A hypothesis to explain the distribution of the great crested newt *Triturus cristatus* in the Highlands of Scotland

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ABSTRACT - The great crested newt *Triturus cristatus* is widespread in Britain but rare or absent over much of Scotland. The species is known from a small number of sites in the Scottish Highlands, but these are separated from the rest of the British population by over 80 km of unfavourable habitat, which has given rise to doubts about the origin of great crested newts in the region. The status as native or otherwise has implications for the conservation of the species in the Highlands. This paper looks at new records (since 2000) of *Triturus cristatus* in the Highlands and discusses whether they clarify the status of the species in the area. It describes how great crested newts could have colonised the region naturally. In particular, it considers the importance of climate history in shaping the current distribution of the species.

BRITAIN is a stronghold for the great crested newt *Triturus cristatus*, which has declined throughout most of Europe (Beebee & Griffiths, 2000). Because of its status within Europe it is legally protected and it has also been identified for action under Scotland's Species Action Framework. It is not common anywhere in Scotland, with populations being fragmented and relatively small (Gaywood, 1997). Indeed a recent study by Wilkinson et al. (2011) suggests that less than 1% of Scottish ponds are suitable for the species.

The great crested newt is rare north of the Highland Boundary Fault, with sites near Aviemore and Inverness (Langton & Beckett, 1995; Alexander, 1997). The 80 km gap between the most northerly Lowland site (in Fife) and the most southerly Highland site at Aviemore has not been adequately explained (Beebee & Griffiths, 2000). It is well in excess of any other disjunctions in great crested newt range in Britain and much greater than newts are known to move without assistance (e.g. Kupfer & Kneitz, 2000). This led Langton & Beckett (1995) to conclude that the great crested newt was probably not native to the Highlands. They recommended surveys near to known sites to find "source ponds" (ibid) but additional surveys in 1997 (Alexander, 1997) did not find any new sites.

The Fife site, Turflundie Wood (NO194142), has been described as the most northerly great crested newt metapopulation in the British Isles (JNCC, 2011) with four breeding ponds (McIntyre, 2003) (although the current study has identified pond clusters that may function as metapopulations in the Highlands). Most of the land between Fife and the Highland sites is mountainous and dominated by upland heath; few areas between them appear to be suitable for the species under present vegetation cover. For newts to have reached Inverness, they would either have had to negotiate the Slochd and Drumochter passes, each of which is more than 400 m above sea level, or take the much longer route along the coast, where there are no great crested newt records despite considerable survey effort (Trevor Rose, pers. comm.). The last Scotland-wide survey found no great crested newt more than 290 m above sea level, with 70% of sites being below 124 m (Alexander, 1997).

The earliest records of great crested newts in the Highlands date from 1875 when Wolley reported animals at four sites in Sutherland (Harvie-Brown & Buckley, 1887). They have never been rediscovered at any of these sites despite repeated surveys (HBRG, 2011), and these records may be erroneous (Collier in Langton & Beckett, 1995). Excluding these sites, there are records for ten ponds in the Highlands prior to 2000. The oldest are

from 'Abernethy' 1896 (Harvie Brown & Buckley, 1896) and 'Forres' 1914 (HBRG, 2010). There are records for both these areas to the present day and the habitat in Forres is typical of that used by the species elsewhere in Britain: a mosaic of mixed woodland, grassland and scrub on the relatively fertile coastal plane. Most of the ten ponds are widely separated and studies of neighbouring ponds did not produce new records (Langton & Beckett, 1995; Alexander, 1997).

The great crested newt usually exists in metapopulations and models have suggested that isolated populations have a high probability (> 95%) of extinction within 20 generations (Halley et al., 1996; Griffiths & Williams, 2000). In the absence of any known metapopulations, the status of great crested newts in the Highlands was at best dubious (Collier in Langton & Beckett, 1995; Beebee & Griffiths, 2000). Further, all but two of the sites were next to schools, houses or main roads. One site was known to be an introduction (Langton & Beckett, 1995) and it was hypothesised that the others may also have been so (Beebee & Griffiths, 2000). Until 1981 biological supply companies and pet shops offered great crested newts for sale and such animals could have been released into Highland ponds.

Since 2000, however, a further 15 great crested newt ponds have been found (HBRG, 2011), including two pond clusters. Rather than being a small isolated pocket, the Highlands holds a fifth of Scotland's recorded great crested newt ponds. The status of great crested newt populations in the Highlands, hence, merits further review, considering whether these populations are likely to have originated through introduction or natural colonisation.

Establishment of Populations by Introduction

At least two Highland sites, in Sutherland (identified after 2000, Iain Macdonald, pers. comm.) and on Skye (Langton & Beckett, 1995), are known to result from introductions. Anecdotal evidence from local people at a third site (Boleskine) suggests that a previous resident, Aleister Crowley, may have introduced the animals to the site for purposes which, given his treatment of other amphibians (Crowley, undated), are best left unknown.

Interviews with local residents and landowners undertaken as part of this study found no evidence of introductions at either of the newly discovered clusters of sites. Both of these are well away from housing, schools or main roads. Until recently, one of these sites was extremely difficult to access, due to the hazardous terrain, and so seems an unlikely site for an introduction.

Excluding the known and possible introductions detailed above, and sites without recent records, great crested newts in the Highlands occur in six groups: Strathpeffer; Black Isle; West Inverness; Culloden; Forres and Aviemore. These are all separated by likely barriers to the spread of newts: areas of land with pond densities below 1 km^{-2}, wide rivers, built up areas or areas of extensive upland heath (Fig. 1). Some of these barriers (e.g. the rivers) are natural. The others have, with the exception of that between Forres and Culloden, been in existence since at least the early 1960s. Thus, unless there were at least five separate introductions, great crested newts must either have been introduced before that time or be native to the area.

It is not impossible that there was a series of introductions, or that newts were introduced before the earliest record in 1896, but it is curious that such a pattern is not found in other densely populated areas of Scotland. Other areas of Scotland have similar summer climates to regions of southern Scandinavia where great crested newts are found, so if there had been introductions to these areas, it would seem likely that at least some populations would have survived long enough to be recorded. Great crested newts have not been recorded from apparently suitable areas of Scotland such as Ayrshire, nor between Montrose and Aberdeen, despite considerable survey effort (Trevor Rose, pers comm.).

A Possible Mechanism for Colonisation of the Highlands

Great crested newts presumably colonised Britain between 10,000 b.p. and 7,000 b.p. when rising seas flooded the southern North Sea, cutting the last land-bridge with mainland Europe. We hypothesise that great crested newts were able to colonise the Highlands some time in the last 7,000

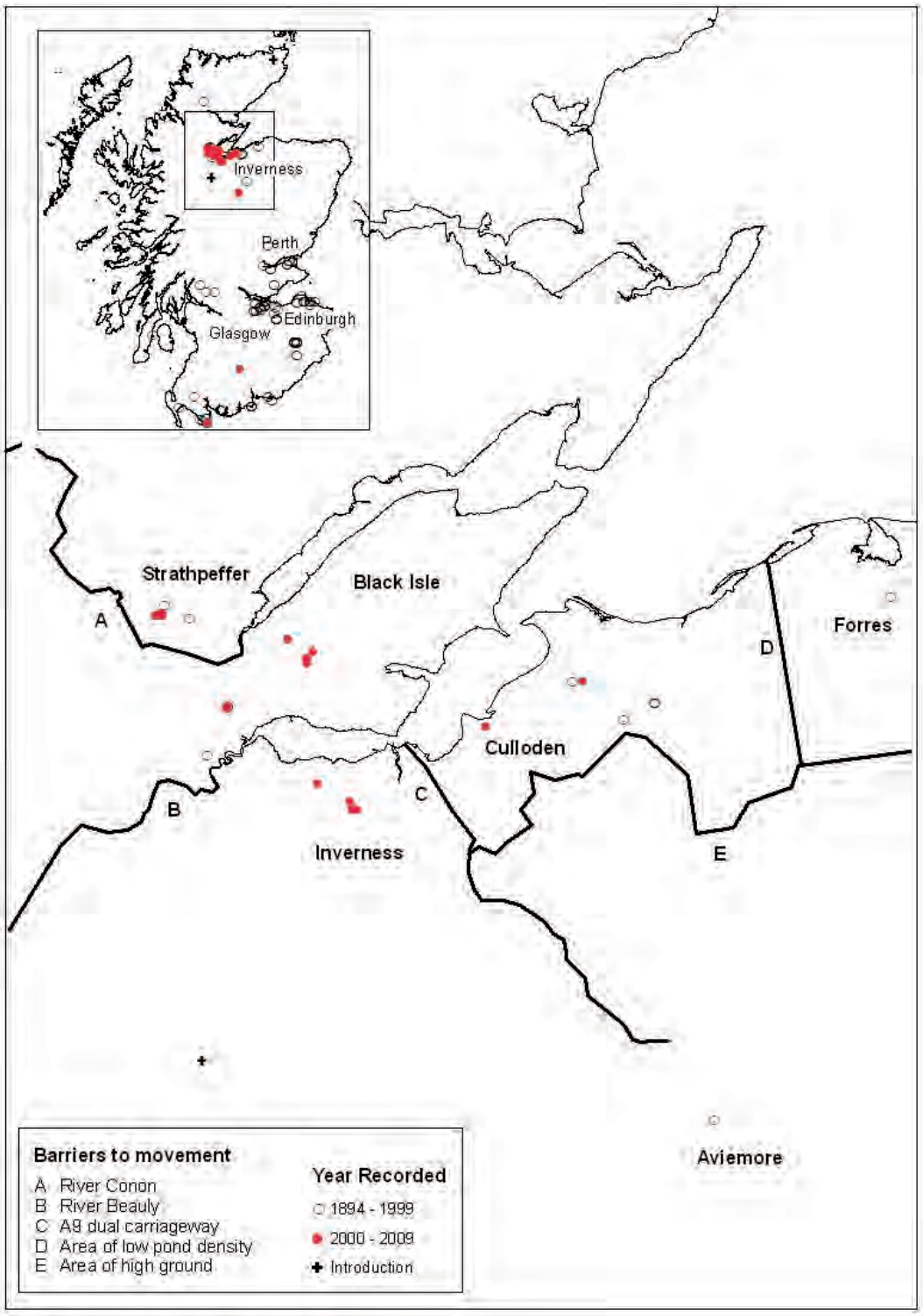

Figure 1. Records of great crested newt in the Highlands and barriers between sites (bold lines).

years, following a lag period as they spread from southeast England northwards. Pollen records suggest that broadleaved and mixed woodland, favourable habitats for the species (Latham et al., 1996), were widely distributed across the Highlands up to 3,000 b.p. (Edwards & Whittington, 2003).

Summer climate was in fact 2-3°C warmer between 5,000-7,000 b.p. than it is now. Around 3,000 to 2,500 b.p., a climatic downturn led to the replacement of woodland by upland heath and blanket bog. Very few populations of British great crested newts occur on upland heath (Swan & Oldham, 1993), which is generally considered to be an unfavourable habitat (Beebee & Griffiths, 2000). Heathland ponds tend to be relatively acidic, and the great crested newt is the least tolerant of the British newts to low pH (Griffiths & de Wijer, 1994).

The last land-bridge connected Britain to Europe via Norfolk, and was lost around 7,000 b.p. (Lambeck, 1995). If great crested newts reached the Highlands before the deterioration in habitat around 3,000 b.p., they would have had at least 4,000 years to cover around 800 km from Norfolk to Inverness, a rate of at least 0.2 km per year. This appears manageable, given that studies of the species' dispersal have shown a maximum range of between 0.5 km per year (Oldham & Humphries, 2000) and 1 km per year (Arntzen & Wallis, 1991), and that it would have taken place when there were many more ponds in the landscape and far fewer human-made barriers than at present.

Thus we believe that great crested newts could have reached the Highlands without human aid. The area around the Moray Firth has a relatively benign climate for its latitude (Thompson, 1974), and the Black Isle peninsula in particular has numerous natural springs of base-rich water as well as lochs and ponds of various sizes. However, isolated populations are at greater risk of extinction and the fact that the habitats are currently suitable for great crested newts does not mean they have always been so.

Limits on Current Distribution in the Highlands

The great crested newt has not been recorded from some areas of the Highlands that appear to offer suitable terrestrial and breeding habitats. Indeed the model proposed by Wilkinson et al. (2011), and confirmed by our own field observation, shows such suitable habitats extending 50 km to the east (Cullen) and 40 km to the north (Brora) of the edge of the observed range of the species. This may be an artefact of under-recording or, given the level of recent recording efforts (HBRG, 2011), it may reflect the impacts of past local climate change.

Climate, and particularly temperature, affect great crested newts' behaviour, reproduction and survival in various ways. In spring, adults do not migrate to breeding ponds until night-time temperatures reach 5°C (Verrell & Halliday, 1985), and their return to hibernacula occurs when temperatures approach similar levels in autumn. Gustafson et al. (2009) found water temperature to be an important factor in great crested newt distribution in Sweden. The development rates of eggs and larvae are in part related to temperature (Griffiths & de Wijer, 1994), and low temperatures are associated with morbidity of eggs.

Great crested newt distribution is likely to relate not merely to where suitable conditions occur now, but where they have occurred in the past. Isolated occurrences can be relict populations surviving beyond the main range edge. Given that climate was significantly warmer 5,000-7,000 years b.p., it is reasonable to expect that great crested newts once had a more northerly 'climate envelope'. In other words, their northern limit was once further north than it is now. The same is true for any species with thermophilic requirements that limit its northern range. For example, subfossil evidence shows that the European pond terrapin *Emys orbicularis* was present in southern Sweden 5,000-7,000 b.p. when summers were warmer but has since become extinct there (Gleed-Owen, 1999). Even in East Anglia, there is evidence that the European pond terrapin, agile frog *Rana dalmatina*, moor frog *Rana arvalis* and pool frog *Pelophylax lessonae* were once present where they are now extinct (Gleed-Owen, 2000).

The effect of a long-term climatic cooling on a species with thermophilic requirements is to make its northern range edge uneven and patchy. Locally favourable conditions allow isolated populations to survive while the main range limit shrinks

southwards in response to climate cooling. The result is a scattering of disjunct populations to the north of the main range edge. It is not uncommon for European herpetofauna to have such patchy northern limits (e.g. Gasc et al., 1997).

If we consider climatic variation specifically in relation to the great crested newt, it seems likely that long periods of poor summers would have the greatest impact. Great crested newts start to breed at the age of three to four (females) or two to three years (males) and live to approximately seven to eight years (Hagström, 1977; Dolmen, 1982), exceptionally to 17 (Miaud et al., 1993). If conditions keep breeding success very low for several years in a row, local extinction is likely to occur. For example, the period of poor summers from 1694 to 1701 that followed the eruption of Mount Hekla in 1693, would be expected to adversely affect the species.

Such prolonged periods of unfavourable climate could have led to the loss of great crested newts across most of the Highlands, restricting them to relict populations around Inverness and the Moray coast, where the climate is relatively mild for the latitude. Such range expansions and contractions may have occurred several times. Indeed, if Highland great crested newts have been isolated from the rest of the British population for up to 3,000 years, and subjected to repeated bottlenecks, there may be interesting differences between these animals and the rest of the British population. Unfortunately, subfossil evidence that might show a former wider distribution of great crested newts in Scotland is not currently known.

Conclusion

We suggest that great crested newts colonised much of Scotland, at least as far north as the Black Isle, during the climatic optimum (5,000-7,000 b.p.), but that this was followed more recently by local extinctions in higher parts of the country during poorer climatic conditions. The populations around Inverness are thus relicts of the former, wider distribution. Climate has more recently improved, certainly since the mid-twentieth century, but insufficient time has elapsed and the intervening habitat may be too fragmented, to allow full re-colonisation of otherwise suitable areas.

Given the possibility of natural colonisation and the unlikely scenario of a series of introductions necessary to have established this number of metapopulations, we suggest that the precautionary approach would favour treating great crested newts as native to the Highlands – at least until further evidence is available. Genetic studies would shed further light on the native status of the Highland great crested newts, as Arntzen et al. (2010) demonstrated the likely natural origin of a cryptogenic population of great crested newts in France. Increasing our knowledge of the distribution of the species would inform land management to protect a potentially distinctive variant of an already uncommon species.

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REFERENCES

Alexander, L. (1997). National survey for the great crested newt *Triturus cristatus*. Battleby: SNH contract report.

Arntzen, J.W. & Wallis, G.P. (1991). Restricted gene flow in a moving hybrid zone of the newts *Triturus cristatus* and *T. marmoratus* in Western France. *Evolution* **45**, 805-826.

Arntzen, J.W., Burke, T. & Jehle, R. (2010). Estimating the propagule size of a cryptogenic newt population. *Animal Conservation* **13** (supplement 1), 74-81.

Beebee, T.J.C. & Griffiths, R.A. (2000). *Amphibians and Reptiles. A Natural History of the British Herpetofauna*. London: HarperCollins.

Crowley, A. (undated). Liber LXX: the cross of a frog.

Dolmen, D. (1982). Zoogeography of *Triturus vulgaris* (L.) and *Triturus cristatus* (Laurenti) (Amphibia) in Norway with notes on their vulnerability. *Fauna Norvegica* Ser. A **3**, 12-24.

Edwards, K.J. & Whittington, G. (2003). *Vegetation change*. In: *Scotland after the Ice Age: Environment, Archaeology and History 8000 BC-AD 1000*. Edwards, K.J. & Ralston, I.B.M. (Eds.). Edinburgh: Edinburgh University Press.

Gasc, J.P., Cabela, A., Crnobrnja-Isailovic, J., Dolmen, D., Grossenbacher, K., Haffner, P., Lescure, J., Martens, H., Martínez Rica, J.P., Maurin, H., Oliveira, M.E., Sofianidou, T.S., Veith, M. & Zuiderwijk, A. (Eds.), (1997). *Atlas of Amphibians and Reptiles in Europe*. Paris: Societas Europaea Herpetologica, Muséum National d'Histoire Naturelle & Service du Patrimoine Naturel.

Gaywood, M.J. (1997). Species action plan: Great crested newt, *Triturus cristatus*. Edinburgh: SNH.

Gleed-Owen, C.P. (1999). The palaeoclimatic and biostratigraphic significance of herpetofaunal remains from the British Quaternary. In: *Late Cenozoic Environments and Hominid Evolution: A Tribute to Bill Bishop.* Andrews, P. & Banham, P. (Eds.). Pp. 201-215. London: Geological Society.

Gleed-Owen, C.P. (2000). Subfossil records of *Rana* cf. *lessonae, Rana arvalis* and *Rana* cf. *dalmatina* from Middle Saxon (c.600-950AD) deposits in eastern England; evidence for native status. *Amphibia-Reptilia* **21**, 57-65.

Griffiths, R.A. & de Wijer, P. (1994). Differential effects of pH and temperature on embryonic development in the British Newts (*Triturus*). *J. Zool. (London)* **234**, 613-622.

Griffiths, R.A. & Williams, C. (2000). Modelling population dynamics of great crested newt *(Triturus cristatus):* a population viability analysis. *Herpetol. J.* **10**, 157-163.

Gustafson, D.H., Andersen, A.S.L., Mikusinski, G. & Malmgren, J.C. (2009). Pond quality determinants of occurrence patterns of great crested newts (*Triturus cristatus*). *J. Herpetol*. **43**, 300-310.

Hagström, T. (1977). Growth studies and ageing methods for adult *Triturus vulgaris* L. and *Triturus cristatus* Laurenti (Urodela, Salamandridae). *Zoologica Scripta* **6**, 61-68.

Halley, J.M., Oldham, R.S. & Arntzen, J.W. (1996). Predicting the persistence of amphibian populations with the help of a spatial model. *J. Appl. Ecol.* **33**, 455-470

Harvie-Brown, J.E. & Buckley, T.E. (1887). *The Vertebrate Fauna of Sutherland, Caithness and West Cromarty*. Edinburgh: David Douglas.

Harvie-Brown, J.E. & Buckley, T.E. (1896). *Vertebrate Fauna of the Moray Basin II*. Edinburgh: David Douglas.

HBRG (2011). *Highland Biological Recording Group Herps dataset*. Accessed 30 May 2011.

JNCC (2011). <www.jncc.gov.uk/protected sites/sacselection/sac.asp> [Accessed: 15 February 2011].

Kupfer, A. & Kneitz, S. (2000). Population ecology of the great crested newt *(Triturus cristatus*) in an agricultural landscape: dynamics, pond fidelity and dispersal. *Herpetol. J.* **10**, 165-172.

Lambeck, K. (1995). Late Devensian and Holocene shorelines of the British Isles and North Sea from models of glacio-hydro-isostatic rebound. *J. Geol. Soc. London* **152**, 437-448.

Langton, T.E.S. & Beckett, C.L. (1995). *A preliminary review of the distribution and status of great crested newts* Triturus cristatus *records in Scotland*. Halesworth, Suffolk: HCI/SNH.

Latham, D.M., Oldham, R.S., Stevenson, M.J., Duff, R., Franklin, P. & Head, S.M. (1996). Woodland management and the conservation of the great crested newt (*Triturus cristatus*). *Aspects of Applied Biology* **44**, 451-459.

McIntyre, N. (2003). Management statement for Turflundie Wood SSSI. Battleby: SNH.

Miaud, C., Joly, P. & Castanet, J. (1993). Variation in age structures in a subdivided population of *Triturus cristatus*. *Can. J. Zool.* **71**, 1874-1879.

Oldham, R.S. & Humphries, R.N. (2000). Evaluating the success of great crested newt *(Triturus cristatus*) translocation. *Herpetol. J.* **10**, 183-190.

Swan, M.J.S. & Oldham, R.S. (1993). National amphibian survey. English Nature Research Report 38. Peterborough: English Nature.

Thompson, F. (1974). *The Highlands and Islands*. London: Hale.

Verrell, P.A. & Halliday, T.R. (1985). The population dynamics of the crested newt *Triturus cristatus* at a pond in southern England. *Holarctic Ecology* **8**, 151-156.

Wilkinson, J.W., Wright, D., Arnell, A.P. & Driver, B. (2011). Assessing population status of the great crested newt in Great Britain. NE Commissioned Report 080.