

THE FLANDRIAN HISTORY OF RARE HERPTILES IN BRITAIN: A CONSIDERATION OF THE HYPOTHESES OF BEEBEE AND YALDEN

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INTRODUCTION

The distribution of the three rare British herptiles *Bufo calamita*, *Lacerta agilis* and *Coronella austriaca* has been described by Beebee (1978). This stimulated a debate on the history of these species in Britain (Yalden, 1980a, b; Beebee 1980) which produced two different hypotheses describing the colonisation of Britain during the Flandrian (Post Glacial) period by these animals. These were summarised by Beebee (1980) as follows:

Yalden's hypothesis

1. Invasion by the three species (among others), 10000-9000 BP (Before Present).
2. Restriction due to forest growth, 9500-500 years BP followed by expansion around developing heathlands etc.

Spellerberg/Beebee hypothesis

1. Invasion over period 7000-500 BP, restricted to a few suitable areas by prevalence of forest.
2. Expansion around coasts or with heaths both after 5000 BP.

Following this both hypotheses suggest that the rare herptile populations would have fluctuated with the changing fortunes of their heathland habitat. Beebee suggested a corridor of heathland through the west midlands to north west England, although as Yalden (1980a,b) points out there is little evidence for this. It is worth noting that Beebee (1980) makes the mistake of assuming that the amount of Royal Forest Protection was positively correlated with the amount of tree cover. This need not be the case. The Royal Forests were areas where the King had a right to keep deer: 'to the medievals a Forest was a place of deer, not a place of trees' (Rackham, 1986).

This paper is concerned with the early history of these rare herptiles in Britain using recent evidence to discriminate between the Yalden and the Spellerberg/Beebee hypotheses and to consider the possible location of glacial refugia.

DISCUSSION

The Colonisation of Britain

Recent palaeontological work by Holman (1985, 1988) has provided fossil evidence which allows one to differentiate between the two hypotheses. He has examined the herpetofauna from two sites in southern England; Ightham Fissures, Sevenoaks, Kent (Holman, 1985) and Cow Cave, Chudleigh, Devon (Holman, 1988). Holman considers both sites to be late Devensian (last glacial) or Early Flandrian in the composition of their mammal faunas. At this date the Spellerberg/Beebee hypothesis would suggest there were no rare herptiles in Britain; however remains of *B. calamita* and *C. austriaca* were found at Ightham Fissures and *B. calamita* at Cow Cave.

There was a fourth British rare herptile, *Emys orbicularis*, which is now extinct and so not considered by Beebee or Yalden. Its fossil occurrences have been reviewed by Stuart (1979). The remains of three individuals of *E. orbicularis* have been recovered from East Wretham, Norfolk. Pollen analysis of associated peats by A.R. Hall (in Stuart, 1979) suggests that they came from pollen zone VIIa (*sensu* Goodwin, 1975) of the Flandrian (this gives a pre *Ulmus* decline date of approximately 6000-7000 BP). If the distribution of *E. orbicularis* in Britain is plotted for all Pleistocene localities (not just the Flandrian) then it exhibits a distribution

similar to that of the modern rare herptiles, being found in southern England as far west as Somerset and in East Anglia (Stuart, 1979. Fig 2). This raises the possibility that the present distribution of rare herptiles in Britain may have been repeated in other interglacials. The modern ecology of *E. orbicularis* suggests that in line with the other rare herptiles it favours warm conditions (July temperatures at least 2°C warmer than currently found in southern Britain) and light soils exposed to the sun (Stuart, 1979).

Both Beebee and Yalden consider the development of heathlands and open conditions of great importance to the history of these species in Britain. The conventional view is that heaths are anthropogenic in origin mainly dating from the Neolithic and later, but some could have been created by Mesolithic activity (Dimbleby, 1984; Rackham, 1986). Recent work by Bush and Flenly (1987) has suggested that open chalk grassland may have existed at some sites throughout the Flandrian. It is not yet clear how common this may have been, but it is obviously of potential importance to the history of such species as the rare herptiles which are found in warm open habitats.

A more exact history of the rare herptiles can now be outlined. The early fossil occurrences of *B. calamita* and *C. austriaca* suggests that they colonised Britain in the Late Devensian/Early Flandrian, possibly along with *L. agilis* and *E. orbicularis*. This means that they can have crossed from continental Europe to Britain via the landbridge which existed until around 9500 BP (Yalden, 1982). This removes the problem inherent in the Spellerberg/Beebee hypothesis of how these herptiles colonised Britain after the English channel had formed. This would have posed particular problems for *B. calamita* which appears unable to survive in salinities greater than 60‰ sea water (Beebee, 1983). The native status of *Triturus vulgaris* and *Lacerta vivipara* in Ireland has also been suggested as evidence of a landbridge, in this case to mainland Britain (Wilson, 1986). The early arrival of *B. calamita* in Britain raises the interesting possibility that it may have been able to reach Ireland by such a landbridge (although the existence of this landbridge is controversial; see Devoy (1986), Yalden (1982) and references there in suggesting the Irish population may be native rather than introduced. Coleopteran evidence suggests that the climate in Britain around this time was at least as warm as to-day (Atkinson, Briffa and Coope, 1987) so that herptile distribution, at least in southern Britain, was unlikely to be limited by climate. The work of Holman (1985; 1988) suggests that in the early Flandrian at least some of the rare herptiles had a wider distribution in Britain than they do to-day.

The uncertainty surrounding the exact date of the fossil deposits at Ightham Fissures and Cow Cave allows the possibility that these faunal assemblages could have been formed during a warm stage of the Late Devensian and these species may not have survived subsequent colder events (eg. the Younger Dryas, 11000-10000 BP, Atkinson *et al* (1987)). Even if this was the case their presence in these faunas demonstrates the ease with which they could colonise Britain when conditions were suitable. This dating uncertainty and the lack of paleobotanical data from the sites prevents any conclusions being drawn about the contemporary vegetation. However if the fossils are indeed Late Devensian/Early Flandrian there could have been warm yet fairly open conditions, with forest not yet fully developed (Huntley and Birks, 1983).

The subsequent history of the rare herptiles in Britain appears to be one of decline. *E. orbicularis* became extinct sometime after 6000 BP presumably due to climatic deterioration. The small number of Flandrian fossils which have been discovered when compared to the more plentiful fossils of some previous interglacials suggests that conditions (climate?) were always marginal for this species in the British Flandrian (Stuart, 1979). For the other three species one can speculate (following Yalden) that they showed a decline between 9000-5000 BP when they were confined to relatively rare non forested sites. They probably expanded somewhat with the decline of the forest and development of extensive areas of open habitat such as heath only to decline again from perhaps the Seventeenth century onwards with the decline of heathland (Rackham, 1986).

GLACIAL REFUGIA

The evidence considered in this paper supports the early colonisation suggested by Yalden. This raises the question: colonisation from where? Where were the glacial refugia for herptiles in Europe? By analogy with the plant data from pollen analysis (eg. Huntley and Birks, 1983) one might suggest that they were in southern Europe, south of the Alps and Pyrenees. Indeed

Beebee (1983) suggests Iberia as a likely refugia site for *B. calamita*. Again fossil evidence is really required to confirm this. However, some support for these ideas can be obtained from modern distributions. If the location of European herptile species of limited distribution (arbitrarily taken as half the area of Iberia or less) is recorded, discounting island forms, using the maps of Arnold and Burton (1978), only one species is found north of the Alps/Pyrenees, while 43 were recorded south of this line. This distribution of non-insular endemics could give an indication of the locations of glacial refugia from which these species have not managed to 'escape' during the post glacial. Whereas the species which colonised Britain and northern Europe migrated from these areas as conditions improved. It is likely that the refugia were confined to southern Europe as north Africa was very arid during the last glaciation (Sutcliffe, 1985).

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