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Dynamics of a declining amphibian metapopulation: Survival, dispersal and the impact of climate

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ABSTRACT

Climate can interact with population dynamics in complex ways. In this study we describe how climatic factors influenced the dynamics of an amphibian metapopulation over 12 years through interactions with survival, recruitment and dispersal. Low annual survival of great crested newts (*Triturus cristatus*) was related to mild winters and heavy rainfall, which impacted the metapopulation at the regional level. Consequently, survival varied between years but not between subpopulations. Despite this regional effect, the four subpopulations were largely asynchronous in their dynamics. Three out of the four subpopulations suffered reproductive failure in most years, and recruitment to the metapopulation relied on one source. Variation in recruitment and juvenile dispersal was therefore probably driving asynchrony in population dynamics. At least one subpopulation went extinct over the 12 year period. These trends are consistent with simulations of the system, which predicted that two subpopulations had an extinction risk of >50% if adult survival fell below 30% in combination with low juvenile survival. Intermittent recruitment may therefore only result in population persistence if compensated for by relatively high adult survival. Mild winters may consequently reduce the viability of amphibian metapopulations. In the face of climate change, conservation actions may be needed at the local scale to compensate for reduced adult survival. These would need to include management to enhance recruitment, connectivity and dispersal.

1. Introduction

Climatic factors may influence population dynamics deterministically or stochastically, and can operate at both local and regional levels. Identifying the role of climatic factors in population declines and extinctions therefore poses significant challenges (e.g. McCarty, 2001; Thomas et al., 2004). For example, short-term fluctuations in rainfall can influence the hydroperiod of a temporary pond in an unpredictable way, and this may impact the survival of aquatic organisms in a stochastic fashion. On the other hand, global warming may result in the pond drying up altogether, and in the longer-term this can result in deterministic extinctions (McMenamin et al., 2008). Equally, local rainfall can interact with hydrology in complex ways so that water levels of adjacent ponds vary asynchronously and unpredictably. Alternatively, a reduced water table at the regional scale can result in synchronous reductions in water level across all water bodies. As the persistence of a metapopulation is ultimately determined by birth rates and death rates, the impact of climate on survival within different subpopulations is fundamental to understanding the dynamics and conservation of the system.

Because many species breed in discrete, patchily distributed water bodies, metapopulation ideas have frequently been applied to the conservation of amphibians (e.g. Gill, 1978; Sjögren, 1991; Sjögren-Gulve, 1994; Sinsch, 1992; Vos and Chardon, 1998; Hels, 2002; Hels and Nachman, 2002; Griffiths, 2004). However, if population sizes are controlled by regional factors (e.g. a regional drought), then all local populations may be impacted in the same way and behave like a single population rather than like a metapopulation that depends on asynchronous dynamics (Hanski, 1999; Liebhold et al., 2004). Consequently, identifying whether a patchily distributed population displays the stochastic extinction–recolonization dynamics required by a metapopulation (sensu stricto) remains problematical (Harrison, 1991, 1994; McCullough, 1996; Baguette, 2004). Managing amphibian populations on the basis that they conform to a metapopulation structure may therefore be an oversimplification (Marsh and Trenham, 2000; Smith and Green, 2005). Because of the lack of clarity in knowing whether amphibian populations meet the assumptions of metapopulation models, here we use the term 'metapopulation' in the broadest sense to refer to a subdivided population that has a spa-

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tial structure (e.g. Harrison, 1994; Wiens, 1996; Marsh and Trenham, 2000).

In this study, we combine capture-mark-recapture data collected over a 12 year period with population viability analysis to explore the impact of variation in survival on the metapopulation dynamics of the great crested newt (*Triturus cristatus*). Declines of great crested newts in Europe have led to provisions under EU legislation that require member states to implement protection measures for this species. Although the great crested newt frequently exists in subdivided populations (e.g. Arntzen and Teunis, 1993; Miaud et al., 1993; Kupfer and Kneitz, 2000; Joly et al., 2001; Griffiths, 2004; Jehle et al., 2005; Meyer and Grosse, 2007), there have been no studies of long-term population dynamics within such subdivided systems. In particular, we test the hypotheses that: (1) annual survival varies between subpopulations; (2) annual survival is related to climatic factors and possibly climate change; and (3) subpopulations display asynchronous dynamics.

2. Materials and methods

2.1. Study site

The study site consisted of four pond systems on the Blean plateau approximately 3.5 km north of Canterbury, Kent, UK at an elevation of approximately 70 m. The ponds were located within a landscape consisting of mixed arable land and orchards, traversed by hedgerows, and with an area of semi-natural woodland to the north and the village of Tyler Hill to the south. The ponds were separated from each other by distances of between 200 and 800 m and all contained great crested newts between 1994 and 2006. As the next nearest newt pond was beyond the normal dispersal distance of great crested newts (i.e. >1 km from any of the studied ponds – see Oldham and Swan, 1997; Kupfer and Kneitz, 2000; Jehle and Arntzen, 2000), the four pond systems were considered to be isolated from other potential newt breeding sites.

The Pylon pond was a rectangular semi-natural pond of c. 185 m^2 and with a maximum depth of about 1.5 m. Most of the water body was covered by submergent or emergent vegetation, but the water level fell during the summer months. The nearest pond to the Pylon pond was the Snake pond, located 350 m to the south.

The Snake pond was a large semi-natural pond of variable surface area and shape, depending on water levels, but normally between 160 and 270 m^2. Maximum water depth was about 2 m. Water levels became severely reduced during most summers. The nearest pond to the Snake pond was the Garden pond system (230 m).

The Garden pond system comprised three butyl-lined ponds situated in the garden of a farmhouse, and constructed c. 1970 (Williams, 1999). The three ponds were within 2 m of each other and separated by a narrow path. Great crested newts appeared to move freely between them, based on the evidence of weekly capture records. All newts captured at these ponds were therefore grouped together as representing a population occupying a single site. The ponds varied in size between 4.5 and 32 m^2, with a maximum depth of about 1 m. The Garden pond system was equidistant between the Snake pond and the Swimming pool (230 m).

The Swimming pool was a disused concrete Swimming pool, constructed c. 1970, and abandoned soon thereafter. The surface area was approximately 45 m^2 and water depth varied from approximately 1.5 m at the shallow end to approximately 2 m at the deep end. The Swimming pool was located 230 m southeast of the Garden pond system.

2.2. Survey methods

Newts were captured using funnel traps (Griffiths, 1985) constructed from 1 l plastic bottles and spaced at approximately 2 m intervals along the shoreline. A total of 108 traps were set each week, 26 at the Garden ponds, 16 at the Swimming pool and 33 each at the Snake and Pylon ponds. Traps were set between 2000 and 2200 h and emptied between 0730 and 0900 h the next morning. Trapping commenced on the Thursday evening nearest to 1st March in each year and continued at weekly intervals in each season until no further newts were caught, usually mid-July. In most years two of the Garden ponds dried up in early summer, reducing the number of traps set from 26 to 12. In some years the Pylon pond also dried and trapping therefore ceased before mid-July at this site. Likewise, the Snake pond also desiccated in some years, and the number of traps set was reduced accordingly.

The belly pattern of each great crested newt captured was photographed (e.g. Hagström, 1973) and compared with those from previous weeks, and years, enabling detailed capture histories for all individuals to be constructed. From 1999 onwards, any great crested newt larvae captured in the traps were also counted. These were used to provide an index of reproductive success in each pond.

Climatic data were taken from cell FG224 of the UK Meteorological Office gridded datasets (Perry and Hollis, 2005), this cell covering the area that included the study sites. Exploratory correlations between annual survival and possible predictor variables revealed four potentially important climatic factors. These were: winter ground frost (WGF), winter mean minimum temperature (WT), spring rainfall (SR) and non-aquatic season rainfall (NAR). Dividing the rainfall data into spring rainfall (SR) and non-aquatic season rainfall (NAR) was regarded as appropriate given the different impacts of rainfall on aquatic and terrestrial stages of newts.

Winter ground frost was defined as the total number of days of ground frost in the months of December, January and February combined. Winter mean minimum temperature was defined as the mean daily minimum temperature (°C) over the period December–February each winter. Spring rainfall was defined as the combined rainfall (mm) in the months of March, April and May each year, whilst non-aquatic period rainfall was defined as total rainfall (mm) over the remainder of the calendar year (January–February + June–December), the period in which most newts were expected to be absent from ponds.

2.3. Mark-recapture analysis

Between-year adult survival based on capture-mark-recapture data was estimated using the Cormack-Jolly-Seber model in program Mark (White and Burnham, 1999). Pre-defined and customised models were used, allowing analyses that were both time and group dependent. “Groups” in this context represented analysis by sex, different ponds, and by sex and different ponds combined. In addition to these, models were also run with climatic data as covariates. Model fit was determined using the quasi-likelihood Akaike Information Criterion (QAICc). We followed Burnham and Anderson (2002) in using the ΔQAICc to determine the best model, and took a ΔQAICc of <2 as evidence of substantial fit, values between 3 and 7 as indicating less support and a ΔQAICc > 10 as having little or no support. Models with a ΔQAICc of over 10 were therefore discounted as unimportant. Goodness-of-fit was tested by means of 1000 bootstrap iterations of the best-fitting model and these were used to estimate the variance inflation factor ($\hat{c}$) for comparing models. Further diagnostic tests for transience and trap-dependence were carried out in U-Care (Choquet et al., 2009). Model assumptions followed Williams et al. (2002), whilst model notation followed Lebreton et al. (1992), viz: phi_i = survival probability from time i to $i + 1$; p_i = probability of detection (i.e. capture or recapture) at time i; (g) = group