

Decline and flounder of a Sussex common toad (*Bufo bufo*) population

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ABSTRACT - Common toads *Bufo bufo* have declined over much of southern and eastern England in recent decades where other widespread amphibian species have remained relatively stable. One such toad decline, at Offham marshes in Sussex, was investigated over the fifteen year period 1998-2012 immediately subsequent to a tenfold decrease in population size between 1989 and 1997. Syntopic amphibians (*Rana temporaria*, *Lissotriton vulgaris* and *L. helveticus*) probably also declined at this site. The surviving toad population continued to recruit new cohorts and had an apparently healthy age structure. Habitat quality (aquatic and terrestrial) remained good and there was no evidence of disease. An invasive species (*Pelophylax ridibundus*) was excluded as a likely cause of toad decline. However, traffic on a neighbouring road rendered more than half the previously available terrestrial habitat for toads essentially unreachable. Furthermore, reduced management of vegetation in ditches where the toads breed apparently increased mortality of developing tadpoles. Future prospects for conserving and increasing the toad population are discussed.

Common toads *Bufo bufo* and other widespread amphibians declined substantially in Britain during the mid 20th century primarily as a result of agricultural intensification (Cooke, 1972). Comparable trends were later identified across much of Europe (Houlahan et al., 2000). The status of *B. bufo* has continued to deteriorate, especially in eastern England (Carrier & Beebee, 2003) and similar declines have been noticed elsewhere (e.g. in northern Italy, Bonardi et al., 2011). Because of this ongoing decrease, common toads were added as a priority species to the UK Biodiversity Action Plan in 2007.

At Offham marshes in Sussex (Fig. 1; also known as ‘The Pells’) common toad numbers have fallen dramatically. The area was scheduled as a Site of Special Scientific Interest (SSSI) in the late 1980s on account of its amphibian community which included a large population of *B. bufo* as well as substantial numbers of common frogs *R. temporaria*, smooth and palmate newts *Lissotriton vulgaris* and *L. helveticus* (Banks 1987; 1988). Marsh frogs *Pelophylax ridibundus* subsequently invaded the area from an established population south of Lewes (Beebee, 1977). Toads at Offham breed in drainage ditches and many migrate to the site from woodland to the west, across a major road (A275) that has generated heavy mortality. A ‘toad patrol’ volunteer group formerly moved animals across this highway and accounts from this team during the early 1990s identified rapidly decreasing toad numbers. By the late 1990s there were too few to warrant retention of the patrol which was therefore disbanded. Unfortunately during this period there were no estimates of toad numbers breeding on the marshes. However, when the problem was appreciated efforts began to assess the toad population size annually and investigate possible causes of, and solutions to, the problems afflicting it. This paper reports the results of these investigations over the fifteen year period 1998-2012 inclusive.

METHODS

The study site

Offham marshes consist of approximately 200 ha low-lying fields intersected by numerous drainage ditches (Fig. 1) which have a sporadic history of dredging to keep them open (see Results section). The north (ditches C, D, E) central (M1 area) and south (Marsh A, ditch B) parts of the marshes have separate owners but all three graze the pasture intermittently from April through to October, mostly with cattle. Management history of the area was provided by these landowners. The ditches are floristically and faunistically rich with abundant growths of water violet *Hottonia palustris* and invertebrates including great silver beetles *Hydrophilus piceus*. All the ditches support fish, including three- and ten-spined sticklebacks (*Gasterosteus aculeatus* and *Pungitius pungitius*).

An assessment of terrestrial habitat structure and its suitability for use by *B. bufo* (Bardsley, 1998) was carried out by Dr L. Bardsley in 1998. Areas up to about 1.5 km west of the marshes (altogether >1.5 km²) were investigated on the basis of four key habitat criteria each ranked from 1 (poor) to 5 (very good): (1) Herb and ground-layer flora using the DAFOR scale, quantified in 5 x 1 m² quadrats per 100 x 100 m habitat section. Large trees and shrubs were counted in 25 x 25 m quadrats with 100 m between each. Poor habitat (grade 1) included heavily grazed pasture while very good habitat (grade 5) included long rank grassland with a litter component. (2) Number of refugia, specifically of dry stone walls, fallen logs, animal burrows and hummocks of grass litter per 25 x 25 m area. Grade 1 was <5, grade was >25. (3) Soil moisture content, measured in the top 2 cm of soil every 10 -20 m using a 'Rapidtest' monitor; grades were from 1 (dry) to 5 (some standing water). (4) Slope, from grade 1 (very steep, 1 metre rise in <2 metres distance) to flat (<1 metre rise over 8 metres distance). Steep slopes on soil

overlying chalk (as here) are prone to rapid desiccation in summer. Final scores summed those for the four criteria. Total scores of >16 were considered excellent, 12-16 of intermediate quality and <12 unlikely to support toads except briefly or during migrations.

Amphibian population monitoring

Anecdotal information about toads at Offham prior to 1987 was obtained by correspondence with local people, in one case from as early as the 1920s. Numbers of all amphibian species on the marshes were assessed by Banks (1987; 1988) prior to SSSI designation by counting *R. temporaria* spawn clumps, *B. bufo* adults by torch at night and newts *L. vulgaris* and *L. helveticus* by netting ditches for a standard time (30 minutes). From 1998 onwards I estimated population sizes of *R. temporaria* by counting spawn clumps and *B. bufo* by counting adults assembling to breed. For *B. bufo* at least three counts were made over the course of each breeding season (usually early – mid March), spaced several days apart and always on warm, still nights following observations of the first arrivals during preliminary visits. Ditches A – E as well as M2 and M3 were walked on each occasion. Use of ditch M1 and those east of the railway line was very rare so these were excluded from study. The highest number of toads recorded over each season was taken as a relative estimate of population size. This method cannot estimate true population size because only a fraction of the numbers present is seen even on the peak night. A capture-mark-recapture (CMR) exercise in 2002 showed that the number of *B. bufo* estimated by this more rigorous approach (c. 1200) was approximately three times higher than the number (382) counted on the peak night (Brede & Beebee, 2006). However it was not practicable to carry out CMR studies every year and I have assumed that peak counts are sufficient to indicate relative changes in the toad population over time. This method is widely used in assessment of common toad populations (Gent &

Gibson, 1998; Scribner *et al.*, 2001).

Newt numbers were not estimated regularly but in 1999 and 2012 a netting survey was repeated exactly as described by Banks (1987). Marsh frogs were recorded when observed basking along ditch banks in summer. A study of ditch preferences by marsh frogs at Offham was undertaken over one summer (Macro, 2004).

Assessing tadpole survival was problematic in the complex array of drainage ditches. A combination of visual estimates in open water with, in some cases, CMR by tail-clipping was carried out by Dr J. Denton between 1998 and 2000, from April to June each year.

Demography of Offham toads

Forty one toads were caught and measured (snout-vent length) in 1998 by Dr L. Bardsley. In 1999 single toe tips were taken (under Home Office licence) from the hind feet of 20 adult toads during the breeding season. The animals were released immediately afterwards. The age of each toad was established by Dr L. Bardsley using skeletochronology as described elsewhere (Hemelaar, 1983).

Tracking adults and toadlets

To investigate terrestrial habitat use by adults, eight male toads caught in ditch C in March 2000 were implanted abdominally with small (< 2g) radio-transmitters (Biotrack, Dorset) following anaesthesia (Denton & Beebee, 1993), all by Dr. J.S. Denton under Home Office licence. The animals were allowed to recover for two days after surgery and then released at their site of capture. The toads were then relocated at approximately weekly intervals, during daytime and using a Yagi antenna, until the batteries expired around early/mid June.

To investigate the fate of newly metamorphosed toadlets, eighty five roof tiles were placed along the margins of ditch C prior to toadlet emergence in June 2000 (Baynes,

2000). Ditch C supported many thousands of *B. bufo* tadpoles in that year. Nine pitfall traps (buckets) were installed, mainly around the eastern end of ditch C where most metamorphosis occurred and in the field corner near convergence of ditches C, D and E (Fig. 1). When dispersal began, drift fences were used to generate nine x 20 m transects across the field north of ditch C at right angles to the main direction of toadlet movement. One square metre sampling areas at 5 m intervals along each transect were each searched for one minute to count toadlets, fifteen times between 0900 -1200 hours every day from June 15 – June 30 and intermittently through July.

Traffic density

Information on traffic flow on the A275 between 1984 and 1996 was provided by Dr Alex Tait of East Sussex County Council.

RESULTS

Population dynamics and demography

Trends in toad numbers at Offham are summarised in Fig. 2. Anecdotal evidence indicated that the population was consistently high for decades prior to its first assessment in the late 1980s. Between 1988 and 1997 it apparently decreased from thousands to hundreds, in accord with reports from volunteers at the toad crossing. Since 1998 the population has remained small relative to pre-1990 but nevertheless fluctuated considerably, maximally up to more than 700 in 2004. No significant overall trend occurred between 1998 and 2012 ($r_s = -0.134$, $P = 0.649$). Because head-counting is an imprecise method small variations between years probably do not represent significant trends. On the other hand the very low count in 2011 was certainly real but may not reflect a change of population size. This was the driest spring ever recorded and some toads may have skipped a breeding season (Muths et al., 2006; Loman & Madsen, 2010).

In the late 1980s large numbers of toads assembled in most of the ditches shown in Fig. 1. Ditches B, C/D and E were the most heavily used and in the late 1990s the pattern was broadly similar except that numbers were disproportionately reduced in ditch B relative to those further north. This pattern has persisted ever since.

Table 1 summarises observations of other amphibians at Offham between 1987 and 2012. Since 1998 frog and newt counts have also been lower than in the late 1980s but marsh frogs increased substantially commensurate with the toad decline.

It was important to discover whether the toads breeding in the late 1990s were constituted mostly by old animals, implying little recent reproductive success, or by a mixed-age population. Table 2 gives estimates of toad sizes and ages in the late 1990s. These indicated that by both criteria the surviving toads reflected a regularly recruiting set of overlapping cohorts (Gittins et al., 1985). Tadpoles were observed every year after 1998 and in every ditch where spawning took place though in most years no attempts were made to estimate numbers. However, reproductive success was assessed between 1998 and 2000 based on numbers of tadpoles in the ditches through the spring months (Table 3). The huge shoals seen in C and E in 2000 followed ditch clearances late in 1999 and produced many toadlets whereas highly vegetated ditches B and D supported few or no tadpoles through to metamorphosis.

Table 1. Amphibians other than *B. bufo* breeding at Offham. Empty space = no records

Year	<i>Rana</i> <i>temporaria</i> (spawn clumps)	<i>Pelophylax</i> <i>ridibundus</i>	<i>Lissotriton</i> <i>vulgaris</i>	<i>Lissotriton</i> <i>helveticus</i>
1987	105	1	49	45
1988	123			
1999	44	10s	17	6
2012	25	10s	13	4

Table 2. Size and age distributions of Offham toads, 1998-1999. The age of one individual could not be determined.

Size range in mm (1998)	Number of individuals
51-60	2 (sex indeterminate)
>60 - 70	24 male, 3 female
>70 – 80	2 male, 4 female
>80	0 male, 6 female
Age (1999)	Number of individuals
3	2
4	10
5	7

Table 3. Tadpole survival at Offham.

Ditch				
Year	M2	C	E	M3
1998	-	10700 (CMR May 7-8) 1000s (May 27) 10s-100s toadlets (June 13)	-	-
1999	-	<30 (CMR May 15-16) No toadlets seen	-	6000 (CMR May 15- 16) 10s toadlets (June 11)
2000	100s (May 6) 1000s (May 29) Few toadlets (June)	10000s (May 6) Huge shoals (May 21) 1000s toadlets (June)	10000s (May 6) Huge shoals (May 21) Toadlets (June)	100s (May 6) 10s (May 29) Few toadlets

Autecology of Offham toads

Evidently the Offham toad population was still breeding successfully in the late 1990s despite its recent size reduction. Further work was therefore carried out to investigate life history outside the breeding season. In the first instance I attempted to find out which

habitats the animals selected in summer. Eight adult males implanted with radio transmitters were tracked for about three months after leaving breeding ditch C in early March 2000. All the toads moved west into the steeply sloping woodland and remained within about 200 m of the ditch throughout the tracking period (Fig. 3). Movement from April onwards was always over short distances and except for one individual which eventually returned to the field next to the ditches, the toads stayed in the woodland habitat. One animal crossed the road and ended up in the woodland immediately west of it. The toads were never directly encountered but were in refugia beneath ground vegetation (mostly ivy), under fallen trees or, in the case of the animal in the field, under thick grass.

It was also desirable to determine the fate of toadlets after metamorphosis as mortality can be very high at this life stage and influence overall population dynamics (Vonesh & De la Cruz, 2002). Mark Baynes followed a large cohort of toadlets (thousands) that metamorphosed from the eastern end of ditch C in June 2000. Very few moved east towards the railway bank, despite its proximity. The great majority moved west, either directly along the southern side of ditch C or along shallow, damp hollows towards ditch D after first migrating north parallel to the railway (Fig. 4). Baynes (2000) also showed that the animals selected corridors of relatively high humidity (damp hollows with long grass) in preference to open, short-turf pasture. The overall directionality of movement was striking, with toadlets converging towards the woodland habitat also used by adults. A single well-grown toadlet was seen in the woods in August. Such directionality towards woodland has been noted in studies with other amphibians (Malmgren, 2002) but not, as far as I am aware, with *B. bufo*.

Terrestrial habitat within 1-2 km westwards from Offham was investigated in 1998. Results are shown in Fig. 5. By the criteria applied, neighbouring woodland as

well as the pasture surrounding the breeding ditches provided adequate habitat for common toads. There were, however, areas of higher quality habitat immediately to the north and also west of the woodland slope high on the downs. Overall there were about 500 ha of potentially suitable terrestrial habitat for *B. bufo* within 2 km west of the breeding ditches. The railway embankment might also be adequate but access for assessment was prohibited and no toads have been seen migrating in from that direction.

Anthropogenic influences on toad population dynamics

Road traffic is well-known as a cause of amphibian mortality and the daily pattern of use on the main A275 in 1996 is shown in Fig. 6A. Vehicle numbers declined through the evening and early night when most toad migration occurred but nevertheless still averaged about 200 per hour. Somewhat surprisingly, traffic flow decreased by 20% over four years during the early 1990s simultaneous with the toad decline (Fig. 7B). This was ascribed by the Local Authority to the newly opened Brighton by-pass diverting traffic that previously used the A275. However, immediately prior to this the traffic use rose steeply, by 30% within three years. It remains a very busy highway.

Another potentially important factor was land use and management by the site owners. Information on this subject was obtained from each of the three families involved in 1999 and is summarised in Table 4. All had grazed livestock on the pasture for decades past and there were no recent alterations in their minor applications of fertilisers or pesticides. Only with respect to ditch management was there evidence of change. Two of the three owners had carried out almost no dredging over the previous decade whereas the one at the north end, on the advice of English Nature, had adopted a policy of half-clearing each ditch longitudinally every five years. Previous to that there was no specific information but in the past it was common practice for farmers to maintain clearance cycles whereby any one ditch would be dredged about every five years. Based on

observations that toad tadpoles seemed to survive well in open water (i.e. in recently dredged ditches) but much less well in densely vegetated water, I recommended that the five-year cycle of ditch management was restored. This was agreed in principle but after implementation starting in 2000 the process was abandoned after a few years and only reinstated in 2012 (Fig. 2). However, toad numbers increased for several years following restoration of ditch management in 2000 and decreased in subsequent years when management ceased. Assuming most toads matured at three or four years of age (table 2), adults resulting from improved larval survival in dredged ditches should have peaked between 2003 and 2007. Average numbers counted in that period = 563 (SD = 136,) more than twofold higher than mean counts between 2008 and 2012 (=245, SD = 156), a highly significant difference (Wilcoxon signed rank test, $U = 0, 25$, exact $P = 0.008$).

Table 4. Past management at Offham (pre-2000).

Activity	North end (ditches C, D, E, M2, M3)	Central (including ditch M1)	South (including marsh A and ditch B)
Ditch management	5-year cycle, half ditch (longitudinal) each time	Once within previous 10 years	One operation within previous 10 years
Grazing (all April-September)	Mostly cattle, sometimes sheep	Cattle, occasional	Cattle
Chemical applications	Nitrogen fertiliser (small quantities) in April; occasional	Nitrogen fertiliser applied annually, April-June.	Very small amounts of nitrogen fertiliser (April). No

herbicide treatment	Occasional	herbicides used.
of ditch dredging to	herbicides to control	
control nettles	thistles & nettles	

DISCUSSION

Common toads declined at Offham by an order of magnitude during the early 1990s when detailed monitoring was not in place. Since then the population has persisted but at a smaller size than in previous decades. The decline was not confined to toads. Other native amphibians (common frogs, smooth and palmate newts) probably also decreased although there are fewer data upon which to make this inference. No species disappeared and amphibian diversity actually increased with the appearance of marsh frogs at Offham. Various possible reasons for the toad decline are considered below.

Climate change

Reading (2007) showed that body condition, survival rates and fecundity of common toads at a pond in Dorset declined as a correlate of increasingly mild winters. He proposed that toad physiology requires a cold spell during hibernation and that climate change was therefore a possible cause of population declines. Numbers of toads and therefore the actual rate of decline were not shown but the most dramatic effects on physiology occurred during the mid-late 1980s, after which there was little change. This time scale did not coincide with the main decline at Offham and although effects of climate cannot be discounted, other explanations seem more likely (see below).

Habitat change

Loss of and damage to habitats are well-known causes of amphibian declines (e.g.

Beebee & Griffiths, 2005). However, habitat quality and extent did not change appreciably in the Offham area during or after the period of toad decline. Water quality in the ditches, as judged by other flora and fauna, has remained high and no amphibian mortality (such as might be induced by fertilisers or pesticides) has ever been seen. In 1998 there were at least 500 ha of good terrestrial habitat within the species' likely range. Much was beyond the top of a steep slope but toads have been found there and *B. bufo* can move to summer habitat 400 m higher than the breeding site (Sztatecsny & Schabetsberger, 2005). In mid Wales adult toad densities in terrestrial habitat were estimated at 23 per ha (Gittins et al., 1980). On that basis Offham could theoretically have supported more than 11 000 individuals although whether habitat qualities in the two areas are strictly comparable is not known.

Disease

No sick or dead amphibians have been reported at Offham, though this might have gone un-noticed during the poorly monitored period of main decline. Nevertheless, disease seems unlikely to have been an important factor. *Ranavirus* is common in south-east England but is more pathogenic to frogs (*R. temporaria*) than to toads (Teacher et al., 2010). Yet frogs survived at least as well as toads at Offham, as they have generally in south-east England (Carrier & Beebee, 2003). The fungus *Batrachochytrium dendrobatidis* (Bd) occurs in British *B. bufo* but not at Offham, where amphibians were tested for its presence in 2007 (Cunningham & Minting, 2008). Although this pathogen can kill common toads, *B. bufo* expanded its range in part of Spain where Bd devastated *A. obstericans*, presumably due to relaxed competition (Bosch & Rincon, 2008).

Displacement by invading marsh frogs

Pelophylax ridibundus increased rapidly at Offham in the period commensurate with toad declines. This invader might oust native species, especially common frogs (Smith,

1951) but in Sussex this concern has not been borne out (Beebee, 1980). Toads breed before most marsh frogs emerge from hibernation. Adult marsh frogs remain in or close to water all summer and were not seen predated toadlets by Baynes (2000). Stomach contents from three adult marsh frogs lavaged by J. Denton at Offham in July 1998 included fragments of alderfly and dragonfly larvae but no toadlets although these were in the immediate vicinity. *Pelophylax ridibundus* actively avoids toad tadpoles (Innocenzi, 1995). There is therefore no evidence to suggest that marsh frogs were responsible for the toad decline.

Traffic mortality

Toads often migrate long distances between summer and breeding habitats. They probably cross roads more often than other British amphibians and are potentially more vulnerable to traffic mortality. Large numbers have been killed on the A275 over many years, but could this account for the population decline? Although traffic intensity decreased on this highway during the early 1990s, in 1996 there was still an average of more than three vehicles per minute during the evening/early night peak migration times. Based on road mortality analysis of amphibians including *B. bufo* at a site in Denmark (Hels & Buchwald, 2001) this traffic intensity would kill more than 50% of toads attempting to cross the A275. Since adults must also make a return journey after breeding and toadlets face the same problem, the overall chances of a toad establishing a home range west of the A275 must now be less than 10%. Cooke (2011) demonstrated that falling numbers of toads killed on roads around three sites in Cambridgeshire between 1990 and 2010 correlated strongly with falling numbers turning up in the ponds. Furthermore, the rate of decrease in casualties (reflecting the population decline) correlated with traffic flow across the various sections of road involved. Traffic intensity

at Offham between 1990 and 1996 was similar to or higher than that estimated by Cooke in Cambridgeshire. It seems likely that traffic deaths have become sufficiently high at Offham to effectively cut off a high proportion of good quality summer habitat (Fig. 1). If the surviving toads mostly use woodland below the road, as indicated by the radiotracking studies, a much reduced area of suitable habitat has become safely accessible. Thus the effect of the road may have been to kill most toads attempting to access good habitat to the west of it, and therefore be the primary driver of population decline. Numbers of dead toads on the A275 have never been counted even during the toad patrol years but, while corpses are still occasionally seen, they are few and imply little recent cross-road migration.

Habitat management

Although Offham habitats have remained generally good, a reduction in ditch clearance frequency has occurred (table 1) and this probably affected the toad population adversely. *Bufo bufo* thrives in relatively large water bodies, especially where fish are present (Beebee, 1985; Laurila 1998). Their tadpoles are distasteful to most vertebrates but more vulnerable than those of frogs *Rana temporaria* to invertebrate predators such as odonate larvae (Manteifel & Reshetnikov, 2002; Alavarez & Nicieza, 2009), probably because *Bufo* larvae are more continuously active (Chovanec, 1992). Clearance generates open water with fewer invertebrate predators than the dense vegetation of unmanaged ditches. Evidence that this has been important at Offham is both direct (larval mortality estimates, table 3) and indirect. Toad declines in the area around ditch B were much more severe than in the northern area. In 1987-8, 22-25% of toads at Offham spawned in ditch B. After 1998 the proportion was never higher than 10% and usually much less (results not shown). However, ditch B is furthest from the main road and close to suburban gardens which are likely to be good toad habitat (Beebee, 1985). But it is in the southern area that

ditch clearance decreased most markedly. Ditches C, D and E were still cleared occasionally throughout the toad decline period, albeit longitudinally, a technique following which open water areas persist for a much shorter time than in the traditional full-dredging days.

Future Conservation

Of three possible causes of toad declines identified at Offham, two are intractable. Climate change is not amenable to any short-term or local action. Evidence that this could be a problem for *B. bufo* comes from a single site in Dorset (Reading, 2007). More research is needed to establish how serious this issue might be. The road will remain a major cause of mortality. *Bufo bufo* can be induced to use under-road tunnels (Lesbarreres et al., 2004) but construction and maintenance of a tunnel with the necessary associated fencing would be impossible (or at least extremely expensive) at Offham because of the very steep and densely vegetated slopes on both sides of the A275. Furthermore the well-drained chalk substrate west of the road is not amenable to constructing new ponds to sustain a population there, a solution which can work in some situations (Schlupp & Podloucky, 1994). However, restoring a regular cycle of ditch clearance in the historical tradition could increase the population to higher numbers than have been typical since the early 1990s. Evidence from recent clearances suggests that tadpole survival, and later adult population size, respond positively to this management which restarted in 2012. The Offham toads remain genetically diverse (Brede & Beebee 2006) and surely have the potential to increase above recent numbers if appropriate ditch management is reinstated and the existing good habitat is maintained.

Declines of *B. bufo* have been widely reported in southern England and it will be interesting to discover whether likely causes identified at Offham are more generally applicable. They are in accord with other evidence that road traffic mortality is playing an

increasingly damaging role in reducing amphibian populations, especially of species such as *B. bufo* that regularly migrate over large distances between summer and breeding habitats. However, synergistic effects of two or more factors, as implied here, may be widespread in nature and it is clearly important to consider more than single causes in complex situations such as alterations in population dynamics. The likelihood that other amphibians have also declined at Offham infers that other as yet unidentified factors might also have affected this apparently pristine site.

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Figure 1. Offham marshes. Figure A: Site location. Marsh A = main *Rana temporaria* breeding area; _ = ditches; B – E = main *Bufo bufo* spawning sites; M1-M3, minor/occasional *B. bufo* spawning sites. ‡ = Railway line on raised embankment. Figure B: *B. bufo* breeding ditch (E).

A



B



Figure 2. Toad numbers at Offham. Bars = Maximum count each year. Only a minimal estimate was available for 1987. * = No counts possible due to foot and mouth disease outbreak. _ = Year in which ditch clearance occurred.

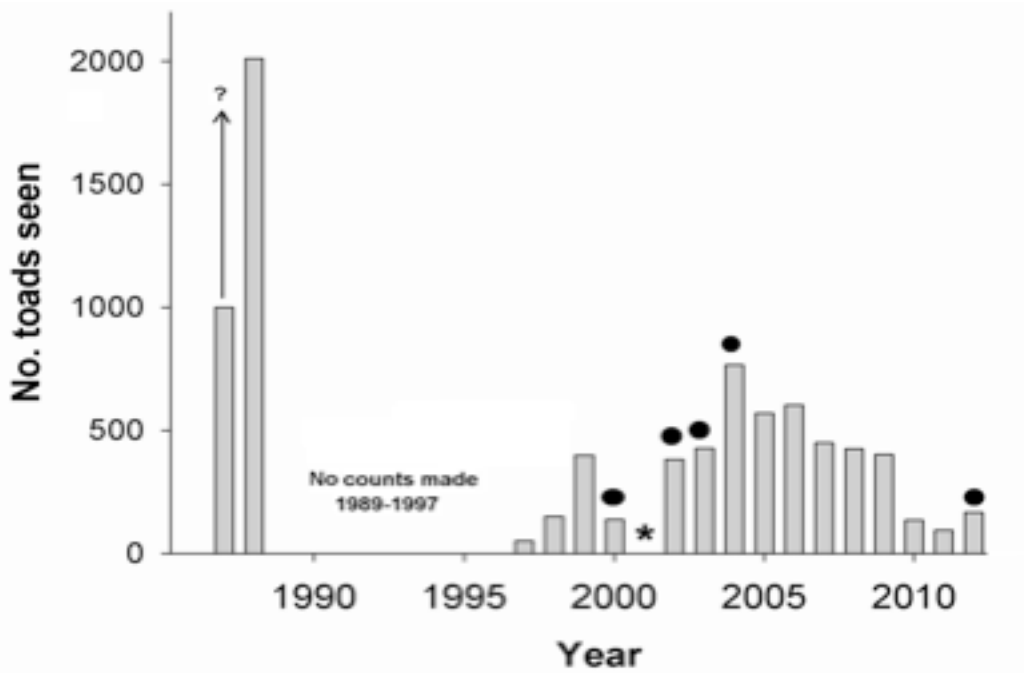


Figure 3. Movements of radiotracked toads, March – June 2000. O, point of leaving breeding site; ↘, Last record.

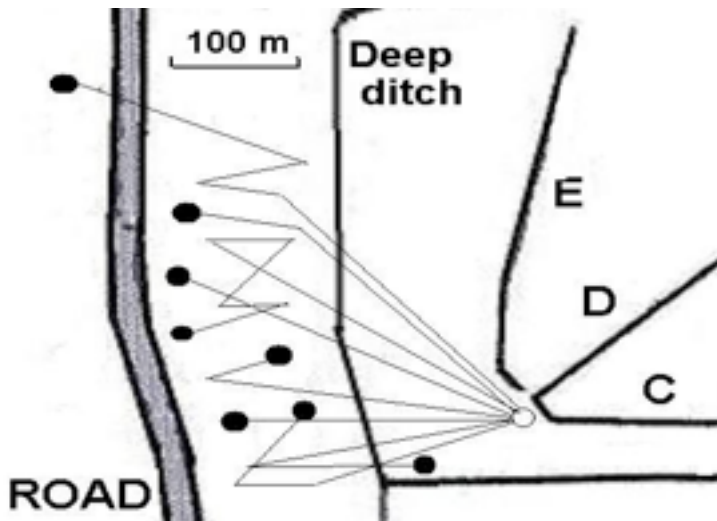


Figure 4. Toadlet movements after metamorphosis, summer (June) 2000. - - - = Toadlet movements; arrow thickness proportional to numbers seen. _ = Last toadlet seen (August 8).

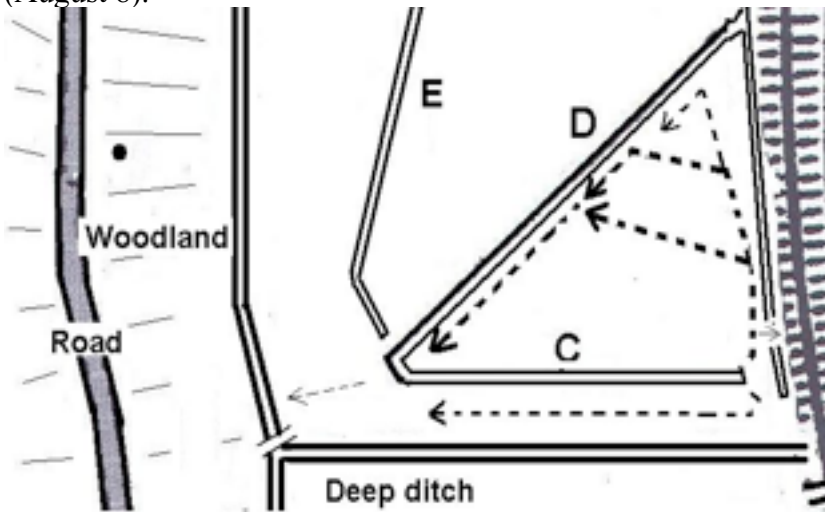
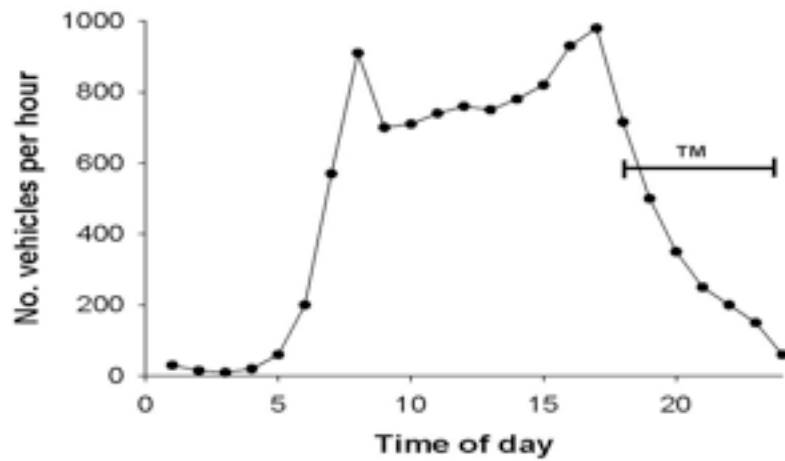


Figure 5. Terrestrial habitat at Offham. Dark grey = optimal, score >16; oblique black bars = intermediate quality, score 12-16; light grey = poor quality, score <12. ? = mostly urban areas, quality not known (but probably good). Areas east of the railway line were not assessed

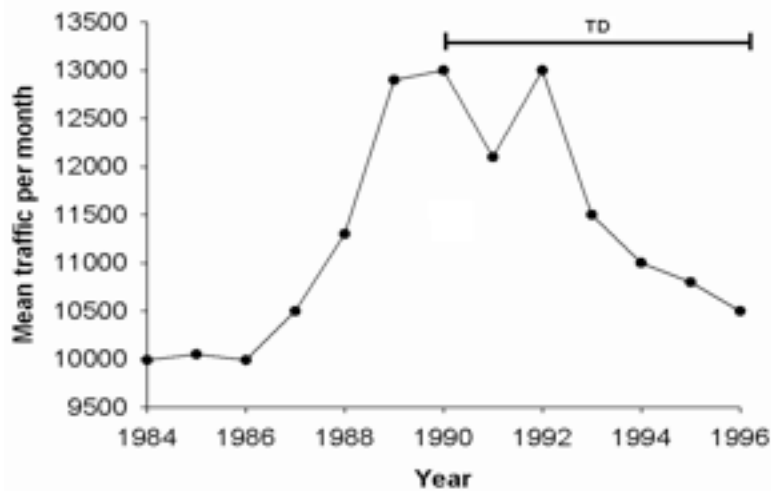


Figure 6. Traffic intensity on the main road (A275). A: Average traffic flow in relation to time of day, February – December inclusive, 1996. TM = Main period of toad migrations. B: Mean traffic (no. vehicles) per month, February and March combined, 1984-1996 inclusive. TD = Main period of toad population decline.

A



B



REFERENCES

- Alvarez, D. & Nicieza, A.G. (2009) Differential success of prey escaping predators: tadpole vulnerability or predator selection? *Copeia* **2009**, 453-457.
- Banks, B. (1987; 1988) Amphibian surveys on the Pells. File Notes, Nature Conservancy Council, UK.
- Bardsley, L.S. (1998) Use and selection of terrestrial resources by adult common toads (*Bufo bufo*) in agricultural landscapes. PhD thesis, De Montfort University, UK.
- Baynes, M (2000) The use of corridors as diurnal dispersal conduits by a population of postmetamorphic common toads (*Bufo bufo*). Project report, University of East Anglia.
- Beebee, T.J.C. (1977) More marsh frogs. *Brit. J. Herpetol.* **5**, 635.
- Beebee, T.J.C. (1980) Habitats of the British amphibians (3): river valley marshes. *Biol. Conserv.* **18**, 281-287.
- Beebee, T.J.C. (1985) Discriminant analysis of amphibian habitat determinants in south-east England. *Amphib-Reptil.* **6**, 35-43.
- Beebee, T.J.C. & Griffiths, R.A. (2005) The amphibian decline crisis: a watershed for conservation biology? *Biol. Conserv.* **125**, 271-285.
- Bonardi, A., Manenti, R., Corbetta, A., Ferri, V., Fiacchini, D., Giovine, G. et al. (2011) Usefulness of volunteer data to measure the large scale decline of “common” toad populations *Biol. Conserv.* **144**, 2328-2334 (2011).
- Bosch, J. & Rincon, P.A. (2008) Chytridiomycosis-mediated expansion of *Bufo bufo* in a montane area of central Spain: an indirect effect of the disease. *Divers. Dist.* **14**, 637-643.
- Brede, E.G. & Beebee, T.J.C. (2006) Large variations in the ratio of effective breeding

and census population sizes between two species of pond-breeding anurans. *Biol. J. Linn. Soc.* **89**, 365-372.

Carrier, J.-A. & Beebee, T.J.C. (2003) Recent, substantial and unexplained declines of the common toad *Bufo bufo* in lowland England. *Biol. Conserv.* **111**, 395-399.

Chovanec, A. (1992) The influence of tadpole swimming behaviour on predation by dragonfly nymphs. *Amphib-Reptil.* **13**, 341-349.

Cooke, A.S. (1972) Indications of recent changes in the British Isles of the frog (*Rana temporaria*) and the toad (*Bufo bufo*). *J. Zool.* **167**, 161-178.

Cooke, A.S. (2011). The role of road traffic in the near extinction of common toads (*Bufo bufo*) in Ramsey and Bury. *Nat. Camb.* **53**, 45-50.

Cunningham, A.A. & Minting, P. (2008) National survey of *Batrachochytrium dendrobatidis* in UK amphibians, 2008. Institute of Zoology, London.

Denton, J.S. & Beebee, T.J.C. (1993) Summer and winter refugia of natterjacks (*Bufo calamita*) and common toads (*Bufo bufo*) in Britain. *Herpetol. J.* **3**, 90-94.

Gent, T. & Gibson, S. (1998) eds. *Herpetofauna Workers' Manual*. Joint Nature Conservation Committee, Peterborough, UK.

Gittins, S.P., Kennedy, R.I. & Williams, R. (1985) Aspects of the population age-structure of the common toad (*Bufo bufo*) at Llandrindod Wells lake, mid-Wales. *Brit. J. Herpetol.* **6**, 447-449.

Gittins, S.P., Parker, A.G. & Slater, F.M. (1980) Population characteristics of the common toad (*Bufo bufo*) visiting a breeding site in mid-Wales. *J. Anim. Ecol.* **49**, 161-173.

Hells, T. & Buchwald, E. (2001) The effect of road kills on amphibian populations. *Biol. Conserv.* **99**, 331-340.

Hemelaar, A.S.M. (1983) Age of *Bufo bufo* in amplexus over the spawning period. *Oikos* **40**, 1-5.

- Houlahan, J.E., Findlay, C.S., Schmidt, B.R., Meyer, A.H. & Kuzmin, S.L. (2000) Quantitative evidence for global amphibian population declines. *Nature* **404**, 752-755.
- Innocenzi, P. (1995) The ecology and conservation of the marsh frog. MSc dissertation, University of Kent, Canterbury.
- Laurila, A. (1998) Breeding habitat selection and larval performance of two anurans in freshwater rock-pools. *Ecography* **21**, 484-494.
- Lesbarreres, D., Lode, T. & Merila, J. (2004) What type of amphibian tunnel could reduce road kills? *Oryx* **38**, 220-223.
- Loman, J. & Madsen, T. (2010) Sex ratio of breeding common toads (*Bufo bufo*) – influence of survival and skipped breeding. *Amphib-Reptil.* **31**, 509-524.
- Macro, J. (2004) Distribution patterns and behavioural ecology of the water frog *Rana ridibunda*. Project Report, University of Sussex.
- Malmgren, J.C. (2002) How does a newt find its way from a pond? Migration patterns after breeding and metamorphosis in great crested newts (*Triturus cristatus*) and smooth newts (*T. vulgaris*). *Herpetol. J.* **12**, 29-35.
- Manteifel, Y.B. & Reshetnikov, A.N. (2002) Avoidance of noxious tadpole prey by fish and invertebrate predators: adaptivity of a chemical defence may depend on predator feeding habits. *Archiv Hydrobiol.* **153**, 657-668.
- Muths, E., Scherer, R.D., Corn, P.S. & Lambert, B.A. (2006) Estimation of temporary emigration in male toads. *Ecology* **87**, 1048-1056.
- Reading, C.J. (2007) Linking global warming to amphibian declines through its effects on female body condition and survivorship. *Oecologia* **151**, 125-131.
- Schlupp, I. & Podloucky, R. (1994) Changes in breeding site fidelity – a combined study of conservation and behaviour in the common toad *Bufo bufo*. *Biol. Conserv.* **69**, 285-291.

- Scribner, K.T., Arntzen, J.W., Cruddace, N., Oldham, R.S. & Burke, T. (2001)
Environmental correlates of toad abundance and population genetic diversity.
Biol. Conserv. **98**, 201-210.
- Smith, M.A. (1951) *The British Amphibians and Reptiles*. Collins, London.
- Sztatecsny, M. & Schabetsberger, R. (2005) Into thin air: vertical migration, body condition, and quality of terrestrial habitats of alpine common toads, *Bufo bufo*. *Canad. J. Zool.* **83**, 788-796.
- Teacher, A.G.F., Cunningham, A.A. & Garner, T.W.J. (2010) Assessing the long-term impact of Ranavirus infection in wild common frog populations. *Anim. Conserv.* **13**, 514-522.
- Vonesh, J.R. & De la Cruz, O. (2002) Complex life cycles and density dependence: Assessing the contribution of egg mortality to amphibian declines. *Oecologia* **133**, 325-333.