

## LONG TERM DECLINE AND POTENTIAL FOR RECOVERY IN A SMALL, ISOLATED POPULATION OF NATTERJACK TOADS *BUFO CALAMITA*

L. VINCENT FLEMING<sup>1</sup>, BARBARA MEARNS<sup>2</sup> AND DAVID RACE<sup>3</sup>

<sup>1</sup>Scottish Natural Heritage, Research & Advisory Services Directorate, 2 Anderson Place, Edinburgh EH6 5NP, UK

<sup>2</sup>Connansknowe, Kirkton, Dumfries DG1 1SX, UK

<sup>3</sup>15 St. Andrews Street, Darlington, Co. Durham DL1 2HD, UK

Changes through time in a small, isolated population of natterjack toads on the Solway Firth are reported. The area and linear length of coastline occupied by the colony have declined since it was first described in 1849. The colony now occupies less than 20% of its former range. The rate of decline has increased since the 1960s and has continued into the present decade. This decline has been accompanied by losses of breeding pools and habitat which can be directly attributed to anthropogenic changes in land-use. Comparison of aerial photographs between 1946 and 1988 show, amongst other changes, a major loss (>60%) of coastal sandy grassland, favoured by natterjacks, to agricultural intensification and to the recreational development which now surrounds the colony. Recent population monitoring (1986-1995) shows a failure of recruitment in five of the six years before 1991. During this period the annual peak counts fluctuated between nine and thirty adult males, well below a previous estimate in 1976 of 100 males. Artificial excavation of breeding pools in 1991 resulted in the subsequent production annually of large numbers of toadlets. A peak count of 79 males in 1995 probably reflects the recruitment to the breeding population of these cohorts and gives the first indication of recovery in this population. Re-occupation of the former range is no longer possible. The expansion of the colony to areas of suitable habitat away from the native site, but with no previous records of natterjacks, is discussed.

### INTRODUCTION

Within Britain there has been a significant contraction in the range and number of populations of natterjack toads *Bufo calamita* Laur. This decline has been most severe on the heaths of south-east England (Beebee, 1976; Banks, Beebee & Cooke, 1994; Arnold, 1995). Populations elsewhere, especially those occupying the sand-dune and saltmarsh habitats of Britain's Irish Sea coast, have been affected less severely. These now represent the stronghold for natterjacks in Britain (Banks *et al.*, 1994). Yet even here colonies have become extinct in recent decades, with small isolated populations being at greatest risk (Beebee, 1992; Banks *et al.*, 1994). However, there have been few published long-term studies on these Irish Sea colonies compared to those on heathlands (e.g. Banks, Beebee & Denton, 1993).

The colonies of natterjacks on the north shore of the Solway Firth, in south-west Scotland, are at the north-western limit of the species' range in Europe (Beebee, 1979; Bridson, 1977). Yet they are important in conservation terms. Collectively, the Solway colonies account for up to an estimated 23% of the total British population (Banks *et al.*, 1994). Southernness represents the furthest point on the Solway to which natterjacks have spread. It is thus of some biogeographical significance (Beebee, 1979, 1989). There are no substantiated records of natterjacks further north or west along the coast from this point (Beebee, 1989). This colony is,

however, isolated from the other Solway populations by the tidal mudflats and estuary of the river Nith (Fig. 1), being 11km in a linear distance from its nearest neighbour at Caerlaverock. It is also small in size with, in 1976, an estimated population of less than 100 males (Bridson, 1977). This paper reports on (a) changes in this colony through time, based on historical and contemporary records, (b) associated changes in land cover assessed from aerial photographs, and (c) recent monitoring to assess population trends, especially in response to recovery initiatives.

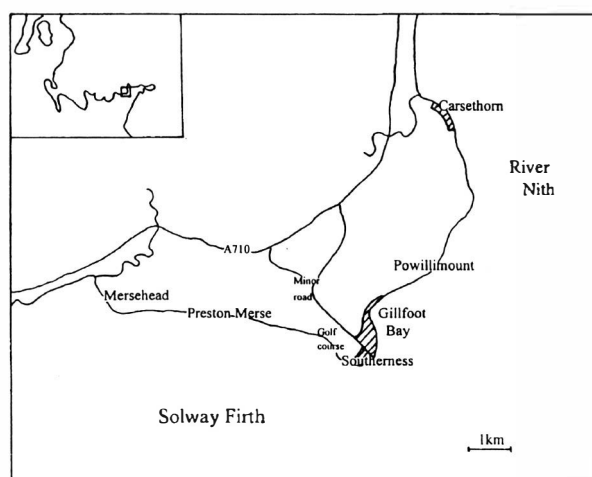


FIG. 1. Outline map of the Southernness area, showing locations referred to in the text.

## METHODS

## PREVIOUS RECORDS

We have searched the literature for references to this colony, and have also contacted local naturalists, record centres and others for information that would enable us to assess any changes through time (Mearns, 1994). The British Museum (Natural History) and seven museums in northern Britain (namely The Observatory, Dumfries; the Stewartry Museum, Kirkcudbright; the Kelvingrove Museum, Glasgow; Royal Museum of Scotland, Edinburgh; Tullie House Museum, Carlisle; the Hancock Museum, Newcastle; and Aberdeen University Museum) were also contacted to see if they had any natterjack specimens, originating from Southernness, in their collections. Additional information was obtained from the files of Scottish Natural Heritage (formerly the Nature Conservancy Council) and from the Biological Records Centre, Monks Wood.

## HABITAT CHANGE

In order to assess changes in habitats or land-use that may have affected use of the area by natterjacks, we compared aerial photographs taken in 1946 (1:9900) and 1988 (1:24000). The study area was defined as land between Carsethorn and Mersehead (Fig. 1) within 500 m distance of mean high water mark of spring tides (MHWS), modified to the nearest field boundary which remained constant between both sets of air photographs. This area encompassed all known records for natterjacks and represented a realistic area to assess the impacts of changes in land management. For the purpose of the analysis, the study area was split into two using the minor road to Southernness as the division (Fig. 1). Details of land-cover from aerial photographs were transcribed on to 1:10000 scale maps for subsequent measurement and analysis. Features of less than 0.25 ha were not included in the analysis. The following land cover categories were recognised:

*Improved agricultural land*: either arable land or intensively managed grassland.

*Coastal grassland*: unimproved or semi-improved pasture, typically very sandy with extensive rabbit activity, also including sand-dune.

*Heath*: dominated by heather or other dwarf shrubs but often merging into sandy grassland; also including golf course fairways.

*Marsh*: including open water, fresh marshland and saltmarsh.

*Urban*: including farmsteads and caravan/chalet parks with areas of amenity grassland.

*Woodland*: both deciduous and coniferous.

*Bare sand*: areas of bare sand above MHWS.

Land-cover categories were validated ("ground truthed") by comparing land cover types, mapped from 1988 aerial photographs, with a field assessment. Maps, ranging from the 1st Edition Ordnance Survey (OS) maps of 1896 (1:57600) to the most recent Pathfinder range (1:25000), with revisions up to 1985, were

compared to record gross changes in features, such as erosion and accretion of the coastline.

## MONITORING

From 1986 to 1995 the colony was monitored annually by us in order to assess numbers of natterjacks and to record parameters of breeding success. Visits were timed to coincide with key stages in natterjack breeding activity. The frequency of monitoring visits varied between years: during 1986-91, five to eight visits were made *per annum*, but from one to three visits *per annum* were made thereafter. At least one visit, but usually more, was made at night. Numbers of adults, especially calling males, were recorded. Any toads captured were sexed and a snout to vent measurement (mm) taken with a hand-held ruler before their immediate release (Smith, 1990). To avoid double-counting within years, only the highest single peak count of natterjacks and only the mean length of the largest single sample of captured toads are presented. Searches were made for spawn strings, tadpoles and emerging toadlets, and their numbers counted or estimated. All identifications were made in the field though not all *Bufo* tadpoles could be identified specifically. Other sites to the west of Southernness, to Mersehead (Fig. 1), were also surveyed periodically for evidence of natterjack activity.

## RESULTS

## RECORDS

The first record known to us of this colony, and for Scotland, was made by Sir William Jardine in an account in Bell (1849), in which he describes natterjacks as being "very abundant" and occurring for several miles along the coast between Southernness and Carsethorn (Fig. 1). Subsequently Service (1895) described the colony at Gillfoot Bay, then thought to be one of only two localities in Scotland. Later, he noted (Service, 1896) the wider distribution of natterjacks on

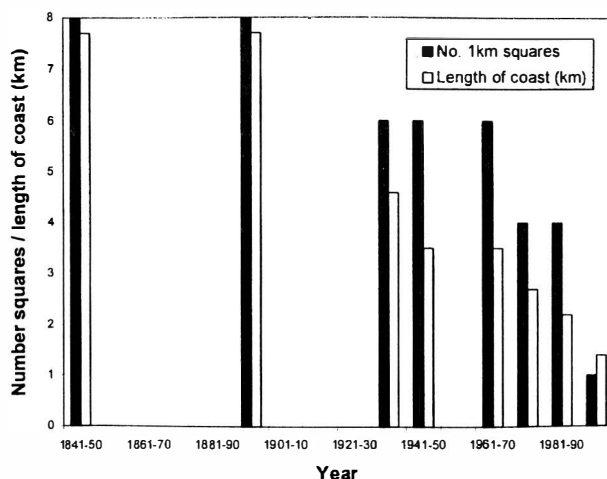


FIG. 2. Number of 1 km Ordnance Survey grid squares and linear length of coastline occupied through time by a declining population of natterjack toads.

the Solway and described the extent of the colony on the west side of the Nith.

We have found few records of this colony in the earlier part of the present century and we were not able to locate any specimens in the collections of likely museums (Mearns, 1994). However, natterjacks were recorded at Southernness in the 1930s and about this time pre-emergent natterjack toadlets were observed in a pool at the House on the Shore (OS grid reference: NX994572), to the north of Powillimount (A. Truckell, personal communication). Between 1939 and 1941, J. Donnan found natterjacks to be common to the west of Southernness lighthouse in an area where these were later recorded by G. Clarke in 1964 (personal communications). There are, to our knowledge, no confirmed records of natterjacks further west along Preston Merse. Taylor (1963) records the presence of natterjacks at Southernness by the indication of a dot on his distribution maps. This record, for 1961-62, represents the earliest record of natterjacks at Southernness held at the Biological Records Centre.

Bridson (1977) subsequently surveyed this colony comprehensively in 1976 and described the location of breeding pools thought then to be confined entirely to Gillfoot Bay (UK grid reference NX95; 3° 35' W, 54° 53' N). Subsequently, in 1988, we discovered two pools with calling natterjacks at Powillimount, 1 km to the north of Gillfoot Bay and 200 m inland, and a further breeding pool 300 m inland from Gillfoot Bay. We have not recorded any natterjacks to the west of the minor road to Southernness.

#### CHANGES IN DISTRIBUTION AND LAND-COVER

Whilst it is not possible to be certain of the exact area occupied by natterjacks in the past, we have attempted a quantitative estimate of the changes in distribution through time. To do so, we plotted all records of location, with dates, on to a 1:25000 scale map of the area. We assumed that natterjack occupancy was confined to a strip within 100 m of MHWS unless we had information to the contrary. For each 10-year period with records, we were then able to count the number of 1 km squares of the OS grid, and to measure the linear length of coastline, then occupied by the colony (Fig. 2). In doing so, we also assumed (a) that any breeding sites known to us now were occupied by natterjacks in earlier years; (b) that occupancy of an area terminated at the latest date for which we have records; (c) that range occupation was uniform for any given period; and (d) that any contraction in range was towards localities with later records. We have taken Carsethorn as the northern limit of this colony's distribution despite the vague reference by Service (1896) to natterjacks occurring up to Kirkconnell (some 8 km to the north of Carsethorn).

All the extant breeding pools now fall within a single 1 km square of the OS grid. Despite the relative crudity of these estimates, this colony clearly now occupies less than 20% of its former range (Fig. 2). Moreover,

TABLE 1. Changes between 1946 and 1988 in area (ha) of different land cover types, derived from aerial photographs, in two study areas at Southernness (for definition of types and study area see text).

| Land-cover            | West of road |      | East of road |      |
|-----------------------|--------------|------|--------------|------|
|                       | 1946         | 1988 | 1946         | 1988 |
| Improved agricultural | 78           | 134  | 241          | 245  |
| Coastal grassland     | 208          | 137  | 63           | 25   |
| Heath                 | 57           | 74   | 0            | 0    |
| Marsh                 | 11           | 36   | 6            | 7    |
| Urban                 | 2            | 3    | 8            | 39   |
| Woodland              | 22           | 10   | 16           | 17   |
| Bare sand             | 32           | 3    | 0            | 0    |
| TOTAL                 | 410          | 397  | 334          | 333  |

the rate of contraction in range has increased since 1960 and has continued into the present decade.

Examination and comparison of aerial photographs suggests significant quantitative and qualitative changes in land cover between 1946 and 1988 (Table 1). It is apparent that land between Southernness and Carsethorn ("east of the road" in Table 1) was already intensively farmed by 1946. Even so, significant areas of heavily grazed coastal grassland remained, concentrated around Gillfoot Bay. By 1988, the area of this habitat had had been reduced by over 60% with losses to agricultural intensification and to recreational developments (caravan and chalet parks) at Southernness. Indeed, two years after the 1988 aerial photographs, a further area (7 ha) of sandy coastal pasture at Powillimount, used by natterjacks, was lost to agricultural improvements. Differences in total area between 1946 and 1988, in both parts of the study area, result from net changes in erosion and accretion of the coastline.

Between Mersehead and Southernness ("west of the road" in Table 1), changes were more dynamic. Improved agricultural land increased at the expense of dune heath and coastal grassland. Despite these losses, significant areas of sandy pasture remain. Although the total area of heathland increased, it is now restricted to a golf course. The net increase in the total area of marsh is due to considerable accretion of saltmarsh at Mersehead. However, this obscures significant erosion of the coastline overall. At least 130 m depth of land along Preston Merse was lost to marine erosion during the period between air photographs. Large areas of bare sand in 1946 give the impression then of a dynamic and eroding habitat. Comparison of maps indicate that, at the western end of Preston Merse, the MHWS mark may have receded by up to 700 m since 1896. Up to 480 m of this loss is marked as being vegetated and presumably represented saltmarsh or sand dune.

#### BREEDING AND TERRESTRIAL HABITAT

The colony is now focused on a narrow strip of ungrazed coastal marshland, 1.4 km in length and up to

TABLE 2. Results of natterjack population monitoring at Southernness from 1986-1995 inclusive ( $n$  for SE of mean length =  $n$  for size range column unless otherwise stated). +, 10's of tadpoles/toadlets; ++, 100's tadpoles/toadlets; +++, 1000's tadpoles/toadlets; F, failed; \* $n=20$ ; \*\* $n=54$ ; nd, no data.

| Year | Maximum number   |                  |          |                      | Mean length<br>of toads ( $\pm$ SE) | Size range (mm)<br>(pooled data) | No.<br>visits |
|------|------------------|------------------|----------|----------------------|-------------------------------------|----------------------------------|---------------|
|      | toads<br>(males) | spawn<br>strings | tadpoles | emergent<br>toadlets |                                     |                                  |               |
| 1986 | 23 (20)          | 1                | ++       | F                    | 55 $\pm$ 7.4                        | 46-76 ( $n=3$ )                  | 6             |
| 1987 | 36 (30)          | 7                | +++      | +                    | 56 $\pm$ 0.5*                       | 42-72 ( $n=32$ )                 | 8             |
| 1988 | 18 (16)          | 2                | ++       | F                    | 53 $\pm$ 0.3                        | 48-56 ( $n=9$ )                  | 5             |
| 1989 | 9 (9)            | nd               | ++       | F                    | 59 $\pm$ 0.6                        | 54-65 ( $n=7$ )                  | 7             |
| 1990 | 23 (23)          | nd               | +        | F                    | 56 $\pm$ 0.8                        | 45-62 ( $n=8$ )                  | 7             |
| 1991 | 6 (6)            | 2                | +++      | +++                  | 52 $\pm$ 2.5                        | 50-55 ( $n=2$ )                  | 7             |
| 1992 | 6 (6)            | nd               | +++      | ++                   | nd                                  | nd                               | 3             |
| 1993 | 2 (1)            | 16               | +++      | ++                   | nd                                  | nd                               | 3             |
| 1994 | 6 (6)            | nd               | ++       | nd                   | 41 $\pm$ 2.9                        | 22-51 ( $n=5$ )                  | 1             |
| 1995 | 90 (79)          | 10               | ++       | +                    | 53 $\pm$ 0.1**                      | 31-64 ( $n=57$ )                 | 3             |

100 m wide, at Gillfoot Bay, bordered to the landward by a recreational caravan site. Vegetation in the marshland is dominated by dense stands of *Phragmites australis* and *Bolboschoenus maritimus*. This area is within the Upper Solway Flats & Marshes Site of Special Scientific Interest (SSSI) designated under the Wildlife & Countryside Act in June 1988. Mown amenity grassland dominates within the caravan site.

Natterjack breeding activity has consistently been associated with two pools at Gillfoot Bay. The main pool, although relatively large (100 x 50 m), is now half its original size as reported by Bridson (1977). The second pool is much smaller, 5 m by 10 m, and with spreading *P. communis*. Both pools may desiccate in dry summers and may be subject to tidal inundation in winter (Beebee, Fleming & Race, 1993). Pools at Powillimount were lost to agricultural drainage and improvement work over the winter of 1989-1990. We have no subsequent records of use of the area by natterjacks. Three other pools have been subject to drainage attempts or have also been lost.

#### CONSERVATION MANAGEMENT

To ensure the availability of suitable breeding habitat, three new pools were mechanically excavated in September 1990 within the Gillfoot Bay marshland. In addition, the two existing pools were cleared out and re-profiled. Not all the new pools have been used by natterjacks: two have been avoided. Despite clearance work, invasion by *P. communis* has intensified in the minor original pool such that little open water remains and recently use by natterjacks has ceased.

#### POPULATION MONITORING

In the years between 1979 and 1985 for which we have records (no data from 1983), toadlet emergence was recorded as poor or failed in all but 1979 and 1980 (Beebee, 1989). Combined results of population monitoring from 1986-1995 are presented in Table 2. Despite the presence annually of tadpoles, no emergence of toadlets was recorded in four of the five years

before 1991. In each case, pool desiccation was responsible for breeding failure. Even in 1987 the emergence of toadlets was inferred rather than observed because there were no obvious factors (such as drought) to have prevented emergence of the few hundred tadpoles present that year. Following the creation of breeding pools, the production of tadpoles has been consistently high. Large numbers of toadlets were recorded as emerging in 1991 and 1992, and similar numbers were likely from 1993 to 1995.

Before 1990, peak nighttime counts of adult natterjacks fluctuated between nine and 30 males, suggesting a total population not exceeding 60-80 individuals (Table 2). The fluctuations between years may be due to monitoring visits missing, by chance, the peak of breeding activity. Counts from Powillimount, between its discovery and destruction, suggest that although no more than 10 adult natterjacks were recorded there, these may have represented then a significant proportion of the total population. Despite the apparent lack of recruitment between 1986 and 1991, there is no evidence of any progressive increase in mean length that might be expected with an ageing population (Smith, 1990). However, sample sizes are small and factors other than age may influence body size (Denton & Beebee, 1993; Halliday & Verrell, 1988). Very low counts from 1991-94 may be an artefact of reduced recording effort. This view is supported by a high single count of spawn strings in 1993, indicating at least 16 females in the population. Indeed, it is more likely that the population was increasing over this period, resulting ultimately in a peak count in 1995. This single count is the largest number of adults recorded at this site and suggests, assuming an equal sex ratio (Banks *et al.*, 1993), an adult population now approaching 200 individuals.

Further evidence of successful recruitment is suggested by the occurrence since 1994 of juvenile toads much smaller than 43 mm in length (Table 2), the apparent minimum size threshold for breeding (Denton & Beebee, 1993). Counts of spawn strings also increased

after 1991, but these results must be interpreted with more caution. In particular, searching for spawn is difficult in the densely vegetated and silty pools characteristic of the site. Pool excavation may also have made the discovery of spawn more easy.

Common toad *Bufo bufo* and common frogs *Rana temporaria*, adults and juveniles, were recorded almost annually. There is no evidence so far of any significant increase in their numbers.

#### DISCUSSION

The long term, and continuing, decline in this natterjack population is probably typical of many other, but less well documented, colonies. Indeed, it is remarkable in many respects that it has persisted at all. Losses of populations in north Wales have been attributed to extensive recreational developments (Beebee, 1976) not unlike those now surrounding the colony at Southernness. The persistence of the colony is almost certainly due to the survival of the marshland at Gillfoot Bay. It is evident from the earliest descriptions of the colony (Bell, 1849; Service, 1895) that, even then, this was a focus of natterjack activity. The contraction in range that we have documented has been towards this core habitat feature. Paradoxically, it is possible that the caravan site, juxtaposed with the marshland, may have contributed to the survival of the colony. Mown amenity grassland, within the site, may have provided natterjacks with more open foraging conditions (Denton & Beebee, 1994) that might not have been available if the area had been, for example, agriculturally improved.

The decline of this colony has been accompanied by changes in, and intensification of, land-use, principally for agriculture and recreation, typical of losses in most coastal natterjack sites (Beebee, 1992). Most importantly at Southernness, the area of sandy coastal grassland, that seems to have been associated with natterjack use, has been significantly reduced. This has been combined with continuing loss and attrition of breeding pools. Of greatest concern, perhaps, is that these losses have continued, and indeed accelerated, into the present decade despite legal protection given to natterjacks, and elements of their habitat, since 1975. Habitat destruction, however, has taken place almost exclusively outside the boundary of the Upper Solway Flats & Marshes SSSI, since its re-notification (and therefore enhanced protection) under the 1981 Wildlife & Countryside Act. These results reflect the relative benefits of site versus species protection recently reviewed by Banks *et al.* (1994).

Results of population monitoring indicate that, in the 1980s, the outlook for this colony was far from promising. Reductions in the extent or quality of habitat continued. Recorded breeding success had also been continually poor with toadlet production being recorded in only three of the twelve years before 1991. Although, the count of 30 males in 1987 is below the 100 individuals formerly estimated by Bridson (1977),

it is within the range of counts (30-40 males) actually reported from 1976. Whilst this might suggest some stability between the two periods, the counts from this study were typically much lower and included those from a number of pools apparently not known to Bridson (1977), suggesting a genuine decline in population.

It is clear that the artificial excavation of breeding pools in late 1990 was both necessary and timely. These recovery attempts were immediately successful, with large numbers of toadlets produced almost annually thereafter. From a nadir in the late 1980s, the adult population now seems to have recovered to, or exceeded, 1976 levels. However, there are few grounds for optimism in the long term. Some of the pools, and certainly the rank vegetation at Gillfoot Bay, may now favour common toads and common frogs, successful competitors with natterjacks (Banks & Beebee, 1987; Denton & Beebee, 1994; Griffiths, Edgar & Wong, 1991). Management of the vegetation by grazing is unlikely to be a realistic option. Equally, if the population is increasing in size, and presumably density, individual toads may be ranging more widely (Denton & Beebee, 1993) yet there is little other suitable habitat available for them to colonise. The former documented range towards Carsethorn is now entirely unsuitable.

Along Preston Merse (Fig. 1), however, there is potentially suitable habitat for natterjacks (Table 1). Immediately west of Southernness, sandy coastal grassland and heath occur within a distance feasible for natural recolonisation (Langton & Beckett, 1995). There are records of natterjacks from the easternmost part of this area as recently as 1964. Establishment would, however, be limited by lack of breeding pools. Further west, at Mersehead, there is also suitable habitat, consisting of grazed dune pasture and saltmarsh, dune slack, sandy flood banks and relic sand-dunes, now in conservation management. Natterjacks are not likely to be able to colonise here unless by translocation. There is scope, therefore, by positive conservation measures, to enable some recovery of the colony's former abundance by expansion into new habitat.

Despite the apparent present and former suitability of Preston Merse (Table 1), however, there are no historic records. Yet, there may once have been considerably more habitat than is present today. Much of the land lost to coastal erosion was likely to have consisted of saltmarsh and sand-dune. By extrapolation from other Irish Sea colonies (Beebee, 1989), this would have been suitable for natterjacks. Another threatened inhabitant of ephemeral pools, *Triops cancriformis*, the tadpole shrimp, was recorded from Mersehead in 1907 and 1948 (Balfour-Browne, 1948) suggesting, perhaps, the presence of pools suitable for breeding by natterjacks. It has also been suggested that the original sites for this species have now been lost to coastal erosion (Bratton, 1991). Since there are no obvious obstacles to natterjacks having occupied this area in the past, it is not unreasonable to consider Preston

Merse within the "presumed natural range" of natterjacks (Nature Conservancy Council, 1983). Beyond Mersehead a long stretch of rocky cliffs would have been an obstacle to the spread of natterjacks. Any proposals to establish natterjacks further west beyond this biogeographical barrier would be unwarranted and unjustified.

#### ACKNOWLEDGEMENTS

Dr. T. J. C. Beebee and two referees provided helpful comments on this paper. We thank the various landowners at Southernness, especially Mr. Mackie of Southernness Holiday Village, for allowing us access for this study. We are also grateful to the various museum curators, amateur naturalists, Biological Records Centre and staff of Scottish Natural Heritage for their assistance. The Royal Commission of Ancient and Historical Monuments for Scotland permitted us access to their archive of aerial photographs for study. One of us (BM) was supported in a search for historical records by a contract from Scottish Natural Heritage. Breeding pool excavation was funded by grant aid from the Nature Conservancy Council and by the British Herpetological Society. All field work was done under licence from NCC and SNH.

#### REFERENCES

- Arnold, H. R. (1995). *Atlas of amphibians and reptiles in Britain*. ITE Research Publication no. 10. HMSO, London.
- Balfour-Browne, F. (1948). Re-discovery of *Apus cancriformis*. *Nature, London* **162**, 116.
- Banks, B. & Beebee, T. J. C. (1987). Spawn predation and larval growth inhibition as mechanisms for niche separation in anurans. *Oecologia* **72**, 569-573.
- Banks, B., Beebee, T. J. C. & Denton, J. S. (1993). Long-term management of a natterjack toad (*Bufo calamita*) population in southern Britain. *Amphibia-Reptilia* **14**, 155-168.
- Banks, B., Beebee, T. J. C. & Cooke, A. S. (1994). Conservation of the natterjack toad *Bufo calamita* in Britain over the period 1970-1990 in relation to site protection and other factors. *Biological Conservation* **67**, 111-118.
- Beebee, T. J. C. (1976). The natterjack toad (*Bufo calamita*) in the British Isles; a study of past and present status. *British Journal of Herpetology* **5**, 515-521.
- Beebee, T. J. C. (1979). A review of scientific information pertaining to the natterjack toad *Bufo calamita* throughout its geographical range. *Biological Conservation* **6**, 107-134.
- Beebee, T. J. C. (1989). Natterjack toad (*Bufo calamita*) site register for the UK. Unpublished confidential report.
- Beebee, T. J. C. (1992). Trying to save the natterjack toad - a case study in amphibian conservation. *British Wildlife* **3**, 137-145.
- Beebee, T. J. C., Fleming, L. V. & Race, D. (1993). Characteristics of natterjack toad (*Bufo calamita*) breeding sites on a Scottish saltmarsh. *Herpetological Journal* **3**, 68-69.
- Bell, T. (1849). *A history of British reptiles*. London: John Van Voorst.
- Bratton, J. H. (ed.). (1991). *British Red Data Books 3. Invertebrates*. Joint Nature Conservation Committee, Peterborough.
- Bridson, R. H. (1977). The natterjack toad - its distribution in south-west Scotland 1976. *Transactions of the Dumfriesshire and Galloway Natural History and Antiquarians Society* **53**, 46-56.
- Denton, J. S. & Beebee, T. J. C. (1993). Density-related features of natterjack toad (*Bufo calamita*) populations in Britain. *Journal of Zoology* **229**, 105-119.
- Denton, J. S. & Beebee, T. J. C. (1994). The basis of niche separation during terrestrial life between two species of toad (*Bufo bufo* and *Bufo calamita*): competition or specialisation. *Oecologia* **97**, 390-398.
- Griffiths, R. A., Edgar, P. W. & Wong, A. L.-C. (1991). Interspecific competition in tadpoles: growth inhibition and growth retrieval in natterjack toads, *Bufo calamita*. *Journal of Animal Ecology* **60**, 1065-1076.
- Halliday, T. R. & Verrell, P. A. (1988). Body size and age in amphibians and reptiles. *Journal of Herpetology* **22**, 253-265.
- Langton, T. E. S. & Beckett, C. L. (1995). *Home range size of Scottish amphibians and reptiles*. Scottish Natural Heritage Review No. 53. Scottish Natural Heritage, Perth.
- Mearns, B. (1994). *The past distribution of the natterjack toad on the north Solway*. Unpublished report to Scottish Natural Heritage.
- Nature Conservancy Council. (1983). *The ecology and conservation of amphibian and reptile species endangered in Britain*. Nature Conservancy Council, Peterborough.
- Service, R. (1895). Natterjack Toad in Dumfriesshire. *The Zoologist* **53**, 350.
- Service, R. (1896). The vertebrate zoology of Kirkcudbrightshire. In *Maxwell's Guide Book to the Stewartry of Kirkcudbright, 6th edition*, pp 175-176. J. H. Maxwell. Castle Douglas: The Advertiser.
- Smith, P. H. (1990). Size differences of natterjack toads breeding on north Merseyside sand dunes. *Herpetological Journal* **1**, 493-498.
- Taylor, R. H. R. (1963). The distribution of amphibians and reptiles in England and Wales, Scotland and Ireland and the Channel Isles: a revised survey. *British Journal of Herpetology* **3**, 95-115.