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CHARACTERISTICS OF NATTERJACK TOAD (*BUFO CALAMITA*) BREEDING SITES ON A SCOTTISH SALTMARSH

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Natterjack toads are associated in Britain with three habitat types: sand-dunes, lowland heaths and upper saltmarshes (Beebee, 1983). Populations on the latter habitat, mostly situated along the northern shores of the Irish Sea, have been relatively little-studied though they include some of the largest in the country (Bridson, 1976; Banks & Beebee, 1988; Beebee, 1989). We have investigated natterjack breeding sites on Priestside Merse, a strip of saltmarsh on the north Solway coast that is about 7 km long and which varies from <50 m to about 500 m in width. The area is dotted with innumerable shallow saltpans, flood-pools and ditches, some of which are used by a natterjack toad population estimated to be in the low hundreds. Common frogs (*Rana temporaria*) and toads (*Bufo bufo*) also occur.

The ponds of Priestside Merse were systematically searched for natterjack adults, spawn and tadpoles during May, the peak of the breeding season, in 1990. Some observations on pond use were also made in earlier years. Water samples were taken from those ponds with healthy spawn or tadpoles (classified as successful breeding sites), ponds with occasional calling males and/or dead spawn (classified as attempted breeding sites) and from a range of ponds with no evidence of natterjack use. Conductivity of these samples was measured using a WPA meter with glass electrode, all at constant temperature, and salinities expressed as percentage seawater (assuming 100% seawater = 2.75% w/v NaCl). During the winter of 1990-1991, further samples were taken from a selection of these ponds at monthly intervals, stored at -20°C, and conductivities subsequently measured as described above.

Natterjack tadpoles and healthy spawn were found in a discrete subset of the saltmarsh ponds (Figure 1A), notably those with relatively low salinities (averaging 7.9% seawater, or about 0.22% w/v NaCl). The highest salt concentration in which breeding looked likely to be successful was 14% seawater (0.39% NaCl); the lowest was about 0.2% seawater (0.06% NaCl, essentially freshwater), but 10 out of the 11 breeding sites showed evidence of some salination and most were in the range 5-10% seawater (0.14-0.28% NaCl) during the May sampling period. Sixteen unused ponds, which were

interspersed with the used ones but often at least slightly closer to the sea, averaged 20% seawater (0.55% NaCl) with a maximum of 34.6% seawater (0.95% NaCl). Two other unused ponds, not included in the analysis of Fig 1A, were essentially 100% seawater. Salinities of used and unused ponds were significantly different by *t*-test after arcsin transformation ($t=5.29$, $df=17$, $P=0.0001$). There were, in addition, three ponds in which breeding was attempted but in which there was no evidence of success; two of these had occasional calling males (14.6% and 30.2% seawater) and the third had some calling and a single, fungus-infected spawn string (73% seawater).

Sampling the three classes of ponds (successful, attempted and unused) through a winter period confirmed that the differences between them were essentially ones of degree (Fig. 1B). High tides flooded the merse at various times throughout the year, but most acutely during the autumn. Ponds used by natterjacks evidently received these saline flushes, but salt concentrations did not reach the levels seen in unused ponds or in those in which breeding was probably unsuccessful during the spring of 1990. Freshwater, presumably as rain and run-off from inland areas, reduced salinities progressively during the winter months though further, relatively minor inundations were detectable at the height of winter (January-February) and more markedly in spring just before the onset of the natterjack breeding season. Many ponds were dry in May 1991, and no sampling was done in June, but a final July sampling indicated the occurrence of a midsummer inundation of at least some of the saltmarsh pools. We do not know how often midsummer inundation happens at this site, but metamorphosis of toadlets usually occurs in June. Successful ponds averaged about half the salinities of attempted and unused ones (9.5%, 16.4% and 15.9% respectively) throughout the measurement period.

It has been known for many years that natterjacks living in coastal regions, particularly in Scandinavia, often breed in pools exposed to salt spray or to occasional inundation from the sea (e.g. Andren & Nilson, 1979; 1985; Schlyter, Hoglund & Stromberg, 1991) though the degree of salinity has rarely been investigated. Exaggerated impressions of salt tolerance have arisen from accounts of natterjacks breeding in rock-pools along the Swedish coast because the low salinity of the Baltic Sea (only about 0.4% NaCl, 15% normal seawater, in bays used by natterjacks) is not always recognised by workers outside Scandinavia. In laboratory trials, early embryogenesis proved more sensitive to salt toxicity than subsequent developmental stages and there were no significant differences in this respect between *B. calamita* and *B. bufo*, nor between inland and coastal populations of *B. calamita* in Britain (Mathias, 1971; Beebee, 1985). Lethal limits for spawn were between 15-20% seawater (0.41-0.55% NaCl), though tadpoles could survive up to about 25% seawater (0.69% NaCl) and possibly higher for short periods. These corresponded closely to the highest salt concentrations at which natterjack reproduction has been recorded in the field, both in this and the earlier studies.

The inundation regime prevalent at Priestside, and probably at other saltmarshes inhabited by natterjacks, may well be crucial to the success of the animal in these habitats. Regular episodes of saline flooding prevent the development of typical freshwater invertebrate communities (Nicol, 1935)

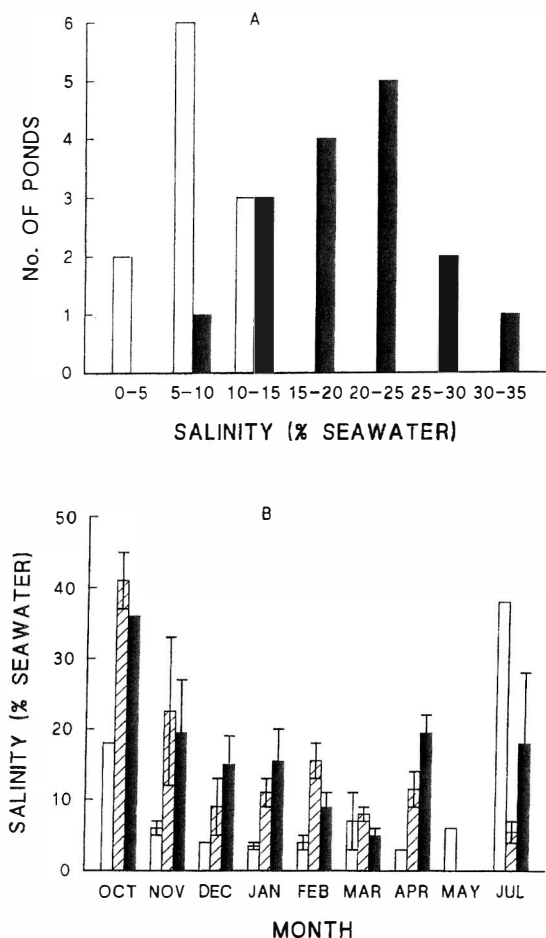


Fig. 1. Characteristics of saltmarsh pools. A: Numbers of ponds successfully used by natterjacks (open bars) or without any evidence of use by natterjacks (solid bars). B: Salinity changes between October 1990 and July 1991 in ponds with natterjack tadpoles or healthy spawn in May 1990 (open bars), ponds with occasional calling natterjacks and/or dead spawn in May 1990 (hatched bars) and ponds with no evidence of use by natterjacks in May 1990 (solid bars). Data are averages from two ponds in each class where error-bars show the ranges of the two estimates; where no error bars are present, only a single pond was sampled on that visit.

and thus maintain low numbers of tadpole predators. This is of vital importance to a species with small larvae highly vulnerable to such predation, and in which metamorphic success rates are inversely proportional to invertebrate predator numbers (Banks & Beebee, 1988). In the Scottish saltmarsh studied by Nicol, invertebrate species diversity was at a minimum and macrophytes virtually absent in the ponds of intermediate salinity and irregular inundation, presumably because neither freshwater nor marine species could establish for long periods. At Priestside at least seven species of tadpole predators have been observed (four species of *Agabus*, *Colymbetes fuscus*, an unspecified *Dytiscus* and *Notonecta glauca*) but numbers were generally low (D. Green, unpublished observations). Aquatic macrophytes were absent from many pools, but water crowfoot (*Ranunculus* species) occurred in some of the most productive natterjack ponds on the upper merse. Overall, faunal and floral diversity was much less than that regularly encountered in dune and heathland

ponds. Furthermore, the spring inundation coincides with the earlier breeding season of the other British anurans (*Rana temporaria* and *Bufo bufo*) and is likely to cause substantial mortality of the eggs and larvae of these competitively superior species, which might otherwise dominate this habitat as they do most others (Banks & Beebee, 1987). Nicol (1935) noted mortality of adult frogs, apparently caught out by high spring tides, in the upper saltmarsh ponds of her study. The inundation pattern is thus ideally suited to natterjack biology, reducing predators and competitors but with a period of lowered salinity in the late spring coinciding with the natterjack breeding season. Any development which altered this pattern, such as a tidal barrage scheme or embankment and reclamation of the upper saltmarsh could well be disastrous for natterjacks in this finely-balanced situation. Finally, our observations indicate that great care is necessary in the creation of new natterjack ponds on saltmarsh habitats to ensure that the appropriate salinity changes are achieved.

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