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Effects of environmental factors and conservation measures on a sand-dune population of the natterjack toad (*Epidalea calamita*) in north-west England: a 31-year study

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A 31-year study monitored Britain's largest natterjack toad population on the Sefton Coast sand-dune system in north-west England. Key objectives were to describe changes in numbers and breeding success, relate these to environmental variables and explore whether conservation efforts have been well targeted. Considerable variation was found in the number of water bodies used for spawning, the number of spawn strings laid and breeding success based on estimated toadlet production. There was a declining trend in annual totals of spawn strings and toadlets. Positive correlations were established between spring and April rainfall and both spawn count and toadlet production. April rainfall for the study area declined between 2000 and 2017. Premature desiccation of water bodies and associated poor breeding success were frequently observed, there being a positive relationship between water-table height and toadlet numbers. A long-term declining trend in the height of the water-table was established. The mean adult population of Sefton natterjacks was estimated at about 1200 individuals, with a peak around 3150. Successful breeding is increasingly reliant on management to excavate appropriately designed and managed "scrapes" that hold water long enough for metamorphosis to occur. Overgrowth of vegetation and loss of dynamism in the dune system threaten both the natural production of new breeding slacks and the natterjack's open terrestrial habitat. Encouragement of dune dynamics by removing trees and scrub, increasing areas subject to livestock grazing and mechanical rejuvenation may offer the best hope of conserving this species in the future.

Keywords: Amphibian; climate-change; rainfall; sand-dunes; vegetation-overgrowth; water-table

INTRODUCTION

The natterjack toad (*Epidalea calamita*) is native to 22 countries in western and northern Europe, as far east as western Russia. Although still locally abundant, especially in southern Europe, it is declining in much of its northern range and is consequently listed as a European Protected Species under Annex IV of the EU Habitats Directive. At the north-western edge of its global distribution, this is a rare amphibian in Britain, having disappeared from 70-80 % of its range between the late 19th century and 1970 (Beebee, 1977). Declines have been attributed to habitat loss through afforestation, urbanisation and agricultural improvement, changes in habitat structure leading to seral succession and displacement by common toad (*Bufo bufo*) and/or common frog (*Rana temporaria*) and, in some cases, acidification of breeding pools (Baker et al., 2011; Beebee, 1983; Beebee et al., 1990; Denton & Beebee, 1994; Denton et al., 1997). By the early 1970s, the natterjack was restricted to around 50 British sites and was thought to be in danger of declining to extinction (Buckley & Beebee, 2004). Populations persisted in coastal north-west England and south-west Scotland and in a few scattered localities in southern and eastern England. Being protected by UK statute since 1975, this species has been the subject of considerable research and much conservation effort (Buckley & Beebee, 2004). The natterjack toad is a good coloniser of shallow, ephemeral ponds with a relatively high pH (6.0-8.0), mainly in sand-dunes, heathlands and on high-level saltmarshes, taking advantage of higher water-temperatures, lower predator numbers and reduced competition from other amphibians. An open, unshaded terrestrial habitat is required with areas of minimally vegetated ground for foraging and burrowing (Baker et al., 2011; Beebee, 1979; Banks & Beebee, 1987a, b; 1988).

The largest remaining natterjack population in Britain occurs on the calcareous sand-dunes of the Sefton Coast in north-west England (Beebee & Buckley, 2014a), where it has been known since the 1830s (Smith, 2009). Populations were evidently large in the late 19th and early 20th centuries but housing and other developments, extensive planting of conifers and introduction of invasive shrubs, such as Sea Buckthorn (*Hippophae rhamnoides*), led to losses of suitable habitat (Smith,

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2009). Following a prolonged drought in the 1970s which caused breeding failures (Smith & Payne, 1980), about 50 "scrapes" were excavated in existing slack basins to create new breeding sites. However, as the water-table rose again in the late 1970s and early 1980s, many of the scrapes became more-or-less permanent ponds and were invaded by large numbers of common toads and invertebrate predators, thereby becoming less suitable for the natterjack (Simpson, 2002; Smith, 2009).

Subsequent surveys highlighted large variations in breeding success, seemingly linked to changes in the water-table, a shortage of suitable wetlands in some parts of the dune system and the growth of coarse vegetation and scrub which adversely affected the natterjack's terrestrial habitat. A Sefton Coast Natterjack Conservation Strategy (Herpetological Conservation Trust, 2003; Simpson, 1992; Smith, 1984) recommended additional breeding pools to reduce population isolation and co-ordinated monitoring of distribution and breeding activity. From 1987 onwards, an annual monitoring report was produced, these data being summarised by Skelcher (2010). His report (updated to 2017) forms the basis for the current study whose main aims were to:

1. Use annual reports and other relevant sources to summarise how natterjack distribution, abundance and breeding success have changed over time.
2. Link these changes, where possible, to environmental factors.
3. Determine whether conservation efforts have been well targeted and make recommendations for future management.

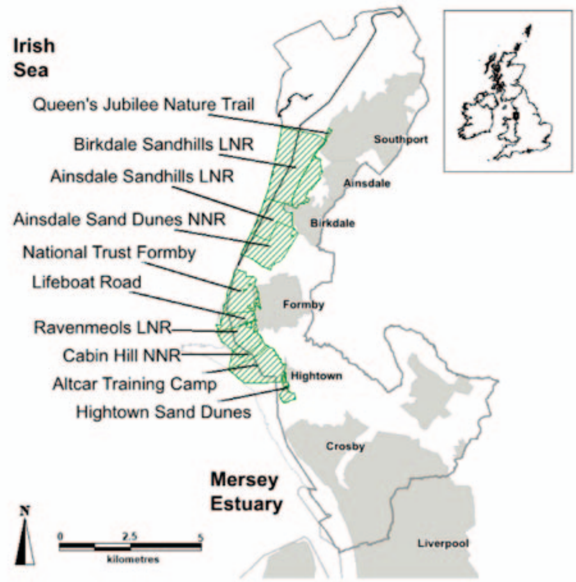

Figure 1. Map of Sefton Coast, north-west England, showing locations of survey units

METHODS

Population measures

The 2100 ha dune system was divided up into nine units (Fig. 1) that could reasonably be covered by individuals or small teams of surveyors made up of trained volunteers and site managers. Using methodology developed during earlier surveys (e.g. Smith & Payne, 1980; Buckley & Beebee, 2004) visits were made at roughly weekly intervals from the start of breeding activity. There was an emphasis on counting natterjack spawn strings and estimating toadlet production at each water-body (site) used for breeding. Female natterjacks usually lay only one pair of spawn strings per year, although a second, smaller pair of strings may be produced on rare occasions (Denton & Beebee, 1996). Therefore, string counts can be used as an index of the breeding female population. The appearance of freshly laid natterjack spawn changes markedly over a few days, making it possible to avoid double-counting strings recorded on earlier visits.

Toadlet numbers give an indication of breeding success but it is usually impossible to obtain accurate counts, so estimates for each breeding site were made on a logarithmic scale (Buckley & Beebee, 2004). Toadlets were often difficult to find and their numbers were probably underestimated in some years.

Supporting information included counts of assembling adults, estimates of tadpole numbers, presence of other amphibians, evidence of mortality, changes in water depth, date at which the site dried up and details of rescue operations.

Monitoring visits commenced at the start of the breeding season, usually late March to mid April, continuing until all metamorphosis had taken place or sites had dried up, often in late June to mid-July. Survey effort was standardised as far as possible by ensuring all potential breeding sites were covered in each year using the same methodology. Several of the same recorders were involved for a large part of the study.

Environmental correlates

To investigate possible relationships between breeding success and environmental variables, monthly rainfall and temperature data were obtained from the Ainsdale Sand Dunes National Nature Reserve (NNR) weather station, situated near the centre of the dune coast. Monthly water-table variations for the dune system have been measured since 1972 using a series of tube-wells. The most representative of overall dune water-table is considered to be tube-well no. 11 in the open dunes of Ainsdale NNR (D. Clarke in litt., 2015), so data from this well were used in the analysis. Based on a Shapiro-Wilk test, the dependent variables (spawn and estimated toadlet counts and their log vales) were considered to have normal distributions, while most of the independent variables (rainfall, temperature and water-table height) were not normal. Therefore a non-parametric test, Spearman's Rank (SR), was chosen to investigate correlations involving the latter variables, while Pearson's correlation coefficient was used for the former.

RESULTS

Adult assembly and spawning

Between 33 and 125 sites potentially suitable for natterjack breeding (mean 84) were monitored annually, the total depending on water-table conditions and whether or not the sites were flooded. Adult natterjacks assembled to between 7 and 96 sites (mean 48), the maximum adult peak count being 2442 in 1987 while the lowest was 15 in 2017 (mean 656). However, the counting effort for adults was inconsistent, so these data should be viewed with caution.

Most spawning took place during April or early May but, exceptionally, it occurred earlier or much later. Ideal conditions for assembly and spawning seemed to be relatively windless, damp and mild weather with a night-time temperature of at least 8 ˚C (personal observations). The number of sites used for spawning varied from a maximum of 78 in 2000 to a low of 7 in 2017 during a prolonged drought, the mean being 42. Annual totals of spawn strings ranged from 1576 (1988) to 77 in 1996 (mean 606). Figure 2 shows great variability in annual spawn counts but with a declining trend over the period of the study of about 70 %.

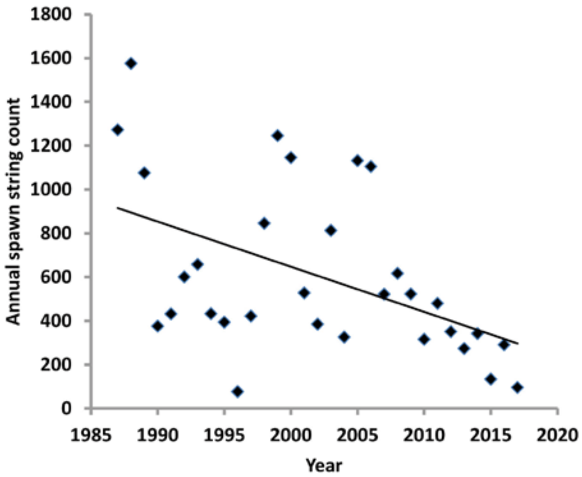

Figure 2. Number of spawn strings counted in each year of the study. (r =-0.485; p = 0.0057)

Contributions of different units to the annual totals of spawn strings varied considerably both within years and over longer time scales. Overall, Ainsdale NNR and the adjacent Ainsdale Sandhills Local Nature Reserve (LNR) provided 30 % and 28 % of total strings respectively. Annual totals at Ainsdale NNR tended to increase from 1987 to 1999 (Simpson, 2002) but then, despite high spawn counts in 2005 and 2006, showed significant declines from 2000 (Fig. 3a), especially so from 2007. Spawn counts for Birkdale Sandhills LNR fluctuated in line with coastwide trends until 2005, when numbers increased to a peak in 2008 before declining (Fig. 3b). This was mainly attributable to colonisation of pioneer slack and embryo dune habitat on the so-called “Birkdale Green Beach” from 1999 (Smith, 2007), while the more mature slacks to the east were progressively abandoned. After 2008, Green Beach spawn counts also fell. Further south, Cabin Hill NNR, together with the adjacent Altcar Training Camp, achieved a peak spawn count of 456 in 1985, just before the current study began (Smith, 2012).

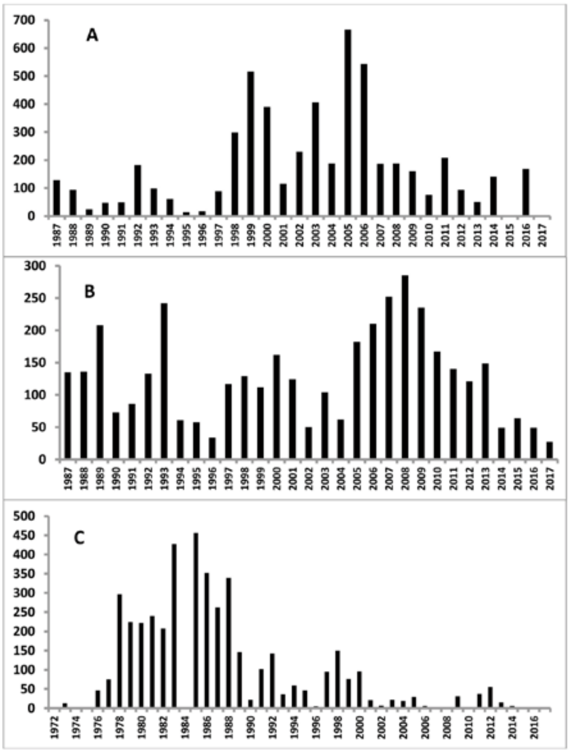

Figure 3. Annual spawn counts for Ainsdale Sand Dunes NNR, 1987-2017 **(A)**, Birkdale Green Beach 2005-2017 **(B)** and Cabin Hill/Altcar, 1972-2017 **(C)**. Ainsdale NNR shows a declining trend from 2000 (r =-0.58, p = 0.012)

There was then a significant decline in annual totals over the next three decades (Fig. 3c), though Altcar showed increased spawning activity in 2011-2013, probably due to the provision of new scrapes. Spawn counts at other units were generally low and trends unclear.

Metamorphosis

Breeding sites often dried up in spring or early summer, so successful metamorphosis occurred at only about half of the sites in which spawn was laid. A mean of 18.4 sites per annum produced toadlets, with a wide range from 48 sites in 2000 to none in 2011.

The use of a log scale to record numbers of toadlets at individual sites makes it difficult to compare annual coastal totals. In an attempt to overcome this problem, it was decided to use the midpoint of log values for each site, so that log 1 = 50 toadlets, log 2 = 500, log 3 = 5000, etc. From these approximations, annual toadlet production ranged from 0 to 526,000 per annum (mean 45,000). Peaks in toadlet numbers occurred in 1987, 1988, 1994, 2000 and 2006. Particularly poor metamorphosis was recorded in 1997, 2009, 2010, 2011 and 2017. After the 2006 peak, a series of five years of falling metamorphic success culminated in no toadlets being found in 2011. Overall, there was a declining trend in toadlet production (Fig. 4). Years with high spawn counts also tended to produce more toadlets than in years with lower spawn totals (Fig. 5).

The importance of excavated scrapes for successful breeding was evident, especially in drier years. Thus,

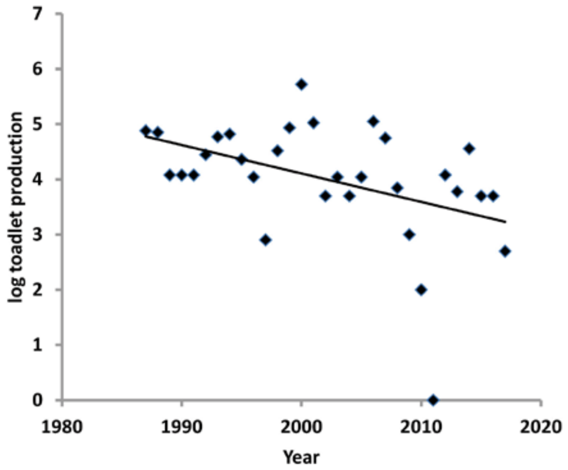

Figure 4. Trend of annual toadlet production. The y-axis is transformed to $\log_{10}$ (r =-0.436, p = 0.014)

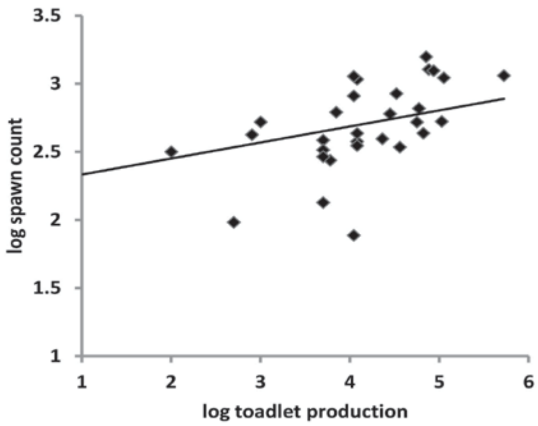

Figure 5. Relationship between $\log_{10}$ annual toadlet production and $\log_{10}$ spawn count (r = 0.401, p = 0.025)

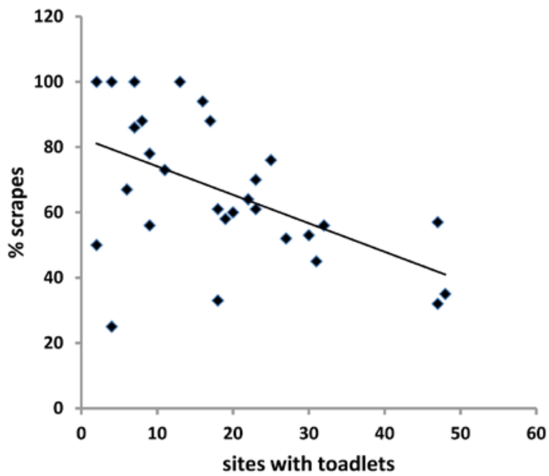

Figure 6. The relationship between the proportion of successful breeding sites that are artificial scrapes and the number of sites producing toadlets in each year (SR =-0.405, p = 0.027)

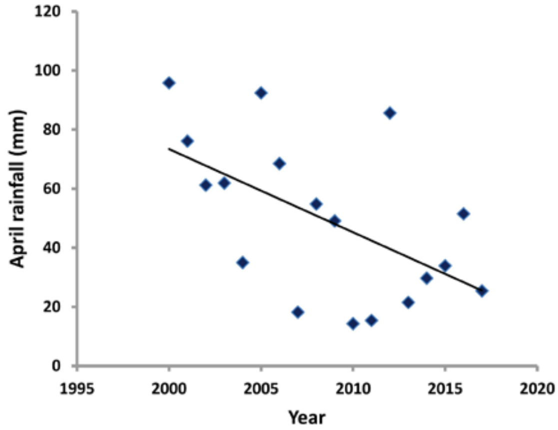

Figure 7. April rainfall trend at Ainsdale, 2000–2017 (SR = -0.567, p = 0.016)

a mean of 10.5 scrapes per year produced toadlets, representing 57 % of successful sites, the range being from 25 % scrapes in 2004 to 100 % in 1996, 1997 and 2017. Figure 6 shows that, in years when fewer sites had successful breeding, the proportion of them that were scrapes was significantly higher.

Environmental variables

With an average annual rainfall of about 820 mm, Sefton is one of the driest places in north-west England. The coast is also relatively windy, resulting in rapid evapotranspiration. Therefore any reduction in precipitation can have an adverse and cumulative impact on the water-table with potential impacts on natterjack breeding success. Monthly rainfall data from the Ainsdale NNR weather station for the study period were combined to provide totals for autumn (September -November), winter (December-February) and spring (March-May). Summer rainfall (June-August) was not included in the analysis as this usually has little impact on the water-table, most summer precipitation being lost to evapotranspiration (Clarke & Sanitwong Na Ayutthaya, 2010). The autumn mean rainfall (268 mm) was considerably higher than the winter mean (220 mm), spring having the lowest mean value (154 mm). There was a highly significant difference between the three sets of rainfall data (Kruskal-Wallis = 32.11, p = 0.0000001).

Autumn rainfall showed great variability, with a slight increasing trend that was not significant. There was no particular trend over time for winter rainfall, while spring totals suggested a decline over time which was not significant. However, rainfall for April, the month in which most spawning takes place, showed a steeper declining trend, this being significant from 2000 (Fig. 7). Since that year, there have been eight particularly dry Aprils with mean rainfall about 50 % of the long-term average. These eight seasons had mean spawn counts of 311, compared with the overall mean annual count of 606, this difference being significant (Man Whitney = 144, p = 0.018). Positive Spearman Rank correlations were found between log toadlet production and spring rainfall (SR = 0.509, p = 0.0041) and April rainfall (SR = 0.45, p = 0.011)

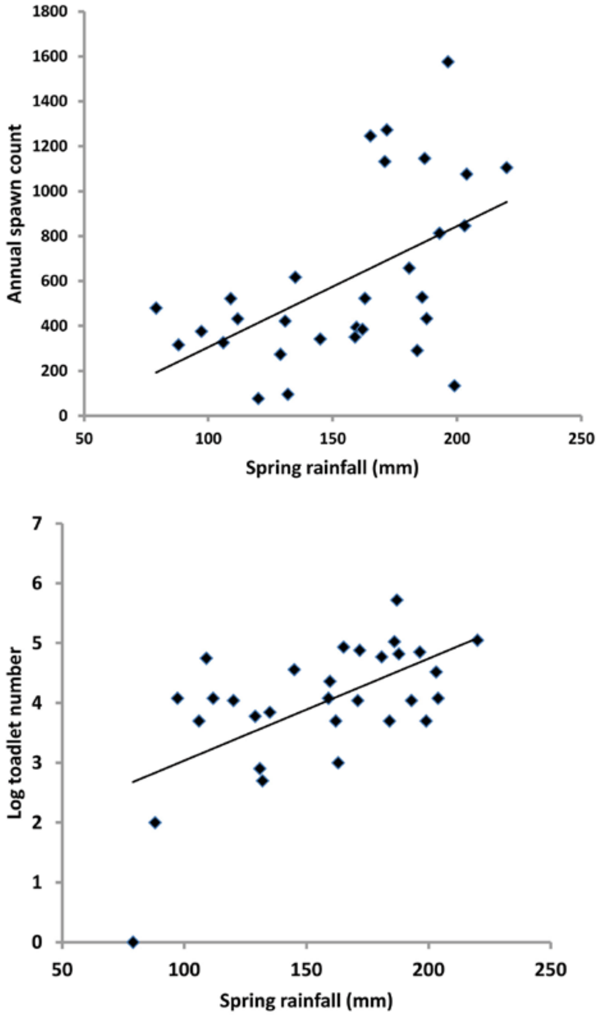

Figure 8. The relationships between annual spawn count (above) and $\log_{10}$ toadlet number (below) and spring rainfall (SR toadlets = 0.509, p = 0.0041; SR spawn = 0.533, p = 0.0028)

and also between annual spawn count and both spring rainfall and April rainfall (Fig. 8). Correlations were not established between either toadlet numbers or spawn counts and annual rainfall.

During the study period, spring mean maximum temperature increased (SR = 0.526, p = 0.0024), while spring minimum mean temperature declined (SR = -0.44, p = 0.013). We had thought that April temperatures would impact on spawning; but correlations were not found between mean minimum or mean maximum April temperatures and spawn counts and between spawn counts and spring mean minimum or maximum temperatures.

Figure 9 shows a declining trend of monthly water-table during the study period for tube-well no. 11 in Ainsdale NNR. The time-line shows the expected seasonal oscillations in water-table, maxima occurring in early spring and minima in summer. In most years, the difference between annual high and low points was about 85 cm, reflecting high rates of evapotranspiration in spring and summer. There was also great variation in annual high and low points, with winter peaks in 1988,

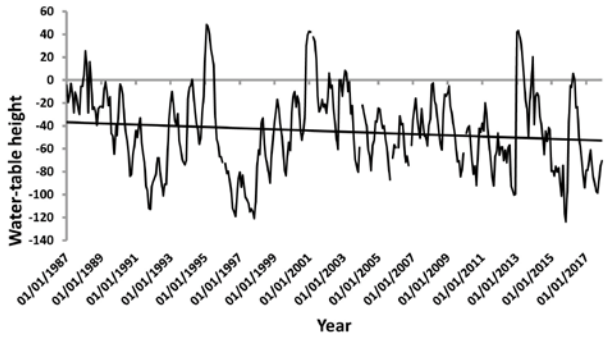

Figure 9. Monthly water-table in well 11 Ainsdale NNR from 1987 to 2014. Zero on the y axis denotes the ground surface; positive values indicate depth of standing water; negative values depth below ground surface

1995, 2001 and 2013, while particularly low values occurred in the summers of 1991, 1997, 1998, 2006 and 2011. Changes over short time-scales could be strikingly large. For example, the water-table declined by 167.5 cm in the 20 months between February 1995 and October 1997. This meant that deeply flooded dune slacks in late winter could be completely dry within a few weeks and remain so for many months.

Surprisingly, no Spearman Rank correlations were found between spawn counts and water-table data expressed either as April water-table (SR = 0.180, p = 0.331) or mean annual water-table (SR = 0.311, p = 0.088). However, there was a correlation between mean annual water-table and log toadlet number (SR = 0.394, p = 0.028) but not between mean April water-table and log toadlet number (SR = 0.29, p = 0.114). There was no relationship between mean March-June water-table and both spawn count and log toadlet number (SR = 0.268, p = 0.144 for spawn; SR = 0.326, p = 0.074 for toadlets).

DISCUSSION

Population dynamics

Continuous survey over many years is the most reliable way of quantifying changes in natterjack populations (Buckley & Beebee, 2004). The 31-year timescale of this study provides a unique opportunity to analyse trends for a large population in a sand-dune habitat, the only other published long-term investigation being a 37 year data-set for a much smaller population of natterjacks on lowland heath in southern England (Beebee, 2011; Di Minin & Griffiths, 2011).

During the current study, annual spawn counts varied greatly, the pattern of peaks being similar to that reported in the UK as a whole by Buckley et al. (2014). Between 1990 and 2009, peak national spawn counts were in 1993, 2000, 2003, 2005 and 2009, while those on the Sefton Coast occurred in 1993, 1999, 2000, 2005, 2006 and 2008. Annual Sefton spawn counts, roughly equivalent to numbers of females breeding in that year, ranged from 1576 to 77 (mean 606). A small proportion of females do not spawn every year, as some may require resources from more than one year to mature a batch of eggs. Also, they assess pond conditions or the presence of competitor larvae before spawning (Beebee & Buckley, 2014b). Spawn counts are likely therefore to underestimate the numbers of females in particular years. Bearing in mind this proviso and assuming a 1:1 sex ratio (Beebee & Denton, 1996), the mean Sefton adult population may have been about 1200 individuals, with a peak around 3150. Some strings were probably missed, so the actual population was probably somewhat larger. Smith & Payne (1980) estimated an adult female population of about 2000 in their 1978 Sefton Coast study, while Davis's (1985) data suggest that just the Cabin Hill adult population averaged about 1400 between 1981 and 1983.

Peak counts of adults (mostly males) at breeding sites were sometimes larger than the number of spawn strings recorded, the largest counts being 2442 in 1987 and 2354 in 1998. However computed, these data represent a high proportion of the UK natterjack toad population, estimated "very approximately" at an average of 4000 adults between 1990 and 2009 (Beebee & Buckley, 2009).

Beebee (2009) examined the relationship between "apparent" breeding population size (from spawn counts) and "effective" breeding population size estimated from genetic (microsatellite) data. The latter is usually much smaller than census size because many adults fail to leave progeny. In a mid-1990s sample year, Sefton had a census size of 896 and an effective size of 97 adults (ratio 9.2:1). An effective breeding size of more than 50, as here, is important because a smaller number promotes genetic drift which is likely to erode genetic diversity and, ultimately, population viability.

Estimated metamorphic success was extremely variable (from 0 to 526,000 toadlets per annum), there being a positive relationship between spawn count and toadlet numbers. Beebee & Buckley (2014b) also reported a positive correlation between spawn counts and $\log_{10}$ toadlet production in a 20-year analysis of UK natterjack populations.

Climatic factors

The great variation and decline in spawn counts and breeding success recorded in Sefton was probably due to many interacting factors, some of which were investigated during this study. Most convincing was the positive relationship between spring (March-May) and April rainfall and both spawn count and toadlet production. Declining April rainfall since 2000, with associated reduction in spawning and metamorphic success, seems to accord with national trends and, according to Hanna et al. (2016), is linked to changes in high pressure blocking over Greenland. This has resulted from a warming trend in that part of the Arctic and has affected the strength of the North Atlantic Jet-stream.

McGrath & Lorenzen (2010) investigated the effect of 25 climatic, site and management variables on British natterjack populations using general linear models. They found that rainfall but not temperature was a predictor of population trends. Surprisingly, however, these trends declined with increasing rainfall, this being mainly due to the dominant influence of three sites in Cumbria, UK, that were subject to high rainfall. No clear relationship was apparent for other sites that experienced lower rainfall. The authors concluded that, while rainfall is needed to trigger natterjack activity, having just enough to maintain shallow breeding ponds is preferable to high rainfall. However, a drier climate coupled with large fluctuations in water-table, as on the Sefton Coast, risks an increasing frequency of breeding pond desiccation. Thus, Banks et al. (1994) showed that from 1970 and 1990 there was a greater risk of natterjack breeding failure for years in which any month between March and May had less than 25 mm of rainfall. In Sefton, the eight driest Aprils since 2000 had a mean rainfall total of 24.2 mm, these springs also having fewer spawn strings. Similarly, Banks & Beebee (1988) found that slack desiccation was a key mortality factor in some years, especially affecting tadpoles at their Drigg dunes (Cumbria, UK) study area. However, desiccation was much less important at their Woolmer (Hampshire, UK) heathland study area, being replaced by tadpole loss to predation as the key mortality factor. Davis (1985) found that invertebrate predation was responsible for 87-97 % of tadpole mortality at Cabin Hill, Sefton, from 1981 to 1983, while pool desiccation accounted for only 2.9 to 12.8 % of tadpole loss. However, his study took place during a period of high water-levels and involved "mature" water-bodies over ten years old, in which invertebrate predator populations were likely to be high. Davis also pointed out that losses due to desiccation often occur late in the season, affecting mature tadpoles that have escaped other forms of mortality.

Unusual climatic conditions were shown by Buckley & Beebee (2004) to coincide with low spawn counts at many British natterjack colonies, thus the exceptionally high water-levels in spring 1995, followed by low levels the following year corresponded with low numbers of spawn strings nationally, as well as in the Sefton dunes. Beebee (2011) used models to test a series of hypotheses on the effects of conservation management and climatic factors on natterjack population dynamics. His results supported those of McGrath & Lorenzen (2010), inferring positive influences of management and negative effects of rainfall. To account in part for the latter, Beebee (2011) suggested that high winter rainfall causes mortality of juveniles by flooding hibernation sites.

A link was established between annual water-table height and toadlet production, it being clear that premature desiccation of Sefton breeding sites in spring and early summer, especially after 2000, caused catastrophic mortality of tadpoles. In some years, water-levels were so low that few breeding sites were available; for example, only seven were used for spawning in 2017. The major fall in water-table between February 1995 and October 1997 coincided with the lowest spawn count of 77 in 1996. Hydrological studies of other British dune systems suggest such variations are not confined to the Sefton Coast. Thus, while the mean annual fluctuation of the Sefton dune water-table is about 85 cm, Kenfig in South Wales averages 81 cm (Jones & Etherington, 1989), Whiteford Burrows 115 cm (Stratford et al., 2012), Braunton Burrows 95 cm (Clarke & Stratford, 2010) and Newborough Warren between 82 cm and 133 cm (Clarke & Stratford, 2010). However, of these localities, only Sefton supports natterjack toads. The fact that there has been an overall decline in the height of the water-table may have increased the likelihood of breeding sites drying out prematurely.

Our study found significant increases in mean maximum temperatures and decreases in mean minimum temperatures during spring over the survey period. Warmer daytime temperatures may increase rates of desiccation of breeding sites, while cooler temperatures at night are less favourable for natterjack breeding activity (McGrath & Lorenzen, 2010).

Conservation

It is well established that a viable natterjack population is dependent on two key habitat resources:

- The availability in spring of suitably shallow, sparsely vegetated water bodies with appropriate water chemistry and few aquatic predators or competitors
- Suitable terrestrial habitat comprising short turf with large open sandy areas for foraging and burrowing (Baker et al., 2011; Beebee & Denton, 1996).

In the past, Sefton natterjacks mainly bred in embryonic slacks created either by wind-erosion or accretion of new dunes (Smith, 2009). However, due to dune-sealing, the rate of slack formation in the Sefton dunes has been low for several decades (Houston, 2008; Smith, 2009), necessitating the excavation of scrapes to mimic this habitat. According to Beebee & Denton (1996), natterjack population size is usually limited by the number of suitable breeding pools. A high density of pools also increases the chance of some having suitable conditions for the immature stages, irrespective of rainfall or other factors that affect temporary water bodies. Between 2010 and 2015, 24 new scrapes were created in the Sefton dune system. Nearly all young scrapes were used successfully by natterjacks, their importance for toadlet production, especially in dry years, having been shown during this study. Indeed, without them, little or no successful breeding could have occurred in most recent years. Ideally, several scrapes of different depths are required at each site to ensure that at least one supports successful metamorphosis each year (Baker et al., 2011; Buckley et al., 2014).

Also important is the distance between breeding sites. Using radio-telemetry, Sinsch et al. (2012) estimated that a maximum distance of 2250 m between natterjack breeding ponds in central Europe was needed to maintain connectivity. In Sefton, as far as possible, suitable breeding sites have been provided at intervals of less than 2000 m.

Previous studies have demonstrated the importance of climatic variables on natterjack populations, especially the deleterious consequences of changes in rainfall (Banks et al., 1994; McGrath & Lorenzen, 2010). In the longer term, climate change could also have an adverse impact on slack habitat. Thus, using a conceptual water-balance model, Clarke & Sanitwong Na Ayutthaya (2010) estimated that the Sefton dune water-table may fall by as much as 1.5 m by the end of the 21st century. Natural England (2014) found a 36 % and 44 % reduction in wetland area at Ainsdale and Birkdale, respectively, between 1989 and 2012 due to slack habitats becoming drier. Older slacks are gradually infilled by blown sand and organic matter (Simpson, 2002; Smith & Payne, 1980), and undergo succession to a densely vegetated condition, rendering them less suitable for natterjack breeding. Many of the older scrapes dug in the 1970s and 1980s have been colonised by emergent aquatic plants, the competitive common toad and aquatic predators such as dragonflies (*Odonata*), to the exclusion of the rarer amphibian (Simpson, 2002). Beebee & Buckley's (2014b) national study showed that a majority of natterjack breeding ponds remained productive for up to 25 years, though many required active management to maintain favourable conditions. Some of the earlier scrapes on Ainsdale NNR were re-profiled in the early 1990s and continued to be used by natterjacks (Simpson, 2002).

As in other West European dune systems, the natterjack's terrestrial habitat has been affected by increasing stability, vegetation overgrowth and loss of dynamism (Houston, 2008; Smith, 2009; 2012). Lower rabbit (*Oryctolagus cuniculus*) numbers in some areas (Simpson, 2002) and aerial deposition of nitrogen (Jones et al., 2004), is likely to have played a role in the development of coarse vegetation and scrub on the Sefton dunes. Over-stabilisation is disadvantageous to natterjacks as it restricts foraging opportunities and encourages colonisation by competitive amphibia (Beebee & Denton, 1996). These factors seem to have led to reductions in previously large populations, especially at Ainsdale NNR, Birkdale LNR and Cabin Hill/Altcar. Arntzen et al. (2017) reported a significant decline of the natterjack in northern France between 1974 and 2011, coastal dune populations being affected by re-growth of vegetation over open areas that had been created by military activities during World War II. Similarly, Stevens & Baguette (2008) drew attention to the natterjack's susceptibility to habitat succession in Belgium.

In an attempt to hold back vegetation succession, domestic livestock have been re-introduced to several Sefton duneland holdings, as recommended for the management of natterjack terrestrial habitat by Baker et al. (2011). However, many of the natterjack breeding sites near the shore lie outside the grazing enclosures. In a review of UK breeding colonies, Beebee & Buckley (2009) found populations on grazed sites were stable or increased slightly between 1990 and 2009, while those on ungrazed sites declined. Simpson (2002) described the beneficial impact that tree and scrub removal followed by livestock grazing had on natterjack terrestrial habitat at Ainsdale NNR. Although it retarded succession at Ainsdale, grazing did not entirely prevent it, leading Millett & Edmondson (2013) to suggest that re-establishment of disturbance to create new slack habitat, followed by grazing, might be a more successful strategy. Evidently, active management is needed to maintain and enhance natterjack populations (Arntzen et al., 2017; McGrath & Lorenzen, 2010). Stevens & Baguette (2008) point out that protection without management leads to habitat deterioration and natterjack extinction. While the considerable (and expensive) management efforts in Sefton seem to have been well-targeted, they have been insufficient to prevent an apparent recent reduction in the population. It is especially concerning that natterjacks appear to be declining on Ainsdale NNR (Fig. 3a), despite the fact that large parts of the reserve are managed in a way that should benefit this species, including provision of scrapes, scrub control and winter-grazing by livestock. Further action is desirable, including creating more scrapes, restoring older ones, increasing livestock grazing, removing invasive scrub and woodland and mowing coarse vegetation in breeding sites. It is hoped that additional resources for management will be allocated through Dynamic Dunescapes, a joint Heritage Lottery Fund and EU LIFE project covering seven coastal dune systems in England and Wales, including the Sefton Coast. The delivery phase, from 2019 to 2023, proposes capital works, such as re-mobilisation, turf-stripping, mowing and scrub control which, if appropriately targeted, could greatly benefit natterjack toad conservation in Sefton.

CONCLUSIONS

The results of this long-term study suggest that the size of the natterjack toad population on the Sefton Coast remains significant in a national context but has declined in recent years and is increasingly dependent on active management to create and maintain suitable breeding sites. These are susceptible both to desiccation, due to low spring rainfall, and invasion by competitive amphibians. Large fluctuations in the water-table often resulted in the premature drying out of dune-slacks and reduced breeding success. Climate change is likely to exacerbate this trend in the future. Many former breeding sites have become overgrown, while vegetation maturation and the development of scrub and coarse grassland have reduced the suitability of terrestrial habitat. Encouraging dune dynamics by removing trees and scrub, increasing areas subject to livestock grazing and mechanical rejuvenation may offer the best hope of conserving this species in the future.

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