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Amphibian Conservation in Britain: A 40-Year History

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Abstract.—**Agricultural intensification, starting during the Second World War, precipitated declines in all seven native species of amphibians in Britain. Problems in the United Kingdom (U.K.) therefore predated recognition of global amphibian declines and were due to relatively simple causes, notably habitat modification and destruction. Pesticides, acid rain, ultraviolet radiation, climate change, and disease have thus far proved relatively minor issues. Amphibian conservation started in the 1970s, initially with status surveys, but by the 1980s research into habitat requirements and proactive management was underway, particularly for the rare *Bufo calamita* (Natterjack Toad). The relatively widespread *Triturus cristatus* (Great Crested Newt) was given the same legal protection as *B. calamita* in 1981 due largely to declines elsewhere in Europe. This protection has become problematic for conservationists on account of the many sites with this newt that regularly come under threat from development. Additional difficulties identified in the 1990s included serious impacts of road mortality on *Bufo bufo* (Common Toad) and inbreeding in urban populations of this species and of *Rana temporaria* (Common Frog). A previously unrecognized rare native, the "northern clade" of *Pelophylax* (formerly *Rana*) *lessonae* (Northern Pool Frog) became extinct in the early 1990s but was reintroduced in the 2000s. In the past 4 decades conservation efforts have stabilized, although not increased, the U.K. *B. calamita* population, but some of the widespread species are still declining, albeit at a slower rate than in the postwar period. Effective methods for amphibian conservation are now available and the outstanding question is whether there will be sufficient funding to make greater gains in future.**

The first inklings of a looming crisis arrived, for me, one bright spring day half a century ago. It should have been another uneventful visit to the field pond, just down the road, that awoke a fascination with amphibians that would last a lifetime. And what a pond it was. I stumbled on the place when just 11 yr old; it was brim full of intriguing animals I had no idea existed. There was an astonishing variety of plants and invertebrates, and five of Britain's impoverished amphibian fauna (there are just seven native species altogether) also bred at the site. Common Frogs *Rana temporaria* and Common Toads *Bufo bufo*, Smooth, Palmate, and Great Crested Newts *Lissotriton* (formerly *Triturus*) *vulgaris*, *Lissotriton* (formerly *Triturus*) *helveticus*, and *Triturus cristatus*, respectively, were abundant and there for the taking. Decades on, I've never come across a more inspiring place, though this judgment might conceivably be tinged with nostalgia.

On this morning, 3 yr later, things were very different. I anticipated a routine trip trying to find the first newts of the season but it didn't turn out like that. A huge machine hovered over the pond and had already in-filled a large part of it with soil from the surrounding field. Within a couple of days this wildlife wonderland was no more than a memory, the foundations for a new housing estate. This wasn't the first environmental disaster I'd seen. A year earlier dead songbirds, killed by pesticides, grotesquely decorated the hedgerows in our garden and similar reports were coming in from all over the country. Not long afterwards, as an undergraduate in East Anglia, I set out to encounter one of Britain's rare amphibians. The area was, historically, a hotspot for Natterjack Toads (*Bufo calamita*). Sadly, another shock was in store. Ted Ellis, a highly regarded old-school naturalist, had lived in East Anglia all his life. His breadth of knowledge on the area's natural history was overwhelming and, generous to a fault, he always made time to impart it to young upstarts like myself. Ted told me that, of the many places he knew with Natterjacks before the war, only two still survived. I later had my first meeting with this engaging amphibian at one of them, but by now it was obvious that all was not well in the British countryside.

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In addition to the much-vaunted social revolution, the 1960s were a period of dramatic environmental changes in Britain. These began during the Second World War when large tracts of semiwild land were "dug for victory" to avert food shortages. Many valuable amphibian habitats were destroyed in the process, but worse was to follow. When the war ended a policy of agricultural intensification, on a previously unimaginable scale, was put in place to eradicate any future risk of starvation. In this respect, development in Britain differed, with respect to primary cause, from that in many less-populous countries. Most of the landscape, including national parks, is subject to moderate or intensive human activities, and even wilderness areas such as the Scottish mountains and moors are used for livestock grazing or managed for game bird (grouse) shooting! In other countries agricultural changes certainly occurred, but were often less widespread and motivated more by the prospect of increased profits rather than threats to survival. Twenty years on, huge areas of countryside had been drained and ploughed up, new fertilizers and pesticides applied with abandon, and unregulated urbanization was under way to cope with an increasing population. England, with almost no wilderness habitats to start with, became a showcase example of habitat loss and degradation. Although damage was mitigated to some extent in subsequent decades by better regulation, agri-environment schemes (paying farmers to include conservation management), and the like, the legacy of this industrialization of the countryside is still with us. For herpetologists in Europe, and Britain in particular, the recent concern about global amphibian declines was distinctly déjà vu. For us it happened much earlier and mostly for obvious rather than enigmatic reasons. This difference in timing, which underpins much of amphibian conservation work east of the Atlantic, was succinctly summarized by Houlahan et al. (2000, Fig. 1.).

The 1970s: Assessing the Situation and the Start of Conservation

Amphibians were one of many taxonomic groups affected by gross habitat alterations in Britain and, by the late 1960s, it was clear that at least some species had suffered substantial declines (Perring, 1966). Popular concern about frogs in particular prompted research by the statutory government agency, the

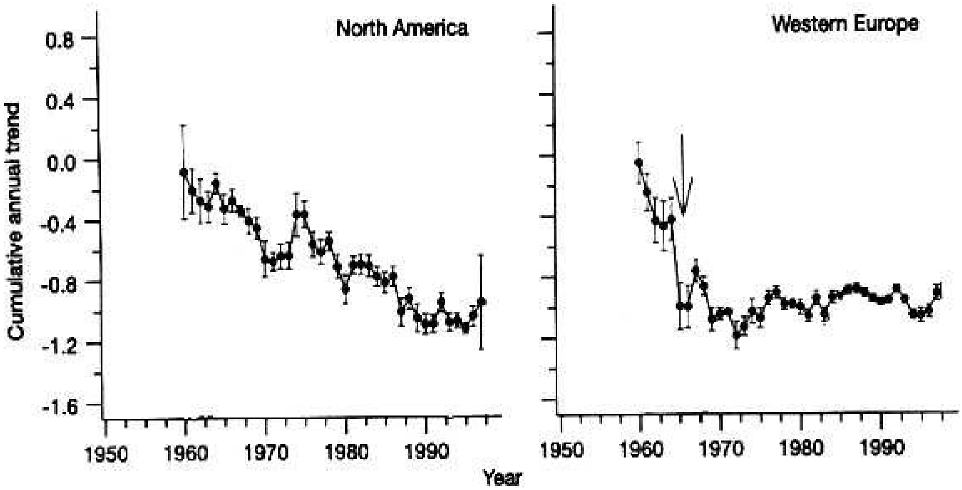

FIG. 1. Pattern of amphibian declines over time (Houlahan et al., 2000). With permission, Nature Publishing Group.

Nature Conservancy Council, based on questionnaire surveys targeted at schools and experienced naturalists. This first attempt at quantitative assessment (Cooke, 1972) confirmed that both *R. temporaria* and *B. bufo* had indeed experienced major recent declines (Fig. 2) and drew attention to a range of possible causes, mostly involving habitat destruction or deterioration. This study, involving statistical analysis of questionnaire returns, set a precedent for future investigations of widespread species for which comprehensive field surveys were not practicable due to the thousands of ponds that would require attention.

One potential cause, large-scale pesticide application, was investigated in detail because these pollutants were increasingly implicated in other wildlife declines. An insecticide (dichlorodiphenyltrichloroethane, DDT) and herbicides (diquat and dichlorobenil) were tested in the laboratory and in field trials. Sublethal and lethal effects on amphibian larvae were sometimes observed (e.g., see Cooke, 1973, 1977). However, habitats with high levels of pesticide application were usually inhospitable to amphibians due to habitat destruction following agricultural intensification. Despite the continued development of new pesticides, some of which are problematic for wildlife, there has been little research into their impact on British amphibians. Endocrine disrupters such as atrazine are proving highly damaging elsewhere (Hayes et al., 2003) but, ironically, early observations of damage to British Common Frogs by this chemical (Hazelwood, 1970) were not followed up. In the Hazelwood study pond, contamination by this herbicide was associated with mass egg mortality and tadpole deformities. It is fortuitous that this chemical, widely applied in North America, has been tightly regulated in Europe and was banned from general application in Britain in 1992.

Another important response in the 1970s was the creation, by the British Herpetological Society (BHS), of a Conservation Committee (BHSCC). The main remit of this nongovernment organization, consisting entirely of volunteers, was to investigate amphibian and reptile declines in Britain and take steps to improve their future conservation. Two amphibians received immediate attention. *Triturus cristatus* was suspected to have undergone more-dramatic declines than the other widespread species, and this fear was confirmed by a questionnaire survey asking experienced naturalists about the fate of populations known to them. The results indicated around a 50% loss of breeding sites across the country in the 1960s (Beebee, 1975). My childhood pond was one of them! *Bufo calamita*, on the other hand, was sufficiently rare that field survey of all known sites, past and present, was feasible. As a specialist largely dependent on open, sandy terrain, Natterjack Toads always had a limited distribution in Britain.

An early aspiration of the BHS, before the conservation committee days, was to elucidate British species distributions, and much information about historic sites was readily available for cross-reference (Taylor, 1963). Now came my first serious involvement with amphibian conservation and it wasn't the best of beginnings. The project started with a great deal of dispiriting fieldwork, searching old Natterjack sites and usually coming up with nothing. Essentially I confirmed Ted Ellis's observations from 1968 and extended the list of losses to include almost all of the species old heathland locations. It was a sharp learning curve; male Natterjacks have a loud and distinctive call, but not distinctive enough to me in those early days to prevent me from chasing churring Nightjars (Caprimulgidae) (from tree to tree, surely a clue there) across desolate heathlands after dark. I was just starting a postdoctoral research project on gene expression, my intended career path, and I still had relatively little field experience. Fortunately coastal populations, mostly on sand dunes and upper salt marshes, fared better and there are happier memories of trying to sleep in a car next to orchestral-volume Natterjack populations still counted in the hundreds. Nevertheless there was an estimated 70–80% decline since the Second World War of an always rare species (Beebee, 1976).

The common conservation dilemma of wanting to act, while at the same time needing more information on which to base action, inevitably emerged in these early days. Some aspects were nevertheless straightforward. Lobbying Parliament resulted in the first protective legislation for British herpetofauna in the Conservation of Wild Creatures and Wild Plants Act of 1975. Weak though it was (among amphibians only *B. calamita* was listed and its habitats remained unprotected), it set the precedent for future and increasingly valuable laws (the Wildlife and Countryside Act of 1981 and the Countryside and Rights of Way Act in 2000), which extended high level protection to other species (notably *T. cristatus* and Northern Pool Frog *Pelophylax lessonae*) and, crucially, to their habitats. These later Acts also provided weaker protection to the other British amphibians.

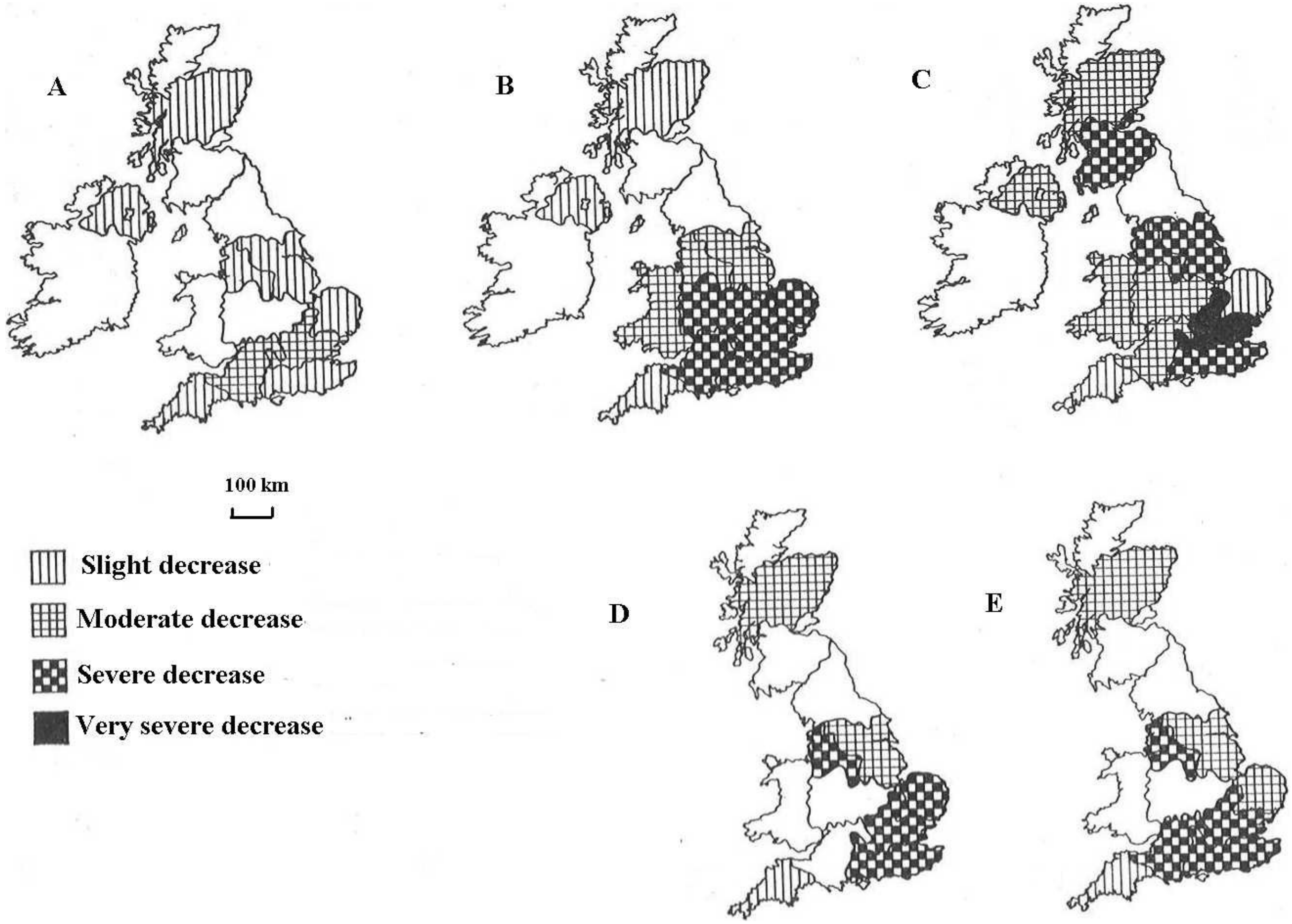

FIG. 2. Changes in status of *Rana temporaria* (A) 1956–1960, (B) 1961–1965, (C) 1966–1970; and of *Bufo bufo* (D) 1961–1965, (E) 1966–1970. Unshaded areas = insufficient responses. All after Cooke (1972). Reproduced with permission from John Wiley and Sons.

Site protection was another aspect simple in principle: as much remaining habitat as possible should obviously be defended from developers and agricultural ambitions. In Britain only a small fraction of the land surface (<5%) was protected in any way at that time. Nature reserves offered the safest option; all the British amphibians occurred on them including some of the best surviving Natterjack populations. The main alternative was designation as a Site of Special Scientific Interest (SSSI) by the Nature Conservancy Council but, in the 1970s, protection against development by this national statute was feeble. Most British amphibians were on completely unprotected land, with the largest remaining population of Natterjack Toads occurring on Merseyside coastal dunes near Liverpool. At this site only one small section of the dune system was protected as a nature reserve and the rest was up for grabs. The fate of these Merseyside toads was an early example of the vulnerability of amphibian populations in Britain. Between 1968 and 1971, tens of hectares of the Merseyside dunes were developed as housing estates and a holiday camp was constructed within an SSSI after (remarkably!) consent was granted by the Nature Conservancy (Fig. 3). In an undoubtedly futile gesture, hundreds of toads were moved out of the developers' way by the BHSCC as the machines rolled in and the pristine habitat was destroyed (Beebee, 1978). All were released in neighboring dune habitat which, of course, was probably already supporting its carrying capacity of Natterjacks. Arguably there was, however, an eventual upside to this catastrophe. The associated publicity from the press resulted in strong protection of virtually all of the remaining Merseyside dune system. The SSSI designation received more "teeth" in both the 1981 and 2000 legislation such that permission for development on them is now almost impossible to obtain, and (in theory at least) appropriate habitat management can be imposed on landowners. By 2012 the SSSI network extended over >8% of Britain and included, together with nature reserves, more than 95% of Natterjack Toad habitat.

In this period most practical work to improve the status of amphibians focused on Natterjacks, deemed to be in the greatest peril and thus demanding urgent attention. Creation of new breeding ponds and the deepening of many existing ones were widely instigated, while clearance of scrub to reverse natural succession on heathlands also got underway. Although based on available knowledge (Beebee, 1977), ecological information was limited and mistakes were made. For example, over-deepening of ephemeral ponds in the hope of improving larval survival had the opposite effect, with predator and competitor numbers (especially *B. bufo*) increasing rapidly. Ultimately *B. calamita* were completely excluded from such sites; an example of taking action before understanding what is really needed. Another early error was trying (and failing) to reintroduce Natterjacks into recently vacated heathland sites without

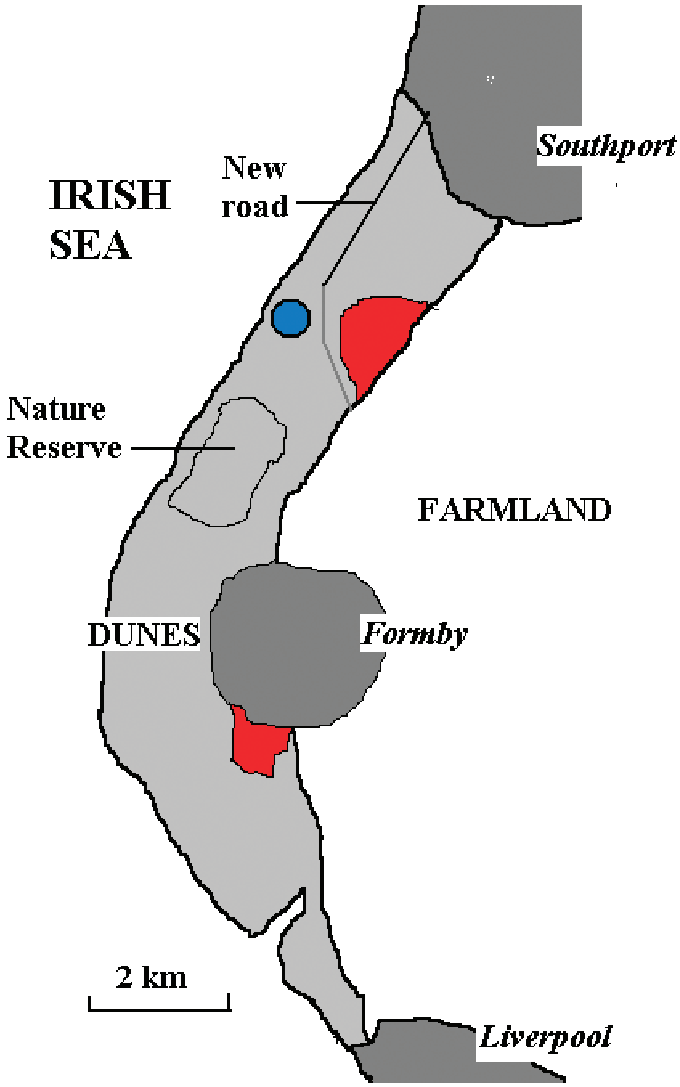

FIG. 3. Unregulated development on the Merseyside dune system, 1968–1971. Red areas = new housing; blue = new holiday camp.

finding out why the species died out in that habitat. The need for evidence-based rather than intuitive management became clear, and an early result of shifting to directed research identified the main cause of reintroduction failures as a preponderance of ponds too acidic to sustain larval development (Beebee and Griffin, 1977).

Finally, a pleasantly surprising positive factor became apparent in the 1970s. Cooke (1972) noted that although Common Frogs and Toads had declined overall, there was increasing colonization of garden ponds. By the end of the decade these small pools were so popular that in Brighton one garden in seven contained a potential amphibian breeding site, and half of these were actually in use, albeit by a limited range of species (Beebee, 1979). This urban reservoir, mostly of *R. temporaria*, *B. bufo*, and *L. vulgaris*, has become commonplace in towns and cities across the country. Investigation was the simplest type of amphibian survey imaginable, often accompanied by generous refreshments from householders delighted to learn about the animals in their back gardens. Subsequent publicity in the form of leaflets and widespread media coverage continues to promote wildlife gardening in Britain, and ponds with amphibians feature strongly.

THE 1980s: RESEARCH AND CONSERVATION, HAND IN HAND

An early development at the start of the 1980s was the addition of a second amphibian, *Triturus cristatus*, to the strictly protected list in Britain. The designation was, and remains, controversial because despite serious declines in the 1960s this newt is still a widespread animal in England. Protection followed a European directive (the Bern Convention of 1979) mostly based on grey literature evidence that Great Crested Newts were in trouble over much of their European range. Partly because of this change in the law but also because interest in (and funding of) amphibian conservation was on the rise, the 1980s were halcyon days for amphibian research in Britain. A number of investigators (Rob Beattie in Nottingham, myself in Sussex, Clive Cummins in Peterborough, Paul Gittins in Wales, Tim Halliday at the Open University, Rob Oldham in Leicester, Chris Reading in Dorset, and Richard Tinsley in London) established active teams, and there were annual meetings of an amphibian ecology group. Future leading lights, including John Buckley, Tony Gent, Richard Griffiths, Tom Langton, and Julia Wycherley, started to make their mark in the 1980s. Much of the work was fundamental rather than applied, with the aim of better understanding behavior, life history, distribution, and autecology as a prerequisite for evidence-based conservation. Most of the many published papers did not have direct application to conservation but provided valuable backgrounds for future action. Productive collaborations and long-lasting friendships emerged at this time, the BHS Conservation committee had its heyday, and after some confrontational discussions the Nature Conservancy Council (1983) produced its first comprehensive plan for herpetofauna conservation in Britain.

Another feature of the 1980s was the recognition of environmental threats posed by acid rain to poorly buffered wetlands. Low pH and consequent solubilization of toxic aluminum salts can cause high mortality of amphibian embryos and larvae (e.g., see Clark and Hall, 1985). Among British species only the Palmate Newt *L. helveticus* is well adapted to reproduction at pH <5 (Griffiths and DeWijer, 1994). In hard-rock areas of Scotland many ponds and lakes were acidified to pH <4.5, and Cummins (1986) showed that both in the lab and the field *R. temporaria* larvae suffered increased mortality that could put local populations at risk. Lowland heath podsols are also susceptible to wetland acidification, and some Natterjack Toad breeding sites were rendered useless by acidification during the early 20th century (Beebee et al., 1990). Diatom analysis of cores sampled from pond bottoms demonstrated that pH dropped from >5.5 to <4.5 over this period at a historic heathland breeding site (Fig. 4), ending up well below the level tolerated by Natterjack spawn and larvae (Beebee, 1986). Fortunately many wetlands have benefitted from emission controls on point-source pollution, and problems from acidification have declined in recent decades. In the short term, breeding ponds were successfully restored by the addition of lime (e.g., for *R. temporaria*, Beattie et al., 1993) or, more sustainably, by removal of acidified substrates from shallow *B. calamita* breeding sites (Beebee et al., 1990).

Efforts to inform *B. calamita* conservation management developed substantially in the 1980s with a major focus on breeding pond requirements ably investigated by Brian Banks, a new friend and colleague. In particular the importance of pool ephemerality, with summer desiccation, was recognized as a primary conservation objective (Banks and Beebee, 1987). On upper salt marshes, inundation of ponds by high tides in early

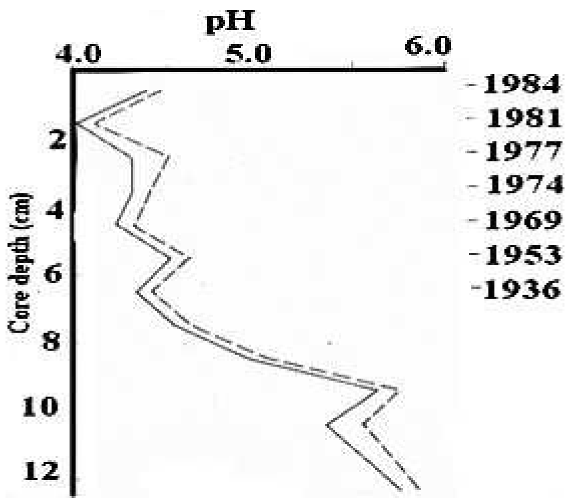

FIG. 4. Acidification chronology of a previous *B. calamita* breeding pond at Woolmer, Hampshire (Beebee et al., 1990). Reproduced with permission from Elsevier.

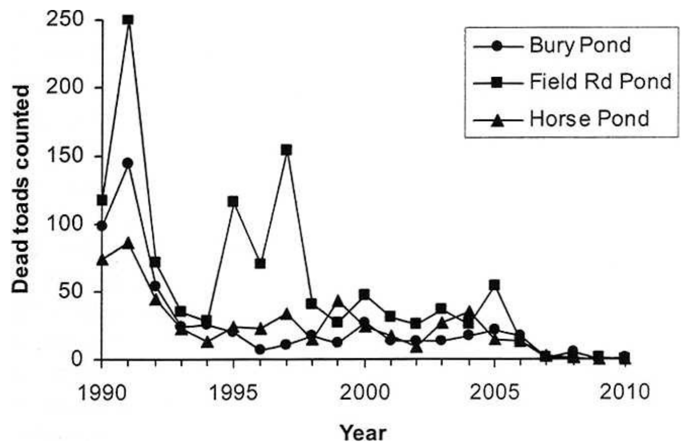

FIG. 5. Decline of toad populations due to traffic mortality (from Cooke, 2011). With permission from Nature in Cambridgeshire.

spring followed by rainwater refill had similar consequences to desiccation (Beebee et al., 1993). Both processes minimized predator and competitor numbers, essential prerequisites to breeding success in *B. calamita*. Improved data collection at all the remaining Natterjack Toad sites in Britain led to the innovation, in 1986, of a national site register for the species. The register documented adult population sizes (judged by cumulative spawn string counts each spring), breeding successes (judged by toadlet production around the pond margins, estimated within an order of magnitude soon after metamorphosis), and conservation management annually. This database was expected, over time, to permit critical assessment of management interventions. Better understanding of Natterjack ecology had an early benefit in the 1980s by informing further translocations which, unlike the earlier efforts, succeeded in establishing some new populations. By the end of the decade *B. calamita* conservation was on a firmer footing; almost all British populations had been identified by continued survey, habitat protection increased from 60% to 83% of all sites, and restorative management was under way on many of them (Banks et al., 1994).

The five more-widespread species, including *T. cristatus*, presented a different problem. Sampling rather than comprehensive surveys, again based on questionnaires, was instigated. Preliminary results indicated that the status of most species stabilized during the 1970s, following the large earlier declines described by Cooke (1972) and Beebee (1975), but that *T. cristatus* continued to decrease (Cooke and Scorgie, 1983). A subsequent and much larger sampling survey involved over 1,000 people and provided information about >11,000 wetlands (Swan and Oldham, 1993). The relative abundances of the widespread species, their occupation of wetlands, and overall distributions were assessed and their habitat associations were analyzed statistically. Landscapes dominated by woodland or grassland were optimal for all these species whereas intensive arable farming was generally inimical. Relatively small, fish-free pools supported the best populations, except in the case of *B. bufo*, which was frequently syntopic with various fish species. A more-detailed study involving both questionnaires and fieldwork was carried out for *T. cristatus* (Oldham and Nicholson, 1986). The results in this case indicated a reduced rate of decline (around 2% between 1980 and 1985) and demonstrated a particular susceptibility of larvae to fish predation, including a strict requirement for fish-free ponds. These results were extrapolated to suggest that a total of 6,000 breeding sites still existed for this newt in Britain (Oldham and Nicholson, 1986). This work also led to the derivation of a "habitat suitability index" for *T. cristatus*, essentially a list of readily assessed habitat features permitting accurate prediction of the species presence or absence (Oldham et al., 2000). This index has enjoyed extensive use ever since to assist surveyors and provide warnings when sites are threatened with development.

Yet another issue that came to the fore during the 1980s was the carnage inflicted by road traffic on amphibians, especially Common Toads, that migrate long distances from winter quarters to breeding ponds every spring. It was unclear whether this was purely an animal welfare issue or whether population viability might be compromised, but efforts got underway to try and reduce the toll. The first of these, including "toads on roads" warning signs, followed pioneering work by Paul Gittins and his collaborators in mid-Wales during the early 1980s. Volunteer groups, often combined with temporary fencing and pitfall traps along roads, subsequently arose to catch amphibians during spring migrations and carry them across the highways. In Britain there were >400 such crossings by the 1980s, transporting >500,000 animals (mainly *B. bufo*) annually. Under-road tunnels (culverts) with fencing to direct migrating animals into them are undoubtedly a better solution and were installed at many locations in Europe and North America by the end of the decade (Langton, 1989). Twenty years on it is surely remarkable that there has been no rigorous and systematic study of road mitigation measures for any wildlife (Lesbarrères and Fahrig, 2012) and alarming because recent research suggests that long-term attrition can indeed exterminate *B. bufo* populations (Cooke, 2011). Numbers killed on local roads declined over time (Fig. 5), commensurate with numbers successfully reaching the ponds and correlated inversely with increasing traffic density, inferring a causal effect of road mortality.

The decade ended on a promising note with the creation of a new nongovernment organization, the Herpetological Conservation Trust (HCT), in 1989. Unlike its predecessor, the BHSCC, the HCT had sufficient funds from the start to employ full-time staff. It developed into a major force in U.K. amphibian conservation, changing its name in 2009 to the Amphibian and Reptile Conservation Trust (ARCT) and carrying out major

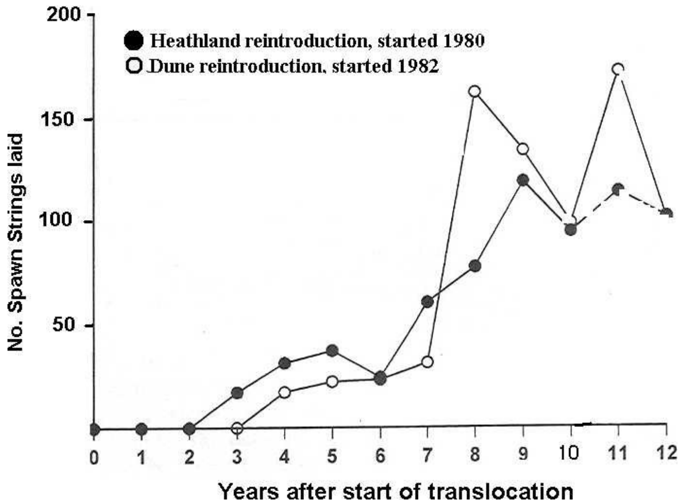

FIG. 6. Increasing sizes of two translocated *Bufo calamita* populations (from Denton et al., 1997). With permission from John Wiley and Sons.

programs of proactive conservation, nature reserve acquisition, and scientific research (www.arc-trust.org). Froglife, another nongovernment organization with an interest in amphibian conservation, was born in the same year (www.froglife.org). For me it was an eventful period, consolidating a tenured university post while simultaneously changing my research focus from gene expression ever more towards amphibian ecology and conservation. Among my recollections of the decade are many days spent clearing scrub around heathland ponds; hard work but lightened by the company of dedicated friends and colleagues.

THE 1990S: CONSOLIDATION AND NEW DIRECTIONS

Following the First World Congress of Herpetology in 1989, herpetologists from around the world began to realize that widespread global declines of many species were under way (Wake, 1991), and this initiated research into possible causes that continues today. An early suspect, especially at high elevations in North America, was extra embryonic and larval mortality due to increased exposure to ultraviolet (UV) radiation, itself a consequence of the Arctic "ozone hole" (Blaustein et al., 1994). In Britain, two species breed in shallow water exposed to the sun and were potentially vulnerable to UV damage. However, laboratory studies with one of them (*R. temporaria*) using UV supplements corresponding to environmental levels had no significant effect on frog embryos (Cummins et al., 1999). Subsequent research in France confirmed minimal impact of UV on this species, even at high elevations, and showed that the jelly surrounding the eggs had a protective role (Marquis et al., 2008). Natterjacks might also be at risk, but studies in Spain also found no extra UV-induced mortality in this species (Oromi et al., 2008). Although this and subsequent research identified complex interactions between UV and other factors for some species, the global impact of UV on amphibian decline is probably limited.

After more than a decade of research, basic autecological studies of Natterjacks in Britain were nearing completion. The benefits of multiple pools to support metapopulation structures had become clear (Beebee et al., 1996), as had the need to maintain open, scrub-free terrestrial habitat for this anuran as demonstrated by Jonty Denton, another welcome newcomer to Natterjack research (Denton and Beebee, 1994). Negative impacts of Common Frogs and Common Toads due to competitive dominance of their larvae in Natterjack breeding ponds was confirmed in the laboratory and the field (Griffiths et al., 1991; Bardsley and Beebee, 1998). This in turn was a consequence of inadequate scrub management facilitating encroachment by these species. An important conclusion was that sustainable methods of terrestrial habitat management were needed to suppress regrowth after initial clearance. Restoration of grazing by domestic animals, the historic but long-since abandoned traditional use of heathlands, was an obvious option. It remains so today but still needs development to optimize its effects. Early suggestions to bring cows back to a heathland used for training by the Ministry of Defence were met with concern that the animals might frighten soldiers on night-time exercises! Happily, a more enlightened approach won the day and cattle again roam there, benefitting Natterjacks as they did for centuries past.

Translation of research into conservation action was given a boost early in the 1990s, following the 1992 Rio de Janeiro United Nations Conference on Environment and Development, by new government directives proposing the development of action plans for protected species including *B. calamita* and *T. cristatus*. An early consequence was funding of a recovery program for *B. calamita* which entailed, over 3 yr, greatly enhanced habitat management and attempts to establish a further suite of new populations by translocation to restored sites (Denton et al., 1997). By this time some of the first successful translocations begun in the 1980s were thriving (Fig. 6). Although basic research on amphibian ecology declined relative to the great days of the 1980s, there were some new kids on the block destined to make significant contributions in years to come including John Baker, Jim Foster, and Charles Snell.

A concern emerging in the 1990s was possible damage to amphibians from fertilizers, especially nitrates, the environmental concentrations of which increased steadily in Britain after the onset of agricultural intensification (Ministry of Agriculture, Fisheries and Food, 1993). Ponds in England typically contained 10–250 mg/liter of nitrate by this time. Nitrate pollution of freshwaters was often manifested as eutrophication, such that ponds with regular run-off from nearby arable fields had dense growths of algae but few macrophytes. Laboratory trials with several amphibian species indicated that although sublethal effects of nitrate on larvae were sometimes seen (e.g., for *B. bufo*, Xu and Oldham, 1997), field concentrations were always well below lethal ones of $>$1,000 mg/liter. Ammonium nitrate was acutely toxic to the frogs *R. temporaria* at levels applied, as granules, to fields in spring (Oldham et al., 1997), but fortunately this risk was not realized because it dissolves rapidly in soil after daytime application before frogs migrate to breeding sites at night. Nevertheless, indirect consequences of nitrate accumulation, such as reduced oxygen concentration and alteration of pond community ecology following eutrophication, could have significant negative impacts on amphibians. Agri-environment schemes became a novel feature of farming in the 1990s and, among other things, aimed to minimize nitrate flux into freshwater by measures that included buffer strips around fields where fertilizer is not applied. As yet their effects have not been substantial, and more research on this subject is still needed.

As if there were insufficient conservation issues for amphibians, another raised its head in the 1990s as genetic analysis was applied to help evaluate population viability. Some of the small and relatively isolated garden populations of Common Frogs and Common Toads had accumulated fitness defects, including reduced larval survival, as a consequence of inbreeding (Hitchings and Beebee, 1997, 1998). Spatial models including a range of parameters indicated that populations of *B. bufo* and *T. cristatus* were unlikely to persist in the long term at the small sizes present in most in garden ponds (Halley et al., 1996). Although urban amphibian sites have provided a valuable stop-gap, they have not reduced the imperative for restoring the large rural populations that were common before the latest agricultural revolution.

By contrast, there was also a pleasant surprise in store for British amphibian conservationists in the 1990s. Conventional wisdom was that Britain had just six native amphibian species and, although European water frogs *Pelophylax lessonae* (Pool Frog), *Pelophylax* (formerly *Rana*) *ridbundus* (Marsh Frog), and their hybridogenetic offspring *Pelophylax* (formerly *Rana*) *esculentus* (Edible Frog) were widespread in some areas, all were believed to descend from well-documented introductions starting in the 19th Century. Snell (1994) drew attention to a relict population of Pool Frogs for which there was circumstantial evidence of earlier origin. This initiated a research program combining historical record trawling, archaeozoology, male vocalization, and molecular genetic analysis—all of which supported the hypothesis that Pool Frogs of a distinct northern clade, found elsewhere only in Scandinavia, did indeed constitute a seventh native species (Beebee et al., 2005). Unfortunately the discovery came just after the demise of the relict population, a result of neglect from conservationists focusing on *B. calamita* on the assumption that all water frogs in Britain were the result of anthropogenic introductions. However, further conservation consequences of this discovery would come later.

The 2000s: Latest Developments

The new millennium brought new issues for amphibian conservation in Britain; one concerned potentially damaging invasive species. Although there is a long history of nonnative species introductions into the U.K., most have failed to spread and therefore caused little concern, as almost all are sympatric with the British natives in mainland Europe. However, the surprising discovery of breeding North American Bullfrogs *Lithobates* (formerly *Rana*) *catesbeianus* in Sussex (Banks et al., 2000) was treated as a serious risk, and the population was eventually eradicated by a combination of methods including pond drainage, archery (!), and sharpshooting. A second population in Essex suffered a similar fate, while efforts are still under way to eliminate a third, again in Sussex. The actual, rather than possible, impact of this species on British fauna has not been investigated.

The specter of devastating amphibian diseases also emerged as a potentially serious problem in Britain, as elsewhere, in the 2000s. Mass mortalities of Common Frogs were reported with increasing frequency, mostly in urban gardens. Subsequent studies confirmed *Ranavirus* as the cause and found that, typically, around 80% of adult frogs were killed during outbreaks, usually followed by a slow population recovery (Teacher et al., 2010). Fortunately the overall impact on what is still a very widespread and common species seems, as yet, to be minimal. The fungal disease *Batrachochytrium dendrobatidis* (*Bd*) was first detected in Britain, in *B. calamita*, in 2004. Thus far, although some British amphibians such as *B. bufo* have proved susceptible to *Bd*-induced mortality under laboratory conditions (e.g., see Garner et al., 2009), there is no evidence of population declines of any species due to this agent. The same is generally true of British species elsewhere in Europe. Indeed, in Spain *B. bufo* actually increased, at least for a while, due to reduced competition when Midwife Toads, *Alytes obstetricians*, were almost exterminated by *Bd* in Penalara National Park (Bosch and Rincon, 2008). There is, therefore, cause for cautious optimism that currently known diseases will not have major impacts on British amphibians.

Then came climate change, which thus far is implicated in two main effects on amphibians. Phenological changes due to milder winters advanced the start of breeding activity in newts (*L. vulgaris* and *L. helveticus*) by up to 2 weeks in central Wales between the 1980s and the 2000s (Chadwick et al., 2006). Common Frog spawning time also advanced across the whole of Britain in recent decades (Carroll et al., 2009) but by much less than was seen with the newts. There is a hypothetical possibility that this asynchrony in timing change might alter amphibian community structures by reducing any advantage that frogs obtain by spawning early. *Rana temporaria* breeds before any other British species and its palatable embryos have, in the past, usually hatched into safer, free-swimming larvae before predatory newts arrive. Now there is often more overlap, but whether this concern is justified remains to be seen. However, a more tangible consequence of climate change might result from the increasing frequency of mild winters. Reading (2007) showed that body condition and survival of Common Toads declined at his study site commensurate with increasing winter temperatures and with a sharp overall decline in the population. This was attributed to failure of gamete production (a significant cold period may be required) and relatively high metabolic rates using resources faster than in previous times. Mild, wet winters were also implicated in reduced survivorship of Great Crested Newts (Griffiths et al., 2010: fig. 7) and of Natterjacks (McGrath and Lorenzen, 2010). Whether these problems will become more acute or be compensated for by local adaptation will not become clear for many years.

The scale of effective conservation was better understood by the 2000s. The idea that a pond and its immediate environs were sufficient to sustain amphibian populations gave way to an emphasis on metapopulations, maintaining a network of ponds interconnected by permeable habitat over substantial distances. Population viability analysis revealed elevated extinction risks for Great Crested Newts in the absence of metapopulation structure (Griffiths and Williams, 2000) and landscape connectivity.

The fate of the widespread species of British amphibians continued to be a cause of concern. It became evident that *B. bufo* experienced further substantial declines in the 1990s (Carrier and Beebee, 2003), perhaps because of its special susceptibility to road mortality and climate change as described earlier. Great Crested Newts posed a dilemma because they are strictly protected but are also still widespread (thus creating heavy casework loads for statutory conservation agencies with limited resources), especially in England. Wilkinson et al. (2011), using a combination of empirical information and habitat modeling, estimated there were around 60,000 breeding ponds for this species in Britain, about tenfold more than the earlier study of Oldham and Nicholson (1986). Although some newt sites were protected on natures reserves, SSSIs, and a new, stronger designation (Special Areas of Conservation, under the European Union's *Natura 2000* scheme), most were not. Threats

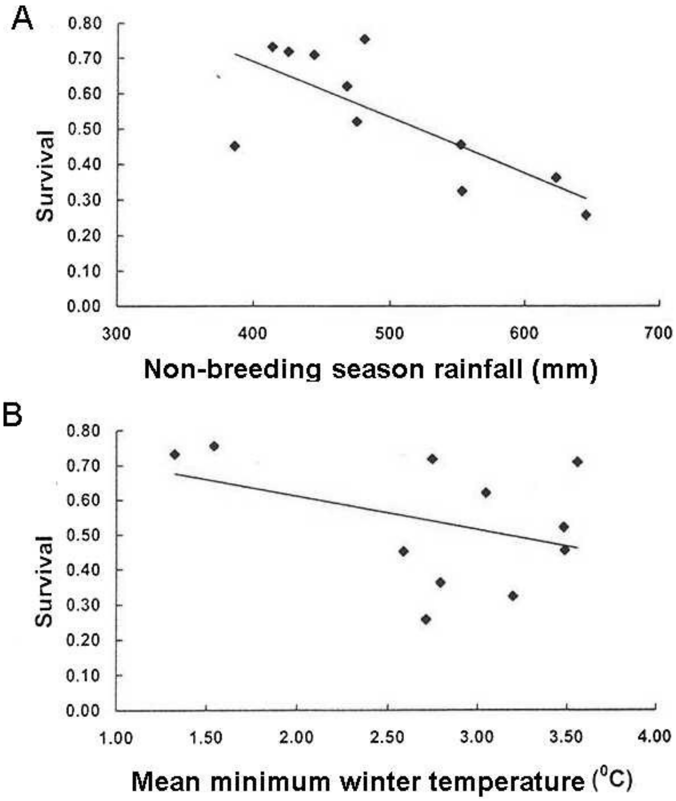

FIG. 7. Survival of *Triturus cristatus* as a function on nonbreeding season (mostly winter) rainfall and winter minimum temperatures (from Griffiths et al., 2010). Reproduced with permission from Elsevier.

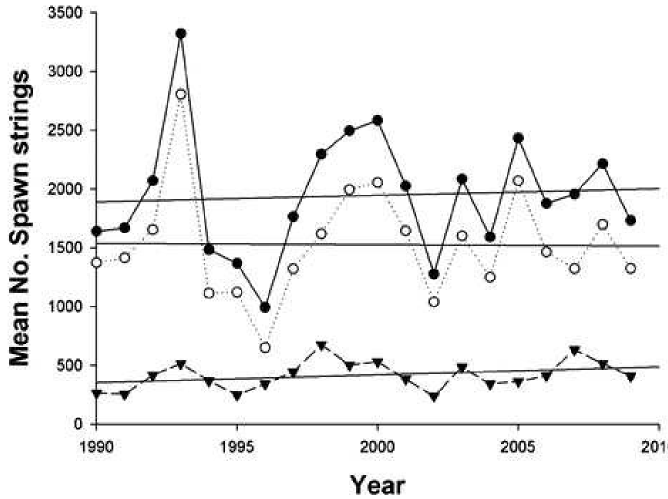

FIG. 8. Trends in the U.K. Natterjack population over 20 yr. Solid circle = total; open circle = native populations; solid triangle = translocated populations. Lines show regressions of spawn counts against year.

usually resulted in mitigation measures; the movement of newts to new sites, accompanied if necessary, by creation of new ponds. Unfortunately the consequences of such mitigation are often dubious (Edgar et al., 2005), and it is very likely that this protected species continues to decline. The time was ripe for setting up a systematic, long-term project to assess status changes of all the widespread amphibians, and this was initiated as the National Amphibian and Reptile Recording Scheme (NARRS) in 2007 (http://www.narrs.org.uk/). Commensurate with that scheme, robust occupancy modeling was developed (Sewell et al., 2010) to ensure the reliability of data collection and analysis. Future conservation priorities should therefore be better informed than in the past.

As for the rare species, data from the Natterjack site register (1990–1999) were used to assess national trends. Overall there was no significant change in the total U.K. population during the 1990s, a substantial improvement on the downward path before that time (Buckley and Beebee, 2004). Recent (unpubl.) analysis using a 20-yr time series suggests that this situation continues (Fig. 8), with occasional local extinctions approximately matched by successful translocations. The importance of grazing terrestrial habitat on Natterjack sites was recognized some time ago (Denton and Beebee, 1996), and wider restoration of this management using domestic livestock offers the best prospects for future increases of this species. Modeling factors that influence Natterjack population viability confirmed that management is along the right lines, but also indicated that at many sites more work is needed (McGrath and Lorenzen, 2010; Di Minin and Griffiths, 2011).

The metapopulation structures of *B. calamita* in Britain were better defined following genetic analysis (Rowe and Beebee, 2007) and, as demonstrated for this species in Belgium (Stevens and Baguette, 2008), maintaining landscape connectivity will be critical to future progress. Indeed, one small and isolated colony of Natterjacks at Saltfleetby on the east coast of England suffered reduced fitness (slow larval growth), seriously reducing survival to metamorphosis as a result of inbreeding (Rowe and Beebee, 2003). A genetic restoration program to revive this population, which failed to respond to habitat management over many years, commenced in 2009. As far as I know this was the first application of genetic restoration to amphibians. Spawn and larvae equivalent to the output of four females, corresponding to about 20% of the recipient population size (following Hedrick, 2005), were collected from the nearest diverse population and released at Saltfleetby over two consecutive years. Ironically, genotyping Saltfleetby larvae in 2010 revealed that a restoration actually started in 2002 when toadlets from a third population, with distinctive microsatellite genotypes, must have escaped during experiments (Rowe and Beebee, 2003) at the site (!). Some effects of this accidental earlier restoration are already apparent. Eleven microsatellite alleles definitely derived from the 2002 escapees were present at high frequency at Saltfleetby in 2010 (altogether averaging 42% per locus), virtually doubling the original Saltfleetby allele number of just 12 across 8 loci (unpubl. results). This implies rapid selection for the presumably very few introduced genotypes which were much fitter, based on larval growth rates, than the Saltfleetby toads (Rowe and Beebee, 2003). There was also limited evidence of increased fitness at the population level (Table 1). Comparing spawn string counts and metamorph numbers in the 4 yr up to 2002 with the 4 yr beginning in 2008 (approximately two toad generations after the 2002 escapes), the latter period experienced slightly though not significantly ($P = 0.313$) elevated spawn deposition but much higher metamorph production (averaging $>550\%$, $P = 0.044$). The intervening period (2003–2007) was essentially unchanged from that preceding the escapes. For many years much of the Saltfleetby spawn has been reared by nature reserve staff in artificial ponds protected from predators and premature desiccation because natural recruitment was unsustainably low. Natural breeding success was also more frequent in the post-2008 period compared with the pre-2002 years. Nevertheless, attributing

TABLE 1. Population parameters of Saltfleetby Natterjacks before and after genetic restorations that started (inadvertently) in 2002.

Period	Average spawn string count per year	Average metamorph production per year	Years with natural metamorphosis
1999–2002	17.5	300–400	1
2003–2007	18.5	400–500	0
2008–2011	23.3	>2,500	2

these apparent improvements unequivocally to genetic restoration would be premature; the Saltfleetby Natterjack population remains precarious and still in need of support, but at least preliminary indications seem favorable.

Finally, an attempt to reintroduce "northern" clade Pool Frogs from their remaining stronghold in Sweden started in 2005. Over four consecutive years, dozens of adults as well as thousands of eggs and larvae were released at a newly managed habitat in eastern England. By 2012 a breeding population was established at the site but it remains small and it is, therefore, too soon to be sure about its long-term viability. Plans are in hand to reintroduce Pool Frogs to other sites, including the site of the last population of Pool Frogs that died out, when habitat is restored.

New blood for the new millennium? Too soon to be sure, but Trent Garner and John Wilkinson are certainly up there among the newest generation of leading U.K. amphibian conservationists.

CONCLUDING REMARKS

How have amphibians fared in Britain over the past 50 yr? Global issues of high concern elsewhere (pesticides, acid rain, increased UV radiation, climate change, and disease) have, as yet, been relatively minor players. Major declines nevertheless occurred, but mostly before these threats arose and for the straightforward reasons of habitat destruction and alteration. In principle, the declines should therefore be readily reversible but, in practice, life is of course never so simple. Progress has occurred but to varying degrees. For the two rare species (Fig. 9) the results are reasonably clear. Massive earlier declines of *B. calamita* were halted, though not reversed, and we have a comprehensive understanding of management methods that work. Improving their implementation in the future looks entirely feasible. The Northern clade *P. lessonae* was entirely lost, essentially through neglect, but its reinstatement is under way. The fate of the five widespread species is less certain. Declines have probably continued, possibly excepting *R. temporaria* and the two small newts *L. vulgaris* and *L. helveticus*, but (in most cases) at a slower rate than inferred by Cooke (1972) and Beebee (1975) in the 1960s. Common Toads are a renewed cause for concern and probably exemplify the serious impact that increased road traffic can have on species that migrate long distances. Mitigation of road mortality on the scale required is hugely expensive and, astonishingly, the available methods are still not scientifically validated. Great Crested Newts (Fig. 9) pose a challenge to conservationists due to the paradox of high protection level and wide distribution in the English countryside. A strategy for their proper protection that accommodates these facts is urgently needed. Simple conservation measures for widespread species can have remarkable results. Restoration of ponds in a London park increased the Common Frog

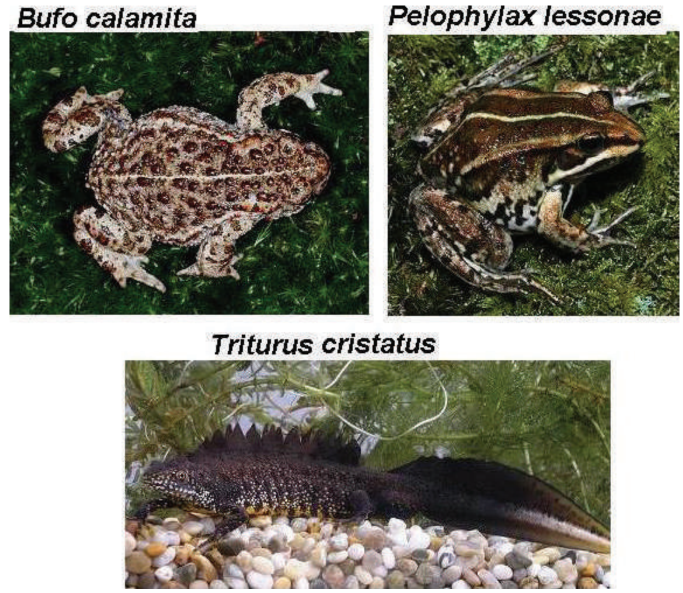

FIG. 9. Britain's strictly protected amphibians.

population nearly 50-fold, from tens to thousands, within 20 yr (Williams, 2005). Amphibians rapidly colonize newly created ponds in Britain (Baker and Halliday, 1999) and a "Million Ponds Project" initiated in 2008 with the optimistic objective of its title has already provided many new breeding sites. In general, though, the best hope for the more common British amphibians resides in agri-environment schemes improving habitat at the landscape level. These schemes can work well for amphibians and much else besides (e.g., see Maes et al., 2008) but will rely on sustaining a policy promoting them at a time when food security is, once again, causing concern and might tip the balance back to yet more-intensive farming practices.

So, what of the future? It is a truism in conservation that each generation relates to its own baseline experience. The baseline of amphibian abundance I enjoyed more than half a century ago would be the stuff of dreams to those beginning their careers today; and the Ted Ellis generation looked with dismay at even those seemingly beneficent times. Recording schemes in Britain have reached the point where we will not lack information about how the species are faring in the coming years. We also know what is needed for effective conservation management. The widespread amphibians will, in my view, nevertheless probably continue to decline because the agricultural revolution has slowed but not stopped, let alone reversed, and the impact of roads can only get worse. Costs of effectively mitigating these developments on a large scale will surely be prohibitive. The best I realistically hope for is a slower rate of overall loss and some improvement of landscape-scale conservation to sustain a network of the best metapopulations. Despite huge efforts, even the rare species (*B. calamita* and *P. lessonae*) still face difficult times. The big challenge for *B. calamita* will be to turn the tide rather than merely hold the fort, which was the main achievement of the last few decades. An upturn for this species undoubtedly hinges on improved grazing regimes. On a positive note, invocation of the European Union's requirement under its 1994 Habitats directive for member states to achieve "favorable conservation status" (FCS, as yet undefined!) for listed species could make a substantial difference to the fate of British amphibians. Combined with agri-environment schemes, working towards FCS could restore optimism and make ours the last generation to experience a better baseline than its successors. Another valuable feature that has developed over the years is the ease of collaboration and communication within a relatively small but convivial group of friends and colleagues, all striving for the same goals. This particularly strong feature of British amphibian conservation has made for increasingly joined-up thinking (at least most of the time!) and might prove a useful export.

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