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CHANGES IN DEWPOND NUMBERS AND AMPHIBIAN DIVERSITY OVER 20 YEARS ON CHALK DOWNLAND IN SUSSEX, ENGLAND

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Abstract

The fate of dewponds, the only substantive wetland habitat on the chalk Downs of southern England, was monitored over an area of 150 km² between 1977 and 1996 together with changes in use by the five species of amphibians that inhabit them. Despite a proactive pond restoration programme there was an overall net loss of seven pools (21% of the initial number of 33) by 1996, although a higher proportion and absolute number of surviving ponds were in good condition in 1996 (58%, 15 ponds) compared with 1977 (24%, eight ponds). Anurans (common frogs Rana temporaria *and toads* Bufo bufo*) were more widespread on the Downs in 1996 compared with 1977, probably because they colonised new ponds effectively, whereas urodeles (smooth newts* Triturus vulgaris*, palmate newts* T. helveticus *and crested newts* T. cristatus*) all declined over the same period.* T. cristatus*, a species ceded maximum protection under the European Union Habitats Directive, occurred in nine sites in 1977 but in just three by 1996. Total destruction of ponds was the most common cause of crested newt extinction, but at two sites the species disappeared following the establishment of fish populations. Various indices of amphibian diversity in dewponds are also compared. © 1997 Published by Elsevier Science Ltd*

Keywords: dewponds, biodiversity, amphibians, *Triturus cristatus*.

INTRODUCTION

Concern about global declines of amphibian populations has been reported from many countries all round the world in recent years (e.g. Wake, 1991; Griffiths & Beebee, 1992; Blaustein et. al., 1994). In Britain there are generally recognised to be only six native species currently extant, one of which (the natterjack toad *Bufo calamita*) is highly localised on account of its specialised habitat requirements (Smith, 1951). The remaining five species are widespread and constituted by two anurans (the frog *Rana temporaria* and the common toad *Bufo bufo*) and three urodeles (smooth, palmate and crested newts, *Triturus vulgaris*, *T. helveticus* and *T. cristatus*, respectively). The distribution and abundance of all these animals has been investigated in some detail at both national and local levels over recent decades (Swan & Oldham, 1993; Buckley 1989, 1991) and probably all have suffered declines to varying degrees (Cooke & Arnold, 1982; Swan & Oldham, 1993). Both anurans and at least one of the newts (*T. vulgaris*) have, however, benefited substantially from the popularity of garden ponds (Beebee, 1979; Banks & Laverick, 1986), somewhat offsetting decreases in the countryside. Of the widespread species, there is most concern about the crested newt *T. cristatus* because (a) it has probably always been less abundant than the other four, (b) it has not adapted well to garden environments, and (c) it has declined faster than other relatively common amphibians not only in Britain but also elsewhere in Europe (Beebee, 1975; Oldham & Nicholson, 1986; Gent & Bray, 1994). Crested newts were legally protected under the Wildlife and Countryside Act in Britain in 1981, and enjoy a similar status in many countries of the European mainland.

The chalk hills ('Downs') of southern England occupy a substantial proportion (more than 15% in the county of Sussex) of the total landscape and were among the first areas to be inhabited and modified by human invaders some 6000–7000 years BP. Natural freshwater bodies are rare on the freely-draining chalk substrate, though a few do occur on impermeable clay overlays. However, livestock farming on the Downs was maintained for many centuries by the provision of artificial pools, known as dewponds, constructed by puddling artificial liners of clay and straw into excavated depressions and allowing them to fill naturally with rainwater (Martin, 1909; Pugsley, 1939). From the 17th century onwards these ponds became very abundant, averaging one per km² on the Sussex Downs early in the

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20th century, until arable intensification starting in the 1940s rendered them increasingly redundant. Dewponds at their best support a rich variety of fauna and flora including all five of the widespread amphibian species, and can be particularly good habitats for crested newts (Beebee, 1977). Unfortunately these ponds have short lifespans and are quickly lost when their artificial bases crack and go unrepaired. More than 70% of those present on the Downs between the rivers Ouse and Adur disappeared between 1950 and 1977 (Beebee, 1977). Evidently, an interesting feature of Downland scenery together with its associated wildlife has been put at risk by this major change in agricultural practice.

All dewponds within the 150 km^2 of Downs between the rivers Ouse and Adur were surveyed for condition and for the presence of amphibians in the spring of 1977. Since that time these hills have been declared an Environmentally Sensitive Area (ESA), a Sussex Downs Conservation Board has been established, and efforts have been made to ameliorate the effects of intensive arable farming. These have included a substantial dewpond creation and restoration programme, and in this paper I report on a resurvey of dewponds during 1995–1996 covering the same area as in 1977.

METHODS

Information concerning dewpond restoration and creation was provided by the Sussex Downs Conservation Board, the National Trust, and in some cases by personal observation during perambulations of the Downs. All ponds within the study area that contained water were surveyed for amphibians during the springs of 1995 or 1996, employing standard procedures for the various species (Beebee, 1977; Griffiths *et al.*, 1996). Thus frog breeding sites were identified by looking in daytime for spawn within the two weeks of peak breeding activity in March; toad sites were also identified by looking for spawn or tadpoles, and by inspecting ponds after dark by torchlight. The presence of newts was established by a combination of netting (using chest waders to reach all parts of the pond) during daytime, searching by torchlight at night and by the setting of live-traps overnight. The presence or absence of newt eggs on the leaves of aquatic macrophytes was also determined; this method can distinguish the larger eggs of *T. cristatus* from those of *T. helveticus* and *T. vulgaris*, but cannot distinguish between those of the latter two species. Newt occupancy was never determined by observations of eggs alone, and most ponds were surveyed at least three times. Only the presence or absence of a species was recorded, and no effort was made to quantify population sizes. The general state of the pond, especially maximum depth and presence of macrophytes, was also recorded in every case.

Data were compared with those obtained in an earlier survey carried out mainly in 1977 (Beebee, 1977) but with a few further observations between 1977 and 1980 using methods similar to those employed in 1995–1996 except that live-trapping and egg-searching were not done in the earlier survey. Standard statistical tests (mostly χ^2) were employed throughout. Numbers of species combinations were compared with the theoretical maximum of 31, i.e. ($2^n - 1$) for $n = 5$ species.

RESULTS

The fate of dewponds

The changing numbers of dewponds within the survey area are summarised in Table 1. The survey also included two larger pools (> 500 m^2 surface area), at least one of which was probably of natural origin. Of 33 ponds present in 1977, only 16 (less than 50%) remained in 1996 and half of these were partly cracked and very shallow (less than 30 cm maximum depth in April). This was despite the fact that 11 of the original 33 ponds had been restored during the intervening period; two of these 11 ponds were already dry, and a further four were in a precarious condition. However, 13 ponds that were dry in 1976, or did not exist even as remnants at that time, have also been created, and thus conservation work has been carried out on a total of 24 ponds in this part of the South Downs. Restored and newly created ponds were with only one exception sited in good (i.e. non-arable) terrestrial habitat, usually rough grassland subject to livestock grazing. Most were also fenced to limit or prohibit access by these animals. Unfortunately there has been a substantial attrition rate with these new ponds as well (three losses and three in poor condition) despite the fact that most were made as recently as the early 1990s, with the result that by 1996 there were still 21% fewer ponds (26 rather than 33) than in 1977.

Table 1. Changes in dewpond numbers and quality 1977–1996

	Original ponds (present in 1977)			New Ponds (b)	Grand total (a + b)
	Total (a)	Restored since 1977	Unrestored		
Total	33	11	22	13	46
Ponds lost 1977–1996	17	2	15	3	20
Ponds in good condition in 1996	8	5	3	7	15
Ponds in poor condition in 1996	8	4	4	3	11
Total left in 1996	16	9	7	10	26

On the other hand, a larger number and percentage of ponds were judged to be in good condition in 1996 (15 ponds, 58% of the total) than was the case in 1977 (eight ponds, 24% of the total). Ponds were assessed to be in good condition if they were at least 0.5 m deep in April and supported extensive growths of macrophytes (covering >25% of the pond base), commonly *Ranunculus* species but also various *Potamogeton* species and other (generally minor) floral components.

Amphibians in the dewponds

Occurrence of all five widespread amphibian species in 1977 and 1996 is summarised in Table 2. Several changes were notable over this period. First, anurans were found more than twice as often in 1996 as in 1976 and both species increased by about the same degree. By contrast, all three species of urodeles declined and the decreases ranged from about 29% (*T. vulgaris*) through 50% (*T. helveticus*) to 67% (*T. cristatus*). This difference between anurans and urodeles clearly had two reasons: (1) Anurans survived better in the old (1977) sites than urodeles did, remaining at 50–75% of sites (*B. bufo* and *R. temporaria*, respectively) compared with 22, 43 and 50% for the newts (*T. cristatus*, *T. vulgaris* and *T. helveticus*, respectively). Even so, the frequencies of amphibians still present in original (1977) ponds in 1996 were not significantly different from those expected by chance based on the overall rate of pond loss, although crested newt declines were twice as great as would be expected from pond destruction alone; (2) colonisation of new ponds varied substantially between species. Thus, total frequencies of amphibian observations (in old and new pools altogether) were significantly different in 1996 from those expected by chance on the basis of losses of old ponds and equitable colonisation rates of new ones ($\chi^2 = 15.51$, d.f. $= 4$, $p < 0.02$). Six of the new pools were occupied by frogs (nearly 50% of those made) and three by toads, constituting 67 and 75% of their total 1996 distributions. Of the five amphibians present on the Downs, *Rana temporaria* was evidently the most efficient coloniser. By contrast, *T. helveticus* had not colonised any of the new ponds and *T. cristatus* only one, which happened to be within a few metres of an old pool lost in the intervening years despite a restoration effort. *T. vulgaris* was the best urodele coloniser and had reached four ponds, though these still constituted only 40% of its total 1996 range on the Downs.

Table 2. Changes in amphibian fauna of dewponds 1977–1996

Species	Number of records (1977)	Number of records (1996) Original ponds	New ponds	Total
Rana temporaria	4	3(2)	6	9(3)*
Bufo bufo	2	1(1)	3	4(3)
Triturus vulgaris	14	6(7)	4	10(11)
Triturus helveticus	6	3(3)	0	3(5)*
Triturus cristatus	9	2(4)*	1	3(7)*

Numbers in parentheses are of expected numbers of observations in original ponds if changes were due only to pond losses, or expected observations in all ponds if new ones were colonised in the same relative proportions as old ponds were occupied in 1977.
*, Situations with large differences between observed and expected results.

Various measures of amphibian success in Downland dewponds are summarised in Table 3. Total records were reduced by 17% in 1996 compared with 1977, though the average number of species per pond (combined used/unused) was essentially unchanged and the percentage of ponds used by amphibians was substantially higher in 1996, presumably reflecting the increased proportion of ponds in good condition. However, the average diversity within individual ponds tended to lower values in 1996, with a small reduction in the number of species combinations recorded (nine instead of 10) and a rather larger reduction (17%) in the average number of species in ponds used by at least one species. This reflected a smaller proportion of used ponds with more than one species in 1996 (55%) compared with 1977 (65%).

DISCUSSION

The contribution of small pond habitats to biodiversity is increasingly recognised in Britain and elsewhere, but commensurate with this realisation have been enormous losses of ponds, mostly consequent upon the changing demands of modern agriculture (Oldham & Swan, 1993; Biggs *et al.*, 1994; Milton, 1994). The South Downs stand out as an area which, having suffered from this change, is now benefiting from a relatively high input of conservation management. They therefore provide an instructive example of how difficult or otherwise it will be to reverse the damage to the British countryside and its wildlife that has been so extensive in recent decades. It is salutary to note that even with a substantial programme that has on average restored or created more than one pond per year since 1977 in an area of some

Table 3. Biodiversity indices for amphibians in dewponds

Index	Year 1977	1996
Total records*	35	29
Percentage of ponds used	55	69
Average no. species per pond surveyed	1.06	1.11
Average no. species per used pond	1.94	1.61
No. species combinations (% of maximum possible)	10(32)	9(29)

Used ponds are those with at least one species of amphibian present.
*, Sum of all species in all ponds, i.e. $\sum$ number of records in Table 2.

150 km^2, there has still been a net loss of water bodies over that period. However, if only high quality ponds are compared then the programme has been much more successful, essentially doubling the number of good freshwater habitats from eight to 15. Clearly it will be important to maintain the momentum of this pond programme to achieve the double goal of both maintaining pond numbers and improving average pond quality.

The 1995–1996 survey included more methods for detecting newts than were applied in 1977–1980 and thus should, if anything, overestimate population survival over the 20 years, but it was nevertheless very clear that amphibian biodiversity in Downland dewponds changed substantially during this period. The older ponds generally supported large and often mixed newt populations but few anurans, whereas the newer ponds have been occupied quickly by anurans (especially frogs) but much less effectively by newts. There are probably two main reasons for this.

First, frog and toad spawn is commonly moved by humans and, in particular, eggs from garden ponds in which both species have prospered enormously in recent decades (Beebee, 1979) are frequently deposited in countryside ponds. Indeed, the Parks and Gardens Department of the Local Authority have assisted people to move spawn in past years. This happens much less with newts, and could go some way towards explaining the apparently greater colonising power of anurans. Its extent is impossible to quantify, but the occurrence of such activity is supported by other observations such as the finding during the survey of ornamental goldfish *Carassius auratus* in a recently created (< 5 year old) dewpond hundreds of metres from the nearest road.

Second, however, anurans may in any case be more agile than urodeles and better able to cross inhospitable terrain between ponds. Frogs and toads are inherently more mobile animals than newts, travel faster and probably cover greater distances on breeding migrations as well as during summer foraging and autumn hibernaculum selection (Glandt, 1986; Sinsch, 1991). The question also arises as to why anurans were relatively uncommon in the older ponds if their colonising powers are better than those of newts. This may be the consequence of a successional process; newts are highly efficient predators of anuran larvae (Cooke, 1974), and their eventual establishment in large numbers (as often happens in dewponds) may in the long term lead to decline or extinction of frogs and toads.

It was notable that the longstanding anuran populations were all in ponds containing fish, selective predators of urodele larvae which may prevent the development of large newt populations (Beebee, 1979). The lower number of species combinations and numbers of species per pond in 1996 may therefore reflect the different frequencies of early and late successional stages in the two surveys.

Smooth newts are the most widespread of the three British urodeles and their general success in dewponds, as well as their relatively efficient colonisation of new ones, was not unexpected. This species also does well in gardens (Beebee, 1979) and again colonisation may have been helped inadvertently by humans by the movement of aquatic vegetation with newt eggs attached.

It was striking that the other two newts, which are virtually absent from garden ponds on the Downs, showed negligible ability to colonise the new dewponds. It was also notable that *T. cristatus* fared especially badly, not only failing to colonise new ponds but disappearing from old sites more than could be accounted for by pond destruction. In fact, the two extra losses had a very specific explanation; in both cases fish were introduced, a mixture of sticklebacks *Gasterosteus aculeatus* and large cyprinids, to ponds very close to human habitation. Crested newts disappeared entirely within a few years of fish appearance. If the present rate of decline continues it will be extinct in the study area within another decade. Nor are the problems of this species confined to Downland habitats; a sample of five crested newt sites identified in the late 1970s in lowland areas north of the Downs was also revisited in 1996, and two of these populations had been lost as a result of pond destruction.

However, the current improving status of dewponds on the Downs offers the opportunity to assist with the conservation of this most endangered of the widespread British amphibians. There are several new or newly-restored dewponds of excellent quality, sited within suitable terrestrial habitat, in which *T. cristatus* should prosper if deliberately introduced. The large areas of inhospitable arable terrain between these ponds and the very few surviving crested newt sites, together with the distances involved (mostly > 1 km), make natural colonisation unlikely. A proactive translocation programme for this species is therefore well worth considering.

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