. Dustin showed no trend. Three-way ANOVA suggests that body condition varies between individuals, gender and years (Table 18).

Table 17: *Results from regression analysis with SMI against year*

Females		Males	
Audrey	**	Bruce	**
Gwyneth	**	Clint	***
Halle	**	Dustin	ns
Kiera	**	Hugh	**
Marilyn	***	Kiefer	*
Renee	***	Mr.T	ns
Terri	***	Richard	***
Whoopie	***	Sean	***

"*" =<0.05, "**"= <0.01, "***"=<0.001, "ns" = no significant trend

Table 18*: Results from 3-way ANOVA with SMI as the response*

	Df	Sum Sq	Mean Sq	F value	P
Gender	1	165.95	165.95	80.28	<0.001
Year	1	206.23	206.23	99.76	<0.001
Individual	12	26.54	19.04	9.21	<0.001
Residuals	110	227.39	2.07		

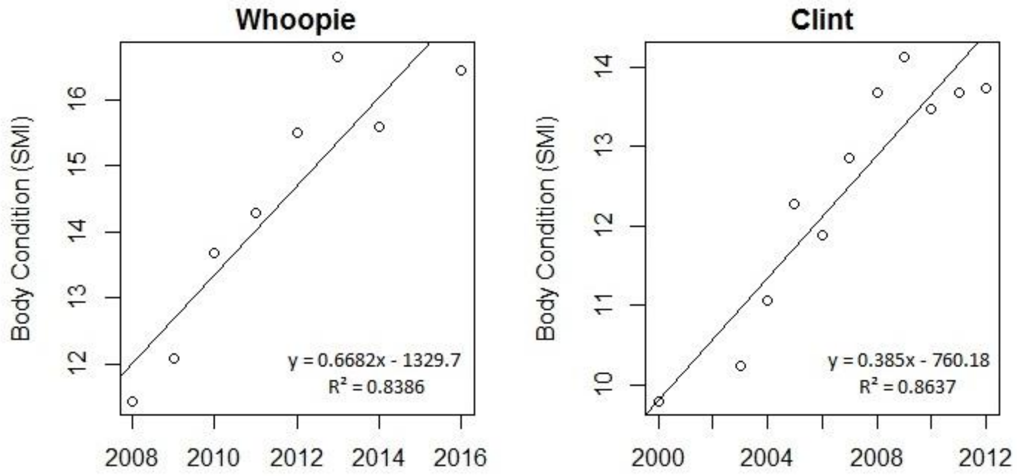

Figure 13: *An example of highly significant changes in body condition (SMI) over time for a female (Whoopie) and male (Clint) great crested newt, both p<0.001. Newts chosen as examples of those with the highest significance.*

Individual Body Condition and Climate

There was no clear pattern in significant relationships between climate and individual body condition of great crested newts. When accounting for Bonferroni corrections ($\alpha/k = p = 0.003$, where $k=16$), there were only four significant relationships between individual body condition and climate, three of which were with the same newt, therefore they have not been classed as important and are not shown.

Discussion

Arrival of Individual Newts

Individual great crested newts did not show any consistent patterns between years in terms of the timing of their arrival at the ponds, which corroborates the lack of change observed for median capture date at the Field Site. Given that no change in median date or arrival were observed for great crested newts at the Field Site, it is still unclear as to whether phenological shifts are as a result of individual adaptation or through a general shift within the population. Prior to Bonferroni corrections there was a notable proportion of significant relationships between the first arrival of individual great crested newts and climate during the winter months. Newts will emerge for migration in late winter only once temperatures reach and are maintained above 4°C and when there has been sufficient rainfall (Jehle et al., 2011; Verrell and Halliday, 1985). Therefore, any change in climate during this period is likely to affect the timing of emergence and migration. British newts exhibit protandry, whereby males arrive at the breeding areas before females (Arntzen, 2002; Chadwick et al., 2006). Despite no changes in arrival date for individual great crested newts over time, they still retained this trait as a species, with males arriving an average of 2 weeks earlier than females. Males were also present in the ponds in more recurrent years than females, which was consistent with the tendency for females not to return to breed every year (Jehle et al., 2011).

Trends in Individual Body Condition

The vast majority of great crested newts showed an increase in body condition (SMI) over the study period. Body condition represents the general fitness of an individual and as such, is indicative of their ability to invest in reproduction, cope with environmental pressures, to feed, to fight and to survive (Green, 2001; Jakob et al., 1996; Jarvis, 2015; MacCracken and Stebbings, 2012; Schulte-Hostedde et al., 2005). Jarvis (2015) suggests that in great crested newts, male body condition is an indication of fat reserves whereas that of females represents fecundity, the former of which may be more reliant on environmental conditions. Chadwick et al. (2006) suggest that the greater degree of plasticity found in male salamanders could relate to lower temperature thresholds and thus greater sensitivity to changes in temperature.

The duration of the aquatic period for great crested newts was longer at the Field Site than at Well Court by an average of ten weeks, suggesting that the newts were likely to be feeding more during the summer before leaving the ponds. This would mean the newts were in better condition prior to hibernation and thus upon emergence the following year. The breeding season typically lasts 4-5 months (Jehle et al., 2011) and newts can sometimes still be found in ponds throughout late summer and early autumn. Duration of newt activity at the Field Site was highly related to rainfall in the previous September. Alongside manual replenishment of the ponds, this factor would determine the starting condition of the ponds for the following breeding season and so could inadvertently affect the duration of the next season.

Climate during the winter months can affect body condition through the quality and duration of the brumation period. Should the winter be milder, newts may emerge from brumation more frequently, thus expending energy with an increase in metabolism (Griffiths et al., 2010). A slight nonsignificant increase in 'days of air frost in winter' was noted throughout the study period, suggesting that winter was increasingly colder over the study period (Appendix 1). This would result in more effective and continuous brumation, thus saving energy and providing newts with a higher body condition upon emergence in spring.

Jarvis (2015) found variation between the body condition of male and female great crested newts across years. Male body condition fluctuated over the five-year study whereas that of the females declined. This contrasts with the findings of this study, whereby both males and females increased in body condition over time, and females more significantly so. Jarvis (2015) found no significant relationship between mean winter temperature and body condition, however the study only spanned a period of five years. This study, covering a 20-year period, found no significant relationships with body condition and climate, supporting Jarvis' findings and suggesting that body condition is more likely to be linked with other characteristics of the habitat, such as resource availability.

By analysing the body condition of newts during peak season, this study eliminated the variation found throughout the breeding season (Arntzen et al., 1999b; Bonetti, 1996; Jarvis, 2015). Given that great crested newts at the Field Site (at both an individual and species level) were not found to show significant changes in first arrival or median date, and thus peak season over the study period, the measurements for each year are comparable.

CHAPTER FOUR: General Discussion

This study aimed to investigate whether two neighbouring metapopulations of newts were responding to climate change over time by altering their breeding phenology, and if the two metapopulations, and three species, were responding in the same way. Phenology was assessed by median capture date, duration of aquatic period, individual arrival and individual body condition.

The data reveal that there have been changes in newt phenology over the study period, though interestingly this varies between pond and species: great crested newts have shown a delay in median capture date and a lengthening in duration of aquatic period at two out of five ponds, plus an increase in body condition; palmate newts have shown a delay in median capture and lengthening of duration at one pond; and smooth newts have shown a lengthening in duration at two of the five ponds. There does appear to be a relationship with climate, but as the changes in phenology have not been observed at all ponds within the same local climatic region, it suggests that the effects of climate change may be indirect. The variation of responses both between and within the neighbouring metapopulations suggests that changes in climate may not be affecting all populations in all ponds in the same way.

Great crested newts showed the greatest changes in the timing and duration of activity, followed by the palmate newt. The smooth newt showed changes in duration at a greater quantity of ponds, although the observed changes were smaller than those found in the other two species.

Smooth newt distribution throughout Europe stretches from Ireland in the east to Russia in the west, and from Greece in the south to Norway in the north (IUCN, 2008c). This geographic range spans a multitude of climates (such as Mediterranean, continental and maritime), suggesting that the smooth newt could be more ecologically plastic and adaptable to a variety of climate. The palmate newt however, is restricted to western Europe, with a northerly limit of Scotland (IUCN, 2008a), suggesting a preference for maritime climates. Therefore, changes in the climate towards hotter and drier trends may affect the distribution and fecundity of palmate newts (Galloy and Denoël, 2010) more so than smooth newts.

Despite showing variation, males and females of all species did not differ in the timing and duration of their breeding activity. This conflicts with the findings of Chadwick et al. (2006) who found greater changes in median arrival for males than females, although methodological differences do not allow for direct comparison with this study. Male newts migrate to ponds before females (Arntzen, 2002; Verrell and Halliday, 1985) but ultimately, if males and females were to alter their phenology differently, this could potentially result in mismatches which would be detrimental to reproductive success and the population itself. This is perhaps supported by the finding that no individual great crested newts showed significant trends in their timing of breeding. It suggests that the trends observed for the populations come about as gradual shifts in the behaviour of the population as a whole, rather than as the accumulated trends of individuals, therefore maintaining behavioural dimorphism as opposed to individual variation.

In the current literature, of 46 amphibian populations studied across Europe and North America, only four were found to show delays in breeding activity (*Ambystoma opacum, Bufo fowleri, Eurycea quadridigitata* and *Bufo bufo*), compared to 23 which were found to be breeding earlier (see Table 1). Of these four species, three were anurans and only one a urodele. This study therefore differs from the majority of current research (Table 1), having found delayed seasonality but no advances, and is the first to document delayed breeding activity in urodeles within Europe.

Common frogs were found to spawn earlier in the west of the UK than in the east, due to warmer maritime temperatures (Sparks et al., 2007). It is possible that this could also explain some of the variation in newt phenology, as contrasting results are found between Chadwick et al.'s (2006) study in the west and the results of this study in the east of the UK. This geographical gradient however, fails to explain the contrast between the neighbouring counties of this study and that of Beebee (1995).

Alongside phenological advancement, Chadwick et al. (2006) reported a lengthening of the aquatic period for both smooth and palmate newts at a pond in Wales. Over a period of 24 years, a mean increase of 21.3 to 28.2 days was observed across both species. This study supports their finding, with a minimum increase of 5.4 weeks and a maximum of 10 weeks in duration of the aquatic phase for all three species over 20 years.

Although projections for the UK point towards increasingly hotter temperatures (DEFRA, 2009), the trends show a significant decrease in maximum August temperature for the study period. This deviation from the overall climatic trend could in part explain why delays were observed in newt phenology. Studies documenting phenological advancement also reported climate patterns that were in line with the overall projections for the UK (Beebee, 1995; Chadwick et al. 2006); the opposite to what was found in this study. It serves as a reminder that study periods encompass only a snapshot of wider climate change and perhaps these short-term trends are of greater importance to short-lived species than long-term patterns expanding further than one or two generations.

The Field Site ponds never fully desiccate as they are usually topped up by researchers, so could prove to be an important resource for newts during particularly hot summers. This combined with the decrease in maximum August temperature could help to explain the increase in body condition for great crested newts and also the increase in duration of aquatic period for both great crested and smooth newts at the Field Site.

Body condition increased for great crested newts at the Field Site. Although the population at the pond has grown over the study period, potentially increasing intraspecific competition, this population appears to be increasing in fitness and thus may be better able to cope with any stresses imposed on them by climate change.

Limitations of this Study

Population size needs to be taken into account when assessing and comparing arrival time as there is a higher probability of detecting arrival in a larger population (Tryjanowski and Sparks, 2001). At all ponds, smooth newt populations were smaller than the other two species, therefore there is the possibility that the population sizes were too small to detect changes over the time period. Occupancy modelling could be a useful tool to identify the effort needed to detect change in long-term monitoring sites.

Other research into urodeles have used first sightings or drift-fences to calculate first and median arrival dates (Beebee, 1995; Chadwick et al., 2006; Todd et al., 2011). This study used funnel trapping around a truncated start date; it did not allow for analysis using exact arrival dates so capture date was the parameter used instead. The ‘median’ was utilised in keeping with other studies into amphibian phenology (Chadwick et al., 2006; Todd et al., 2011). In order to try and account for this truncation, modal date i.e. peak, was also analysed. Aside from one instance, there was little correlation and significance between modal date over time and in conjunction with median date. Quantities of newts in the ponds appeared to gradually increase over time (Appendix 3), so perhaps the use of modal date is best suited to analysing explosive breeders with more defined migrations such as anurans (Sinsch, 1988).

The climate is a complex system and climate change even more so (Loarie et al., 2009). Some of the variables analysed displayed trends which seemingly contradicted those observed for the UK as a whole. This is likely due to climate data being analysed for just the years of the study period, and only Central England and South East/Central South data were used. Therefore, although the CET are thought to be generally representative of the UK (Duncan, 1991), the climate data analysed were only a snapshot in time and location of a much larger process.

Selecting for climate variables is somewhat arbitrary; we can use the best of our collective knowledge on what might impact the natural history of a species but every aspect of an animal's life cycle is affected by a multitude of environmental factors, many of which are intertwined in ways that we are not yet aware of or do not understand. Few studies have analysed soil temperature as a measure of climate, likely due to a lack of available data. Further studies may want to consider this variable as a potential cue to migration (Sexton et al., 1990; Wisniewski et al., 1980).

The surveying methods of this study did not allow for much flexibility in climate analysis; with a truncated start date, analysis into the 30-90 days prior to first arrival (such as Todd et al., 2011) was not possible to determine. Climate was analysed in monthly blocks, which is convenient for analysis but not necessarily reflective of amphibian time scales (Chadwick et al., 2006). Gamboni (2005) found no significant relationships between newt migrations and temperature in a single yearly study, suggesting that the effects of weather may be delayed, though the extent to which is still unknown. There is uncertainty in how to select the climatic effects which may have the greatest effects on amphibians, and research into phenology has shown a wide range of relationships with climate variables and time scales. There is a likely possibility, supported by some of the models produced in this study, that amphibians are affected more so by interactions between environmental variables than by individual aspects alone.

Implications for Populations

In terms of climate change, the study has discovered some relationships which could further affect the phenology of newts and potentially in different localities. In great crested newts, a lagged decrease in maximum August temperature and a decrease in the quantity of autumn rain days suggests later breeding, whilst a lagged decrease in September rainfall points towards a lengthening of the breeding season. In palmate newts, a decrease in minimum spring temperature and an increase in March air frost may lead to delayed seasonality, whereas an increase in March frost and a decrease in maximum temperature during July may lengthen the breeding season. Smooth newts may show a lengthening of the breeding season alongside a lagged decrease in September rain and a lagged decrease in maximum August temperature.

Changes in the phenology of newts can have cascading impacts on the wider community. Later breeding activity could put newt larvae at greater risk of predation pressure if invertebrate predators are not also changing their phenology; dragonfly nymphs for example, will be much larger and thus a greater threat once newt larvae hatch later in the season (Chadwick et al., 2006; Lewis, 2012). On the other hand, a greater length of time spent in ponds over the summer will increase the predation pressure by newts on the aquatic invertebrate communities (Jehle et al., 2011). It would be beneficial to include monitoring of dependent species i.e. predators and prey of newts, to further assess the impacts of such alterations.

As well as affecting interactions between wider taxa, variation in the responses between sympatric species could have unforeseen effects; later breeding activity of small newts could put their larvae at greater risk of predation by larger great crested adults and/or larvae. An increase in the duration of the aquatic phase could affect egg-laying dates and therefore larval survival. A longer time spent in the water could mean that females are able to lay eggs both early and later on in the season. Early eggs are likely to result in larvae that metamorphose before pond desiccation. Later eggs will yield larvae that may overwinter and emerge the following spring as larger metamorphs with greater survival, however they run the risk of desiccation if rainfall over summer and winter is low (Griffiths, 1996). This strategy of egg-laying could enable newts to survive despite uncertain hydroperiod. Larvae which overwinter before metamorphosis become larger adults (Bruce, 1982). Fewer instances of this could affect survival and reproductive opportunity, as female great crested newts show preference for larger males (Hedlund, 1990), whilst female palmate newts prefer males with a smaller body size (Haerty and Secondi, 2007). On the other hand, there could be an increase in overwintering individuals, in which case the reverse would be seen.

The consistent increase in body condition of great crested newts suggests that the fitness of the population at the Field Site has increased over time and therefore has a greater chance of survival and reproduction. A lengthening of the aquatic phase however could threaten a reduction in adult survival, as newts exhibit higher mortality rates during the aquatic phase (Kalezic et al 1994).

The effects of climate change need to be taken into account when planning conservation management for amphibians. Finding a balance between creating and maintaining ideal habitat for great crested newts e.g. with little shade on ponds, but also attempting to reduce premature desiccation risk via increasing temperatures and decreasing precipitation will be a challenge. Although regular desiccation of ponds is beneficial for reducing invertebrate predators, drying out too early will hinder amphibian reproductive efforts and may have long term effects on population numbers and fitness (Gervasi and Foufopoulos, 2008). Shoo et al. (2011) identified a selection of management actions for reducing amphibian biodiversity loss in the face of climate change to be tested and incorporated into conservation management. Such actions include providing supplementary refuges to reduce thermal stress and desiccation, manipulating pond canopy cover to maintain optimal temperatures, and manipulating water levels to increase larval survival during varying precipitation regimes.

Future Research

It would be interesting to analyse the body condition of great crested newts at ponds within the Well Court metapopulation to see if similar patterns are observed within the same climatic envelope. Jarvis (2015) found that due to the close proximity and similar microhabitat of his study ponds, the body condition of great crested newts did not vary between ponds. However, the body condition of common toads has been found to vary between sites (Reading, 2010; Sztatecsny and Schabetsberger, 2005).

This study is the first to document delayed seasonality in urodeles within Europe and only the second to document such a trend in urodeles in the current literature (Todd et al., 2011). Each of the studied species has a wide distribution across Europe (IUCN, 2008a, b, c) and it is currently unknown how different populations are responding to climate change across the species' ranges. To identify whether there are any latitudinal trends or if the observed responses are unique to each individual population, similar analysis and comparison should be carried out for newt populations across the ranges of the species studied. This would create a bigger picture of how climate change is affecting newt populations, which could guide and refine essential conservation efforts and management. *Bufo bufo* provides an example of how a single amphibian species can vary in its phenological response to climate across its range (Arnfield et al. 2012; Reading 1998, 2003; Sparks et al. 2007; Tryjanowski, Rybacki, and Sparks 2003). Alongside this study, these findings highlight how little we know about amphibian responses to climate change and therefore bring attention to the need for a greater understanding in how a variety of species may be adapting or facing detrimental effects due to climate change.

With the right tools and knowledge, many of the threats facing amphibians and other taxa, such as habitat loss and invasive species, can be managed and even reversed. Climate change however, is inevitable and irreversible (Jenkins et al., 2009; Parry et al., 1998); the uncertainty lies in the degree of change that is likely to occur and this is dependent on human behaviour and mitigation measures (Karl and Trenberth, 2003). In effort to tackle the extinction crisis (Ceballos et al., 2015; Wake and Vredenburg, 2008), it is essential that we have a continuation of and an increase in long-term monitoring projects. Without such monitoring it is currently difficult, if not impossible, to predict the responses of species and populations to changing environmental pressures. Once we have this knowledge, mitigation actions can then begin to focus on compensating for climate change to conserve biodiversity. To further improve the long-term monitoring at the Field Site, it is recommended that surveying starts earlier in the year in order to identify the start of the season and to allow for analysis of first arrivals in the future.

This study analysed the effects of climate change on adult newts but due to their complex life cycles, amphibians are likely to respond to changes in varying ways at each life stage (Beebee, 1996; Griffiths, 1996). Eggs and larvae are less mobile and much more dependent on aquatic bodies, whereas the adults of some species are largely, if not wholly, terrestrial (Griffiths, 1996) and so exhibit different adaptive mechanisms to changes in the environment (Jehle et al., 2011). In order to fully understand the impacts of a changing climate on species and populations, it is necessary to study all life stages and all aspects of each stage i.e. behaviour, physiology and reproduction (Carey and Alexander, 2003). It is then essential that findings from such studies are implemented into conservation policy and legislation in order to mitigate the threat to potential population declines.

Conclusion

The effects of climate change are complex and the responses of newt populations to climate change vary even on a local scale. This study is unique in its analysis of two neighbouring metapopulations using two long-term datasets and is believed to be the first to document: a) a delay in median date for great crested and palmate newts, and b) a lengthening of the aquatic period for great crested newts, adding to our understanding of phenological responses to climate change in urodeles. Studies into *Bufo bufo*, for example, have found a variety of phenological responses in different localities (Arnfield et al., 2012; Reading, 2003, 1998; Sparks et al., 2007; Tryjanowski et al., 2003), reaffirming that amphibians appear to be responding to climate change on a population-basis rather than at species level (Sparks et al., 2007).

On a wider scale, this study contrasts with the majority of literature. Multiple studies in the USA have found delayed migrations in avian populations (Bezzel and Jetz, 1995; Bradley et al., 1999; Gatter, 1992; Oglesby and Smith, 1995), however very few, if any, temperate species of any taxa have displayed delayed reproductive phenology. The majority of research in this area documents that many bird species have shown advanced egg laying dates (Bergmann, 1999; Brown et al., 1999; Dunn and Winkler, 1999; Goodenough et al., 2010; MacInnes et al., 1990; McCleery and Perrins, 1998; Sæther et al., 2000; Winkel and Hudde, 1997), butterflies are appearing earlier (Forister and Shapiro, 2003; Roy and Sparks, 2000; Stefanescu et al., 2003) and flowering, bud burst and harvest date have advanced in a variety of plant species (Cayan et al., 2001; Hannah, 2011; Menzel et al., 2003; Parmesan, 2006). As mentioned previously, the few studies that have found delays in phenology concerned anurans, primarily in North America (Arnfield et al., 2012; Blaustein et al., 2001; Todd et al., 2011). Only one population of salamander in the USA has shown delayed phenology (*Ambystoma opacum*) (Todd et al., 2011) yet this species is an autumn breeder and so exhibits a rather different life history to the newts found in the UK (Lannoo, 2005). What we cannot yet derive from these findings, is whether or not climate change will be detrimental, especially as the majority of species studied in relation to climate change are not threatened (Winter et al., 2016).

Despite long-term datasets of amphibian phenology dating back to 1846 (Terhivuo 1988), and the widespread distribution and abundance of smooth, palmate and great crested newts, it is surprising that very little is known about the reproductive phenology of these species over time. By analysing the responses of two neighbouring metapopulations consisting of multiple ponds, this study was vital in highlighting the potential variation in responses to climate change both between and within species of amphibians and localities. The key finding of delayed seasonality in great crested and palmate newts contrasts with the majority of research in this area and therefore highlights a lack of understanding in how coexisting species are adapting to changes in the climate. Great crested newts are of particular interest due to their status as a European Protected Species yet only one other study exists which analyses their response to a changing climate. Climate change is inevitable and it is clear from these results that we are not aware of how individual populations, let alone species, are responding and what the impacts of these responses will be on the wider population and communities. Without this knowledge, it will be impossible to implement effective conservation management strategies to reduce the loss of amphibian biodiversity, not just in the future, but now.

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Appendix 1

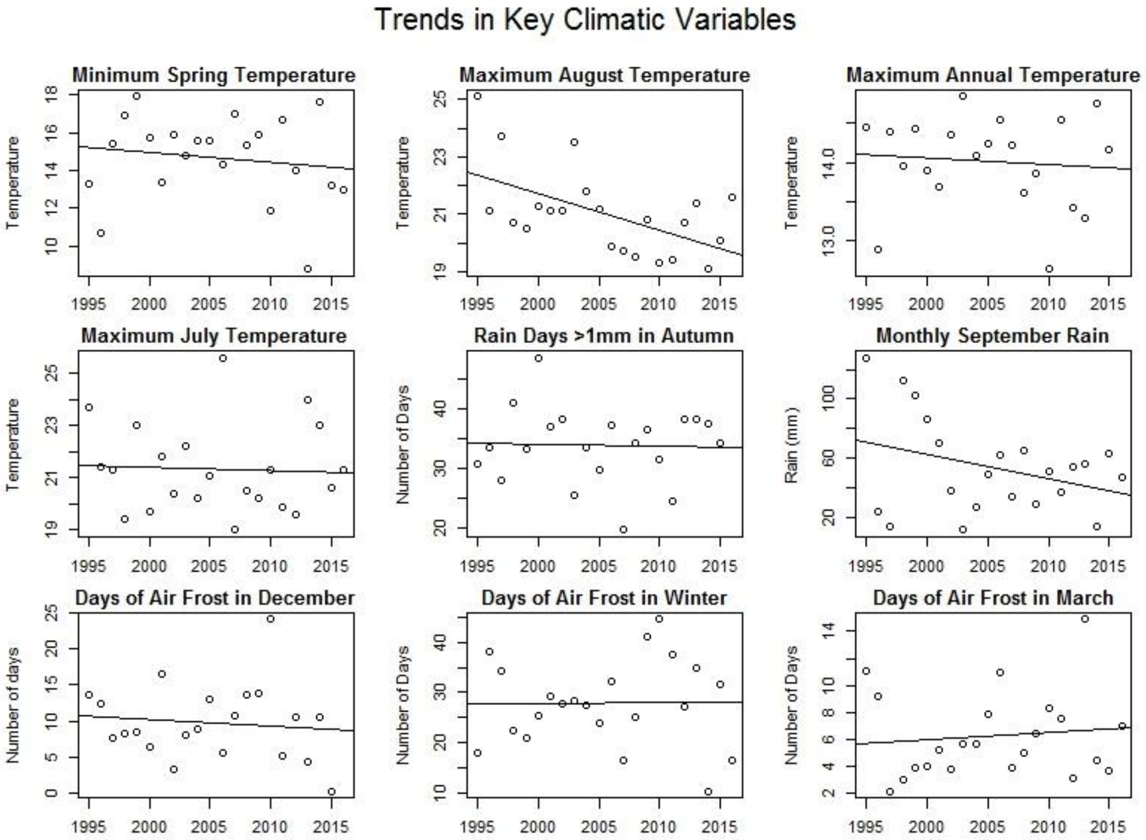

__Figure 14__: Trends in key climatic variables as used in model averaging. Data taken from Hadley Centre, Met Office, UK.

Appendix 2

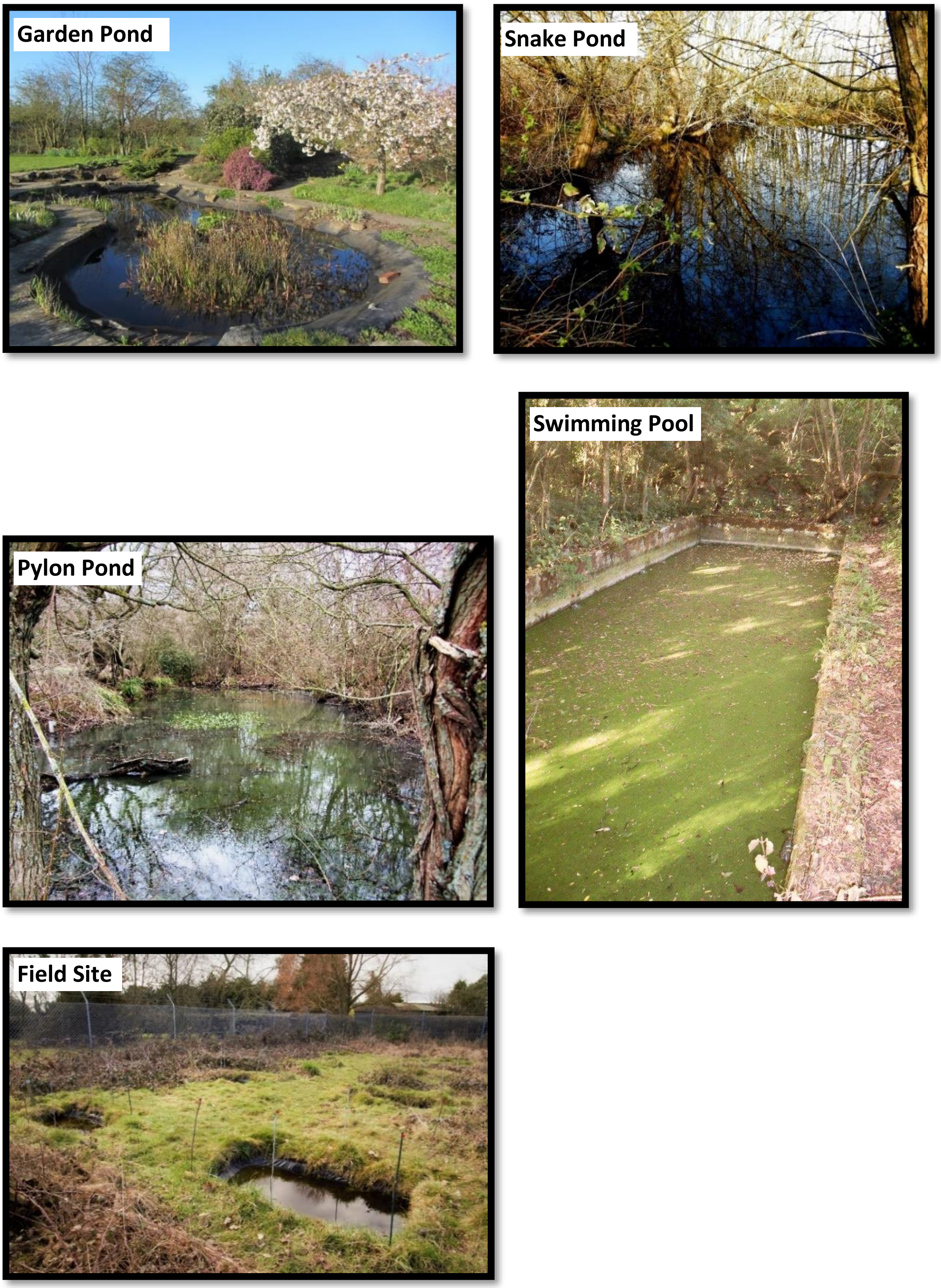

Figure 15: Photographs showing the ponds at the two study sites. The top four photos are at Well Court and the bottom photo is the Field Site.

Appendix 3

Changes in Capture Rate over Time

Capture effort has remained relatively stable over the study period with a standardised start date. Some years did have more/less survey weeks but this was usually dependent on captures of newts and so is not biased by human effort. Regression was used to look at how the number of *captures* of newts had varied over time at each pond.

Results

There was an increase in the number of great crested newts captured at the Field Site as the study period progressed, but a decrease in the number of captures of the same species at the Garden Pond, Pylon Pond and Swimming Pool. There was no change at the Snake Pond. Smooth newt captures decreased at the Snake Pond and Swimming Pool and remained unchanged at the other ponds. Similarly, palmate newt captures decreased at the Snake Pond but remained unchanged at the other ponds. Only those which were statistically significant are displayed below (Figure 16).

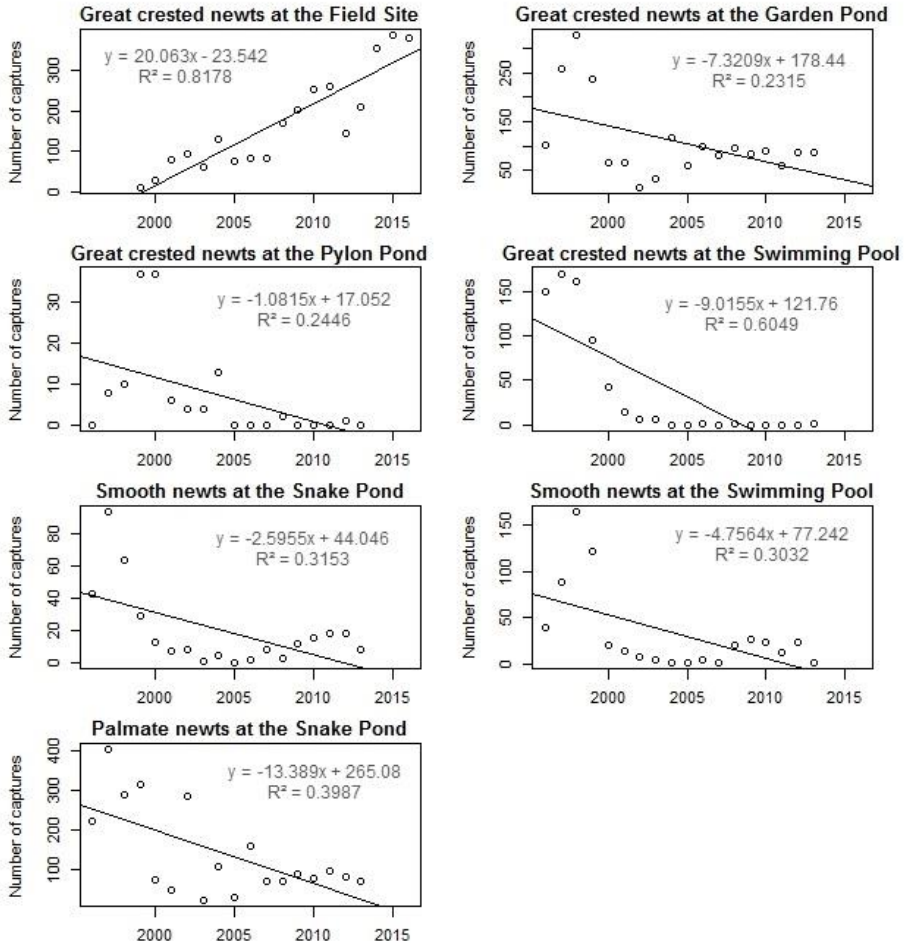

Figure 16: *Significant changes in the quantity of newts captured during the study period, 1996 – 2016*

Great Crested Newts at the Field Site

Capture rate of great crested newts increased at the Field Site (Figure 16), and capture-mark-recapture data allowed for identifying the quantity of individuals caught each year, showing that the population is increasing (Figure 17). There was a significant relationship between the number of different individuals caught and year (r (12) = 0.89, p = 1.65 x10^{5}).

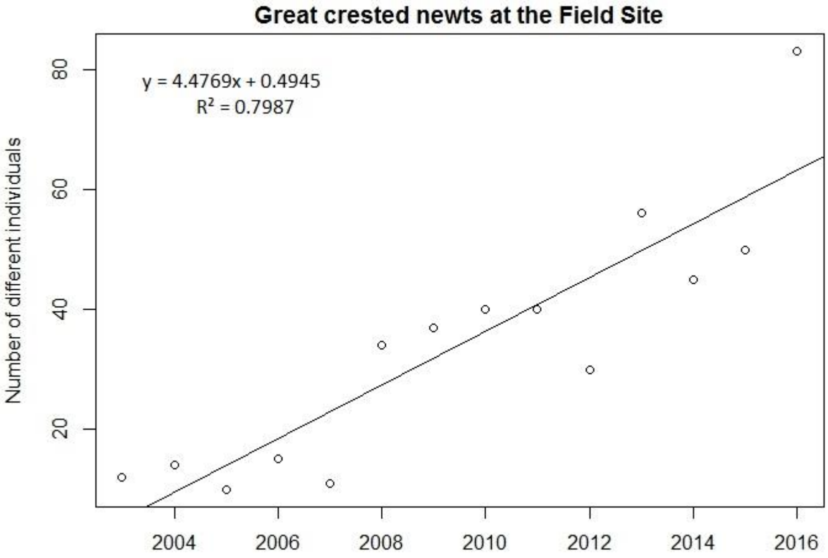

Figure 17*: The quantity of different individual great crested newts caught between 2003 and 2016 at the Field Site*