Management history and climate as key factors driving natterjack toad population trends in Britain

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Abstract

Along with other amphibian populations in Europe and elsewhere, natterjack toad *Bufo calamita* populations in Britain have declined since at least 1960. Conservation management since the 1970s has aimed to halt the decline and maintain viable populations at key sites throughout the species' recent historical range. Here, we assess population trends from 1985 to 2006 at 20 British *B. calamita* sites and evaluate the role of active management in maintaining good conservation status. We investigated the effects of 25 climatic, site-characteristic and conservation management variables on population trends using general linear models. In single-variable analyses, rainfall variables showed negative relationships with population trends. Among the site characteristics, being located at the very edge of the species' range (northern Irish Sea coast) and occurrence of common toad (*B. bufo*) were negatively related to *B. calamita* population trends. Management history (populations established via translocation as opposed to native populations) had a significant positive effect; as had sites that received greater translocation releases, undergone Species Recovery Programme management, and where common toad was absent. In multiple-variable analyses, the combined effects of management history and average pre-breeding season rainfall accounted for inter-site variation in population trends. The rainfall effects in single- and multiple-variable analyses were strongly influenced by three sites with very high rainfall whilst no clear effect was apparent for the remaining sites. This study highlights the role of climatic factors in population decline, and the importance of conservation management in stabilizing population trends. Climate change over the next 50–100 years is predicted to have limited impacts on most *B. calamita* populations in Britain, but strongly positive impacts on the most threatened populations located at the very edge of species' range that will benefit from reduced precipitation. A need for active conservation management will remain for the foreseeable future.

Introduction

Globally, amphibian populations have been declining since the 1960s (Houlahan *et al.*, 2000). Causes of global amphibian declines have been identified as habitat loss, disease, overexploitation, pollution, alien species, exposure to ultraviolet-B radiation and climate change (Kiesecker, Blaustein & Belden, 2001; Beebee & Griffiths, 2005; Pounds *et al.*, 2006). Amphibian population responses to these factors are increasingly being considered context dependent, varying depending on the species, where it resides and what influences exist locally (Blaustein & Kiesecker, 2002). Multiple-factor testing is necessary to untangle the complexity of potential natural and anthropogenic causes of amphibian population declines (Collins & Storfer, 2003; Storfer, 2003). The natterjack toad *Bufo calamita* in Britain is a case in point: populations are known to have declined since at least the 1960s. Targeted conservation management measures

have been instituted since the 1970s but variation in population trends (including stability, growth and decline) persists between sites. An exploration of the many possible reasons for this is needed to help natterjack toad conservation managers tackle population declines in a more informed way and may provide information that can be applied more widely to the conservation of other amphibian species that are under threat.

The natterjack toad *B. calamita* is found in central and western Europe and is declining in countries at its north-western edge including Britain, where it is endangered. Population decline in Britain has historically been attributed to habitat change through afforestation, urbanization, agricultural practice, seral succession on neglected heathlands, acidification of breeding ponds by acid rain and invasion by competitively superior species (Beebee, 1977; Beebee *et al.*, 1990; Denton & Beebee, 1994). Conservation management intervention to aid the recovery of populations began in the
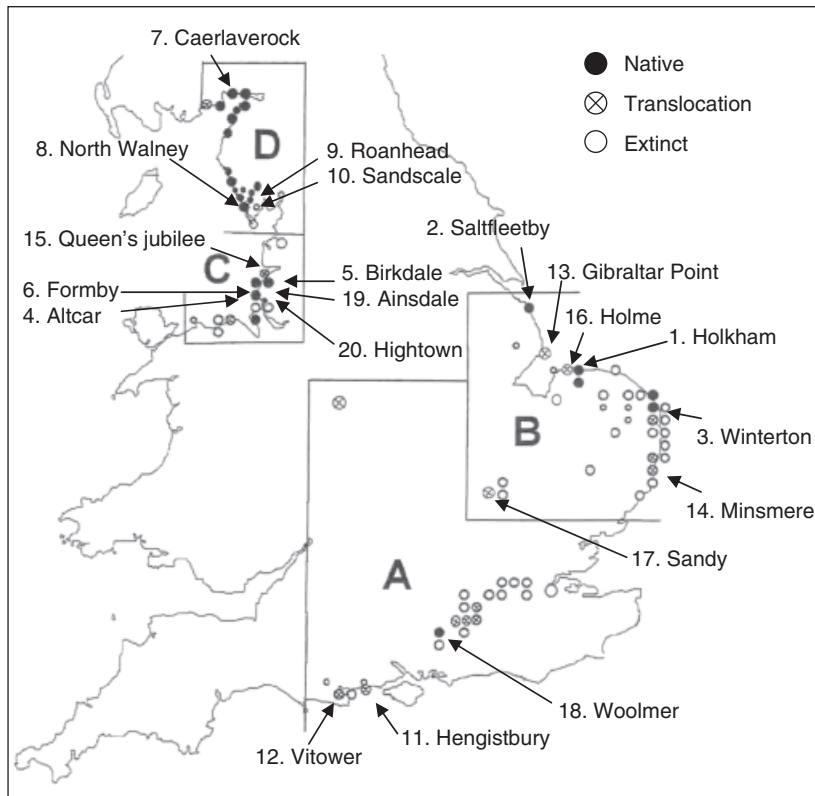
Figure 1 Map of *Bufo calamita* sites in Britain indicating regions A, B, C and D (map courtesy of the Herpetological Conservation Trust).

1970s focusing on aquatic and terrestrial habitat conditions, translocations from wild and captive sources to re-establish extirpated populations and control of competitors and predators. The Natterjack Toad Species Recovery Programme (SRP) (1992–1995) aimed to increase management significantly at key sites and re-establish more populations to their historic range (Denton, Hitchings & Beebee, 1995). SRP management involved a combination of terrestrial habitat management, creation or restoration of breeding ponds, countering anthropogenic acidification of breeding ponds (prevalent at the time) and translocation for re-introduction to suitable sites where the species was absent but had historically been present. As a result, *B. calamita* sites in Britain consist of native sites, where toads continue to persist, and those that have been re-established via translocation, either before the SRP or as part of it. Management continues to-date as directed by the Species Action Plan for the natterjack toad and is thought to have ensured the survival of some populations (Banks, Beebee & Denton, 1993; Denton *et al.*, 1997).

The conditions faced by conservation managers differ between populations due to site-characteristic factors. Three different habitat types of sand dune, saltmarsh and heathland are used by *B. calamita* in Britain and each face unique threats (Beebee, 1983; Buckley & Beebee, 2004). Habitat area and population size vary between sites and some face competitive and predatory threats to population status from the common toad *Bufo bufo* (Banks & Beebee, 1987;

Griffiths, 1991; Beebee & Buckley, 2001). While most sites are isolated from one another, metapopulations may exist where nearest neighbour distance is short enough along the Merseyside Coast and in the Duddon Estuary (Rowe, Beebee & Burke, 2000). The sites occur in four distinct regions (south/central England, eastern England, south Irish Sea and north Irish Sea; Fig. 1) which differ according to predominant habitat type, metapopulation presence and climatic conditions (Beebee & Buckley, 2001). These site-characteristic differences could be responsible for determining differences in population trends between sites.

For amphibians like *B. calamita* that rely on shallow ephemeral ponds for breeding, a delicate balance exists between the need for rainfall as a cue for breeding, the need for low rainfall levels to maintain shallow breeding ponds and the need for enough rainfall to prevent early drying (Blankenhorn, 1972; Beebee, 1983; Denton & Beebee, 1994). Similarly, temperatures need to be high enough for breeding and developmental needs but low enough to ensure evaporation of breeding ponds is not too rapid (Banks & Beebee, 1986; Banks, Beebee & Cooke, 1994; Beebee, 1995). Future climatic conditions in Britain are predicted to be drier and warmer (Hulme *et al.*, 2002). Such conditions are associated with population decline for some amphibian species (Rohr & Madison, 2003; Rohr *et al.*, 2004; Daszak *et al.*, 2005). However, *B. calamita* is at the edge of its range in west and north-west Britain where average annual rainfall is about twice as high as in the centre of the species' range which

includes central Europe and south-east Britain (European Environment Agency, 2003). Hence impacts of climate change on the British populations may not necessarily be negative. Population changes likely to be induced by climate change could be better predicted, planned for and managed with greater understanding of the relationship between *B. calamita* population trends and climate variables.

We assessed the status of *B. calamita* populations in Britain by estimating population trends. We carried out single- and multiple-variable analyses using a general linear model (GLM) to examine whether conservation management, site-characteristic and historical climatic explanatory variables could explain differences in population trends between sites. The hypotheses tested in relation to these explanatory variables are summarized in Table 1. We then examined the likely effects of predicted changes in future climate on *B. calamita* population trends.

Materials and methods

Estimation of population trends

Data for the response variable population trends were obtained from the Natterjack Toad Site Register (NSR) which documents *B. calamita* spawn string counts from over 60 sites across Britain from 1970 to 2006 (Beebee & Buckley, 2001; Buckley, 2006). Spawn string observations are made throughout the breeding season and the cumulative sum recorded. Here, data for a sample of 20 sites (Table 2) over the period 1985–2006 were used. These sites were selected according to whether the number of years of monitoring data was > 10 years and monitoring was sufficiently often enough during the breeding season such that counts of spawn strings are reliable (Beebee & Buckley, 2001; Buckley & Beebee, 2004). Data were truncated from 1985 as monitoring is thought to be consistent between years from then onwards for natterjack sites across Britain (T. J. C. Beebee, pers. comm.). The sites in the sample were representative of the different conditions found in Britain in terms of translocation and native sites, habitat type and regional distribution.

Long-term population trends were estimated for each site by linear regression of log-transformed cumulative spawn string counts, as a proxy for female breeding population, against year of observation (1985–2006). The slope of the regression is the exponential rate of population change. Population trends for sites re-established via translocation were calculated using spawn string data beyond initial translocations over 3 years used to establish populations.

Explanatory variables

Climate

The climatic explanatory variables chosen were those directly linked to *B. calamita* life history with the potential to affect population trends through positive or negative effects on population status in different life stages (spawn, tadpole,

metamorph, juvenile and adult). The rainfall and temperature variables considered were categorized according to the months in which they occurred and were directly related to the foraging (April–October), winter (October–March), pre-breeding (March–April) and breeding (April–July) periods of *B. calamita* life history. The rationale for inclusion of these climatic variables in the analysis through their links to *B. calamita* population status is detailed in Table 1.

Data for the climatic variables were obtained from records taken at the sites themselves and Meteorological Office and Forestry Commission historic station data (Forestry Commission, 2008; Meterological Office, 2008). These data sources offer long-term records for mean maximum temperature ($^{\circ}$C), mean minimum temperature ($^{\circ}$C) and total rainfall (mm) per month for *B. calamita* sites and various weather stations around Britain. Data collected from maximum and minimum thermometers and rain gauges at each station are available in daily records. Where on-site climatic data were not available, the closest weather station to the site was selected to provide proxy data for climate trends.

The candidate explanatory climate variables used in this analysis are listed in Table 1. The estimate for average maximum winter (October–March) temperature was derived from the average mean October–March maximum temperatures computed for each year (1985–2006) and then averaged over this time period. The same method was used to calculate the other temperature variables as specified (Table 4). Similarly, estimates of average winter (October–March) rainfall were calculated from the average total monthly rainfall per year (1985–2006) averaged over this period.

Site characteristics

The sites investigated were classified according to their management history based on whether they had been initiated through translocation as part of early conservation management efforts or the SRP (translocation sites) or had persisted since records began (native sites) (Denton *et al.*, 1995; Beebee & Buckley, 2001) . Translocation success is measured as breeding by at least the second generation of animals and translocation sites analysed here are mostly considered successful with the exception of Queen's Jubilee, which is currently unproven (Denton *et al.*, 1997). The regional classifications (A, B, C or D) attributed to each site were based on regional groupings used in the NSR (Fig. 1; Beebee & Buckley, 2001). Habitat type was assigned according to whether sites were predominantly dune, heath or marsh (Table 2).

Best-available habitat area (ha) estimates available for natterjacks were obtained from the NSR (Beebee & Buckley, 2001). Six figure National Grid reference locations provided in the NSR were used to calculate the nearest neighbour distance for each site. Using the eastings and northings, the straight-line Euclidean distance (square root of the sum of the squares of the differences between the corresponding coordinates of the sites) between each site and all other sites

Table 1 Explanatory variables with brief rationale for inclusion

Variable	Rationale for inclusion	Abbreviation	Unit or levels
Climatic variables			
1. Average maximum winter temperature (October–March)	Winter temperatures can impact upon juvenile and adult overwinter survival	Av.tmaxOM	°C
2. Average minimum winter temperature (October–March)		Av.tminOM	°C
3. Average maximum pre-breeding temp (March/April)	Warmer pre-breeding season temperatures can promote earlier migration to breeding ponds	Av.tmaxMA	°C
4. Average minimum pre-breeding temp (March/April)		Av.tminMA	°C
5. Average. maximum breeding season temperature (April–July)	Breeding season temperatures are important for ensuring ponds are sufficiently warm ($>20\,°C$) for tadpoles to develop rapidly and for metamorphosis to occur before there are substantial predatory losses	Av.tmaxAJ	°C
6. Average minimum breeding season temp (April–July)		Av.tminAJ	°C
7. Average winter rainfall (October/March)	Shallow breeding pools (<10cm) are needed for spawn deposition	Av.rainOM	mm
8. Average pre-breeding rainfall (March/April)	Higher proportion of females breed in wetter springs	Av.rainMA	mm
9. Average breeding season rainfall (April–July)	Early pool desiccation may prevent successful metamorphosis but if well-timed it may reduce reproductive success of competitors	Av.rainAJ	mm
10. Average foraging rainfall April–October ($t-1$)	Foraging period rainfall influences female foraging activity and may impact upon breeding success	Av.rainAO($t-1$)	mm
Site variables			
11. Management history	Translocation sites hold reintroduced populations and vary according to date of initiation, supplementary releases and success. Native sites have been subject to conservation management initiatives targeting particular threats faced	Man.hist	Native, translocation
12. Region	The Natterjack Toad Site Register groups *Bufo calamita* sites into four distinct regions	Region	A, B, C, D
13. Habitat type	Three main habitat types are occupied by *B. calamita* in Britain: heathlands, dunes, saltmarshes	Habitat.type	Dune, heath, marsh
14. Adult population size	Populations of *B. calamita* across Britain vary in size holding small (10s), medium (10s to 100s) or high (100s to 1000s) adult numbers	Adult.N	Average number of adults (1985–2006)
15. Habitat area	Available habitat for *B.calamita* populations ranges from 1 to 800 ha	Area.ha	Habitat area (ha)
16. Nearest neighbour distance	Populations from sites in close proximity may form a metapapoulation	NN.dist	Km
17. Common frog	Common toad *Bufo bufo* and Common frog *Rana temporaria* tadpoles predate *B.calamita* spawn and can have inhibitory effects on natterjack tadpole growth	Common.frog	Present, Absent
18. Common toad		Common.toad	Present, Absent
Management variables			
19. Wild–wild translocation	Translocations have been implemented using spawn/tadpoles from nearby wild sources or captive populations	Wildwild.yrs	Number of years implemented
20. Captive–wild translocation		Captivewild.yrs	Number of years implemented
21. Aquatic habitat management	Aquatic habitat management has included maintenance of pool water levels, clearance of aquatic vegetation and liming (addition of Ca OH^2)	Aquatic.yrs	Number of years implemented
22. Terrestrial habitat management	*B. calamita* are adapted to early successional terrestrial habitats – management involves removal of scrub and woodland, the treating of scrub or tree stumps with herbicide and livestock grazing	Terrest.yrs	Number of years implemented
23. Competitor/predator control	Removal of common toad, common frog and predatory invertebrates and construction of wire mesh to protect natterjack spawn from predatory birds	CPcontrol.yrs	Number of years implemented
24. Any form of management	Wild-wild, Captive-wild, Aquatic, Terrestrial and Competitor/predator control years combined (variables 19–23)	Man.yrs	Number of year implemented
25. SRP management	Intensive conservation management was carried out during the Species Recovery Programme, 1992–1995, which aimed to increase management significantly at key sites and re-establish populations to their historic range	SRPMan	Yes, no

Table 2 Characteristics of *Bufo calamita* sites

Number	Site	History (year initiated)	Success	SRP management	Habitat type (metapopulation)	Region	Number of years data (1985–2006)
1	Holkham	Native	–	Non-SRP	Dune	B	20
2	Saltfleetby	Native	–	Non-SRP	Dune	B	19
3	Winterton	Native	–	Non-SRP	Dune	B	13
4	Altcar	Native	–	Non-SRP	Dune (M)	C	21
5	Birkdale	Native	–	Non-SRP	Dune (M)	C	21
6	Formby	Native	–	Non-SRP	Dune (M)	C	21
7	Caerlaverlock	Native	–	Non-SRP	Marsh	D	20
8	North Walney	Native	–	Non-SRP	Dune	D	13
9	Roanhead	Native	–	Non-SRP	Marsh (NI)	D	16
10	Sandscale	Native	–	Non-SRP	Dune (NI)	D	17
11	Hengistbury	Trans (1989)	Yes	SRP	Heath	A	17
12	Vitower	Trans (1993)	Yes	SRP	Heath	A	13
13	Gibraltar Point	Trans (1992)	Yes	SRP	Dune	B	13
14	Minsmere	Trans (1985)	Yes	SRP	Heath	B	16
15	Queen's jubilee	Trans (1995)	Unproven	Non-SRP	Dune (M)	C	11
16	Holme	Trans (1982)	Yes	Non-SRP	Dune	B	21
17	Sandy	Trans (1980)	Yes	Non-SRP	Heath	B	20
18	Woolmer	Native	–	SRP	Heath	A	21
19	Ainsdale	Native	–	SRP	Dune (M)	C	18
20	Hightown	Native	–	SRP	Dune (M)	C	19

Regions refer to A, South and Central England (Dorset, Hampshire, Staffordshire and Surrey); B, Eastern England (Bedfordshire, Lincolnshire, Norfolk and Suffolk); C, South Irish Sea (Flintshire, Lancashire and Merseyside); D, North Irish Sea (Cumbria and Dumfriesshire). Metapopulations refer to M, Merseyside metapopulation; NI, North Irish Sea.

was calculated and the shortest distance used as that to the nearest neighbour (Ordnance Survey, 2008). Adult population size was estimated using the average cumulative spawn strings (1985–2006), assuming females deposit one spawn string per breeding season and the sex ratio is 1:1 (Beebee, Denton & Buckley, 1996). Sites were also classified according to the presence or absence of common toad and common frog to determine whether these species in particular had a significant effect on *B. calamita* population trends.

Conservation management

Detailed information on management activities at all sites was extracted from the NSR. Habitat management for *B. calamita* has taken place in the aquatic and terrestrial environment targeting the distinct aquatic and terrestrial life cycle phases. Specific management approaches used varied between sites dependent on particular conditions and threats faced. However, all approaches aimed to achieve the same standard of habitat condition acceptable in each environment to meet *B. calamita* requirements and improve population status. Therefore the variable aquatic habitat management (Aquatic.yrs) refers to any management in the aquatic environment covering the approaches of pond creation, neutralization of acidic breeding ponds, the clearance of pond vegetation and scrub/vegetation around the pond and maintenance of pond water levels. Terrestrial habitat management (Terrestrial.yrs) represents occurrences of the removal of invasive scrub and woodland, the treating of

scrub or tree stumps to prevent re-growth and the implementation of livestock grazing schemes. Categorizing these approaches as two distinct variables allowed a clear distinction between the effects of management efforts in these distinct environments.

Translocations to both native and translocation sites have taken place as a direct means of enhancing populations. Approaches using wild-sourced (including those that were head-started) and captive-sourced individuals have been used and here they were considered as separate management efforts (Wild–wild.yrs and Captive–wild.yrs). The effects of these management variables were measured as management effort according to the number of years in which the management method was implemented over 1985–2006 (Table 1). The variable Man.yrs combines the number of years in which any of the above forms of management were implemented. The final variable investigated classified sites as subject to SRP management or not. This encompasses establishment of populations via translocation and aquatic and terrestrial habitat management of native sites and translocation sites.

Statistical analyses

Effects of explanatory variables

The presence of correlations among the explanatory variables was tested using Pearson's product moment correlation with a two-sided test. We used a GLM with Gaussian

errors and the identity link (the linear combination of values for the explanatory variables is not transformed) for single- and multiple-variable analyses. Stepwise forward selection was used in the multiple-variable analysis to identify the minimum adequate model, iteratively including at each step the most significant remaining variable until no remaining variables were significant. Statistical analyses were carried out using R, version 2.6.2 (R Development Core Team, 2009).

Population trend predictions under future climate change

Climate change impacts on population trends were predicted by applying the minimum adequate model to climate predictions for 2050 and 2100. Predictions for the climate variable that remained in the minimum adequate model, average pre-breeding season rainfall, were obtained from the UK Climate Impacts Programme (UKCIP). The UKCIP stochastically generated daily climate predictions for eleven meteorological stations across the UK (UK Climate Impacts Programme, 2007). Average pre-breeding season rainfall predictions were obtained for each *B. calamita* site by averaging daily rainfall values for the UKCIP station in closest proximity to the site.

Results

Factors driving recent population trends

Natterjack population trends in 1985–2006 varied significantly among sites. Five of the 20 sites analysed showed positive population trends, five showed negative trends and 10 trends were not significantly different from zero (Fig. 2). On an average, population trends were negative in unmanaged (non-SRP) native sites but positive in translocation and managed (SRP) native sites.
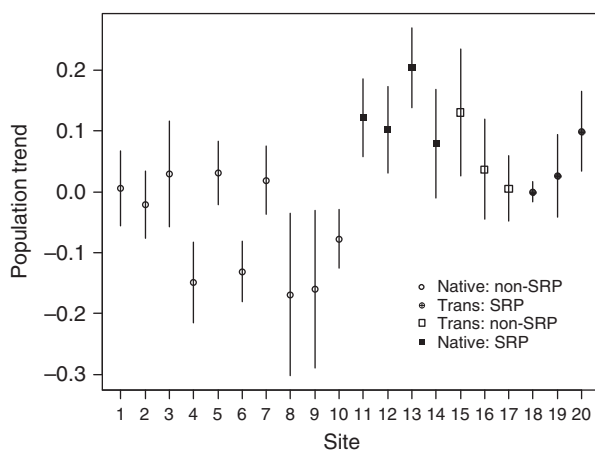

Figure 2 Population trend (1985–2006) by site with 95% confidence intervals. Sites 1–20 correspond to sites as numbered in Table 2.

A correlations matrix was used to investigate whether correlations between explanatory variables could cause confounding in the GLM (supporting information Appendix S1). As may be expected, significant correlations existed among several temperature variables and among rainfall variables. All rainfall variables were also negatively correlated with average maximum breeding season temperature (April–July). The habitat management variables were also correlated, indicating that aquatic habitat management, terrestrial habitat management and predator/competitor control were implemented together. Common toad presence on sites was negatively correlated with management history such that fewer translocation sites were known to be inhabited by common toad. Compared with other regions, region D had lower temperatures, higher rainfall, more native sites and no sites that underwent SRP management.

The GLMs predicting population trends from individual explanatory variables are summarized in Table 3. Of the climate variables, all rainfall but none of the temperature variables were significant predictors of population trend. Population trends declined with increasing average winter, pre-breeding season, breeding season and foraging period rainfall (Table 3, Fig. 3). Non-linear models of population trends–rainfall relationships were also tested but none improved the fit over that provided by the linear model based on comparisons between degrees of freedom, deviance and generalized cross-validation scores (Wood, 2006). Visual examination of Fig. 3 suggests that the population trends–rainfall relationship is strongly influenced by three sites subject to extremely high levels of rainfall (sites 8, 9 and 10 from area D) while no clear relationship is apparent for the remaining sites at which rainfall was much lower.

Of the site variables, site establishment by translocation had a positive effect on population trend (Table 3, Fig. 4). The mean population trend for translocation sites was significantly positive (0.0972 ± 0.0246) while the mean trend for native sites was not significantly different from zero (-0.0382 ± 0.0245). Sites located in region D had a significant negative impact on trend, as did common toad presence. Of the management variables, years of translocation of wild animals and SRP management were significant predictors of population trend (Table 3, Fig. 5). However, the relationship between years of translocation of wild animals and population trend (Fig. 5a) does not remain significant when the outlier with 12 years of releases is removed from the analysis ($P = 0.2$). By contrast, neither releases of captive bred animals nor individual habitat management variables influenced trends significantly.

In the multi-variable GLM, management history (sites established by translocation vs. native sites) and average pre-breeding season rainfall (March–April) provided the minimum adequate model after forward selection (Table 4). Both variables were also the most highly significant individual predictors. As discussed above, site establishment by translocation was positively correlated with years of wild translocations and negatively correlated with site location in region D, hence the variable 'management history' effectively accounts for these confounded factors. Likewise, all

Table 3 General linear model output for individual explanatory variables with population trend as response

Variable	Estimate	Standard error	t-value	P
Climate variables				
Winter				
Av.tmaxOM	0.0226	0.0364	0.6203	0.5428
Av.tminOM	0.0430	0.0250	1.7159	0.1033
Av.rainOM	**−0.0012**	**0.0004**	**−2.9150**	**0.0092****
Pre-breeding season				
Av.tmaxMA	0.0185	0.0370	0.4987	0.6240
Av.tminMA	0.0270	0.0213	1.2690	0.2206
Av.rainMA	**−0.0017**	**0.0005**	**−3.1892**	**0.0051****
Breeding season				
Av.tmaxAJ	0.0390	0.0203	1.9219	0.0706
Av.tminAJ	0.0365	0.0207	1.7657	0.0944
Av.rainAJ	**−0.0026**	**0.0008**	**−3.1560**	**0.0055****
Foraging period				
Av.rainAO(t-1)	**−0.0021**	**0.0007**	**−3.0389**	**0.0071****
Site Variables				
Man.hist: Trans	**0.1354**	**0.0381**	**3.5505**	**0.0023****
Region: B	−0.0260	0.0631	−0.4115	0.6861
Region: C	−0.0735	0.0646	−1.1371	0.2722
Region: D	**−0.1713**	**0.0698**	**−2.4548**	**0.0259***
Habitat.type: Heath	0.0605	0.0535	1.1316	0.2735
Habitat.type: Marsh	−0.0716	0.0771	−0.9277	0.3665
Area.ha	0.0001	0.0001	0.5363	0.5983
NN.dist	0.00005	0.0001	0.4049	0.6903
Adult.N	−0.0001	0.0001	−1.0801	0.2944
Common.frog	−0.0109	0.0664	−0.1635	0.8720
Common.toad: Present	**−0.1283**	**0.0592**	**−2.1685**	**0.0438***
Management variables				
Wildwild.yrs	**0.0176**	**0.0068**	**2.5779**	**0.0190***
Captivewild.yrs	0.0369	0.0537	0.6861	0.5014
Aquatic.yrs	−0.0013	0.0048	−0.2644	0.7945
Terrest.yrs	−0.0016	0.0044	−0.3733	0.7133
CPcontrol.yrs	0.0011	0.0040	0.2783	0.7840
Man.yrs	0.0003	0.0046	0.0755	0.9407
SRPMan: Yes	**0.1249**	**0.0401**	**3.1164**	**0.0060****

Significant variables shown in bold.

*$P < 0.05$.

**$P < 0.01$.

OM, October–March; MA, March–April; AJ, April–July; AO, April–October.

rainfall variables were correlated and it is not surprising that only one rainfall variable was included in the minimum adequate model.

Population trends under future climate

Pre-breeding season rainfall to 2050 and 2100 is predicted to decrease for the majority of sites, but to increase for some. These rainfall trends are reflected in predicted future population trends, which improve dramatically for sites 8, 9 and 10 (in region D, at the north-western edge on the species' range) but show only moderate changes, mostly positive but sometimes negative, for other sites (Fig. 6). The model predicted fewer sites to have negative changes in trend in the longer term to 2100 (three native and one translocation

= 20% of all sites) than to 2050 (five native and one translocation = 30% of all sites).

Discussion

Our study provides a systematic assessment of the effects of climate variables, site characteristics and conservation management on recent *B. calamita* population trends in Britain. It thus extends a previous, more descriptive analysis of trends in British *B. calamita* populations (Buckley & Beebee, 2004). Based on our statistical modelling of climate influence on recent population trends, we also predict likely effects of climate change on future trends.

Rainfall had a significant, negative impact on population trends over the range of rainfall levels observed. This result
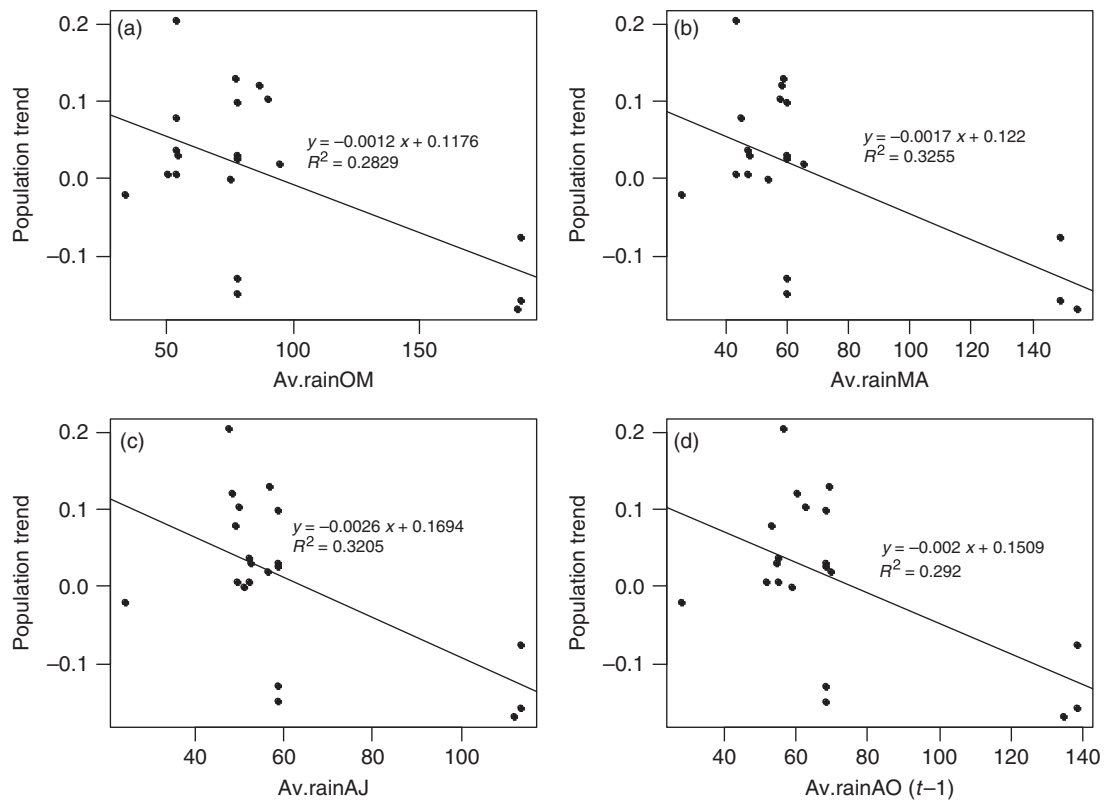
Figure 3 Climatic variables significantly related to population trend. (a) Average winter rainfall (October–March), (b) average pre-breeding rainfall (March–April), (c) average breeding season rainfall (April–July) and (d) average foraging rainfall (April–October, t–1).

was strongly influenced by sites at the north-western edge of the species' range (Region D) which were subject to extremely high average rainfall and showed strong population declines. By contrast, no clear relationship with rainfall was apparent within the set of remaining sites. To exclude the possibility that negative growth rate estimates in high rainfall sites may be related to sampling problems (reduced visibility of spawn strings in high rainfall years), we examined within-site data on rainfall and spawn string counts but found no significant or apparent correlations. We therefore conclude that very high levels of rainfall are detrimental to *B. calamita* populations whilst variation within the range of rainfall found across central and eastern Britain may not have strong impacts on populations. This result supports the hypothesis that whilst rainfall is needed to trigger *B. calamita* breeding activity, having only enough rainfall to maintain shallow breeding ponds provides better breeding conditions than high rainfall (Smith & Payne, 1980; Beebee, 1983). However, a severe lack of rainfall causes premature pond desiccation and thus, reproductive failure (Pechmann *et al.*, 1989; Banks, Beebee *et al.*, 1994; Beebee, 1995; Rowe & Dunson; 1995; Stewart, 1995). Reduction in breeding pond size may also have indirect adverse impacts on population size by affecting food supply, tadpole density, metamorph size and predation pressure (Pearman, 1995; Brady & Griffiths, 2000; Carey & Alexander; 2003). Hence

the positive effect of rainfall on population trends must be interpreted with caution and should not be extrapolated beyond the range of rainfall levels historically observed.

The effect of management history (translocated vs. native populations) was most likely the result of faster growing populations at translocation sites where the populations expanded into areas where they had been re-established. Many translocation sites also underwent SRP management. In addition, fewer translocation sites had common toad present. It is therefore likely that faster growth rates at translocation sites were also encouraged by ensuring that habitat conditions were amenable to successful establishment before translocations occurred. This result lends support to previous findings that the reintroduction of *B. calamita* into suitable sites through translocation of wild animals can contribute substantially to amphibian conservation, particularly when combined with habitat restoration and maintenance (Denton *et al.*, 1997; Seigel & Dodd, 2002; Buckley & Beebee, 2004). Our analysis was restricted to populations which had been monitored for over 10 years and therefore may over-represent successful translocations. Translocation attempts often fail to establish new populations (Denton *et al.*, 1997; Gent, 2004). Examining translocation success data from the NSR for 1970 to 2006 using categories adapted from Denton *et al.* (1997); we found that of 34 translocations initiated during this period, seven were
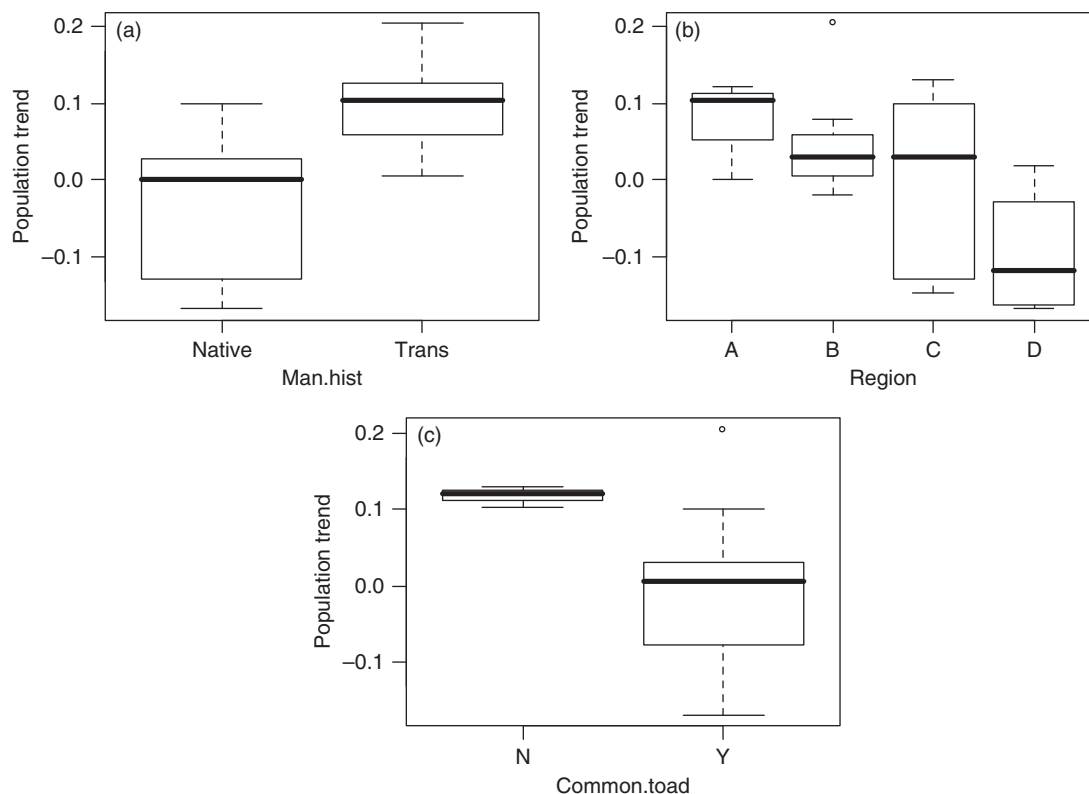
Figure 4 Site variables significantly related to population trend. (a) management history, (b) region and (c) common toad presence.
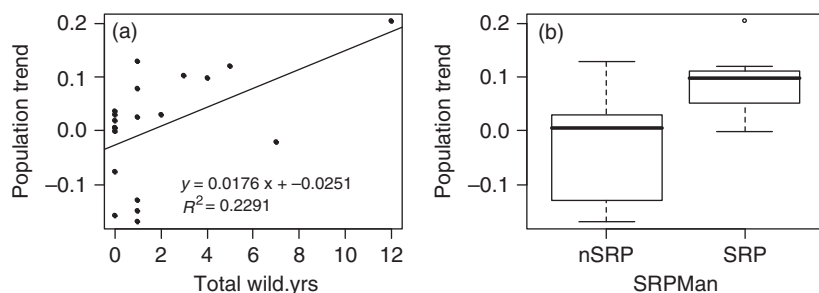

Figure 5 Management variables significantly related to population trend. (a) Number of years wild *Bufo calamita* released and (b) Site subject to Species Recovery Programme (SRP) management. nSRP, non-SRP.

completely successful (breeding continued at the site for at least 5 years), a further 15 showed intermediate success (adults returned to breed within 3 years) and one showed initial success (emergence of toadlets in reintroduction years). Six translocations were considered definitive failures and for the remainder, the outcome is uncertain. Causes of failure include early pond drying, predation and aquatic vegetation encroachment. However, as our results show, those translocations that are successful at initial establishment can give rise to viable and growing populations with long-term conservation benefits.

The positive impact of integrated management is highlighted by our finding that SRP management (combined terrestrial habitat management, creation or restoration of breeding ponds, countering acidification of breeding ponds and translocation) had a significant positive effect on

Table 4 General linear model forward selection results with population trend as response

Variable	Estimate	Standard error	*t*-value	*P*
(Intercept)	0.0538	0.0408	1.32	0.2044
Man.hist: Trans	0.1044	0.0354	2.948	0.009
Av.rainMA	−0.0012	0.0005	−2.578	0.0195

population trends. The approach taken may be used as an example to amphibian reintroduction programmes taking place in other parts of the world, which have had partial or low success (see Griffiths & Pavajeau, 2008 for a summary).

The meta-analysis by Houlahan *et al.* (2000) shows rapidly declining amphibian populations in western Europe in the 1960s, but stable populations since the 1970s. Our
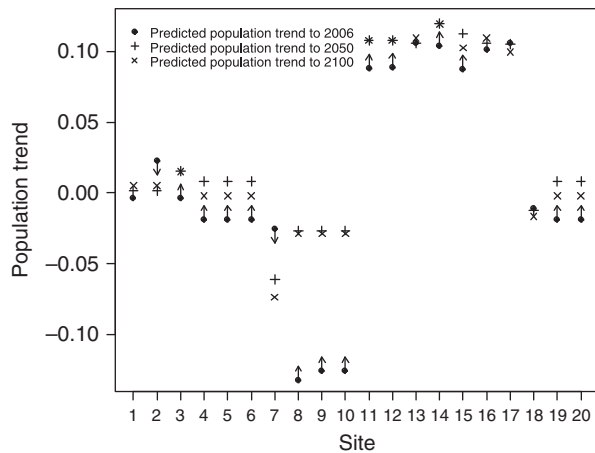
Animal Conservation ▮▮ (2010) 1–12 ⓒ 2010 The Authors. Journal compilation ⓒ 2010 The Zoological Society of London

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Figure 6 Observed and predicted population trends to 2006 and predicted trends under average rainfall (March–April) projections to 2050 and 2100.

results suggest that in the case of the *B. calamita*, stability of average population trends has been the result of conservation interventions and that without such interventions, the populations would have continued to decline.

Our analysis suggests that future climate change, with a predicted decline in pre-breeding season rainfall, will have strongly positive impacts on population trends in sites at the north-western edge of the species' range. Population trends in the remaining British *B. calamita* sites are expected to change less dramatically, but mostly in a positive direction. This prediction is consistent with the fact that the north-western sites are at the very edge of the species' range and receive substantially higher rainfall than the central part of the range including central and eastern Britain. However, increasing rainfall with negative impacts on population trends has been predicted for some sites. In addition, very dry climate could eventually lead to increased occurrence of premature breeding pond desiccation. Hence continued monitoring and responsive conservation management action will remain necessary, despite a generally positive outlook for *B. calamita* populations. This is particularly important at sand dune and saltmarsh sites, where groundwater and sea-level changes will have direct impacts on breeding pond water level and quality (Buckley & Beebee, 2004; Clarke & Sanitwong-Na-Ayuttaya, 2007).

References

Banks, B. & Beebee, T.J.C. (1986). Climatic effects on calling and spawning of the natterjack toad *Bufo calamita* – discriminant analyses and applications for conservation monitoring. *Biol. Conserv.* **36**, 339–350.

Banks, B. & Beebee, T.J.C. (1987). Spawn predation and larval growth inhibition as mechanisms for niche separation in anurans. *Oecologia* **72**, 569–573.

Banks, B., Beebee, T.J.C. & Cooke, A.S. (1994). Conservation of the natterjack toad *Bufo calamita* in Britain over the period 1970–1990 in relation to site protection and other factors. *Biol. Conserv.* **67**, 111–118.

Banks, B., Beebee, T.J.C. & Denton, J.S. (1993). Long-term management of a natterjack toad *Bufo calamita* population in southern Britain. *Amphib.-Reptilia* **14**, 155–168.

Beebee, T.J.C. (1977). Environmental change as a cause of natterjack toad *Bufo calamita* declines in Britain. *Biol. Conserv.* **11**, 87–102.

Beebee, T.J.C. (1983). *The natterjack toad*. Oxford: Oxford University Press.

Beebee, T.J.C. (1995). Amphibian breeding and climate. *Nature* **374**, 219–220.

Beebee, T.J.C. & Buckley, J. (2001). *Natterjack toad Bufo calamita site register for the UK 1970–1999 inclusive*. Unpublished report by University of Sussex and The Herpetological Conservation Trust.

Beebee, T.J.C., Denton, J.S. & Buckley, J. (1996). Factors affecting population densities of adult natterjack toads *Bufo calamita* in Britain. *J. Appl. Ecol* **33**, 263–268.

Beebee, T.J.C., Flower, R.J., Stevenson, A.C., Patrick, S.T., Appleby, P.G., Fletcher, C., Marsh, C., Natkanski, J., Rippey, B. & Battarbee, R.W. (1990). Decline of the natterjack toad *Bufo calamita* in Britain: palaeoecological, documentary and experimental evidence for breeding site acidification. *Biol. Conserv.* **53**, 1–20.

Beebee, T.J.C. & Griffiths, R.A. (2005). The amphibian decline crisis: a watershed for conservation biology? *Biol. Conserv.* **125**, 271–285.

Blankenhorn, H.J. (1972). Meteorological variables affecting onset and duration of calling in *Hyla arborea* L and *Bufo calamita calamita* Laur. *Oecologia* **9**, 223–234.

Blaustein, A.R. & Kiesecker, J.M. (2002). Complexity in conservation: lessons from the global decline of amphibian populations. *Ecol. Lett.* **5**, 597–608.

Brady, L.D. & Griffiths, R.A. (2000). Developmental responses to pond desiccation in tadpoles of the British anuran amphibians *Bufo bufo*, *B calamita* and *Rana temporaria*. *J. Zool. (Lond.)* **252**, 61–69.

Buckley, J. (2006). *Natterjack Toad Bufo calamita Site Register updates 2000–2006*. Unpublished report by The Herpetological Conservation Trust.

Buckley, J. & Beebee, T.J.C. (2004). Monitoring the conservation status of an endangered amphibian: the natterjack toad *Bufo calamita* in Britain. *Anim. Conserv*. **7**, 221–228.

Carey, C. & Alexander, M.A. (2003). Climate change and amphibian declines: is there a link? *Divers. Distrib*. **9**, 111–121.

Clarke, D. & Sanitwong-Na-Ayuttaya, S. (2007). Water balance at Ainsdale National Nature Reserve 1975–2100. In *Report of the Sefton Coast Partnership Research Meeting 14th July 2006, Edge Hill University College*: 30–35. Wisse, P. & Lymbery, G. (Eds.) Bootle: Sefton Coast Partnership.

Collins, J.P. & Storfer, A. (2003). Global amphibian declines: sorting the hypotheses. *Divers. Distrib*. **9**, 89–98.

Daszak, P., Scott, D.E., Kilpatrick, A.M., Faggioni, C., Gibbons, J.W. & Porter, D. (2005). Amphibian population declines at savannah river site are linked to climate, not chytridiomycosis. *Ecology* **86**, 3232–3237.

Denton, J.S. & Beebee, T.J.C. (1994). The basis of niche separation during terrestrial life between two species of toad *Bufo bufo* and *Bufo calamita*: competition or specialisation? *Oecologia* **97**, 390–398.

Denton, J.S., Hitchings, S.P. & Beebee, T.J.C. (1995). *Natterjack toad Species Recovery Programme project 1992–1995*. Final report. English Nature Research Reports No. 151.

Denton, J.S., Hitchings, S.P., Beebee, T.J.C. & Gent, A. (1997). A recovery program for the natterjack toad *Bufo calamita* in Britain. *Conserv. Biol*. **11**, 1329–1338.

European Environment Agency. (2003). *Europe's water: An indicator-based assessment. Topic report No 1/2003*. Copenhagen: European Environment Agency.

Forestry Commission. (2008). Meteorology. Available at http://www.forestry.gov.uk/website/forestresearch.nsf/By-Unique/INFD-5ZYHDG (accessed on 30 April 2008).

Gent, T. (2004). Herpetological reintroductions. In *Restoration, re-introduction and translocation*. Rooney, P, Nolan, P. & Hill, D (Eds). Southport: Proceedings of the 20th conference of the Institute of Ecology and Environmental Management.

Griffiths, R.A. (1991). Competition between common frog, *Rana temporaria*, and natterjack toad, *Bufo calamita*, tadpoles: the effect of competitor density and interaction level on tadpole development. *Oikos* **61**, 187–196.

Griffiths, R.A. & Pavajeau, L. (2008). Captive breeding, reintroduction, and the conservation of amphibians. *Conserv. Biol*. **22**, 852–861.

Houlahan, J.E., Findlay, C.S., Schmidt, B.R., Meyer, A.H. & Kuzmin, S.L. (2000). Quantitative evidence of global amphibian population declines. *Nature* **404**, 752–755.

Hulme, M., Jenkins, G.J., Lu, X., Turnpenny, J.R., Mitchell, T.D., Jones, R.G., Lowe, J., Murphy, J.M., Hassell, D.,

Boorman, P., McDonald, R. & Hill, S. (2002). *Climate change scenarios for the United Kingdom: the UKCIP02 scientific report*. Norwich, UK: Tyndall Centre for Climate Change Research, School of Environmental Sciences, University of East Anglia.

Kiesecker, J.M., Blaustein, A.R. & Belden, L.K. (2001). Complex causes of amphibian decline. *Nature* **410**, 681–684.

Meterological Office. (2008): Historic Station Data. Available at http://www.metoffice.gov.uk/climate/uk/stationdata/index.html (accessed on 27 March 2008).

Ordnance Survey. (2008): Calculating the distance between two points using their National Grid references. Available at http://www.ordnancesurvey.co.uk/oswebsite/aboutus/reports/misc/calculate.html (accessed on 26 March 2008).

Pearman, P.B. (1995). Effects of pond size and consequent predator density on two species of tadpoles. *Oecologia* **102**, 1–8.

Pechmann, J.H.K., Scott, D.E., Gibbons, J.W. & Semlitsch, R.D. (1989). Influence of wetland hydroperiod on diversity and abundance of metamorphosing juvenile amphibians. *Wetl. Ecol. Manag*. **1**, 3–11.

Pounds, J.A., Bustamante, M.R., Coloma, L.A., Consuegra, J.A., Fogden, M.P.L., Foster, P.N., La Marca, E., Masters, K.L., Merino-Viteri, A., Puschendorf, R., Ron, S.R., Sanchez-Azofeifa, G.A., Still, C.J. & Young, B.E. (2006). Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* **439**, 161–167.

R Development Core Team. (2009). *R: A Language and Environment for statistical computing*. Vienna: R Foundation for Statistical Computing. Avaialble at http://www.R-project.org (accessed 15 January 2009).

Rohr, J.R., Elskus, A.A., Shepherd, B.S., Crowley, P.H., McCarthy, T.M., Niedzwiecki, J.H., Sager, T., Sih, A. & Palmer, B.D. (2004). Multiple stressors and salamanders: effects of an herbicide, food limitation, and hydroperiod. *Ecol. Appl*. **14**, 1028–1040.

Rohr, J.R. & Madison, D.M. (2003). Dryness increases predation risk in efts: support for an amphibian decline hypothesis. *Oecologia* **135**, 657–664.

Rowe, C.L. & Dunson, W.A. (1995). Impacts of hydroperiod on growth and survival of larval amphibians in temporary ponds of central Pennsylvania, USA. *Oecologia* **102**, 397–403.

Rowe, G., Beebee, T.J.C. & Burke, T. (2000). A microsatellite analysis of natterjack toad *Bufo calamita* metapopulations. *Oikos* **88**, 641–651.

Seigel, R.A. & Dodd, C.K. (2002). Translocations of amphibians: proven management method or experimental technique? *Conserv. Biol*. **16**, 552–554.

Smith, P.H. & Payne, K.R. (1980). A survey of natterjack toad *Bufo calamita* distribution and breeding success in the North Merseyside sand-dune system, England. *Biol. Conserv*. **19**, 27–39.

Stewart, M.M. (1995). Climate driven population fluctuations in rain-forest frogs. *J. Herpetol*. **29**, 437–446.

Storfer, A. (2003). Amphibian declines: future directions. *Divers. Distrib* **9**, 151–163.

UK Climate Impacts Programme. (2007). Available at http://www.ukcip.org.uk (accessed on 26 November 2007).

Wood, S.N. (2006). *Generalized additive models: an introduction with R*. London: Chapman & Hall.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Correlation matrix of explanatory variables. Numbers 1–25 correspond to variables: 1. Av.tmaxOM, 2. Av.tminOM, 3. Av.tmaxMA, 4. Av.tminMA, 5. Av.tmaxAJ, 6. Av.tminAJ, 7. Av.rainOM, 8. Av.rainMA, 9. Av.rainAJ, 10. Av.rainAO(t–1), 11. Man.hist, 12. Region, 13. Habitat.type, 14. Adult.N, 15. Area.ha, 16. NN.dist, 17. Common.frog, 18. Common.toad, 19. Wildwild.yrs, 20. Captivewild.yrs, 21. Aquatic.yrs, 22. Terrest.yrs, 23. Cpcontrol.yrs, 24. Man.yrs, 25. SRPMan (See Tables 1–3). * $P < 0.05$

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