Investigating the Great Crested Newt Landscape in a pond rich environment: Developing a landscape scale management perspective

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Abstract

This thesis investigated graph theoretic analysis of connectivity and habitat availability for landscape scale management of *Triturus cristatus,* the Great Crested Newt. The ecological foundations of wider landscape management concepts and knowledge base on *T. cristatus'* habitat requirements, dispersal and migration were explored. Species presence, and aquatic and terrestrial habitat on the Cholmondeley Estate, Malpas, Cheshire, UK was mapped and land cover characterized for suitability and traversibility by *T. cristatus.* Habitat area available and accessible from ponds were identified.

Analysis and modelling of pondscape connectivity using Probability of Connectivity (PC) and related indices, was carried out using Euclidean and Cost Weighted Distance and pond clustering at ecologically relevant scales was examined. Association or correlation of presence with proximity to breeding ponds, pond cluster size, proximity and available quantity of terrestrial habitat, proximity to roads and moving water, and connectivity of breeding ponds were examined at Cost Weighted and Euclidean distances.

Connectivity, (PC index), pond count in clusters at 250 and 500m thresholds of connectivity, and proximity to core habitat (broadleaved woodland and rough grassland) using Cost Weighted distances were positively associated with breeding presence. Road proximity and density, proximity of core habitat at Euclidean distances and mean inter-pond distance were not significantly associated with breeding presence. Proximity to moving water was negatively associated with breeding presence. Resistance to movement of various land cover types has important implications for habitat availability and connectivity, and important questions are raised in terms of "rule of thumb" guidelines for estimation of connectivity between pond populations and habitat availability around breeding ponds.

Graph analysis was used to identify priority areas for maintenance of landscape level connectivity, and enhancement of habitat connectivity and availability on the local population scale, with prioritization of pond creation/protection sites against their contribution to connectivity and habitat availability, examining various scenarios.

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Chapter 1 - Biodiversity conservation and the wider landscape

The focus of nature conservation in the UK and Europe has historically been the designation of discrete sites. Increasingly, the past 30 years have seen shifts in the biodiversity conservation paradigm away from a tight focus on discrete site or species based conservation, towards conservation at the wider landscape scale. This has resulted from a growing realisation of the inherent limitations of site based conservation (Adams *et al.* 1994, Bromley 1997, Lawton *et al.* 2010). Discrete reserves, by their nature, are vulnerable to degradation due to pollution, drainage modification by external actors, invasion by exotic or undesirable competitive species, catastrophic disturbance and development pressures that impinge from the surrounding landscape, from which their often relatively small isolated nature may preclude effective long term recovery.

Management of such widespread and relatively small sites is generally fraught with difficulties and is complex and expensive in time, money and effort, but has in the past been a relatively straightforward proposition, compared with the growing problems inherent in attempting this against the background of complex changes at landscape, ecosystem and global climatic scales (Gaston *et al.* 2006, Tyldesley 2009). An inevitable consequence of species or habitat based approaches on discrete sites in the landscapes of the developed world, especially in the context of global climate change, is reserves becoming disconnected, isolated from (yet, paradoxically, vulnerable to) natural periodic or stochastic disturbance.

> *"Despite the important contribution designated sites have made, England's wildlife habitats have become increasing fragmented and isolated, leading to declines in the provision of some ecosystem services, and losses to species populations."* (Lawton *et al.* 2010 p. vi)

Such sites become progressively hemmed in by a landscape mosaic of fragmented and more or less degraded natural and semi-natural environments, intensive "factory farm" agriculture and spreading urban development, leaving their target species or biotopes vulnerable to the migration of its/their climatic envelope (Piper *et al.* 2006). Restricted in their ability to migrate, individuals and local populations face isolation in biotope patches or reserves being transformed around them by changes in the prevailing conditions, and population distributions adjustment to shifting climatic envelopes are constrained. A realization of the need to address these problems through management of connectivity and habitat availability in the wider landscape is finding its way into theory and policy (Lawton *et al.* 2010, DCLG 2012).

The single species or designated site approach has broadened to accommodate the integrity and connectivity of the wider landscape and species assemblages, with attention to single species frequently focused on so called umbrella species, with habitat requirements and conservation needs often seen as encompassing and supporting those of a suite of additional species (see for example Diamond 1975 and 1981, Adams 1996, Simberloff 1998, Poiani *et al.* 2000). Views of biodiversity conservation (and to an extent policy – Council of Europe 1992a and 1992b, DEFRA 2002, The Wildlife Trusts 2009, Tyldesley 2009, Lawton *et al.* 2010, DCLG 2012) have expanded to recognize the necessity for conservation activity at all levels - genes, populations, species, communities, ecosystems and landscapes, with each level of biological organization displaying its own level of complexity of composition and structure, each relating to the others through dynamic and complex patterns and processes, at multiple and nested scales.

Restoration, maintenance and enhancement of the connectedness, connectivity and permeability of the landscape has become a focus for attention. Landscape connectivity has been defined as (bold type for my emphasis, not in original):

> *"The degree to which the landscape* **facilitates** *or* **impedes** *movement among resource patches"* (Taylor *et al.* 1993)

or

> *"...the functional relationship between habitat patches, owing to the* **spatial contagion of habitat and the movement responses of organisms to landscape structure"** (With *et al.* 1997),

or again, as the landscape function which expresses the degree to which sub-populations are **interconnected as a functioning demographic unit** (Baudry and Merriam 1988). This concept is similar, but not synonymous with connectedness (Fry 1994), referring to the structural links between landscape elements (see Tischendorf and Fahrig 2000a and 2000b).

Habitat fragmentation – the shredding of once continuous biotopes and habitats into smaller parcels, separated by distances of potentially hostile "matrix", has numerous effects – many beyond the scope of this study such as on carbon storage, community structures and more (Laurence 2008). Indeed, the term 'habitat fragmentation' is often used inconsistently and too broadly, applied to many patterns and processes that accompany landscape change. As Lindenmayer and Fisher (2007) point out, this has in many respects made it a panchreston - an explanation or theory used so broadly as to purge it of meaning and confuse discussion and debate. In this study the term should be understood in terms of effects on:

> "*Species perspective of a modified landscape*"

> "*Perception of* [*sensu* ability to interact effectively with] *a landscape by a given (*non-human*) species; important features include sources of food and shelter, and appropriate climatic conditions*",

and the breaking of

> "*Functional linkages between habitat patches for a given species, a species-specific entity*" *and* "*Functional separation of habitat patches for a given species: a species-specific entity and the opposite of habitat connectivity*"
> (Lindenmayer and Fisher (2007), table 1, p138).

The development of ecological network approaches has been a significant response to this shift in paradigm in an effort to develop more holistic, integrated, spatially coherent and sustainable conservation management practices at landscape and regional scales. The ecological network approach (applicable at any scale from global to local) seeks to maintain and support populations, metapopulations and communities through management at landscape scales, supporting special reserves, designated sites or other statutorily un-designated areas of high conservation capital over the long term, through maintaining their functional and structural relationships with the wider landscape and each other. Corridors and stepping stone patches constitute the key elements of the ecological network from the point of view of connectivity. They may serve multiple functions, but fundamental to their role within the network is their linking function, supporting dispersal and migration, providing movement corridors or conduits. They may also constitute habitat patches in their own right. Buffer zones, minimizing negative impacts on the periphery of core, corridor or stepping-stone elements may take a range of forms; physical barriers (such as vegetated strips alongside watercourses or still water bodies, to buffer against excessive run off or chemical pollutants and sediments entering the water body), or may simply constitute an area free of certain land uses (development, intensive agriculture and application of agri-chemicals, or recreational activities (see for example Jongman and Pungetti 2004).

The relatively recent introduction of the ecological network concept results in direct empirical evidence for the efficacy of ecological networks as a whole, especially at larger scales and over the longer term, being in relatively short supply. The concentration of this thesis, however, is at the fine scale, at a resolution where core areas constitute key ponds and pond clusters, with their adjacent terrestrial habitat and corridors are vegetated strips on field margins and along hedge-lines. At this level, theoretical, empirical and experimental evidence for the function of the various network elements is now substantial and has developed rapidly over recent years. Ecological network thinking rests on a substantial body of ecological theory. Without flows of individuals and genes between habitat patches and populations or groups of interacting populations (metapopulations), apparently stable, vital populations may become extinct quite rapidly. The "corridor" proposition was, certainly in the early stages of the development of the network concept, accepted more intuitively than on the basis of empirical evidence, sceptics frequently pointing in the literature to a shortage of high quality studies relating to corridor function, their physical properties, utilisation, and identification of species to one extent or another reliant on corridors for persistence (Simberloff and Cox 1987, Simberloff *et al.* 1992). In direct response, from the 1990's to date, a far larger body of literature, and more compelling evidence in the form of species and landscape ecological studies and mathematical and GIS based spatial modelling has been developed, which substantially underpins the theoretical basis for the ecological network concept.

This thesis sets out to contribute to the "tool kit" available for delivery of Favourable Conservation Status[1] (FCS, Jones 2002, Halahan and May 2003) for the Great Crested Newt, *Triturus cristatus*. *T. cristatus* primarily occurs in the UK in lowland pastoral environments (Swan and Oldham 1993), although the species has a higher profile due to development conflicts and planning requirements of protected species legislation in urban or urban-fringe environments. This has been notably the case in Cheshire, where *T. cristatus* records are particularly widespread due to the extensive pastoral landscape of small fields, hedgerows and scattered woodland with high density of ponds – certainly one of the highest, and possibly the highest such density, in England and Wales. Populations of *T. cristatus,* though widespread, generally persist at low levels of abundance (dealt with in Chapter 4). This has made the species vulnerable to not just local stochastic, developmental, and deterministic extinction threats (the latter largely aquatic habitat loss to hydroseral succession and farm management changes) - but also to a particularly "bad press".

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[1] Conservation status for a species is defined in Article 1(i) [Council of Europe 1992, 92/43/EEC] as follows:

Conservation status for a species means the sum of the influences acting on the species concerned that may affect the long-term distribution and abundance of its populations within the territory referred to in Article 2 [Council of Europe 1992, 92/43/EEC]

The conservation status of species is considered favourable when:

a) Population dynamics data on the species concerned indicate that it is maintaining itself on a long-term basis as a viable component of its natural habitats, and
b) The natural range of the species is neither being reduced for the foreseeable future, and
c) There is, and will probably continue to be, a sufficiently large habitat to maintain its populations on a long-term basis.

(Council of Europe 1992, 92/43/EEC)

Substantial media attention has focused on the high financial costs (and could well have raised the issue of the high environmental cost, when production, transport and disposal of large amounts of plastic fencing is taken into account) of mitigation, as compared to small (sometimes very small) numbers of individuals "saved" from development (see for example Sunday Mirror 2006, Bell 2006, Salkeld 2008, Stote 2008, Wilkes 2008, Knowles 2009). Such "exposés" are essentially media reflections of industrial and political lobbying against conservation legislation perceived as onerous and deleterious to the interests of economic and infrastructure development. Such articles frequently turn logic on its head, complaining of the small numbers of animals involved, as if suggesting that endangered or protected species conservation measures would be more cost effective the more abundant the species in question. This in part arises from the nature of the legislation itself, which may arguably be described more as "animal welfare" oriented than to species conservation, focusing on very local populations, individuals and habitat patches, rather than FCS at landscape and regional scales. These factors have significantly coloured policy discussion in relation to the species including, worryingly, raising questions over the species' listing under the Habitats Directive (Council of Europe 1992a, incorporated into UK law as The Conservation (Natural Habitats, andc.) Regulations, 1994).

Continued attrition of breeding pond numbers and local populations is a significant threat to such a thinly distributed and pond dependent species. This thesis proceeds in part, however, from the proposition that concentration on animal welfare aspects of species protection and mitigation of individual localised impacts such as development projects contributes to delivery of FCS only to a limited extent relative to the financial and environmental costs of implementation. Planning protection for critical populations ('critical' understood as, for example, significance of size or location of a breeding site) is clearly important. This thesis, however, advances from the position that far more important for the long term persistence of species throughout their range in the UK than persistence at individual sites, is the maintenance of the species viability at landscape scales. This is thrown into particular relief when the level of success of many mitigation projects and translocations is considered (see for example Edgar *et al.* 2005, and Lewis *et al.* 2007). It could reasonably be proposed for example, that the expenditure of many tens of thousands of pounds per animal on exclusion fencing, site monitoring, capture and translocation with dubious success, of animals at the A 5117 road works in Cheshire (the subject of an "exposé" (Bell 2006) referenced earlier), could far more profitably have been spent on widespread pond and terrestrial habitat creation to reinforce surrounding populations on farmland (or elsewhere through Biodiversity Offsetting initiatives for example), potentially generating income (through long term agri-environment scheme (AES) supported management) for farm economies into the bargain.

To address these issues, this thesis focuses on:

- the theory underpinning the landscape scale ecological network approach to habitat connectivity enhancement and maintenance,
- the autecological knowledge base available to inform this approach in relation to a target species: *Triturus cristatus*, the Great Crested Newt,
- an examination of spatial targeting of conservation effort to this end, through the application of graph theory (using the software package CONEFOR Sensinode v2.5.8 beta, Saura and Torne 2009, Saura *et al.* 2011).

The aims and objectives of the thesis are therefore;

Objective 1: To develop a landscape scale perspective on conservation management for *Triturus cristatus*, through:

> **Aim 1:** an examination of the basis in ecology theory for the ecological network/wider landscape approach
>
> **Aim 2:** a synthesis of long standing and current research relating to the species' habitat requirements and interactions with landscape, and
>
> **Aim 3:** an examination of the species distribution and landscape associations with its pond occupation and particularly breeding presence, within a landscape typical of its core range in the UK

Objective 2: To examine use of graph theoretic techniques for focusing on key loci of connectivity and habitat availability, through

Aim 4: identification of key existing sites for protection of habitat connectivity and habitat availability arising from their position within the landscape

Aim 5: identification and selection of key sites for habitat creation or restoration arising from their position within the landscape

1.1 Structure

This chapter has briefly described the shift in the biodiversity conservation paradigm away from discrete site based conservation, to the "wider landscape" approach. It outlined the nature of this paradigm shift in relation to the growing understanding of the landscape scale impacts of habitat fragmentation, erosion and degradation and the consequent fragility and exposure of discrete sites to landscape scale ecological, and local and global anthropogenic processes. The gradual acceptance and embedding of this new approach into policy frameworks and conservation practice has as a consequence the need to develop techniques for its implementation. Having outlined its aims and objectives, this thesis now goes on to examine the implications of landscape scale management as applied to a focal species capable of acting as an umbrella species for a suite of other species with similar habitat requirements: *Triturus cristatus*, the Great Crested Newt.

Chapter 2 - Conservation in the Wider Landscape examines the literature on the fundamental basis in ecological theory for the key concepts of ecological networks: core areas, linked by corridors and stepping stone patches. It examines the contribution of key concepts and paradigms - Island Biogeography and Metapopulation theory - to theoretical developments as they relate to practical implementation. Structural elements of ecological networks are examined and the theoretical and empirical backing for the concept and implementation of wildlife corridors and stepping-stone patches, the targeting of which is central to the thesis, are explored. The implications of landscape scale management and ecological network implementation for the attitudes of land managers and stakeholders and the norms and complex interrelationship of ends and means involved in creation or restoration of habitats and the extension or re-establishment of species distributions and presence is explored.

Chapter 3, "The Great Crested Newt (*Triturus cristatus*) and the wider countryside" examines the autecological knowledge base relating to the target species, *T. cristatus,* the Great Crested or Warty Newt, and the terrestrial and aquatic habitat requirements of the species, which must inform any management planning for its conservation. It examines the importance of pond density and dispersion in relation to *T. cristatus* distribution and looks at *T. cristatus*' dispersal and migration capacities, and landscape scale barriers to the animal's movement and associated mortality factors. Population and metapopulation persistence, decline and fluctuation at landscape scales is examined. Analysis, quantification and modelling of landscape connectivity using graph theory and Least Cost or Cost Weighted Distance approaches are explored and the CONEFOR Sensinode landscape graph analysis package (Saura and Rubio 2010) used in this study is introduced. This section also examines the use of graph theoretic indices of connectivity in the landscape ecological context, looking at applications and development of the technique in the literature. It examines in detail some of the more recently developed indices and techniques employed in this thesis, specifically the Probability of Connectivity Index, and related indices of habitat availability (Pascual-Hortal, and Saura 2006, Saura and Rubio 2010, Saura *et al.* 2011, Schick and Lindley, 2007).

Chapter 4 deals with the criteria for study site selection and candidates for selection. A description of the Cholmondeley Estate, Malpas, Cheshire, which was ultimately selected, is provided, giving a detailed description of the study area location, extent, superficial geology and topography, drainage and transport infra-structure.

Chapter 5 deals with terrestrial and aquatic habitat survey methodologies, data processing and techniques for analysis and classification of terrestrial and aquatic habitat are explained. The Habitat Suitability Index (Oldham *et al.* 2000, ARGUK 2010), used in this study as a measure of habitat quality in the weighting of habitat patches during connectivity and habitat availability analysis is explained.

Chapter 6, Results, deals with the findings of terrestrial and aquatic habitat survey and analysis of these. It describes the composition of the Cholmondeley landscape in terms of distribution of aquatic and terrestrial habitat, quantifying the latter in terms of totals within the study area and quantity accessible from ponds. It further characterizes land cover types in terms of habitat suitability and traversibility for *T. cristatus.* Salient features of the Cholmondeley pondscape are outlined and discussed, in terms of distribution, morphology, density and clustering. The clustering of ponds at ecologically relevant spatial scales (130m, 250m and 500m inter-pond distances considered relevant in migration and dispersal) is examined from the perspective of both Euclidean ("as the crow flies") and effective, or Cost Weighted ("as the newt crawls") distances, and the implications of this discussed. The distribution of *T. cristatus* (mainly confirmed breeding presence), is related to rates of occurrence as indicated by previous surveys at Cholmondeley, and across Cheshire. The effects of shading and seral succession are briefly discussed in terms of their effect on species presence. Various hypotheses are tested to examine levels of association and correlation of occurrence to factors in the surrounding landscape and pondscape, such as proximity to *T. cristatus* breeding ponds, size of pond clusters at relevant spatial scales, the characteristics, proximity and quantity of terrestrial habitat, proximity to roads and moving water bodies, and levels of connectivity of breeding ponds (at Cost Weighted, and Euclidean distances).

Chapter 7 "Application of graph analysis to conservation planning in the actual landscape of Cholmondeley" examines the application of graph theoretic analysis and modelling to landscape scale management for *T. cristatus.* It examines the use of graph theoretic techniques (using the CONEFOR Sensinode 2.5.8 beta software package) to identify priority areas of the Cholmondeley pondscape for management aimed at both maintenance of existing key areas for pondscape connectivity at whole landscape level, and for management aimed at enhancement and improvement of habitat availability. In terms of the latter, it focuses on a priority area, working at a multi-farm level, at the pond/pond cluster population scale. It examines the use of indices of connectivity and habitat availability generated in CS2.5.8 in the prioritization of potential pond creation sites for their contribution to connectivity and habitat availability, examining various scenarios. The first scenario considers prioritization based on multiple criteria, with the aim of maximizing conservation benefits, while minimizing effort and cost. The second considers prioritization for habitat availability, and the third at prioritization based on benefits to improvement and maintenance of existing pondscape connectivity.

Chapter 8, Conclusions and discussion, identifies key findings and reservations regarding their validity and applicability, assesses the level of success achieved by the thesis in meeting its aims and objectives, and identifies key contributions and questions raised by the research outcomes, proposing areas for subsequent research.

Numerous studies have been published (Cook 1985 and 1986, Franklin 1993, Hayward *et al* 2000, Jehle 2000, Jehle and Arntzen 2000, Kupfer and Kneitz 2000, Malmgren 2002) of *T. cristatus* relationship to landscape features and pondscape, but at much smaller scales. This study is unique, to the author's knowledge, in being the only one to examine a complete landscape at this scale and is also to tie together examination of landscape scale features of *T. cristatus* presence and breeding with examination of the potential for spatially targeted and prioritised management at the same spatial resolution. "Conclusions and Discussion" draws together the various strands of the examination, appraising its conclusions and critically reflecting upon its strengths and weaknesses. Future plans for research in this area (both figuratively and geographically) are summarised and briefly discussed and the value of its findings for future practical conservation application evaluated.

Chapter 2 – Ecological Foundations.

2.1 Niches, patches, "islands" and the landscape matrix

Chapter 2 addresses the first aim of this thesis: to examine the basis in ecology theory for the ecological network/wider landscape approach. That species perceive the environment as composed of parcels, or patches, satisfying their needs to some degree or not at all, and that specialist species may be confined to one small part of a biotope patch, while generalists may find several biotope patches comprise their habitat, are long established ecological concepts (e.g. Grinnell 1904, MacArthur 1972). Individual habitat patches may be contiguous, be set in a matrix of unsuitable habitat, or form part of a landscape mosaic of patches meeting different habitat requirements or constituting non-habitat for the target species (Wiens 1995), which may change in spatial arrangement over time with seasonality, disturbance and succession. In nature, "boundaries" between habitat types are gradational, if sometimes abrupt at human scales of perception (Bunce and Jongman, 1993, Bunnel 1999). McIntyre and Barrett (1992) proposed that a fragmented landscape model, of patches or remnants isolated within hostile matrix, is an often inappropriate approximation to reality. They proposed a landscape model they characterised as a variegated shifting mosaic of varying suitability (see also McIntyre and Hobbs 1999, Debinski *et al.* 2001, and Vandermeer *et al.* 2010). This landscape mosaic model offers a closer approximation to reality than the simpler patch-matrix model, which assumes homogeneity within patches and well-defined patch/matrix boundaries. It may, however, be problematic to model and represent.

A species' perception of habitat homogeneity is highly scale sensitive. A biotope patch perceived by one as homogenous habitat, might to another, with different habitat requirements and interacting with the environment at different spatial and temporal scales, be perceived as patchy and fragmented. Habitat fragmentation shreds once continuous habitats and, to access sufficient habitat area or particular habitat types (for foraging, shelter or breeding), organisms must embark upon potentially hazardous journeys through new and possibly hostile environments, overcoming barriers (physical or behavioural) to dispersal and migration. Isolation and habitat fragmentation have been long standing areas of concentration for ecological research, seen as undermining species persistence in several ways (Wilcove *et al.* 1998, Hilty *et al.* 2006):

1. Reducing the immigration rate and so potential for "rescue" of a declining population
2. Reducing potential for colonisation of new habitat patches (Terborgh 1975, Simberloff and Cox 1987)
3. Reducing potential for re-colonisation of habitat patches following local extinction
4. Inhibiting gene flow, producing problems of inbreeding and genetic drift (but see also Crowley 1981, below)
5. Preventing utilisation of sufficient area of required habitat
6. Hindering or preventing seasonal migration
7. Inhibiting re-alignment of species distributions, as the effects of climate change alter habitat suitability, on regional and global scales (Hill *et al.* 1994, Walker and Steffen 1997, Piper *et al.* 2006)

The underlying assumption is that a species' response to land cover may be such that it constitutes a physical or behavioural barrier to its movement, migration or dispersal. Identification of the nature and consequences of such barriers for particularly species, and population dynamics in general, has been central to ecological and especially Landscape Ecological study for decades. Studies are numerous relating to bird, fish, insect, mammal and arboreal marsupial species, in a range of environments, e.g. Keitt *et al.* (1997), Cassady St.Clair *et al.* (1998), Brooker *et al.* (1999), Laurance and Laurance (1999), Bolger *et al.* (2001), Spens *et al.* (2007) and Ahlroth *et al.* (2010). These and other studies relate empirical data on critical gap sizes, preparedness to cross matrix, to predictive models of dispersal behaviour, landscape connectivity, and the potential for genetic variation across landscapes, throwing light on dispersal and migration capacities of species in particular environments.

Island biogeography provided the dominant paradigm in conservation biology until the late 1980s, dealing with patches of habitat on fairly large scales. A patch of habitat (or "island") will, according to biogeographical theory, hold more species if it is near to a source of potential colonisers (other "island" patches or "the mainland"), and if it is large, than if it is small and/or distant from sources of colonisers. MacArthur and Wilson (1963, 1967) described an equilibrium theory of island biogeography to provide explanation for two empirically observed trends:

- First, the relationship between the size of the area studied and the number of species to be found in it - the species area relationship (Preston 1962; reviewed by McGuiness 1984, see also Boecklen and Gotelli 1984, Oertli *et al.* 2002).
- Second, that "island" faunas become progressively "impoverished" (i.e. have fewer species than the equivalent area of "mainland") with distance from the nearest "landmass" (Preston 1962, Moore 1962).

Before MacArthur and Wilson's work (1963, 1967), one explanation for relative species poverty of remote patches was lack of time for colonisation, implying that given enough time, even remote patches may approach the species richness and diversity of near ones. MacArthur and Wilson modified the theory by considering extinction of established species. The number of species becoming extinct on an "island" should increase with species richness. Three of MacArthur and Wilson's detailed predictions are relevant to the discussion in this thesis:

- Chaotic fluctuation around equilibrium;
- Species turnover as some become extinct and are replaced by immigration;
- Patches not at equilibrium (due to environmental change or disturbance) "relax" over time to a new equilibrium (Diamond 1972).

Brown and Kodric-Brown (1977) developed these concepts still further, describing a "rescue" effect, where extinction is less likely in nearer than more distant patches, due to recurrent immigration boosting species' populations and gene pools, decreasing the effect of isolation on species richness. A special case was also proposed by Brown (1971) and developed by Diamond (1974) by considering species incapable of crossing gaps - no new species of this type arrive, creating a dis-equilibrium and spiral to extinction of such species. This model predicts that species richness in a patch of habitat reflects the balance of two processes - extinction and colonization; that equilibrium occurs because, when fewer species than the equilibrium number are present, immigration to fill the vacant niche should compensate for extinctions and *vice versa*. Extinctions are fewer on an equivalent "mainland" patch because it is not so isolated from the surrounding habitat; its immigration rates are higher and some of its resident species populations are maintained (or rescued) by immigration from the surrounding habitat (Preston 1962). MacArthur and Wilson extended the theory further, introducing the idea of "stepping stone patches" enhancing immigration rates of species from a source to a target patch beyond the stepping stone (MacArthur and Wilson 1967).

It is no great intuitive leap to conclude from this theoretical basis, that were "corridors" suitable for an organism to move through to connect suitable patches, otherwise inaccessible patches may become available. The lower the immigration rate in a patch, the greater the potential for selective loss of sensitive species over time (Diamond and May 1976), so corridors as conduits for migration and dispersal, and stepping stones as intermediate staging posts enabling dispersal or migration for species capable of some movement in the matrix, by putatively increasing the potential for migration, may allow sensitive species to re-colonise (Terborgh 1975). Simberloff and Cox (1987) pointed out that the same effect should lower the extinction rate, through the operation of the rescue effect, or the replenishment of depleted populations, both in terms of individuals and gene flow, from neighbouring patches. The intuitive attraction of corridors and stepping stones for conservation practitioners is obvious. In some cases, there may be need for successful reproduction within and along the length of the corridor (for example in plants, see Tikka *et al.* 2001, but also other taxa, Burel 1989; Bennett 1990, Haddad *et al.* 2003). In other cases the corridor may be seen as facilitating movement only, with reproduction confined to the habitat patches. Caution is needed, however, as evidence suggests that functional connectivity between structurally connected populations will not always be achieved by the construction or retention of a corridor and that functional connectivity cannot be inferred solely from the presence of individuals, or breeding populations, within corridors (Horskins *et al.* 2006).

2.2 Metapopulation theory.

Metapopulation theory was developed first to describe populations of invertebrates in small-scale mosaic habitats (Hanski 1989, and 1998a). The basic proposition is that the numbers of any given species may fluctuate greatly in small patches of habitat to the extent of becoming locally extinct in some, but that the species will persist in an archipelagic collection of island patches because either re-colonisation takes place from those where extinction has not taken place, or populations are supplemented by immigration and extinction is avoided. The genetic viability of metapopulations is maintained when there is sufficient connectivity between sub populations to allow gene flow, yet sufficient disconnectedness and asynchrony of population fluctuations to prevent the sub-populations effectively becoming unified, which is necessary, if genetic drift and possibly the synchronisation of stochastic extinction events, are to be avoided.

The intuitive appeal of corridors is supported, and the logic of corridor efficacy and close spacing of habitat patches is derived from these theories, proposing that following a local extinction, re-colonisation is likely to be quicker across a small gap or along a corridor, than in the absence of corridors or across larger gaps. Alternatively, these same structural features will facilitate supplementation of a sub-population by immigration, avoiding local extinction in the first place, allowing species persistence in the patch system as a whole, even where extinction may be inevitable in individual patches. It is the movement of individuals and genes between sub-populations and patches that are essential to metapopulation theory; corridors and stepping-stones potentially offer a means through which the process may be manifested. It is necessary to make an important distinction here, between a true metapopulation and a previously continuous population which has become fragmented through environmental change or degradation. These may appear superficially similar - both can have the patch-matrix model applied to them, but there are fundamental ecological differences between these two states which must be accounted for. Patches in a fragmented system constitute remnants (Forman and Godron 1986) of previously continuous habitat isolated from each other by a non-habitat matrix; species that have evolved relatively continuous populations in relatively homogenous habitat may not have the ability to traverse the matrix between habitat patches if previously homogenous habitat becomes fragmented, say by human activity. A *bona fide* metapopulation patch, however, may be considered an environmental patch, a result of natural landscape heterogeneity. Areas of natural non-habitat through which a species is adapted for movement in search of suitable patches, may not present as much of a barrier. If a fragmented population is to act as a metapopulation, then the individual within patch fragments of the population must be functional as demes, within minimum habitat area thresholds and capable of exchange of individuals and genes between patches. Fragmentation and loss of habitat is associated with population reduction and habitat degradation, which may inhibit or prevent this if populations are reduced to sub-minimum viable population numbers and fall below minimum habitat area thresholds.

The rate of colonisation and establishment in new patches, and/or the re-colonisation of old patches after stochastic local extinction events, must equal or exceed that of local extinction if a metapopulation is to persist. Early and simple metapopulation models assumed that all patches are equal sources of colonisers, i.e. that there is no distance effect and habitat patches are homogenous (see Hanski and Gilpin 1991). However, organisms occupying a series of habitat patches do not in reality occupy homogenous habitat, but a collection of some more and some less suitable patches, the less suitable requiring replenishment from the more suitable for persistence of species within them, necessarily overcoming or bypassing behavioural or physical constraints upon migration and dispersal. In other words, sub-populations of a metapopulation are likely to be as much or more affected by the type and proximity of other patches as by the resources and other conditions in the patch or patches where they are found. Pulliam (1988) defined patches operating as net exporters of individuals as source, and those as net importers of individuals as sink, patches. Therefore, direct and detailed knowledge of the population processes working in conservation areas may be necessary to avoid or mitigate the effects of the attempted conservation of sinks without their sources, to the possible detriment of the metapopulation as a whole. These processes may not be fixed, however, but shifting and spatially unstable (Vandermeer *et al.* 2010), and tracking them should be part of the long term, on-going monitoring element of conservation management planning.

Delibes *et al.* (2001a and 2001b) proposed that sinks can attract dispersing animals if high mortality or breeding failure is difficult for them to detect and suggested that this may not be an uncommon result if individuals lack cues associated with reduced fitness inside sinks, and consequently they select their habitat inappropriately (see also Foppen *et al.* 2010). In this "attractive sink" scenario, small changes in the proportion of sink habitat may have disproportionate effects on the population's persistence. This does not mean, however, that sink populations do not contribute to metapopulation survival. Even if the population cannot fully sustain itself, it is a member of the patch community, contributing to its biodiversity, affecting other populations within the community and forming part of the metapopulation's genetic resource. Without immigration of course a sink population must eventually become extinct; its persistence may, however, be a common phenomenon in natural situations and contribute to the persistence of the metapopulation. Foppen *et al.*'s (2010) study of Reed Warbler (*Acrocephalus scirpaceus*) in the Netherlands demonstrated that sinks may under certain conditions support the stability of source patches and metapopulations, at least prolonging their survival in decline, thereby perhaps promoting the species persistence in the landscape.

Furthermore, local populations may fluctuate between source and sink status with variation in local environmental conditions. Dynamically this fluctuation represents an intermediate phase between persistence and extinction – from which rescue through immigration, and restoration to steady source status can potentially take place (Vandermeer *et al.* 2010). This may require fewer individuals than the colonisation of a new patch (Sjögren 1991), or the re-colonisation of a patch after local extinction. However, the potential for the latter is questioned by Thomas (1994) who argued that causes of stochastic extinction allowing for available habitat for potential re-colonisation later are uncommon (less than convincingly it must be said, since a number of ephemeral or transitory causes of local extinction such as temporary disturbance, point pollution events, or pathogens may readily be envisaged, particularly in dynamic, self-contained biotopes such as ponds). Numbers required for colonisation of new patches may be an important consideration, depending on species characteristics, for example in species requiring external fertilisation of eggs. Under some circumstances, the most efficient use of individuals (viewed as a species resource) could be in supporting sink populations, as opposed to re-colonisation of vacant patches (Sjögren 1991).

Hanski (e.g. 2001) has stressed that distance may have a major effect in metapopulations - short distances between patches increasing the re-colonisation rate, but also increasing probability that fluctuations in all patches may be correlated, even synchronised. For example, Telfer *et al.* (2001) examined the spatial distribution of water vole populations in four consecutive years, investigating regional population processes (extinction, re-colonisation and migration) influence on distribution and persistence, and how these processes were influenced by spatial variation in habitat quality. Their findings showed re-colonisation rates were influenced by isolation and habitat quality, and indicated that dispersing voles actively selected habitat on the basis of its quality and proximity. Others, such as Commins and Noble (1985) and Debinski *et al.* (2001) have stressed "patch dynamics", with fluctuations in habitat patches and the species and populations occupying them being correlated in a complex interplay between patch scale, movement patterns and habitat sampling. Vandermeer and Carvajal (2001) through use of a variety of modelling techniques showed that matrix quality can be extremely important in determining metapopulation dynamics. A higher-quality matrix may generally act as a buffer against extinction; however, in some situations an increase in matrix quality could generate chaotic subpopulation dynamics, where stability had been the rule in a lower-quality matrix.

In other words, by forcing metapopulation dynamics on a fragmented collection of stable subpopulations, the probability of simultaneous extinction of all subpopulations may actually be increased. Thus, it cannot be automatically assumed that increasing matrix quality or patch connectivity through corridor construction will lower the probability of global extinction of a population. Pickett and Thompson (1978) developed theory accounting for the significance of area, related to Webb's (1993) distinction between biotope and habitat patches. Each biotope patch may consist of several habitat patches, within each of which a species may become extinct and then re-colonise from adjacent patches. Study of these internal dynamics should establish the "minimum dynamic area", or the area of biotope patch necessary for retention of sufficient habitat patches to prevent extinction. These habitat patches may reflect natural heterogeneity, or be the result of rotationally managed or disturbed habitats. Corridors, by extending the area of a biotope patch, could assist in providing this minimum area, but too high a level of connectivity within a metapopulation could be disadvantageous and in practice, this serves to reinforce the need for regular monitoring and observation of target populations and biotopes.

Maintenance of levels of connectivity, without elevating these levels such that complete synchrony is achieved, may be crucial to the stability and persistence of a population (Crowley 1981). In other words, metapopulation theory suggests that connectivity should be sufficient to dampen stochastic population fluctuations in habitat patches (so that local extinction and dramatic genetic effects are rare), but not so extensive as to synchronise population fluctuations within the habitat patch system. There is evidence from modelling studies that the relationship here is far from simple. Orrock (2005) found in simulation that connecting a stable but isolated population to an unstable one requiring periodic recovery (sink patch) could be beneficial or problematic, depending on disturbance levels. Where disturbance levels were low, fixation of beneficial alleles and loss of harmful alleles was increased, however, where disturbance levels were high the reverse was the case, and so by changing fixation, corridor connection could promote adaptation or extinction depending on conditions and species' genetic characteristics.

As mentioned above, different species perceive habitat in different ways depending on issues of physiology, behaviour and scale. A corridor link across inhospitable matrix for one species or group of species may paradoxically constitute a barrier to movement to another, whose habitat is in those patches perceived as matrix by the other (for example see Forman and Godron 1981, Adams and Dove 1989, Verkaar 1990, Woiwod and Thomas 1993). Often the literature on corridors takes as the conservation model that of natural habitat such as continuous primary forest fragmented by timber resource exploitation or clearance for agriculture, where the target species are those of the native natural habitat. There may not always be so clear cut a scenario, and identification of species or habitats to be conserved so easy, for example in regions such as the UK, where clearance of natural habitat took place so long ago, or where it has taken place over a less protracted period, but has been so intensive, that little if any natural habitat remains. In such cases clearly there are major implications for the design and location of corridors, which may raise complex questions of conservation priorities, and stakeholder interest.

2.3 Structural elements of ecological networks.

The concept of habitat features operating as conduits, or stepping stones, for the movement of organisms through the landscape between core habitat areas arises from general consideration of degraded and fragmented habitats, and barriers to dispersal. The intuitive appeal of the concept is obvious, particularly from a practitioner point of view. However, it has often been seized upon without adequate consideration, and it is well worth briefly examining here the development of the literature on these structural elements, upon which the functioning of ecological networks at any scale rests. The efficacy and viability of ecological corridors has been the topic of recurring debate for some decades. An early rapid expansion of publication on the concept, combined with its intuitive appeal, saw the corridor proposition readily become "fashionable" with practitioners. After appearing in prestigious and influential publications (e.g. IUCN 1980) a discussion developed in the theoretical literature regarding the validity of the proposition, particularly following the publication of papers critical of the concept (e.g. Simberloff and Cox 1987).

Dawson (1994a and 1994b) identified a substantial body of literature advocating the creation or retention of linear features, potentially functioning as landscape conduits, up to his time of writing (e.g. Diamond 1974, 1975; Wilson and Willis 1975; Diamond and May 1976; Forman and Godron 1981; Noss 1983; Wittig and Schreiber 1983; Bridgewater 1987; Burgman *et al.* 1988, Adams and Dove 1989; Saunders and Hobbs 1989; Grove and Schermeister 1990; Moore 1991; Council of Europe 1992a), citing also Harris and Scheck (1991) and Helliwell (1975) as reviewers of related conservation practice.

Dawson (1994a and 1994b) reviewed solely the concept of corridors as "conduits" (Bennett 1990; Forman 1991; Peterken 1993) or "travel corridors" (Johnson and Beck 1986), "biotic corridors" (Spellerberg 1989) and "movement corridors" (Merriam 1991b). Spellerberg and Gaywood (1993), however, reviewed the literature on all aspects of corridors and "linear habitats", including a summary of studies suggesting conduit function. Corridors may and do serve a range of aesthetic, recreational and other functions (Forman and Godron 1986; Noss 1987; Moore 1990; Low 1991; Forman 1991; Hobbs 1992; Spellerberg and Gaywood 1993, Bryant 2006, Ignatieva *et al.* 2011,) and may deserve recognition by ecologists and conservationists simply as elongated habitat patches in their own right, regardless of any connector function (Adams and Geiss 1983; Arnold 1983; Osbourne 1984; Forman and Godron 1986; Simberloff and Cox 1987; Noss 1987; Adams and Dove 1989; Lynch and Saunders 1991; Merriam 1991b). Concern that species may become trapped in isolated reserves and natural areas, latterly as climatic change renders their environment unsuitable, has been an additional spur to interest in corridors as conduits for migration and range adjustment (Wilcox 1980, Peters and Darling 1985, Peters 1988, Grove and Schermeister 1990, Warren and Key 1991, Hobbs and Hopkins 1991, Briers 2001, Shafer 2001, Piper *et al.* 2006), (see Fig 1, below).

Figure 1; Conceptual illustration of corridor systems suggested to promote movement at a range of spatial (and temporal) scales (from Dawson 1994a).

Numerous studies have demonstrated inter-patch movement happening more easily in corridors than the matrix, or movement within and occupancy of corridors as habitat patches, without necessarily demonstrating functionality as conduits, though these have often lacked unconnected controls. Even these studies are, however, sufficient to show that corridors can help meet size threshold requirements of species, or provide migration routes, especially for terrestrial animals such as mammals, amphibians and birds. One of the earliest and best studies, which met the requirements of hypothesis testing, Pollard *et al.* (1974), was on the distribution of Dogs Mercury (*Mercurialis perennis*) in hedgerows extending from a wood in Northamptonshire, UK. This study is particularly interesting in that while it demonstrates movement (or extension of area); the rate of movement along the hedgerow corridors was so slow as to make the demonstration of readily visible results within the scale of a human lifetime difficult, which emphasises the question of scale, both spatial and temporal, in assessment of conduit function.

While some more recent studies dealing with corridor effectiveness have provided positive support (e.g. Castellon and Sieving 2006, Damschen *et al.* 2006, Baker 2007) others do not or at least raise cause for caution (Collinge 2000, Hoyle and Gilbert 2004, Rantalainen *et al.* 2005). Examples of "good" corridor studies (i.e. testing hypotheses by comparison with experimental or natural control situations, replication, and rejection of a null hypothesis in statistical tests) are relatively rare, while studies stating that "corridors" would be useful in a given situation often without justification within presented findings, are common (e.g. the otherwise admirable Roe and Georges 2007). Gilbert-Norton *et al.* (2010) made a meta-analysis of a selection of 78 experiments (drawn from 130 laboratory and field studies dating from 1985 to 2008), using only studies with replicated corridor and control treatments. Overall, 60 experiments showed positive effect sizes, suggesting corridors increased movement between habitat patches, and 18 showed negative effect sizes. They reported that across all the studies the mean effect size was positive, of medium strength and highly significant, representing an approximately 50% increase in movement between habitat patches connected by corridors relative to movement between unconnected habitat patches. Invertebrates, non-avian vertebrates and plants showed no significant difference in amount of movement, but with all three taxa showing more movement through corridors than birds, and natural experiments showing more movement through corridors than experiments with created corridors. This said, 23% showed that corridors were less effective than non-habitat matrix in facilitating movement between patches, suggesting (potential for misclassification of habitat as non-habitat and poor corridor design or execution aside) that while corridors may be useful for many species, they are unlikely to be used by all species, and their relevance in particular cases may depend on the species targeted for management.

The use of the term "corridor" itself can be problematic (as indeed can the range of terms applied by writers in their efforts to not use the C-word, and so invoke its implication of conduit function - see Hesse and Fischer 2001). Numerous researchers working with corridors have noted that lack of a clear and consistent terminology leads to confusion about the goals of corridors (Saunders and Hobbs 1991, Loney and Hobbs 1991; Simberloff *et al.* 1992, Lindenmayer *et al.* 1993 and 1994; Rosenberg *et al.,* 1995, 1997 and 1998; Hobbs and Wilson 1998, Bennett 1999 and Hess and Fischer, 2001). A much greater degree of specificity and terminological consistency regarding corridor function and attributes would assist clarity, particularly in relation to differentiation between corridors as conduits, and corridors as habitat patches. Use of "corridor" in game management, island biogeography, and metapopulation literature is focused on function, while a structural usage of the term has arisen in conservation management and landscape ecology. "Corridor" is now used to describe both structural and functional aspects of landscape features, often implicitly, in a wide range of disciplinary literature and lack of a clear and consistent terminology has significant implications in terms of confusion in relation to design and conservation management of corridor features. Hess and Fischer (2001) pointed out that appropriateness and proper design and management of a corridor depend critically on a clear and explicit statement of its intended or inherent functions, rejecting succinct definitions because of the complex and multiple functions a corridor may serve. Instead, they suggest, somewhat hopefully perhaps, that conservationists and planners consider and document explicitly the possible functions of corridors when considering and designing them.

The efficacy of corridors, relative to that of the preservation of as much habitat as possible, and extension of area of existing habitat patches is another contentious issue. Substantial literature supports the proposition that persistence and abundance in larger, unconnected patches (potential for in-breeding depression aside) is better than in smaller connected patches (e.g. Falcy and Estades 2007, Hodgson *et al.* 2011). There is also (e.g. Martensen *et al.* 2008) support for the proposition that well connected fragments may sustain a broader range of species and greater abundance of individuals, with the additional connectivity providing opportunity for use of multiple fragments, and habitat types. The preservation of as many and as large fragments, especially in areas of genuinely natural habitat, should always be a conservation aim but connectivity between fragments can enhance the area functionally connected and is beneficial to all functional groups and therefore should also be a conservation priority, with balance and careful selection of approach on a case by case basis the aim. The answers to conservation ecological questions are rarely simple.

A range of situations and differing purposes for which corridors may prove advantageous can be listed:

- **Re-colonisation**; Corridors may allow species in a single habitat patch to be saved from, or the patch to be re-colonised after, local species extinction events (Diamond and May 1976; Forman and Godron 1981; Adams and Dove 1989; Bennett 1990; Soulé and Gilpin 1991; Merriam 1991b; Hobbs 1992, Taylor *et al.* 2005, Dixon *et al.* 2006, Remonti *et al.* 2008).
- **Size Threshold effects**; Corridors may allow individual animals, by facilitating movement between two or more otherwise mutually inaccessible patches, to find enough habitat types and area for day-to-day survival, where one of the patches in isolation would provide insufficient resources to support them (Sullivan and Schaeffer 1975; Forman and Godron 1981; Simberloff and Cox 1987; Goldstein-Golding 1991; Merriam 1991a and 1991b; Hobbs 1992, Martensen *et al.* 2008).
- **Migration**; Migratory animals may use corridors to facilitate their regular seasonal movement between habitats they exploit (Adams and Dove 1989; Merriam 1991b; Hobbs 1992), so meeting the requirements of survival, either as individuals or populations.
- **Climate change**; Species may need to follow their habitats as their distribution changes under the effects of climate change. Corridors may provide the linkages necessary for these changes in distribution (Hill *et al.* 1994, Peters 1988, Peters and Darling 1985, Walker and Steffen 1997, Piper *et al.* 2006).

- **Gene flow**; Enhancing the connectivity of potentially isolated populations corridors may facilitate gene flow across the landscape (Forman and Godron 1981; Merriam 1991b, Shirk *et al.* 2010).
- **Incidence**. Corridors may enable species or individuals not in any danger of extinction or death to range more widely than the permeability of the matrix would otherwise allow, giving them more access to their required habitat (conservation of the common).

2.4 Stepping Stones and connectivity

Gilpin (1980) built on the McArthur/Wilson island theory (McArthur and Wilson 1963; 1967) by allowing that individual species differ in their ability to survive on relatively small stepping stone patches or "islands", using a similar model to the peninsular effect. Gilpin considered that in the absence of stepping stones, most species would be present on the island all the time, or not at all. This theory consequently suggests that the presence or absence of stepping stone patches would influence very strongly a particular group of species: those which sometimes occur on the island, and are capable of crossing matrix to some degree. As with corridors, this sub group of species would also tend to be those with intermediate powers of dispersal; sedentary or very poorly dispersing species with physiological or behavioural aversions to the matrix not benefiting at all from stepping-stones, and strongly dispersing species able to traverse matrix unhindered, benefiting from stepping-stones only in the special case of "staging posts" for long distance migrants. At bottom, the function of corridors and island patches are effectively the same in the context of an ecological network – to facilitate the movement of organisms between habitat patches. As observed above, the essential difference may actually be one of scale, and species characteristics. For example, a wetland site used as a stopping off point in a regional or global scale migration corridor for migratory birds would have to be considered a stepping-stone, albeit perhaps on the larger scale seen as part of a corridor, and at smaller scales a habitat patch. In the case of a low vagility amphibian species intermediate, more isolated ponds, located between well connected pond clusters may play key stepping stone roles in dispersal, colonisation and re-colonisation.

Keitt *et al.* (1997), in their study of dispersal and movement patterns of Mexican spotted Owls (*Strix occidentalis lucida*), demonstrated that stepping stone patches, located at critical points in a network, may play a role in the network disproportionate to the inherent quality or size of the patch itself. Stepping stone patches may be the locations of abrupt scale dependent changes in levels of connectedness and connectivity, indicating that connectivity of landscapes themselves is highly scale dependent, with marked transitions at distances characteristic to particular species, and varying significantly for organisms with differing dispersal capacities and behaviour. More importantly, they showed that the sensitivity and importance of landscape pattern is also scale dependent, peaking at scales associated with percolation transitions (Stauffer and Aharony 1985, Gardner *et al.* 1989, 1992). This allows analysis to identify *critical* "stepping stone" patches that, when removed from, or established in, the landscape, cause large changes in connectivity, related not only to the spatial distribution of habitats across a landscape, but also on the scale at which organisms interact with landscape pattern (Merriam 1984, Gardner *et al.* 1989, Noss 1991). Thus, landscape patterns can act as scale-dependent "filters", relating differentially to the movement of species operating on different spatial scales. Landscape connectivity does not depend on scale alone, however; the configuration or spatial arrangement of habitats in a landscape is also an important determinant of connectivity (Forman and Baudry 1984, Henein and Merriam 1990, Gardner *et al.* 1992, Taylor *et al.* 1993, Alderman *et al.* 2005, Baguette and Van Dyck 2007, Pascual-Hortal and Saura 2006).

Keitt *et al.* (1997), presented a multi-scale analysis of landscape connectivity, based on an extension of uniform percolation theory to non-uniform landscape graphs (Cantwell and Forman 1993), developing both aggregate measures of landscape connectivity and patch-based measures of individual patch contributions to overall connectivity. An important finding of their analysis was that habitat loss has a highly scale-dependent effect on landscape connectivity. For organisms that perceive the landscape at fine scales, landscape configuration and stepping stone patches must be addressed at scales appropriate to them. Similarly, movements of species capable of long-range dispersal will not be strongly influenced by the configuration of individual patches. Near the species specific percolation transition, however, landscape configuration may play a significant role in determining landscape connectivity - near the percolation transition, individual patches can act as corridors or stepping-stones, bridging gaps in habitat distribution.

Species using different modes of dispersal will interact with landscape patterns in different ways. The Keitt *et al.* (1997) model, was based on the dispersal behaviour of Mexican Spotted Owls (*S. o. lucida*); however, an organism that must walk, run or slither over a landscape will encounter different barriers, and experience them differently. However, the general approach may easily be modified to incorporate other modes of dispersal and more detailed spatial and species information. Examinations of actual species dispersal rates show that many do not require corridors, because they are physically and behaviourally adapted to cross inhospitable matrix between patches without their use. Others, such as clonal woodland plant species, disperse so slowly even through favourable habitat, that colonisation of new patches is unlikely in time scales realistic in a human frame of reference. These two groups can benefit little if at all from corridors as anything other than habitat patches in their own right. This implies, however, an intermediate group, identification of which requires detailed species and habitat specific data, but which will be able to utilise corridors and experience severe difficulty or be unable to cross the matrix successfully over fairly specific distances, and which would benefit from corridors and stepping-stones. Published examples of studies relating to this proposition include Laurance and Laurance (1999), Lode (2000), Perault and Lomolino (2000), Sieving *et al.* (2000), Trombulak and Frissell (2000), Andreassen and Ims (2001), Berggren *et al.* (2001), Bolger *et al.* (2001), Coffman *et al.* (2001), Fernandez-Juricic, (2001), Joly *et al.* (2001), Mech and Hallett (2001), Palomares (2001), Pryke and Samways (2001), Tikka *et al.* (2001), Tull and Krausman (2001), Dover and Settle (2009), Bosschieter *et al.* (2010).

The evidence suggests that populations benefiting most from corridors will be specialist, disperse poorly and have been lost from remote or small fragments. Evidence for movement along corridors, and not across matrix and barriers, confirms the value of corridors in providing movement and migration routes and meeting size threshold requirements. From a conservation point of view the weight of evidence, and the undoubted cost of replacing lost corridors in contrast to the ease of retaining them, strongly suggests that the precautionary principle (O'Riordan and Cameron 1994) should be exercised, even when rigorous proofs of reliance on corridors as conduits are absent. In other words, where corridors exist they should be retained, and enhanced wherever possible. Where they do not, resources permit and their construction is not contra-indicated by other factors, their creation should be considered. At the very least, corridors should be seen as having intrinsic value as habitat patches in themselves and their preservation or creation considered from that point of view.

The situation with regards to stepping-stone patches is less straightforward. Clearly all the statements relating to the intrinsic benefits of corridors as habitat patches in their own right apply equally well to stepping-stones. Circumstances can be envisaged (if perhaps limited ones) in which the potential disadvantages of structural connection by corridors could be overcome by creation of stepping-stone patches for particular species, enhancing connectivity as perceived at that species' spatial scale, but not at others. The strategic creation of stepping-stones within the context of a network may be used to generate abrupt changes in connectivity at different spatial scales, to increase but also (by judicious removal) reduce (for example as a control measure against pathogens or invasive species) connectivity. The application of the network concept into planning and land use decisions could avoid the destruction or loss to natural succession of seemingly less valuable habitat patches (from the point of view of their own intrinsic habitat quality), the loss of which in the stepping stone context could produce major and unforeseen reductions in landscape connectivity.

2.5 Structural barriers to functional connectivity, migration and dispersal.

Anthropogenic barriers, such as roads and man-made features other than inhospitable matrix habitat, may present barriers to movement for species and individuals otherwise physically and behaviourally capable of crossing the matrix. This may be either due to unsustainably high fatality rates or behavioural inability to cross the barrier. Harris and Scheck (1991) listed the many aspects of a cultural landscape that may be a barrier to animal movement, some of which they considered as effective a barrier as the sea in classic island studies. Trombulak and Frissell, (2000), in their review of the ecological impacts of roads, highlighted not only the direct effect of roads as physical barriers to dispersal, but the less obvious effects of changes to soil density, temperature, soil water content, light levels, surface waters, patterns of runoff, and sedimentation, as well as heavy metals, salts, organic molecules, ozone, and nutrient pollution (see also Vos and Chardon 1998). It should be noted that directionality is an issue here, as while a road may represent a barrier to movement perpendicular to it, suitably vegetated verges may represent corridors facilitating movement and dispersal parallel to it (e.g. Tikka *et al.* 2001).

At least in the case of small mammal species, it has been demonstrated that the road itself (rather than emissions or traffic) is actively avoided, with the implication that traffic reduction or calming would be ineffective, and that relatively low traffic frequencies may not necessarily diminish the barrier effects of roads (McGregor *et al.* 2008, Shepard *et al.* 2008a and 2008b). Lode (2000), studied the effects of a motorway on mortality and isolation of populations for a range of species. The results showed that road mortality considerably affected vertebrate populations with animal mortality exponentially increasing with traffic volume, to almost 100% of migrants where no mitigation passage existed (see also Forman and Hersperger 1996, Alexander and Waters 2000, Mumme *et al.* 2000). Roe *et al.* (2006), in a study of water snake species of differing vagility, demonstrated that the effects of mortality on species varies with vagility – perhaps counter intuitively, more mobile species (through consequent higher probability of encounters with road crossings) suffering substantially higher mortality compared with more sedentary species (in this study 14-21% and 3-5% of population per year, respectively). Corridors may in these circumstances literally as well as metaphorically constitute a “bridge” (or indeed tunnel) facilitating movement and dispersal.

Studies involving roads and other such barriers (Merriam *et al.* 1989, Mader *et al.* 1990, Bennett 1991a and 1991b) have suggested some species rarely cross them or do indeed incur high mortality in doing so. It should be noted though, that studies simply show most such barriers are a hindrance to re-colonisation, not that they prevent it. However, for individual animals to achieve minimum habitat threshold and migrants to complete seasonal movements, they must have a reasonable probability of survival. Furthermore, for the use of corridors to be justified in most cases, the total prevention of possible colonisation/re-colonisation without them is not a pre-requisite; simply that corridor provision would enhance otherwise marginal or unacceptably low probabilities.

Low colonisation rates of suitable habitat ultimately arise through failure to leave the source, or failure to arrive at the target patch. A poor corridor may be a lethal trap, particularly to less readily dispersing, or vulnerable species – poor quality, or interrupted habitat and increased predation due to edge effects in the corridor may elevate mortality rates (Orrock *et al.* 2003, Orrock and Damschen 2005), and the corridor itself may act as an “attractive sink” (Delibes *et al.* 2001a and 2001b). The common assumption regarding isolation - that it is inherently a “bad thing” - needs careful consideration in itself. Isolation is not always necessarily deleterious to the persistence of rare or endemic species. In addition to the genetic arguments raised in Vandermeer and Carvajal (2001), Crowley (1981), Simberloff and Cox (1987), and Panetta and Hopkins (1991), the competition aspects warned of by Walker and Steffen (1997), i.e. that immigrants and exploiters of corridor improved connectivity may be predominantly invasive competitor species which may displace target species, or predators (Burkey 1997, Holyoak 2000) and danger of pathogen dispersal (Hess 1994 and 1996) are real concerns. Weldon (2006) demonstrated in a study examining the effect of increased corridor connectivity on Indigo Bunting (*Passerina cyanea*) nesting success, that nest predation was increased in connected sites as compared to unconnected sites, identifying the mechanism as associated with edge/area ratio increase in the connected sites.

It has also been suggested (though inconclusively and on limited evidence) that corridors may be exploited by mammalian predators as prey-traps, with prey species being effectively funnelled into areas of high concentration, raising the possibility that use of corridors by predators may reduce the effectiveness of passages in conserving other forms of wildlife. Little *et al.* (2002) reviewed the literature and concluded that evidence for the existence of prey-traps is scant, largely anecdotal and tends to indicate infrequent opportunism rather than the establishment of patterns of recurring predation. More research will be needed in this area. Most corridor studies record no evidence of predation (though do not generally deal specifically with this) in or around corridors and conversely, there is some evidence that predator species use differently configured corridors than their prey (Little *et al.* 2002). On balance, the weight of evidence falls on the side of the beneficial or at least neutral effects of corridors on species persistence within and dispersal between patches, but careful consideration of location and design issues must be a fundamental prerequisite of any corridor proposition.

2.6 Lines on maps and lines in the sand.

Put simply, ecological networks and wider landscape management seek to re-connect fragmented landscapes and ecosystems; clearly in the human dominated landscapes of Northwest Europe, this means cooperative management across the administrative and property boundaries superimposed upon those landscapes and ecosystems. Consequently both ecosystem function and process, and stakeholder perceptions, participation, and long term social and economic planning processes must be encompassed by the ecological networks concept (Boothby and James 2002); effective ecological networks must be made up of "actor networks" (Selman and Wragg 1999) as well as physical and administrative constructs (James *et al.* 2000).

Through these means, the scope of conservation management outside designated sites may be broadened, crossing cadastral and property boundaries to form a closer approximation to ecologically bounded areas and functions, rather than being restricted by human social constructs such as designated special conservation areas and the limits of property boundaries (Smith 1995a and Boothby 2004).

Ecological networks of any kind or scale have no legal status in the UK despite the terms' appearance explicitly in the National Planning Policy Framework (DCLG 2012) and structural plans, and will therefore require the use of "soft levers" such as inducements from Agri-environment Scheme (AES) funding where possible. Indeed, a somewhat loose commitment to the network approach resulting from treaty and agreement commitments has been translated into concerted effort on the part of government to develop them only recently (Lawton et al. 2010, DCLG 2012). The realisation of ecological networks is not intended to result in any new form of conservation designation, replace or undermine any existing ones. Any part of a network receiving designation could not do so by virtue of the creation of such a network and or its place within it *per se*. However, lines on maps in themselves (Boothby 2004) may be a contentious issue. Ultimately, the creation of a network cannot proceed without the prior identification of core areas, corridors, stepping-stones and buffers. Consequently lines on maps are inevitable and the act of their creation, privately or publicly, with legal status or without, may be controversial.

The generation of even hypothetical boundaries may create antagonisms, hidden or explicit, due to real or perceived issues of ownership and control (Julien *et al.* 2001, MacFarlane 2000a and 2000b, Morris and Potter 1995). The identification of core areas, whether some legal nature conservation designation already applies or not, will undoubtedly bring with it additional responsibilities (at least in perception). This effect may in some ways be more pronounced in the case of habitat creation or enhancement areas and connecting corridors as a result of their essentially creative purpose - be it of new or improved habitat, or landscape connectivity and connectedness. By undertaking the enhancement of the "conservation estate" outside designated areas, land deserving of formal designation may (hopefully will) be generated over time. Resistance to voluntary agreement to create networks may well be seen by many land managers as a necessary defence against future land use restrictions arising from increased occurrence of protected species or biotopes worthy of designations such as Site of Special Scientific Interest (SSSI) or Special Area of Conservation (SAC).

Property, particularly in land, holds crucial economic and social significance and requires that boundaries should be clearly and precisely defined, an aspect central to their meaning. Mereotopology (the relationship between wholes and parts) offers some useful insights (Smith 1997). Smith (1995a and 1995b) proposed that the "real" world is made up of complete "*Bona fide*", "real" objects, and created objects defined by human actions, "*fiat*" objects. *Bona fide* boundaries include physical entities, such as continental plates, coasts, river banks and lakesides – with boundaries (however ephemeral or indeterminate) existing irrespective of any human conceptualisation or efforts to delineate them, resulting from qualitative discontinuities in nature. "*Fiat*" boundaries remain entirely conceptual - though sometimes acquiring greater significance in economic, political and social terms than many *bona fide* boundaries - owing their existence to human administrative, legal, political or cognitive decision making processes.

Included in this category would be political and administrative units, property lines and most forms of "habitat boundary" (representing as they do a gradational scale dependent progression, with the point of transition from one to another unfixed, qualitative change being a matter of species perception, the "boundary" as perceived by humans, being a human construct). Smith (1997) also defines incomplete, "fuzzy" edged spatial objects lacking well defined or lasting exterior boundaries –such as flocks of birds, shoals of fish, population and species distributions; objects which are not the products of human cognition and assignment of arbitrary or conventional boundaries, but also are not necessarily representative of some underlying natural spatial discontinuity. As Boothby (2004) observes, the concept of incompletely bounded objects is directly relevant to the potentially controversial boundaries generated by ecological network development.

A very small proportion of sites which may be considered valuable to nature conservation receive any kind of conservation designation. In designating as valuable and applying conservation designation, *bona fide* boundaries (if "incomplete" or "fuzzy" natural boundaries) are (hopefully) subsumed into (complete) *fiat* boundaries. Indefinable or incomplete boundaries are a central feature of wildlife censuses and habitat surveys - maps of species distributions are generalised abstractions, delineating likely rather than literal presence, often based on proxy evidence, such as climate envelopes or particular habitat characteristics. Species distribution, though not necessarily presence, may track underlying contours in nature - specific habitats (as perceived by particular species) are *bona fide* objects, and *bona fide* objects may have indeterminate and ephemeral boundaries as well as determinate fixed ones. The creation, through survey and buffering in GIS of core areas and so on, *may* correspond to *bona fide* boundaries - soil chemistry, geology - but more likely in the highly fragmented, production dominated landscapes of the developed countries, consist of collections of both *fiat* and *bona fide* objects, given *fiat* status through management agreements.

Success in the objectives of conservation efforts could well confer *bona fide* status on the components of the conservation area - over time their *fiat* status as management areas being converted into tangible restored (semi-)natural habitat. This conversion, or merely the potential for it, could present some stakeholders with difficulties. The presence of "new" species and habitats could bring with it duties and responsibilities that the stakeholder would prefer not to entertain, such as for example the restraints imposed by the illegality of interfering with a protected species or its habitat. An ecological network for *Triturus cristatus* for example, would define its habitat as not just the pond in which it breeds and surrounding terrestrial feeding and overwintering habitat, but the pond cluster(s) which support its (meta)population(s) and the connecting corridors and island stepping stones which link them. Creation of new ponds and terrestrial habitat would potentially extend the population range through colonization and so extend, or create new and additional, protected habitat.

Insights made possible through the concepts of mereotopology can provide a means of conceptualising the complex interrelationship of ends and means involved in the creation or restoration of habitats and extension or re-establishment of species distributions and presence. Actions to promote species can become tools for habitat protection, species protection methods help to protect habitats, which consequently promote species persistence. Mereotopology also forces (and allows) consideration of the ontology of landscape, helping define those consisting of variegated, shifting or ephemeral and patchy features - which have typically in the past been considered as aggregations of disparate individual elements, for example in relation to pond conservation. Through this a contribution can be made to solving the problems of whole landscape management and planning.

The concept of ecological networks and landscape scale conservation considered in this thesis is by necessity partial, controversial, unsupported and unfettered by legal definition, delineating planners' intention and *fiat* perhaps as much as *bona fide* nature. However, the lines on maps they consist of have the power to generate anxiety, controversy, debate, animosity and resistance. The spatial characteristics and objectives of the network must, however, be disclosed at some point, to facilitate their realisation and to produce assessable wildlife outcomes (Kleijn *et al.* 2001, Kleijn and Sutherland 2003 and Peach *et al.* 2001). Through stakeholder involvement and genuine participation from the outset, anxiety may be reduced, resistance so far as possible disarmed, or at least forced to articulate itself in such a way as to make a possibly workable compromise attainable. In essence, ecological networks and wider landscape management to one extent or another represent a move towards a "fuzzy edged" spatial planning, where designations become de-stabilised, rights exclusive boundaries less restrictive and more balanced against responsibilities and co-operative management across property boundaries. This very "Fuzziness", paradoxically, heightens the need for precise spatial targeting if conservation efforts are not to be dissipated. Means to expedite this level of targeting are at the centre of this thesis.

This chapter has examined the theoretical underpinnings of the ecological networks concept and structures, and has considered the evidence base for the efficacy of their application as management tools within wider landscape conservation management. The following chapter will examine the autecological knowledge base in relation to *T. cristatus* and its interaction with habitat at landscape scales to identify the key parameters which landscape analysis will need to address:

- Terrestrial movement capacity in pre- and post- and breeding migration between terrestrial and aquatic habitat and dispersal,
- the importance of proximity and connectivity of aquatic habitat for *T. cristatus* occupation and breeding presence,
- the importance of proximity and quantity of core habitat for occupation and breeding presence.

This will inform subsequent graph theoretic analysis of the configuration of key habitat patches in a landscape typical of the species core range, as the basis for spatial targeting of habitat creation, preservation and enhancement.

Chapter 3 The Great Crested Newt (*Triturus cristatus*) and the wider countryside

3.1 The focal species (*Triturus cristatus*).

Triturus cristatus (Laurenti, 1768), the Great Crested Newt, was selected as the focal species for its fulfilment of criteria which the focal species should meet, and the ready availability to the author of a substantial quantity of data on the distribution and breeding presence of the species across the Cheshire and North Wales area within which study sites were under consideration. Criteria for selection of the focal species were that it should;

- have limited/intermediate dispersal/migration capacity and so be part of the sub-set of species most likely to benefit from landscape scale management for connectivity (see chapter 2).
- have habitat requirements making it suitable for consideration as an "umbrella" species, management in favour of which would be likely to support the conservation of a suite of other species.
- be a species of recognised conservation interest, preferably specifically identified in existing AES provision as one for which funding to support management in its favour is available.

T. cristatus is a short distance dispersing, philopatric species, whose terrestrial habitat requirements are shared with a wide variety of vertebrate and invertebrate species of conservation interest. The species is strictly protected under provision of the Wildlife and Countryside Act 1981 (as amended), (HMSO 1981), and the Conservation of Habitats and Species Regulations 2010 (HMSO 2010), and listed as a species of principal importance for the conservation of biodiversity in both England and Wales under Sections 41 and 42 (respectively) of the Natural Environment and Rural Communities (NERC) Act 2006, (HMSO 2006). It is included in Annexes II and IV of the Habitats Directive (Council of Europe 1992a), and both the species and its aquatic habitat in particular are targeted for funding within existing AES provision. Management for provision of Favourable Conservation Status (FCS) of the species must include management of both terrestrial and aquatic habitat, and necessarily involve landscape features (extensive pond networks and intervening terrestrial habitat) straddling multiple land holdings.

In the UK, *T. cristatus* is found across a range of mainly lowland habitats; a high density of suitable ponds, with adjacent daytime refugia and hibernation sites, in a mosaic of extensive or relatively unimproved grassland and broad leaved woodland provides what is generally considered optimal terrestrial habitat (Langton *et al.* 2001, Swan and Oldham 1993); see Table 1, below. Extensive coniferous forestry plantations are generally considered sub-optimal, since their sparse herb layer provides limited foraging potential and cover for adults. Their generally low pH ponds, generally macrophyte poor due to low light levels, warm slowly in spring and provide limited egg laying substrate and invertebrate prey for larvae.

Table 1; Recorded population densities of T. cristatus in a range of favourable habitat (from Oldham 1994), after Cooke (1985, 1986), Oldham and Nicolson (1986), Franklin (1993) and Horton and Branscombe (1994), with population estimates from the Cheshire Triturus cristatus Site Inventory (CTcSI 2008).

Site	Habitat	Est. pop. Density (no. ha^{-1})
Little Wittenham	Large area of woodland	50 -1,500
Shillow Hill	Small area of woodland, surrounded by agricultural land.	25 - 1,250
Leicestershire Ag. Land	Agricultural mosaic	20 - 250
Lomax Brow	Agricultural and old industrial land	~20
CTcSI[1] (derived from all available records, habitat quality not accounted for).		
	Count	%[3]
Total records	894	100.0
No population Estimate available in record	673	75.2
Pop. Est. Low (1-10)[2]	128	14.4
Medium (11-100)	59	6.5
High (101+)	34	3.7
[1]Estimates in CTcSI records are either in, or are converted for use here, to English Nature categories (English Nature 2001) from other systems in use over the period covered at time of writing (1910 – 2007) or from raw maximum capture/count where available. [2]Refers to maximum capture/count. [3]Note percentages do not sum to 100 due to rounding.		

3.2 The Landscape Matrix.

Joly *et al.* (2001) examined the effects of variation in characteristics of the habitat matrix on three co-occurring species of newts, including *T. cristatus,* in European agricultural land. Though their study examined only the effects of presence of cultivation and woodland upon species distribution, specifically filtering out the effects of other major causes of habitat fragmentation, such as road networks and urbanisation, it throws useful light on key factors. They examined the effects of a range of breeding pond site variables (pond depth and area; bank slope; proportion of area with floating vegetation cover and presence of fish) and terrestrial landscape variables (proportion of woodland, proportion of cultivated land, hedgerow length, number of ponds, angle of the uncultivated sector, i.e. the angular sum of all directions for which a straight line from the pond to woodland did not cross cultivated land) in 50ha areas within a 400m radius centred on each pond. Within a subset of samples examined to isolate the influence of cultivation from forest presence (20 sites selected for forested area within a limited range) high abundances were observed only where the un-cultivated angle exceeded 140 degrees. Overall, Joly *et al.*'s (2001) findings broadly concurred with those of Swan and Oldham (1993). The relationship between *T. cristatus* abundance and cultivated angle followed a skewed bell curve – abundance increased with cultivated area until a threshold level was reached, beyond which decline was rapid, suggesting newt abundance was enhanced in areas where levels of cultivated area were intermediate, possibly reflecting levels of landscape heterogeneity or (perhaps) reflecting crowding due to lack of other suitable breeding habitat in the surrounding matrix, as suggested by Grayson (1994). Association was also found with increasing pond density (high when exceeding 5ha^{-1}).

Other landscape variables (except woodland area) negatively influenced the abundances of all three species examined, with pond area, fish presence (possibly conflated since larger ponds tended to be commercial fish breeding ponds in the study area and large ponds are generally associated with higher likelihood of fish presence), hedgerow length and a high proportion of cultivated area being negatively related to abundance. The only surprise here would be the negative relationship between abundance and hedgerow length. A possible explanation for this is that the supposed beneficial effects of hedgerow length (frequently seen as potential habitat and movement corridors for newts) were masked by some other variable(s), as was suggested by the authors. Possibly, this reflects a shortfall in the study, which apart from its fairly crude spatial analysis of the arrangement of landscape components, is that there was no assessment of the quality of terrestrial habitat elements, other than area or length. It cannot be ruled out that what is actually being measured in this negative relationship between hedgerow length and newt occurrence and abundance is the importance of the quality of this feature for newts (as other key habitat presence, quality or area diminish), if the quality of the hedgerows (e.g. discontinuity, connectedness, width of gaps, hedge bottom vegetation etc., were sufficiently low (see Clements and Tofts 1995). The positive relationship between the uncultivated area and presence and abundance of newts validates the hypothesis that this constitutes the main component of connectivity between aquatic and terrestrial, and probably between terrestrial habitats for newts. For *T. cristatus* the relationship between woodland area and abundance was not significant, suggesting connectivity was the main landscape determinant for the species. The relationship between width of uncultivated sector and newt abundance suggested to the authors that the broader this was the more use newts were likely to make of it.

3.3 Pond density and dispersion.

Pond density is relatively high in pastoral areas of lowland Britain (Swan and Oldham 1993, see Tables 2 and 3, and Fig. 2, below); grazing pressure provides suitable foraging and dispersal habitat and often maintains suitable pond marginal habitat, and arable is scattered and relatively infrequent. Associated hedgerows, copses, scattered woodland and ditches also provide both additional potential habitat and putative dispersal corridors. In areas of the highest pond density, such as northwest England and most notably Cheshire, populations are widespread in networks of farm pond clusters, where they are often considered to constitute extensive metapopulations (Swan and Oldham 1993, Langton *et al.* 2001), usually at low levels of abundance (see Table 1 above). This is considered far more robust and resilient for population persistence than areas where the "pondscape" is fragmented by intensive agriculture, urban, industrial and infrastructure development. Here, populations tend to persist in, or are centred upon, small numbers of isolated breeding ponds, making populations much more vulnerable to long term declines due to inbreeding depression or deterministic factors such as habitat loss and fragmentation, or stochastic local extinction events.

However, (as demonstrated by Smith and Green, 2005) assumption of metapopulation function, rather than patchy population distribution based on assumption of short range dispersal capability, should be approached with caution, since, as will be demonstrated, although the majority of dispersal events are undoubtedly short range, relatively rare dispersal events may take place over much greater distances and link populations separated by many kilometres. Perret *et al.* (2003), in a study of Alpine newt (*Ichthyosaura alpestris*, formerly termed *Triturus alpestris* and *Mesotriton alpestris*) in SE France, identified a transience rate of 35.5%, with no significant difference between sexes, and that adult dispersal may contribute significantly to between-population migrations (as suggested previously by Miaud *et al.* 1993).

The majority of British lowland ponds originated as marl pits dug in the eighteenth and nineteenth centuries to provide a base rich clay used as a soil improver, which subsequently persisted as watering points for stock. This accounts for their often being found in quite dense clusters, frequently at hedge line intersections, over widespread areas - a particular feature of the Cheshire landscape. Pond numbers, density and distribution have been reduced by pond removal due to housing, industry, transport infrastructure development, agricultural intensification and changes in management techniques promoted by short sighted past agricultural incentive schemes (Boothby, 1999).

Swan and Oldham (1993) suggest a minimum pond density of 0.7 km^{-2}, with only 31% of areas with lower densities supporting *T. cristatus,* by comparison with 58% above it. Occupancy rises appreciably at higher levels, in excess of 3 ponds km^{-2} (see table 3, below). These findings are supported by breeding site distribution in Cheshire, recorded in the Cheshire *Triturus cristatus* Site Inventory. *T. cristatus* was the only amphibian species with a minimum pond density threshold suggested by the National Amphibian Survey (NAS, Swan and Oldham 1993), occurring in only about a third of areas with densities below 0.7 km^{-2} (see table 3, below). Arable cultivation is the predominant land use of just over half the farmed area of lowland Britain which, particularly intensive arable, imposes restrictions on *T. cristatus* distribution. Pesticides and monoculture reduce the availability of invertebrate prey, fertiliser runoff causes (often severe) eutrophication of ponds and toxicity directly affects animals where period of application coincides with migration (Berger *et al.* 2012), and large numbers of ponds in arable areas have been ploughed out (at a slightly higher rate according to Swan and Oldham, (1993), than those in pastoral areas), as have hedgerows, ditches and woodland habitat. Disturbance from ploughing, harrowing and rolling among other management practices may further reduce overwintering success (by destroying hibernation sites and their occupants) and also interfere with and increase mortality during dispersal movements (Swan and Oldham 1993, Berger *et al.* 2012).

Table 2; Pond density associated with various land use types (in 60 survey areas across the UK (from Swan and Oldham 1993), in Cheshire[1] generally (Pond Life Project) and the Cholmondeley study area).

Land-use type	Density (km^{-2})				
	Median	Mean (SD)	Max.	Min.	n
Lowland agricultural					
Built up area with gardens absent.	1.2	1.8 (1.6)	5.5	0.2	33
Built up area with gardens present	2.0	3.3 (3.4)	10.9	0.3	14
Mineral extraction sites in area	3.3	3.5 (2.2)	6.2	1.2	4
Upland areas	0.1	0.5 (0.8)	2.3	0.04	8
Dune slack	4.6	-	-	-	1
Pond density in Cheshire[2]	6.29	6.74 (3.2)	17.0	0.25	@12,000
Pond density at Cholmondeley[3]	19.05	19.64 (8.5)	45.92	0.00	325

[1]Cheshire vice county, VC58. [2]Kernel Density Interpolation from point data set, 275m cell size, 1928m search radius. [3]Kernel Density Interpolated from point data set, 50m cell size, 500m search radius, using pond point locations up to 1km distant from study area boundary to minimise edge effects.

Table 3; Pond dispersion and density in the Triturus cristatus pondscape (from Swan and Oldham 1993).

	Pond density (ponds km^{-2})	Range of dispersion (km)
Suggested Great Crested Newt presence threshold	0.7	1.2
Observed pond density in much of central Britain	0.1 – 2.0	3.0 – 0.7
Median occupied pond density within distributional range	0.4	1.6
Observed threshold for highest % occupancy	3.0	0.6

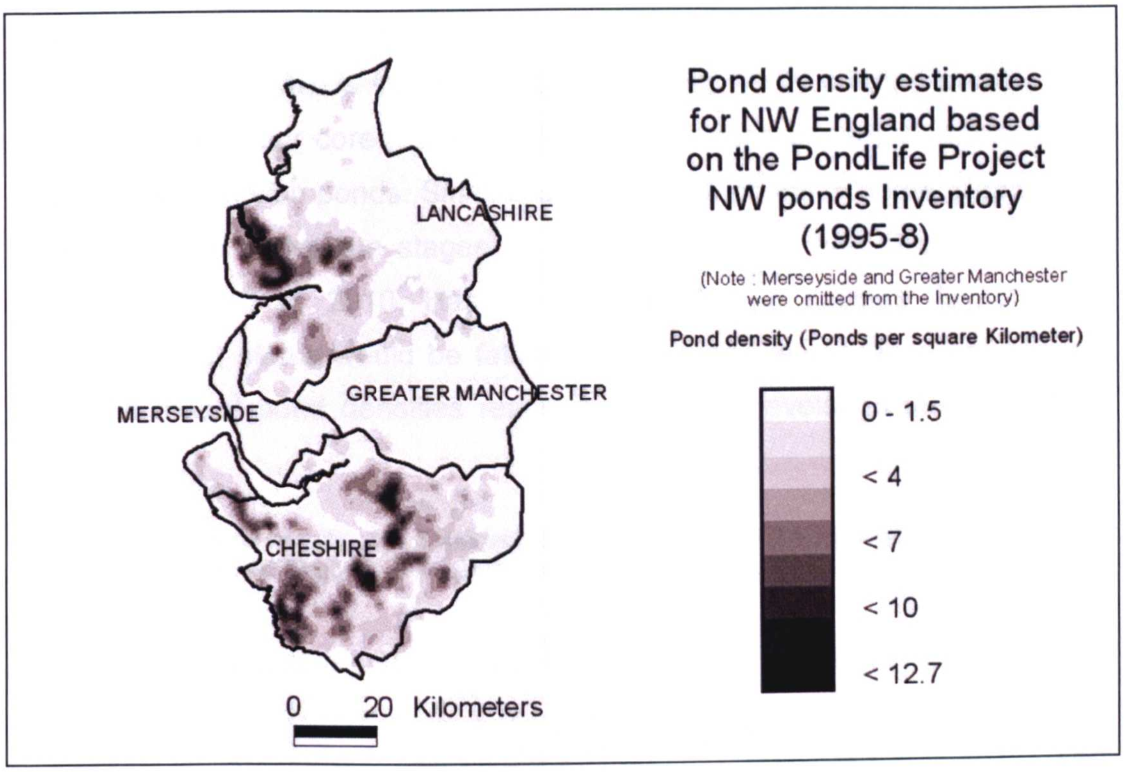
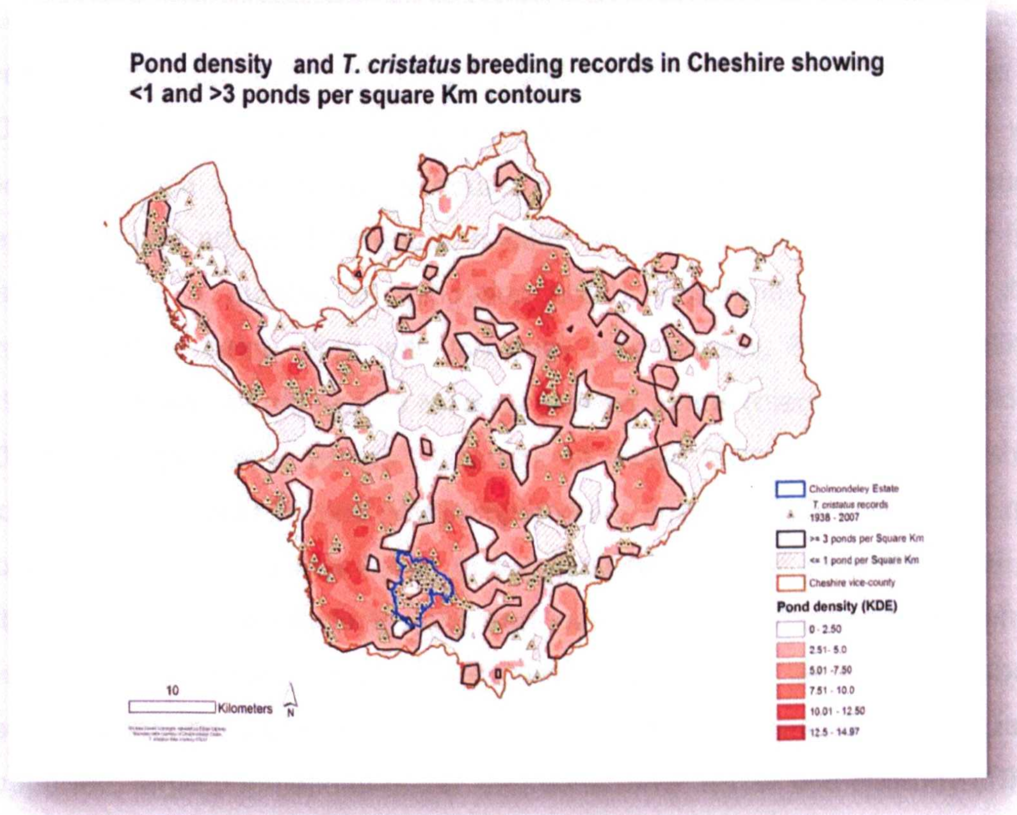


Figure 2; Estimated pond density, NW UK (derived from Pond Life Project NW Pond Inventory

As Fig. 3 below indicates, *T. cristatus* records tend to cluster within the higher density areas well above 3 ponds km^{-2}, with only 9 recorded breeding sites in areas with estimated pond densities below 1 km^{-2}, and only 2 below the 0.7 km^{-2} observed by Swan and Oldham (Hollinshead 2006, CTcSI 2008). Where breeding records occur with densities below 3 ponds km^{-2}, these tend to be older, and this may well reflect historic pond densities more closely than current densities.

Largely shorn of the purpose which ensured their persistence by the advent of piped water, and consequently without active management or regular disturbance, seral succession has arguably become the major threat to the regional pondscape. Many farm ponds have become silted up and dried out, or too heavily shaded by marginal shrubs and trees to provide suitable habitat (Hassall *et al.* 2012). While over management of ponds is undesirable (since ponds at a range of seral stages in any area will promote maximal pond biodiversity (see Hassal *et al.* 2011, 2012 and, Boothby 1997), where suitable ponds are not being created or developing at a rate faster than attrition and succession reduce their numbers in the landscape, this must eventually result in loss of suitable breeding habitat. Though *T. cristatus* is frequently said to favour newly created ponds, as will be seen, their core aquatic habitat preferences appear concentrated on mid succession ponds. Since around half the ponds in some areas are known to be in the late stages of succession (Swan and Oldham 1993, Hollinshead *et al.* 2010, Hassall *et al.* 2012) the species' favourable conservation status would be fatally compromised long before pond loss *per se* meant pond densities reached untenable levels (Boothby 1997).



[1]Kernel density Interpolated from point data set, 275m cell size, 1928m search radius. [2]Cheshire vice county, VC58

Figure 3; Pond density[1] *(km^{-2}) and T. cristatus records in Cheshire*[2] *showing <1 and < 3 ponds* km^{-2}.

In recent years, pond loss to anthropogenic causes has apparently slowed and the trend possibly reversed (Swan and Oldham 1993, Boothby 1999), pond numbers appearing to have stabilised at a country wide figure of around 400,000 (Ponds Conservation 2011). However, though substantial numbers of ponds have been dug, many ostensibly for conservation purposes, many new ponds are sub-optimally located, and have frequently been dug for fishing, waterfowl or other amenity purposes not always necessarily to the benefit of wildlife in general and of *T. cristatus* in particular (Hollinshead *et al.* 2010, Hassall *et al.* 2011).

Poor siting of ponds may be an issue even where new ponds have been specifically created to mitigate negative environmental impacts on *T. cristatus*, such as from road and housing development. Between 14th May and 23rd June 2006, 50 ponds (a stratified random sample from the 500 Cheshire ponds within the 1000 in North West England surveyed as an adjunct of the 1995-1999 Pond Life project (Boothby 1999) were re-surveyed using the same methodology and surveyor (Guest 2006 (unpublished), Hollinshead *et al.* 2010, Hassal *et al.* 2012). A 35% reduction in *T. cristatus* presence was recorded which was mainly attributed to successional changes in aquatic vegetation and adjacent terrestrial habitat, along with the introduction of fish, particularly in a number of mitigation ponds apparently targeted by illicit anglers due to being sited with too easy road access. Baker and Halliday (1999) examined 49 old and 78 recently created ponds (median 5 years old, 1-20 years respectively) across 3000 km^2 of mixed farmland in Bedfordshire, North Buckinghamshire and Northamptonshire in the UK. Occupancy of new ponds by *T. cristatus* was found to be significantly lower (only 2%) than for other amphibians, particularly frogs and toads, and was the case only where the nearest neighbour ponds were within 400m (however, as observed above as a problem, many of the new ponds were specifically created for, or at least supported, large populations of fish and waterfowl). Baker and Halliday (1999) also found a lack of detectable effects of terrestrial habitat on pond colonisation by amphibians, other than proximity to the pond, in contrast to the findings of numerous other studies - for example Beebee 1985, Laan and Verboom 1990, Pavignano *et al.* 1990, Swan and Oldham 1993).

3.4 *Triturus cristatus* dispersal capacity.

T. cristatus dispersal distances may vary greatly with the age of the individual, habitat quality and availability and quality of the intervening matrix. Dispersal is commonly observed up to 500m (Franklin 1993, Oldham and Nicholson 1986, English Nature 2001). At most sites, the majority of adults probably stay well within 250m of the pond (Langton *et al.* 2001; Jehle and Arntzen 2000) and remain loyal to the breeding site the following season. Where density related factors weigh sufficiently heavily, or the extent of high quality habitat and refugia extends beyond 500m, newts may disperse over much greater distances. Kupfer (1998) records single *T. cristatus* migrating 1290m in approximately one year, and colonisation of ponds over 1000m from any known occupied pond in their first year is recorded in France (Arntzen and Teunis 1993) and Germany (J. Guest, pers. comm. June 2006), though ponds over 1000m distant from occupied ponds may take several years to colonise. There is evidence from a study in France based on range extensions (Arntzen and Wallis 1991) of a dispersal rate of up to 1km a year over a 30-year period. Little is known of metamorph dispersal or the detail of adult migration patterns, but *T. cristatus* may make significant migrations in autumn (Glandt 1986, cited by Jehle 2000) and dispersal events could be rare, take place other than immediately after breeding or alternatively most dispersal could take place at the juvenile stage (Kupfer and Kneitz 2000), as has been shown for some nearctic salamanders and toads (Gill, 1978a and 1978b; Breden 1987).

A radio tracking study of *T. cristatus* and the closely related *T. marmoratus* in Western France (Jehle and Arntzen 2000), in which *T. cristatus* individuals were tracked for between 5 and 28 days, found that newts leaving the breeding pond migrated with high directionality up to 137m into refugia, commonly small mammal burrows. Movement after the first night was mostly over short distances (< 6.8m) and underground, with 64% of tracked newts staying within 20m of the pond edge, though migrations up to 146m from the pond edge were recorded. Jehle (2000), in a similar study, identified buffers, including 95% of *T. cristatus* "localisations" - defined as locations where the individual was resident for at least 24 hours - with radii of 12.2 - 32.2m. A similar study by Schabetsberger *et al.* (2004), at relatively high altitude (c. 1280m a.s.l.) in the Northern Calcareous Alps, Austria, during 2000/1 radio tracked *Triturus carnifex carnifex* captured from the shoreline of a small, shallow, periodically flooded lake (Amiesensee) shortly before emigration and after beginning entering the terrestrial phase. After transmitter implantation and a recovery period, individuals were released at two locations adjacent to the lake where most emigrating newts were observed. Newts were tracked until individuals remained in a terrestrial refuge without apparent movement for at least one week. Newts moved over a period up to 7.8 days after release. Movement took place during day and night, with significant directionality (X^2 test, $p<0.001$). During the first night after release, 89% of females and 62% of males changed position between localisations, this percentage dropping the next day to 20 and 9% respectively). Individuals migrated between 13 and 299m before reaching their terrestrial refuge.

In both years individuals preferred a NW direction, with no animals crossing a gravel road to the SE of the lake. Of the tracked individuals, 49% could be tracked to their terrestrial refuges, at the edge of or in forest. 72% were in small mammal burrows under tree roots, 20% in cavities under flat overgrown rocks, or cracks in boulders, 8% were in rotten tree stumps. Depths below ground were 0.05m to 0.80m, no movement exceeded 1m after newts reached their underground shelters, which were therefore taken to be hibernaculae. The terrestrial refugia of *T. c. carnifex* were 4-8 times further away from origin than those of *T. cristatus* and *T. marmoratus* in Jehle and Arntzen's (2000) study, and migration speed was roughly the same but generally lasted more than one day. It is worth while noting, as did Schabetsberger *et al.* (2004) themselves, that there was no snake presence at Amiesensee, whereas three *T. marmoratus* and *T. cristatus* were predated by snakes in Jehle and Arntzen's (2000) study, and that population density of *T. c. carnifex*, *I. alpestris* and *L. vulgaris*, as well as other amphibian species were high (> 10,000 adults), so this population probably faced relatively lower rates of predation, and higher levels of intra and inter specific competition for refugia (20% of all hibernation sites were multi occupied, by individuals of more than one species), and prey, which may account for the differences in migratory pattern.

Kupfer and Kneitz (2000), in a seven year study of *T. cristatus* populations in North Rhine-Westphalia, Germany, (a mosaic of farmland, woodland and built up areas), noted a marked dissimilarity in migration patterns and site fidelity between adults and metamorphs, with adults showing greater site fidelity than metamorphs, who were recorded in their study as more frequently migrating to neighbouring ponds, to a maximum recorded distance of 860m.

There is therefore, given short recorded dispersal distances, substantial cause for concern as to the continuing fragmentation of *T. cristatus* metapopulations. Individual isolated ponds may have high breeding populations, though this may reflect a crowding effect, due to the paucity of alternative suitable sites in the area, rather than inherent site suitability. *T. cristatus* have been found to thrive most successfully in sites consisting of clusters of ponds in close proximity (i.e. < 500m inter pond distance). In such a system, viewing the pond cluster, rather than individual pond, as the habitat patch upon which sub-populations of a metapopulation are based, may be more appropriate than a "pond as patch" model (Jehle *et al.* 2005, Pannel and Obbard 2003).

3.5 Barriers to movement and migration mortality factors.

The multiphase life cycle of amphibians necessitates migration between terrestrial and aquatic habitats, and movement between varied terrestrial habitat for foraging, daytime shelter, winter dormancy and dispersal. Migration and dispersal carry increased energy costs and mortality risks, since much of the landscape matrix may be outside the species' niche, unsuitable or hostile (Holt 1996, Ims and Yoccoz 1997). Particularly for ground dwelling species of low vagility, the character of the landscape matrix, its level of permeability and connectivity heavily influence presence and population persistence. Research into newt dispersal and migration capabilities, and ability to traverse land cover of different types, is relatively sparse compared to aquatic preferences and terrestrial land cover correlates with presence and abundance at breeding sites. Most studies have (largely of necessity) concentrated on migrating adults (e.g. Franklin 1993, Madison and Farrand 1998, Jehle 2000, Jehle *et al.* 2001, Perret *et al.* 2003, Schabetsberger *et al.* 2004, Rittenhouse and Semlitsch 2006). Dispersal and migration of juveniles is under studied, largely due to the current impracticality of radio tracking juveniles. The few mark-release-recapture and PIT tagging studies of dispersing juveniles (e.g. Kupfer and Knietz 2000, Hayward *et al.* 2000, Cummins and Swan 2000, Malmgren 2002) have demonstrated dispersal capacity, but have thrown little light at all on what newts have been doing between captures. Few experimental treatments of the subject have been published and assumptions about newt capacity to traverse land cover of different types is therefore fraught with uncertainty (see, however, Rothermel and Semlitsch 2002 for an experimental investigation of movement capacity within various vegetation cover types of migrating juvenile salamanders). However, the assumption that areas suitable for foraging or shelter are also likely to compose the most suitable terrain for movement between ponds and breeding sites during seasonal pre and post breeding migration and dispersal seems reasonable in light of what evidence is available, communication with practitioners and field experience.

Limiters on amphibian dispersal ability are likely to include increased exposure to predation, desiccation, UV light, and physical difficulty in negotiating dense vegetation, such as dense ryegrass (*Lolium* var.) leys. Land cover of various types will fall, in the physical ability or behavioural preparedness of newts to traverse it, along a continuum ranging from complete aversion/total barrier effect to no barrier at all being presented and animals moving freely within it. Quantifying newt ability to traverse land cover, and identifying where along this continuum any particular land cover will fall remains largely in the realm of assumption based on limited evidence in the literature, practical experience (of where individuals are most frequently found), and ecological "intuition". This is, however, the subject of planned future research, not part of this study, at the Cholmondeley study area and Cheshire Wildlife Trust's Gowy Meadows Nature Reserve, Ellesmere Port. Frequent studies (see as examples Adriaensen *et al.* 2003, Drielsma *et al.* 2007a and 2007b, Driezen *et al.* 2007, Fahrig 2007, Liu 2008, Rodriguez-Gonzales 2008), including this one, have assigned multipliers to various land cover categories which are then applied in GIS to Euclidean distances traversed in crossing them, to generate a "cost surface" representing an approximation of the permeability of the landscape for the target species. It should be noted that buildings, in addition to restricting movement in some respects, particularly in the more intensive agricultural landscapes constitute an abundant source of refugia and may support large numbers of over wintering animals. An additional impact of arable in the context of the pastoral landscape, where it tends to take the form of crops such as maize grown for whole crop silage, fodder beet etc., or occasional grain crops is at least in part due to its unstable shifting nature, with land cover shifting between fodder crops and grassland as requirements change. In addition, over recent years, developments in grain commodity prices and new demands on arable production for bio-fuels have increased the area and altered the distribution of land under crops. This may significantly alter the permeability and connectivity of the landscape in some areas, certainly at local levels where land cover in close proximity or adjacent to breeding ponds is changed abruptly, and possibly on a cyclical basis, as was demonstrated at the Cholmondeley study site of this thesis.

Movement over appreciable distances frequently involves encounters with roads in the agricultural landscapes of northern Europe. Road traffic may be destructive to animal populations through a range of direct and indirect processes (Forman and Alexander 1998). Aside from direct fatality on the road, the fragmentation of populations and habitat (Mader, 1984; Mader *et al.* 1990; Andrews 1990; Groot Buinderink and Hazebroek 1996; Reed *et al.* 1996) and related genetic and behavioural effects (Shepard *et al.* 2008a), the effects of noise (Bee and Swanson 2007), vibration, disturbance by light pollution at night (Buchanan 1993) and pollutants such as salt, oil, and exhaust emissions impact negatively. Mortality resulting directly from movement across roads can be substantial (van Gelder, 1973, Oldham and Swan 1991). Kuhn (1987 - see also Reh and Seitz 1990) estimated 24-40 cars hour^{-1} killed 50% of migrating *Bufo bufo*, while Heine (1987, cited in Reh and Seitz 1990) estimated the survival rate could decline to zero at a rate of 26 hour^{-1}. Fahrig *et al.* (1994) demonstrated possible depression of anuran population densities due to the effects of road traffic in Ontario, Canada, by showing significant negative correlation between population density and traffic intensity in areas of otherwise similar habitat composition and quality. Though other factors may be important, direct mortality rates would seem likely to vary spatially to a substantial degree, with diurnal variation in rates of traffic flow – newt movement being preponderantly at night, when traffic levels in rural areas tend to be reduced considerably even on major roads. Other disturbance factors may make substantial contributions at long distances –

which may be surprisingly long, Houlahan and Findlay (2003) demonstrated impacts associated with increasing road density even as distant as 3000 and 4000m on species richness and occurrence respectively. Herrmann *et al.* (2005) in their New Hampshire study, did not find any significant effect on species richness of density of roads at smaller scales, and found it difficult to disentangle road density from forest cover, strongly correlated at larger scales (more than 750m).

Vos and Chardon (1998) demonstrated a significant negative effect of road density on the occupation probability of ponds by moor frogs (*Rana arvalis*) in the Netherlands. They found that road density strongly affected the likelihood of pond occupation in 55% of their study area with occupation probability lowered to less than 30% of that expected in some areas. Hels and Buchwald (2001) studied the diurnal movement patterns of six amphibian species, including *T. cristatus*, for five breeding seasons between 1994 and 1998, addressing the likelihood of an individual amphibian becoming a road casualty and what fraction of the amphibian population is killed by traffic. They point out, citing also Huijser and Bergers (1997) and Mallick *et al.* (1998) that presence alone of a large number of individuals of a particular species as road kill may reflect the presence of a large and thriving population, rather than necessarily indicate the decimation of a struggling one. Mazerolle (2004) made a study based in New Brunswick, Canada, of amphibian road crossings and road kills on a road bordering 30 potential breeding sites for 11 species of amphibians between 1992 and 2002. Mazerolle was unable to detect any cumulative effect on amphibian abundance over the time period, though species dependent variation in change in numbers of fatalities with variation in traffic intensity was detected.

Hels and Buchwald's (2001) study differed from most in establishing the proportion of the population killed on the road and assessing the importance of this for population persistence, demonstrating a relationship between the probability of mortality on the road and the velocity of the animal, its diurnal activity pattern and traffic intensity and diurnal pattern. They concluded that the overall effect of road kills on population density would be dependent upon whether the main determinants of the regulation of the population were density-dependent (predominantly intra-specific competition, mainly among larvae) or density-independent (e.g. climate variables). Where density independent determinants prevail, road kill will tend to have an additive effect and thus be important in population regulation. If density dependent determinants prevail, road kill may be compensated for by increased larval survival and its impact negligible. At sufficiently high levels of road density, however, road mortality could reach levels where the population's reproductive output is reduced such that stochastic processes have increased importance for population persistence (Hels and Buchwald 2001).

3.6 Population persistence, decline and fluctuation.

Global amphibian population decline and species extinctions have been a particular spur to amphibian research over recent years (Alford and Richards 1999, Alford *et al.* 2001; Collins and Storfer 2003, Nystrom *et al.* 2007). Population decline can be considered straightforwardly as a protracted downward trend in numbers of individuals, but identifying or confirming this in species with high or even moderate levels of natural population fluctuation is problematic and, in some cases, fluctuating population sizes are not necessarily tightly coupled with the probability of extinction (Blaustein *et al.* 1994; Schoener and Spiller 1992). It is the complex interaction of a population's demography, environmental changes and the connectivity of populations on landscape scales that determine population persistence (Bolger *et al.* 1991; Hanski 1998b; Moilanen 1998, Marsh and Trenham 2000, Bascompte *et al.* 2002, Johst *et al.* 2003). The probability of local extinction should therefore be correlated with high population fluctuation and habitat alterations that have fragmented or isolated populations (Thrall *et al.* 2000), which as Gardener *et al.* (2007) and Cushman (2006) point out, seems a more convincing likely cause and perhaps more deserving of large scale research attention than the effects of some of the more novel stressors associated with amphibian decline (increase in UV exposure, novel pesticides and pathogens etc.).

Several authors have highlighted the deterministic nature (i.e. arising from long term or permanent degradation of the breeding site) of amphibian extinctions as opposed to stochastic (i.e. occasional chance occurrences in ostensibly suitable patches). Beebee (1997) noted that either pond destruction or introduction of fish could explain most recent disappearances of *T. cristatus* from dewponds in Sussex for example, and Hollinshead *et al.* (2010) showed that an apparent reduction of over 30% in pond occupancy by *T. cristatus* in the 2006 re-survey of Cheshire ponds recording presence in 1995/6 could be best explained by the arrival of fish and degradation of terrestrial habitat. Sinsch (1997) showed that local extinctions of Natterjack toads (*Epidalea calamita*) were due to habitat destruction. As observed previously, pond loss through natural succession is perceived as one of the major threats to *T. cristatus* populations, Sjögren-Gulve and Ray (1996) made similar observations in respect of Pool frog (*Rana lessonae*) populations. Skelly *et al.* (1999) found terrestrial habitat succession to be a key factor in explaining population turnover in amphibian assemblages in Michigan, USA.

Amphibian population persistence can be thought of as a storage model, with terrestrial adults and juveniles representing the storage stage. Terrestrial adults and juveniles have a limited "shelf life", however. Modelling the marbled salamander (*Ambystoma opacum*), the 10-year life span of which is similar to that of *T. cristatus*, Taylor *et al.* (2005) found the adverse effect of catastrophic breeding failure was relatively small: the probability of extinction due simply to catastrophic failures was just 2% in 50 years with a 50% annual risk of catastrophic failure. Clearly, this probability rises substantially for species with shorter life spans or breeding habitats with greater frequencies of failure. For pond-breeding amphibians generally, abundances would appear more sensitive to post-metamorphic processes than to pre-metamorphic ones (e.g., Marsh and Trenham 2001; Biek *et al.* 2002; Vonesh and De la Cruz 2002). Taylor *et al.*'s (2005) study of *A. opacum* supports the idea that modest reductions in terrestrial survival can jeopardize persistence. They concluded that if conservation efforts are to be successful, protection must be extended beyond the aquatic habitat, or even the immediately adjacent terrestrial habitat. Depending on factors that include life span and risk of catastrophic failure, amphibians breeding in incompletely predictable or vulnerable habitats may require management on spatial scales that encompass additional breeding ponds to offer good prospects for rescue or re-colonisation when the inevitable occurs.

A growing literature suggests that terrestrial habitat plays a key role in determining amphibian population dynamics. Schwartzkopf and Alford (1996) demonstrated the importance of shelter site quality as an important determinant in growth of *Bufo marinus* and Loredo *et al.* (1996) demonstrated the importance of ground squirrel burrows for *Ambystoma californiensis* (California Tiger Salamander), suggesting a strong negative consequence of their loss for the species. Skelly *et al.* (1999) make a strong case for the effects of succession in terrestrial habitat in terms of local extinction and in-pond population dynamics. In addition to local demography, terrestrial habitat characteristics may strongly influence regional dynamics. Marsh and Trenham (2001) summarised studies which have examined the influence of isolation of breeding ponds from terrestrial core habitats on breeding pond use. Where isolation from terrestrial habitat has been assessed it has been correlated with amphibian abundance or diversity in every case, and in several (e.g. Laan and Verboom 1990, Edenham 1996) terrestrial isolation effects were stronger than aquatic (pond to pond) effects so pond occupancy may be more indicative of the spatial arrangement of terrestrial habitat than that of breeding pond quality for some species at least (Marsh and Trenham 2001). Semlitsch (1998) used movement data for salamanders to estimate appropriate terrestrial buffer sizes for wetlands used by salamanders. Trenham (1998) found California newts (*Taricha torosa*) disperse over much longer distances between ponds and terrestrial habitats than between ponds. A pond based metapopulation study of these animals would therefore seriously underestimate the mobility of individuals, the spatial scale and habitats needing to be monitored or protected for conservation of the species.

Pond breeding amphibians, particularly species with apparently demanding habitat requirements and high pond dependency such as *T. cristatus*, may be particularly susceptible to demographic threats from habitat fragmentation and loss of connectivity. Many populations may be restricted to isolated habitat remnants, such as single isolated breeding ponds, which may result in dangerously low effective population sizes (N_e) at the landscape scale, with loss of alleles and genetic drift dominating structural dynamics (Jehle and Arnzen 2000). N_e is the most important determinant of the amount of genetic drift, with low N_e increasing the probability of population extinction (Newman and Pilson 1997). The N_e or the related parameter N_b (the effective number of breeding adults) for temperate amphibians breeding in small ponds has been variously estimated (Merrell 1968; Gill 1978b; Easteal 1985; Berven and Grudzien 1990; Scribner *et al.* 1997; Driscoll 1999; Funk *et al.* 1999; Seppa and Laurilla 1999, Jehle *et al.* 2001) as mostly below 100 individuals, with capture records and population estimates for *T. cristatus* recorded in the Cheshire *T. cristatus* Site Inventory (CTcSI 2006) supporting this level of estimate for *T. cristatus*. N_e and N_b are expected to be low when variance in female reproductive success is high, multiple matings are rare and the sex ratio is skewed (Nunney 1993, 1996).

T. cristatus (as with all European *Triturus* species) generally has a sex ratio of 1:1, with females often receiving spermatophores from several males (Halliday 1998), although Jehle *et al.* (2001) speculate that some elements of sub-optimal aquatic habitat quality could affect N_e, for example by disruption of spermatophore transfer in turbid ponds where the pond substrate is organic peats or mud. It follows that a key conservation objective from the point of view of maintaining high N_e (though not by any means the exclusive conservation concern) among *T. cristatus* populations should be maintenance, and appropriate enhancement where necessary, of landscape connectivity, thereby maximising access to breeding sites and potential N_e and N_b.

3.7 Dispersal and the terrestrial landscape

Amphibians have tended to be seen as highly philopatric organisms with limited dispersal abilities and short dispersal distances (Sinsch 1990; Blaustein *et al.* 1994, Duellman and Trueb 1994), which has led to the view that pond isolation, measured as some function of inter-pond distance and/or pond density, should be a key determinant of population viability (Laan and

Verboom 1990, Sjögren 1991, Bradford *et al.* 1993, Blaustein *et al.* 1994). Understanding the role of pond isolation is critical, as loss of breeding habitats and disruption of dispersal routes through terrestrial habitat, habitat fragmentation and degradation, leaves remaining habitats increasingly isolated from one another (Swan and Oldham 1993; Oldham 1994, Sjögren-Gulver and Ray 1996; Semlitsch and Bodie 1998). However, the dispersal capabilities of amphibians need not be as limited as has been suggested. Long distance dispersal is very difficult to detect, and what is more, concentration of survey time has (for understandable reasons of difficulty of detection in terrestrial environments) been on breeding sites rather than the extent of terrestrial habitat included in home ranges, estimates of which appear conservative in light of findings in Marsh and Trenham (2000), and Smith and Green 2005. The application to amphibian conservation is clear - assumption in favour of a metapopulation based conservation approach on the hypothesis of ponds as patches, and subsequent focus on protection of those patches without testing whether the habitat critical to the species survival was indeed encompassed, mean it is possible that the truly important terrestrial habitat may not be protected.

Dispersal capability is often underestimated in mark recapture studies (Porter and Dooley 1993). Szymura and Barton (1991) found, using genetic estimates of dispersal rates in fire bellied toads (*Bombina bombina*), dispersal distance estimates double those from mark-recapture studies, and that rare long distance movers may move up to 11 km. A number of studies of some of the better dispersing amphibians show dispersal distances sometimes exceeding 10 km. Although such long distance dispersal may be a rarity, it may significantly affect breeding habitat colonisation and patterns of spatial dynamics (Kot *et al.* 1997; Lewis 1997). In the specific case of *T. cristatus*, Swan and Oldham (1993) suggest a maximum inter-pond distance of 1.6 km, based mainly on analysis of distribution of occupied ponds, but with limited focus on availability and quality of terrestrial habitat. Studies of landscape composition effects have found relationships between land cover extent (typically forest) and amphibian presence at spatial scales ranging from 100m or less to 3000m in radii (Hecnar and M'Closky 1996, Knutson *et al.* 1999, Lehtinen *et al.* 1999, Guerry and Hunter 2002, Houlahan *et al.,* 2001, Trenham and Shaffer, 2005). Houlahan and Findlay (2003) examined amphibian assemblages at 75 wetlands (mean 66.7ha) in South-eastern Ontario, Canada looking at wetland characteristics and land use (road density, forest cover, building density, proportion of lakes or rivers, proportion of wetlands, and distance to nearest wetland) in 16 bands from 0-4000m from the wetland edge. Effects (not always significant and possibly confounded by spatial autocorrelation in wetland and forest dispersal) were identified at distances in excess of 2000m and as far as 3000m, around wetland proportion, forest cover and road density. Though a proportion of the species identified are known to migrate and disperse over distances significantly greater than *T. cristatus* (up to 2000m regularly) and are much more generalist and matrix tolerant than *T. cristatus*, and clearly land cover is not the only factor at work, the study does indicate that factors operating over local and landscape scales are an essential consideration, and that these operate at distances well in excess of the standard dispersal distances attributed to many amphibian species.

A number of amphibian metapopulation studies have found no detectable effect of pond isolation, while others have found significant effects (see Marsh and Trenham 2001). Two genetic studies (Reh and Seitz 1990 and Hitchings and Beebee 1997) found steep increases in genetic differentiation with increased inter pond distance, a common feature of these genetic studies being very disturbed habitats and urbanisation positively correlated with genetic divergence among populations. A number of other studies have found roads and urbanisation to be limiters of amphibian dispersal and abundance. In contrast, studies finding no significant isolation effect tended to be carried out in areas of relatively undisturbed inter-pond habitat (Gill 1978a; Berven 1995; Trenham 1998; Seppa and Laurilla 1999; Skelly *et al.* 1999). Studies looking at inter-pond dispersal in relatively undisturbed habitat have found dispersal rates in the order of 20% per generation (Marsh and Trenham 2001). As Marsh and Trenham (2000) observe, because many amphibian species appear to be well adapted for regular inter-pond dispersal, isolation effects may not be inherent aspects of amphibian spatial dynamics, for many species at least.

Semlitsch (2008), in a review aimed at differentiating between true dispersal, characterized as *"unidirectional movements from natal sites to breeding sites that are not the pond of birth and not part of the local population… tending to be greater in distance than for migrating adults, probably occur[ing] only once in a lifetime, and…inter-populational in scale"* (p262), and migration (pre- and post-breeding movement between terrestrial and aquatic habitats, and secondary migration between terrestrial habitats), made some observations of particular significance for this thesis. Here, Semlitsch cited an earlier study, Rittenhouse and Semlitsch (2006), giving estimates of extents encompassing core habitat based on kernel density estimations from radio tracking studies (averaged over 13 studies and 11 species) which included 50%, 95%, and 99% of populations, respectively yielding 93m, 664m, and 852m radii from the breeding site (see Fig. 4 below; from Semlitsch 2008). These distances indicated that the probability distribution of individuals migration distances is strongly skewed, with more individuals found close to the breeding site. This held even for more vagile species moving longer distances (such as frogs and toads), with 95% estimates still averaging only 703m.

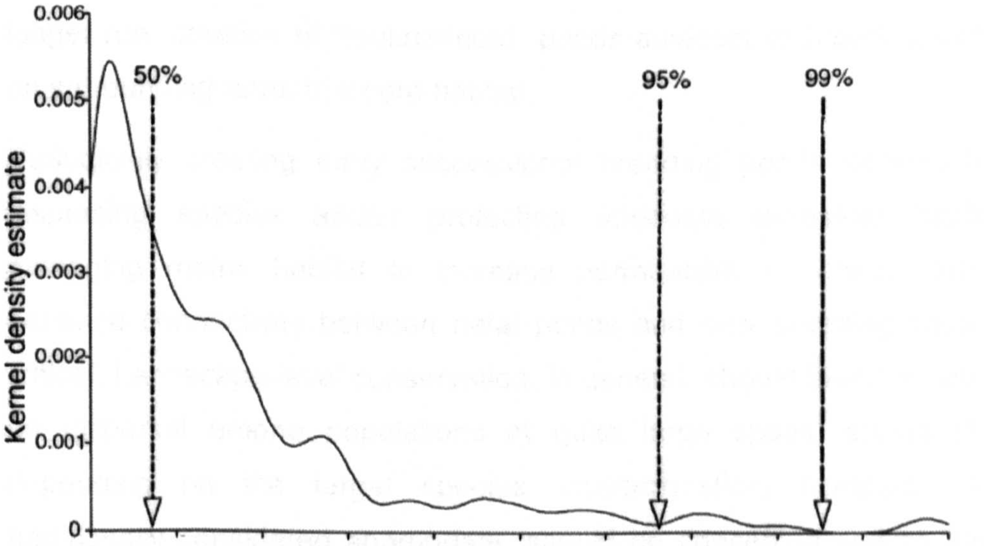


Figure 4; Univariate kernel density estimation of amphibian dispersal distances from 408 individuals from 13 radiotelemetry studies (composite estimate calculated from

1000 bootstrap samples drawn equally from each study to correct for sample size differences among studies), from Semlitsch 2008, after Rittenhouse and Semlitsch 2006).

Semlitsch (2008) therefore concluded that population-level conservation in general should be focused on spatial scales of less than 1.0 km from natal sites, with attention focused on the majority of the adult population nearest to them. Juvenile dispersal on the other hand, from direct observation of individuals and genetic evidence, may be seen to operate at different scales, and depending on species may operate at greater distances, with metapopulation-level processes occurring at distances in the region of 2.0–10.0 km (Smith and Green 2005). Zamudio and Wieczorek (2007) for example, demonstrated through fine-scale genetic analyses for spotted salamanders (*Ambystoma maculatum*), that non-random genetic structure occurs at a scale of approximately 4.8 km. There are significant management implications inherent in these findings. As Semlitsch (2008) observed, short-term sub-population level efforts might be best directed at the core terrestrial habitat of a local population, while long-term metapopulation scale efforts may be best focused upon larger scale connectivity among populations and improvement of intervening matrix habitat. For philopatric species with late successional requirements, resources might be best deployed through medium term management aimed at protection and restoration, and in the longer run, creation of "replacement" ponds adjacent to breeding ponds, and on surrounding terrestrial core habitat.

Periodically creating early successional breeding ponds needed by many dispersing species and/or protecting adequate terrestrial habitat, and managing matrix habitat to increase permeability or create corridors to enhance connectivity between natal ponds and new breeding sites may be critical. Landscape-level conservation, in general, should therefore be focused on dispersal among populations at quite large spatial scales (1–10 km depending on the target species' characteristics) compared to those traditionally considered appropriate, should be conceptualised as functioning over much longer periods of time than is often the case, and on the importance of pond density and spatial distribution, terrestrial habitat connectivity, and isolation effects due to land use (see also Marsh and Trenham 2001).

The strength of isolation effects may therefore be related not so much to pond density or inter pond Euclidean distance as effective distances as defined by the nature of the terrestrial habitat and the degree to which the intervening landscape has been altered by human activity such as agricultural intensification, forestry and development. Marsh and Trenham (2001) suggested that in many cases where inter-pond or pond cluster landscape disturbance and fragmentation is high, translocation into extinct or declining populations would be a more cost effective strategy for maintaining regional distribution and population persistence than mitigation, habitat and/or corridor creation. This may be the case for some amphibian species, and some highly disturbed and modified landscapes. However, the findings of Oldham and Humphries (2000), Edgar *et al.* 2005 and Lewis *et al.* 2007 suggest in most cases there is insufficient evidence for, and substantial evidence against, relocation success in the case of *T. cristatus*.

Semlitsch (2008) suggested that juvenile dispersal may be divided into a number of discrete events, allowing individuals time, in terrestrial habitat adjacent to the natal pond initially, to reach a body size making terrestrial movement more manageable than immediately upon emergence and enabling them to travel longer distances (of up to several thousand metres) with greater survivability. Movement in the first year he has suggested, is most likely into foraging habitat close to the natal pond, then to over-wintering sites. In the second or third year, when juveniles are larger, they may then move greater distances with higher levels of survivability, which is consistent with the observations of long distance colonisation, and arrival of more mature juveniles at new breeding ponds (Smith and Green 2005). Mullner (2001) observed in a study in Lower Saxony, Germany, what she described as "movement on a wide front" on the part of emerging *T. cristatus* juveniles, moving faster and further than and with equal directionality to adults (an unusual observation, since most accounts record amphibian juvenile movement as slower and shorter – see for example Sinsch 1997, Rittenhouse and Semlitsch 2006). The relatively large body size at metamorphosis of *T. cristatus* may make some individuals large enough to disperse overland without any delay. Studies examining dispersal of newt metamorphs may actually be looking at movement behaviour and distances during initial migration into the terrestrial environment, and not any one stage move to an ultimate destination.

Little evidence has been found to suggest that juvenile amphibians generally have specialized perceptual abilities to find new or alternative breeding sites (as opposed to returning to their natal pond in years subsequent to emergence for those domiciled around their natal pond), such as water-finding ability. Mullner (2001), however, did make observations of directionality towards woodland in particular which might indicate that juveniles exhibit target-oriented dispersal, i.e., directed movement toward a specific habitat (Sjögren-Gulve 1998), yet made no reference to correlation with movement patterns of *earlier* emerging adults (Malmgren 2002), which could also account for these observations. No study has been found of *T. cristatus* juvenile movement displaying patterns suggestive of searching behaviour (e.g. looping movements Heinz *et al.* 2006), and recorded behaviour appears either related to those of earlier emerging juveniles and adults, or (as with most amphibians) tends to be in directions perpendicular to the pond edge. Semlitsch (2008) proposes, as the simplest explanation, that newly metamorphosed individuals disperse from natal ponds in a random pattern relative to landscape features beyond the pond perimeter (i.e., acknowledging there is non-random dispersal at the pond edge). In the case of *T. cristatus,* this statement could be "fine-tuned" to include some tens of metres of pond adjacent terrestrial habitat in "pond edge", and apply mainly to later emerging juveniles, who subsequently find new or non-natal breeding ponds primarily by chance. This random dispersal hypothesis is consistent with Gill's (1978b) model where he proposed that the pattern of dispersal is best described by the probability of colonizing a new pond being likely a consequence of density of ponds in the landscape, distance travelled, barriers, and habitat resistance (see also Rothermel and Semlitsch 2002). By virtue of their numbers, a few individuals should occasionally reach ponds some kilometres away which is consistent with observations of long distance colonisation.

T. cristatus, as is with many amphibian species, is well adapted for regular inter-pond dispersal, and longer distance dispersal, though very difficult to detect, may be more of a feature of its population persistence than is frequently suggested. Studies of landscape composition effects for a range of amphibian species have found relationships between land cover extent (typically forest) and amphibian presence at spatial scales ranging from 100m or less to 3000m. The implication for conservation management is clear – that factors operating over *both* local (pond, pond cluster and adjacent terrestrial habitat) *and* landscape scales are essential considerations, and that these operate at distances well in excess of the standard dispersal distances attributed to many amphibian species. The probability distribution of an individual's migration distances is strongly skewed to the local, with more individuals found close to the breeding site, but less common longer distance dispersal may have a significant role to play in long term population persistence at landscape scales and long term time scales.

As outlined above, in order to provide suitable terrestrial habitat to support a *T. cristatus* population, an area must contain permanent areas of refuge habitat to provide hibernaculae and shelter, daytime refuges, foraging habitat and dispersal opportunities. Permanent refuge habitat may take a range of forms, such as underground crevices, old tree root systems, mammal burrows (abandoned or occupied), old walls, piles of stone, rubble or even fly tipped refuse. Hibernaculae may even simply be voids deep in loose soil, at or close to their summer resting places. At many sites, *T. cristatus* over winter in woodland, where tree canopy, shrub layer, herbage and debris help suppress levels of exposure to frost. At sites with high levels of scrub or woodland around the pond site, dense pond edge vegetation and a high density of potential refuges, adults and immature individuals are more likely to over winter close to the pond edge, or in the water body itself (Langton *et al.* 2001). Thick vegetation, tussocky rough grassland, scrub, woodland, hedge bottoms and ditch bank vegetation utilised as shady daytime refuges also serve as foraging habitat.

Recent EU Life project studies in the eastern Baltic (Rannap and Briggs 2006, Rannap and Briggs 2010,), provide the most detailed, comprehensive and recent studies of *T. cristatus* immediately pond adjacent habitat requirements. Rannap and Briggs (2006, 2010) examined the terrestrial habitat features in a 50m buffer around each surveyed pond (see table 4, below). They found that the composition of the habitat complex in the 50m around the pond was essential. Extensive grazing (χ^2= 3.87, p=0.049), contrary to findings in the UK (Swan and Oldham 1993) coniferous forest (χ^2= 7.84, p=0.0051), and deciduous forest (χ^2= 6.92, p=0.0085) and grassland in general (χ^2= 5.31, p=0.021) were the favoured constituents. The presence of deadwood appeared to have a positive, but not strongly significant effect (χ^2= 3.11, p=0.078). Urban areas, shrub (χ^2= 2.65, p=0.1) and cultivated fields (χ^2= 1.40, p=0.2) did not have any significant influence on occurrence. The presence of the above habitat classes beyond 50m out to a 500m buffer was not shown to have any association with *T. cristatus* presence (χ^2= 0.12, p=0.7). The proximity of the pond to forest was analysed and it was concluded that there was an association with nearby forest (χ^2= 7.10, p=0.0077), optimally between 2 and 80m from the pond, with occurrence declining at greater distances and if the pond was actually within the forest with trees on the margins. Herrmann *et al.* (2005) investigated the influence of landscape and wetland characteristics on amphibian assemblages in South-central New Hampshire, USA. Though there was substantial variation in strength of effect between species, species richness was most strongly associated with proportion of forest cover within 1000m, being low where this was less than 40% and high where more than 60%.

Table 4; Percentage of T. cristatus presence in relation to land cover within 50m of ponds (after Rannap and Briggs 2006).

Habitat type	n (ponds)	*T. cristatus* presence (%)
Deciduous forest within 50m	85	58.8
No deciduous forest within 50m	124	39.5
Coniferous forest within 50m	33	69.7
No deciduous forest within 50m	176	43.2
Dense shrub within 50m	62	38.7
No dense shrub within 50m	147	51
Deadwood within 50m	16	68.8
No deadwood within 50m	193	45.6
Fields within 50m	105	51
No fields within 50m	104	43.3
Grassland within 50m	68	58.8
No grassland within 50m	141	41.8
Extensive grazing, no agrochemicals within 50m	26	65.4
Intensive grazing within 50m	21	38.1
No grazing within 50m	140	49.3
Urban areas within 50m	30	50.0
No urban areas within 50m	146	46.9
In forest	82	47.6
Forest 2 – 80m from pond	41	68.3
Forest > 80m (100-400m)from pond	41	48.8
Forest > 80m (450-2000m) from pond	45	26.7

Conclusions to be drawn from the above review will now be summarised. Proximity of the pond to a river or substantial stream was found by Swan and Oldham (1993) to be the most important negative correlate with *T. cristatus* occupancy. This may reflect both a barrier effect to dispersal and increased potential for the presence of fish, major predators of newt larvae and possible competitors to adult newts for food. In the 2006 re-survey of ponds in Cheshire, a major factor in the increase in recorded presence of fish was proximity to streams or large drainage ditches from which fish (notably sticklebacks, *Gasterosteus aculeatus aculeatus* or *Pungiteus pungiteus*) could access the pond during flooding events. Populations frequently persist for long periods, though probably in suppressed numbers, in the presence of fish (Swan and Oldham 1993). Such ponds may represent "attractive sink patches", as larval production and subsequent recruitment is drastically reduced, while breeding adults may continue to occupy or re-colonise the pond due to failure to detect its unsuitability (see Delibes *et al.* 2001a and 2001b). The effect of the presence of ditches was found by the Swan and Oldham (1993) to be dependent upon the predominance of other habitat and landscape features in the landscape. Where ponds occurred predominantly in improved grassland or arable, the presence of ditches was associated with increased rates of *T. cristatus* occurrence, where they occurred within 10 – 500m of the pond site. This trend was reversed where the pond was located in unimproved grassland or woodland. It was suggested that this reflected the relative hostility of the land cover for *T. cristatus* migration, and that ditches were operating as corridors for movement in migration or dispersal. It could also be reasonably supposed that ditch bank vegetation and the water bodies themselves would provide additional suitable habitat for foraging.

Dispersal is commonly observed up to 500m, with uncommon records of greater distances such as 860m and 1290m, with metamorphs recorded more frequently migrating to neighbouring ponds. At most sites, the majority of adults probably stay well within 250m of the pond, with commonly recorded post breeding migrations with high directionality between 13 and 135m into refugia. Individual isolated ponds may have high breeding populations, though this may reflect a crowding effect, due to the paucity of alternative suitable sites, and *T. cristatus* have been found to thrive most successfully in sites consisting of clusters of ponds in close proximity. This information informed the selection of distances at which levels of connectivity and clustering were analysed using graph theoretic techniques later in this study. They also informed the buffer distances within which the composition of adjacent and surrounding terrestrial habitat were measured and analysed, and hypotheses with relation to association between *T. cristatus* presence and pond proximity, density and connectivity tested.

Analysis of this pond landscape was based on assessment of traversibility of the landscape for *T. cristatus*. There is likely to be a great deal of variation in connectivity both across the dispersal/migration distances examined and between the Euclidean and Cost Weighted conceptions of dispersal distance. This was assessed by the generation of a resistance surface in GIS, informed by the review above. Land cover types were assigned multipliers which were then applied in GIS to Euclidean distances to generate a "cost surface" representing an approximation of the permeability of the landscape for the target species. It was these Cost Weighted distances which were used in graph theoretic analysis of connectivity, and in the generation of buffers to examine terrestrial habitat availability around ponds. Road density was examined and the hypothesis tested that increasing road density is negatively associated with *T. cristatus* presence in the landscape of the study area.

Population persistence is determined by the interaction of demography, environmental changes and the connectivity of populations on landscape scales, consequently terrestrial habitat availability, configuration and quality plays a key role both locally and at landscape scales. *T. cristatus* is susceptible to demographic threats from habitat fragmentation and loss of connectivity. The availability of habitat – aquatic and terrestrial – on the Cholmondeley study site landscape will be examined through analysis of pondscape connectivity and of quantity and quality of terrestrial habitat available to individual ponds and within pond connected pond clusters. Variation between quantities of habitat available within pond clusters across the range of levels of connectivity investigated will be examined. Association and correlation between *T. cristatus* presence and proximity and quality of surrounding terrestrial habitat will be examined in the study area. Population-level conservation efforts need to focus on spatial scales of substantially less than 1.0 km from natal sites (within the 0 – 500m range from occupied ponds), with attention focused on the majority of the adult population nearest to them. On the other hand, from direct observation of individuals and genetic evidence, juvenile dispersal, and occasional adult transience, may be seen to operate at different scales, and, depending on species, may operate at greater distances, with metapopulation-level processes occurring at distances in the region of up to 10.0 km. Short-term sub-population level efforts are best directed at the core terrestrial habitat of a local population, while long-term metapopulation scale efforts may be best focused upon larger scale connectivity among populations and improvement of intervening matrix habitat.

For philopatric species with late successional requirements, resources might be best deployed through medium term management aimed at protection and restoration, and in the longer run, creation of "replacement" ponds adjacent to breeding ponds, and on surrounding terrestrial core habitat. Management of existing aquatic habitat (in favour of *T. cristatus*, effectively maintaining ponds at mid to late successional stages) may tend to lead to reduced or suppressed alpha, beta and gamma diversity (but should not be ruled out, especially in the presence of species of high conservation interest and specific habitat requirements satisfied by a given pond). However, for maintenance and enhancement of aquatic habitat availability, pond density and clustering, emphasis should be placed on pond creation in close proximity (ideally within 250m and up to 4-500m) to existing ponds, maintaining a broad pond age and successional profile across the landscape. The strength of isolation effects may therefore be best assessed not so much by analysis of pond density or Euclidean distance between ponds, or ponds and terrestrial habitat, as effective (Cost Weighted) distances and levels of connectivity and habitat availability across the pond landscape. It is from this stand point that the use of graph theory to analyse habitat availability and connectivity at both landscape and pond cluster scales proceeds. As a consequence of requirements in terms of dispersal and migration capacity, and avoidance of close proximity to negatively associated landscape features, precise spatial targeting of pond creation is required. It is this requirement which the use of graph theoretic analysis addresses through identification of key existing ponds (for sighting of new pond creation in close proximity) or locations for new pond creation (to enhance connectivity and habitat availability) are focused.

3.8 Modelling and Measuring Landscape Connectivity and Graph Theory

As seen above, definitions of landscape connectivity can be summarised as the degree to which landscape facilitates or impedes movement of species between source patches (Taylor *et al.* 1993, Tischendorf and Fahrig 2000a). This definition emphasises that connectivity depends not only upon landscape structure, but also upon species movement and behavioural characteristics (functional connectivity; Tischendorf and Fahrig 2000a and 2000b; Moilanen and Hanski, 2001). Patch connectivity is usually calculated as a measure of the cost to move between patches and is usually assumed to be a function of patch proximity, expressed as the Euclidean "straight line" distance between nearest neighbour patches, or sometimes as more complex measures, for example where all surrounding patches within a stipulated dispersal distance contribute to the measure of connectivity. In most cases, however, only structural measures are used and landscape characteristics of the between patch matrix are not incorporated. There is, however, a growing awareness of the importance of matrix characteristics for species movement (e.g. Wiens 1996, Tischendorf and Fahrig 2000a and 2000b, Moiainen and Hanski 2001, Ricketts 2001, Adriaensen *et al.* 2003, Schadt *et al.* 2002, Jules and Shahani 2003, Revilla *et al.*, 2004, Li and Wu 2010, Pereira *et al.* 2010,) and the effect of barriers (e.g. Verboom and van Apeldoorn 1990, Vos and Chardon 1998, Lesbarrères *et al.* 2006, Frantz *et al.* 2010).

More recent studies have examined the use of "least-cost" modelling as an approach to incorporating detailed geographical information (Nikolakaki 2004, Drielsma *et al.* 2007a, Janin *et al.* 2009, Decout 2010) as well as behavioural aspects, and species perceptual range (Pe'er and Kramer-Schadt 2008) into connectivity measures. "Least Cost" in this context refers to using a "Cost Weighted" distance surface, i.e. one in which measurable Euclidean distances are weighted according to the "cost" of movements, "cost" being a measure relating to factors such as the "friction" effect of resistance to movement afforded by land cover or behavioural aversion, physiological responses or elevated mortality rates due to movement through varying terrains. Least cost modelling as a tool is itself derived from Graph Theory, and tools and algorithms based on this concept are available "off the shelf" as part of the tool kits incorporated within most current GIS packages (e.g. ArcGIS 9.3, this study) as well as some specialised applications both commercially available and free for use (e.g. the Landscape Genetics toolbox for use with ArcGIS (Etherington 2011), and the Pathmatrix extension originally written for use with Arcview 3.2 (Ray 2005), and the underlying algorithms are similar to the method proposed by Knaapen *et al.* (1992) and outlined in Adriaensen *et. al.* (2003).

Graph theory is a well and long established analysis and modelling technique used in a range of disciplines to describe relationships and connections between objects and within systems. The application of graph theory usually takes place where studies are concerned with flows of energy, materials or information. Commonly, this has included transport route maps, computer networks, electrical circuit diagrams, molecular graphs, representations of internet connectivity and, perhaps most recently, social networks. Graph theory is particularly applicable to conservation biology and analysis of landscape connectivity, metapopulation function and genetic relatedness between populations. Graph based models in landscape ecology and landscape genetics provide a spatial representation of landscape that can be examined in relation to land cover and land use. Graph theory provides a clear mathematical framework, increasingly well understood by researchers and practitioners, for quantification of the impacts of land cover and management decisions on connectivity and habitat availability. Landscapes are represented as sets of nodes (e.g. habitat patches) and edges or connections (both structural and functional) between them. Attributes may be assigned to both nodes (such as for example habitat quantity and qualities, population size) and edges (directedness, i.e. directionality of flow, permeability, and energy costs of traversing the edge). Urban *et al.* (2009) reviewed several landscape ecological applications of graph theory.

Graphs have been used for representation of spatial relationships between patches of habitat (e.g. Urban and Keitt 2001) and among individuals within landscapes (e.g. Fortuna *et. al.* 2008), connectivity between Nature Reserves has also been modelled (e.g. Fuller *et al.* 2006). Graph theory has also been used to produce raster models of landscape where connectivity may be analysed and examined at the scale of individual raster cells (e.g. Adriaensen *et. al.* 2003, Drielsma *et al.* 2007b, McRae *et al.* 2008, Pinto and Keitt 2009). Galpern *et al.* 2011 present a review of studies using graph theory to model connectivity among habitat patches, and identify questions of conservation importance that can be answered by graph theoretic modelling, and discuss appropriate applications.

Graph theory particularly lends itself to analysis of consequences for connectivity and connectedness of addition or removal of connections (vertices) between landscape patches and addition or loss of habitat patches (nodes). If graph edges are taken as representing structural or functional connections within a landscape, they can be assigned attributes relating to Euclidean, or Cost Weighted Distance. Connections can be constrained by the weightings applied to edges, e.g. maximal or mean dispersal distances of target organisms, or probabilities of dispersal derived from mark-release-recapture or radio-telemetry studies. These may themselves be weighted according to a "friction" or "cost surface" relating to the preparedness of the organism to traverse different habitat types or matrix, allowing modelling of landscape connectedness and connectivity as perceived by the target organism. As the threshold of adjacency reduces edges or nodes are removed - the landscape as perceived by the target organism becomes more fragmented, the landscape graph becoming less well connected and potentially breaking into numbers of sub-graphs or components, themselves further fragmented as threshold distances decrease still further.

Habitat patches may have importance in the landscape in several different ways; most significant from the point of view of this thesis are:

- a patch may contribute towards the minimum viable area of particular habitat,

- a patch may influence overall recruitment, as a source or sink,
- a patch may contribute to the traversibility of the landscape, as an element in a corridor, or as a stepping stone.

Clearly, in each of these cases the contribution of the patch is in many ways determined by its connectedness with other habitat patches. Particularly in the latter, the importance of the contribution of the patch may be disproportionate to its inherent qualities, particularly if it constitutes a "cut-node" and its removal (or possibly creation) would cause major changes in connectivity. A small stepping stone patch could be crucial for connectivity, without directly contributing to recruitment in its own right, especially if this connectedness were to allow long distance rescue effects to manifest. The fully rounded out value of a discrete habitat patch can only be assessed therefore in a network context. The value of a patch in relation to natality, population size, or carrying capacity may be low, but it may still be important for the persistence of a species if its position within the landscape graph is extremely important for connectivity.

Keitt *et al.* (1995, 1997, see also Urban and Keitt 2001) analysed distance relationships among potential Mexican Spotted Owl (*Strix occidentalis lucida*) habitat patches, identified from satellite imagery of three states in the S.W. USA. Their analysis identified two distinct types of patches contributing to landscape connectivity. These were

- Large core patches providing regional dispersal routes largely because of their size and extent, operating as hubs within the landscape.
- Small stepping-stone patches contributing disproportionately to size or quality by virtue of spatial location, or network position as cut-nodes within the landscape graph.

Clearly, in this illustration of the principle, *S. o. lucida*, an avian species with long distance dispersal capacity, is a fundamentally different organism from *T. cristatus*, a terrestrial, strongly philopatric species of low vagility. However, the principle remains directly applicable to analysis of landscape, though at radically different spatial scales. The application of Graph Theory may be best suited to representation of landscapes that can be (from the point of view of the target organism at least) represented as discrete patches in a matrix that can be generally treated as non-habitat. However, the quality of intervening habitat (or mosaic landscapes) can be represented by careful integration of matrix quality into inter-patch distance by assignment of resistance values to each cover type through which the edge passes. This may be achieved by derivation of a "resistance surface" from resistance values attributed to cover types and permeability of relative barriers (such as roads of differing traffic density, or where culverts etc. are installed).

Nodes may be represented in one dimension as points, or two dimensions as polygons, the choice of which becomes more relevant with larger (map) scale – for smaller (map) scale analyses, say for example coral reef patches in the Pacific (Treml *et al.* 2008), point nodes are perfectly satisfactory given the vastly greater inter-patch distances compared to patch sizes. Where nodes represent elongate or very irregularly shaped patches, or patches have large area relative to inter-patch distance (and/or dispersal distances are short), node geometry is important, as using points (say patch centroids) may bias spatial location of nodes, thereby distorting inter-patch distance calculations. Two-dimensional geometry can be computationally expensive, but permits greater accuracy in calculation of inter-patch distances, because these can be calculated between patch boundaries. Node attributes are typically allocated after graphs are constructed using Euclidean or Least Cost weighted distances. They are then used as variables in calculation of graph connectivity metrics. Node attributes are generally used to weight calculation of patch importance, describing properties such as area, habitat quality or suitability, and as such seldom influence linkage except in the case of links representing flux as a function of node weightings (for example in metrics relating to habitat availability, and probabilistic measures of connectivity (see Pascual-Hortal and Saura 2006, Saura and Rubio 2010, Saura *et al.* 2011, Schick and Lindley, 2007). Graph metrics are required to quantify the connectivity of the graph. These may be classified as metrics of entire graph connectivity, metrics measuring properties of groups of nodes (components – sub graphs, and

compartments – designated sub-sets of nodes within a component or fully connected graph), or metrics assessing connectivity of single nodes.
Pascual-Hortal and Saura (2006) proposed that landscape connectivity be considered within the wider context of overall habitat availability in order to allow its successful application to landscape planning, and this approach has been developed through a series of subsequent studies at a range of spatial scales and resolutions. The approach recognises that for easy availability of a given habitat for a species, the habitat needs to be both abundant and well-connected at a scale appropriate to the species under consideration. Therefore, habitat availability for a species may be low if habitat patches are poorly connected, but also if the habitat is scarce despite high patch connectivity (Pascual-Hortal and Saura 2006). The habitat availability concept then, is based in considering a patch itself as a space where connectivity occurs, integrating habitat patch area (or some other attribute relevant to its intrinsic value as a habitat patch) and connections between different patches in a single measure (Pascual-Hortal and Saura 2006).

In their 2006 study, Pascual-Hortal and Saura put forward the Integral Index of Connectivity (IIC). This index showed improvement on previous indices in that it responded appropriately to relevant changes in network properties (including indicating lower levels of connectivity in response to increased fragmentation) and recognized the most critical landscape elements (patches, corridors) for maintaining overall landscape connectivity. IIC, however, as all of the indices considered in their 2006 study, is a binary index, i.e. each habitat patch pair is either connected (at whatever critical distance) or not, with no modulation of connection strength or dispersal feasibility (Cantwell and Forman 1993, Fagan 2002, Jordan *et al.* 2003). The binary model may be considered over simplified (see Moilanen and Niemenen 2002) since it ignores intra-patch connectivity and regards inter-patch connectivity as equally strong in all cases. Saura and Pascual-Hortal (2007a) therefore presented a new probabilistic index, Probability of Connectivity (PC). They illustrated its use and effectiveness with a case study on Goshawk (*Accipiter gentilis*) in Catalonia, north-eastern Spain and compared it with ten other indices, including IIC, testing against 13 criteria, including several relating to data format and interpretability of results (see also Li and Wu 2002), demonstrating improvement in that it indicated lower connectivity with increasing patch separation, attaining maximum value when a single habitat patch covered the entire landscape (an issue with many previous indices which in these circumstances considered connectivity to be zero, needing at least 2 patches for connection) and indicated lower connectivity with increasing fragmentation (assuming constant habitat area). Additionally, the index considered as negative the loss of a patch, connected or isolated, reduction in patch size (assuming no variation in other landscape pattern characteristics) and detected as *more* important the loss of larger patches (assuming no variation in other landscape pattern characteristics).

Higher importance was also detected for key stepping-stone patches (assuming no variation in other landscape pattern characteristics), and lesser importance of the loss of key stepping-stone patches, when the loss of the patch leaves most of the remaining habitat area connected (assuming no variation in other landscape pattern characteristics). Importantly as well, the index was able to handle patches which were adjacent or contiguous (yet distinguished from each other by some *bona fide* variation in inherent quality, or some other *fiat* consideration, such as ownership or protected status). Saura and Pascual-Hortal (2007a) concluded that most tested indices met some, but not all, of the criteria, but that the PC index was the only index that systematically fulfilled them all. The binary index IIC fulfilled all but two; being unable to deal well with adjacent patches and over simplifying patches connection (a feature of all such binary indices). Both indices tend (as do other metrics) to assign greater importance to larger patches. As stated above, habitat patches may contribute to connectivity and habitat availability in different ways, irrespective of patch size. To assess these Saura and Rubio (2010) presented methodological developments on the habitat availability concept and PC metric by partitioning it into three key components, based on the same concept and measured in the same units, which are directly comparable and can be summed within the unifying framework of PC, quantifying different contributions. PC is the probability that two points randomly placed within the landscape fall into habitat areas that are interconnected (in other words that an organism placed at a location selected randomly within the network could find its way from there to any given other randomly selected location) given a set of n habitat patches and direct connections (links) between them (Saura and Pascual-Hortal 2007a), see equation 1 below (from Saura and Rubio 2010).

$$PC = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n} a_i \times a_j \times p_{ij}^{*}}{A_L^2} = \frac{PCnum}{A_L^2} \qquad 1)$$

Where a_i and a_j are attributes of patches i and j. A_L is the maximum attribute across the landscape – if the patch attribute is habitat area, A_L is total landscape area, including both habitat and non-habitat. P*ij is the maximum product probability of all the possible paths between patches i and j).

If i and j are distant, or have weak direct connections, the shortest path will consist of several steps through intermediate stepping stone patches. Prioritisation and ranking of landscape elements (both patches and links) by their contribution to landscape connectivity and habitat availability can be calculated from the percentage of the variation in PC caused by the removal of each element from the landscape (Keitt *et al.* 1997, Urban and Keitt 2001 and Saura and Pascual-Hortal 2007a). PC is a relative metric. Absolute values of PC will be dependent on the definition of the study area boundary (A_L) and not the habitat pattern, and low values of PC may be obtained when habitat patches and total area are very small compared to the entire landscape extent.

Saura and Rubio (2010) partitioned PC into Intra, Flux and Connector fractions. The Intra fraction is the contribution of a patch in terms of intra-patch connectivity (i.e. the available habitat area, or some other relevant attribute, such as habitat suitability) provided by the patch itself. The value of Intra is therefore completely independent of how a patch is connected to other patches, does not relate to focal species dispersal distance, and is the same for a completely isolated or highly connected patch (intrinsic patch quality/area being equal). The Flux fraction depends both on the attribute (area, suitability etc.) - all other factors being equal, a patch with a larger area will produce more flux - and on its position within the landscape network. This fraction measures how well a patch is connected in terms of flux, but not the patches importance in terms of maintaining connectivity between the rest of the patches in the network. This is achieved through the Connector fraction, which measures the contribution of each patch or link to the connectivity of the network as a connecting element or stepping stone between other patch's. This fraction is therefore completely independent of area or any other attribute, and a certain patch or link will contribute to network PC when it is part of the best path for dispersal between two other patches. So, Intra measures intra-patch connectivity, or the significance to the network of the discrete patch; Flux and Connector measure inter-patch connectivity as related to a certain landscape element. A given habitat patch will have some level of importance due to one or more of the fractions because of its topological position in the network and its intrinsic characteristics.

At short dispersal distances Intra is the fraction which contributes most to overall habitat connectivity and availability (see Fig 5, below). Connector, reflecting the role of links and patches as stepping stones contributes most at intermediate dispersal distances. Flux tends to have a larger importance values than Connector, because removing a starting or ending patch will completely eliminate flux between them, while loss of an intermediate patch may reduce flux between start and end patches, but not necessarily impede it entirely, provided alternative paths exist after the element is lost. A particular patch may be of little importance as an origin or destination of dispersal flux, but be important as a stepping stone between other large, important or numerous patches, which would result in its Connector value being larger than its Flux value.

Figure 5; Relative contribution of the intra, flux and connector fractions of the Probability of Connectivity Index (PC), to the importance of landscape patches and links for connectivity and habitat availability as a function of median dispersal distance (from Saura and Rubio 2010).

Connector is a measure of landscape pattern which is to a great extent independent of area based prioritisation of habitat patches. There is some degree of correlation, however, because large habitat patches will probably fall between more of the other habitat patches in the network and provide a stepping stone between them. High values of this fraction suggest that the loss of the patch in question would have a large and negative impact on the overall connectivity of the network. Critical patches as determined by this metric may differ significantly from those based on their intrinsic habitat attributes alone, however, At very long or short dispersal distances, PC correlates strongly with patch area (Saura and Rubio 2010), since at very low dispersal distances, connectivity is low and intrinsic patch attributes become the dominant factor, while as dispersal distance increases, beyond a certain point determined by the characteristics of the dispersion of habitat patches, increase in species dispersal distance adds nothing to connectivity, and the role of intrinsic patch characteristics becomes more important.

Patches may play differing roles depending on their topological position and intrinsic habitat characteristics, in a given landscape and for a given focal species. For species with low vagility, or when examining interaction with the landscape at short distances (say in terms of seasonal pre/post breeding migration, or inter-terrestrial habitat patch movement, in the case of *T. cristatus*), habitat attributes within patches are much more important than the area made available through dispersal to other patches which may be weakly connected. For species with longer distance dispersal abilities, or when examining broader scale interaction with the landscape, such as post emergence dispersal, or at perhaps larger scales the dispersal behaviour exhibited by the probably relatively small percentage of individuals responsible for occasional long distance dispersal, habitat patches become utilised as part of a more or less functionally continuous habitat (at least within certain critical thresholds). It is at intermediate dispersal distances that Saura and Rubio (2010) found that individual patches and links can play a critical role, and their loss cause a significant drop in connectivity and habitat availability – indicated by higher values of the Connector fraction for the patch.

Baranyi *et al.* (2011) analysed thirteen commonly used graph indices and their performance in analysis of the forest habitat network of goshawks in NE Spain to evaluate how the patch rank orders derived from these indices differ from each other and identify which indices tend to quantify the same characteristics and which address topological characteristics not considered by the rest. They found that most of the variability in patch rankings can be captured by only three network indices. The largest group of redundant indices corresponded to those measuring flux received by a given patch. The connector fraction of the integral index of connectivity (IIC) and probability of connectivity (PC) indices stood out as quite unique by focusing on the way habitat patches act as connecting elements between other habitat areas. No particular landscape indicator in isolation, however, is able to single out the most important landscape elements. In practice, several measures, used simultaneously, will provide a more complete over view of the role of particular landscape elements in maintaining connectivity and in the functioning of ecological networks. They suggested that most of the variability in the patch rankings provided by the wide (13) set of indices they examined could be in fact captured by three different aspects: the amount of flux a patch is estimated to receive, the degree to which a patch is valuable in upholding the connectivity between other habitat areas different from itself, and the intrinsic patch attributes (e.g. habitat area or quality) that capture the non-spatial and network independent importance of a patch. These three aspects match very well the three fractions (intra, flux, connector) of the measures of habitat availability (reachability) at the landscape scale (*d*IIC, *d*PC).

The PC, Intra, Flux and Connector metrics can be utilised in decision making in terms of consideration of the relative importance of intrinsic habitat patch characteristics and the role of intrinsically sub-optimal patches occupying *important topological positions* for overall connectivity. They simultaneously quantify habitat availability and connectivity, minimising the risk of over weighting consideration of either patch area/quality or connectivity (Saura and Rubio 2010). If levels of inter-patch connectivity are not a serious threat to species persistence at the appropriate threshold of connectivity in a given landscape (say at the long or short dispersal distances mentioned above) then PC will prioritise habitat patches according to their intrinsic patch attribute and conservation funding and effort can be prioritised towards these. If patch connectivity is a major issue on the other hand, PC should provide adequate weighting for determination of key patches for connectivity, either existing in the landscape or for creation.

The application of the PC index values is, however, limited in that they are dependent on the definition of the study area boundaries, which in most cases are likely to be set arbitrarily around focal habitat patches (as with the focus area in this study), or within *fiat* bounded areas within which management is to take place, or research carried out. Also, very low PC values may be obtained in practice when the habitat patch areas are small (or attribute values of individual patches small) compared to the total landscape area (or total available attribute value) in the network, as is the case in this study, and as reported in Neel (2008), cited in Saura *et al.* 2011, both studies identifying PC values under 0.00001. Saura *et al.* (2011), further developed the approach through the concept of Equivalent Connected Area, where the patch attribute considered is habitat area (ECA) or Equivalent Connectivity (EC), where the patch attribute is suitability, carrying capacity or some other appropriate variable. EC/A is much more easily interpreted in the context of identifying and quantifying the effects of temporal change, or evaluating modelled changes.

EC/A is defined as the size or attribute value of a single habitat patch (maximally connected) that would provide the same value of PC as the actual habitat pattern in the landscape. EC/A value will not be smaller than that of the largest/highest attribute value patch in the landscape, avoiding the very low values that may be generated with PC, and will coincide with the habitat area/attribute existing in the landscape when connectivity is maximised (all the habitat is confined in a single habitat patch with no fragmentation, or when the habitat is dissected into different patches but there is maximal inter-patch connectivity). EC/A takes into account the connected area existing within the habitat patches, the estimated dispersal flux between different habitat patches in the landscape, and the contribution of patches and links as stepping stones or connecting elements that uphold the connectivity between other habitat areas (Saura and Rubio, 2010, Saura *et al.* 2011). The EC/A index shares units (of area/suitability) with the patch attribute while at the same time maintaining the properties and appropriate reaction to spatial changes it derives from PC (Pascual-Hortal and Saura, 2006; Saura and Pascual-Hortal, 2007a; Saura and Rubio, 2010, Saura *et al.* 2011). The relative variation in EC/A after a particular spatial change (or set of changes) in the landscape (*d*EC/A, defined as the difference between the EC/A value after and before the spatial change, divided by the EC/A value before that change) can be directly compared with the variation in the total habitat attribute in the landscape after the same change (*d*A).

The inputs for analysis in CS2.5.8 are both the spatial structure and configuration of the landscape mosaic and the movement capability of the focal species (e.g. dispersal distance). Outputs consist of statements of overall indices for the network and node importance indices and/or fractions according to user specification, and delineation of components (groupings of connected nodes, and unconnected nodes). Both inputs and outputs consist of numerical delimited text files generated by or incorporated into GIS. Habitat patches are prioritized by their contribution to landscape connectivity, providing objective criteria for the selection of the most critical habitat areas for landscape conservation planning purposes (whether these are already existing, or for evaluation of planned habitat creation sites). For these purposes, connectivity is conceptualised with the assumption that probability of direct dispersal between nodes is calculated as a decreasing exponential function of inter-node distances (in this case, for *T. cristatus*), such that a distance of 130m corresponds to a probability of .75, 250m corresponds to a probability of 0.5, and probability approaches 0 at 1000m (see Fig. 7, page 103, after Saura and Pascual-Hortal 2007b).

3.9 Pond clustering and resistance multiplier estimation

For the purposes of this study, a pond cluster is defined as a grouping of two or more ponds with an inter-pond distance equal to or less than a given value of either "strait line" Euclidean, or "Cost Weighted" distance (in this study 130m, 250m and 500m). Clearly, migration and dispersal may occur at distances less than or in excess of and intermediate to these distances, the intention is the delineation of aquatic and terrestrial habitat most likely to be functionally connected at the most commonly observed dispersal and migration distances, and within and between which the exchange of individuals and genes is most likely to take place. Thus, the ponds constituting a given cluster, together with adjacent terrestrial land cover (at Euclidean or cost weighted distances based on estimated "friction" or "resistance" effects of movement through varying land cover) may be considered as actual (where occupied by *T. cristatus*) or potential habitat patches of varying size and quality.

Clearly land-cover varies spatially, as will perception of it by a target species as habitat or inhospitable matrix. Sometimes this variation may present as a continuous gradation at a land-cover boundary, e.g. from grassland to scrub, sometimes as a binary distinction between classes e.g. vegetated field margin to ploughed field - either habitat or matrix with no gradation at boundaries. This in itself is a scale dependent distinction. At scales perceptible to humans and larger vertebrates the vegetated margin/ploughed field interface presents as a distinct binary boundary, but at scales experienced by smaller vertebrates and invertebrates may be perceived as a continuous gradation, or a patchy, "fuzzy" margin. Problematically, published cases are rare in which detailed study and measurement of the "friction effect" of different land-cover types on the movement of a given species are recorded. Friction values are therefore frequently estimates, based on the best available evidence in the literature, the field experience and knowledge of the researcher, personal communication with practitioners and researchers in the field and judgements regarding data resolution and reliability (but see Epps *et al.* 2007, and Wang I.J. *et al.* 2009 and Wang Y-H. *et al.* 2009 for examples of use of landscape genetics to throw light on this, as is planned at the Cholmondeley study area in a future study subsequent to this thesis). The estimation must take into account all factors affecting the species' ability to traverse terrain (degree of physical resistance, behavioural aversion and physiological responses to environmental conditions associated with different land-cover types), but more complex models, based on many criteria, do not necessarily produce more reliable results and frequently obscure the uncertainties of the modelling processes, giving the impression of improbable or impossible levels of precision. Development of resistance values is generally an inexact process.

Resistance multiplier values are applied to the land-cover map of a study area to produce a "friction" or "resistance surface"; this "surface" is then applied as a multiplier to Euclidean distances to produce a "cost weighted" or "effective" distance surface. The surface can then be interrogated in GIS to generate cost weighted point to point measurements, distance buffers etc. Measures of a given Euclidean distance will generate identical or similar buffers (of equal area and perfectly circular at the designated distance from a point feature, or of irregular shape and area but with a boundary equidistant from the perimeter of a polygon feature). Those calculated using a cost weighted surface are likely to be complex in shape and highly variable in area and perimeter, reflecting variation in the resistance values of the surface and the heterogeneity of the underlying land cover (see Figure 6 below).

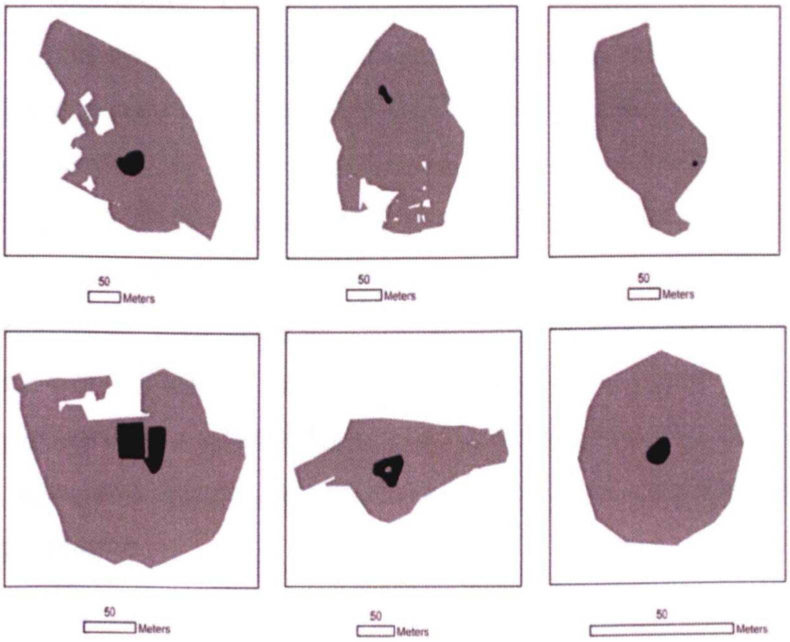


Figure 6; Typical Cost Weighted distance buffers (grey) at 250m effective distance from pond polygons (black). Note areas internal to buffers considered inaccessible, i.e. "beyond" the buffer distance due to land cover characteristics (white in grey).

Conceptualised as a binary state (connected / not-connected), at inter-patch distances below a certain threshold level patches are considered connected, or not-connected where this threshold distance is exceeded. Conceptualised as a probabilistic process, all patches are potentially connected, but with the strength of the connection mediated by some level of probability, a function of distance moderated by difficulty or cost associated with traversing the distance. In this study, both these conceptualisations are explored and utilised, since while the probabilistic conceptualisation is clearly a closer approximation to actual situations, the binary concept has utility from a planning perspective, and is that in common application in census and survey. The distribution curve identified by Semlitsch (2008) and Rittenhouse and Semlitsch (2006) can inform estimation for modelling purposes (when considered in conjunction with the current state of knowledge of the dispersal capacity of *T. cristatus*, from radio tracking and mark release re-capture studies), of dispersal probabilities. At the finest spatial scale (within which the majority of individuals utilising a pond for breeding purposes could be expected to find daytime shelter, forage and occupy hibernacula over winter), inter-pond distances of <130m, inter-patch/pond migration may be expected at a very high probability (0.75 and higher). At the intermediate spatial scale, <250m, a high (0.75-.5) probability of inter-pond dispersal could be expected, for example particularly in successful breeding years, or periods of heightened density dependent intra-specific competition). At the coarser spatial scale, <500m inter-pond distance over which inter-pond migration and dispersal is commonly observed, a substantially less frequent probability (0.5-0.25) can be expected, with, at distances in excess of 500m, probability approaching 0 with increasing distance.

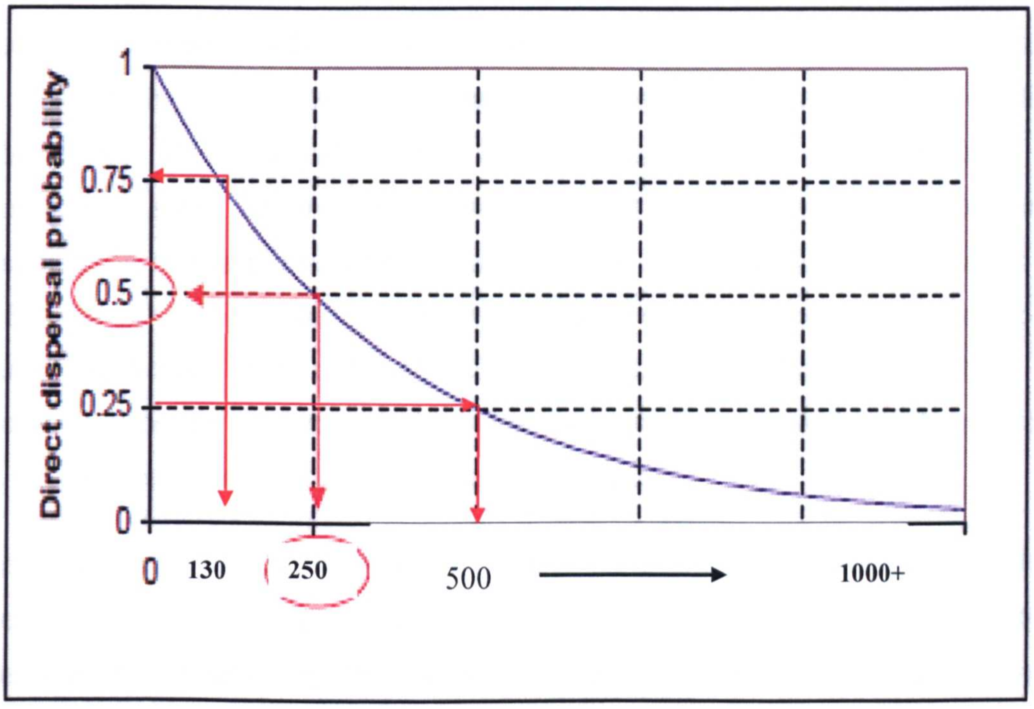


Figure 7; The probability of direct connectivity between nodes calculated in CONEFOR Sensinode 2.5.8 beta (CS2.5.8) as a decreasing exponential function (after Saura and Pascual-Hortal 2007b).

3.10 Habitat patch Quality/Suitability weighting

The analysis carried out in this study will examine patch connectivity, and also habitat availability which this connectivity generates. Consequently, a measure of habitat quality, or suitability, is applied to each node/patch. The measure used in this study is the well-established Habitat Suitability Index for *T. cristatus,* which was originally developed by Oldham *et al.* (2000), and its assessment subsequently modified slightly in light of field experience (Amphibian and Reptile Groups of the United Kingdom (ARGUK) 2010). HSI is a numerical index with values between 0 and 1 (0.01 is used as the lowest SI score to avoid scores being reduced to 0 during calculation of the final index, see below), 0 indicating completely unsuitable habitat, and 1 representing optimal habitat. Ponds with high HSI scores are statistically more likely to support *T. cristatus* populations than those with low scores – HSI is a supporting tool for survey, rather than a substitute for it, and is not sufficiently precise to conclude that any particular pond with a high score will support newts, or that any pond with a low score will not. There is, however, a positive correlation between HSI scores and the numbers of *T. cristatus* observed and in general; high HSI scores are likely to be associated with greater relative abundance of *T. cristatus*. HSI is not necessarily a good predictor of population size, as the relationship is not sufficiently strong to allow estimations of the abundance of newts in any particular pond. Calculation of HSI is of value in assessment of general pond suitability, comparison of pond suitability across and between different areas, evaluation of suitability of potential receptor ponds and identifying habitat management priorities, which is the context in which it is employed in this study.

To summarise the key findings of extensive literature review: the key terrestrial determinants of *T. cristatus* presence in ponds are identified as high pond density and connectivity (the latter defined by areas of uncultivated land - grassland, scrub and woodland), with presence and abundance increasing with area of woodland and rough grassland. Presence and abundance increase with levels of cultivation within the landscape at low to intermediate levels. Increased presence of *T. cristatus* is seen to be associated with close proximity to both nearest neighbouring ponds and ponds with recorded *T. cristatus* presence, and high pond density (presence increasing significantly above 3 km^{-2}), and with close proximity to adequate quantities of core terrestrial habitat. Distance from the nearest road appears to be negatively associated both in terms of barrier effects of the road itself, and the increased likelihood of fish introduction associated with close proximity to roads; it is hypothesised that presence will decrease with proximity to roads and increase in road density. Monitoring and mitigation guidelines relating to *T. cristatus* (e.g. English Nature 2001) refer frequently to Euclidean measurements of distance (e.g. distance to nearest neighbour pond, distance to nearest terrestrial habitat), frequently, however, effective distances as experienced by the species, in terms of behavioural and physiological "resistance" to movement may be underestimated using Euclidian measures of distance. It is hypothesized that levels of connectivity demonstrated at Cost Weighted distances will be significantly less than those displayed at Euclidean distances. This has key implications for consideration of likely long term persistence of the species at individual breeding sites (ponds or pond clusters) and within landscapes.

High levels of connectivity and connectedness may mean that a pond can play an important role in species persistence, despite low levels of intrinsic suitability as a habitat patch in themselves. It is hypothesized that levels of connectivity demonstrated at Cost Weighted distances will be significantly less than those displayed at Euclidean distances. However, in the context of a pondscape with a high proportion of shaded-out ponds, rendered unsuitable by seral succession and management changes, long term declines in habitat availability, despite high levels of connectivity, will eventually result in decline and local extinctions. It is hypothesised that a high proportion of ponds within the study area landscape will be subject to high levels of shade, and that this will be negatively associated with *T. cristatus* occupation. The Habitat Suitability index, a general indicator of habitat quality/suitability (ARGUK 2010) was used as a habitat quality weighting in calculation of habitat availability and connectivity indices. HSI score in relation to *T. cristatus* breeding presence was examined, testing the hypothesis of increased HSI score being associated with increased breeding presence across the study site.

Chapter 4 Study Area and Surveys

4.1 Study area requirements and identification

This section describes the field study area, the criteria for the selection of which were that the site should:

- be of sufficient extent to encompass several land holdings,
- comprise a landscape typical in character of the lowland UK range of the target species *T. cristatus* (i.e. a pond rich pastoral landscape mosaic of small fields, hedgerows and scattered small woods).
- be readily accessible for survey of terrestrial and aquatic habitat.

Candidate sites/areas were, in descending size order (see Fig. 8 below);

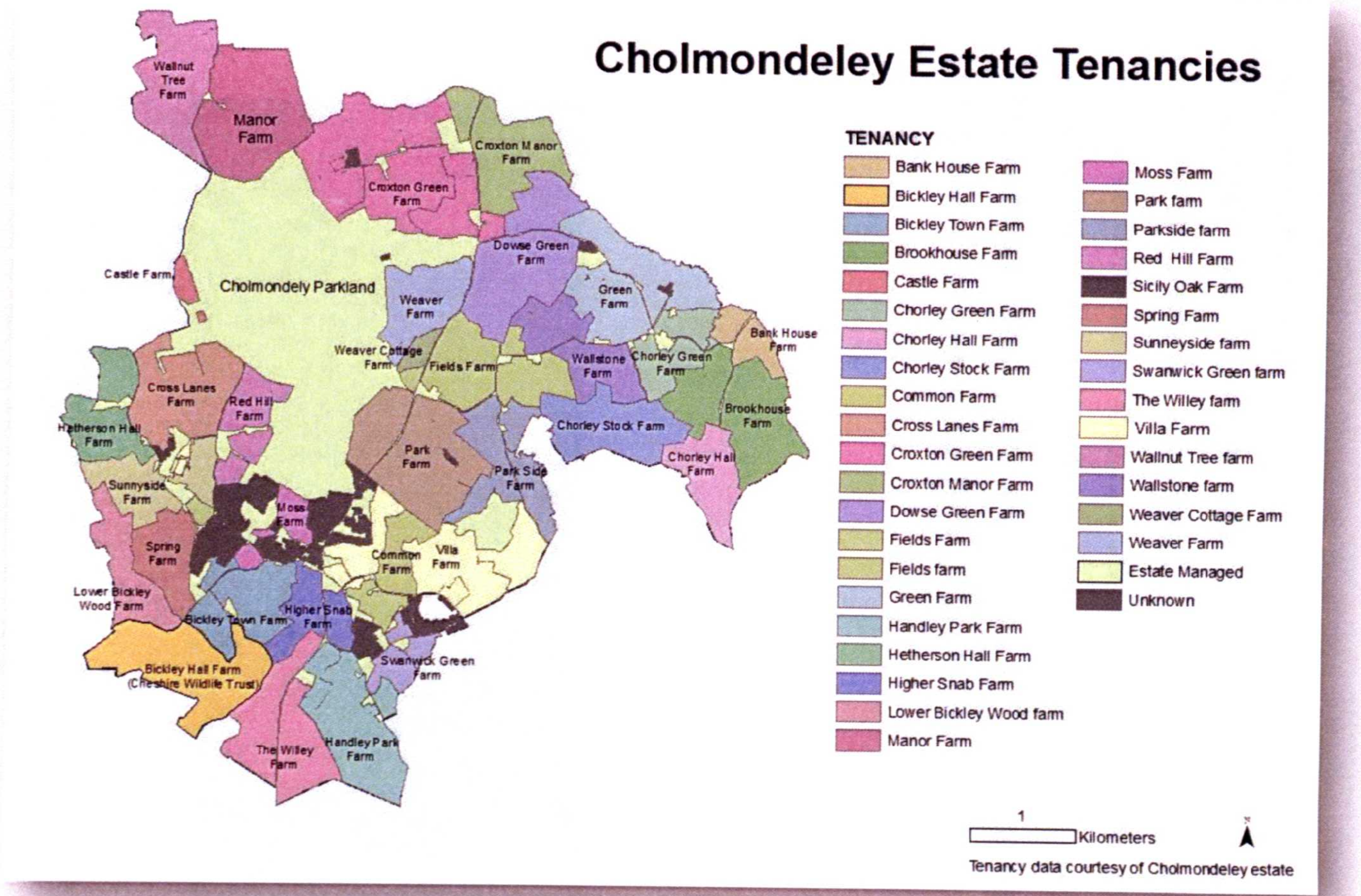
- One of three areas of appropriate size selected for typicality from within an extensive area of North East Wales, including Flintshire, Wrexham and lower lying Northern parts of Denbighshire, for which historic *T. cristatus* data (presence and breeding, though no demographics) were available through contacts in Countryside Council for Wales (CCW), and for which extensive (and at the time recent) Phase 1 Habitat Survey data were available.
- A large estate in South Cheshire, the Cholmondeley Estate owned by the Marquis of Cholmondeley, with a total land area of approximately 4,700 ha, for which very limited *T. cristatus* survey data (presence and breeding, no demographics) were available from the Pond Life Project and Cheshire *Triturus cristatus* Site Inventory databases.
- Shotwick Park, near the villages of Shotwick and Saughall, close to the Welsh border in West Cheshire, approximately 1,150 ha, owned at the time by Chester City Council. Some habitat and hedgerow survey, and extensive pond survey (including *T. cristatus* presence/breeding records, no demographics), had been carried out by the Farming and Wildlife Advisory Group (FWAG) in conjunction with the Pond Life project, and these data were available to the author.

Figure 8; Candidate study sites, NE Wales, Cholmondeley, Shotwick Park.

Use of the whole NE Wales study area for a lower resolution study was examined in detail, but rejected despite the attraction of comprehensive coverage of recent Phase 1 Habitat Survey. Three smaller areas were examined in detail; however, the quality of *T. cristatus* data which was made available, though reliable as species identification and distribution data at 1km tetrad resolution was of insufficient spatial precision to be usable to the high resolution, small map scale, and pond specific study envisioned. Work done in preparation was written off and the areas rejected. The area, and the associated *T. cristatus* data, later became the focus of a larger, lower resolution GIS habitat suitability modelling exercise examining determination of FCS, to which the author contributed data and observations on the structuring of habitat suitability modelling (Amphibian and Reptile Conservation and Cafnod 2010).

The Shotwick estate (SJ 3571), had the benefit of being both compact and distinct, being comprised of a number of contiguous tenancies, the holdings overall being owned by Chester City Council. Most had long standing tenants (though vacant tenancies were a problem on the estate at that time, as with many local authority owned farms). Survey and field work would be facilitated by detailed mapping and previous survey of terrestrial and aquatic habitat, and proximity of the site to the author's home. However, the Local Authority was extremely uncooperative and uncommunicative, and their relationships with tenants seemed problematic. It was initially felt that the difficulties this was likely to generate could be overcome, and significant work towards the pre-survey desk exercise was carried out in preparation, however, this proved not to be the case. Ultimately, the problems regarding access and cooperation outweighed the intrinsic benefits of the estate as a potential study area, so the work done was written off and the site rejected.

The Cholmondeley Estate (SJ550 507) was significantly larger (around 4,000 ha total area including non-estate owned land within the estate's external boundary, extensive mixed and coniferous plantation woodland, parkland and formal gardens and several sizeable meres), but with a broadly similar tenure arrangement. The number of tenants varies (it was at the time of site selection declining, with average holding size increasing), but during the time of survey some 27 tenants were leasing their holdings from one landowner (see Fig. 9, below), Cholmondeley Estates. Bickley Hall Farm, to the Southwest margin of the estate, is leased by Cheshire Wildlife Trust and was included in the survey. The Cholmondeley Estate supplied details of property boundaries and tenancies and a letter of introduction to tenants and estate staff, operating in a classic "gate keeper" role, and greatly facilitating the work. No extensive Phase 1 Habitat data were available, and little *T. cristatus* presence/breeding data were available. That which was, mainly relating to a few ponds in the North of the estate, was contained in the CTcSI, arising from survey carried out by United Utilities prior to infrastructure development work, and the Pond *Life* Project data base.



Tenancy data courtesy of Cholmondeley estate

Figure 9; The Cholmondeley Estate and tenancy boundaries.

4.2 Cholmondeley Estate

The Cholmondeley Estate was eventually selected as the study area because of its typical lowland pastoral landscape (see Figs 10 to 13 below), its compactness, and cooperation forthcoming from the estate manager and tenants and consequent manageability of extensive survey. The estate is situated straddling the boundary between the newly created unitary authorities of Cheshire East, and Cheshire West and Chester, which were established with the abolition of Cheshire County Council and its six district councils (previously - and at the time of the survey - the estate straddled the boundary between the Crewe and Nantwich District Council and Chester City Council). It lies to the Northeast of Malpas and to the West of Nantwich, and includes the small settlements of Croxton Green, Dowse Green and Chorley. Nearby villages include Bickerton to the Northeast, Bulkeley to the North, No Man's Heath to the Southwest, and Bickley Moss to the South.

Figure 10; A typical view across the Cholmondeley Estate N. towards higher ground at Bickerton, central background (author's photo).

Figure 11; A typical view across the Cholmondeley Estate SE towards Chorley from a point close to the Cholmondeley castle gate house on the A49 (author's photo).

Figure 12; Looking NW towards higher ground at Bickerton (central background), (Photo John Mulder).

Figure 13; Holsteins graze on the margins of a large field pond, Dowse Green Farm (T. cristatus eggs were found in low numbers on Myosotis scorpioides), (author's photo).

4.2 Topography, geology, drainage, roads and pondscape

Topography

As would be expected from a site situated on the Cheshire plain and selected, at least in part for its typicality, the area consists of essentially low lying, gently rolling grassland between approximately 60 and 180m, mainly below 100m above mean sea level (see Fig.14, below, Figs 10 – 13 above). The general slope of the terrain trends from Northwest to Southeast.

Figure 14; Topography of the Cholmondeley Estate.

Underlying superficial geology

The superficial geology of Cholmondeley estate is also broadly typical of the Cheshire plain, consisting of glacial deposits (diamicton) with fluvial deposits and pockets of peat within the heavier, less freely draining clay soiled areas to the north east, west and south of the estate (see Fig. 15, below). Areas of sand, gravel and peaty pockets run north/south through the centre, and along the southern margins of the estate - the central area being the location of several meres and an extensive conifer plantation, itself the site of a mere drained in the late eighteenth century and established as woodland in the nineteenth (Hall, J. pers. comm., June 2007).

Figure 15; Superficial geology of the Cholmondeley Estate.

Surface Drainage.

The trend of drainage is from NW to SE, following the general slope of the land, and several large meres are significant landscape features (see Fig. 16 below). Drainage features shown in Figure 16, are those considered to potentially constitute substantial barriers to *T. cristatus* dispersal and migration (i.e. large standing water bodies and moving water). Smaller tributary streams and drainage ditches occur throughout. The extreme southern boundary of the estate is defined by a section of canal. Though occasionally substantial landscape features, drainage ditches are not generally considered barriers, and indeed may reasonably be hypothesised as dispersal/migration corridors for *T. cristatus*. They are utilised for feeding and occasionally breeding where flow rates are slow or negligible (though this is not recorded at Cholmondeley). Breeding success in these circumstances, given the high probability of presence of predatory fish such as Stickleback (*Gasterosteus aculeatus aculeatus* or *Pungiteus pungiteus*), is likely to be low however. The small rivers and streams on the estate are relatively fast flowing in all but the driest periods and are likely to constitute barriers to dispersal, though the effectiveness of this barrier effect is difficult to establish, and the target of future planned research on the estate using landscape genetics techniques, outside the scope of this study. The likely major effect of both drainage ditches and moving water in the form of rivers and streams on the distribution of *T. cristatus* across the estate would seem to be depression of breeding success and pond occupation by acting as vectors for dispersal and sources (in times of flood) of fish, in particular Sticklebacks (*Gasterosteus aculeatus aculeatus or Pungiteus pungiteus*). Angling fish are present in larger ponds throughout the estate, and are more likely introduced by deliberate human agency (also the case for Goldfish *Carassius auratus auratus* in a few ponds adjacent to roads and close to settlement).

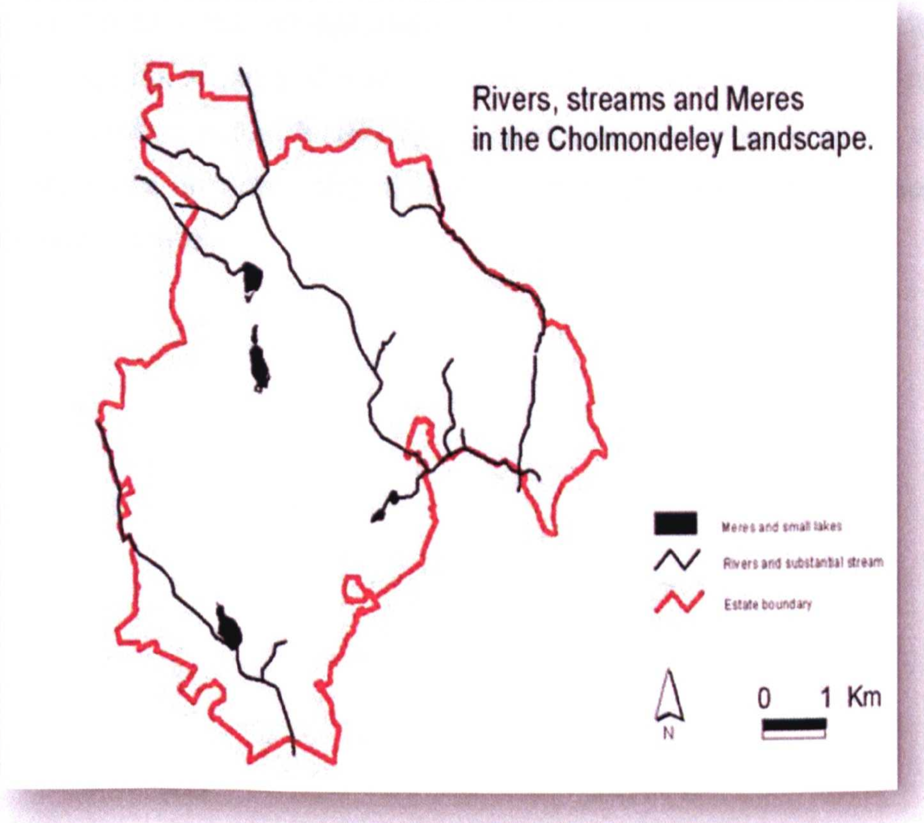


Figure 16; Major surface drainage features of the Cholmondeley Estate.

Roads

The estate is traversed by a number of roads, though while there are some substantial metaled roads carrying heavy traffic - both in terms of volume of traffic flow and vehicle axle weight - the only one felt likely to represent a substantial physical barrier to dispersal and migration (due to width, structural features and traffic volume day and night) is the A49, running generally N-S through the estate (see Fig. 17 below). The majority of metaled roads are narrow, often single lane tracks, carrying low or very low traffic flows even during the day, and little if any after dark. Night time traffic flow rates (i.e. at the times most likely to impact on *T. cristatus* movement) are low in this rural area, by-passed as it is by a number of major routes. The A49, however, retains a substantial rate of flow with a substantial proportion of traffic being multi-axle heavy goods vehicles during the night, with obvious impacts from chemical, noise and light pollution, and heavy ground vibration. There is substantial potential for disturbance of and collision with animals attempting a road crossing. Avian and mammal road kill was very much in evidence during survey, though actual fatality rates, particularly for small animals such as *T. cristatus,* are unknown and difficult to establish (though see section 3.6 and references therein).

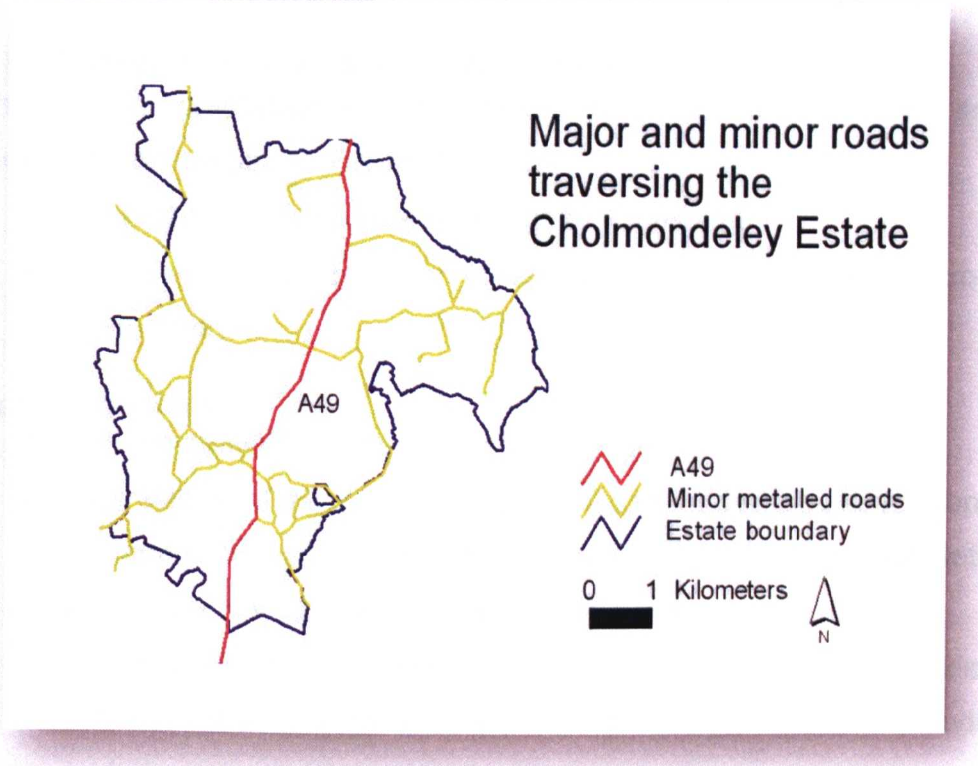


Figure 17; Major and minor metaled roads traversing the Cholmondeley Estate.

Chapter 5 - Methods

5.1 Terrestrial and Aquatic Habitat Survey

This section summarises pre- and post-field survey desk exercises and the terrestrial and aquatic survey methods used to collect data on:

- the distribution and breeding status of *T. cristatus*
- the quantity and distribution of terrestrial and aquatic habitat across the study area

Survey rationale

In line with the analytical aims of the study:

- examination of the species distribution and landscape associations with its pond occupation and particularly breeding presence within a landscape typical of its core range in the UK,
- identification of key existing sites for protection of habitat connectivity and habitat availability arising from their position within the landscape and
- identification and selection of key sites for habitat creation or restoration arising from their position within the landscape,

the primary aim of the survey (to delineate the terrestrial and pond landscape and general situation of *T. cristatus* within it) required the establishment of species presence/probable absence, and delineation and quantification of terrestrial habitat available to it. A "broad brush" survey was undertaken in preference to a more detailed survey of a representative sample of ponds in order to establish the most comprehensive possible picture of the location, distribution and spatial arrangement of ponds (both occupied and unoccupied by *T. cristatus*) and intervening terrestrial biotopes. A detailed survey of a representative sample of ponds would not have achieved this aim, nor could multiple visits to generate population size estimates and other demographic data practically be carried out over the full extent of the pondscape, as this would have been prohibitively expensive both in terms of money and time. A Phase 1 Habitat Survey was undertaken, supported by reference to aerial photography (to assist in confirmation and calculation of land cover patch extents etc., see JNCC 2007), to delineate terrestrial biotopes and land use.

Pond inventory and pond site identification.
The Cholmondeley pondscape was first mapped out as a desk exercise in GIS through collation of available pre-existing data; the Cheshire coverage of the Pond *Life* Project NW Pond Audit, The Cheshire *T. cristatus* Site Inventory (served through the NBN Gateway, see CTcSI Partnership 2006), and ponds mapped in the current OS 1:10000 raster map series. Point locations of approximate pond centres from these sources were combined into a pre-survey pond audit map. During the period 1995-98 the EU *Life* environment programme funded the Pond *Life* project (PLP - Boothby 2000), a partnership project led by researchers at Liverpool John Moores University. An early output was a GIS based pond inventory of northwest England (specifically the Watsonian Vice Counties of Cheshire and Lancashire, excluding the urbanized areas of Merseyside and Greater Manchester). Locations of all recorded ponds were derived from historical (first edition onwards) to then current Ordnance Survey (OS) maps, aerial photography (AP) and some limited on-the-ground survey. Data were collated in GIS (Environmental Systems Research Institute, Arcview 3.2, 1992). These data were made available to the author by Dr. John Boothby and Prof. Andrew Hull. At this point, it should be noted that a degree of spatial error exists in the PLP NW Pond Audit. Since the primary purpose of the audit was to derive a pond count and density rather than record the precise location of ponds, precision in digitisation of the original data set was not rigorous. Occasionally, pond data points in the audit data set do not coincide precisely with mapped locations. A consequence of this is ambiguity in identification of certain ponds where digitized locations do not coincide with mapped locations: is this point location representative of an inaccurately digitized pond, or an accurately digitized unmapped pond, and is a mapped pond which has not been allocated a digitized point location actually there?

The Cheshire *T. cristatus* Site Inventory (CTcSI Partnership 2006) was developed by the author in a nine month project funded by United Utilities plc., in partnership with (the then) English Nature, Cheshire Wildlife Trust and the Cheshire county biological recording centre, rECOrd. The project was funded in part mitigation of disturbance resulting from major water pipeline works passing through the Cholmondeley study area. The inventory collates records of precisely located ponds where *T. cristatus* presence has been recorded in Cheshire. The inventory is a collation of data:

- from English Nature/Natural England Science and Education protected species license returns and within English Nature/Natural England regional offices
- DEFRA Development and Mitigation license applications and reports,
- sufficiently precise spatial resolution (i.e. eight figure OSGB national grid references or better, verified by at least one cross referencing source) records extracted from data supplied by rECOrd
- reports held by local authority planning departments within the vice county of Cheshire
- utility companies such as United Utilities, Transco etc.
- the Environment Agency
- NGOs such as the RSPB, Cheshire Wildlife Trust and the National Trust
- education and research centres such as Liverpool John Moores University and the University of Liverpool (Ness Botanic Garden)
- and data provided by a number of participating and competent private individuals and ecological consultants

The Inventory carries 12 figure Ordnance Survey of Great Britain (OSGB) National Grid References for approximate pond centres derived by examination of original survey data and cross referencing site plans with other available data. While the majority of the records relate to water bodies identified in the Cheshire Pond Audit data, locations of many were re-digitised with a more rigorous approach to spatial precision, and a substantial minority are not included in the original PLP audit (either not included at all, or with ambiguity, due to the locational precision errors mentioned above). Those present on the estate were incorporated into the study area pre-survey audit data set as detailed below.

The current 1:10000 map series, in raster format, was supplied through EDINA Digimap under the CHEST agreement. Ponds recorded in this map product were point digitised (to a distance of 1km external to the estate boundary, see below). Where point locations within the estate boundary in the PLP dataset and those digitised from the OS maps clearly represented the same pond, the PLP data was accepted. Where there was ambiguity, both locations were accepted as presumed pond sites. The 1875 edition of the OS County Series 1:10560 map, available as GeoTIFF image files (Landmark Information Group Limited, 2010, available through Edina Digimap) provided information on the historic distribution of ponds on the estate (see Fig. 18, below) and enabled a "triangulation" approach in conjunction with locations from the PLP data set, and the current OS 1:10000 raster series. Pond features in the 1875 1:10560 map series may be difficult to identify – the GeoTIFF images are created by fairly high resolution scanning of the historic maps and the geo-referencing of the file with OSGB national grid coordinates to allow use in GIS with other (e.g. current) map products. However, smaller features may occasionally be obscured by pixellation or corruption of the original map sheet (occasional stains, fold marks, tears, stretches and missing patches) reproduced in scanning, rendering the symbol difficult to interpret. Identifiable ponds were point digitised and a similar process of verification against the PLP audit/OS map composite data set was carried out, with locations identified as identical in each data set being accepted, otherwise both locations being included as presumed pond locations.

In some cases therefore, one or both of the OS mapped location(s) and the PLP Audit recorded location were mapped as presumed pond sites, because potentially, each location could be the site of permanently or seasonally separate ponds. Where this was the case, actual and precise pond locations were established during on the ground survey, as was recording of ponds lost to various causes, and of ponds present on the ground but not represented in the pre-survey audit (i.e. not previously mapped or recorded in available aerial photography). No recent aerial imagery was available either from the estate management, Cheshire County Council or the local authorities where the estate was then situated (Crewe and Nantwich, and Chester City). However, Google Earth had at the time of the survey recently updated its imagery of the area. This was of sufficient resolution to allow verification in most cases of the presence of ponds identified in the existing datasets and to identify a number of pond locations (or possible locations) which could be noted in the pond data set and confirmed or otherwise by direct "ground truthing" survey (see Fig 19, and Fig. 20, below).

Figure 18; An area around Chorley Stock Farm, roughly centred on GR SJ 57067 50397, features identified as ponds from the 1875 edition of the OS County Series 1:10560 map indicated in red (Historic map data Landmark Information Ltd., 2010, available through Edina Digimap).

Figure 19; Google Earth imagery used to support Phase 1 Habitat Survey and pond identification. This image (eye altitude equivalent 371m, scale approximately 1: 1000) shows a pond at Park farm. T. cristatus eggs were present in small numbers on Nasturtium nodiflorum (image Google Earth © 2011 Tele Atlas, Europa technologies, Infoterra Ltd. and Bluesky).

Figure 20; Approximately the same area as shown in Fig. 18 above, currently existing ponds indicated in red (T. cristatus breeding ponds indicated by orange arrows, scale approximately 1: 10000, image Google Earth © 2011 Tele Atlas, Europa technologies, Infoterra Ltd. and Bluesky).

Cholmondeley Estate in addition identified locations of a small number of recently created ponds (created under Countryside Stewardship and/or for conservation/education purposes); these were incorporated into the pond data set. This produced a composite map of pond locations for use in field survey. Prior to survey on individual farm holdings, the tenant or land manager was consulted and details of any un-mapped (recently created, temporary/ephemeral, or very small) pond locations and background information on pond permanence were noted. Unmapped ponds and/or temporary/ephemeral pond sites not inundated at the time of survey were located with the use of hand held GPS or compass triangulation during Phase 1 Habitat Survey or Amphibian survey.

5.2 Survey period and access

The survey was carried out by the author during May, June and July 2007. Two land managers refused access for survey to be carried out (including one whose refusal to cooperate with mitigation works around United Utilities (UU) infrastructure works in 2004/5 resulted in the funding by UU of the CTcSI project). The Estate land agent, whose association with the survey positively influenced cooperation in some cases, was willing to intercede and exert the estate's influence as land owner to grant access, however, it was decided that good intentions notwithstanding, this was undesirable, and to accept the offer unethical. The majority of tenants allowed access freely, sometimes enthusiastically, regardless of the estate's cooperation, or in a few cases though at first wary, acquiesced when informed of the estate's cooperation with the study. This does not necessarily reflect the heterogeneous nature of attitudes or tenure generally. Overt imposition of authority by the estate hierarchy to enforce cooperation (however, diplomatically) could (undoubtedly would in some cases where relationships between the tenant and estate were strained), sour relations between the author and tenants, making later cooperation with the study difficult if not impossible to obtain and would have compromised the ethical imperative to secure cooperation through free and informed consent.

5.3 Pond/Amphibian survey methods.

Several standard methods are used to identify and monitor the status of *T. cristatus* populations. Each of these methods carries with it strengths and limitations to effectiveness in terms of applicability and data gained, survey timing, duration, effort and surveyor skills or experience levels required for effective use. Adverse impacts on the target and associated species or their habitat, financial cost, and license issues where the target species or associated species in the same habitat patch enjoy legal protection (as with *T. cristatus* and the Lesser Silver Water Beetle *Hydrocara caraboides*, recorded at Bickley Hall Farm) must also be considered carefully. Relevant methods have been tested and assessed for effectiveness in numerous studies (see for example Griffiths 1985, Beebee 1990, Griffiths and Raper 1994, Heyer *et al.* 1994, Cooke 1995, Griffiths *et al.* 1996, Baker 1999, and Bibelreither 2006). The standard methodologies for *T. cristatus* survey in the UK are outlined and reviewed in English Nature (2001), Griffiths and Raper (1994), Griffiths *et al.* (1996).

Clearly, the establishment of species absence is virtually impossible.

> *"'Presence/absence' surveys may determine presence but in fact it is virtually impossible to demonstrate absence. The guidance here is designed to suggest a reasonable level of effort that, at the majority of ponds, will detect the presence of newts. However, where survey conditions are difficult, or where very small populations are involved, it can be exceedingly difficult to detect great crested newts. It is feasible, for example, that using the ... methodology at a site with a very small population, four visits could be carried out with no great crested newts detected, but a fifth visit might find them."* (English Nature 2001, p26)

Methodologies specified as best or required practice under the Great crested newt mitigation guidelines (English Nature 2001) are employed generally as pre-development measures aimed at avoiding damage and disturbance to *T. cristatus* individuals, populations and their habitat. In effect, they are aimed at the establishment of probable absence with a high degree of reliability, since presence is relatively easily established and the presence of one egg, larva or adult within or near a development footprint is usually sufficient to trigger stringent licensing and mitigation requirements.

Standard methodologies

Egg search is the primary technique, generally considered the most readily effective method for detecting presence, and responsible for identification of presence and of course breeding, in 65% of the cases where survey technique is recorded in the CTcSI. This consists of careful search of living and senescent vegetation and other potential egg deposition substrate on the entire accessible perimeter and, where appropriate and accessible, at points within the water body, for enfolded *T. cristatus* embryos. Where presence is at low densities, where vegetation is very dense or complex, or very sparse and difficult to access, eggs may prove difficult to find. Searching may be destructive, exposing embryos to mechanical damage, increased ultra-violet light levels (see for example Blaustein *et al.* 2003) and risk of predation. This potential for damage arises as it usually proves necessary to open the egg fold to confirm the species from physical characteristics of the embryo, though it is not usually necessary to systematically un-wrap large numbers of egg folds, as one egg is sufficient to confirm presence, and little quantitative information on population size can be gained from egg counts. It should be further noted that the presence of eggs in folds is no indicator of breeding success and recruitment. Fifty per cent of *T. cristatus* eggs are sterile due to a genetic trait of *T. cristatus* and the closely related *T. marmoratus* (MacGregor and Horner 1980), and breeding may frequently take place in ponds containing high densities of predators, particularly fish, or which are subject to dropping of water levels below that at which eggs had been deposited, or drying out completely before hatching or larval metamorphosis is completed.

The use of a long-handled dip-net to capture *T. cristatus* adults and larvae by sampling the area around the pond edge and accessible areas within the water body is the next most readily utilized technique. Netting can be conducted by day or night, but daytime netting is easier and safer for the surveyor and for netted organisms. This method can be a source of considerable disturbance to marginal vegetation and can result in substantial damage to eggs and larvae; it should therefore be employed subsequent to egg search and torch counting where this technique is also employed. A perimeter walk, as with torch surveys, is recommended, and there should be at least 15 minutes of netting per 50m of shoreline. Netting is cheap, though of limited effectiveness, and can be useful in finding larvae and juveniles in the later part of the survey period. In the C*Tc*SI, of 602 cases where survey methods responsible for capture or recording of *T. cristatus* was recorded, netting was recorded in 307 cases, with netting of adults recorded in 259 cases, and larvae or/and juveniles in 54 cases. Great care is needed to avoid damage to smaller larvae and the gills of larger larvae. Any physical damage may easily result in infection and prove fatal. Again, netting is not particularly useful for gaining an indication of population size or breeding success in terms of recruitment.

The use of a powerful (500,000 - 1,000,000 candle power) torch to illuminate newts floating in the water column is a third, slightly more demanding, relatively low intensity survey method. This simple and effective means of identifying newts may be ineffective where ponds are heavily vegetated, have a dense covering of floating vegetation such as Pondweeds (*Potomageton* spp.) or Duckweed (*Lemna* spp.) or are highly turbid. Torch survey should not take place immediately after netting as turbidity levels are likely to be increased and the disturbance is likely to have caused newts to stay hidden in vegetation or move into the depths of the pond for some considerable time. A further consideration is that the illumination is itself a considerable disturbance, which may impact on survey results adversely and possibly disrupt breeding by causing individuals to take refuge in vegetation and avoid the clear shallows where display and mating takes place. The whole pond perimeter (where accessible – this activity by necessity takes place at night, so safety is not a trivial consideration) should be walked and checked for newts. Effectiveness of torch survey varies considerably with weather conditions and is most reliable when night-time air temperatures are greater than 5°C, in still air, on a rainless night (English Nature 2001 and references).

Bottle (or funnel) trapping, the setting of traps (normally cheaply made from 2-litre plastic bottles) around the pond margin and leaving the traps set overnight is considered the single most definitive survey technique. Studies referenced above indicate that bottle trapping is the most reliable method for detecting the presence of great crested newts, and it is especially useful for surveying turbid or weedy ponds. The main disadvantages are that the technique is time consuming and there is susceptibility to damage by vandals and possible harm to trapped newts. Bottle trapping can be used to catch adults during the breeding season and larvae during summer (one trap per two metres of shoreline is recommended). It should only be relied on when the night-time air temperature is >5°C, but very high temperatures can increase the likelihood of harm to trapped newts, especially larvae.

Pitfall trapping, capture on land using pitfall traps, flush with a drift fence, and commonly used in conjunction with a ring fence, or length of drift fence encircling the breeding pond is a good method of sampling immigration and emigration. Capture rates are highly dependent on timing and weather conditions particularly in summer when great crested newt terrestrial above ground movements are usually limited to rainy periods, and the technique is highly intensive in terms of financial cost and effort (erection of drift fencing, setting of traps, frequent and regular visiting to empty traps and record captures since captured animals are rendered vulnerable to predation, desiccation, loss of condition or even death if traps are not installed properly or attended regularly, then removal and disposal of fencing and traps). It is often employed in conjunction with refuge search, which mainly consists of placing refuges such as carpet tiles and plywood boards on a site to increase the chances of finding newts occupying a terrestrial refuge. Lifting and searching underneath naturally occurring refuges (including rubble and fly tipped refuse close to ponds) appears to be a very inefficient method, and is generally at least partially, and often totally, destructive of the refuge site. These methods are generally utilized where trapping for re-location as part of development mitigation is taking place. Neither technique was considered appropriate for this study.

Survey methods employed

Considerations in selection of survey methods to employ were:

Survey effort; the study area contains several hundred ponds and extends over approximately 4,000 ha Consequently the methods chosen must minimize survey time and expense per pond, and the weight and complexity of equipment, which must be transported off-road by hand.

Effectiveness and output; given the requirements of the survey for presence/probable absence assessment only, effective detection was more important than assessment of population abundance, age structure etc.

Negative impact; invasive and destructive impacts of techniques upon the animals or their habitats, given that no development or other threat to them was known to be in any way imminent, must be minimal. Methods which could be terminated immediately upon the establishment of presence and having minimum impact on individuals and the overall integrity of the site were therefore preferred.

Timing; an important but subsidiary consideration in the decision on survey methods was that a considerable constraint upon the survey was the timing of the survey period, given extraneous time constraints imposed upon the author and the duration of the optimal period for reliable detection of *T. cristatus.*

Refuge search, pitfall and bottle trapping were ruled out (the last reluctantly) due to cost and high levels of survey effort required, but also as the primary outputs of these methods (reliable abundance and demographic data) were not required. Consequently, the methods selected were egg search and netting, with consideration to be given to torch survey on a pond by pond basis, should egg search and netting not identify presence, but pond characteristics suggest a high probability of it.

Although *T. cristatus* displays considerable loyalty to its natal pond, in many cases ponds are utilised on a discontinuous basis, as satellite ponds of established breeding ponds. Therefore, non-detection or detection (particularly of adults only) in a given year is not necessarily always indicative of occupation in subsequent years. For example, re-survey of a sub-set of ponds on the estate took place during June 2009 to detect presence of the non-native Alpine newt (*Ichthyosaura alpestris*, previously *Lissotriton alpestris*, and *Mesotriton alpestris*), and an unidentified alien frog, possible populations of which have been tentatively identified at 2 locations on the estate. During this survey a small number of *T. cristatus* larvae were bottle trapped in a pond which had been identified in 2007 as sub-optimal aquatic habitat, with good terrestrial habitat and sources of colonists nearby, but in which the species was not detected. On that occasion it was considered possible that the species was simply not detected, but present in very low numbers, but that more probably the pond may have constituted a satellite pond, which would be utilized when breeding competition and or success was high in primary ponds nearby, and density dependent factors drove dispersal, which the findings in 2009 seem to bear out.

As stated above, it was considered that a less stringent survey requirement than that called for by the Mitigation Guidelines (English Nature 2001) would be sufficient and practical; i.e. up to two visits, using three methodologies (egg search, netting, and in the case of high quality ponds late in the season, torch survey) as appropriate and necessary. A pond survey protocol was therefore established and is included as Appendix 1.

5.4 Phase 1 Habitat survey

Unavailability of reliable remotely sensed imagery at suitable resolutions, and the establishment of Phase 1 Habitat Survey (JNCC 2007) as the most widely used standard methodology for rapid habitat classification were the decisive factors in the choice of Phase 1 Habitat Survey for delineation of terrestrial land cover. The Cholmondeley estate was surveyed between late March and mid-August, 2007. The surrounding area to a distance of approximately 500m was included to ensure that habitat data outside the estate boundary associated with ponds close to or on the estate boundary would be captured.

Internal and external estate and holding boundaries were provided digitally by the Cholmondeley Estate in Neutral Transfer Format (NTF) and converted to Esri ArcGIS coverages via Arc Toolbox. Field survey maps (1:10000) were produced using the Ordnance Survey MasterMap (OSGB 2011) map product. Survey was on foot, and direct where access was granted (most cases), but where full access was not available, survey was carried out as fully as possible from adjacent land to which access was given, and from Public Footpaths and roads, where necessary with binoculars. Verification of areal extents (in these latter circumstances particularly, but throughout) was supported by Google Earth imagery, facilitated by (at the time) recent high resolution updates imaged in summer 2006, which covered the Cholmondeley estate. It is inevitable that some recording error will have taken place in these areas, but this was minimised as far as possible. An adapted version of standard Phase 1 Habitat Survey methodology was applied; land-cover types not classified within standard Phase 1 Habitat Survey, e.g. roads and some other elements of the built environment were assigned classifications for incorporation into the survey map to ensure that a continuous "seamless" raster land cover layer could be generated in GIS.

Adopting the least cost approach, reclassification of the habitat suitability land cover classes derived from Phase 1 Habitat Classes (see Fig. 21 below) was carried out, with these classes being assigned a "friction" or "resistance" multiplier value according to the extent to which it was considered to hinder or facilitate the movement of *T. cristatus* through the landscape, with this resulting resistance or cost raster forming the basis for the generation of a Cost Weighted distance surface. For the purposes of this study, a relatively simple habitat suitability index, based on four land-cover classes was used (see Table 5 below).

Table 5; *Definition of habitat suitability classification, associated resistance value and corresponding Phase 1 Habitat codes (JNCC 2007).*

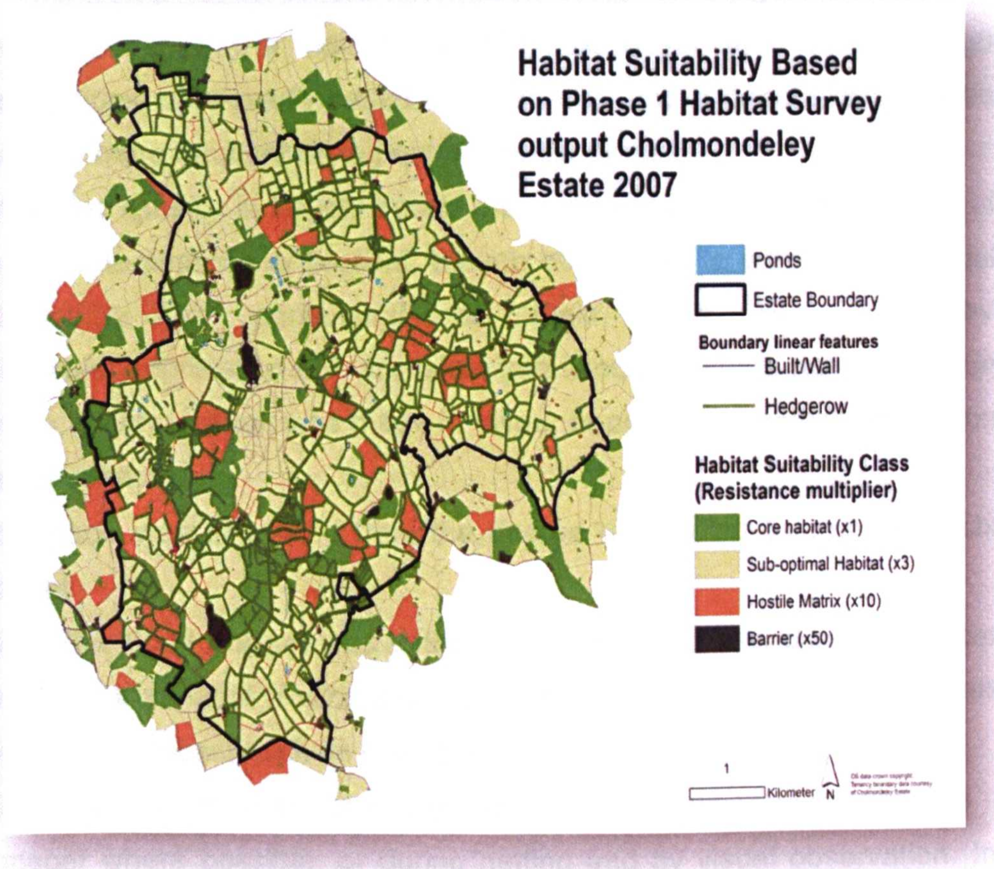


Figure 21; Habitat Suitability based on Phase 1 Habitat Classes, with resistance multiplier (bracketed)

5.5 Habitat Suitability Index

Habitat Suitability Index (Oldham *et al.* 2000) was calculated for each surveyed pond (n=289) using the methodology outlined in ARGUK (2010). The Habitat Suitability Index (HSI) score was derived from combination of ten suitability indices, scored on factors affecting *T. cristatus* occupancy:

SI1 Pond location is scored according to the location of the pond in the UK, with all ponds at Cholmondeley falling in Zone A, consequently scoring 1.

SI2 Pond area was scored on the basis of field observations supported by GIS data derived from the OS MasterMap coverage, or features created using data derived from GPS readings, compass triangulation and pond size estimation in the field.

SI3 Pond drying was generally either established in discussion with the land manager before survey or deduced from examination of the vegetation communities present. Where information could not be gained from the land manager, and or the indications from field observation were ambiguous, assumptions were made based on pond size and a general presumption in favour of more frequent drying out of smaller ponds.

SI4 Water quality is largely based on an appreciation of the diversity of the invertebrate community present, though other cues to water quality, such as vulnerability to agricultural or main road run off, obvious pollution/eutrophication etc. are taken into account. Where ponds were dry on survey, a presumption was made in favour of poor water quality (erring on the side of caution).

SI5 Shade was estimated from the degree of shading by trees and shrubs present.

SI6 Water Fowl impact was estimated from field observation of numbers of fowl other than Coot (*Fulica atra*) or Moorhen (*Gallinura chlorophos*) present, and signs of impact such as over grazing, abundant droppings etc.

SI7 Presence of Fish was assessed through discussion with the land manager where possible, or during netting and by visual observation. In the absence of obvious signs of presence arising from angling (fishing platforms etc.) or fish visible in the water body, where netting was not considered to have been of sufficient duration to establish absence with any confidence, a presumption was made in favour of probable presence, a record of absence was only made where this was established through a substantial duration of netting which produced no fish, and discussion with the land manager. It would seem likely that this causes an over estimation of fish presence, however, the at least temporary presence of Stickleback (*Gasterosteus aculeatus aculeatus* or *Pungitius pungitius*) is common in Cheshire ponds when close enough to ditches and streams to be colonised during flooding events. The presence of Goldfish (*Carassius auratus auratus*) in ponds adjacent or close to and easily accessed from roads is also quite common, as is the presence of angling fish in larger ponds close to roads. These considerations indicate that presumption in favour of presence is justified.

SI8 Pond Count of ponds within a 1km radius excluding ponds beyond substantial barriers such as main roads and moving water (an indicator of connectivity with other ponds in the landscape) was established in GIS.

SI9 Terrestrial Habitat quality was assessed from observation in the field (i.e. record of suitable refugia/resting sites such as log piles, spoil heaps, mammal burrows etc.), and GIS analysis of the amount of core habitat present within 250m of the pond (and on the nearside of substantial barriers such as main roads and moving water etc.). The amount of core habitat was calculated as a percentage of the area of the 250m Euclidean distance buffer around the pond, and criteria in ARGUK (2010) applied.

SI10 Macrophyte cover was estimated from field observation (estimations of cover extents were made at the time of survey and sketch plans of pond vegetation patterns and digital images made, which were used to support estimation of macrophyte cover), using the guidance provided in ARGUK (2010).

The HSI is the geometric mean of these ten indices; HSI = (SI1x SI2x SI3x SI4x SI5x SI6x SI7x SI8x SI9x SI10) /10. Field scores are both categorical and numerical, with numerical scores converted to SI scores by reading from graphs after Oldham *et al.* (2000). HSI scores can be allocated to a categorical scale of pond suitability (ARGUK 2010), see Table 6 below), each surveyed pond was allocated to an HIS category according to its calculated HSI score. HSI having been calculated for all ponds in the survey, the scores were categorised using the scale in Table 6 below.

Table 6; Categorisation of HSI scores (from ARGUK 2010).

HSI Score	Pond Suitability
0 – 0.49	Poor
0.5 – 0.59	Below Average
0.6 – 0.69	Average
0.70 – 0.79	Good
0.80 – 1.00	Excellent

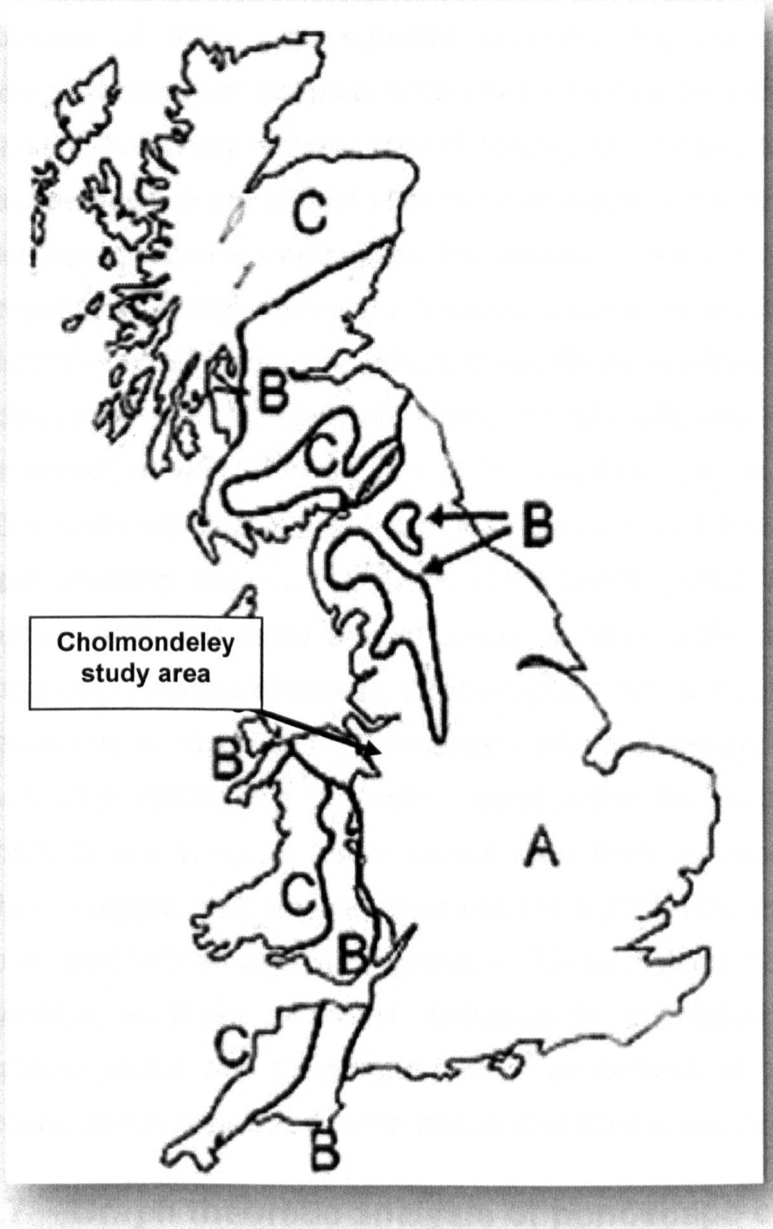


Figure 22; HSI factor SI_1, Geographic location, from ARGUK 2010, Zone A = Optimal (SI=1), Zone B, location marginal (SI=0.5), Zone C, location unsuitable (SI=0.01).

5.6 Pond clustering

For the purposes of this study, a pond cluster is defined as a grouping of two or more ponds with an inter-pond distance equal to or less than a given value of either "straight line" Euclidean and "Cost Weighted" distance. The inter-pond distances used in allocating ponds to clusters were defined by observed and generally accepted characteristics of *T. cristatus* dispersal and migration capabilities, and set at 130m, 250m and 500m. The maximal inter-pond distance of 500m was selected to reflect the commonly observed and accepted dispersal distance, which has informed the requirements of Natural England for survey in the vicinity of development sites. Mark release recapture studies point to an optimal inter-pond distance in the region of 250m, which also reflects and encompasses the extents of the majority of recorded post breeding migration from radio tracking studies. In addition, a more minimal distance of 130m was set, reflecting the distance within which the majority of adult individuals migrated with strong directionality into refugia, in which they remained, or which formed foci of "localizations" (areas of a diameter up to 30m within which any movement took place) until the commencement of the next breeding season in Jehle and Arntzen's (2000) radio tracking study. Buffers were calculated around ponds at 130m, 250m and 500m Euclidean and Cost Weighted distances. Cost weighted distance buffers were created by generating a cost weighted distance surface of distance to pond polygons, then interrogating this to identify areas within the relevant distance of the pond. These areas in raster format were then converted to vector format. These polygon features were then used to capture data on the quantity of land cover and habitat suitability classes within each pond buffer – i.e. potentially available at these threshold distances to populations occupying ponds. Isolated ponds and their buffers were considered as patches, and buffers around ponds connected at the above distances (clusters) were merged.

5.7 Graph theoretic analysis of pondscape connectivity at Cholmondeley

Graph theoretic analysis of pondscape connectivity was carried out in the application CONEFOR Sensinode v2.5.8 (beta), (Saura and Torne 2009, Saura *et al.* 2011). A beta version of v2.5.8 was supplied to the author by the developers, in which PC and IIC are calculable with the fractions Intra, Flux and Connector. Analysis was carried out based on the conception of the pond as the focal habitat patch. The vector polygon coverage of ponds identified in Phase 1 Habitat Survey, were used for this process. Euclidean distance calculation (pair-wise calculation of straight line Euclidean distance between all pond features) was carried out in ArcGIS 9.3.2 using standard tools available within Arc Toolbox. A raster resistance surface was generated in ArcGIS 9.3.2, using the multipliers, and applied to the habitat suitability raster re-class of the Phase 1 Habitat Survey map. This provided the cost surface used in the Cost Weighted Distance calculations (pair-wise calculation of least cost distance between all pond features). These were carried out using the Landscape Genetics ArcGIS toolbox Cost Distance tool (Etherington 2011) to calculate a cost distance matrix, which was then converted to a pair-wise table for use with CS2.5.8, using the Matrix to Pairs tool from the Landscape Genetics ArcGIS toolbox. Pond nodes were weighted as habitat patches for connectivity index calculation by allocation of the *T. cristatus* Habitat Suitability Index calculated for each pond (see Oldham et al. (2000) and (Amphibian and Reptile Groups of the United Kingdom (ARGUK), (2010) as patch weighting factor.

5.8 Data processing and collation

Data collected in the Phase 1 Habitat Survey exercise were transferred into GIS (ArcGIS 9.3.2, Environmental Systems Research Institute 1992) using OS MasterMap (OSGB 2011) 1:10000 scale data to provide the base map. Fence and hedge line features to be mapped in the Phase 1 Habitat Survey were abstracted from the MasterMap Lines layer, modified as necessary, or were digitised from Phase 1 Habitat field maps and classified according to the nature and quality of the feature. Some additional digitization of vegetation features, hedgerows, fences and some other land parcel boundary and linear features not included in the MasterMap layers, was required. A continuous vector land cover map which could easily be converted into continuous raster surfaces when required was produced. All data were stored and projected in the OSGB National Grid coordinate system using a Transverse Mercator projection. All pond sites identified through the pre-survey desk exercise were visited where access was granted, presence confirmed and surveys carried out. Ponds not represented in the MasterMap Polygon layer or in aerial photography (recently created, smaller, ephemeral or temporary ponds, or ponds in woodland patches) were represented by polygon digitization or, in the case of very small or ephemeral ponds of indistinct boundary, generation of circular buffers around the relevant pond point features (derived from GPS or map and compass triangulation) according to the size of the pond as established during pond survey, for incorporation into the data set. A number of ponds recorded as present from map or aerial photo evidence were found to have been lost permanently (in-filled or drained for agricultural purposes or lost to development). These were removed from the data set. A further sub-set of the inventory were found to be dry at the time of survey, but evidence at the site showed that this was due to seasonal or occasional drying (the early part of the survey was particularly dry and a number of seasonal/temporary ponds dried earlier than normal, though during the later period which saw unusually high rainfall, many of these were again inundated). These pond sites remained in the data set.

After digitisation of the Phase 1 Habitat Survey field maps, terrestrial land cover across the study area was quantified using ArcGIS 9.3.2. Land cover to the extent of a 500m buffer around the estate was included in these calculations to minimise "edge effect" artefacts of the technique employed in calculation of density estimations, cost surfaces and habitat availability for ponds on the estate perimeter (i.e. effects such as depressed pond density at the margins due to the lack of sample points beyond the study area, or truncation of pond buffers around ponds at the margins of the study area). Area of land cover per land cover patch was aggregated to produce totals per class for the whole estate. Clearly, only a fraction of this potential habitat is accessible to individuals or populations resident at particular ponds, or to the species resident within the pondscape as a whole. Buffer areas were generated at distances of 130, 250 and 500m (Euclidean and Cost Weighted) around pond perimeters and assigned the unique identifier associated with the pond they centred on. Land cover area within these buffers was aggregated by class, and totals per class, per pond buffer were calculated. Phase 1 habitat classes were re- classified into four habitat suitability classes. The area of these four habitat suitability classes were calculated on the same basis, i.e. by habitat patch, across the study area and within pond buffers.

Pond dimensions

Perimeter, diameter, mean and maximum depth and hydro-period of ponds are variable, subject to change over both long and often very short time scales in response to variation in rainfall, evaporation and drainage of adjacent fields, as well as background levels of draw down and inundation in response to seasonal changes in the level of the local water table. This was particularly in evidence during the 2007 survey which was characterised by a protracted dry period prior to and at the beginning of the survey, with mid and later stages taking place in and being followed by one of the wettest late springs and summers on record. Not infrequently during the latter period, the actual pond margin (i.e. mean high water mark and fringing marginal vegetation – and with it, potential egg deposition sites) could not be identified as it was completely inundated by temporary flooding (see Fig. 23 below). For these reasons it was decided to designate each pond to a size class, rather than record precise dimensions at the time of survey. Where ponds were dry or much reduced by draw down estimations were based on the apparent mean high water level. Size classes to which ponds were assigned were recorded in six categorical bands; 1 = < 100 m^2, 2 = 101-250 m^2, 3 = 251-500 m^2 4 = 501-750 m^2 5 = 751-1000m^2 6 = >1001m^2.

Figure 23; A small field edge pond in an arable field, pond margins lost due to temporary flooding following recent heavy rainfall (author's photo).

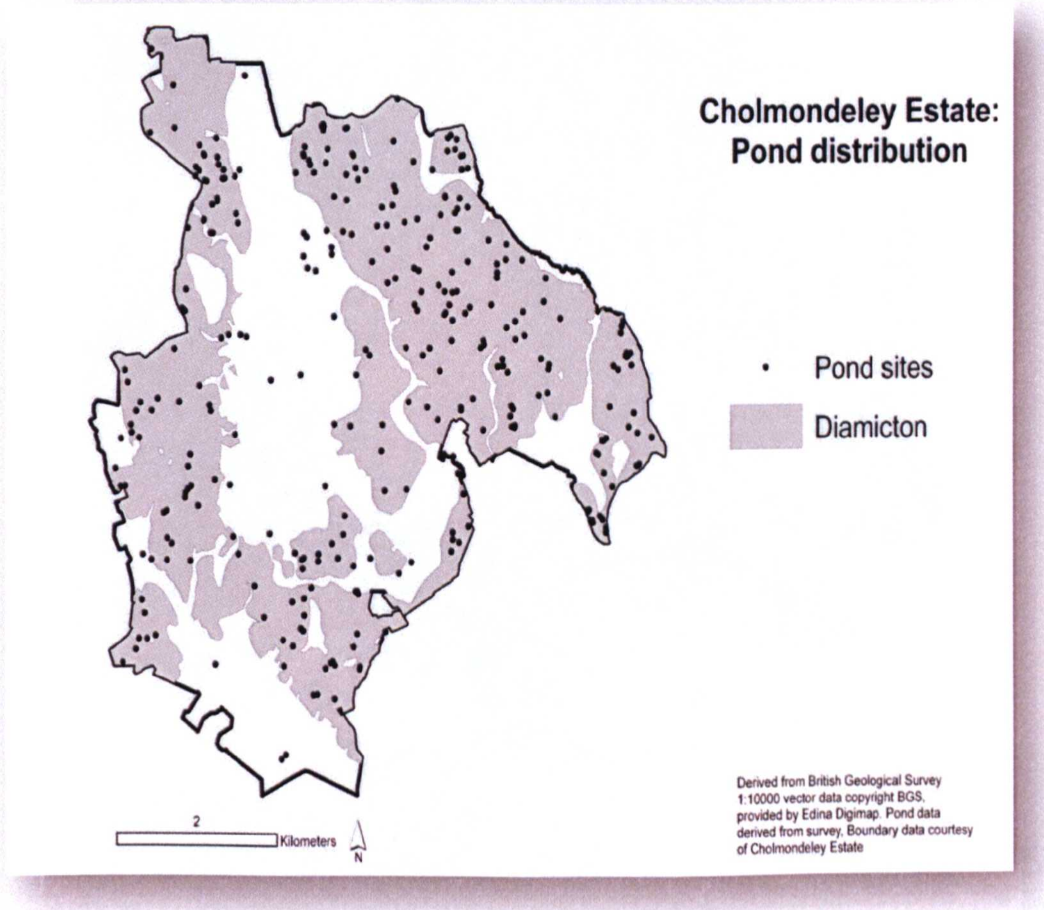
Statistical analysis

Statistical analysis (Mann-Whitney U test) of mean HSI, proximity to roads and moving water, road density, proximity to broad leaved woodland, rough grassland and other core habitat, area of core habitat within Euclidean and Cost weighted distance buffers, proximity to breeding ponds, node importance (*varIIC*, *varPC*), between breeding ponds and non-breeding ponds, and correlation between pond count within graph components and breeding pond occurrence (Kendall's *Tau-b* rank correlation) was carried out using SPSS v17 (SPSS 2008).

Chapter 6 Results

6.1 Pond density

Pond density varies considerably across the estate (see figure 25 below), this variation mainly reflecting underlying superficial geology (see fig 24 and table 7, below).



Derived from British Geological Survey 1:10000 vector data copyright BGS, provided by Edina Digimap. Pond data derived from survey, Boundary data courtesy of Cholmondeley Estate

Figure 24; Distribution of ponds on the Cholmondeley Estate in relation to heavy clay glacial substrate (diamicton).

Table 7; Pond occurrence in relation to the superficial geology of the Cholmondeley Estate.

Superficial Geology	Number of overlying Ponds
Diamicton	281
Clay, Silt, Sand and gravel	15
Sand and Gravel	28
Peat pockets	0

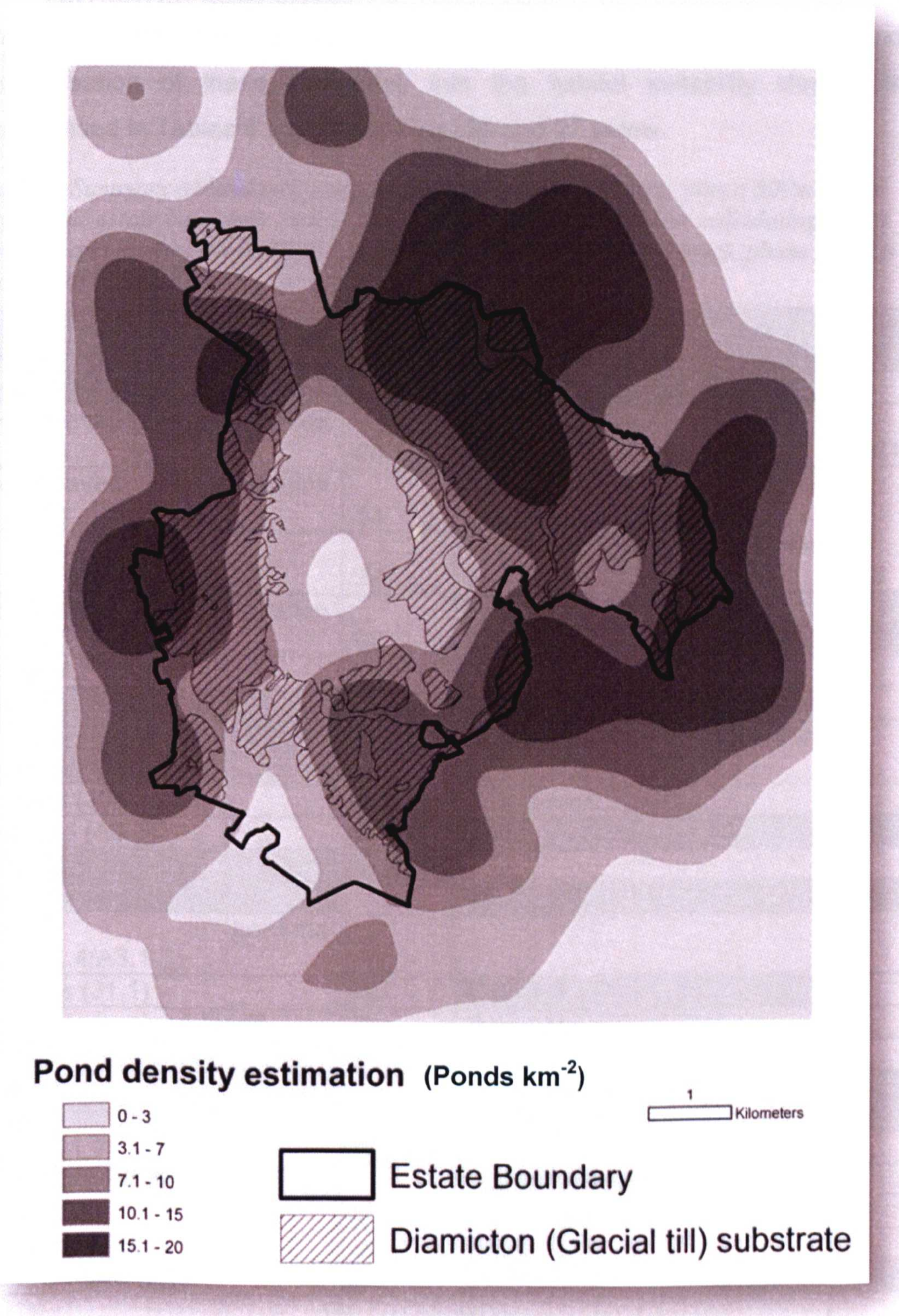


Figure 25; General trends in pond density (ponds km^{-2}) across the Cholmondeley Estate showing areas of glacial till (diamicton) superficial geology (kernel density estimation cell size 6m, search radius 1.2km).

6.2 Terrestrial land cover

Terrestrial land cover across the entire estate plus a 500m buffer, and generalisation of these categories into the habitat suitability classes is summarised in Tables 8 and 9, and Figs. 26 and 27 below.

Table 8; Summary of land cover across the Cholmondeley Estate, plus a 500m buffer beyond the estate boundary included to minimise edge effects when calculating raster surfaces and habitat availability (derived from Phase 1 Habitat Survey, phase 1 codes bracketed).

Land-cover Type	Area (ha)	Land-cover Type	Area (ha)
Woodland		Grassland	
Broadleaved Semi-natural (A1.1.1)	80	Improved Grassland (B4)	3081
Broadleaved Plantation (A1.1.2)	14	"Rough"/Semi-improved/unimproved Grassland, poor quality (poor B4/B2.2/ B2.1/B5)	548
Mixed Plantation (A1.3.2)	34		
Coniferous Plantation (A1.2.2)	98	Total	3629
Scrub (A2.1/A2.2)	13		
Total	239	Rough vegetation	
Grass/scattered trees		Roadside vegetation (C3.1,J1.3)	46
Orchard (J5)	0.04	Tall ruderal (C3.1)	1
Parkland (A3.3)	66	Total	47
Total	66		
Gardens/amenity land		Arable (J1.1)	467
Formal gardens (J1.1/J1.4/A3.1-3)	10		
Gardens (J1.1)	56	Wetland	
Amenity grassland (J1.2)	5	Swamp/reed-bed (F1)	5
Total	71	Flush/Spring (E2.1)	1
Non-pond Lentic Water bodies		Total	6
Mere (G1.2)	29		
Lotic Water bodies		Track/Ride/ Road	
Canal (G2)	2	Track/Ride	10
Wet ditch G2)	9	Road	46
River/Stream (G2)	9	Total	56
Total moving water	20	Built and environment (J3.6)	66

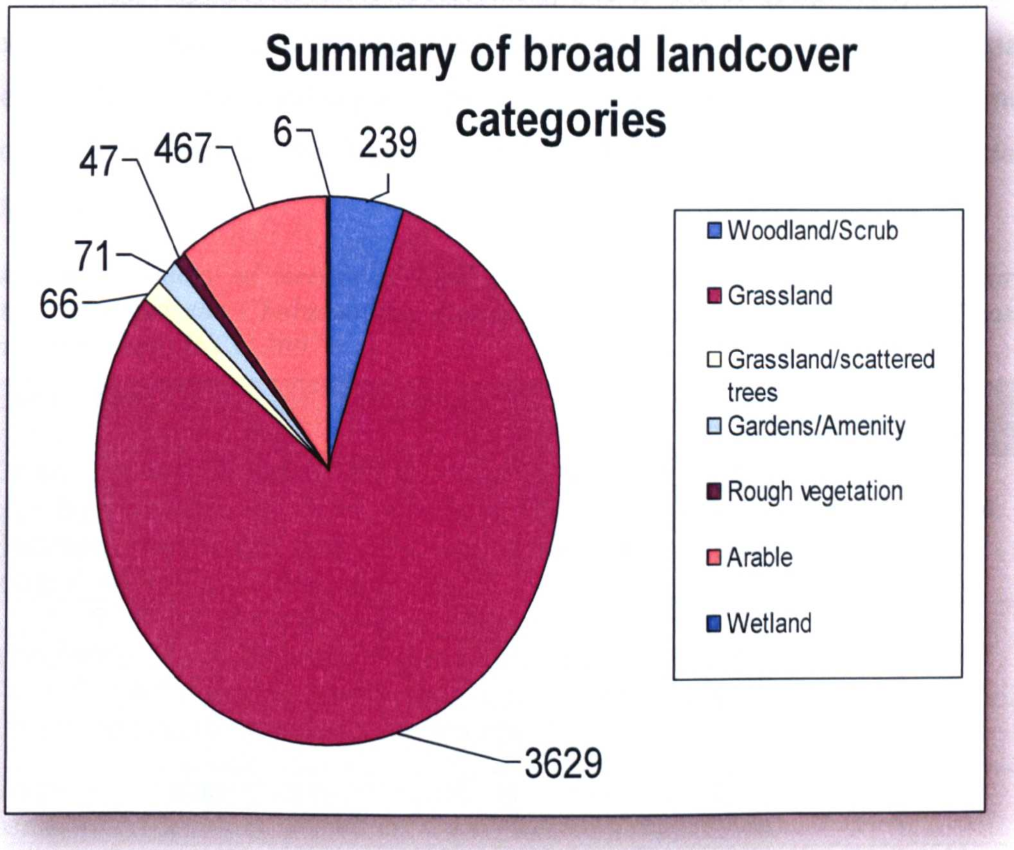


Figure 26; Summary of land cover (area ha) across the Cholmondeley Estate plus 500m buffer (derived from Phase 1 Habitat Survey). Wetland category constitutes several meres, ponds not included).

Land cover is predominantly (77.3%) grassland (see Fig. 26 above), approximately 84.8% of this being species poor Rye grass (*Lolium perenne*) leys, with the remainder rough tussocky grassland including degenerate leys, semi- improved and some small patches of unimproved grassland. Woodland (semi natural and plantation broadleaved, and coniferous plantation) makes up approximately 5% of the total land area, lower than the national percentage, said to be around 8.4%, but in line with findings for Cheshire (vice county), at 4 -5.9% in 1998 (Smith and Gilbert 1998). The largest component of this woodland cover is, however, coniferous plantation (around 2% of total estate land area), the rest comprising scattered small woods, plantations and copses. After grassland, however, the largest component of the estate's land cover by area is fairly scattered arable cultivation. Table 9 below summarises the estate's land cover in terms of the habitat suitability classes into which

Phase 1 Survey results were reclassified; this is shown graphically in Fig. 27 below. From this, it can be seen that slightly less than 16% of the total area of the estate can be considered core *T. cristatus* habitat. However, a much smaller proportion of this habitat is available for exploitation by *T. cristatus* populations.

Table 9; Summary of terrestrial land cover in terms of habitat suitability for T. cristatus across the Cholmondeley Estate plus 500m buffer (derived from Phase 1 Habitat Survey (JNCC 2007).

Land Cover	ha	% Cover
Class 1 (core) Broadleaved woodland, Scrub, Rough, Marshy, unimproved and semi-improved grassland, Swamps, reed beds and flush/spring vegetation, Tall ruderal vegetation, informal gardens.	784.6	15.84
Class 2 (sub optimal/matrix, dispersal) Coniferous woodland, Mixed woodland, orchards and Parkland, Formal gardens, Improved grassland, Wet ditches, Tracks and rides, Roadside vegetation	3354.3	70.97
Class 3 (hostile matrix) Amenity Grassland, Arable fields.	472.3	9.99
Class 4 (barrier) Roads, built environment, Large areas of open water (meres), moving water (rivers and streams, Canal).	151.5	3.20
Total	4726.5	100.00

Table 10 below summarises the land cover as derived from Phase 1 Habitat Survey, falling within Euclidean buffers at 130, 250 and 500m distances. As can be seen, and would be expected, the quantity of available habitat may be substantially reduced with decreasing buffer distance. This effect is dramatically heightened when terrain effects are taken into account by buffering using cost weighted distance. Table 11 below, summarises land cover within cost weighted buffers of the same effective dimensions, showing (figures in brackets) land cover available as a percentage of that available within Euclidean distance buffers. Table 12 below, summarises the same data in terms of the reclassified Habitat Suitability, demonstrating that availability of core habitat within Cost Weighted buffers is reduced to between 57.9 – 62.1% of that available within the more extensive Euclidean buffers.

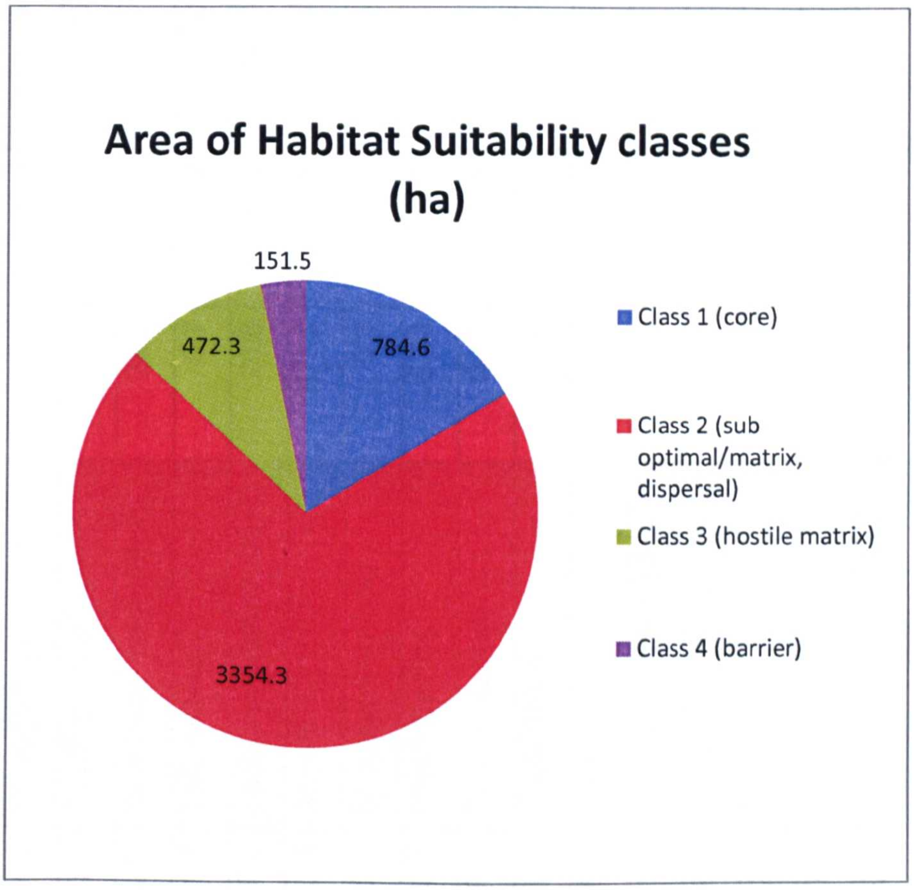


Figure 27; Summary of land cover (ha) classified by habitat suitability for T. cristatus across the Cholmondeley Estate plus 500m buffer, derived from Phase 1 Habitat Survey (JNCC 2007).

Table 10; Land cover area (by total area of land cover type aggregated for all buffers, (ha) within buffers around ponds at Euclidean distances of 130, 250 and 500m.

Land-cover	**130m**	**250m**	**500m**	**Land-cover**	**130m**	**250m**	**500m**
Broadleaved Semi-natural	37.0	48.0	75.0	**Improved Grassland**	1806.7	2333.6	835.0
Broadleaved Plantation	4.0	12.3	14.0	**“Rough” Grassland**	225.6	309.5	483.0
Mixed Plantation	12.3	27.9	33.2	**Total grassland**	2032.3	2643.1	3318
Coniferous Plantation	28.3	51.2	92.9	**Roadside vegetation**	28.3	33.7	43.1
Scrub	2.8	7.2	11.1	**Tall ruderal**	0.7	0.9	1.2
Total woodland/scrub	84.6	146.6	226.2	**Total roadside/ruderal**	29.0	34.6	44.3
Orchard	0.2	0.2	0.4	**Arable**	307.3	355.6	428.9
Parkland	45.1	52.8	65.6	**Swamp/reed-bed**	0.1	0.1	5.0
Total orchard/parkland	45.4	53.0	66.0	**Flush/Spring**	0.03	1.3	1.3
Formal gardens	5.3	6.6	9.3	**Total wetland**	0.13	1.4	6.3
Gardens	18.7	30.1	47.4	**Track/Ride**	2.0	5.3	8.6
Amenity grassland	1.8	4.7	5.2	**Road**	27.6	33.3	41.5
Total amenity	25.8	41.4	61.9	**Total road/track/ride**	29.6	38.6	50.1
Mere	8.3	20.6	28.9	**Built and environment**	18.5	31.2	54.1
Canal	0	2.1	2.2				
Wet ditch	2.8	3.9	7.0				
River/Stream	3.8	6.1	8.1				
Total open water	6.5	12.1	17.3				

Table 11; Land cover area within Cost Weighted buffers around ponds of 130, 250 and 500m (aggregated for all buffers, by land cover type). Bracketed figures are area as % of the area within the equivalent Euclidean distance buffers).

Land-cover	130m	250m	500m	Land-cover	130m	250m	500m
Broadleaved Semi-natural	24.6 (66.5)	31.1 (64.8)	46.7 (62.3	**Improved Grassland**	1258.7 (69.7)	1527.8 (65.5)	1969.8 (69.5)
Broadleaved Plantation	1.3 (32.5)	10.6 (86.2)	12.3 (87.9)	**“Rough” Grassland**	136.1 (60.3)	187.5 (60.6)	273.0 (56.5)
Mixed Plantation	2.9 (23.6)	6.3 (22.6)	17 (51.2)	**Total grassland**	1394.8 (68.6)	1715.3 (65.9)	2242.8 (67.6)
Coniferous Plantation	13.3 (47.0)	19.3 (37.7)	37.2 (40.0)	**Roadside vegetation**	16.8 (59.9)	21.3 (63.2)	29.1 (67.5)
Scrub	2.3 (82.2)	2.6 (36.1)	5.5 (49.5)	**Tall ruderal**	0.6 (85.7)	0.7 (77.8)	0.8 (66.7)
Total woodland	44.4 (52.5)	69.9 (47.6)	118.7 (52.5)	**Total roadside/ruderal**	17.4 (60.0)	22.0 (63.6)	29.9 (67.5)
Orchard	0.1 (50.0)	0.2 (100.0)	0.2 (100.0)	**Arable**	224.4 (73.0)	268.3 (75.4)	316.5 (73.8)
Parkland	44 (97.6)	45.1 85.4)	45.3 (69.1)	**Swamp/reed-bed**	0.1 (100.0)	0.1 (100.0)	1.3 (26.0)
Total orchard/parkland	44.1 (97.1)	45.3 (85.5)	45.5 (68.9)	**Flush/Spring**	0.03 (100.0)	0.03 (2.3)	1.3 (100.0)
Formal gardens	1.9 (35.8)	6.1 (92.4)	6.3 (67.7)	**Total wetland**	0.13 (100.0)	0.13 (9.3)	2.6 (41.3)
Gardens	8.2 (43.9)	13 (43.2)	25.7 (54.2)	**Track/Ride**	0.2 (10.0)	0.7 (13.2)	2 (23.3)
Amenity grassland	0.4 (22.2)	1.3 (27.7)	3.0 (57.7)	**Road**	16 (58.0)	21.8 (65.5)	29.6 (71.3)
Total amenity	10.5 (40.7)	20.4 (49.3)	35 (56.5)	**Total track/road**	16.2 (54.7)	22.5 (58.3)	31.6 (63.3)
Mere	8.3 (100.0)	8.3 (100.0)	18.1 (62.6)	**Built and environs**	5.3 (28.6)	12.1 (38.8)	20.9 (38.6)
Canal	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)				
Wet ditch	0.8 (28.6)	2.3 (59.0)	3.6 (51.4)				
River/Stream	1.8 (47.4)	2.9 (47.5)	4.5 (55.6)				
Total open water	2.6 (40.0)	5.2 (43.0)	8.1 (46.8)				

Table 12; Summary of land cover classified by habitat suitability across the Cholmondeley Estate, plus 500m buffer, at three Euclidean and Cost Weighted buffer distances (130, 250 and 500m), bracketed figures = area within Cost Weighted buffers as % of area within equivalent Euclidean buffers).

Euclidean distance buffers						
Class	**Area (ha) 130m**	**% total**	**Area (ha) 250m**	**% total**	**Area (ha) 500m**	**% total**
1	303.1	40.5	427.4	57.1	663	88.6
2	1931	57.6	2515.2	75	3095.0	92.3
3	309.1	65.4	360.3	76.3	434.1	91.9
4	58.1	87.9	93.4	61.7	134.7	89
Total	**2601.3**	**55.0**	**3396.3**	**71.9**	**4326.8**	**91.5**
cost weighted distance buffers						
Class	**Area (ha) 130m**	**% total**	**Area (ha) 250m**	**% total**	**Area (ha) 500m**	**% total**
1	188.1 (62.1)	25.1	258.8 (60.6)	34.6	383.8 (57.9)	51.3
2	1338.9 (69.3)	39.9	1629.2 (64.8)	48.6	2110.4 (68.2)	62.9
3	224.9 (72.8)	47.6	269.7 (74.9)	57.1	319.6 (73.6)	67.7
4	31.4 (54.0)	20.8	45.2 (48.4)	29.9	73.1 (54.3)	48.3
Total	**1783.3 (68.6)**	**37.7**	**2202.9 (64.9)**	**46.6**	**2886.9 (66.7)**	**61.1**
Class	**Total available (Cholmondeley Estate plus 500m buffer)**			**% total area**		
1	748.6			15.8		
2	3354.3			71		
3	472.3			10		
4	151.3			3.2		
Total	**4726.5**			**100**		

As Table 12 shows, however, the proportion of core habitat present in the Cost Weighted and Euclidean distance buffers around ponds is low as a proportion of the habitat available across the estate. Table 13, below summarises habitat classes of immediately pond adjacent mapped land cover (NB more than one class may apply to each pond).

Table 13; Land cover immediately pond adjacent (derived in GIS from Phase 1 survey map). C= Coniferous, BL = Broad Leaved

Abutting Phase 1 habitat class	No. of features	Habitat classification	% Tot. Features
"Rough" Grassland	45	2	12.7
BL Woodland Semi-nat.	35	1	9.9
BL Woodland Plantation	2	1	0.6
Mixed Woodland Plantation	5	1	1.4
Scrub	34	1	9.6
Swamp/reed-bed	3	1	0.8
Flush/Spring	1	1	0.3
Tall Ruderal	3	1	0.8
Gardens	15	1	4.2
Total	**143**		**40.5**
Improved Grassland	144	2	40.8
C Woodland Plantation	10	2	2.8
Formal gardens	6	2	1.7
Roadside vegetation	7	2	2.0
Parkland	1	2	0.3
Total	**168**		**47.6**
Arable	28	3	7.9
Total	28	3	7.9
Road	6	4	1.7
Built and environs	8	4	2.3
Total	**14**		**4.0**
Total all Classes	**353**		**100.0**

6.3 Pond Characteristics

Totals numbers and percentages of the 288 ponds to which direct access for survey was given within each size class are recorded in Table 14, below.

Table 14; Pond size class distribution of occupied and unoccupied ponds (NB for 288 ponds accessible for survey).

Pond size class (m^2)	No. in class[1]	%. All ponds[2]	No. occupied[1]	% occupied ponds in class[2]	% ponds in class occupied[2]
< 100	85	29.5	10	11.6	11.8
101-250	69	24.1	22 (1)[3]	26.8	33.3
251-500	78	27.1	24 (1)[3]	29.1	32.1
501-750	19	6.6	12	14.1	63.2
751-1000	10	3.5	4	4.7	40.0
>1000	27	9.4	12	14.1	44.4
Total	288	100	86	100	

[1] Ponds to which direct access for survey was given. [2]Does not sum to 100 due to rounding. [3]Adults present, no evidence of breeding.

Percentage shading was recorded at each Cholmondeley pond and is recorded in Table 15 below. Overall, some 53.6% of ponds at Cholmondeley were shaded around more than 50% of their perimeter, over 32.5% being shaded around more than 70%, the level at which significant reduction in newt occupancy can be expected according to Swan and Oldham (1993). Swan and Oldham (1993) also found that occupancy rates were depressed in ponds with very low levels of shade, they speculated possibly due to exposure or homogeneity of surrounding terrestrial land cover. This, however, was not reflected in the 2007 survey (see Table 15 below), in which 29.8% of ponds where presence and breeding were recorded had less than 10% shade, and 47.7% less than 30% shade. Rannap and Briggs' (2006) findings of occupation peaking at intermediate levels of shading were reflected to some extent, with 39.3% of records occurring in ponds with levels of shading between 31 and 70%, with 27.4% in the 51-70% bracket.

Table 15; Estimated degree of shading of ponds across the Cholmondeley pondscape as a whole, and T. cristatus breeding ponds (NB includes estimates based on aerial imagery where access was not granted for on the ground survey).

% Shade (Est.)	All Ponds (n=323)	% all ponds[2]	Breeding ponds (n=84)	% breeding ponds[2]
< = 10	91	28.2	25	29.8
11 - 30	35	10.8	15	17.9
31 - 50	24	7.4	10	11.9
51 - 70	68	21.1	23 (2)[1]	27.4
71 - 80	66	20.4	11	13.1
> 80	39	12.1	0	0.0
Total	323	100	84 (2)[1]	100

[1] Adults present but no evidence of breeding. [2] Does not sum to 100 due to rounding.

Table 16; Pond count and summary of pond condition at Cholmondeley in 2007.

Pond Status	**Pond Condition**	**Count**	**Comments**
All Ponds	Present	291	Includes pond sites with no open water, but signs of recent inundation and/or aquatic/semi-aquatic vegetation, either directly surveyed or not surveyed but clearly visible on survey
	Assumed Present, access denied	32	Either visible in Aerial Photography, or mapped, but obscured in Aerial Photography.
	Total	**323**	
Ponds not surveyed (access unavailable)	Visible in Aerial Photography	10	Open pond visible in Aerial Photography
	Evidence in Aerial Photography	22	Pond condition indiscernible in Aerial Photography.
	Visible but no access.	3	
	Total	**35**	
Surveyed	Present	288	Includes pond sites found to be dry or marshy at time of survey (so amphibian survey limited to egg search and netting of patchy pools).
Dry or shaded out Ponds	Seasonal or long term drawn down	21	Marshy, possibly rarely has open water.
	Dry on Survey	17	Dry, regularly inundated, possibly remnant aquatic vegetation.
	Shaded out, no aquatic vegetation	36	Inundated at time of survey.

6.4 Cluster Sizes and Composition

Connectivity varies greatly across the range of spatial scale examined here. Table 17 summarises the indices of overall network connectivity calculated in CS2.5.8 for all Euclidean and Cost Weighted distance thresholds of connectivity. Note these indices were calculated using the Habitat Suitability Index score as the node attribute used in weighting probability of connectivity calculations. Indices can be briefly summarised here as follows:

Indices of connectivity

NL - Number of Links, as a landscape is more connected, it will present a larger total number of links (connections between habitat nodes in the landscape).

NC – Number of Components. Pond clusters in this instance are nodes, but isolated ponds also are considered as nodes (i.e. a locus of intra-nodal connectivity), so this index equates to the total number of pond clusters plus the total number of isolated ponds. As a landscape is more connected, the number of components decreases.

IIC – Integral Index of Connectivity – (Pascual-Hortal and Saura 2006) ranges from 0 – 1 for individual nodes, increasing with connectivity at a node.

PC Probability of Connection – (Saura and Pascual-Hortal 2007a), ranges from 0 – 1 for individual nodes, increasing with connectivity. The PCnum is an overall summary of this index for the network as a whole, increasing with increased connectivity.

IICnum/PCnum is an overall summary of this index for the network as a whole, increasing with increased connectivity.

Table 17; Variation in connectivity as shown by variation in binary and probabilistic connectivity indices at 130, 250 and 500m Euclidean and Cost Weighted inter-pond distances (pond n = 323).

	Euclidean distance			Cost Weighted Distance		
Overall Indices	500m	250m	130m	500m	250m	130m
NL	1716	625	260	399	188	108
NC	9	65	158	125	197	245
IICnum	2546.738	589.602	262.071	389.981	229.867	183.348
PCnum	3238.818			892.354		

With a simple binary conceptualisation of connectivity, at the maximal threshold (the commonly observed dispersal distance of 500m Euclidean inter-pond distance), connectivity of the pondscape presents as strong and extensive, with all but two isolated ponds included in seven mostly large connected components, or pond-clusters (max. 144 ponds, cluster 4 in Fig. 28, below, See Table 18, page 148). Figure 28 (with subsequent Figs. to Fig. 34) represents the pond connectivity graph with straight line connections (vertices) between connected ponds (nodes) which are represented as points. Buffers around ponds within clusters are merged, representing the area of land cover associated with pond clusters at this threshold distance. Pond buffers around isolated ponds are shown grey.

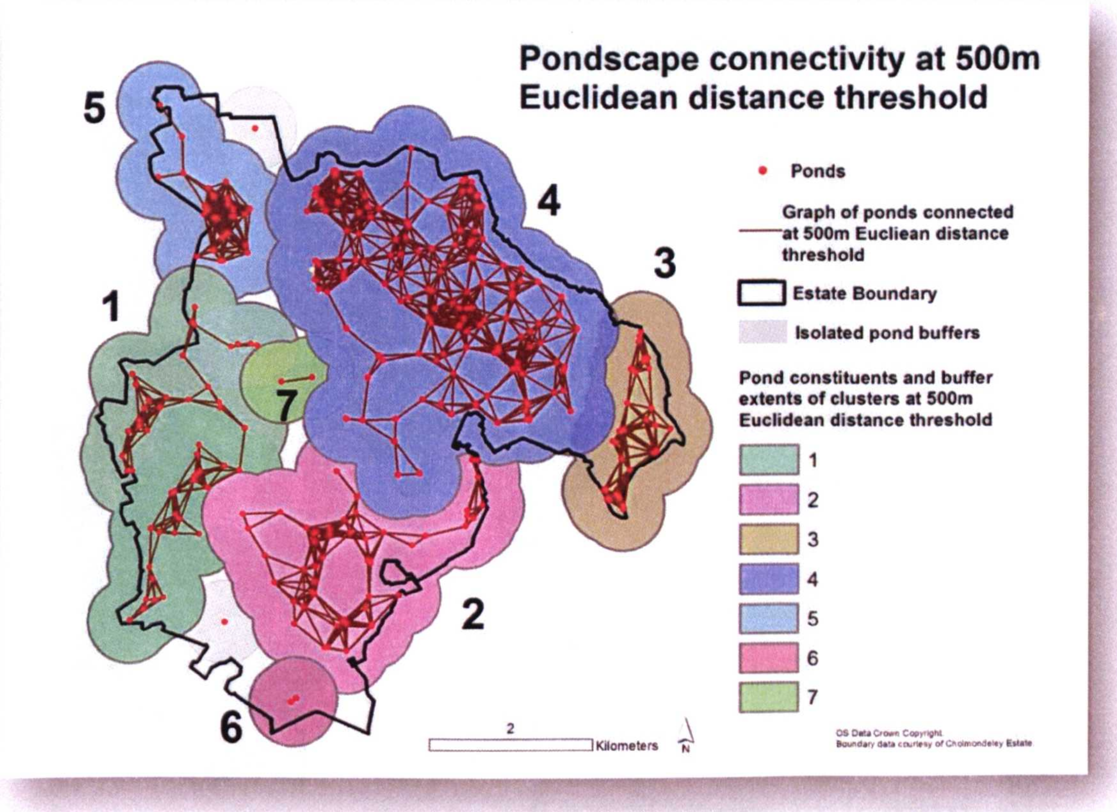


Figure 28; Graph of connected pond clusters with pond buffer extents at 500m Euclidean distance.

As can be seen, at 500m Euclidean distance, over 91% of the estate and the adjacent 500m buffer, falls within pond/pond cluster buffer. However, as Table 12 shows, a relatively small proportion (15.8%, 748.6 ha) of the total area of the estate and land immediately adjacent can be said to constitute core habitat for *T. cristatus*, with still less (88.6% of total core habitat present, or 587.5 ha) available within pond buffers. Fig 29, below shows the pond connectivity graph representing 250m Euclidean inter-pond distance. At this threshold distance connectivity is substantially reduced, with the number of connected components (pond clusters) increasing from 7 to 42, and mean cluster size decreasing from 45.86 (SD 44.38) to 7.29 (SD 7.14) ponds, with the number of isolated ponds increasing more than ten-fold from 2 to 24. The core habitat area falling within pond/cluster buffers at this threshold distance decreases to 57.1% of total available (or 427.4 ha).

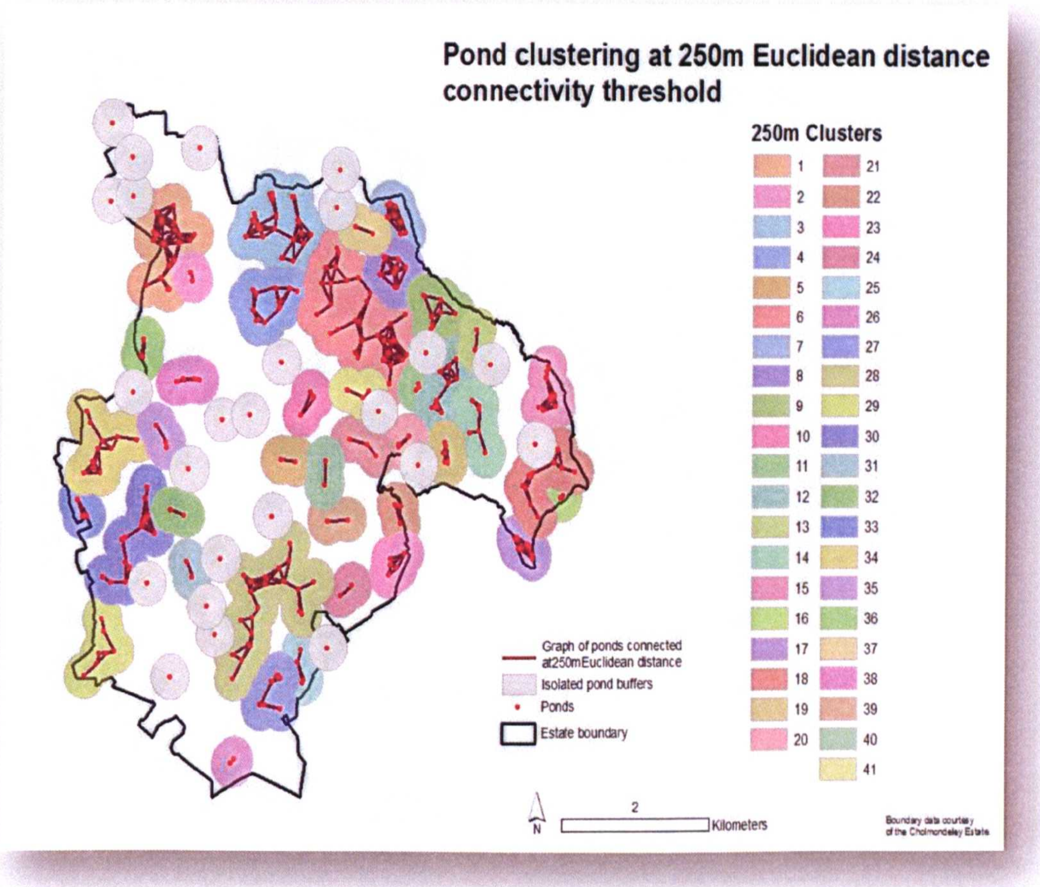


Figure 29; Graph of connected pond clusters with pond buffer extents at 250m Euclidean distance.

As the inter-pond connectivity threshold distance decreases to 130m, connectivity is reduced massively, with the pondscape consisting of 72 clusters (mean cluster size 3.29, SD 1.98) and 86 isolated ponds, though it should be noted that even at this low inter-pond distance, the great majority of ponds (237, 73.37%) are still part of a cluster of at least 2 ponds. The area of core habitat available within pond buffers at this threshold distance is reduced further, to 303.1ha, 40.5% of total.

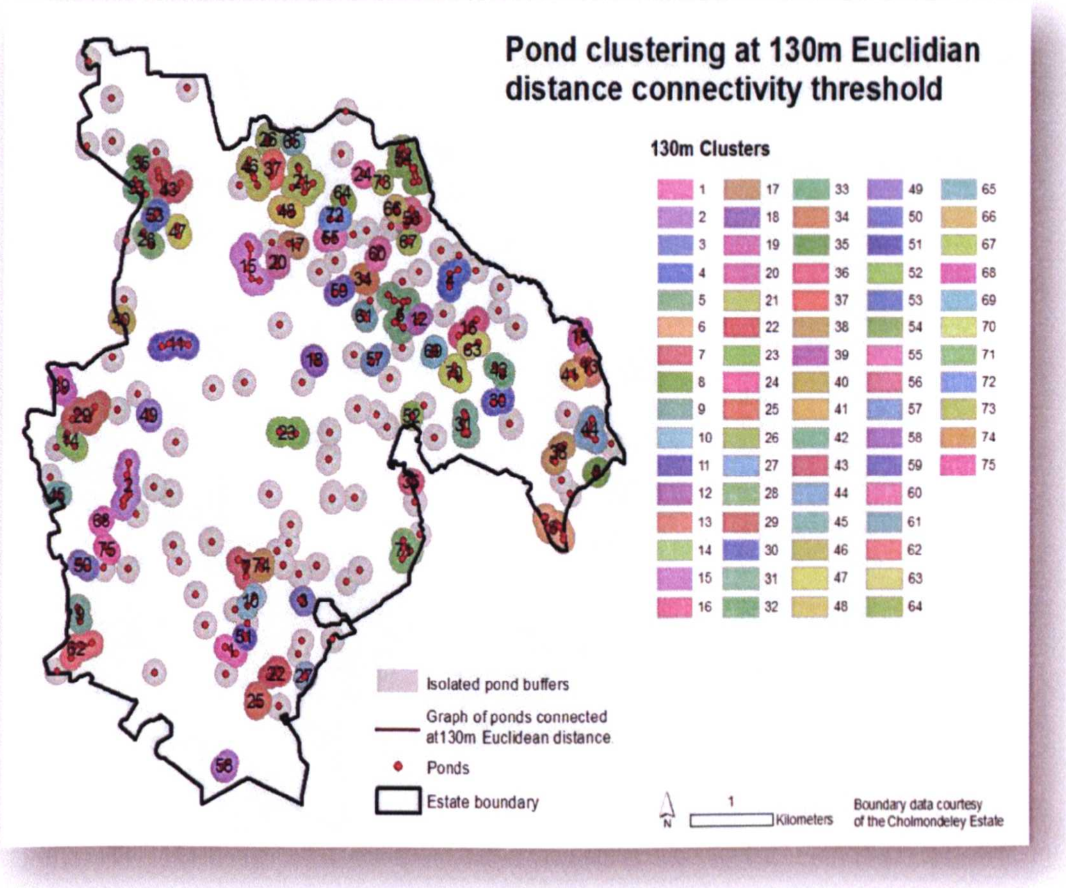


Figure 30; Graph of connected pond clusters with pond buffer extents at 130m Euclidean distance.

The effect of including terrain effects in assessment of pondscape connectivity by using a Cost Weighted distance calculation is substantial, with a marked drop in connectivity at all levels; increase in numbers of pond clusters and isolated ponds and decrease in cluster size (see table 18, below). At 500m cost weighted distance, the number of pond clusters rises substantially, from 7 at 500m Euclidean distance, to 55 (see Fig. 31 and tTable 18), the number of isolated ponds from 2 to 70, and the maximum cluster size drops from 144 to 28 (mean 4.60, SD 4.15). At this distance threshold, the quantity of available core habitat within pond buffers decreases to 51.3% of the total available (57.9% of that available within Euclidean distance buffers, 383.8 ha), from 88.6% (663 ha)

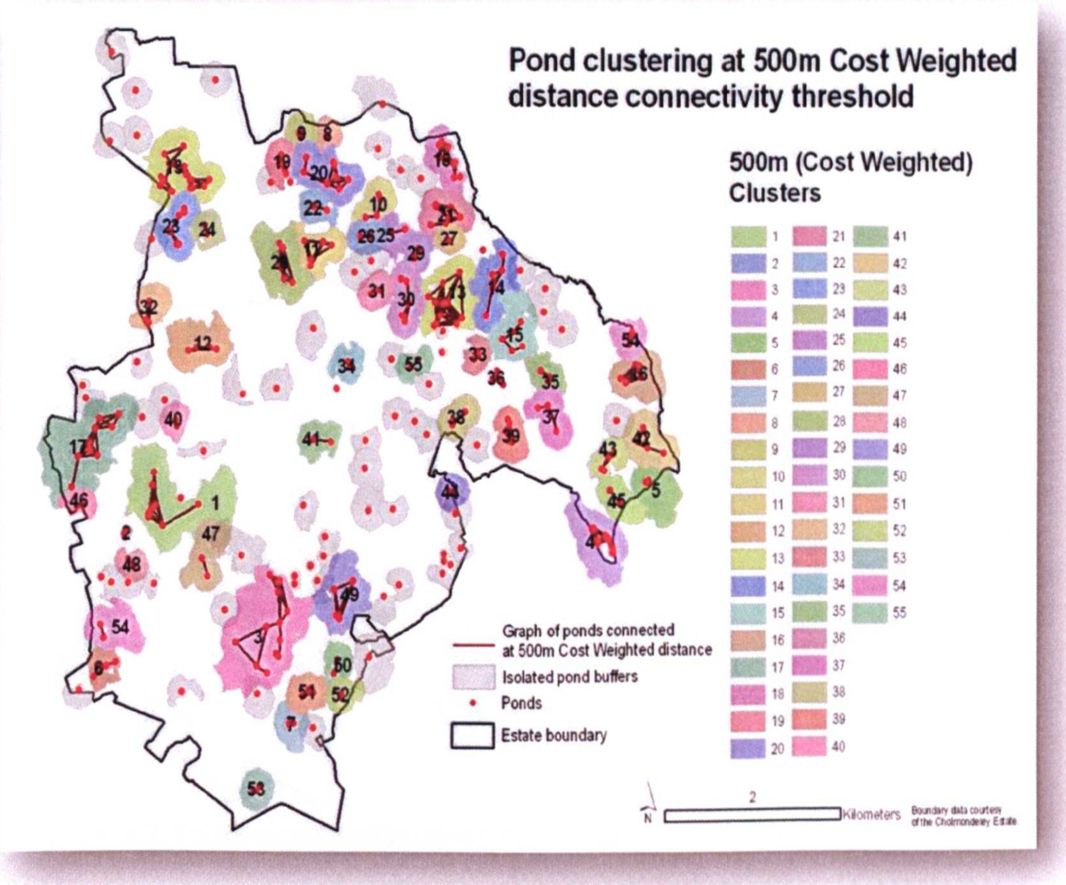


Figure 31; Graph of connected pond clusters with pond buffer extents at 500m Cost Weighted distance.

At the 250m cost weighted distance, (see Fig. 32, below) the increase in number of clusters is smaller (from 55 to 65) as increased isolation reduces mean cluster size (mean 2.93, SD 1.83, with a maximum cluster size of just 13 ponds) and produces a substantial increase in the number of isolated ponds from 70 to 132. The area of core habitat available declines again to 258.8 ha, 34.6% of the total available (60.6% of that available in the 250m Euclidean distance buffers).

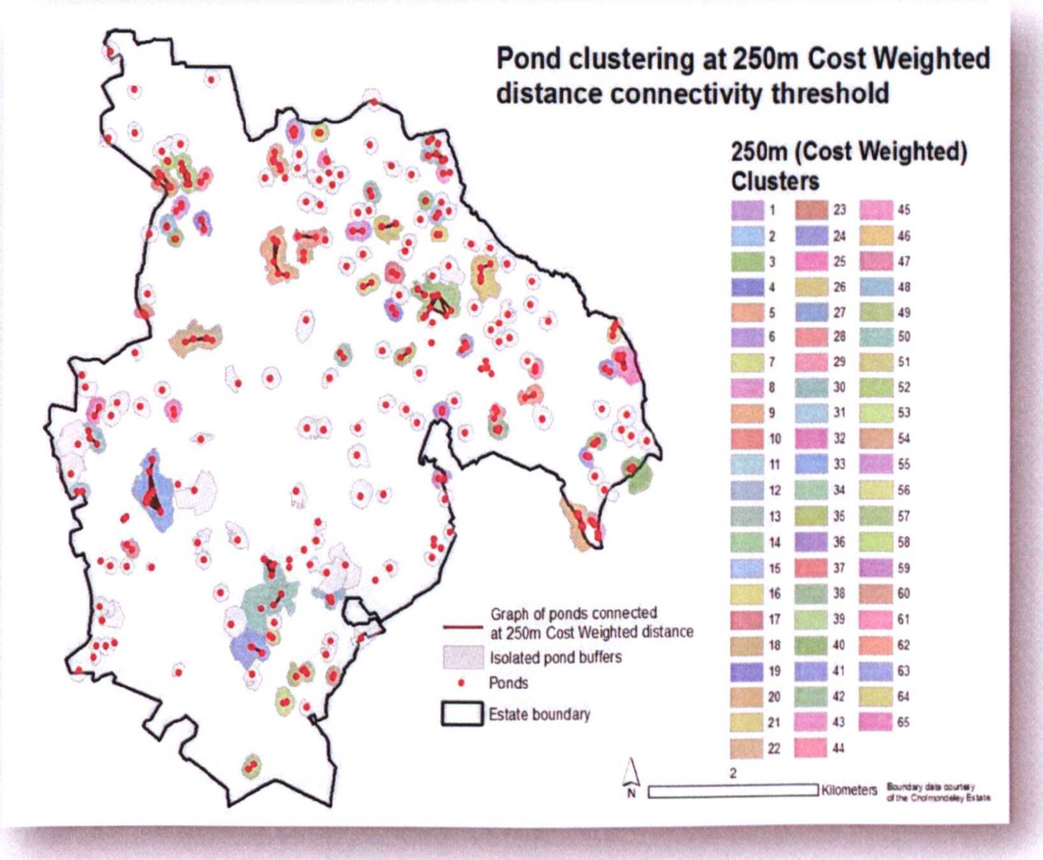


Figure 32; Pond clustering at 250m Cost Weighted distance threshold.

At 130m cost weighted distance (see Fig. 33, below) the number of component pond clusters actually reduces to 48, the maximum cluster size remaining unchanged, but with some reduction in mean cluster sizes (2.60, SD1.11) compared to 2.93, SD 1.83, at 250m cost weighted distance. The majority of ponds (198, 61.3%), are now isolated from a pond cluster at the 130m threshold. The available area of core habitat is also reduced to 25% of the total available, 188.1 ha (62.1% of that available at the 130m Euclidean threshold distance). Change in connectivity (number of clusters and mean cluster sizes) across the range of spatial scales are summarised in Table 18. Figure 34 below shows the stepwise disconnection of the pondscape as threshold of connectivity decreases.

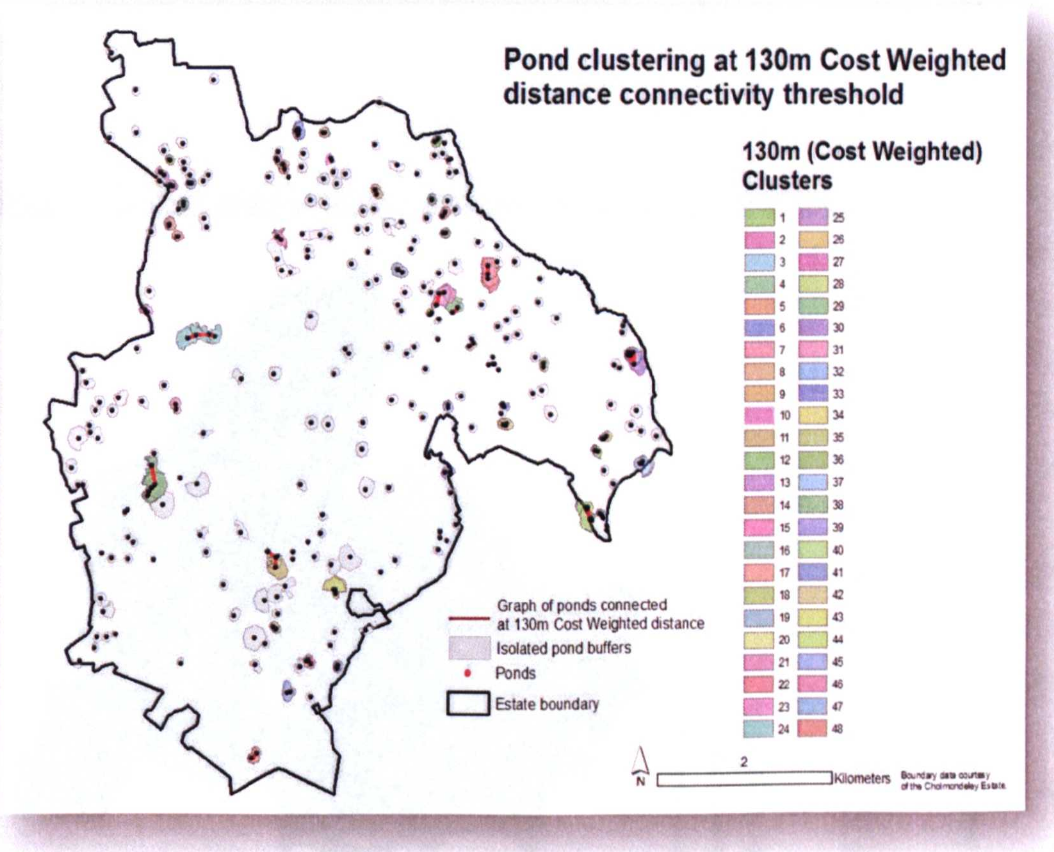


Figure 33; Graph of connected pond clusters with pond buffer extents at 130m Cost Weighted distance.

Table 18; Variation in pond cluster size, number of clusters and number of isolated ponds at 130, 250 and 500m Euclidean inter-pond distances.

Inter-pond distance	Number of clusters	Number of Isolated ponds	Maximum cluster size	Minimum cluster size	Mean cluster size	SD cluster size
Euclidean Distance						
130m	72	86	12	2	3.29	1.98
250m	42	24	32	2	7.29	7.14
500m	7	2	144	2	45.86	44.38
Cost Weighted Distance						
130m	48	198	7	2	2.60	1.11
250m	65	132	13	2	2.93	1.83
500m	55	70	28	2	4.60	4.15

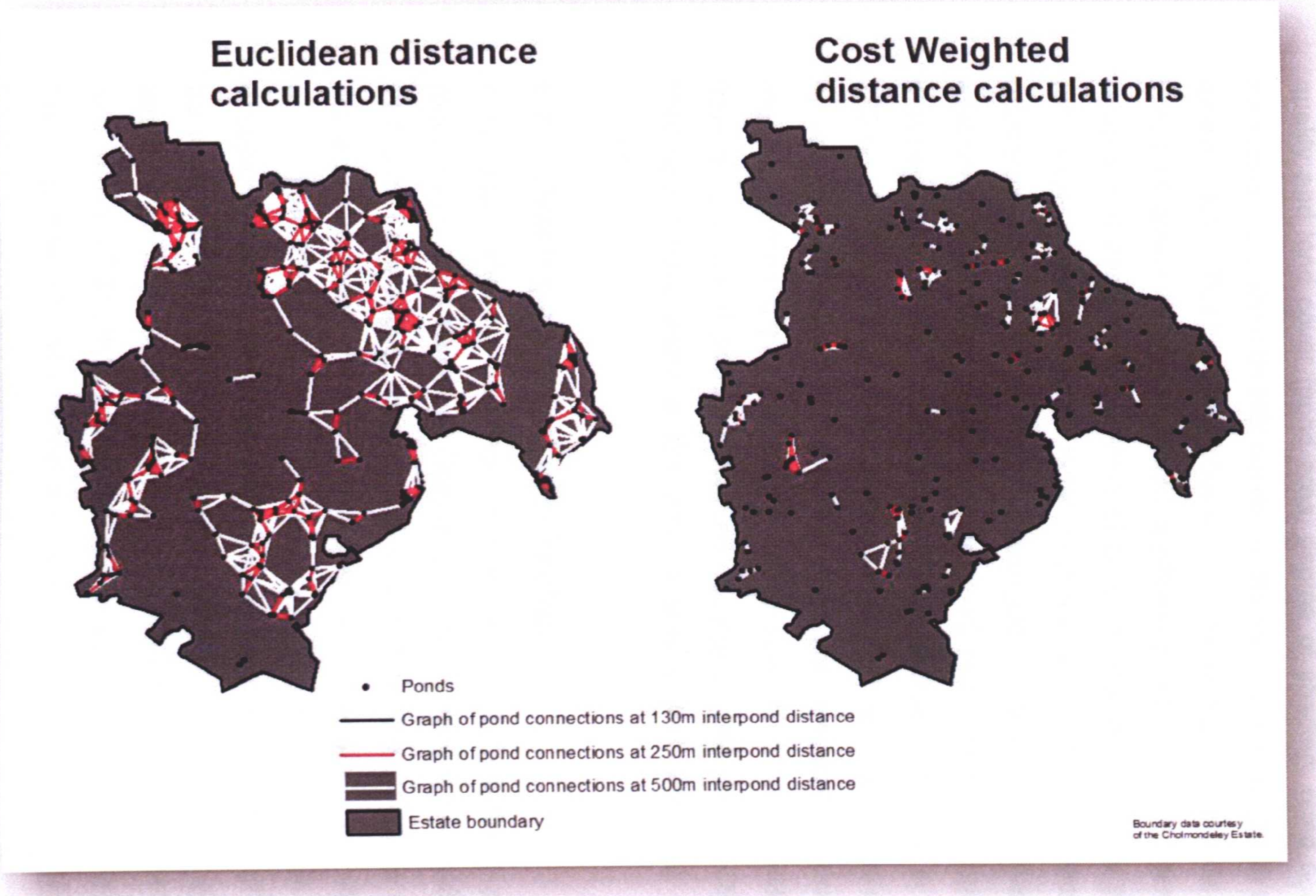


Figure 34; Connectivity graphs showing variation in connectivity between Cost Weighted and Euclidean distance thresholds at 130, 250 and 500m inter-pond distances..

6.5 Presence of *Triturus cristatus*

This section describes the distribution of *T. cristatus* breeding ponds across the Cholmondeley estate and the relationship of this distribution to terrestrial habitat characteristics, pond attributes associated with terrestrial habitat quality and land cover (pond area, degree of shading, pond density, habitat suitability (as defined by HSI score), relationship to barriers such as roads and moving water. The characteristics of *T. cristatus* breeding ponds in relation to levels of connectivity, specifically association with pond clustering, and the relative and absolute importance of breeding ponds within the pond network (as represented by pond node importance for the connectivity of the pondscape graph at the three thresholds of connectivity discussed) are examined. *T. cristatus* were recorded in 86 ponds of the 283 ponds holding standing water at the time of survey, with breeding confirmed in 84. Of these 283 ponds, *T. cristatus* were not found in any of the 12 identified as temporary or seasonal; however, this probably does not constitute all ponds liable to regular seasonal drying out, as this information could not be reliably obtained from tenants for all ponds. Recorded occupation rate was 30.39% for ponds holding standing water at the time of survey, with breeding confirmed in 29.68%.

6.6 Shading and seral succession

Percentage shading was recorded at each Cholmondeley pond and is recorded in Table 19 below. Overall, and comparable to the findings from the PLP data base above, some 54.2% of ponds at Cholmondeley were shaded around more than 50% of their perimeter, and over 30% were shaded around more than 70%, the level at which significant reduction in *T. cristatus* occupancy can be expected according to Swan and Oldham (1993). As can be seen from Fig. 35, below showing proportion of sampled ponds in each shade class, in line with the findings of Swan and Oldham (1993) and Rannap and Briggs (2006), the occurrence of *T. cristatus* in each class broadly follows the proportion of each in the pondscape (χ^2 = 28.060, p<0.000), showing some association with intermediate levels until high levels of shade, exceeding 75 – 80%, are reached. Lower than expected occurrence at the <10% level of shading is demonstrated, again in line with Swan and Oldham's (1993) findings, although occupation in the <10% class could be considered somewhat higher than might be expected from their findings. Mann – Whitney 2 sample rank testing between ponds with recorded breeding presence (median class 3, 31-50%), and no record of presence (median class 4, 51-75%) showed a significance difference between median shade values ($W_{204,84}$ = 31755.0, p = 0.0003 (adjusted for ties), with the non-breeding ponds having a significantly higher median shade value (p = 0.0001, adjusted for ties).

Table 19; Estimated degree of shading of ponds across the Cholmondeley pondscape as a whole, and T. cristatus breeding ponds (NB includes estimates based on aerial imagery where access was not granted for on the ground survey).

% Shade (Est.)	All Ponds (n=323)	Surveyed ponds (n=288)	Breeding ponds (n=84)	% all ponds	% surveyed ponds[2]	% breeding ponds[2]
< = 10	91	81	25	28.2	28.1	29.8
11 - 30	35	30	15	10.8	10.4	17.9
31 - 50	24	21	10	7.4	7.3	11.9
51 - 70	68	60	23 (2)[1]	21.1	20.8	27.4
71 - 80	66	57	11	20.4	19.8	13.1
> 80	39	39	0	12.1	13.5	0
Total	323	288	84 (2)[1]	100	100	100

[1] Adults present but no evidence of breeding. [2] Does not sum to 100 due to rounding.

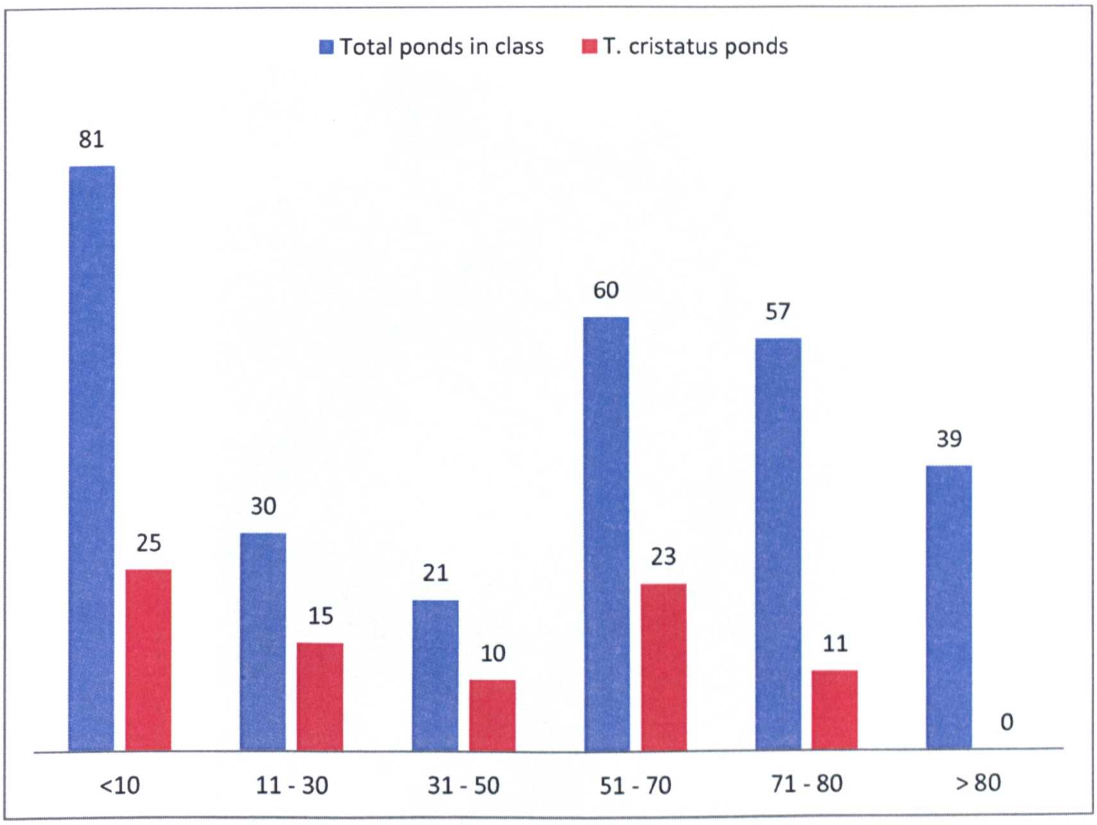


Figure 35; Numbers of ponds (accessible to survey, n=288) per shade class (%) and number of T. cristatus breeding ponds per shade class.

6.7 Pond Density and dispersion

Mean pond density was 15.21 km^{-2} (min 1.94, max 32.89, SD 6.59) , as derived from a Kernel density estimation surface calculated using pond feature centroids (6m cell size 1200m search radius) for the Cholmondeley pondscape as a whole. For *T. cristatus* breeding ponds, the corresponding figure was 14.84 ponds km^{-2} (min. 3.39, max. 26.95, SD 5.81). Testing the hypothesis of association between high pond density and increased breeding presence in ponds, Mann Whitney U test for difference in distribution of values between the breeding pond group and non-breeding group showed no significant difference between the distribution of pond density values of the two groups (Mann Whitney U = 8237.5. p = 0.699). Pond density across the estate is generally high, and no significant relationship (at the 95% confidence level) was identified between density alone and *T. cristatus* occupancy ($\chi^2 = 6.675$, p = 0.154).

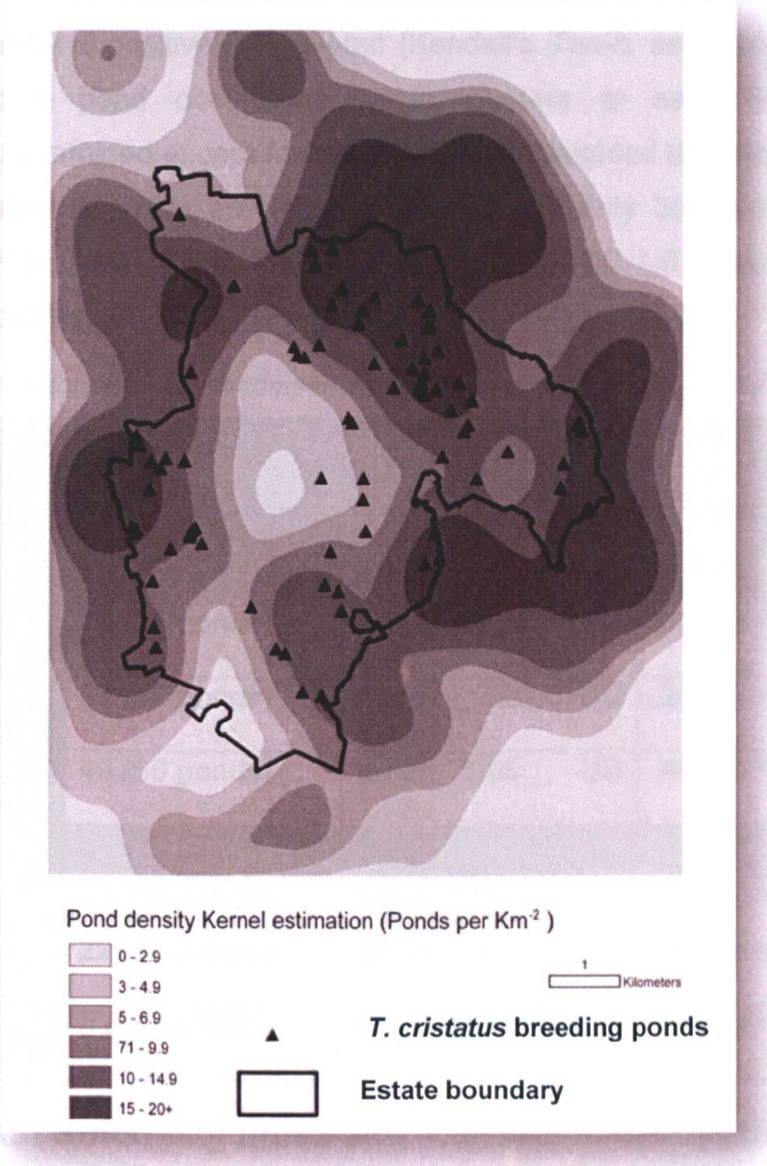


Figure 36; Distribution of T. cristatus *breeding ponds and pond Kernel density estimation (6m cell size, 1200m search radius).*

6.8 Pond Clustering (Euclidean and Cost Weighted connectivity thresholds) and *T. cristatus* presence

The Cholmondeley pondscape is significantly clustered, with a mean nearest neighbour distance of 118.49m, as against an expected 162.08m (Average Nearest Neighbour Distance Observed/Expected = 0.73, Z = 9.35 SD, $p < 0.001$). *T. cristatus* breeding ponds are also significantly clustered, with a mean nearest neighbour distance of 261.57m, as against an expected 332.95m (Average Nearest Neighbour Distance Observed/Expected = 0.79, Z

= -3.75 SD, p < 0.001). Pond count in network components (pond clusters and isolated ponds) is positively correlated (Kendall's *Tau-b,* see table 20 below) with breeding pond occurrence within clusters at each threshold of connectivity examined except for the 130m Cost Weighted threshold, at which most components (197) are isolated ponds, with only 25 breeding ponds occurring in a cluster (16 clusters, mean size 1.56, SD 1.0, max. 4 breeding ponds per cluster).

Table 20; Correlation between component pond count and breeding pond occurrence.

Threshold of Connectivity	Occupied Clusters (Breeding ponds)	Cluster size	Kendall's *Tau-b* (Component size x no. breeding ponds)
Cost Weighted			
130	16 (25 ponds)	Mean 1.56, SD 1.00	.079, p = 0.209
250	27 (42 ponds)	Mean 7.32, SD 7.13	.201, p = 0.003
500	40 (66 ponds)	Mean 1.65 , SD 1.28	.463, p < 0.0001
Euclidean			
130	43 (64 ponds)	Mean 3.57, SD 2.2	.381, p <0.0001
250	22 (68 ponds)	Mean 7.45, SD 6.5	.601, p < 0.0001
500	5 (84 ponds)	Mean 63.4, SD 41	.877, p < 0.002

6.9 Habitat Suitability Index and *T.cristatus* occupation.

Table 21; T. cristatus occupation (count and %) by Habitat Suitability Index class.

HSI Class	No. Ponds	% (Tot.)	No. Occupied	Proportion Occupied
Poor	29	8.98	3	0.10
Below Average	35	10.84	1	0.03
Average	88	27.24	7	0.08
Good	96	29.72	46	0.48
Excellent	41	12.69	29	0.71
Not Calculated[1]	34	10.53	Unknown	Unknown
Total	323	100.00	86	

[1] Includes all the ponds for which access was denied by the tenant, plus ex-field ponds "annexed" into private gardens, which could not be accessed for survey, and were heavily modified (high fish density, waterfowl, artificial "water features" and exotic planting).

Table 21 above and Fig. 37 below summarise *T. cristatus* pond occupation in 2007 in relation to classified HSI score. As would be expected, they show a strong positive association with HSI scores of ponds - as pond HSI score increases from 'Below Average' to 'excellent', so does the proportion of ponds occupied by breeding *T. cristatus* ($\chi^2 = 82.680$, $p < 0.0001$). Mann - Whitney U test for differences in distribution of HSI values between breeding and non-breeding pond group showed a significant difference with a significantly lower median HSI in the non-breeding group (Mann Whitney U = 2995.5, $p < 0.0001$, see Fig 37 below).

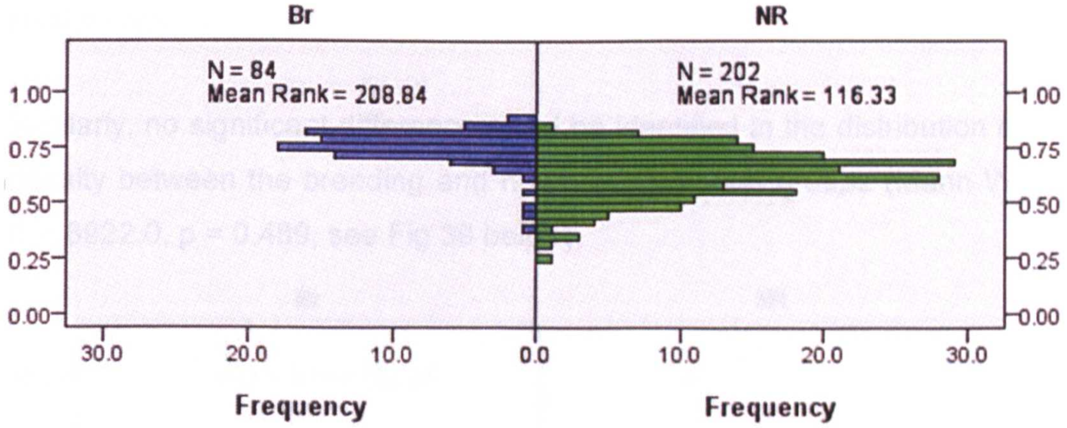


Figure 37; Visualisation of Mann Whitney U test for difference between distribution of pond HSI values of breeding and non-breeding (NR) pond groups.

6.10 Terrestrial landscape and Habitat characteristics

Roads

No significant difference was found between the distance to the nearest road between the breeding pond (median Euclidean distance 160m) and non-breeding pond (median Euclidean distance 120m) groups (Mann Whitney U = 7939.5, p = 0.393, see Fig. 38 below). Euclidean rather than Cost Weighted Distance is considered because the likely factors impacting upon *T. cristatus* are noise, light, vibration and pollutant run off rather than *T. cristatus*' ability to traverse the intervening land cover.

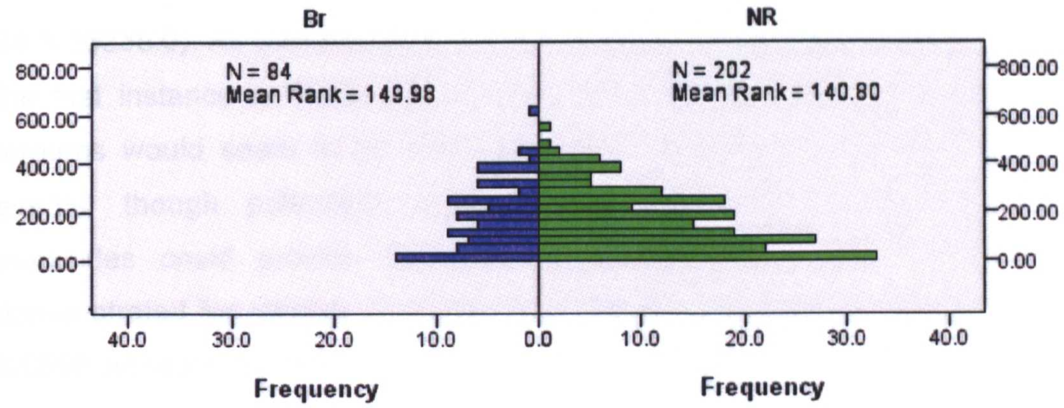


Figure 38; Visualisation of Mann Whitney U test results for differences between distribution of distances to the nearest road of Breeding (Br) and non-breeding (NR) pond groups.

Similarly, no significant difference could be identified in the distribution of road density between the breeding and non-breeding pond groups (Mann Whitney U = 8922.0, p = 0.489, see Fig 39 below).

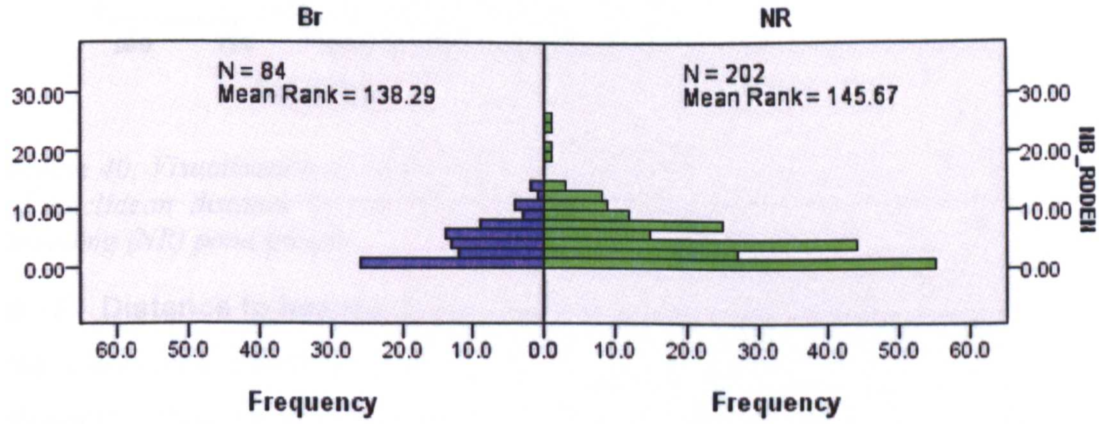


Figure 39; Visualisation of Mann Whitney U test results for differences in distribution of road density estimates (from GIS line density estimation surface) between breeding (Br) and non-breeding (NR) pond groups.

No association could be identified between road density and breeding presence. ($\chi^2 = 4.589$, p = 0.589).

6.11 Moving Water – rivers and streams

A significant difference in the distribution of distances to nearest river or stream was identified between the breeding and non-breeding groups (Mann Whitney U = 64785.5, p = 0.002, see Figure 40 below), with non-breeding ponds having a shorter median distance (p = 0.0007 adjusted for ties, W202, 84 = 36235.0). As with distance to roads, Euclidean distance was examined in the first instance as likely impacts upon occupancy of distance to rivers or streams would seem to be from dispersal of fish during localised flooding events, though potentially rougher more structured vegetation around banksides could provide suitable foraging habitat. A similar trend was demonstrated for median Cost Weighted distance (W202, 84 = 28424.0, p = 0.0505 adjusted for ties), but the difference in distribution of distance values between the two groups was not significant (Mann Whitney U = 7475.0, p = 0.113).

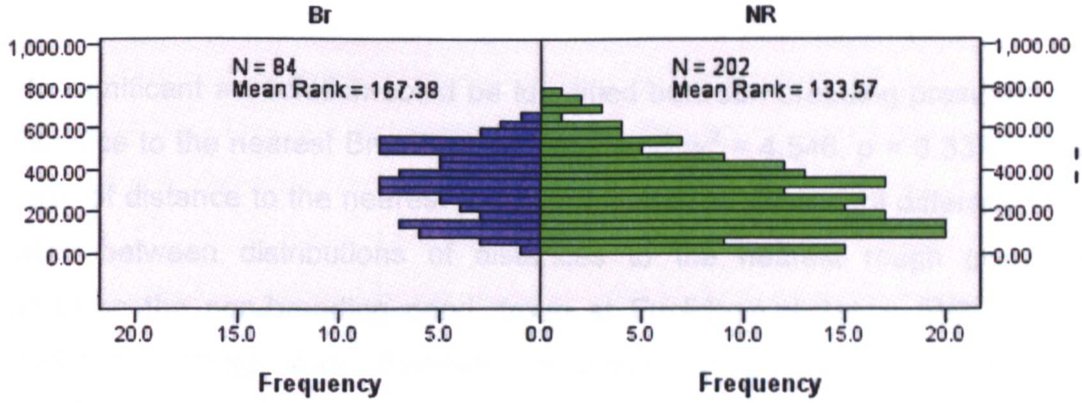


Figure 40; Visualisation of Mann Whitney U test results for differences in distribution of Euclidean distance to the nearest river or stream of breeding (Br) and non-breeding (NR) pond groups.

6.12 Distance to nearest broadleaved woodland or rough grassland

No significant difference was found in the distribution of values for Cost Weighted distance to the nearest rough grassland, between the non-breeding and breeding pond groups (Mann Whitney U = 7737.0, p = 0.240, see Fig. 41, below).

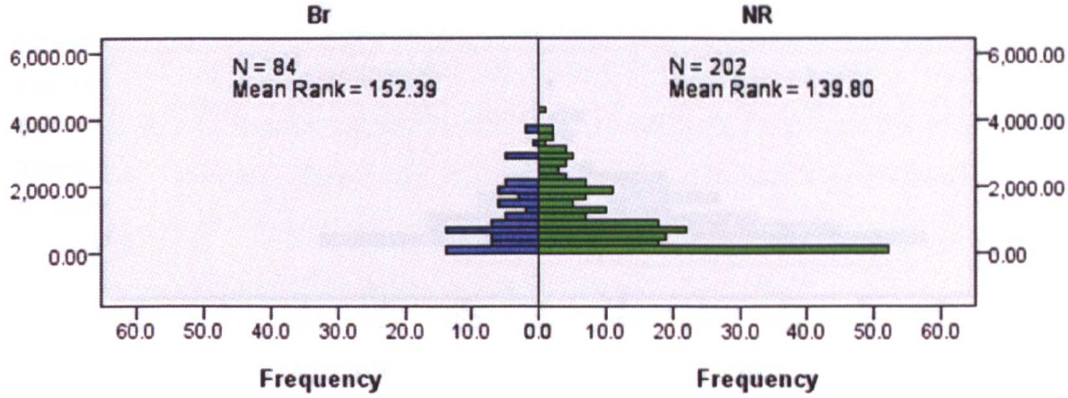


Figure 41; Visualisation of Mann Whitney U test results for differences in distribution of Cost Weighted distance to the nearest rough grassland between breeding (Br) and non-breeding (NR) pond groups.

No significant association could be identified between breeding presence and distance to the nearest Broadleaved Woodland (χ^2 = 4.546, p = 0.337). In the case of distance to the nearest rough grassland, no significant difference was seen between distributions of distances to the nearest rough grassland between the non-breeding pond group at Euclidean distance (W202, 84 = 30436.0,). There was, however, a significant difference between the distribution of values between non-breeding and breeding groups (Mann Whitney U = 9956.5, p = 0.021, see Fig 42 below) at Cost Weighted distances, with a significantly longer median distance for the non-breeding group (median cost weighted distance 635.2m for non-breeding ponds, 496.7m for breeding ponds, W202,84 = 30970.0, p = 0.001). No significant association (at the 95% confidence level) could be identified between breeding pond presence and distance to the nearest rough grassland however, (χ^2 = 7.425, p = 0.115).

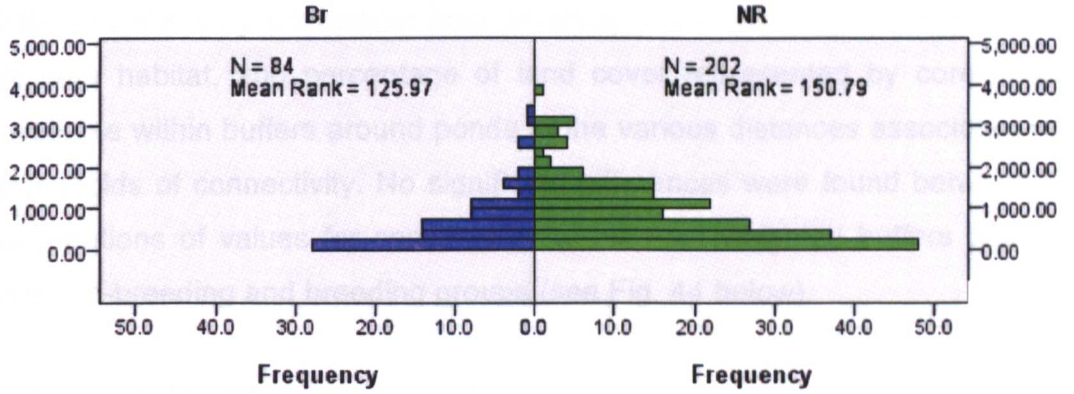


Figure 42; Visualisation of Mann Whitney U test results for differences in distribution of Cost Weighted distance to the nearest broadleaved woodland between breeding (Br) and non-breeding (NR) pond groups.

Broad Leaved Woodland and Rough Grassland were tested here for significant relationships to proximity of breeding ponds, but other land cover classes are demonstrated in the literature to fall into the category of Core Habitat, and all of these were taken into account in relation to proximity, by measurement of distance to the nearest Core Habitat as reclassified from the Phase 1 Habitat Survey GIS coverage. No significant difference in distribution of values for distance to Core Habitat between the non-breeding pond group and the breeding pond group was identified (Mann Whitney U = 7987.5, p = 0.408, see Fig. 43 below).

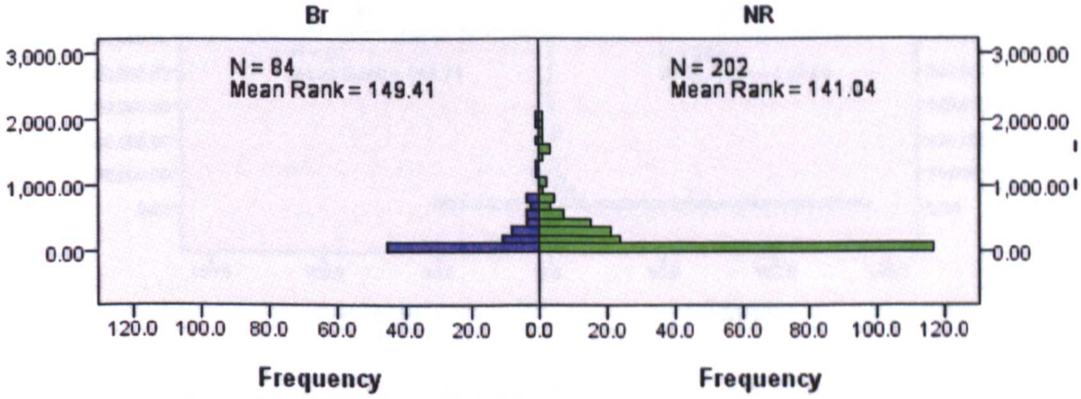
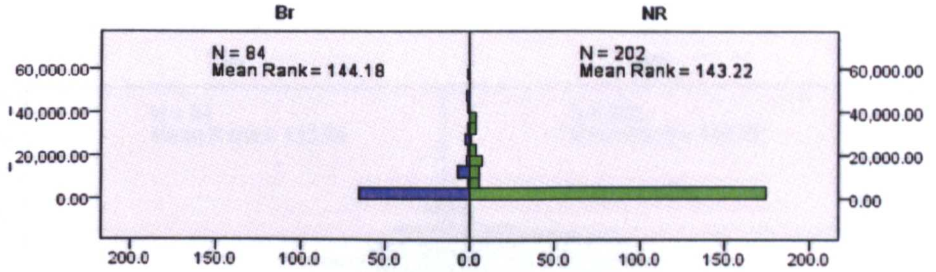


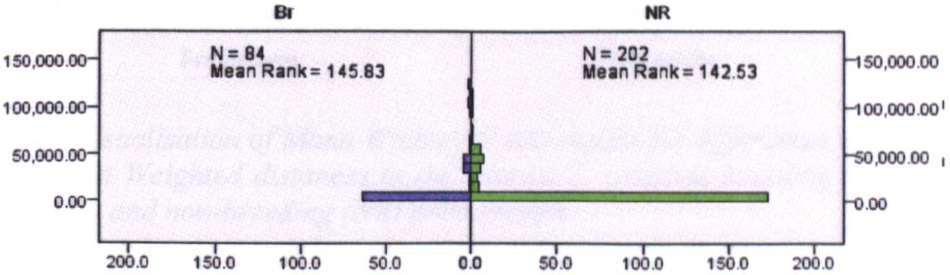
Figure 43; Visualisation of Mann Whitney U test results for differences in distribution of Cost Weighted distance to the nearest core habitat between breeding (Br) and non-breeding (NR) pond groups.

Habitat availability (as distinct from proximity) was examined in terms of area of core habitat, and percentage of land cover represented by core habitat available within buffers around ponds at the various distances associated with thresholds of connectivity. No significant differences were found between the distributions of values for core habitat within cost weighted buffers between the non-breeding and breeding groups (see Fig. 44 below).

130m Cost Weighted distance buffers



250m Cost Weighted distance buffers



500m Cost Weighted distance buffers

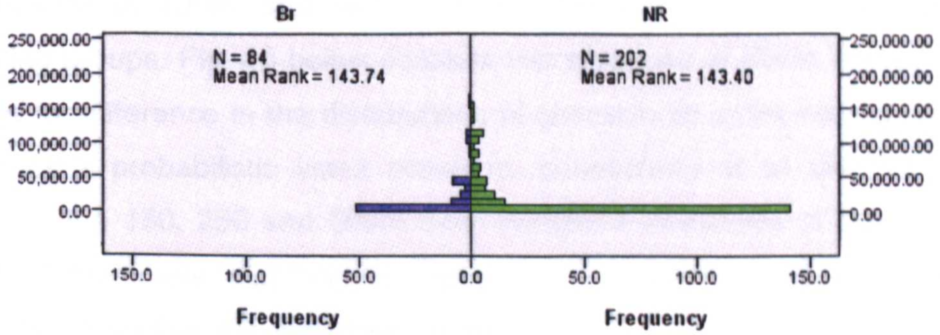


Figure 44; Visualisation of Mann Whitney U test results for differences in distribution of quantity of core habitat within Cost Weighted distance buffers between breeding (Br) and non-breeding (NR) pond groups.

6.13 Proximity to *T. cristatus* breeding ponds

No significant difference in median inter-pond distance was demonstrated (Mann-Whitney 2 sample rank test) between the non-breeding pond group (median 695.7m) as compared with the breeding pond group (median 665.5m), ($W_{202,84}$ = 30267.0, p = 0.1098). No significant difference (at the 95% significance level) was identified between the breeding and non-breeding groups in terms of the distribution of values (Mann Whitney U = 9291.0, p = 0.205, see Fig 45 below).

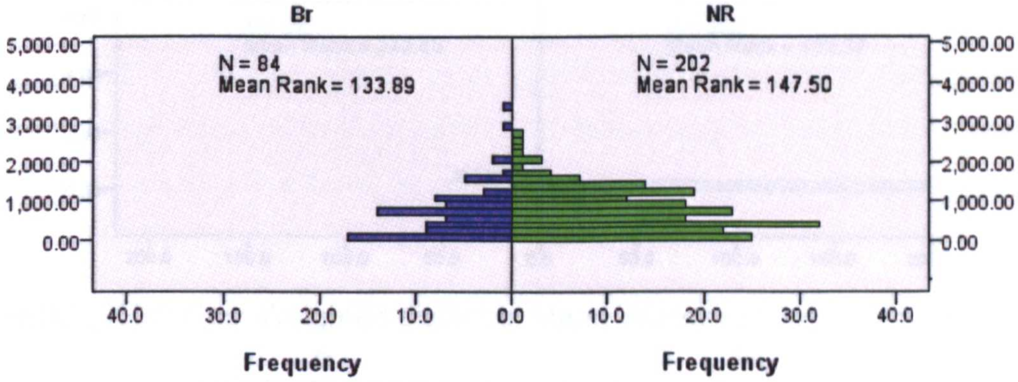
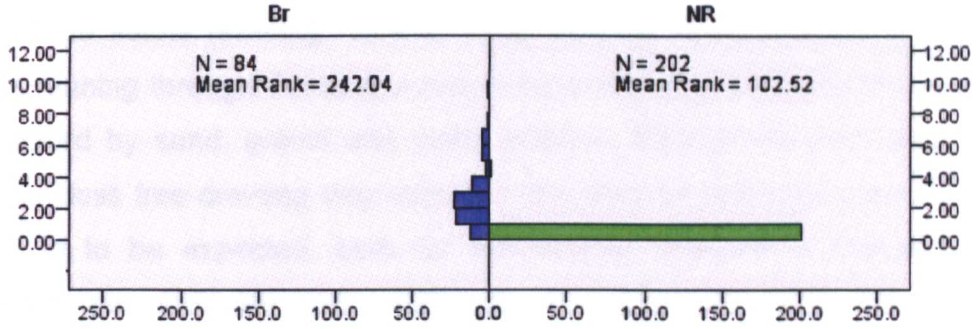


Figure 45; Visualisation of Mann Whitney U test results for differences in distribution values of Cost Weighted distances to the nearest T. cristatus breeding pond between breeding (Br) and non-breeding (NR) pond groups.

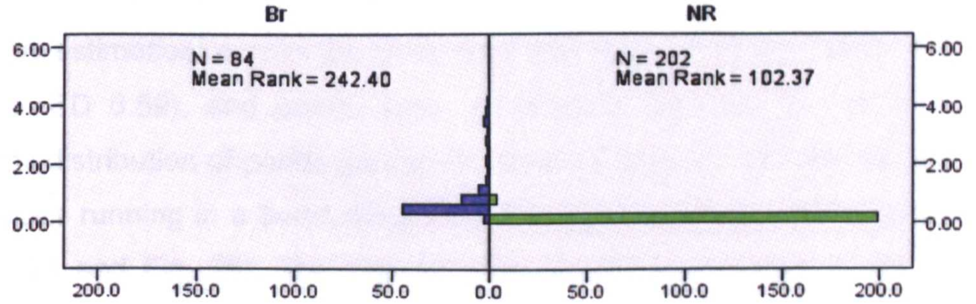
6.14 Node importance of *T. cristatus* breeding ponds.

Mann Whitney U tests showed that there were significant differences in the distributions of *varIIC* and *varPC* scores between the Breeding and non-breeding groups. Fig. 46 below contains visualisations of Mann Witney U test results for difference in the distributions of connectivity Index scores (*varPC* , which as a probabilistic index considers connectivity at all distances, and *varIIC* at the 130, 250 and 500m Cost Weighted thresholds of connectivity), which demonstrate significantly higher ($p < 0.0001$) scores among the breeding group than the non-breeding group.

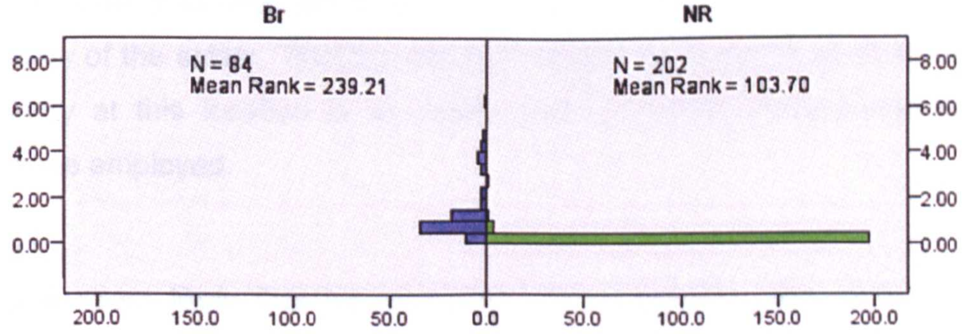
varPC (Mann Whitney U 206.5, p = 0.0001)



varIIC (130m Cost Weighted Distance, Mann Whitney U 176.0, p = .0001)



varIIC (250m Cost Weighted distance, Mann Whitney U 444.0, p = 0.0001)



varIIC (500m Cost Weighted distance, Mann Whitney U 616.0, p = 0.0001)

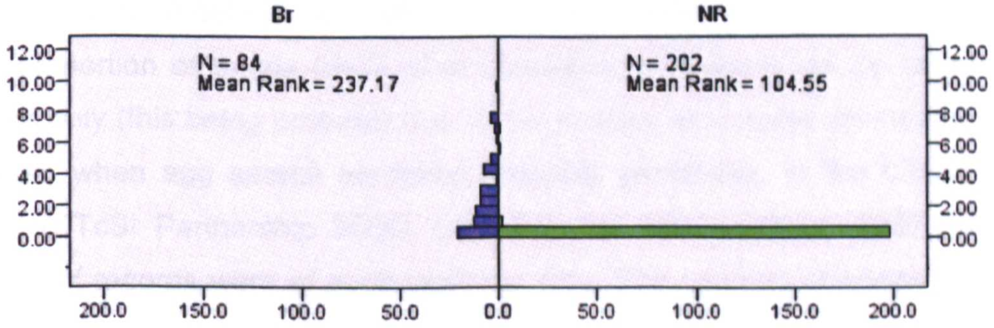


Figure 46; Mann Whitney U test for difference in distribution of connectivity/habitat availability scores across the Cholmondeley estate between breeding (Br) and non-breeding (NR), Var scores on the vertical, frequency on the horizontal axis.

The underlying superficial geology clearly influences the distribution of ponds across the estate (see Fig. 15 and Table 7). Very few ponds are present in areas running through the centre and along the southern margin of the estate dominated by sand, gravel and peaty pockets. Most ponds are situated on heavier, less free draining clay soils; that the majority of ponds occur in these areas is to be expected, both for the obvious reasons of drainage, and perhaps less obviously, their origins as marl pits. In addition to underlying superficial geology, the central relatively pond free area is the location of several meres and an extensive conifer plantation. Mean pond density (Kernel density estimation) across the study area was high, 15.21 km^{-2} (min 1.94, max 32.89, SD 6.59), and ponds were significantly clustered ($p < 0.0001$). The overall distribution of ponds across the estate is uneven, with the highest pond densities running in a band along the north eastern margin of the estate (see Figs. 24 and Fig. 25). The apparent dense cluster of ponds at the western margin of the estate (see Fig. 25) should be disregarded, as these are recently created densely stocked fish ponds at an angling centre some way beyond the boundary of the estate. That the density "hotspot" appears to cross the estate boundary at this location is an artefact of the kernel density interpolation technique employed.

It would seem likely that the recorded total occupation rate of 30.39% for ponds holding standing water at the time of survey (with breeding confirmed in 29.68%) is an under estimate allowing for false negatives and in respect of the low proportion of ponds (n=2) where presence was identified by capture of adults only (this being probably due to the number of surveys where sampling ceased when egg search identified breeding presence). In the CTcSI data base (CTcSI Partnership 2006) excluding the Cholmondeley 2007 survey, 54.3% of records were of adult captures only. The majority of ponds (53.6%) at Cholmondeley were shaded around more than 50% of their perimeter, with over 32.5% shaded around more than 70%, the level at which significant reduction in newt occupancy can be expected according to Swan and Oldham (1993). *T. cristatus* were found to be present in all shade classes, but there was a significant difference between median shade values of ponds with recorded presence and probable absence($p = 0.0003$), with the non-breeding ponds having a significantly higher median shade value ($p = 0.0001$). The hypothesis that breeding presence would be positively associated with increased pond density was not supported, there being no significant difference in pond density between pond locations where presence was recorded and probable absence recorded ($p = 0.699$). No significant relationship (at the 95% confidence level) was identified between density alone and *T. cristatus* occupancy ($p = 0.154$).

The hypotheses that presence would be positively correlated with cluster size (pond count in network components i.e. pond clusters and isolated ponds) was supported. Breeding ponds were shown to be significantly clustered ($p < 0.0001$), and a positive correlation was demonstrated between pond count in components and breeding pond occurrence within clusters at all thresholds of connectivity ($p = 0.002$ to $p < 0.0001$) except for the 130m Cost Weighted threshold ($p = 0.209$), at which most components (197) are isolated ponds. However, no significant difference in median inter-pond distance (at the 95% confidence level), was demonstrated ($p = 0.1098$) between ponds with recorded presence and probable absence. The hypothesis that *T. cristatus* breeding ponds would be better connected (as reflected in node importance measured as *var*IIC and *var*PC) was supported, with significantly higher scores for these indices among the ponds where breeding was recorded, than where probable absence was recorded ($p < 0.0001$).

A positive association of breeding presence with HSI scores of ponds ($p < 0.0001$) supported the hypothesis of increased presence with higher HSI class, with ponds recording no breeding presence having a significantly lower median HSI score ($p < 0.0001$). No support could be demonstrated for the hypothesis of reduced presence with increasing proximity to roads ($p = 0.393$) and increasing road density ($p = 0.489$). The hypothesis of reduced presence with increased proximity to moving water was supported, with a significantly shorter median distance to the nearest running water demonstrated for ponds where no breeding presence was recorded ($p = 0.0007$). The hypotheses that presence is positively associated with proximity to broadleaved woodland and rough grassland was tested using both Euclidian and Cost Weighted distances, however, the hypothesis was not supported at Euclidian distances for both broad leaved woodland (p = 0.240) and rough grassland (p = 0.1361). However, it was supported when Cost Weighted distance measures were used for both broadleaved woodland and rough grassland (p < 0.0001). No significant difference in distance to Core Habitat could be found between ponds with no breeding recorded and ponds with probable absence recorded (p = 0.408), nor were significant differences found between the mean areas of core habitat within cost weighted buffers between the non-breeding and breeding groups.

It is clear from the analysis of connectivity and clustering, that conceptualising connectivity at Euclidean distance, making no allowance for the quality of the intervening landscape matrix (unless this intervening land cover constitutes core habitat, i.e. resistance multiplier = 1) must almost inevitably lead to serious over estimation of the extent of available habitat, and of levels of connectivity within the pondscape. In the case of Cholmondeley, comparison of the connectivity graphs and buffer extents between the Cost Weighted and Euclidean estimations shows that the 250m Euclidean estimations are comparable to Cost Weighted 500m calculations, and Euclidean 130m estimations comparable to 250m Cost Weighted estimations. Clearly, these estimations differ in detail, and the landscape configuration around particular ponds in actual landscapes must be considered case by case, but for "in the field" estimations of available habitat, significant questions are raised regarding distance guide lines in "rule of thumb" terms. The availability of core habitat is low (slightly less than 16% of total land cover), with a much smaller proportion being available within the areas around ponds accessible to actual breeding populations or around ponds generally. At Euclidean distances, only 40.5% of the total is available within 130m, 57.1% within 250m and 88.6% within 500m of ponds. With effective distance taken into account, using measures of Cost Weighted distance, this level of availability falls sharply, with only 62.1% of that available at Euclidian distances (25.1% of the total habitat extent) within a cost weighted distance of 130m, 60.6% (34.6% of total) within 250m and 57.9% (51.3% of total) available within 500m.

The following chapter (chapter 7) will proceed to examine and demonstrate applications of graph analysis of cost-weighted connectivity to conservation planning, using the whole landscape of the Cholmondeley estate. It should be remembered that the *fiat* object (Boothby 2004, Smith 1995a) which the Cholmondeley pondscape (i.e. those ponds and their surrounding terrestrial habitat falling within the perimeter of the estate) constitutes is not "hard bounded" by the Cholmondeley Estate perimeter. The Cholmondeley pondscape is connected to the wider Cheshire pondscape, sections of it doubtless better connected and with more interaction with ponds "off" the estate than those "on" it. The distinctly bounded, very "real", but *fiat* estate boundary in many ways bounds our ability to interact with the pondscape, but for the organisms targeted for conservation management this "boundary" is irrelevant, bounded as their existence is by generally "fuzzy", but *bona fide* environmental gradients and physical or behavioural barriers to their movement and interaction. Any examination of species distribution, conservation status, habitat availability - landscape scale relationships and processes unbounded by *fiat* human constructs - is therefore dogged by the question; "where do we draw the line?" Wherever the line is drawn (unless it can be drawn to coincide with some ecologically coherent *bona fide* boundary such as a river catchment) the result will only be a partial representation.

Chapter 7 - Application of graph analysis to conservation planning in the landscape of Cholmondeley

As examined in chapter 3, effective landscape scale management for pond breeding amphibians such as *T. cristatus* requires management at two levels of temporal and spatial resolution (e.g. see Semlitsch 2008);

- short to medium-term population level efforts directed at core terrestrial and aquatic habitat availability and quality for local populations. Such management would involve immediately pond adjacent habitat, surrounding terrestrial habitat, and neighbouring ponds at distances up to 500m in the case of *T. cristatus*, with conservation effort applied to aquatic habitat aimed at protection and judicious restoration in the short term, and in the longer term, creation of "replacement" or "reinforcement" ponds adjacent to (i.e. within minimal/optimal dispersal/migration distance, identified as 130-250m) of breeding ponds,
- long-term metapopulation scale efforts focused upon larger scale connectivity at distances of 500m – 1km (and possibly more widespread, depending on land cover) among populations and improvement of intervening matrix habitat.

As demonstrated in Chapter 6, consideration solely of Euclidian distances will result in a substantial overestimation of available habitat and under estimation of effective distances. Distances were therefore calculated as Cost Weighted, based on the habitat suitability classes and resistance values as discussed in chapters 5 and 6. From this starting point, this section addresses the related aspects of habitat availability and pondscape connectivity at two scales:

1. the scale of the entire mapped pondscape of Cholmondeley, in relation to the existing pondscape, for
    a. assessment of key pond sites for maintenance of pondscape connectivity, and
    b. prioritisation of locations for protection, enhancement and creation of habitat patches for improvement of local connectivity and habitat availability.

2. the scale of a multi farm "focus area" through an exercise in location selection for aquatic habitat creation aimed at increasing breeding habitat availability and connectivity between breeding ponds, identifying and prioritising in terms of habitat availability and connectivity improvement for minimal conservation effort.

7.1 Connectivity and Habitat Availability Indicators at Cholmondeley Estate Scale

At the scale of the whole Cholmondeley pondscape, graph analysis may be utilised, through the use of the Probability of Connectivity Indices, particularly of *d*PC(EC) and its fractions, to answer questions such as which are the key ponds and clusters to target for management with the specific aim of maintaining existing levels of connectivity across the estate? Which of a range of potential locations for new pond creation would produce the greatest effect in terms of connectivity enhancement? Which elements of the estate's pond network are least well connected and/or make the least contribution to habitat availability? Use of *d*PC(EC) facilitates temporal comparison in modelling scenarios and analysis of data derived from on-going or long term monitoring. Figure 47 below, shows the *d*PC(EC) and fractions across the estate.

Further insights for assessment of key pond sites for maintenance of pondscape connectivity can be achieved through use of the flux and connector fractions. For key stepping stone ponds, with high value for connectivity regardless necessarily of intrinsic habitat attribute, this can be achieved through identification of ponds with higher connector fraction values. Areas for prioritisation of connectivity improvement can be identified by targeting regions of the landscape with low levels of connectivity as measured by both the flux, and also connector fractions, either for protection/restoration of ponds if this is desirable and practical, or pond creation in areas adjacent to the existing pond(s), and measures aimed at improvement of the landscape matrix (Fig. 47 below). Key areas for maintenance of existing pond connectivity are identified in Fig 48 as the selected focus area, and sites identified within boxes 1 to 4.

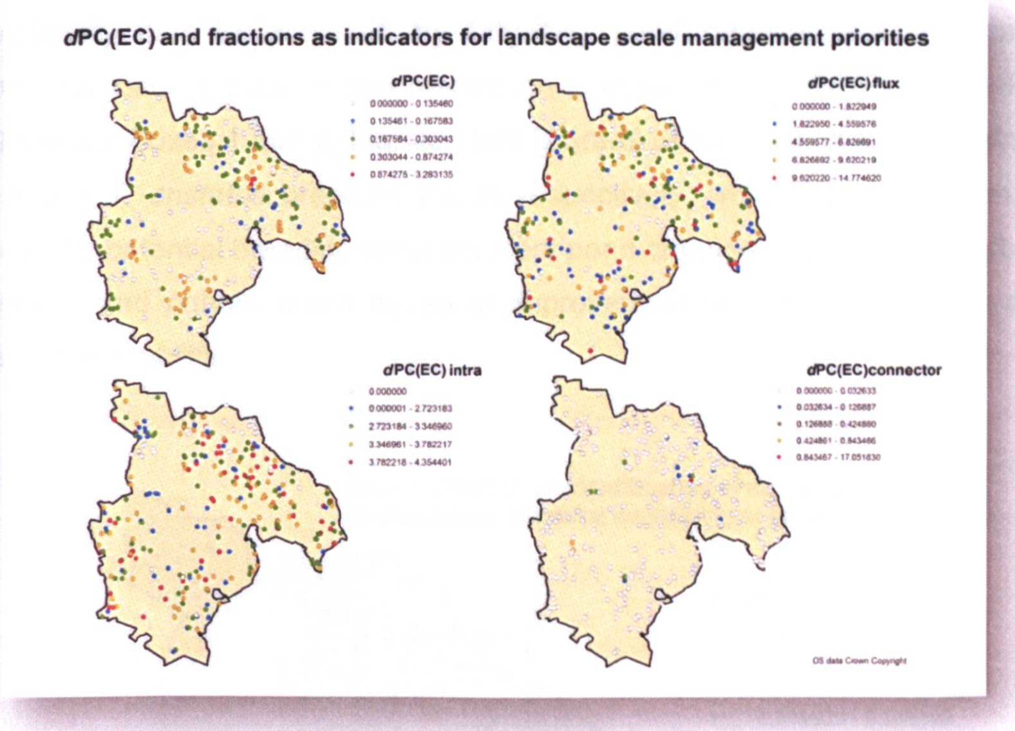


Figure 47; dPC(EC) and fractions as indicators for landscape scale management priorities.

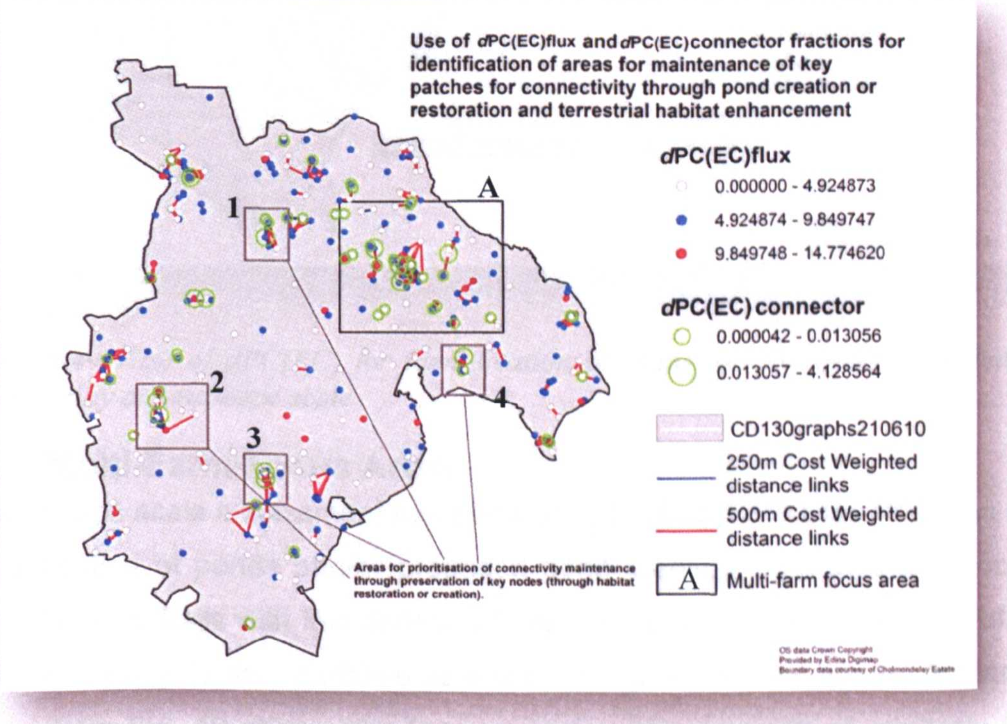


Figure 48; Use of dPC(EC)flux and dPC(EC)connector fractions for identification of key areas for connectivity.

Identification of areas for prioritisation of general improvement to habitat availability can be achieved by targeting pond creation and associated terrestrial habitat creation and restoration in areas of low *d*PC(EC), *(*see Fig. 49 below*)*. Boxes 1 and 2, Fig. 49 identify areas of low connectivity containing 4 and 1 *T. cristatus* breeding ponds respectively, which identifies them as areas for potential breeding pond adjacent pond creation and terrestrial habitat creation and enhancement aimed at improvement of pond connectivity and habitat availability.

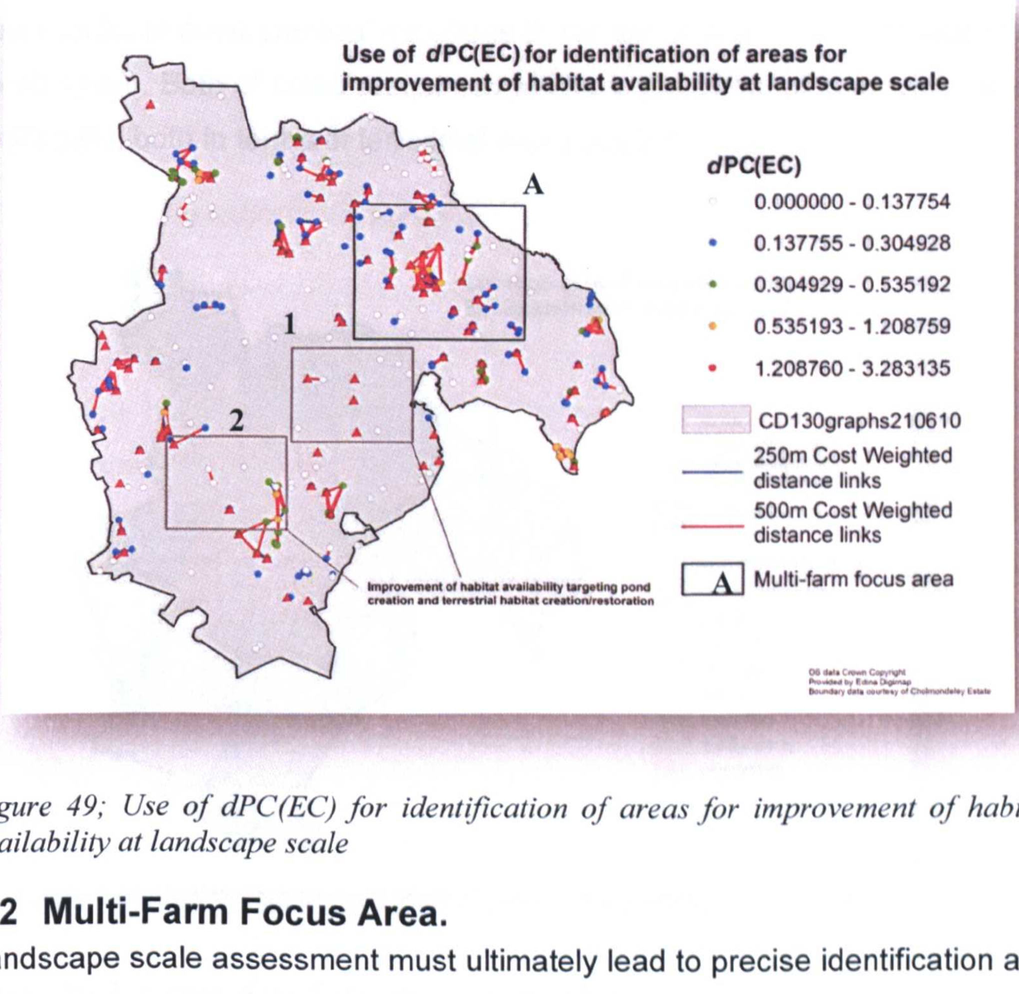


Figure 49; Use of dPC(EC) for identification of areas for improvement of habitat availability at landscape scale

7.2 Multi-Farm Focus Area.

Landscape scale assessment must ultimately lead to precise identification and prioritisation of ponds and/or proposed pond creation sites at a local scale. This section deals with this aspect through focusing directly on an area of the Cholmondeley Estate, identified as box A, in Figs 48 and 49, above. As can be seen from Fig. 49 above, this focus area is within a region of relatively high pond density, and with good connectivity (as represented by *d*PC(EC) *connector*), within a number of disconnected component pond clusters but which, as can be seen from Fig. 49, above, makes a relatively low contribution to habitat availability (*d*PC(EC), *d*PC(EC)*flux*), due to this disconnection of network components, and the below average HSI aquatic habitat provided by a substantial proportion of connected ponds. Figures 50 and 51 below show the "focus area" and its location within the Cholmondeley Estate. Expressed most simply, two means are available to improve pondscape connectivity; effective inter-pond distances may be reduced by generation of more traversable intervening land cover (from the perspective of the target species), or "real" Euclidean inter-pond distances can be reduced, through creation of new ponds. In most practical situations these are of course likely to operate in combination. Both of these responses will have the effect of improving habitat availability, both in terms of terrestrial and aquatic habitat.

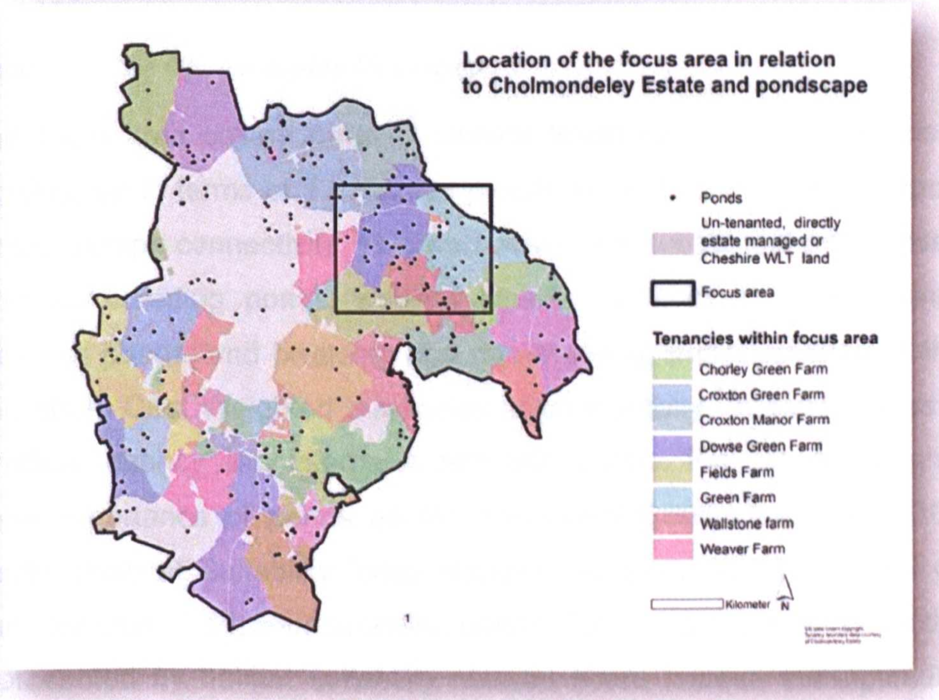


Figure 50; Location of the focus area in relation to the Cholmondeley Estate and pondscape

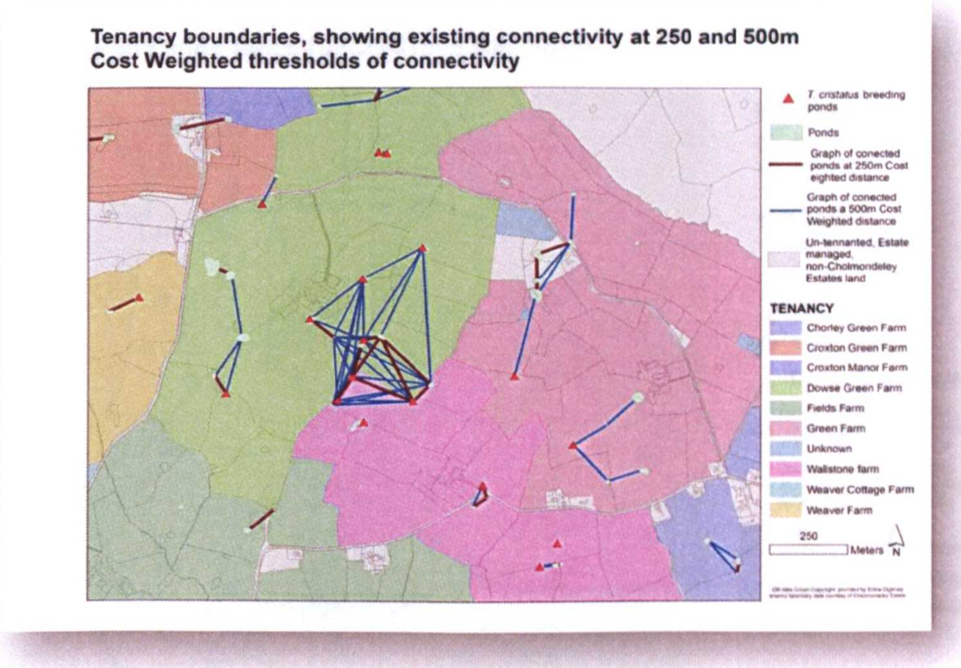


Figure 51; The Cholmondeley focus area.

The focus area covers parts of several tenancies, and was selected for its significance in terms of *T. cristatus* presence, and its importance topologically for pondscape connectivity. The area contains a substantial linked cluster of *T. cristatus* breeding ponds, several smaller pond clusters containing single breeding ponds, and breeding and non-breeding ponds isolated at the 250m and 500m Cost Weighted thresholds of connectivity. In some cases clusters straddle tenancy and internal estate boundaries. Fig. 52, below shows the node importance of ponds as PC Equivalent Connectivity (*d*PC(EC)) pond quality (Habitat Suitability Index showing Excellent and Good HSI classes), and indicates *T. cristatus* breeding ponds. Surrounding terrestrial land cover is represented by habitat suitability classes (Core habitat, sub-optimal habitat, hostile matrix, and barrier) generated from the Phase 1 Habitat Survey in GIS.

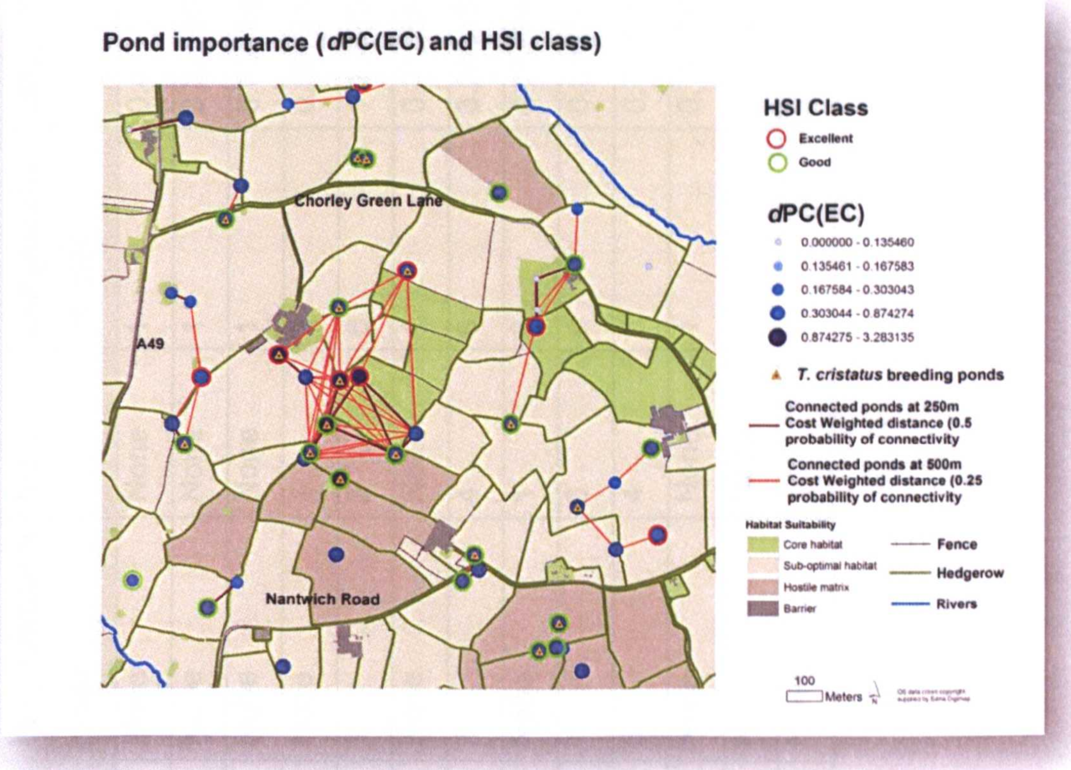


Figure 52 Pond importance and surrounding terrestrial land cover in the focus area.

The area putatively under management contained 32 ponds at the time of survey, 13 with recorded *T. cristatus* presence, slightly higher than the overall rate of occupation, but generally reflecting levels of occurrence across the estate. At the 250m (probability of connectivity 0.5) Cost Weighted threshold of connectivity, 23 ponds were part of seven clustered components, (see Table 32, below for detail). These included in three cases links to ponds outside the management area, across Chorley Green Lane and Nantwich Road. Six of the remaining ponds were *T. cristatus* breeding ponds not considered connected to any pond at this threshold of connectivity, and 3, though linked at this distance, were not linked to ponds with records of *T. cristatus* presence (see table 32 below). Of these, 2 were of Below Average HSI score, and 1 was of Average HSI score.

Table 22; Triturus cristatus breeding pond connectivity (dPC(EC), habitat availability and HSI at time of survey in the multi-farm focus area.

Pond ID	Tenancy	HSI	Clustered	Directly Links to breeding pond	Direct links	No. ponds in component/ cluster	*d*PC(EC)
30	Dowse Green Farm	0.762759, Good	No	None	None	1	0.471016
125	Dowse Green Farm	0.717178, Good	No	None	None	1	0.225953
132	Dowse Green Farm	0.817505, Excellent	No	None	None	1	0.559242
141	Dowse Green Farm	0.799465, Excellent	Yes	None	1	2	0.567317
145	Dowse Green Farm	0.817505, Excellent	Yes	1	2	6	1.208759
148	Green Farm	0.754765, Good	No	None	None	1	0.31568
150	Wallstone Farm	0.762759, Good	Yes	3	4	6	3.283135
154	Dowse Green Farm	0.745927, Good	Yes	None	1	2	0.252943
156	Wallstone Farm	0.719791, Good	Yes	1	3	6	0.810799
158	Wallstone Farm	0.724774, Good	Yes	3	4	6	0.752282
162	Wallstone Farm	0.774431, Good	No	None	None	1	0.161979
165	Green Farm	0.675222, Average	No	None	None	1	0.200023
373	Wallstone Farm	0.745927, Good	Yes	None	1	3	0.285573

The purpose of this exercise is to demonstrate the potential of graph analytic techniques applied to strategic siting of ponds at farm scale landscape levels, for maximisation of benefit in terms of pondscape connectivity, with minimal conservation effort expended. The measures concentrated on in this section therefore are pond creation, 6m field boundary buffers and un-cultivated field corners in grassland and arable fields, hedgerow creation and management, and pond buffers (i.e. in ecological network terminology core areas, corridors and stepping stones, and buffers) with the aim of achieving direct connection of breeding ponds to at least one pond with a Good to Excellent HSI score within the 250m Cost Weighted Threshold of connectivity, and minimising the number of disconnected components in the local network. Clearly, other modifications to farm practices, constituting in the main matrix quality improvement (modification of cultivation and cutting schedules to take account of newt seasonal presence and migration, de-intensification of grazing and discontinuation or reduction in agri-chemical applications in total and/or during migration/dispersal periods, re-seeding of leys with more diverse plant communities to encourage broader diversity of potential invertebrate prey and a more open, tussocky sward), would be beneficial. In actual application, the potential for these would be highly dependent on individual farm economy, land manager attitudes and AES funding availability (overall allocations, levels of up-take and calls on funding etc.). It is intended that this area will form the basis of a subsequent study at Cholmondeley, and is not dealt with here. All of these measures are supported to varying degrees within the ES Higher and Entry Level Schemes, and the corresponding Organic Stewardship (OS) schemes).

Pondscape connectivity was identified through analysis in CS2.5.8, and buffer distances to ponds at the 250m and 500m Cost Weighted distance had already been generated for examination of surrounding terrestrial habitat using the resistance surface created from the Phase 1 Habitat Survey map. The extent of these buffers (merged where ponds form parts of clustered components), are shown in Fig. 53, below.

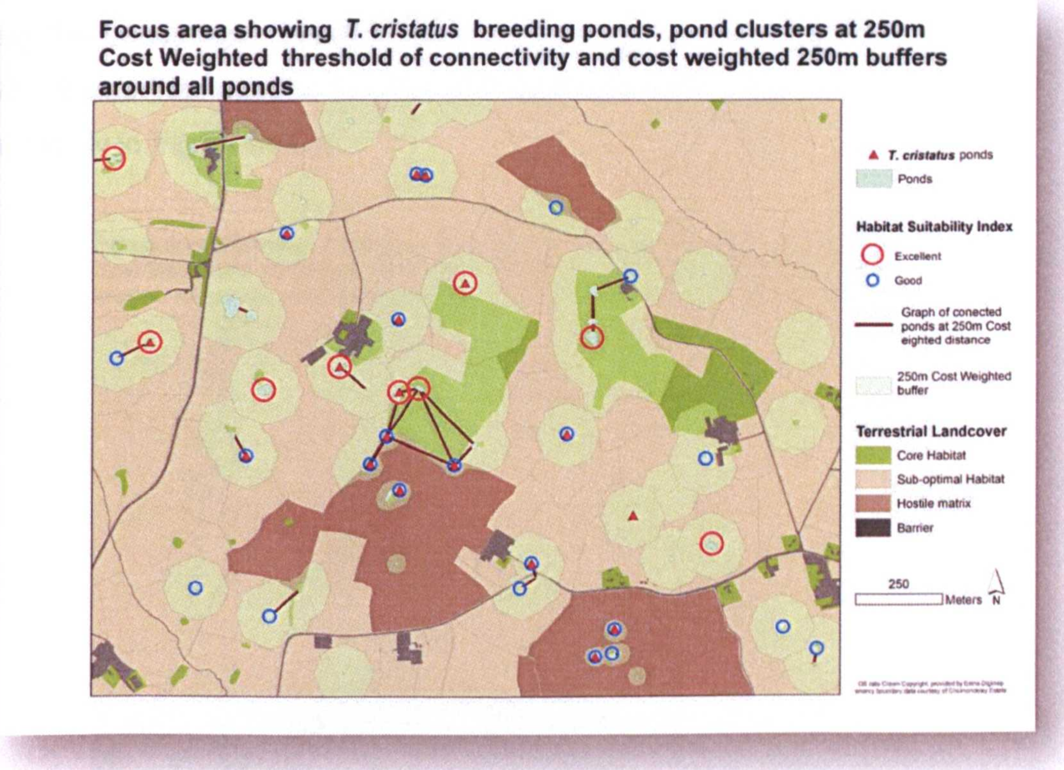


Figure 53; Focus area showing breeding ponds, clustered components and extent of 250m Cost Weighted distance threshold of connectivity.

Pond buffer perimeters bisected by field margins linking non intersecting buffers, and buffers intersecting but not to the extent constituting direct inter pond connectivity (such that pond polygon margins were within 250m of each other), were identified. This process identified field boundaries where margin enhancement by creation of 6 meter field margin buffer strips could contribute to connectivity improvement by reducing effective inter-pond distances. Corridors in the form of 6m field margin buffer strips were identified with a view to linking isolated ponds and linking clustered components. Some requirement for hedgerow planting was identified to replace post and wire field boundaries, providing additional habitat and "spines" for these linking corridors, where hedgerows were identified as currently either non-existent of poor quality. These buffers were then incorporated into the resistance surface (on the assumption of their value after establishment as tussocky, relatively forb rich rough grassland as core habitat with a resistance multiplier of 1). The Cost Weighted distance surface was then re-calculated using this modified resistance surface, and new Cost Weighted pond buffers generated. A new connectivity matrix was calculated for ponds already existing in the landscape, using the Landscape Genetics toolbox (Etherington 2011) within ArcGIS 9.3. CS2.5.8 was then used to re-calculate connectivity Indices. Results are shown graphically in Fig 54 below.

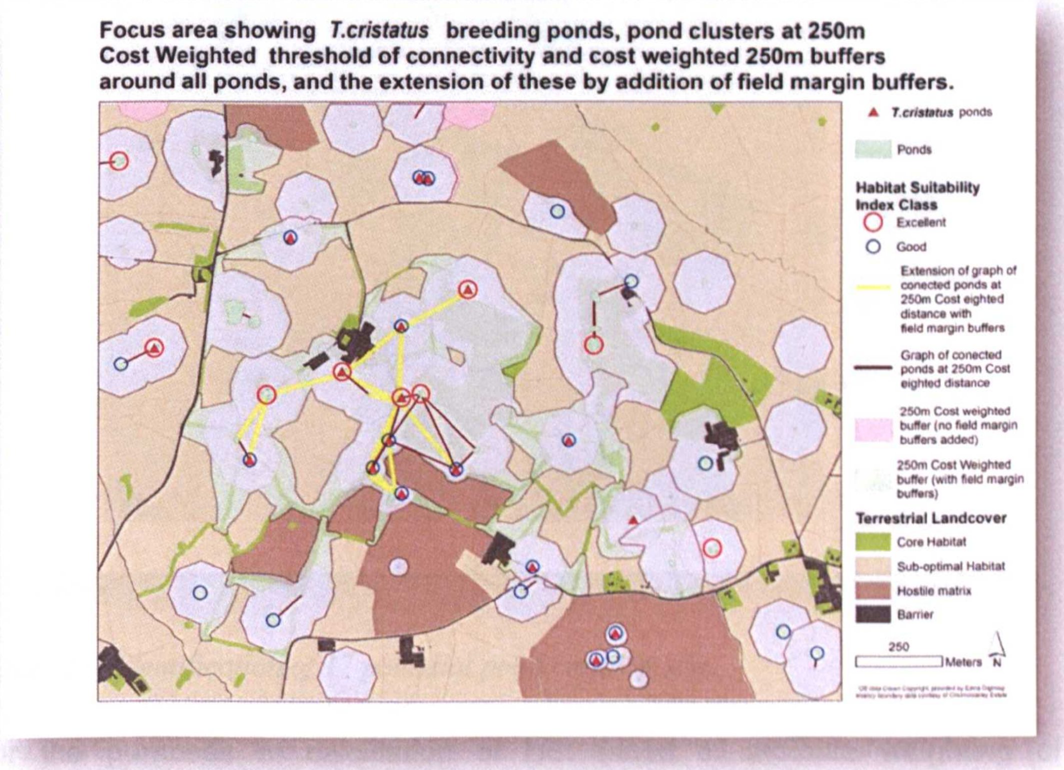


Figure 54; Improvement of inter-pond connectivity through addition of 6m field margin buffers.

As Fig. 54 above shows, simply the addition of field margin buffers provides some enhancement of connectivity at the 250m Cost Weighted threshold among the concentration of *T. cristatus* ponds to the centre west of the focus area, but alone is inadequate to achieve the aims of direct connection of breeding ponds to at least one pond with a Good to Excellent HSI score within the 250m Cost Weighted Threshold of connectivity.

After examination of the revised pond buffers at 250m Cost Weighted distance, seventeen potential locations for pond creation were identified, at suitable points along the identified field margin buffer corridors with the aim of enhancing connectivity and providing additional breeding habitat within buffers associated with *T. cristatus* breeding ponds. These are shown in Fig 55 below.

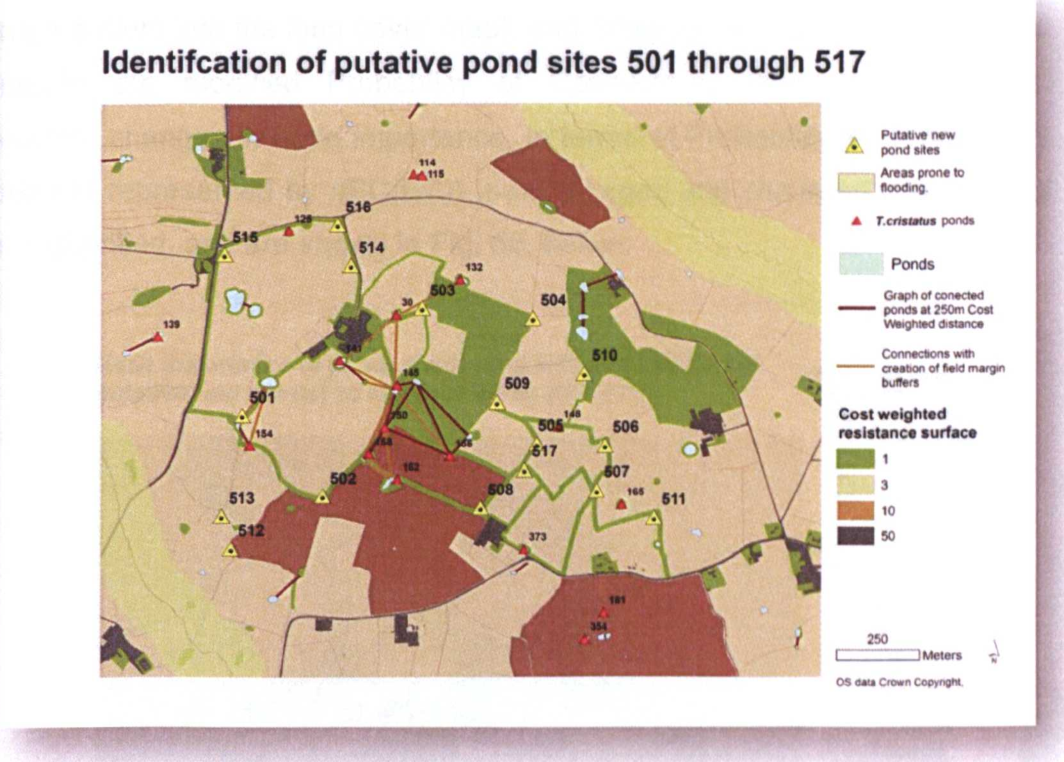


Figure 55; Identification of 17 potential pond creation sites.

For the purposes of calculation of HSI (used in attribute weighting of connectivity and habitat availability calculations) these ponds are considered to be of the optimum area indicated by the literature and the analysis of Cholmondeley ponds, i.e. in the range 125 – 750m^2, to dry out no more frequently than two years in 10 or only in drought, to have moderate water quality, to be shaded around less than 60% of their perimeter, to have minor wildfowl impact, to not have fish present, to have the number of ponds within 1km appropriate to the site location, to have moderately good surrounding terrestrial habitat and to have matured sufficiently to have submerged and emergent aquatic vegetation cover in the region of 60%. This results in an HSI score of 0.892446 (classed as Excellent) for each pond. These values and the final score are considered reasonable on the assumption of pond design and excavation and establishment carried out so as to optimise value for *T. cristatus*.

Inter-pond Cost Weighted distances between all ponds (actual and putative) were re-calculated (using the Landscape Genetics toolbox (Etherington 2011) in ArcGIS 9.3 and the resistance surface generated with inclusion of field margin buffers into the land cover map), and analysis carried out in CS2.5.8 to generate the modified Probability of Connectivity Index and fractions. Resultant changes in node importance, in terms of Probability of Connectivity Index (as represented by *d*PC(EC)), new linkages and clustered components were identified, and are shown in Fig. 56, below.

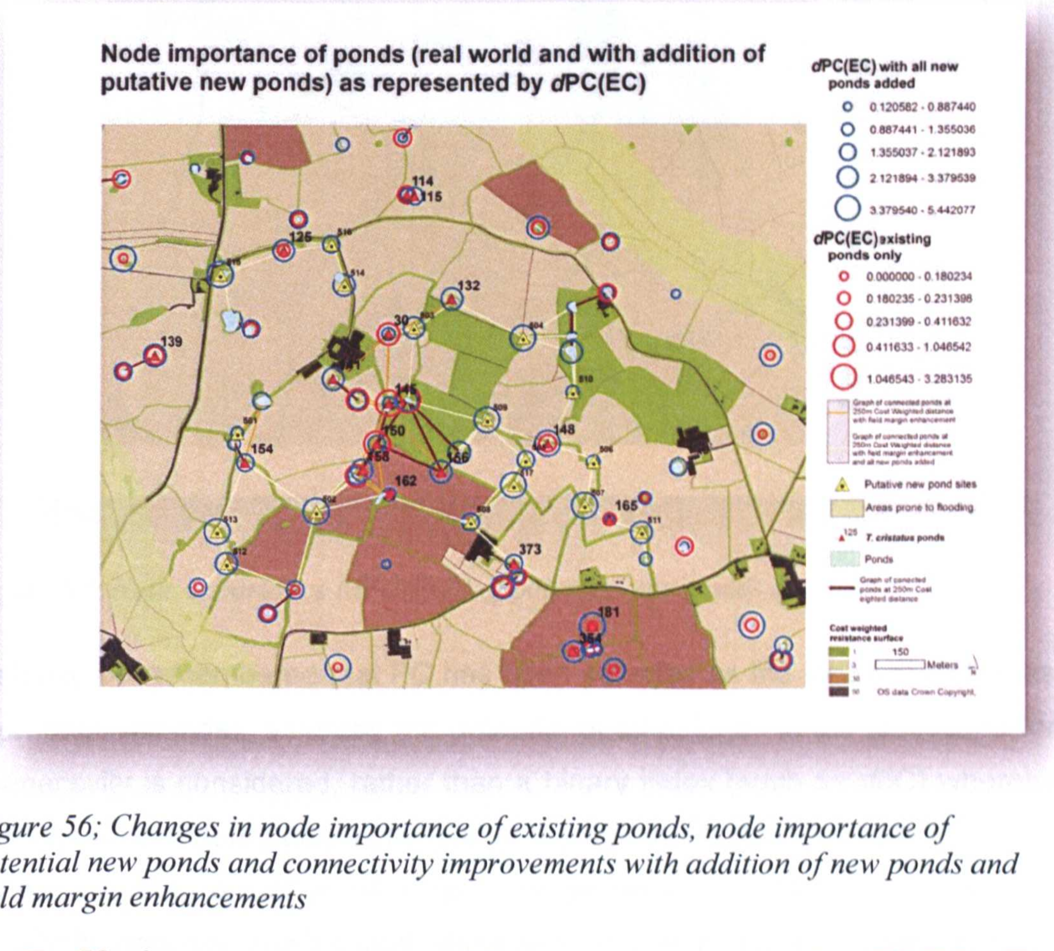


Figure 56; Changes in node importance of existing ponds, node importance of potential new ponds and connectivity improvements with addition of new ponds and field margin enhancements

As Fig 56 above, shows, substantial change is generated in *d*PC(EC). The most immediately apparent feature of the change in *d*PC(EC), The general reduction in node importance of the most important nodes, and increase in importance of less important existing ponds, most notably those directly connected to proposed new ponds at the 250m threshold of connectivity, reflects the relative importance of the new pond introductions of high habitat weighting and generally good levels of connectivity. The calculation of PC(EC) allows quantification of the specific contribution of each pond site to habitat availability. Node importance and node linkages of potential pond sites are shown in Fig. 57 below.

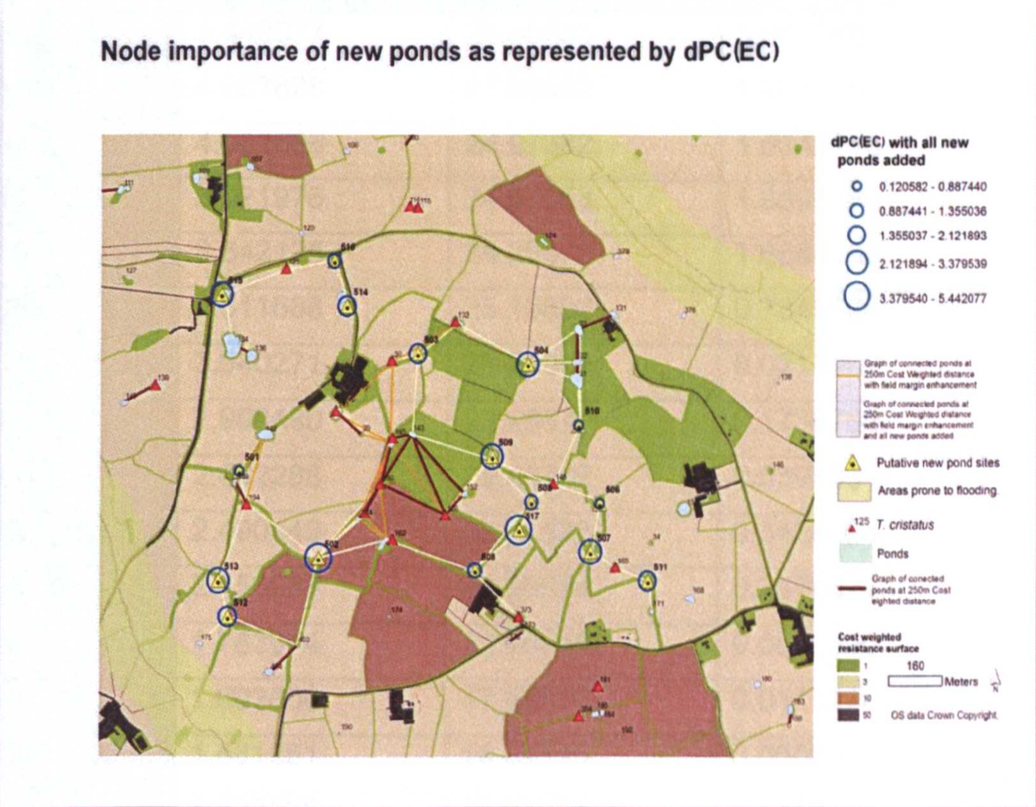


Figure 57; Node importance (dPC(EC)) of potential new ponds only.

It should be remembered that PC has been selected as the index of choice as a probabilistic index, whereby the potential of all patches in the landscape for connectivity is considered, rather than a binary index (such as *d*IIC) whereby nodes are considered connected within the threshold of connectivity identified for examination, or not at all. Direct connection at the 250m Cost Weighted threshold, however, carries particular significance in that it represents the point at which probability of connectivity reaches the 0.5 level. Values of *d*PC(EC) and its fractions for each potential pond site (calculated for the sub-set of ponds within the focus area), are shown in table 33, below. These have been discussed earlier and in Saura and Rubio (2010), but to briefly recap:

Table 23; Potential pond creation sites 501-517 ranked by dPC(EC) *(note:* dPC(EC)intra *is the same for all potential pond creation sites, 5.60576).*

Pond/Node	***d*PC(EC)**	***d*PC(EC)flux**	***d*PCECconnector**
502	5.442077	26.45451	3.8676590
517	4.687628	27.00402	1.9885750
504	4.002666	24.97382	1.6143710
513	3.921976	24.07053	1.8896060
515	3.842125	24.20578	1.6584100
509	3.611688	25.10892	0.7349904
507	3.540271	26.21019	0.0218909
514	2.908480	23.26679	0.1738765
511	2.662288	22.45342	0.0396331
512	2.490449	20.94323	0.3424854
503	2.456088	20.90524	0.2879621
516	1.783814	18.10515	0.0072350
508	1.693600	17.57810	0.0117274
505	1.481361	16.34145	0.0000000
506	1.328535	14.93034	0.1313305
510	1.073418	13.57981	0.0000000
501	1.004649	12.92970	0.0333718

at very short dispersal distances, the *d*PCintra fraction makes the largest contribution to overall habitat connectivity and availability; for a sessile species incapable of movement any distance outside habitat patches, the only available habitat will be that within the patch it inhabits. For a large dispersal distance, the relative contribution of *d*PC(EC)intra will be relatively minor. The value of *d*PC(EC)intra fraction is completely independent of how a patch is connected, and does not depend on the dispersal distance of the focal species (being the same even if a patch is completely isolated from all other patches). The *d*PC(EC)intra fraction, since all the putative ponds received the same weighting, based on the same notional HSI score, is the same in all cases (*d*PC(EC)intra = 5.60576). For the purposes of this exercise, which concentrates on connectivity and involves creation of additional habitat, the attributes of which can to a great extent be controlled, it will make only a small contribution to site prioritisation and selection, although at short dispersal distances such as those under consideration it makes a substantial contribution to the PC indices.

*d*PC(EC)flux represents the patch attribute-weighted dispersal flux through the connections of a patch to or from all the other patches in the landscape. Therefore, *d*PC(EC)flux depends on the attribute of a patch (patches with higher attribute values producing more flux, all else being equal) *and* on its position within the landscape network (better connected patches producing more flux, all else being equal). This fraction therefore measures how well a patch is connected in the landscape (in terms of the amount of flux) but *not* how important that patch is for *maintaining* connectivity between the other patches in the landscape. Again, at short dispersal distances such as those considered here, the flux fraction will determine almost all habitat connectivity and availability, and values of the flux fraction will tend to be much larger than the connector fraction (see Table 23, above).

The *d*PCconnector fraction, measuring the role of both links, and patches that function as stepping stones, makes its greatest contribution at intermediate dispersal distances, and the flux fraction tends to be greater than the connector fraction because, for a given dispersal flux, removing the starting or ending patch will completely eliminate that flux, while the loss of an intermediate patch or link may reduce flux between starting and ending patches, but not necessarily impede it entirely. The value of the connector fraction, depends solely on the topological position of a patch in the landscape, and is completely independent of any patch attribute. A patch may have a weak role as an origin or destination of dispersal fluxes (low *d*PC(EC)flux) but may still be important as a stepping stone between other big, productive or numerous patches, resulting in *d*PC(EC)connector being larger than *d*PC(EC)flux for that patch. A patch will only contribute to PC through the connector fraction when it is part of the best (not necessarily, but all else being equal, shortest) path for dispersal between two other patches.

In prioritising, and ultimately selecting from the list of putative patches, consideration should be given to the performance of the potential location in two respects.

- from the point of view of pond creation adjacent to existing breeding ponds, with the aim of reinforcing the existing breeding habitat and providing replacement breeding habitat for any lost through natural succession (since management to maintain suitability for *T. cristatus* of individual ponds may tend to be to the detriment of other species).
- from the point of view of connectivity between sub-populations in individual ponds, and within and between pond clusters occupied by *T. cristatus* (sub-)populations.

In the first case, this is a "simple" question of pond creation at locations ideally less than 130m (Cost Weighted), but optimally within up to 250m (Cost Weighted) of existing ponds, with appropriate terrestrial habitat enhancement around them within the 130m range. In these cases (i.e. pond creation in close proximity to existing breeding ponds to replace those becoming unsuitable through hydro-seral succession and, within the pondscape as a whole, increasing or maintaining numbers of potential breeding sites), *d*PC(EC)connector is not necessarily a priority or indicator of site suitability. These locations will by definition be within the threshold of connectivity. Higher *d*PC(EC)flux values (relating as this fraction does to wider landscape connections and habitat availability together) would be advantageous, however, as this will reflect the level of potential for dispersal/migration at the new pond location. Generally, aside from identification of ponds adjacent to which they should be located, choice of specific pond creation location at the lower end of this range of proximity to existing ponds (i.e. less than 130m) is unlikely to be informed by the connectivity indices or their fractions in any meaningful way. At the upper end of the range, in relation to the specific siting relative to existing ponds, however, connector and flux will play a role in informing site location choice.

Figure 58 below, shows the resultant additional direct connectivity (0.5 Probability of Connectivity) at the 250m Cost Weighted threshold (connections between existing ponds and potential pond creation sites in red, between potential pond creation sites only, in blue).

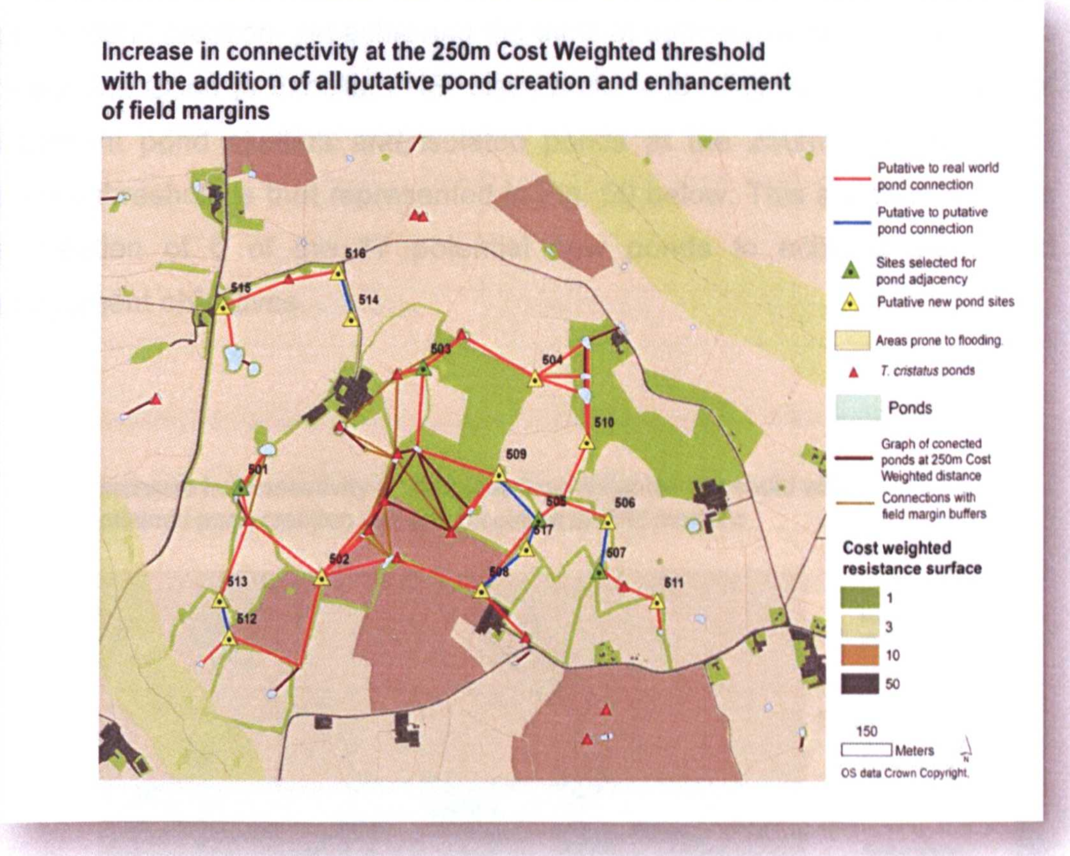


Figure 58; Increase in connectivity at the 250m Cost Weighted threshold with addition of all putative pond creation and enhancement of field margins.

The use of graph analytic techniques allows site selection to be informed by the objective quantification of improvement to levels of connectivity and habitat availability at relevant scales. Prioritisation and selection of these potential sites for pond creation, as Table 23 and Figure 58 above show, can be substantially informed by the rank ordering of *d*PC(EC) and its fractions, which are relatively easily interpreted. Prioritisation of some sites for their pond adjacency, and others for their contribution to connectivity (best measured in this context through the flux fraction) demonstrates, however, that as with any practical conservation management decisions, "trade-offs" are likely to be necessary and an element of subjective assessment involved; sites desirable for their pond adjacency are unlikely to add greatly to connectivity; sites desirable for their contribution to connectivity may not – indeed are unlikely to

- be immediately adjacent to existing breeding sites. Site selection may be further complicated by the connectivity relationship between potential pond sites, necessitating the testing of multiple scenarios. A scenario requiring minimal pond creation, yet achieving the aims of connecting breeding ponds to at least one Good to Excellent HSI class pond, and minimising the number of component pond clusters and isolated ponds at the 250m Cost Weighted distance threshold is that represented in Fig. 59 below. This scenario requires the creation of 6 of the 17 potential new ponds to achieve the stated management objectives.

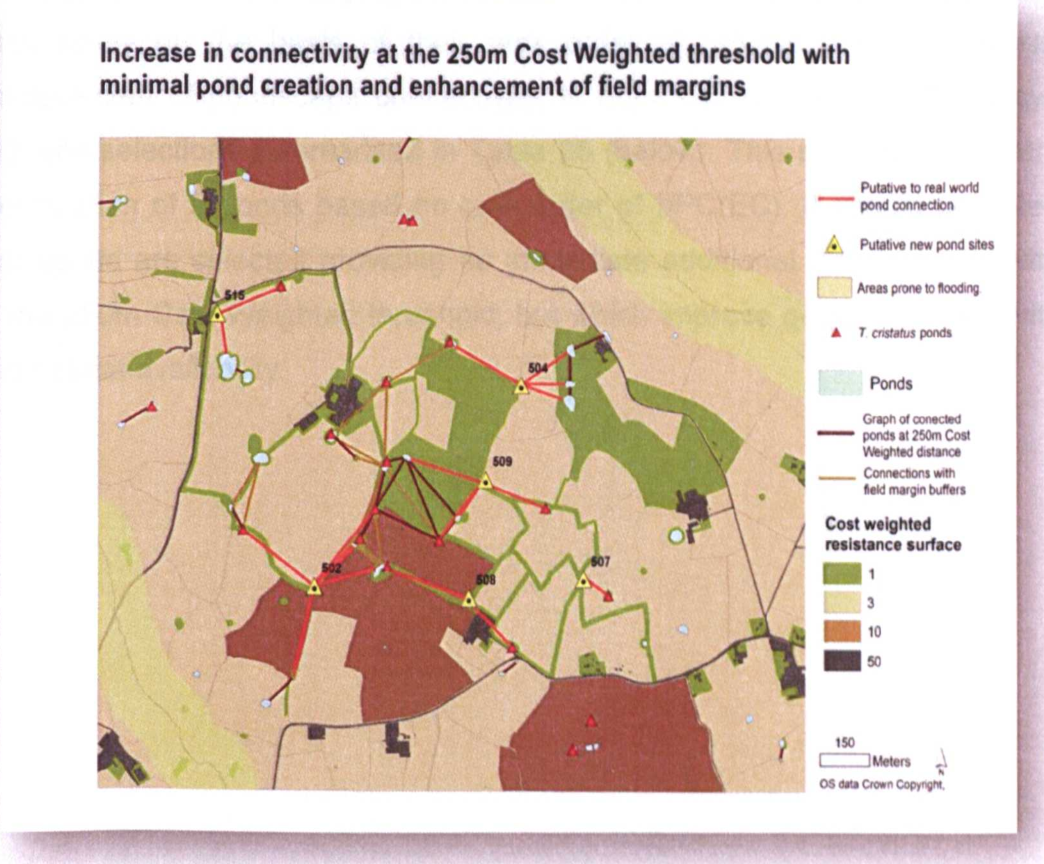


Figure 59; Connectivity improvement scenario requiring minimal pond creation.

The putative pond sites selected by this scenario are summarised in Table 24, below.

Table 24; Potential pond creation sites selected for the minimal pond creation scenario presented in Figure 59.

Site/ Node	*d*PC(EC) rank	*d*PC(EC)	*d*PC(EC)flux	*d*PC(EC)con.
502	1	5.4420770	26.4545100	3.8676590
504	3	4.0026660	24.9738200	1.6143710
515	5	3.8421250	24.2057800	1.6584100
509	6	3.6116880	25.1089200	0.7349904
507	7	3.5402710	26.2101900	0.0218909
508	13	1.6936000	17.5781000	0.0117274

A similar scenario, with slightly more emphasis on pond creation but selecting sites solely on the basis of their rank order of *d*PC(EC), i.e. for overall improvement of pondscape connectivity, is represented in Figure 60 Below, with site selections summarised in Table 25 (below). This scenario considers the creation of 9 ponds based on rank order of *d*PC(EC). It should be noted that ponds are selected providing no immediate additional direct connectivity at the 250m Cost Weighted threshold, but which improve general connectivity and habitat availability.

Table 25; Potential pond creation sites selected by ranked dPC(EC).

Site/ Node	*d*PC(EC) rank	*d*PC(EC)	*d*PC(EC)flux	*d*PC(EC)con.
502	1	5.4420770	26.4545100	3.8676590
517	2	4.6876280	27.0040200	1.9885750
504	3	4.0026660	24.9738200	1.6143710
513	4	3.9219760	24.0705300	1.8896060
515	5	3.8421250	24.2057800	1.6584100
509	6	3.6116880	25.1089200	0.7349904
507	7	3.5402710	26.2101900	0.0218909
514	8	2.9084800	23.2667900	0.1738765
511	9	2.6622880	22.4534200	0.0396331

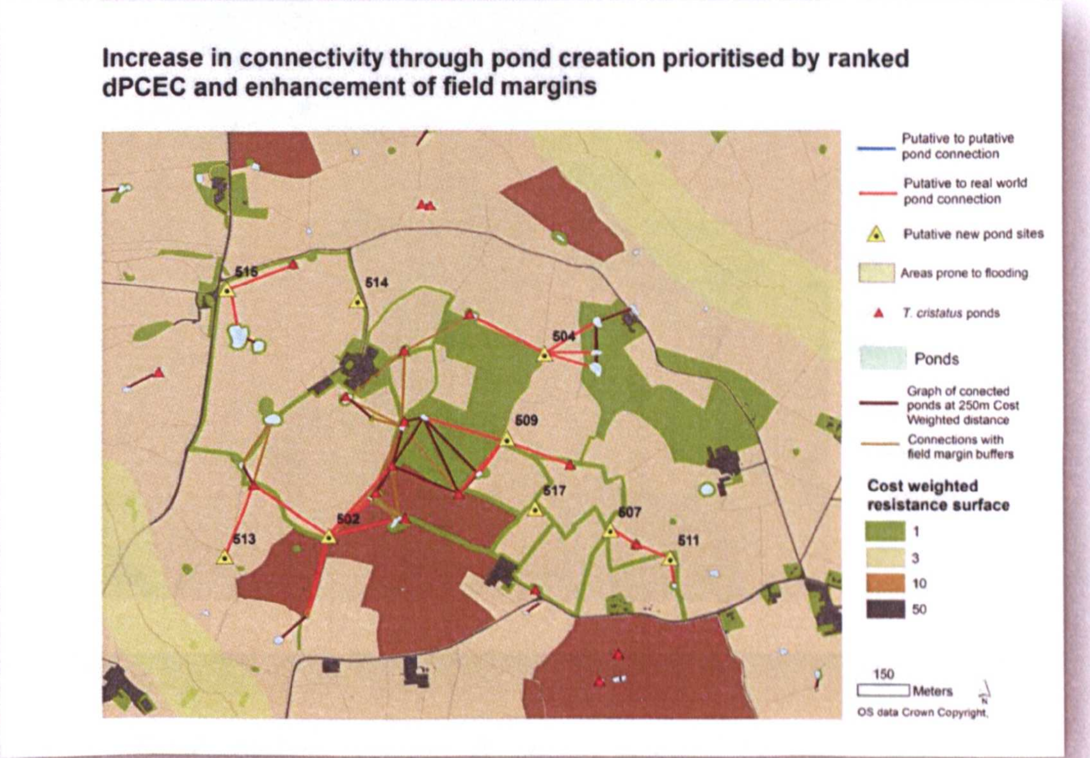


Figure 60; Pond creation scenario (9 ponds) based on ranked dPC(EC).

A third scenario, in which selection of the nine sites (for comparison directly to the previous scenario) contributing most through their contribution to connectivity, as opposed to overall habitat availability would, if it examined *d*PC(EC)flux in this landscape, produce the same result as rank ordering *d*PC(EC) (since flux is the main component of *d*PC(EC) in these scenarios due to the short dispersal distance examined and the uniform high patch attribute). Examination of the *d*PC(EC)connector fraction, i.e. selecting specifically for their role in adding to and maintaining the connectivity of the pondscape, irrespective of patch quality (not so relevant here in that all potential sites are considered equal in terms of patch attribute) is represented in Figure 61, below, and selected sites summarised in Table 26, below. Table 27, below, summarises the variation in potential pond sites prioritised, and ranking of these within each of the scenarios above.

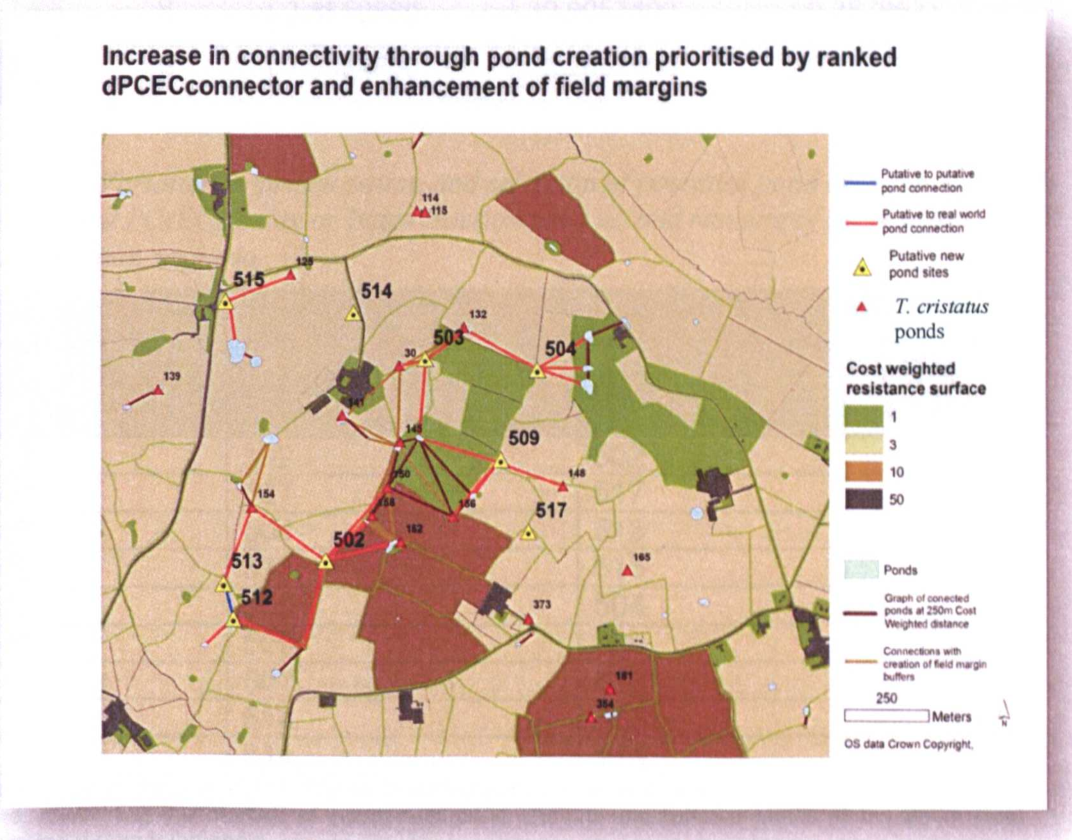


Figure 61; Pond creation scenario (9 ponds) selected by rank order of their dPC(EC)connector fraction.

Table 26; Potential pond creation sites selected by rank order of their dPCEconnector fraction.

Site/ Node	Rank *d*PC(EC)con	*d*PC(EC)	*d*PC(EC)flux	*d*PC(EC)con
502	1	5.4420770	26.4545100	3.8676590
517	2	4.6876280	27.0040200	1.9885750
513	3	3.9219760	24.0705300	1.8896060
515	4	3.8421250	24.2057800	1.6584100
504	5	4.0026660	24.9738200	1.6143710
509	6	3.6116880	25.1089200	0.7349904
512	7	2.4904490	20.9432300	0.3424854
503	8	2.4560880	20.9052400	0.2879621
514	9	2.9084800	23.2667900	0.1738765

Table 27; Variation in prioritisation and selection of potential pond creation sites with criteria and PC(EC) Index or Index fraction used in, and ranking of these within, each pond creation scenario.

Scenario 1 (No rank ordering) Mixed criteria*	Scenario 2 *d*PC(EC) rank order. (Habitat Availability)	Scenario 3 *d*PC(EC)connector rank order. (Pondscape Connectivity)
502	502	502
504	517	517
507	504	513
508	513	515
509	515	504
515	509	509
	507	512
	514	503
	511	514

*Minimal pond creation, connecting all breeding ponds to at least one Good to Excellent HSI class pond, minimising the number of component pond clusters and isolated ponds at the 250m Cost Weighted distance threshold

Undoubtedly, in an actual application of the techniques demonstrated, further constraints upon free and objective selection of sites for enhancement and creation of new habitat would apply, arising from factors of farm economy and management practices, land manager attitudes to and perceptions of the value or appropriateness of conservation management and potentially not least, pre-existing relationships with neighbours with whom cooperative management would need to take place. Figure 62, below, shows the extent to which scenarios examined could require collaborative management across tenancy boundaries.

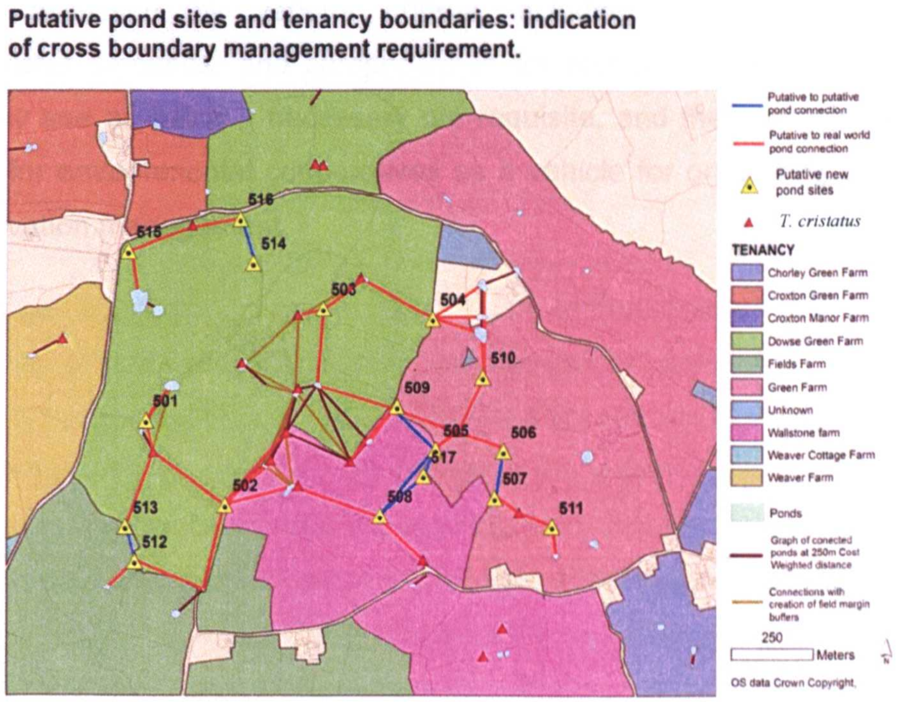


Figure 62; Potential pond sites and tenancy boundaries: indication of potential requirement for cross boundary management.

As can be seen from Figure 62 above, pond creation sites and field margin buffer corridor creation extends across four tenancies and could potentially require cooperation from a fifth, third party, landholder (neither the Cholmondeley Estate, nor one of its tenants). As discussed earlier, this raises complex issues of suitability of existing AES instruments for targeting of management and land manager attitudes and perceptions. At the time of writing, discussions are on-going with colleagues at LJMU, the University of Liverpool, Salford University and the Cholmondeley Estate management, and it is proposed that approaches be made to tenants, with a view to enlisting their cooperation with further multi-disciplinary research in this area of interest. This is envisaged to involve presentation to land managers of concrete proposals for cross boundary management activity on the actual landscape of their own farms and elicitation of their responses on an individual and group basis through interviews, questionnaires and focus groups. The aim of this research would be to assess drivers and inhibitors of the preparedness of land managers to participate in cooperative cross boundary management, the kind of AES assessed by various criteria including spatial target-ability, administrative demands, and compensation for production income foregone which they see as being a necessary pre-requisite, and their attitudes to the potential for environmental cooperatives as a vehicle for organising this form of conservation management.

Chapter 8 Conclusions and discussion.

The first objective of this thesis was to develop a landscape scale perspective on conservation management for *Triturus cristatus.* This was achieved through examination of the theoretical basis for the wider landscape and ecological networks approach, a synthesis of the research relating to the species' habitat requirements and interactions with landscape, and examination of the species distribution and landscape associations with pond occupation (particularly breeding presence) within a landscape typical of its core range in the UK. The second objective was to examine use of graph theoretic techniques for landscape analysis and targeting of landscape scale conservation activity, focusing on key loci of connectivity and habitat availability, through identification of both existing sites of importance for protection of habitat connectivity and availability, and putative sites for habitat creation or restoration providing optimal improvement in habitat connectivity and availability for conservation effort expended. The Cholmondeley study area was selected for its apparent typicality of the lowland pastoral core range of *T. cristatus* in the UK. This was confirmed by analysis of land cover as mapped during field survey. Land cover is predominantly grassland (approximately 77%) of which approximately 85% was comprised of species poor Rye grass (*Lolium perenne*) leys. The remainder consisted of rougher tussocky grassland including degenerate leys, semi-improved and some small patches of unimproved grassland and roadside verge vegetation. Woodland (semi natural and plantation broadleaved, and coniferous plantation) makes up approximately 5% of the total land area, lower than the national percentage, said to be around 8.4%, but in line with findings for Cheshire (vice county), at 4-5.9% in 1998. Pond numbers and density are slightly higher than the Cheshire average, both higher again than the UK lowland average, but not atypical of landscapes within *T. cristatus'* core UK lowland distribution.

The examination of the theoretical foundations and evidence base for the wider landscape and ecological networks concepts as overarching management strategies drew on a wide literature and varied disciplines, ranging from population ecology, to genetics, geography and topology. While debate may still continue in relation to the efficacy of some elements of the concept in specific practical applications - for example the utility of wildlife corridors for connectivity enhancement in relation to corridor attributes and target species - the concepts are well established theoretically, have a wealth of empirical and experimental evidence in support of them and, though debate continues, this in the main centres not on the validity of the overarching proposition, but on the most cost effective and efficient means and appropriate circumstances for their application, which is now widespread.

Though the longstanding and intuitively attractive designated site approach has in no way been completely supplanted, the wider landscape conservation and ecological network approaches have now become established and have over the last two decades become embedded in national and global policy frameworks. The fragile, potentially unstable, and often ineffective nature of many designated sites is increasingly recognised as inherent, particularly in the face of global climate change, rather than always merely the result of local management deficiencies. The necessity of responding to stressors on population persistence at the spatial scale at which they operate has been a major driver in this realization and policy shift. The management traditionally addressed to *T. cristatus* is intensely site specific and (outside larger SSSIs and SACs designated for their value to *T. cristatus* – by definition "special" and unusual sites) is insufficient to respond to landscape scale stressors on species persistence, since it has generally targeted individual breeding ponds or small pond clusters, and usually then only in response to immediate development threats. In general, while having provided much needed protection against adverse development for the species and its core habitats, this legislation has failed to deliver species FCS (see Langton 2009). Concentration on individual habitat patches occupied by identified populations fails to account for the effects of natural succession on pond suitability at landscape level. Management of the *pondscape*, in both the immediately pond adjacent area and at the landscape scale, is clearly demonstrated to be necessary to address delivery of FCS for the species, rather than piecemeal preservation of individual habitat patches. This necessitates management which transcends the limitations of cadastral boundaries, through spatial targeting of the most effective locations for management and creation/restoration of habitat - migration and dispersal do not stop at farm boundaries and pond clusters may straddle, but are not divided by, property lines.

Consequently, the requirement for cooperative management across the administrative and property boundaries superimposed upon landscapes and ecosystems by human activity asserts itself from the earliest stages of any conservation initiative. The establishment of any such initiative cannot take place without the prior identification of core areas for conservation and linking terrestrial habitat management areas, whether corridors of whatever configuration, or stepping-stones. Consequently and inevitably, lines on maps and the act of their creation, privately or publicly, with legal status or without, may arouse concern and controversy. The preparedness of farmers and other land managing stake holders to participate in the kind of cooperative management envisaged, bringing with it responsibilities and obligations to neighbours (in the context of current and past relationships of varying quality) and potentially to habitats and species with legally protected status, cannot be taken for granted. Nor is it well supported by existing agri-environment provision. Much more research is needed in this area, and will form the focus of future research activity by the author (see below).

In the key area of the autecological foundations of the study, synthesis of the research on *T. cristatus'* habitat requirements and landscape interactions produced mixed results. Detailed knowledge of the aquatic habitat requirements of *T. cristatus* is well developed in the literature, since work on the species has focussed tightly on the pond habitat, which is easily identified, self-contained and where species presence is seasonally predictable. The same cannot be said for the terrestrial habitat where individuals usually spend most of their time. Detailed knowledge of the dispersal and migration behaviour of *T. cristatus*, its preferences for and behaviour within terrestrial habitat is sketchy (other than during immediately pond adjacent pre- or post-breeding movement, or in and around pond adjacent daytime shelter and hibernaculae). Numerous radio-telemetry and mark-release-recapture studies have been carried out, but substantial questions remain unanswered. There is a reasonable knowledge of the immediately post emergence migration behaviour of probably the majority of domiciled adults moving from the breeding pond into terrestrial foraging habitat and daytime shelter, and from there into hibernaculae (Jehle 2000, Jehle and Arntzen 2000, Malmgren 2002, Mullner 2001). Evidence suggests, however, that a relatively small proportion (perhaps up to 30%) of adults are transient, displaying considerably less association with particular ponds (Jehle *et al.* 2005) – but to what extent these individuals may be responsible for long(er) distance inter-breeding-pond migration (as opposed to dispersal proper, being considered as movement from the natal pond to a new pond for first breeding) is unknown, as is the detail of their behaviour between captures, and beyond the battery life of transmitters during telemetry studies (usually no more than a few weeks, see for example Jehle 2000, Jehle and Arntzen 2000).

Though several studies have examined directionality of post emergence movement of juveniles and the relationship between this movement and that of adults, this has raised at least as many questions as it has answered – how significant a role do juveniles play in dispersal? When – immediately post dispersal, or at some other time after a period of terrestrial existence? Malmgren (2002) identified two phases in the directionality of movement in emergent juveniles – movement of early emerging juveniles correlating positively with that of adults into terrestrial habitat, and later emerging juveniles avoiding paths of earlier emerging adults and juveniles – are these juveniles more responsible for dispersal, or is the relationship simply that their post emergence migration into terrestrial habitat is more randomly oriented? In either case, what is the contribution of these individuals to dispersal? That late emerging individuals are avoiding adults and earlier emerging juveniles, probably in search of unoccupied terrestrial habitat, is a reasonable hypothesis, providing obvious adaptive benefits – could these individuals also be moving with more random directionality and further afield into the landscape, and so potentially encountering new aquatic habitat at considerable remove from the natal pond? What is the effect of distance on levels of relatedness between populations across the Cholmondeley estate? To what extent is this relatedness affected by putative landscape barriers such as relatively built up areas, roads and fast moving water, and so how effective are these as barriers to dispersal? Further research attempting to answer these questions is planned (see below), however, conclusions from examination of the literature on terrestrial landscape associations with presence, abundance and dispersal/migration capacity, can be summarised as follows:

Increase in presence *and* abundance is associated with:

- intermediate to high levels of landscape heterogeneity (though when high levels of landscape homogenisation sufficiently reduce terrestrial and aquatic habitat availability, quite large populations may be recorded at isolated ponds due to "crowding" effects).
- increase in area of uncultivated land (most notably broad leaved woodland and rough grassland).

Increase in presence is associated with:

- higher pond density and pond clustering, with infrequent occurrence below 0.7 km^{-2} with highest levels of occurrence in higher density areas above 3 ponds km^{-2}.
- an indicated maximum inter pond distance of around 1.6km,

Decrease in presence *and* abundance is associated with:

- increase in road density,
- increase in cultivated area in close proximity to the pond (although populations may persist for some time after adverse modification to adjacent terrestrial land cover).

Decrease in presence is associated with:

- proximity to the nearest road.
- proximity to the nearest river or stream.

- The majority of individuals (possibly upwards of 70%) stay well within 250m of natal pond (over 60% within 20m in one study) where sufficient suitable terrestrial habitat is available.

- Dispersal is commonly observed up to 500m, with inter pond distances less than 250m apparently optimal.
- New ponds are occupied, but mainly in areas of high pond density and close proximity (< 400m) to source populations.
- Colonisation at distances of around 1000m of the nearest known source of dispersers are infrequently recorded, though it is not known when these migrations take place, or if they constitute true dispersal (post emergence migration to first breeding) as it is not known whether colonisation was carried out by adults or juveniles (or if the latter, which seems improbable in one migration event, whether this was after a period, perhaps extended over one or two years or even longer, of terrestrial existence).

Empirical evidence derived from survey across the Cholmondeley pondscape is either supportive of these conclusions or inconclusive in relation to pondscape connectivity, pond density and inter pond distance. No significant association ($p = 0.154$) could be identified between pond density and presence, or difference in mean pond density at pond sites between ponds with recorded presence and probable absence ($p = 0.699$). However, this remains inconclusive, in that most of the estate area is well within the range of densities and inter pond distances associated with significantly elevated presence, and while not significantly different, the lower end of the range of densities is higher, with lower standard deviation (mean 14.84 ponds km^{-2}, min. 3.39, max. 26.95, SD 5.81) for breeding ponds than that of the Cholmondeley pondscape as a whole (mean pond density 15.21 km^{-2}, (min 1.94, max 32.89, SD 6.59), and in line with findings from the literature. *T. cristatus* breeding ponds were significantly clustered, with a mean nearest neighbour distance of 261.57m, as against an expected 332.95m ($p < 0.001$). Increased pond count in clusters was positively correlated with increased breeding presence within clusters at all thresholds of connectivity ($p = 0.002$ to $P < 0.0001$) except for the shortest threshold distance examined (130m Cost Weighted, $p = 0.209$) at which most ponds were isolated. *T. cristatus* breeding ponds were better connected (as reflected in node importance according to measures of connectivity (*var*IIC and *var*PC), with significantly higher scores for these indices among the ponds where breeding was recorded, than where probable absence was recorded ($p < 0.0001$).

Similarly, the empirical evidence relating to landscape associations with presence and probable absence was divided in terms of support for the conclusions derived from literature review between support and inconclusiveness. Presence was not significantly reduced with increased proximity to roads ($p = 0.393$) and increasing road density ($p = 0.489$). Reduced presence with increased proximity to moving water was supported, with a significantly shorter median distance to the nearest running water demonstrated for ponds where no breeding presence was recorded ($p = 0.0007$). Positive association with proximity to broadleaved woodland and rough grassland was tested using both Euclidian and Cost Weighted distances, but was not supported at Euclidian distances for either broad leaved woodland ($p = .240$) or rough grassland ($p = 0.1361$). However, importantly, it was supported when Cost Weighted distance measures were used for both broadleaved woodland and rough grassland ($p < 0.0001$). No significant difference in distance to core habitat could be found between ponds with no breeding recorded and ponds with probable absence recorded ($p = 0.408$), nor were significant differences found between the mean areas of core habitat within Cost Weighted distance buffers around ponds between non-breeding and breeding ponds. Findings in relation to road proximity and density may be considered inconclusive in the sense that road density, and weight of traffic across the estate is low, possibly well below that at which significant effects will register, and the primary effect of road proximity and density is reduced abundance, rather than presence, which was not measured in the survey. The effect in relation to proximity to moving water may well be stronger, in that the effect is most probably derived from probability of fish presence, following local flooding events, impacting over the longer term on abundance and ultimately long term persistence, rather than inherent qualities of the water bodies themselves.

Overall, no significant difference in median inter-pond distance was demonstrated ($p = 0.1098$) between ponds with recorded presence and probable absence. Again, this may be considered an inconclusive result, in that the high pond density and clustering of the Cholmondeley pondscape confounds the effect. *T. cristatus* breeding ponds (as reflected in node importance measured as *var*IIC and *var*PC) were better connected, however, with significantly higher scores for these indices among the ponds where breeding was recorded, than where probable absence was recorded ($p < .0001$).

Calculated on Euclidean distance, over 90% of the landscape fell within the 500m distance associated with the commonly observed and accepted dispersal distance. However, a small proportion (15.8%, 748.6 ha) of the landscape can be said to constitute core habitat for *T. cristatus*, with a much smaller proportion being available within the areas around ponds accessible to actual breeding populations or around ponds generally. Only 88.6% of total core habitat present, (587.5 ha) is available within 500m of a pond. However, at this distance, pondscape connectivity was strong and extensive, with all but two ponds included in seven mostly large connected components (with a maximum component (cluster) size of 144 ponds). As the threshold of connectivity examined (500, 250 and 130m) decreased, however, available core habitat area fell precipitately, as did the level of connectivity of the pondscape, with the number of disconnected components increasing and mean component (cluster) sizes decreasing rapidly, until, at the 130m distance connectivity is reduced massively, with the pondscape consisting of 72 clusters (mean cluster size 3.29, SD 1.98) and 86 isolated ponds. The area of core habitat available within pond buffers at this threshold distance is reduced further, to 303.1ha, 40.5% of total core habitat available.

The effect of including terrain effects in assessment of pondscape connectivity by using a Cost Weighted distance calculation is substantial, with a marked drop in connectivity at all levels, increase in numbers of pond clusters and isolated ponds and decrease in mean cluster size. At 500m cost weighted distance, the number of pond clusters rises almost eightfold, from 7 at 500m Euclidean distance, to 55, the number of isolated ponds from 2 to 70, and the maximum cluster size drops from 144 to 28 (mean 4.60, SD 4.15). At this distance threshold, the quantity of available core habitat within pond buffers decreases from 88.6% (663 ha) to 51.3% of the total available (57.9% of that available within Euclidean distance buffers, 383.8 ha). At the 250m cost weighted distance, the increase in number of clusters is smaller (from 55 to 65) as increased isolation reduces mean cluster size (mean 2.93, SD 1.83, with a maximum component cluster size of just 13 ponds), almost doubling the number of isolated ponds (from 70 to 132). The area of core habitat available declines again to 258.8 ha, 34.6% of the total available (60.6% of that available in the 250m Euclidean distance buffers). At 130m cost weighted distance the number of component pond clusters actually reduces to 48, the maximum cluster size remaining unchanged, but with some reduction in mean cluster sizes (2.60, SD1.11) compared to 2.93, SD 1.83, at 250m cost weighted distance. The majority of ponds (198, 61.3%), are now isolated from a pond cluster at the 130m threshold. The available area of core habitat is also reduced to just 25% of the total available, 188.1 ha (62.1% of that available at the 130m Euclidean threshold distance). The highly significant positive association between reduction in Cost Weighted distance to the nearest broadleaved woodland and rough grassland, and breeding presence ($p < 0.0001$), as compared to the lack of a significant association when Euclidean distance measures were used ($p = 0.240$ and $p = 0.1361$ respectively) gives added weight to these findings.

Perhaps most noteworthy, and one of the main original contributions of this thesis are these findings in relation to the terrain effects on distances at which effects are realised and upon effective distances at which habitat is accessible to populations domiciled at ponds and within pond clusters. Taking account of terrain effects and the resistance to movement of various land cover types has important implications for habitat availability and landscape connectivity, and important questions are raised in terms of "rule of thumb" guidelines for estimation of likely levels of connectivity between pond populations and availability of suitable habitat surrounding breeding ponds. It should be remembered, however, that the resistance surface applied to Euclidean distances in this exercise is a model only, and most of the assumptions used in this study upon which this was based, of necessity drew heavily upon evidence provided by research into close congenerics of *T. cristatus'*, such as *T. marmoratus* or *T. carnifex* (morphologically similar and frequently hybridising where distributions overlap), and the general literature relating to amphibian migration and dispersal capacity, in addition to such *T. cristatus* based studies as do exist.

A recent study by Rayfield *et al.* (2010) using artificial landscapes of various configurations and assignments of resistance values (to "habitat", "hospitable matrix" and "inhospitable matrix") demonstrated that the spatial location of least-cost routes (and thereby from the point of view of this study levels of connectivity between particular locations, such as breeding ponds), was sensitive to differences in the relative cost values assigned to land cover types. They found that the *degree* of sensitivity depended on the landscape's spatial structure, with highest levels in fragmented landscapes with between 20 and 50% what they termed "hospitable matrix" (equivalent to Habitat Class 2 this study, at 70.97% in the Cholmondeley landscape); sensitivity decreased with decreasing habitat fragmentation and increase in the amount of hospitable matrix. Implications for the validity of this study from these findings are relatively minor, if anything pointing to lower sensitivity, but this does stress the importance of developing the knowledge base in relation to the migration capacity of *T. cristatus*. The Cost Weighted distance surface which is the output of this model is still sensitive to initial resistance values assigned to land cover types, though the set of values applied were consistently based on the best information available in the current literature. Empirical testing of their validity and that of surfaces generated using them is problematic. Further research and refinement of these values will improve the overall reliability of the approach. One means of testing this is the use of landscape genetic techniques to quantify effects upon relatedness between populations of intervening land cover and barriers. Further research is needed in this area (see below).

Conservation management in light of the above, must address two levels of spatial scale; management aimed at supporting local populations at the scale of immediate pond adjacency and distances up to 500m from ponds, and landscape scale efforts aimed at maintenance and improvement of pondscape connectivity and terrestrial habitat connectivity and availability at distances from 500m to 2km of a given population centre (pond or pond cluster) or perhaps further, where and if extensive landscape areas could be integrated into a coordinated management scheme. Pond centred management in favour of pond morphological and vegetation characteristics associated with one species across potentially at least 30% of ponds (the approximate current occupation rate identified for *T. cristatus* in the region) would undoubtedly have significant impacts upon a range of species, including potential adverse effects on species of conservation concern. While not ruling out judicious in-pond management of vegetation and silting, and of shade from scrub and trees on margins when circumstances demand it, this thesis proposes that a far more suitable orientation in terms of effort, cost, and collateral effects upon overall pond biodiversity, working with rather than against the grain of landscape trends, would be maintenance of a more balanced pond age profile (benefitting pond biodiversity generally), and enhancement of available breeding habitat, through spatial targeting of pond creation. For a philopatric species, with mid to late successional requirements such as *T. cristatus*, resources might be best deployed through short to medium term management aimed at protection and judicious restoration, and in the longer run creation of "replacement" ponds adjacent to breeding ponds, and on surrounding terrestrial core habitat. At the broader spatial scale, targeting of pond creation and terrestrial habitat restoration and creation for connectivity maintenance and enhancement is proposed. By this means, replacement of breeding ponds naturally declining in suitability for *T. cristatus* through hydroseral succession, and enhancement of landscape connectivity and habitat availability would take place simultaneously over time.

Addressing objective 2, the application of graph theoretic techniques to prioritisation of areas of the pondscape for management at these scales, for habitat management or connectivity improvement, demonstrated the viability of these for application at the scale of the multi-farm local population management area, and across the pondscape. At higher resolution, the techniques were shown to be applicable for maintenance of habitat availability through management of local connectivity and strategic siting of pond creation, addressing the issues of connectivity at local population scales, the scales of immediate post emergence migration to terrestrial habitat and dispersal, and intra-pond cluster movement within breeding aggregations. The techniques were also shown to be applicable at lower resolution – that appropriate to pondscape level management, where overall pondscape connectivity and longer distance migrations and dispersal take place, for maintenance and enhancement of overall connectivity and addressing issues of landscape scale pond loss due to gradual attrition of numbers arising from hydro-seral succession and discontinuance of traditional management practices. The efficacy of these approaches will be tested in the Cholmondeley landscape through future research to be carried out by the author (see below).

A potential draw back of the technique is that it was found to be somewhat data hungry, in that there is a requirement for the delineation of the whole pondscape in some detail, both within the immediate management area and on its periphery for some distance. That said, such baseline survey would be a requirement of any management initiative intended to operate at landscape level (and, though perhaps not so extensively, of any management process), and the identification of the landscape scale being the necessary scale of conservation operations carries with it consequences in terms of the scale and extent of the data it is necessary to capture in order to take management forward. Overall, the technique was demonstrated to be flexible and reasonably easily interpreted (Saura and Rubio 2010). The approach has been shown to be a useful guide to conservation planning and strategic spatial targeting of management (though not a "silver bullet") and sufficiently promising to merit practical application for formal assessment over a protracted period. The Cholmondeley Estate farms are in Entry Level Environmental Stewardship almost in their entirety through whole farm agreements, and a substantial area of the estate is under Higher Level Environmental Stewardship agreement, which will substantially enhance the potential for such a trial, which has been the subject of preparatory discussion with the estate manager.

This thesis has achieved its objectives, contributing substantially to the current knowledge base through:

- its development of a landscape scale perspective on conservation management for *Triturus cristatus*, both in terms of an overarching appreciation of the concept and its theoretical foundations in relation to what is generally considered a relatively short distance dispersing, pond dependent species,
- its review and synthesis of the available literature specifically relating to *T. cristatus,* and amphibian ecology in general, in relation to the terrestrial landscape,
- its landscape scale examination of the terrestrial landscape associations with presence and probable absence, and the connectivity and availability of core habitat, in particular highlighting the importance of inter pond connectivity and clustering, and terrain effects upon habitat availability,
- Its exploration of the applicability of graph theoretic approaches to pondscape analysis and its utility for targeting of conservation effort at varying spatial resolution.

A number of areas for further research are suggested by the findings and experience of this study. Further collaborative research is proposed involving the author and colleagues at Liverpool and Salford Universities, including detailed population studies using mark-release-recapture, radio tracking and landscape genetic studies of *T. cristatus* in the Cholmondeley estate study area. This research will be aimed at;

- delimiting *T. cristatus* metapopulation structure and effective population sizes,
- examining spatial variation in relatedness between *T. cristatus* local populations across the study area,
- relating this to spatial variation in land cover types across the estate and through this

- investigation of dispersal abilities and effectiveness of geographical barriers (e.g. roads, moving water), and levels of 'resistance' posed by various vegetation and land cover types to dispersal and migration.

Research into the dispersal and colonisation capacity of *T. cristatus*, utilising the creation of a novel *T. cristatus* pondscape is planned at Cheshire Wildlife Trusts Gowy Meadows reserve. This research at the Gowy Meadows reserve will involve experimental pond creation (10 new ponds), sited using graph theoretic techniques and also semi-randomly, to examine colonisation processes, and throw further light on dispersal capacity and movement patterns in the terrestrial phase of existence. The author and Professor Andrew Hull participated in a successful bid in relation to the establishment of the Meres and Mosses of the Marches Nature Improvement Area. The resulting work relevant to this study will involve tenants across the Cholmondeley Estate in inter-disciplinary research into land managers attitudes to and their preparedness to participate in cross boundary management activity. This will include development and presentation of concrete proposals targeting the landscape of their own farms in favour of *T. cristatus* conservation, and eliciting their responses, both on an individual and group basis through interviews, questionnaires and focus groups. The aim of this research would be to assess drivers and inhibitors of land manager participation in cooperative cross boundary management, the kind of AES which they see as being a necessary pre-requisite for this, assessed by various criteria including spatial target-ability, administrative demands, and compensation for production income foregone, and their attitudes to the potential for environmental cooperatives or other such collaborative organisations as a vehicle for organising landscape level conservation management.

Glossary of Acronyms

AES (Agri-Environment Scheme). Agri-environment schemes are government programmes set up to help farmers manage their land in an environmentally-friendly way. Agri-environmental schemes are important for the conservation of farmed environments of high nature value, for improved genetic diversity and for protection of agro-ecosystems.

ARGUK (Amphibian and Reptile Groups of the United Kingdom). The representative body for Amphibian and Reptile Groups (ARGs) based in England, Scotland, Wales and N Ireland. ARGUK aims to promote the conservation of UK native amphibians and reptiles by supporting the work of the ARGs.

CS2.2/2.5.8 beta (ConeforSensinode Version 2.2/2.5.8 beta). Graph theoretic analysis software packages ((Saura and Pascual-Hortal 2007a), used in the analysis component of this thesis).

CTcSI (Cheshire *Triturus cristatus* Site Inventory). The CTcSI is a web based inventory of *Triturus cristatus* occupied ponds in the Cheshire Vice County (VC51, Cheshire West and Cheshire, Cheshire East, Wirral, Halton and Widnes local authority areas). The inventory contains 12 figure grid references, date and survey information and was derived from survey reports, protected species licence returns, mitigation monitoring reports and historical records.

DCLG (Department for Communities and Local Government). The UK government department responsible for policy on supporting local government; communities and neighbourhoods; regeneration; housing; planning, building and the environment.

DEFRA (Department for the Environment Food and Rural Affairs). The UK government department responsible for policy and regulations on the environment, food and rural affairs.

ES (Environmental Stewardship). Environmental Stewardship is an agri-environment scheme that provides funding to all farmers and other land managers in England to deliver environmental management on their land at two "levels", Entry and Higher. There is additionally an Organic Entry Level Stewardship open to all farmers not receiving Organic Farming Scheme aid, and Uplands Entry Level Stewardship to support hill farmers with payments for environmental management, which replaces the Hill Farm Allowance.

ELS (Entry Level Stewardship). The lower tier of ES a "broad and shallow" AES which provides a relatively undemanding approach to environmental stewardship of the countryside, through simple and effective land management going beyond the Single Payment Scheme requirement to maintain land in good agricultural and environmental condition. It is open to all farmers and landowners.

FCS (Favourable Conservation Status). Conservation status (the sum of the influences acting on the species concerned that may affect the long-term distribution and abundance of its populations within the territory referred to in Article 2 [Council of Europe 1992, 92/43/EEC], is considered favourable when it is maintaining itself on a long-term basis as a viable component of its natural habitats, and the natural range of the species is not being reduced for the foreseeable future, and there is, and will probably continue to be, a sufficiently large habitat to maintain its populations on a long-term basis.

GeoTIFF (Geo-referenced Tagged Image File Format). TIFF is a file format for storing images, a GeoTIFF is a public domain metadata standard which allows geo-referencing information to be embedded within a TIFF file, allowing display of such images in conjunction with geographical data such as digital map files, environmental spatially related data etc., within a GIS.

GIS (Geographical Information System/Science). A GIS is a system of hardware and software used for storage, retrieval, mapping, and analysis of geographic data. Practitioners also regard the total GIS as including the operating personnel and the data that go into the system. The term GI Science refers to the academic theory behind the development, use, and application of geographic information systems.

GPS (Global Positioning System). A satellite based navigation system providing accurate spatial location and time information.

HLS (Higher Level Stewardship). The Higher tier of Environmental Stewardship involving more complex types of management tailored to local circumstances and targeted at BAP priority species. HLS applications are assessed against specific local targets and agreements offered where they meet these targets and represent good value for money.

HSI (Habitat Suitability Index). An index of pond habitat suitability for *Triturus cristatus* derived from a range of terrestrial and aquatic habitat features. Originally developed by Oldham *et al.* (2000), and its assessment subsequently modified slightly in light of field experience (Amphibian and Reptile Groups of the United Kingdom (ARGUK) 2010).

IIC (Integral Index of Connectivity) A graph theoretic binary connectivity index (Pascual-Hortal and Saura 2006). Nodes are either connected or not connected at a given threshold distance. IIC ranges from 0 – 1 for individual nodes, increasing with increase in connectivity at a node. The IICnum is an overall summary of this index for the network as a whole, increasing with increased connectivity. varIIC is a metric referring to the amount of variation of IIC caused by the removal of a node, that the node is responsible for.

IUCN (International Union for the Conservation of Nature). The International Union for Conservation of Nature is the world's oldest and largest global environmental organization, founded in 1948.

KDE (Kernel Density Estimation). Kernel density estimation is a widely used spatial interpolation tool for estimating a continuous distribution based on points drawn from a sample distribution. It creates a continuous surface of interpolated values at a pre-defined resolution and geographical extent.

NAS (National Amphibian Survey). A volunteer survey, targeting the nationally widespread amphibians in the UK: the great crested newt, smooth newt, palmate newt, common toad and common frog. The purpose of the survey is to provide robust assessments of their conservation status.

NC – (Number of Components). A binary graph theoretic connectivity index. This index equates to the total number of connected components (pond clusters in this study), plus, as loci of connectivity themselves, the total number of isolated nodes (ponds). As a landscape is more connected, the number of components decreases.

NL – (Number of Links). A binary graph theoretic connectivity index. As a landscape is more connected, it will present a larger total number of links (connections between habitat nodes in the landscape at predefined thresholds of connectivity).

NBN/NBN Gateway (National Biodiversity Network). The National Biodiversity Network (http://www.nbn.org.uk/) is an organisation comprised of a wide number of collaborating bodies for the collation and dissemination of biodiversity data. It is administered by the NBN Trust as a charity, and its main means of dissemination is through the NBN Gateway, an interactive data portal whereby biological data can be viewed, mapped and downloaded, subject to conditions of confidentiality and sensitivity of records.

OSGB (Ordnance Survey of Great Britain). An executive agency and non-ministerial government department of the United Kingdom Government, it is the national mapping agency for Great Britain, responsible for producing and disseminating maps of Great Britain.

PC (Probability of Connection). A probabilistic graph theoretic connectivity index (Saura and Pascual-Hortal 2007a), whereby all nodes within a network have a probability of direct connectedness. The probability of direct connectivity between nodes is calculated as a decreasing exponential function of distance. The index ranges from 0 - 1 for individual nodes, increasing with connectivity. The PCnum is an overall summary of this index for the network as a whole, increasing with increased connectivity. *d*PC refers to *delta*PC, or the dimension of PC at a given node. The metric varPC refers to the amount of variation of PC caused by the removal of a node, as a percentage of the total, that the node is responsible for. PC is partitioned into three component fractions. The Intra fraction is the contribution of a patch in terms of intra-patch connectivity, corresponding to the available habitat area (or some other relevant patch attribute) provided by the patch itself. The flux fraction corresponds to the area-weighted dispersal flux through the connections of patch to or from all of the other patches in the landscape when the patch is either the starting or ending patch of that connection or flux. *d*PCflux depends both on the attribute (e.g. area) of a patch (a patch with a higher attribute value produces more flux, if the rest of the factors are equal) and on its position within the landscape network. The connector fraction is the contribution of a patch or link to the connectivity between other habitat patches, as a connecting element or stepping stone between them. This fraction depends only on the topological position of a patch or link in the landscape network. The calculation of *d*PCconnector for a certain habitat patch is independent of its area or any other attribute considered.

PC(EC/A)(Probability of Connection (Equivalent Connectivity / Connected Area). For PC see above. ECA is defined as the size of a single habitat patch (i.e. maximally connected) that would provide the same value of the probability of connectivity as the actual habitat pattern in the landscape. ECA presents the advantages of having area units, a more reasonable and usable range of variation, and, more importantly, an easy and straightforward interpretation especially when directly compared with temporal changes in habitat area. EC (equivalent connectivity) can substitute for ECA whenever the patch attributes used correspond to habitat characteristics other than area, such as habitat quality, probability of occurrence of a particular species, population sizes, carrying capacity, etc. These metrics are also themselves partitioned between the intra, flux and connector fractions, as is PC.

PLP (Pond Life Project). An EU *Life* Environmental Program funded project, led by Liverpool John Moores University, running from late 1995 to early 1999 to gather information on ponds in the North West of England and encourage local support to survey and protect local ponds. A "satellite" project of the PLP carried out detailed survey of 1000 ponds in North West England.

SAC (Special Area for Conservation). A Special Area of Conservation is defined in the European Union's Habitats Directive (92/43/EEC), and is a statutorily protected site for the protection of 220 habitats and approximately 1000 species listed in Annexes I and II of the directive which are considered to be of European interest, following criteria given in the directive.

SSSI (Site of Special Scientific Interest). A Site of Special Scientific Interest is a conservation designation denoting a statutorily protected site for nature or geology in the United Kingdom.

Appendix 1 - Pond Survey Protocol

On approach to the pond;

Observe the pond from a distance to identify surrounding land cover characteristics, presence of waterfowl and other noteworthy characteristics as they present themselves.

At the pond

Walk the perimeter of the pond at some distance to identify composition and configuration of vegetation and small scale landscape features of note (e.g. potential refugia such as concentrations of small mammal burrows, woodpiles and tree stumps) and the best approach and viewing point(s) offering the most characteristic view(s) of the pond.

Photograph the pond from the selected viewing point(s).

Sketch plan the pond, noting configuration and relative extent of the dominant stands of vegetation, shade trees, poaching, fences, position relative to hedges, banks etc., presence of deadwood, mammal burrows etc. in the immediate margins of the pond, estimate and record level of shading and percentage of open water/macrophyte cover.

Note any other significant features of interest, e.g. presence of badger sets, or flora and fauna of particular conservation interest.

Make an egg search around the entire accessible perimeter and internal vegetation stands. Upon identification of *T. cristatus* eggs, discontinue the search to avoid unnecessary disturbance.

Note any additional features of interest observed, such as presence of other amphibian species, fish and invertebrate community characteristics, pond flora, nature of the substrate and water conditions.

If egg search fails to confirm presence, net the shallows and any suitable stands of vegetation within the water body for a minimum of 15 minutes per 50m of pond shoreline. Stop netting as soon as adult, juvenile or larval *T. cristatus* are netted to avoid unnecessary disturbance. Note any additional features of interest such as the presence of other amphibian species, fish and notable invertebrate species or community characteristics and move on to the next pond.

If netting fails to identify the presence of *T. cristatus*, assess the suitability of the pond for torch survey (vegetation, water conditions, bank side access etc.). If torch survey is appropriate, note this and record intent to torch survey. If torch survey is intended, note on pond sketch plan approaches to the pond and any significant hazards to be avoided in night time approach. If torch survey is inappropriate, note this and record intent to second visit to egg search/net.

After completion of the survey, ensure notes are complete, net, waders and other equipment are cleaned of mud, debris etc. (which may contain pathogens and propagules) and disinfected, and move on to the next pond.

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