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Relating spawn counts to the dynamics of British natterjack toad (*Bufo calamita*) populations

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Counting cumulative numbers of spawn strings deposited by female natterjack toads *Bufo calamita* is widely used in Britain as a surrogate estimator of trends in population size. We analysed long-term data from 20 of the best recorded British natterjack populations to assess the relationship between spawn count and population dynamics. Spawn count, toadlet production and numbers of ponds producing toadlets were all correlated. However, high spawn deposition was more likely the cause of high toadlet production than a converse mechanism in which high toadlet production might subsequently increase adult population size. Good toadlet years did not generally correlate with spawn deposition three years later, the expected delay for cohort maturation. Conversely, new ponds could trigger large increases in spawn deposition within a year of their construction. This situation presumably arose because only a fraction of the available adult females usually breed in any one year. We conclude that although spawn string counts and actual female population size were not demonstrably synonymous, spawn counts probably do reflect relative sizes between populations and temporal trends within them except when numbers of productive ponds also change significantly over short timescales. Individual ponds can remain productive of toadlets for at least 25 years provided the habitat is managed appropriately.

Key words: Bufo calamita, natterjack toad, population estimation, spawn counts, UK

INTRODUCTION

Amphibians are declining at alarming rates over most of the world and their conservation is of increasing interest and priority (e.g., Stuart et al., 2004; Beebee & Griffiths, 2005). The crisis began earlier in Europe than in the Americas (Houlahan et al., 2000) and many British species declined severely in the early/mid 20th century. Among them was the natterjack toad *Bufo calamita*, always rare in Britain and the victim of a >70% decline in the decades before 1970 (Beebee, 1976). Subsequent conservation efforts for this species included extensive surveys and improved monitoring of surviving populations as well as pond creation/restoration and terrestrial habitat management, including grazing by domestic livestock which apparently benefits this amphibian (Buckley & Beebee, 2004; Buckley et al., 2013). Central to these efforts was the establishment of a UK natterjack toad site register (Beebee & Buckley, 2001) in which spawn string counts, toadlet production and management work were recorded, as far as possible annually at every location where the species still occurred. This register provides a database from which population trends and the effectiveness of management methods can be assessed.

We analysed data from 20 of the most thoroughly documented UK natterjack populations/subpopulations (about one third of the UK total; see Rowe & Beebee, 2007 for population and subpopulation definitions) to test the hypothesis that annual cumulative spawn string counts at a locality are reliable indicators of trends in female population sizes and, by default (because natterjack populations have, on average, an equal adult sex ratio; Denton & Beebee, 1993a), in trends of the entire adult population sizes. This assumption has been widely used to assess relative population sizes and trends over time because comprehensive spawn string counting is a relatively reliable and easy procedure for this species (Smith & Payne, 1980; Buckley & Beebee, 2004). However, we know little about how spawn string counts relate to actual female population sizes and possible variation in this relationship between years. To investigate this question we analysed data on spawn string counts from multiple UK natterjack populations over many years and related these to two factors: firstly reproductive success, as judged by toadlet emergence, to assess whether good breeding years led to increased spawn counts when the cohort matured; and secondly the consequences of new pond creation to investigate whether this led to apparent increases in population size (as judged by spawn string counts), again when the first cohorts from these ponds matured. Finally, we also examined the long-term abilities of individual ponds to support successful reproduction as judged by toadlet

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production. This was considered important from the conservation perspective as natterjacks are a pioneering species liable to local extinction caused by successional processes in some habitats.

METHODS

Our analysis was based on data from the *Natterjack Toad Site Register* (Beebee & Buckley, 2001) which is updated annually and collates information on breeding success of *B. calamita* at all locations in Britain where the species persists. We selected 20 sites with the most complete and extensive records of spawn string counts and toadlet production, estimated to within an order of magnitude, as shown in Table 1. Although chosen primarily on the basis of data quality and extent, the locations listed in Table 1 were broadly representative of the British natterjack site complement. Five sites were on heathland habitats, one was on upper saltmarsh and the remaining 16 were on coastal dunes or marshes. Seven sites (Frensham, Hengistbury, Holme, Minsmere, Sandy, Talacre and Mersehead) were translocations while the remaining 13 were native populations or subpopulations. Grazing by domestic animals, a management method that can benefit natterjacks, occurred on 12 of the 20 sites during at least some years of the study period. Methods for these assessments were described and justified elsewhere (Buckley & Beebee, 2004). We also included numbers of 'productive' ponds in this analysis, notably those producing natterjack toadlets in at least one of the study years, because it was arguably a more reliable measure than quantitative estimates of toadlet production. Most of the data were obtained between 1990 and 2009, with time series for individual sites varying from seven to 20 years (average=15.5 years). Data analysis was carried out using Statistix v.7 (Tallahassee, USA).

RESULTS

Characteristics of study sites

Trends of spawn string counts over time were slightly positive when averaged over the full 20 sites (average number of spawn strings x year after 1990, r_s=0.079) but marginally higher on grazed (r_s=0.085) than on ungrazed (r_s=0.069) sites. Average extents of suitable habitat in grazed (127 ha) and ungrazed (134 ha) sites were similar, as were average productive pond numbers (3.6 and 2.7 respectively, Wilcoxon Rank Sum Test exact p=0.305) but average spawn string counts per ha were four times higher at grazed (1.97) than at ungrazed (0.44) sites.

Toadlet production, productive ponds and population dynamics

Average spawn string counts, average toadlet production and average numbers of productive ponds were all correlated (Fig. 1) as found in earlier studies with fewer sites and shorter time periods (Beebee et al., 1996): spawn strings and toadlets, r_s=0.618, p=0.004; toadlets and productive ponds, r_s=0.575, p=0.009; spawn strings and productive ponds, r_s=0.536, p=0.016. If spawn string trends are dependent solely on local site factors, no correlation among sites over time is anticipated. By chance we expected just nine (190/20) significant correlations at p=0.05, where 190=total number of pairwise comparisons

Table 1. Sites used in pond effects comparisons. Numbers of years are those for which complete data for both spawn string counts and pond productivity were available.

Site	Number of years with complete data	Habitat type	Region
Frensham	16	Heath	SE England
Hengistbury	20	Heath/dune	S England
Woolmer	20	Heath	SE England
Holme	17	Dune	E England
Minsmere	15	Heath	E England
Sandy	16	Heath	E England
Winterton	16	Dune	E England
Ainsdale	20	Dune	NW England
Altcar	20	Dune	NW England
Birkdale	19	Dune	NW England
Formby	20	Dune	NW England
Talacre	13	Dune	N Wales
Annaside	9	Dune/marsh	NW England
Anthorn	7	Saltmarsh	NW England
Caerlaverock	19	Marsh	SW Scotland
Eskmeals	10	Dune	NW England
Haverigg	15	Dune	NW England
Mersehead	7	Dune	SW Scotland
Sandscale	14	Dune	NW England
Sellafield	17	Dune	NW England

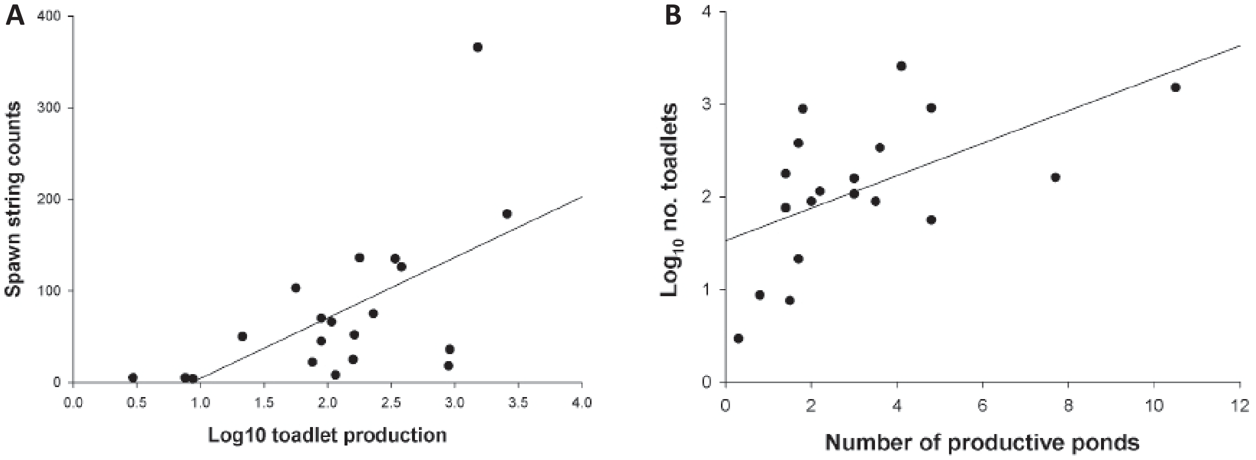

Fig. 1. Spawn string count, toadlet production and productive ponds. A) Numbers of spawn strings laid per year and numbers of toadlets emerging per year. B) numbers of toadlets emerging and numbers of productive ponds. All data were averages over 7–20 years between 1990 and 2009 for the 20 sites listed in Table 1.

among patterns of productive pond numbers over time in our sample of 20 populations, but we actually found 19 such relationships. The eight strongest correlations, some with clear regional connections, are shown in Table 2. These results implied significant regional effects on pond productivity, most likely accounted for by widely acting environmental factors such as climate.

We previously found a weak, positive relationship between toadlet production and spawn string numbers at one site (Woolmer) three years later (Banks et al., 1993). These results implied cause and effect, with toadlet production acting as a determinant of adult population size. However, in the present longer and more extensive study this inference was not supported. As shown in Fig. 2A, at Woolmer the correlation between spawn string count and number of emerging toadlets was strongest in the same year and progressively weaker when spawn string counts were compared with toadlet production in previous years, up to the three years typically taken for natterjacks to reach maturity. A similar pattern was observed at Hengistbury with respect to productive pond number although in this case the best correlation was with year -1, a time within which no toads could have reached maturity. Eighteen out of 20 sites showed positive correlations between spawn string counts and toadlet production in the same year (average r_s=0.356) while 10 of the 20 sites showed negative correlations between spawn string counts and toadlet production three years earlier (average r_s=0.115).

A burst of pond creation and restoration at Caerlaverock starting in the late 1990s (Phillips et al., 2002) also provided information about natterjack population dynamics. Average numbers of productive ponds rose from c. 15 in the period 1996–2000 to c. 36 in 2001–2005. Spawn string counts also rose dramatically between these two periods (Fig. 3A), from an average of c. 31 (1996–2000) to >120 (2001–2005), a highly significant difference (Wilcoxon Rank Sum Test exact p=<0.001). Toadlet production was strongly correlated with spawn string count in the same year (r_s=0.878, p=<0.0001) as expected from Fig. 1 but was not correlated with number of new/managed ponds each year (r_s=0.142, p=0.569). Spawn string count correlated with the total number of productive ponds (r_s=0.908, p=<0.0001) but the correlation between spawn count and number of new productive ponds was strongest (r_s=0.833, p=<0.001) the year immediately after pond creation (Fig. 3B).

Continuity of breeding pond success

Data on toadlet production were analysed from 15 individual ponds at seven sites, in some cases with records for up to 25 years (Table 3). All remained productive over the time span investigated and only three showed significant trends (Minsmere pond 6, Sandy pond 1 and

Table 2. Sites where numbers of productive ponds correlated over time.

Sites	Correlation (r_p)	Probability
South-east/eastern England		
Frensham x Woolmer	0.703	0.024
Frensham x Holme	0.542	0.045
Woolmer x Holme	0.662	0.004
Sandy x Hengistbury	0.598	0.015
North-west England		
Ainsdale x Talacre	0.608	0.162
Ainsdale x Birkdale	0.740	<0.001
Formby x Birkdale	0.552	0.014
Formby x Altcar	0.498	0.025

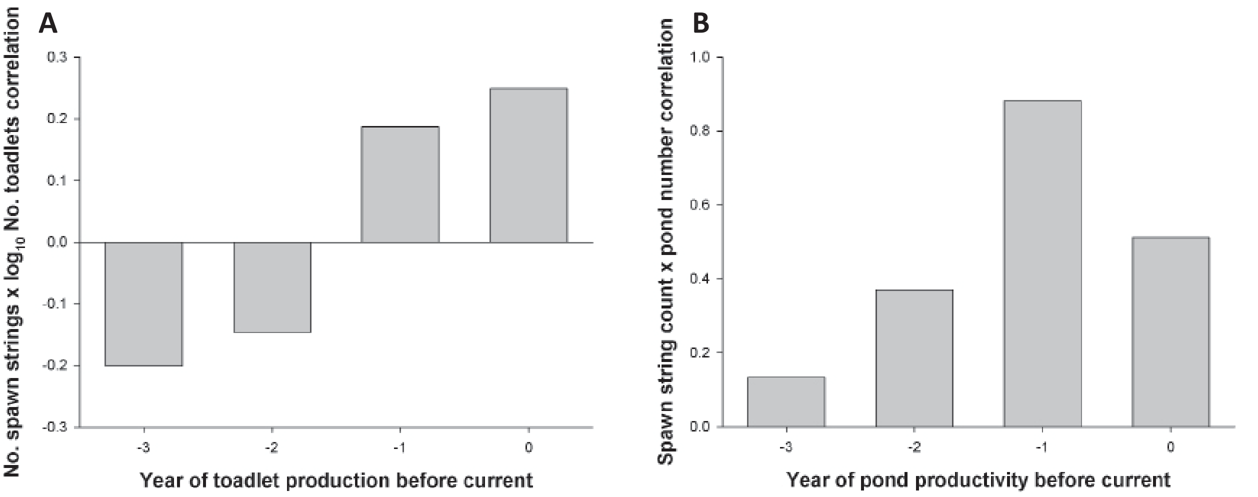

Fig. 2. Synchrony of spawn string counts and toadlet or productive pond numbers. A) Correlations of spawn string count against number of toadlets produced in the same year (0) and produced up to three years previous to the population size estimate at Woolmer. B) Correlations of spawn string count against number of productive ponds in the same year (0) and up to three years previous to the population size estimate at Hengistbury.

Ainsdale pond 159), all negative, over time. Productive ponds generated toadlets on average in 58% of the years for which data were available. The single set of saltmarsh ponds was consistently successful despite regular tidal inundations that killed entire spawn or larval cohorts early in the breeding season. Elsewhere, ponds with artificial liners experienced the highest average success rate (61%) but included two out of the three ponds with significant long-term declines. Dune slacks (average 47%) and heath pools (average 42%) were broadly similar and differences among the lined, dune and heath pool samples were not significant (Kruskal-Wallis ANOVA statistic=4.79, p=0.09).

DISCUSSION

This study confirmed positive relationships among spawn string counts, toadlet production and numbers of productive breeding ponds in accord with previous results based on a smaller data set (Beebee et al., 1996). However, a simplistic interpretation of cause and effect with high toadlet production generating high adult population sizes (at least, as judged by spawn counts) was not supported. In general, good years for toadlet production were not followed by increases in spawn string counts three years later when most toads from the cohort would mature (Denton & Beebee, 1993a). This implied that adult population dynamics were

Table 3. Continuity of pond use. Individual ponds at each site are annotated.

Pond	Period with data (no. years with data)	No. years producing toadlets (%)
Heathland		
Woolmer L	1985–2009 (25)	13 (52)
Woolmer I	1986–2009 (24)	12 (50)
Woolmer N	1985–2009 (25)	10 (40)
Woolmer M	1985–2009 (25)	8 (32)
Woolmer Pond	1985–2009 (25)	9 (36)
Liner ponds		
Minsmere 6	1989–2009 (16)	14 (88)
Vitower 2	1996–2009 (14)	13 (93)
Sandy 1	1985–2009 (21)	21 (100)
Formby 7	1992–2009 (16)	7 (44)
Dune ponds		
Ainsdale 3N	1985–2009 (23)	8 (35)
Ainsdale 5	1985–2009 (23)	11 (46)
Ainsdale 158	1985–2009 (24)	11 (41)
Ainsdale 159	1985–2009 (24)	12 (50)
Ainsdale 169	1985–2009 (25)	16 (64)
Saltmarsh ponds		
Anthorn	1997–2009 (13)	13 (100)

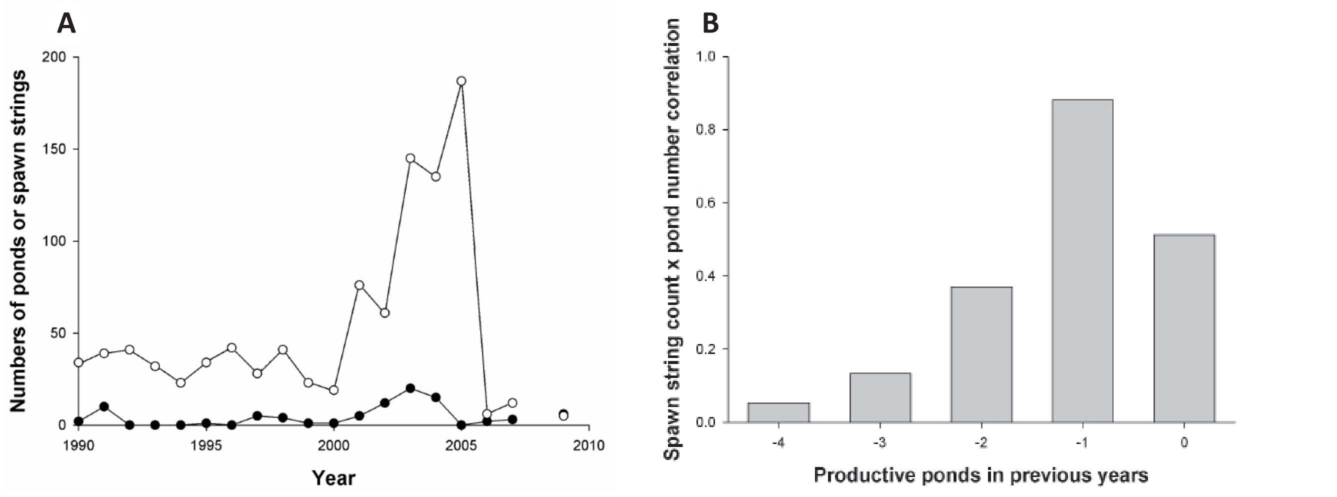

Fig. 3. Temporal relationship between new pond creation and spawn string counts. A) numbers of ponds cleared out or newly created (solid circles) and spawn string counts (open circles) at Caerlaverock, Scotland 1990–2009. B) Correlations between spawn string counts and numbers of ponds restored or created at Caerlaverock relative to times of pond creation.

driven primarily by other factors such as long-term survivorship or juvenile mortality, or that spawn string counts did not accurately reflect adult population size. These explanations are not mutually exclusive and all could contribute to the observations. The widespread correlation of spawn string counts and metamorph success in the same year implied a possible cause and effect in the direction of good spawning years resulting in high toadlet production, rather than the other way round with a time-to-maturity lag. This interpretation was supported by the observation that at Caerlaverock the large-scale creation of new ponds was followed by an increase in spawn deposition almost immediately, without an intervening time sufficient to increase adult numbers by improved recruitment.

This analysis therefore indicates that spawn string counts may significantly underestimate the numbers of adult natterjacks present at a site. Earlier capture-mark-recapture studies at one locality (Woolmer) during the 1990s indicated that in any one year only 35–64% of females known to be present actually spawned although this was partially offset by 10–17% of females spawning twice in a season (Denton & Beebee, 1993b; 1996). Nevertheless, if Woolmer is typical it seems likely that in most cases only a fraction of the female natterjacks at a site will spawn in any given year. Some adult females at Woolmer were seen entering the ponds and even being amplexed by resident males, but still left without spawning (Denton & Beebee, 1996). One possible explanation for these observations is that females may sometimes require resources obtained over more than a single year to mature batches of oocytes. There are precedents for biannual spawning in other amphibians, including bufonids (Muths et al., 2010; Loman & Madsen, 2010). However, another possibility is that females assess pond conditions before deciding whether to invest in oviposition. This could be particularly important for species such as *B. calamita* that usually spawn in temporary pools and which might judge likely hydroperiod from current depth. Female natterjacks can certainly discriminate against ponds already containing large numbers of competitor species larvae (Banks & Beebee, 1987) and late spawners might do the same if many conspecific tadpoles are already present.

Despite the lack of absolute correspondence between spawn string count and adult population size, spawning effort should nevertheless correlate with true population size over time providing circumstances, especially available pond number, remain broadly constant. This assumption has been used to assess relative population sizes and trends (Buckley & Beebee, 2004) and seems robust to variation in spawn effort and detection rates between sites and years (Buckley et al., 2013). Only five of the 20 sites reported in this study experienced significant changes in productive pond number over the 20 year time period. At Haverigg a significant but recent increase in productive ponds was not associated with any trend in spawn string counts. However, at both Anthorn and Talacre there were significant increases in spawn counts (Anthorn r_s=0.953; Talacre r_s=0.824) and in productive pond numbers (Anthorn r_s=0.874; Talacre r_s=0.602) over time, possibly compromising conclusions about population size if a progressively larger fraction of the population spawned. Similarly, at Eskmeals and Winterton spawn string counts (Eskmeals r_s=-0.501; Winterton r_s=-0.814) and productive ponds (Eskmeals r_s=-0.523; Winterton r_s=-0.796) decreased over time.

Evidently spawn string counts cannot be invoked in an uncritical way to assess the value of pond management or creation for natterjack conservation although it remains likely that population size does respond positively, over time, to increasing productive pond number. New ponds are often colonised rapidly by natterjacks (e.g., Ruhi et al., 2012) and modelling suggested that pond creation improves population viability but also confirmed the significance of juvenile mortality to overall population dynamics (Beebee, 2011; Di Minin & Griffiths, 2011). The long lifespan of suitable ponds, many producing toadlets regularly for 20 years or more, was interesting because in habitats utilised by *B. calamita* overgrowth due to successional processes can, in the absence of management, render them useless as breeding sites. In Germany, for example, gravel pit pools are commonly used by *B. calamita* but typically have individually short lifespans. Survival of metapopulations relies on intermittent creation of new sites (Sinsch, 1988; 1992; Sinsch & Seidel, 1995). In Britain, seral succession at natterjack sites is mostly prevented by combinations of dune sand mobility, tidal inundation and livestock grazing. However, lack of sufficient favourable management at Caerlaverock after the phase of pond creation probably explains the dramatic fall in spawn string counts in the late 2000s (Fig. 3B).

In summary, we recommend that cumulative spawn string counts are used with caution to assess trends, relative natterjack population sizes and management effects and that possible complications arising from changing pond numbers on the proportion of females choosing to breed should be taken into account when interpreting results.

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