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SUMMER AND WINTER REFUGIA OF NATTERJACKS (*BUFO CALAMITA*) AND COMMON TOADS (*BUFO BUFO*) IN BRITAIN

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ABSTRACT

We have investigated the refugia used by *Bufo calamita* and *Bufo bufo* throughout the year on heathland, sand dune and saltmarsh habitats in Britain. On the first two habitats, natterjacks mainly lived at depths of >20 cm in burrows of their own making and these burrows insulated animals very effectively against temperature fluctuations during the summer. In saltmarsh habitats natterjacks used a variety of refugia and at all sites common toads were found in mammalian burrows and under stones, logs and piles of leaf litter. Natterjacks at the saltmarsh site vacated areas following tidal inundation with no evidence of mortality attributable to this event. At the heathland site, male natterjacks adopted two distinct strategies for refugia use during the breeding season: commuters travelled to and from the ponds every night, returning before dawn to their summer burrows, while residents took up temporary abode near the ponds for the duration of the breeding season. On heaths and dunes natterjacks usually used the same burrows for hibernation that were used in the summer months, but buried themselves more deeply. Common toads also used similar sites to those occupied in summer, but often these were selected following an autumn move towards the breeding ponds. At the saltmarsh and other coastal sites in Cumbria, most natterjacks and all common toads hibernated under piles of stones or logs, or in the burrows of small mammals.

INTRODUCTION

The natterjack is the rarest amphibian in the British Isles and is declining over much of its European range. Information on the habitat components that are important for breeding and foraging by this species is now extensive (e.g. Beebee, 1983; Banks & Beebee, 1987*a*; 1988; Sinsch, 1989*a*; Denton, 1991), but much less is known about refugia use, especially during the winter months. Indeed, there have been very few studies on the hibernacula of European amphibians with most information on this subject being anecdotal and often the result of accidental, unsystematic discoveries. However, attempts have been made to identify winter refugia of tree frogs *Hyla arborea* in the Netherlands (Stumpel, 1990), common toads have been studied in winter by the use of thermosensitive radiotransmitters (Van Gelder *et al*., 1986), and there have been more general reports on hibernation sites of several species (e.g. Hagström, 1982; Sinsch, 1989*b*). We have recently quantified summer refugia selection by natterjacks and common toads at four study sites in Britain (Denton & Beebee, 1992). Natterjacks mostly used burrows of their own making on sandy sites while common toads usually sought shelter beneath debris. Burrowing behaviour is highly adaptive with benefits including protection against temperature extremes, desiccation and predation (Hoffman & Katz, 1989). In this study we set out to characterise the refugia used by the two toad species on the three habitats in which both can be found in Britain, notably lowland heath, coastal dunes and upper saltmarsh.

STUDY SITES

Observations were carried out over four years (1988-1991 inclusive) at the following sites:

(1) Woolmer Forest, a lowland heath in southern England supporting a relict population of about 100 natterjacks and with an even smaller number of common toads.

(2) Ainsdale and Birkdale sand dunes, on the Merseyside coast of north-west England. This extensive (several hundred ha) dune system supports several thousand natterjacks and tens of thousands of common toads.

(3) Dunnerholme, an upper saltmarsh in Cumbria (north-west England) supporting several thousand natterjacks and a much smaller number of common toads.

In addition, some observations were made at Millom ironworks, another coastal site in Cumbria consisting mainly of rocks and debris with a shallow pond and several thousand natterjack toads. All these sites are described in detail elsewhere (Beebee, 1989; Denton, 1991).

METHODS

All the study sites were visited many times by day and any likely refugia investigated. Natterjack burrows on banks were often identified by the characteristic semicircular opening; those on flat ground were found by searching for newly-exposed sand piles on the surface. Other refugia were detected by systematic lifting of stones, logs and other debris (Denton & Beebee, 1992). Refugia use was also studied by radiotelemetric monitoring of tagged animals. For the hibernation studies, totals of 14 natterjacks and two common toads were tagged on Merseyside; six natterjacks and five common toads at Woolmer; and 12 natterjacks and one common toad at Dunnerholme. Tags were implanted and tracking carried out as described elsewhere (Denton, 1991; Denton & Beebee, 1993). Hibernation sites were investigated by implanting toads with 100-day transmitters in late autumn and following the animals into hibernation, and transmitters were removed the following spring. At Woolmer, individual natterjacks were marked by toe-clipping or identified by individual throat-spot patterns.

At all sites, some of the refugia were subjected to detailed study. Depth, temperatures and relative humidities at the point occupied by the toad were measured in 18 burrows at Merseyside and in 25 at Woolmer. Air, ground-surface and burrow temperatures and humidities were recorded using a Hanna H8564 thermohygrometer. Burrow depths and substrate types were also recorded.

RESULTS

GENERAL FEATURES OF SUMMER REFUGIA

The numbers of refugia investigated for both species at all study sites are listed in Table 1. At dune and heath sites, natterjacks almost always used refugia on sandy substrates. This was true whether refugia consisted of true burrows or of cells dug under debris, but in the Cumbrian sites where sand was rare or (as at Millom) completely absent, typical refugia for this species included mammalian burrows, hollows under large stones on clay soils, and gaps in piles of slag or drystone walls. Most natterjacks in summer burrows lived at depths of >20 cm from the burrow entrance, though on dunes this was usually a horizontal rather than a vertical distance. Thus the average depth at which toads were found in 18 burrows on Merseyside was 30 cm (range 10-45 cm). At Woolmer, however, burrows were dug vertically into virtually flat ground. Toads in 25 burrows at the heathland site averaged 23 cm below ground, with a range of 5-45 cm. Only in spring and autumn was there any substantial use of surface refugia, mostly as cells dug immediately beneath flat tiles, at Woolmer (Denton & Beebee, 1992). Common toads were only found in surface refugia or in burrows dug by other animals at all sites; as shown in Table 2, dense vegetation, especially moss at the base of *Salix repens* stems in wet slack basins was a favourite place and rabbit burrows were utilised on both dunes and heathland. Common toads of all sizes were frequently found under logs and other debris, including metal sheets.

Burrows dug by natterjacks in sandy substrates were effective homeostatic refugia protecting the animals within from extremes of heat and drought. The daily fluctuations of ground air, ground surface and natterjack body temperatures around and inside one particular burrow at Merseyside over a twelve hour period in August are shown in Fig. 1, a single example from the 18 investigated. Whereas sand surface temperatures fluctuated over a range of 48°C during this time, with a maximum of about 60°C at midday, the thermally-tagged natterjack 30 cm below ground level maintained a temperature of around 24°C (±1°C) throughout. Sand surface temperatures of >50°C were recorded regularly on these dunes in summer while night-time temperatures often dropped to <12°C. During such hot dry periods, natterjacks remained inactive in their burrows for up to several weeks at a time. At Woolmer, minimum temperatures in summer were much lower than on the dunes and often dropped to around 0°C. Night-time (22.00-24.00 hours) temperatures in 25 burrows with aestivating natterjacks at this site were always warmer than ground surface temperatures, by an average of 1.6°C on one particular and typical summer night (t=2.14, df=24, P<0.03). Mean humidity was also significantly higher in burrows, averaging 90% compared with 60% in surface air (t=9.09, df=24, P<0.0001) on this same occasion.

study site	refugia numbers	
	total investigated	studied by radiotelemetery
Merseyside		
natterjack	45(42)	28
common toad	23(0)	12
Dunnerholme		
natterjack	143(21)	17
common toad	14(0)	2
Woolmer		
natterjack	57(55)	15
Common toad	11(0)	4
Millom		
Natterjack	83(0)	0
common toad	4(0)	0

TABLE 1. Numbers of refugia studied, 1988-1990. Refugia constituted by self-dug burrows are given in parentheses.

	site	
refugia	Merseyside	Woolmer
logs or litter	5	6
dense vegetation	14	3
rabbit holes	4	2
total	23	11

TABLE 2. Characteristics of common toad refugia.

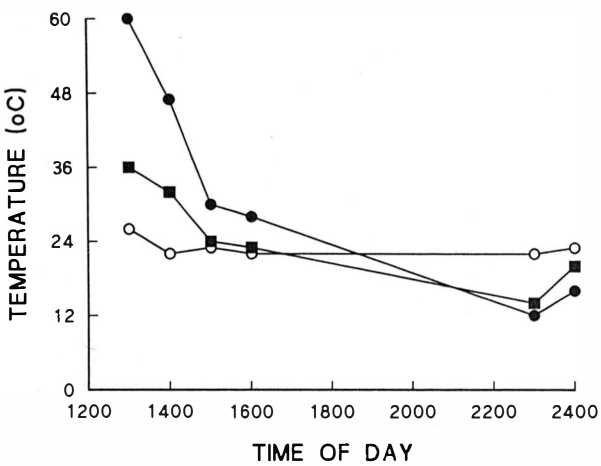

Fig. 1. Temperatures in and around a natterjack burrow. Measurements were made at Merseyside during a single day in August 1990. filled circles, sand surface; filled squares, ground air; open circles, toad in burrow with thermal transmitter.

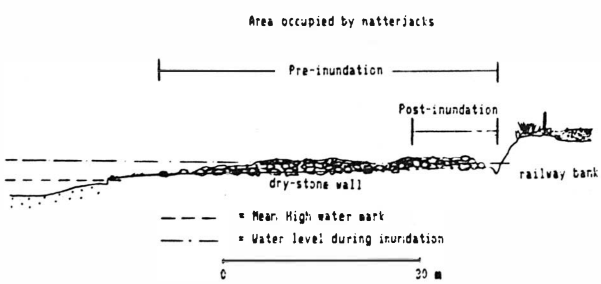

Fig. 2. Refugia changes associated with tidal inundation. The figure shows the distribution of natterjacks in refugia before and after a tidal inundation at Dunnerholme during September 1989.

Refugia use	n	number of animals seen: 1 season	2 seasons	>3 seasons
Nightly migration to pond from winter/ summer burrows	18	2	5	11
Temporary occupation of new refugia near ponds	21	8	5	8

TABLE 3. Refugia selection by breeding male natterjacks at Woolmer. Observations were cumulative over four breeding seasons (1988-1991 inclusive). n=total number of individuals monitored. Each individual was observed a minimum of three times in each breeding season.

Refugia selection by natterjacks at saltmarsh sites was influenced by episodes of tidal inundation. At Dunnerholme the distribution of natterjacks varied from month to month through the summer on this account. Thus in June 1988 a drystone wall which extended from a railway embankment across grazed saltmarsh to the beach (Fig. 2) was occupied by over 80 animals. These were found under collapsed stones along the entire length of the wall. In September 1988, following a tidal inundation, only 15 toads were found in the wall and none were found more than 15 m from the railway embankment end. Many of the more seaward stones concealed marine crustaceans at this time. Natterjacks had also abandoned strand-line flotsam which, before the inundation, was heavily used as a refugium. How toads survived these episodes was not discovered, but no dead animals were found in the flooded areas.

REFUGIA SELECTION BY NATTERJACKS DURING THE BREEDING SEASON

Bufonids of all species are compelled to visit ponds during the breeding season, and this inevitably entails movement away from previously-occupied refugia. Male natterjacks were studied individually at Woolmer, and two equally favoured strategies were apparent at this time (Table 3). Throughout the breeding season, some males commuted to the ponds on every night that they were encountered, returning before dawn to their summer (and winter) home range areas in round trips of up to 300 m. Other males adopted refugia in the vicinity of the ponds for at least one night and often for much longer during the 8-10 week calling period. These males either made new burrows near the pond or hid under debris or in dense vegetation such as *Molinia* tussocks, and invariably started calling before the commuters arrived. The resident strategy seemed slightly more hazardous than the commuter strategy since a substantial proportion of males adopting the former (40%) were seen only for a single breeding season, whereas the comparable figure for commuters was just over 10% (Table 3). Nevertheless, comparing survival rates for up to two seasons with those for more than two seasons there was not quite a significant difference between the two strategies (χ =3.53, df=1, P>0.05). Since all males were recorded during their calling bouts, these data were not biased by differential capture probabilities. Females almost invariably commuted to the pond for a single night, spawned, and returned to the summer/winter home range immediately afterwards. Only on eight recorded occasions out of more than 50 observations, when temperatures dropped low enough to prevent spawning (Banks & Beebee, 1987*b*) did females remain in the vicinity of the ponds for an extra day.

study site	n	no. animals using: same refuge as in summer	new site
Merseyside			
natterjack	14	8	6
common toad	2	0	2
Dunnerholme			
natterjack	12	4	8
common toad	1	0	1
Woolmer			
natterjack	6	6	0
common toad	5	1	4

TABLE 4. Hibernacula selection by natterjacks and common toads. All data were from radiotracked animals. n=number of individuals tracked into hibernation.

HIBERNACULA SELECTION BY NATTERJACKS AND COMMON TOADS

Animals were followed into hibernation by radio-tagging in late autumn, and results are summarised in Table 4. Individual natterjacks at Woolmer always hibernated in the same burrows they occupied during the summer months, but dug down to depths of >50 cm in winter. These hibernacula were invariably on flat, level ground and not in the various banks available at the site. In addition to radiotracking data, 43 natterjacks with known home ranges at Woolmer were first observed in spring in the same areas they occupied the previous summer, also indicating hibernation sites in or near the refugia used in summer months. Some burrows were occupied by more than one individual, and juveniles (<40 mm long) were found with adults. On mobile dunes at Merseyside, natterjacks hibernated in burrows at the base of marram (*Ammophila*) clumps, 8 out of 14 using the same ones occupied during the summer. All four of the radio-tracked natterjacks using burrows on the most seaward dune ridge, however, moved to burrows on the east-facing leeward side of the ridge for hibernation, perhaps minimising risk of exposure by wind erosion on the seaward facing slopes during winter gales.

The Dunnerholme site was dominated by saltmarsh habitat with only small outcrops of mobile dunes. Eight of the 12 natterjacks followed into hibernation by radiotracking moved from their summer refugia into new sites for the winter: two moved less than 5 m, and secreted themselves at depths of around 25 cm in burrows of small mammals; one moved from a pile of railway sleepers into a bank of loose clinker; one moved from a drystone wall, and two more from under stones, to bury themselves in a sand bank; and two dug new burrows within 10 m of their summer refugia in the same sand bank. By contrast, two remained in the sleeper pile, one remained in the drystone wall and another in its summer sand burrow. One male hibernated at the base of a bank >20 cm below the level reached by high winter tides. At Millom, where no sand at all was available, natterjacks hibernated in spaces between coarse slag particles in large banks of this material. In April 1991 63 natterjacks emerged at this site from three holes less than 10 cm apart, all of which led to underground cavities formed among piles of building debris.

The hibernation sites selected by common toads were similar at all three study sites. Radio-tracked animals resorted to hiding places in dense vegetation, under piles of logs or in leaf litter. Both tagged animals at Merseyside, the one at Dunnerholme and four out of five at Woolmer moved to new sites for the winter. Some individuals made substantial (>500 m) moves towards the breeding ponds in autumn before settling in a hibernation site, a behaviour never seen with natterjacks. Mammalian burrows, especially rabbit and vole holes, were also used at Woolmer and Birkdale.

DISCUSSION

Both toad species of this study probably spend more than 90% of their lives in refugia, yet there have been few reports on the nature and location of these places, especially with regard to hibernation sites. Our observations extend those of others on natterjacks which, for the most part, were the results of chance encounters in both summer and winter (reviewed in Beebee, 1979; 1983). Water availability may be a major factor governing refugia selection by amphibians in the sandy, relatively arid habitats favoured by natterjacks in Britain. Burrowing enables natterjacks to utilise substrate moisture, whereas common toads are dependent on surface water sources. Sand is also a poor conductor of heat and temperature fluctuations dampen rapidly as a function of depth from the surface; yellow dunes favoured by natterjacks are subject to daily temperature variations which are much greater than those on the more mature grey dunes (Chapman, 1964) and the ability to burrow is therefore an important adaptation of *Bufo calamita* for existence in otherwise exposed, open habitats. *Bufo bufo*, by contrast, generally selected equable conditions by utilising surface refugia in dense vegetation. At Woolmer, three out of eight common toads radio-tracked in their summer home ranges were eaten by grass snakes *Natrix natrix* while none of six tagged natterjacks were lost to this predator. The snakes caught toads by day, and it seems likely that surface refugia were more accessible to them than the burrows (often completely covered by collapsed sand) inhabited by natterjacks.

The survival of toads in areas subject to occasional tidal inundation needs more study. The duration of these episodes rarely exceeded two hours and it is possible that animals survived in air spaces during the flooding period. Subsequent vacation of flooded sites may be a behaviourial response to residual salinity in groundwater; juvenile natterjacks avoid substrates saturated with >46% seawater when given a choice (Piearce, 1978). Although *B. calamita* is considered to be a euryhaline amphibian, its upper limit of salt tolerance is lower than that of *B. viridis* and is lower in winter than in summer, probably because reduced metabolic rates in cold weather limit the accumulation of plasma urea (Sinsch, Seine & Sherif, 1992).

We do not know whether the two strategies adopted by male natterjacks at Woolmer during the breeding season are used at other sites. Both have apparent dangers; moving long distances every suitable calling night for several weeks risks being caught by nocturnal predators (though we have seen no evidence of such at Woolmer) and being immobilised by falling temperatures. We have found males moving away from ponds late at night almost immobilised by cold, with body temperatures <4°C, but again we have no evidence of consequent mortality. Residents, on the other hand, often hide in vegetation rather than burrows and may be at increased risk from snake attack during daytime. This might be a particular feature of the Woolmer site, where burrowing opportunities around some of the best breeding ponds are severely limited by dense vegetation and impacted substrates; residence may well be a safer and more common strategy at other natterjack localities where burrowing is easier near the breeding pools.

Natterjacks in Britain only inhabit non-sandy sites at coastal localities in Cumbria and Scottish Solway. The climate of these places is strongly influenced by the Gulf Stream and is characterised by mild winters with few severe frosts. Toads living at such sites may be under less pressure to live and hibernate in deep sandy burrows, and thus be free to occupy slightly wider ecological niches, than elsewhere in Britain. Inland natterjack populations in southern and eastern England occur on sites that experience not only severe winter frosts but sub-zero temperatures at night at any time of year between September and June (unillustrated data). This may well deter natterjacks from moving off sandy substrates in these areas.

Our observations have some implications for conservation management of natterjacks. Clearly it is important that in places without sandy substrates alternative hibernation sites (drystone walls etc) are always available. Areas surrounding breeding ponds may benefit from management designed to provide abundant burrowing facilities, such as banks of soft sand without dense or rank vegetation, thus making life safer for resident males. Finally, removal of log and litter piles may help to disadvantage competitively-superior common toads which can, in some situations, cause local extinction of natterjacks when numbers rise to the point where their tadpoles dominate the breeding ponds (e.g. Banks & Beebee, 1987*c*; Griffiths, 1991; Griffiths, Edgar & Wong, 1991). There is some evidence that in open habitats refugia availability is an important factor governing common toad population density (R. Oldham, personal communication).

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