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An Assessment of Mitigation Translocations for Reptiles at Development Sites

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Abstract

All native reptile species are protected against harm through their inclusion on UK legislation. With the exception of two species, this protection does not extend to reptile habitat. As a result, reptiles are frequently subject to mitigation translocations to facilitate the development of land. However, there are few published studies of the effects of mitigation translocation on reptile populations and whether such translocations are effective conservation interventions. The effectiveness of translocation was tested through a combination of: 1) field surveys of sites subject to mitigation across England and Wales; 2) the radio tracking of translocated adders; 3) the monitoring of a population of slow-worms at site where they were released 20 years ago; and 4) a penning experiment to test whether viviparous lizards attempt to disperse from the release site.

Very few translocated reptiles were encountered during the monitoring of release sites. This paucity of recaptures is either due to post-release mortality, imperfect detection or dispersal. Translocated male adders dispersed farther and had larger home range sizes than resident conspecifics. Some male adders undertook large unidirectional migrations back to the donor site crossing areas of unsuitable habitat as they did so. A population of slow-worms persisted at an isolated site two decades after translocation, albeit in relatively small numbers. Body condition improved over 20 years and the population resumed breeding and recruitment. The temporary penning of viviparous lizards was effective in preventing post-release dispersal and resulted in an increase in recapture rates of greater than 16 times when compared to unpenned viviparous lizard populations. The fact that no lizards were recaptured in the unpenned areas provides strong evidence for the effect of post-release dispersal. Although, mitigation translocations may prevent the immediate death of animals that would otherwise be destroyed with their habitat, there is little evidence that they are compensating for the loss of populations on a broad scale.

Keywords: reptiles; mitigation; development; receptor site; dispersal; radio telemetry; penning

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1.0 Introduction

1.1 Global Declines in Wildlife

The Chinese Curse

"*May you live in interesting times*"

Anonymous

Human activities are having an extremely profound effect on the world. Indeed, these effects are so far reaching that scientists have proposed a brand new epoch, the Anthropocene (Zalasiewicz et al., 2012; Waters et al., 2016). The Anthropocene, as the name implies, is the period in which the activities of humans have influenced the environment to a greater extent than at any time during the earth's history (Zalasiewicz et al., 2012). Evidence of human activities can be found in the earth's climate, geology, hydrology and environmental chemistry.

One of the primary attributes of the Anthropocene is human-induced global declines in biodiversity (Pievani, 2014). So extreme are these declines that many authors have described them as the sixth mass extinction (Wake & Vredenburg, 2008; Barnosky et al., 2011; Ceballos et al., 2015). To be considered a mass extinction, there must be a loss of at least 75% of all species within a relatively short geological era (Barnosky et al., 2011). Currently, the International Union for the Conservation of Nature (IUCN) only lists 799 'modern' species as extinct. Despite this, others have estimated that as many as 130,000 modern species may have gone extinct in recent times (Régnier et al., 2015). Régnier et al. (2015) argue that the discrepancy between values is due to relatively few invertebrates being Red Listed, and herein lies a fundamental problem. Given the sheer enormity of diversity, most estimates of extinction rates are, out of necessity, based on small groups and extrapolated up. Régnier et al. (2015) for instance, based their assessment on a single group of invertebrates, the land snails. However, extinction risk is not equal amongst taxonomic groups (Tolley et al., 2016) and it is unlikely that land snails are representative of all invertebrates.

Extinction is ubiquitous throughout the history of the earth. As many as 99% of species that have evolved in the past 3.5 billion years have since died out (Barnosky et al., 2011). Some researchers have argued that extinctions are a necessary driver of speciation (Pievani, 2014). However, speciation is a slow process and biodiversity can take many millions of years to fully recover following an extinction event. It is therefore important to prevent extinctions whenever possible. Unfortunately, the current rate of extinction is estimated to be 1,000 greater than normal background rates with this figure expected to rise to 10,000 in the future (De Vos et al., 2014). Indeed, the current rates of extinction are greater than during any of the first five mass extinction events (Barnosky et al., 2011).

The IUCN (2004) lists five broad factors that are thought to be key drivers behind the current loss of biodiversity:

- habitat loss and degradation;
- the introduction of invasive species;
- the over-exploitation of natural resources;
- pollution and disease; and
- human-induced climate change.

Of these, habitat loss and degradation is assessed as the greatest threat by the IUCN. Of the key indicator groups for which an analysis has been undertaken, the IUCN (2004) has concluded that the loss of habitat is affecting nearly 4,000 species of amphibians and 2,000 species of mammal. However, vertebrate species represent a small proportion (< 5% of described species) of all biodiversity and a far greater number of invertebrates are likely to be declining as a direct result of habitat loss.

1.2 Global Reptile Declines

Whilst much attention has been paid to high profile declines of groups such as amphibians (Stuart et al., 2004), birds (Birdlife, 2004) and mammals (Schipper et al., 2008), other taxa have also been declining albeit on a subtler scale. Gibbons et al. (2000) first flagged the issue of a possible global decline in reptiles. The authors presented IUCN data that suggested 253 species of reptile (c. 3%) were threatened with extinction. More recent papers, however, have calculated this figure to be closer to 20% with a further 19% that are Data Deficient (Böhm et al., 2013; Bland & Böhm, 2016; Tingley et al., 2016). These declines are not spread equally across all reptilian taxa however. Species of reptile that exhibit slow growth, low fecundity, selective feeding regimes, and occur within highly specialised habitats are likely to be more vulnerable to change (Maritz et al., 2016). Within the Chelonians (turtles), as many as 57% are assessed as threatened (Buhlmann et al., 2009). In a study of African reptiles, the highest extinction risks were found within the Blanidae (worm lizards), Boidae (boas) and Geoemydidae (turtles) (Tolley et al., 2016). On Madagascar, all four species of terrestrial tortoises are assessed as Critically Endangered whilst 53 of the 76 species of chameleon are listed as threatened or near-threatened (Jenkins et al., 2014). Outside of Africa, reptile populations are faring equally badly. Of the 100 or so species of lizard found in New Zealand, both species of tuatara, 24% of geckos and 50% of skinks are assessed as threatened (Towns et al, 2001). In this instance, the introduction of invasive mammal species is thought to be a key driver of the declines. Other key regions of reptile diversity, such as

Australia and Asia, are globally the least assessed areas by the IUCN making it difficult to identify population trends (Meiri & Chapple, 2016).

Gibbons et al. (2000) argue that the well-documented threats behind the decline of amphibians, which are the same five drivers as listed by the IUCN above, are equally deleterious to reptile populations. A study by Reading et al. (2010), in which 67% of observed snake populations were declining, suggested that the deterioration of habitats was a factor (albeit amongst several possible factors). Indeed, habitat loss and degradation appears to be the principal cause behind many reptile population declines (Shine, 1991, Maritz et al., 2016; Meng et al., 2016; Tolly et al., 2016). The nature of these habitat losses vary geographically. Losses in Africa and Australia largely arise from the growth of subsistence farming and pastoralism (Webb et al., 2014; Tolly et al., 2016). In USA, the draining of wetlands has adversely affected many species of snake and turtle (Bennett & Nelson, 1991; Buhlmann, 1995; Dorcas et al. 1998). In the UK, changes in agricultural practices and urban expansion have been implicated as causes in the decline of reptile populations (Beebee & Griffiths, 2000; Baker et al., 2004). Indeed, the demand for land that can be developed is fast becoming one of the most important drivers of habitat loss (Germano et al., 2015).

1.3 Reptile Status in Europe

There are 151 species of terrestrial and freshwater reptile that are known to occur within Europe; of these, nearly 50% are endemic to the region. The group is dominated by lacertid lizards (n = 65 species), 75% of which are endemic. Reptile diversity is not distributed evenly across Europe. During the last glaciation event (110,000 years ago), many reptiles migrated south to the Iberian, Italian and Balkan peninsulas, which all avoided the encroachment of ice (Stewart, 1969). Once the ice began to retreat (c. 11,700 years ago), the group slowly migrated north again; however, the southern peninsulas remain the most diverse regions in Europe for reptiles (Spain = 65 species, Greece = 55 species, Italy = 50 species). In contrast, northern Europe supports fewer reptile species (Denmark = seven species, Sweden = six species) (Cox & Temple, 2009). Presumably this is because the cooler climate is less conducive for ectothermic animals.

The IUCN has recently undertaken a broad assessment of the status of reptiles within Europe (see Cox & Temple, 2009). Of the 139 species of reptiles that were included within this assessment, six were listed as Critically Endangered, 11 as Endangered and 10 as Vulnerable (Cox & Temple, 2009). A further 18 species are listed as Near-Threatened. In total, nearly one-fifth of the assessed species were listed as threatened.

The threats facing European reptiles are in accordance with that of the global picture. Habitat loss and degradation is by far the most prevalent threat, affecting 22 of the 27 species of threatened reptiles (Cox & Temple, 2009). Included under habitat loss and degradation are:

- agricultural intensification;
- urban sprawl;
- infrastructure (including roads); and
- replacement of forests with plantation.

Other key threats include accidental mortality, persecution, changes in native species dynamics and human disturbance. The severity of these threats will vary on a case-by-case basis; however, it is important to understand that these threats do not occur singularly and the cumulative impact is likely to be greater than the sum of its parts.

Approximately 42% of European reptile populations are thought to be declining (Cox & Temple, 2009). To arrest further declines, European countries and European Union member states are signatories to a number of conventions aimed at conserving biodiversity.

1.3.1 European Protection

The Convention on the Conservation of European Wildlife and Natural Habitats (the Bern Convention).

The Bern convention, which was adopted in Bern, Switzerland in 1979, is a binding international legal statute. Its primary purposes are to:

- ensure the conservation and protection of flora and fauna in their natural habitats (currently there are 21 species of reptile listed in Appendices II of the Convention);
- to increase the co-operation between contracting parties; and
- to regulate the exploitation of those species (including migratory species) listed in Appendix III.

All signatories to the Bern Convention meet their obligations through the implementation of Council Directive 92/43/EEC on the Conservation of Natural Habitats and of Wild Fauna and Flora (the Habitats Directive).

1.3.2 European Union Protection

The Habitats Directive is the primary mechanism by which the European Union (EU) sets out its approach to the conservation of nature. In accordance with the aims of the Bern Convention, the Habitats Directive seeks to promote the maintenance of biodiversity by requiring Member States to take measures to protect natural habitats and wild species. To achieve this, the Habitats Directive provides the mechanism for the designation of a coherent network of Natura 2000 protected sites. Member States are required to identify sites of European importance and put in place long-term management to protect them. Special Areas of Conservation (SAC) are designated for either habitats (listed on Annex I) or species (Annex II) that require strict conservation measures. In addition to the above, the Directive requires Member States to afford stringent protection to species listed on Annex IV, which currently includes 22 species of reptile. Annex V lists species whose taking from the wild can be restricted by European law to ensure sustainable exploitation.

The Convention on International Trade in Endangered Species (CITES) was adopted in Washington DC in 1973. CITES aims to regulate international trade in species which are endangered or which may become endangered if their exploitation is not controlled. Species covered under CITES are listed in three Appendices, according to the level of protection or regulation of trade that they need. Appendix I includes the most highly endangered species for whom trade is strictly regulated. Appendix II lists species that are not threatened currently but uncontrolled trade could lead them becoming threatened. Finally, Appendix III includes species that have been included at the request of a member state; for instance, to help prevent the illegal import and export from/to other member states. CITES is implemented within Europe via two EC Regulations (EC 338/97 and EC 865/06 as amended). Currently included on Appendices I and II of CITES are all crocodilians, all sea turtles, 24 species of lizards and ten species of snakes.

1.4 The Situation in the UK

1.4.1 UK Legal Protection

The Conservation of Habitats and Species Regulations 2010 (as amended)

The UK government ratified the Bern Convention in 1982. In 1994, the Conservation (Natural Habitats &c.) transposed the requirements of the Habitats Directive into UK law. In 2010, this was succeeded in England and Wales by The Conservation of Habitats and Species Regulations. In Scotland, the Habitats Directive is transposed through a combination of the Habitats Regulations 2010 and the original 1994 Regulations. Finally, in Northern Ireland, the Habitats Directive is transposed into the Conservation (Natural Habitats, &c.) Regulations (Northern Ireland) 1995 (as amended).

The respective Regulations require the designation and protection of SACs, the protection of European Protected Species (EPS) and the adaptation of planning and other controls for the protection of European Sites. Although both the sand lizard and smooth snake are listed under Annex II of the Bern Convention and are almost exclusively found on protected sites, they are neither the primary nor secondary designated feature of any SAC in the UK.

The Regulations make it an offence to deliberately capture, kill, disturb, or trade in any species of animal listed on Schedule 2; although these actions can be made lawful through the granting of licences by the appropriate statutory agencies. The legal protection afforded by the Regulations extends to habitat used by Schedule 2 species for resting or shelter.

Britain’s future membership of the EU is uncertain as are the ecological protections that derive from it. Given the degree of overlap between the distribution of sand lizards and smooth snakes and the boundaries of protected sites, the extent to which these species depend on legal protection is clear.

Wildlife and Countryside Act 1981 (as amended)

The Wildlife and Countryside Act 1981 is the primary domestic legislation in the UK. It consolidates and amends existing national legislation to implement the Bern Convention Equivalent provisions for Northern Ireland are contained within the Wildlife (Northern Ireland) Order 1985 and the Nature Conservation and Amenity Lands (Northern Ireland) Order 1985. Since its Royal assent in 1981, the Act has been modified by several amendments including the Countryside and Rights of Way (CRoW) Act 2000.

The Act itself comprises a series of Schedules relating to the protection afforded to different taxa. All native species of reptile receive legal protection under Schedule 5 of the Wildlife and Countryside Act 1981 (as amended). Under this Act, reptiles are protected from killing or injuring (part of Section 9(1) or selling or being advertised for sale (Section 9 (5a,b)). The sand lizard and smooth snake are also subject to the provisions of Section 9.4 (b,c), which prohibit disturbance whilst occupying a place of shelter or the obstruction of a shelter. Unlike EU legislation, the protection afforded to animals under the Wildlife and Countryside Act 1981 does not extend to their habitat. For instance, all widespread reptiles are under Schedule 5 but their habitat is not; the result of this is the removal of these species from the site of development thereby fulfilling the developer’s legal requirements (to prevent harm).

The Wildlife and Countryside Act 1981 also enables the notification of Sites of Special Scientific Interest (SSSI). These sites, protected by law, are cited for their flora, fauna, geological or physiographical features. SSSIs form the basic unit of UK protected area networks and many higher designations, such as SAC, are superimposed onto existing SSSIs. The Act places a duty of care on to the owners or managers to maintain the site in a favourable status (as determined by the cited feature). Guidelines for the designation of SSSI for reptiles have been prepared and currently there are 54 SSSI designated for reptiles. Of these, 48 cite sand lizard, smooth snake or a combination of both; the remaining six SSSI are designated for their ‘reptile assemblages’.

Natural Environment and Rural Communities Act 2006

All British reptiles are listed under Section 41 of the Natural Environment and Rural Communities (NERC) Act 2006 as a ‘Species of Principal Importance for Conservation England’. The equivalent for Wales was Section 42; however, this was replaced by the Environment (Wales) Act 2016. Both pieces of legislation place a duty of care on the competent authority to consider priority habitats and species as a material consideration when discharging their normal duties. The list of priority habitats and species was drawn from the now defunct UK Biodiversity Action Plan (BAP).

As the rarer species occur largely within protected sites, they are less frequently threatened by development and rarely subject to translocation. As such, neither the sand lizard nor smooth snake feature in any of the translocations reported within this study.

1.4.2 British Reptile Fauna

The UK supports six species of terrestrial reptile and a small number of non-natives that have become established. The six native species comprise the slow-worm (*Anguis fragilis*), viviparous lizard (*Zootoca vivipara*), sand lizard (*Lacerta agilis*), grass snake (*Natrix natrix*), adder (*Vipera berus*) and smooth snake (*Coronella austriaca*). The reptiles are broadly divided into two groups based on their distribution: the ‘widespread’ species (slow-worm, viviparous lizard, grass snake and adder) that are found throughout much of the UK, and the ‘rare’ species (sand lizard and smooth snake), which are highly restricted in their distribution. Coinciding with this split in distribution, the rarer species receive a higher level of legal protection than the widespread species.

Slow-worm

Slow-worms belong to the family Anguidae (glass lizards and alligator lizards) and are the only representative of this group found in the UK. They are a small (c. 500 mm total length) legless species with a relatively long tail.

The slow-worm is a largely fossorial species, spending much of its time beneath vegetation, within leaf litter or compost, or under refuges such as logs and rocks. This has limited our understanding of the species’ ecology. Slow-worms occur within a wide variety of habitats, including open woodland, meadows, heathland and brownfield. Because of their preference for the latter, slow-worms are often encountered within urban areas, favouring semi-disturbed sites such as urban waste ground, churchyards and private gardens (Platenberg, 1999).

The slow-worm occurs throughout the mainland Britain but is likely to be under-recorded. The species’ cryptic lifestyle means that the status of the slow-worm in the UK is largely uncertain. The IUCN list the slow-worm as ‘Least Concern’ and report that, although fragmented, populations are stable. A questionnaire survey, carried out in the 1970’s to establish UK reptile population trends, identified dramatic declines in slow-worm populations during the 20th century (Cooke & Scorgie, 1983). A follow-up survey was undertaken during the 1980’s, which identified further declines in slow-worm populations (Hilton-Brown & Oldham, 1991). Baker et al. (2004) repeated the questionnaire focusing solely on the slow-worm and the adder. Baker et al. (2004) reported that the decline in slow-worms appears to have abated to non-significant levels.

Viviparous Lizard

The viviparous lizard is the smallest UK reptile, measuring just 150 mm total length, although approximately two-thirds of this is tail. Unlike the slow-worm, viviparous lizards can be readily seen basking and foraging in the open. The species occurs throughout much of Britain and Ireland, where it occupies a variety of habitat types. Viviparous lizards have been encountered in open woodland rides, grassland, wet and dry heathland, moorland, coastal cliffs, road verges, brownfield and uncultivated arable field margins (Edgar et al., 2010). Favoured habitats include those that are structurally complex and encompass ecotones (the boundary of two discrete habitat types). Many brownfield sites typically satisfy these criteria, which have resulted in viviparous lizards occurring within and adjacent to urban areas (UK BAP: *Zootoca vivipara*, 2010).

The IUCN have assessed the viviparous lizard as ‘Least Concern’. Although the species is extremely widespread across Europe and northern Asia, it is patchily distributed and populations are thought to be both fragmented and in decline.

Grass Snake

The grass snake is the largest species of snake to occur in Britain. An important aspect of grass snake biology is that it is oviparous and requires access to suitable egg-laying sites. Little is known about where grass snakes deposit their eggs; however, warmth and moisture appear to be key (Beebee & Griffiths, 2000). The grass snake can be found throughout much of mainland UK with the exception of most of Scotland. Other habitats frequently occupied include open woodlands or woodland edges, wet heathland, rough grassland, allotments and moorland.

The grass snake is assessed as Least Concern by the IUCN although the last iteration of the assessment dates back to 1996. It occurs throughout much of Europe and into western Asia. The IUCN does not provide any information of the current population trends for this species.

Adder

The adder is a medium-sized terrestrial viper that occurs throughout much of Europe and in to Asia. The adder is the UK’s only venomous snake species. Typical of the viperids, adders are largely ambush predators and feed primarily on small mammals (voles, mice, shrews) and lizards (Prestt, 1971); to a lesser extent, adders will also predate nestling birds and common frogs (*Rana temporaria*). The adder is found throughout much of mainland Britain, although it has a patchy distribution and appears to be more abundant in the south of England (Beebee & Griffiths, 2000). It is known to occur within woodland, heathland, grassland and coastal dunes. Different habitat types are occupied at different times of the year depending on the needs of the individual (Phelps, 2004). Foraging grounds typically comprise lowland meadows, woodland edges and heathland. Hibernation sites by contrast tend to be higher, southward facing and densely vegetated. The distance moved between feeding and hibernation sites is dependent on the habitat structure, quality and topography, but can range between 50 and 200 m per day (Beebee & Griffiths, 2000).

The IUCN list the adder as ‘Least Concern’ but identifies that populations are declining and that local extinctions have occurred within the past century. All three questionnaire surveys (Cooke & Scorgie, 1983; Hilton-Brown & Oldham, 1991; Baker et al. 2004) have identified dramatic declines in the adder. Baker et al. (2004) describe the status of adders as ‘unfavourable’ given that “… there were more population decreases reported than would be expected to maintain stasis”. In particularly, adders within the Midlands are undergoing significant declines. Since 2004, several national surveys for the herpetofauna in general (National Amphibian and Reptile Recording Scheme) or specifically the adder (Add an Adder, Make the Adder Count) have been carried out. The 2007-2012 NARRS report (Wilkinson & Arnell, 2013) confirmed that, of the sites surveyed, adders had a very low occupancy rate. This means that to identify changes in population status of 20% or 30%, a vast number of surveys would be required. The authors argue that given the low occupancy rate and difficulty in statistically identifying change, concerns should be raised regarding the conservation status of adders in Britain. In 2016, a two-day conference was undertaken to identify and discuss the approach to managing the conservation of the adder.

1.4.3 Threats

The single greatest threat to reptiles is the historical and continued loss and degradation of habitat. Since the introduction of strict legal controls, the loss of habitat largely applies to the widespread reptiles. Of particular note are urban expansion and changes in land management practices (Baker et al., 2004). The UK Biodiversity Action Plan (UKBAP) specifically attributes declines in slow-worms and viviparous lizards to the redevelopment of brownfield sites. Indeed, in 2016 the UK Government launched a campaign to prioritise the redevelopment of brownfield sites. Seventy-three councils in England were tasked with preparing a register of brownfield sites that could be fast-tracked through planning. The Government aspiration was to construct 900,000 homes on brownfield sites. It is hoped, though by no means assured, that sites containing the most ecologically sensitive habitats (i.e. those that meet the criteria to be assessed as the priority habitat under 'open mosaic on previously developed land') will not appear on this register.

Outside of brownfield sites, urban expansion continues to play a significant role in the reduction of reptile populations. Direct losses of habitat notwithstanding, urban expansion can result in other indirect impacts on reptiles. Anthropogenic impacts (such as dog walking, photography, fires or persecution) can have a particularly adverse effect on small, fragmented populations (Langton, 1986). Indeed, a recent study of pet ownership identified that 17% of UK households contained a domestic cat, with a cumulative population of 7.5 million animals (PFMA, 2016). Although Hilton-Brown and Oldham (1991) played down the impact of cat predation, a recent study by the Mammal Society reported that of a sample of 14,370 prey items brought home by cats, 144 (0.01%) were reptiles (Woods et al., 2003). Although the annual loss of 144 animals is unlikely to be significant, the authors then scaled up the figure assuming nine million households contained cats, which brought the expected annual cat predation to five million reptiles and amphibians (unfortunately, no distinction between the two are made). Assuming that the proportion of reptile and amphibian mortalities remained consistent and correcting the figure for 7.5 million homes, cat predation likely results in the loss of over 833,000 reptile and amphibians per annum.

Another major cause of habitat loss is the transition from traditional agricultural methods to modern intensive agriculture practices. Of note is the loss of hay meadows, which is known to have a particularly deleterious effect on slow-worm populations (Cooke & Scorgie, 1983). A by-product of agricultural intensification is the loss of landscape diversity (Robinson & Sutherland, 2002). This, coupled with the removal of hedgerows, addition of chemicals and the formation of fewer but larger farms results in a substantial reduction in the availability of habitat (Cooke & Scorgie, 1983).

1.5 Reptiles and Development

1.5.1 Planning Considerations

In the UK, the mechanism for mitigating the impacts of development on protected species and habitats is either through the legislative or the planning systems. The nature of the mitigation itself is often determined through a series of existing governmental or non-governmental guidance documents (see Table 1.1). The burden of collecting the necessary baseline data and the preparation of appropriate mitigation strategies typically lies with the developer's appointed ecological consultant. However, a recent survey has demonstrated that 66% of local planning authorities either completely lack - or only have partial access to - the in-house ecological expertise required to assess these strategies (Oxford, 2013). This highlights the importance of the information contained within published guidance in the decision-making process. Natural England, the largest government agency concerned with the protection of wildlife, currently has in place a moratorium on the publication of updated guidance documents. Although numerous non-government organisations, such as the Bat Conservation Trust, have engaged in publishing taxa specific guidance, the organisations concerned with reptiles have not. This has resulted in the information contained within the guidance documents becoming very outdated but still citable (e.g. HGBI, 1998; Froglife, 1999). Where updates have been published (i.e. Sewell et al., 2013), they have not been widely disseminated or adopted.

Table 1.1: Current UK guidance documents relating to the survey and assessment of reptiles

Title	**Reference**
Evaluating Translocation Programmes – Maintaining Best Practice	HGBI, 1998*
Froglife Advice Sheet 10: Reptile Surveys	Froglife 1999
The Herpetofauna Workers' Manual	Gent & Gibson, 2003
Reptiles: Guidelines for Developers	English Nature, 2004
The Design Manual for Roads and Bridges – Volume 10, Section 4, Part 7 Reptiles	Highways Agency, 2005
Reptile Mitigation Guidelines (subsequently withdrawn);	Natural England, 2011
Survey protocol for UK herpetofauna	Sewell et al. 2013
Reptiles: Surveys and Mitigation for Development Projects	UK Government, 2014

***** despite being nearly 20 years old, planning authorities still reference this document

1.5.2 Mitigation

Globally, a hierarchy of mitigation is applied to impacts arising from development (IFC, 2012; CIEEM, 2016; US Fish & Wildlife Service, 2016). In descending order of preference, impacts should be avoided, mitigated or compensated. Avoiding adverse impacts, perhaps by relocating the project to another less sensitive area, is always the preferred option; however, the high demand for suitable sites in the UK means that this is rarely possible. As such, many developments require some form of mitigation to alleviate deleterious effects on wildlife (Germano et al., 2015).

Much of the mitigation contained within the published guidance appears to be biased towards the alleviation of short-term impacts (i.e. to avoid immediate effects such as killing and injury). The long-term effects of mitigation are rarely considered. Maintaining reptiles within their current range is the preferred mitigation option (Natural England, 2011). To achieve this, a developer might be asked, for example, to reduce the footprint from two-thirds of a site to one-third, thereby leaving sufficient room for the species to remain *in situ* (often termed ‘mitigation by design’ or ‘embedded mitigation’). The remaining area is typically augmented with ‘enhancements’ designed to potentially offset the reduction in carrying capacity and maintain the population at its current level. Reptiles would then be removed and excluded from the development footprint thereby minimising the risk of harm. Whilst strategies such as this appear sensible, they rarely consider how the affected population would respond in the medium or long-term. For example, such reductions in space invariably result in higher population densities than would occur naturally. In response to high population densities, individuals could either choose to remain *in situ* where they would experience elevated levels of intraspecific competition, or migrate out of the population and forced to occupy suboptimal habitat. Those that do remain may experience reductions in body condition and fecundity (Platenberg & Griffiths, 1999) and increased risk of disease transmission (Storm et al. 2013; Aiello et al., 2014). Furthermore, inappropriate habitat enhancement measures, such as the creation of hibernacula when the availability of prey items is the limiting resource, would exacerbate intraspecific competition. Those animals that migrate away are unlikely to contribute either demographically or genetically to the population (Ebrahimi & Bull, 2014). This combination of factors is likely to result in increased risk of local extinction.

There is currently no centralised collation of reptile mitigation data and, although it is encouraged, there is no obligation on practitioners or developers to lodge their data with a regional or national recording scheme. To save the costs associated with an ever increasing repository of information, a common practice by Local Planning Authorities is to remove access to online material once a planning decision is reached. However, even where reports are accessible, a recent study of great crested newt mitigation showed that less than 10% contained informative population monitoring data (Lewis, 2012).

1.5.3 Translocation

One of the most frequently employed forms of 'short-term biased' mitigation is translocation. Translocation refers to the deliberate movement of a species or group by humans from one area to another. Translocations can be broadly categorised into two groups depending on the motives (but see Burke (1991) for a historical discussion of definitions):

- conservation translocation: the reintroduction or restocking of an ailing population, undertaken to improve the species conservation status; and
- development-led translocation: these include the relocation of populations to ensure compliance with the appropriate legal framework and the relocation of problem species.

The IUCN (2013) released general guidance on how to plan, implement and monitor translocations. Although principally aimed at conservation translocations, much of what is included within the document is equally pertinent to development.

There is currently no formal mechanism for recording the number of development-led translocations that are undertaken annually in the UK. However, the practice appears to be both widespread and frequent (Platenberg, 1999; Platenberg & Griffiths, 1999; Whiting & Booth, 2012; Germano et al., 2015). Indeed, six of the eight documents listed in Table 1.1 detail good practice approaches to translocation.

1.5.4 Evidence of Successful Translocations

A successful translocation has been defined as one that results in a self-sustaining and viable population (Griffith et al., 1989). To establish whether these criteria have been met, post-translocation monitoring is required. The IUCN (2013) divides the monitoring into three phases, the establishment, growth and regulation phases, all three of which should be covered by the monitoring to establish success. Depending on the species concerned, this monitoring may need to extend over several decades (Dodd & Seigel, 1991). However, of the documents presented in Table 1.1, the maximum period recommended for monitoring development-led translocation is just five years but this only applies to larger populations, higher impacts or rarer species (Natural England, 2011).

As of March 2017, the Conservation Evidence website (www.conservationevidence.com) did not contain any studies relating directly to the translocation of reptiles. Moreover, none of the guidance documents listed in Table 1.1 provide any case studies relating to translocation. Despite being a widely recognised technique for mitigating human-wildlife, no evidence can be found as to whether translocation is an effective approach.

1.6 Aims of this Study

Given the frequency at which development-led translocation is undertaken coupled with the uncertainty of its outcome, there is a need to establish the long-term effects of the approach on the species concerned. This information would enable ecological consultants to assess whether translocation is a suitable approach to mitigation and, if so, to undertake steps to maximise the likelihood of success. This development of knowledge will in turn inform future approaches to policy and legislation.

As the rare reptiles, for the most part, occur within protected sites, the effect of development are highly localised rather than widespread; as such, the focus of this study will be on the widespread species only. The current study will seek to address the following questions:

- How do reptiles respond to translocation in the medium-term (up to three years)?
- How do reptiles respond to translocation over longer timescales (20+ years)?
- What factors appear to affect the success of translocations?

To address these questions, assessments will be undertaken of populations of widespread reptiles that have been subject to development-led translocation. Many of these studies follow real-world development mitigations and therefore accurately reflect the current status. This study will seek to undertake:

- An assessment of post-translocation establishment and dispersal (Chapter 2);
- An assessment of the spatial ecology of adders following translocation (Chapter 3);
- An assessment of a slow-worm population some 20 years post-translocation (Chapter 4); and
- An investigation of the effects of penning translocated animals (Chapter 5).

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Chapter 2: Monitoring the Fate of Reptiles Translocated from Development Sites

2.1 Summary

Global reptile populations are undergoing catastrophic declines. In an attempt to arrest these declines, researchers, conservationists and practitioners are implementing a suite of practical interventions including translocation. There are broadly two types of translocation, ‘conservation’ and ‘development-led’. Although often applied to very different situations, both are undertaken with the expectation of minimising impacts on natural populations. However, a lack of post-translocation monitoring means that the fate of reptiles translocated from development sites is largely unknown.

Here I describe six case studies from throughout the UK, all of which involved the translocation of the four ‘widespread’ species of reptiles (see Chapter 1). Although each translocation was different in terms of the numbers and species moved and geographic location, they were all considered to be ‘typical’ examples of mitigation practices in the UK. Very few translocated individuals were encountered during follow-up surveys at the receptor sites. The mean number of reptiles translocated from the sites was 98 (SE 19.61), of which a mean of 1.5 (SE 0.72) individuals or 1.6% of the population were recaptured during multiple surveys at the receptor sites. Indeed, no recaptures of translocated reptiles were made at three of the study sites. Although pre-translocation surveys revealed no reptiles at two receptor sites, post-translocation surveys indicated the presence of non-translocated animals which must have been missed and/or colonised the site naturally. Translocated slow-worms were more than twice as likely to be encountered than viviparous lizards.

The low recapture rates of translocated reptiles could be due to mortality, imperfect detection (including inaccurate identification of individuals) or post-translocation dispersal. Currently, there is limited evidence to support each of the possible options; however, post-translocation dispersal is considered to be the most likely explanation.

2.2 Introduction

Reptile translocations are occurring throughout the world in an attempt to combat global declines or, at the very least, to prevent further losses. Conservation translocations are primarily focused on reintroductions and the reinforcement of declining populations. Mitigation translocations typically seek to avoid further losses by moving reptile populations from the footprint of impending development. Although the motivations differ, the goal of translocation is the establishment of a viable and self-sustaining population (Griffith et al., 1989). The only way to establish success is through monitoring programmes.

The duration of monitoring programmes should be guided by their goals (IUCN, 2013). To establish the success of mitigation translocations, monitoring should be sufficiently long to ascertain population trends (i.e. recruitment and losses). For a population to remain stable and viable, recruitment (births and immigration) needs to broadly equal losses (deaths and emigration). To be considered ‘self-sustaining’, the offspring of translocated animals should themselves form an active part of the breeding population. How long this takes will depend upon the species involved. For instance, slow-worms require between three and five years to become sexually mature (Platenberg, 1999), whilst viviparous lizards typically only require three to four years (Bauwens & Verheyen, 1987). A monitoring programme involving these species could take eight years or more to establish success.

To facilitate an assessment of population trends, detailed data beyond simple counts need to be collected during the translocation. In particular, the ability to re-identify individuals is essential. This can be achieved through the collection of photographic records, PIT tagging or marking (see Plummer & Ferner, 2012 for a comprehensive review). Morphometric measurements would enable an assessment of body conditions, which can be used as a proxy for population fitness and extinction risk (required to ascertain ‘viability’). Recording the proportion of animals that have lost part or all of their tails could allow an assessment of predation pressures.

In the UK, it is unlikely that ‘standard’ monitoring programmes of mitigation translocations are able to demonstrate success or otherwise. Currently, there are eight guidance documents pertaining to the survey and assessment of reptiles in the UK (see Chapter 1), most of which are out of date. Of these, six present ‘good practice’ approaches to translocation; however, none specify a need to collect data beyond simple counts. Indeed, the longest monitoring period described is just five years and is reserved for large development causing ‘substantial’ impacts. Given the importance placed on these documents by local planning authorities (see Chapter 1) coupled with developers drive to cut costs associated with surveys, it is unlikely that the data needed to assess success is being collected.

Dodd and Seigel (1991) reported that reptile translocations had very low success rates and that herpetofauna in general were unsuitable for translocation. This does seem to be at odds with the fact that many species of reptiles and amphibians have successfully ‘invaded’ new areas (*Boa constrictor* in the Florida everglades, *Boiga irregularis* in Guam, *Bufo marinus* in Australia, *Podarcis muralis* in the UK *etc*.). Following Dodd and Seigel (1991), several more authors have reported limited success for reptile translocations. Butler et al. (2005) reported that just 19% of reptile translocations were successful and, of these, none involved snakes. Germano and Bishop (2008) undertook a meta-review of 91 herpetological translocations and again reported low success rates, albeit higher than those of Dodd and Seigel (1991). The authors did, however, identify the motivation for translocation (i.e. conservation or development-led) as an indicator of success. The highest levels of failure (63%) were associated with development-led translocations involving reptiles. It follows that if conservation translocations, for which very detailed risk assessments are carried out, cannot guarantee success, development-led translocations are unlikely to result in successful outcomes. Indeed, the one issue in which many authors do agree upon (Dodd & Seigel, 1991; Reinert, 1991; Germano & Bishop, 2008) is the need to report on apparent failures.

In one of very few studies that included detailed population monitoring of translocated reptiles, Platenberg & Griffiths (1999) describe the continued persistence of slow-worms two years after the translocation. The authors reported that the slow-worms had lower body conditions than nearby natural populations and showed no evidence of breeding within the monitoring period. As the population persisted in the short-term, standard monitoring (based on count data only) would indicate success; however, more detailed quantitative data led the authors to question the conservation value of such translocations.

In addition to the paucity of population data, there is also a clear lack of post-release distribution data. In a meta-review of published studies, Wolf et al. (1999) reported that just 45% of 336 mammal and avian translocations involved either banding or radio telemetry (techniques that would allow individuals to be followed). The majority of post-translocation studies of reptiles involve snakes and these are considered in detail in Chapter 3. However, there are a small number of studies detailing the post-release movements of tortoises (Tuberville et al., 2005) and lizards (Knox & Monks, 2014; Fitzgerald et al., 2015). These studies highlight the importance that ‘post-translocation dispersal’ has on the success of translocations. Le Gouar et al. (2012) define post-translocation dispersal as the temporary or permanent departure of animals from the release area. Mass emigration can inhibit the establishment of a population as there will be fewer individuals to contribute demographically or genetically (Ebrahimi & Bull, 2014). It is, however, feasible that emigrating individuals could establish a population elsewhere. In the UK, there have been very few studies of post-release dispersal and, to the author’s knowledge, all involved radio tracking the movements of snakes.

2.2.1 Aims and Objectives

The paucity of detailed monitoring data means that the fate of translocated individuals is largely unknown. Without this knowledge, it is impossible to determine whether current approaches to mitigation benefit reptile populations. This is a fundamental shortcoming in our knowledge of translocations and is likely to be a contributory factor in the high levels of failure reported for development-led reptile translocations (Germano & Bishop, 2008).

In this chapter, I report on the outcome of six reptile translocations carried out to mitigate the impacts of development. Through detailed post-translocation monitoring, I sought to establish the proportion of translocated individuals that remain at the release site.

2.3 Methods

2.3.1 Site Selection Protocol

Request for Sites

All sites reported in this thesis are real world examples of current mitigation practices. Apart from providing a protocol for photographing and measuring individual animals for follow-up monitoring (see section 2.3.3), I remained strictly impartial and made no attempt to advise, modify or otherwise influence the design or execution of the projects which were carried out by professional ecological consultants on behalf of developer clients.

To identify and secure appropriate sites, I made a number of requests directly to the ecological consultancy community. This included:

- Publicising the research project and requesting details of potential sites at CIEEM's (2011) Reptile Mitigation Conference and the Amphibian and Reptile Groups UK (ARG UK) Herpetofauna Workers Meeting (2011 & 2012); and
- Targeted emails were sent to approximately 100 consultants listed within the CIEEM Professional Directory.

Site Selection Criteria

The criteria for determining the appropriateness of sites is presented below:

- The impacted site should support a population or community of 'widespread' reptile species;

- The impacted site will be subject to development, either partially or fully, within the anticipated timescales of this study; and
- Access to the receptor site would be granted for the author to undertake follow-up surveys of the translocated reptiles.

Of the 12 sites initially offered for the project, only six sites were secured for the study. The reasons for this 50% reduction included failure to secure planning permission for development and landowners refusing access to sites for monitoring. For each of the six secured sites, I requested information on methods and results for pre-translocation surveys of both the donor and receptor sites and descriptions of the donor site.

2.3.2 Study Sites

Site 1

A major trunk road was being upgraded from a single to a dual carriageway to alleviate traffic congestion. To accommodate this expansion, 50 m either side of the affected trunk road was cleared of vegetation, which comprised a mosaic of scrub and grassland.

Surveys of the donor site, undertaken by the developer's consultant, identified a population of viviparous lizards, although neither the original data or report were available for review. A reptile exclusion fence was erected around the affected area and between August and October 2012 the consultants undertook a programme of translocation. A daily capture log was provided by the consultants but no details of the applied methodology were available despite this information being requested. The trapping period comprised 24 visits during which a population of 172 viviparous lizards were captured and translocated to a country park situated approximately 3 km from the donor site.

The receptor site included approximately 10 ha of amenity land (sports pitches), semi-improved and marshy grassland along with secondary broadleaved woodland connected by a series of tarmac walkways. Two areas of the park were augmented with purpose-built hibernacula constructed from earth and inert rubble. The park was used by local residents for recreational purposes principally including dog walking and sports. Targeted surveys of the receptor site, undertaken by the consultants ahead of the translocation, apparently did not identify any existing populations of reptiles, but no details of the survey were available. The receptor area was not enclosed by physical barriers other than to the north, where residential housing bounded the site.

I undertook four post-translocation monitoring visits in years 1 (2013) and 3 (2015) (8 in total). Methods are provided in Section 2.3.3.

Site 2

In 2014, plans were submitted to redevelop a derelict railway depot. The site had been left derelict for over a decade, which had allowed typical brownfield habitats, such as scrub, tall ruderals and secondary birch woodland, to develop. The 4 ha site was bordered by an active railway line to the north and a river to the south. The development proposals required the clearance of the whole site and the loss of all habitats present.

An earlier survey of the donor site, undertaken by ecological consultants in September 2013, identified a ‘large’ population of viviparous lizards; no details of the earlier surveys were available. A peak count (the maximum number of adult lizards recorded during a single survey) of 16 viviparous lizards were recorded on two occasions, indicative of a medium-sized population based on Natural England (2011) criteria. Between mid-August and mid-October 2014, the consultants implemented a programme of translocation at the donor site, but detailed methodology of the translocation was not available. Over the course of 47 daily visits, a total of 102 viviparous lizards were relocated to an active golf course situated 8 km from the donor site. Although no translocation report was available, the consultants did state that a large number of gravid females were included within the relocated population (pers. comm.).

The lizards were released on a golf course in area of rough grassland, largely surrounded by amenity (mowed short) grassland. Beyond the release site, the habitats were typical of golf courses and included a mosaic of amenity and rough grassland, scrub, trees and open water; the total area of the golf course was greater than 100 ha. The release site was partially connected to the wider landscape by contiguous suitable habitats interspersed by short (c. 30 m) strips of amenity grassland. Prior to the release of the translocated lizards, the consultants carried out a survey of the receptor site comprising artificial cover objects and visual encounter techniques. The survey comprised seven visits during June 2014. Fifty artificial cover objects were placed within suitable habitat throughout the receptor site. The survey identified the presence of a small population (Natural England, 2011) of grass snake but no lizards.

The author undertook four post-translocation monitoring visits between April and May 2015.

Site 3

An area of railway sidings was scheduled for upgrades as part of Network Rail's ongoing improvements to the rail system. Typical of railway land, the sidings comprised a mosaic of bare ground, grassland, tall ruderals, scrub and secondary birch woodland. To facilitate the proposed upgrades, the entire site needed to be cleared.

Surveys of the donor site, undertaken by the developer's consultant in 2012, identified a population of viviparous lizards; no details of the survey were available. Between July and August 2012, the consultants erected a reptile exclusion fence and implemented a programme of translocation including 44 visits, but no detailed methodology for the translocation was available.   A total of 114 viviparous lizards, comprising 73 adults, 24 sub-adults and 17 juveniles were relocated to a nature reserve situated 25 km from the donor site.

The release area comprised a 21 ha restored grassland / wetland that was jointly managed as a surface water catchment area and a reserve for a range of taxa. The receptor site consisted of a series of large densely vegetated earth mounds set within a mosaic of rank grassland and scrub. These habitats extended beyond the receptor site to the north, east and south and there were no physical barriers to movement.   Populations of adders, grass snakes and slow-worm were known to be present at the receptor site ahead of the translocation but no viviparous lizards (pers. comm.).

The author undertook four post-translocation monitoring visits per year for three years (12 in total), beginning in 2013 and ending in 2015.

Site 4

In 2012, the site of a derelict garden nursery site was proposed for redevelopment to residential housing. The 12 ha plot of land contained predominantly brownfield habitat, with bare ground, tall ruderals, scrub and a large number of non-native ornamental species of flora (presumably a remnant of the land's previous use).

A survey of the donor site was undertaken by the developer's consultants in 2013, which identified populations of slow-worm, viviparous lizard and grass snake. In March 2013, the donor site was enclosed using exclusion fencing; 45 reptiles comprising 28 slow-worms, 15 viviparous lizards and two grass snakes were translocated to a country park 2.6 km from the donor site; no other methodological details of the translocation were available. Neither the original data nor the subsequent reports were available for review despite numerous requests for this information.

The receptor site, which had been fenced off to prevent public access, comprised a 1 ha mosaic of rough grassland, scattered scrub and secondary birch woodland. Three piles of brash had been created and were being used as a point of release for the reptiles. The wider release area consisted of pasture, rough grassland and walkways. The boundary fence would not prevent reptiles from migrating into or out of the receptor site.

In 2014 and 2015, the author undertook eight and six post-translocation monitoring visits respectively (14 in total).

Site 5

In 2012, government permission was granted for an existing Open Cast Coal Site (OCCS) to extend its extraction boundaries. The extension included two large fields of unmanaged grassland and an area of partially-vegetated earth mounds. Attached to the permission was a condition that a large vegetated overburden mound was reinstated to farmland, a process that would require the stripping back of vegetation and topsoil. Upon completion of the mining operations, all three areas were expected to be restored to low-level agriculture.

It is not known whether pre-translocation surveys of the donor site were undertaken; however, the site is subject to stringent environmental monitoring requirements and annual ecological surveys are a component of this monitoring. Between April and June 2012, 53 translocation visits were undertaken comprising primarily artificial cover objects. One hundred and fifty artificial cover objects were placed in suitable habitat and checked on a daily basis. A cumulative total of 111 reptiles, comprising 27 slow-worms and 84 viviparous lizards, were relocated to a receptor site.

The 1.3 ha receptor site was constructed on an area of previously worked and restored habitat within the quarry, situated approximately 1 km to the south-west of the operational site. A range of habitat types were present within the receptor site including sparse grassland, marsh and scattered scrub. To prevent translocated reptiles from wandering near to watercourse reinstatement works, a reptile exclusion fence was erected along the eastern and northern boundaries. No fence was located to the west or south, rather a densely wooded valley demarked the extent of the receptor site. Beyond the wooded valley was further suitable habitat comprising rough grassland and scattered scrub.

The author undertook 31 post-translocation monitoring visits to the release area between 2013 and 2015.

Site 6

In 2013, permission was granted for the redevelopment of a 15 ha portion of a 75 ha disused golf course (circa 20 %). The footprint of the development was focused on the north-east corner of the site and included a mosaic of bare ground, densely vegetated earth mounds and rough grassland.

Surveys of the donor site, undertaken by the developer's consultants in 2014, identified a large population of adders. Between April and August 2014, 45 adders were translocated by the consultant from the donor to the receptor site; no detailed methodology for the translocation was available.

Both the donor and receptor sites were located within the same disused golf course; however, they were separated by over 500 m of mixed habitats. The receptor site comprised a mosaic of rough grassland, scrub and secondary woodland, largely enclosed by amenity grassland. Three hibernacula were created in the receptor site by the consultants using brash and grass clippings. The wider release area included habitats typical of a golf course. Further details are provided in Chapter 3.

The author undertook six post-translocation monitoring visits during 2015.

Summary of Study Sites

Table 2.1: A summary of the study sites showing the size and species composition of translocated populations

Site	**N**	**N***				**Year of Translocation**	**Monitoring**	
		Zv	***Af***	***Nn***	***Vb***		**Year(s)**	**No. Visits**
Site 1	172	172	0	0	0	2012	2013, 2014	8
Site 2	102	102	0	0	0	2013	2014-2015	4
Site 3	114	114	0	0	0	2012	2013 - 2015	12
Site 4	45	15	28	2	0	2012	2013-2015	14
Site 5	111	84	27	0	0	2012	2013-2015	31
Site 6	45	0	0	0	45	2013	2014-2015	6

N – total number translocated; N* - breakdown of N by species; *Zv* – viviparous lizard, *Af* – slow-worm, *Nn* – grass snake, *Vb* – adder

2.3.3 Field Survey Protocol

Translocation

During the translocation, the consultants engaged to carry out the work were asked to take identification photographs from all individuals. All four widespread species reptiles found in the UK are readily recognisable from natural markings and scalation (Carlstrom & Edelstam, 1946; Sacchi et al., 2010). The identification of adders was based solely on the number and arrangement of cranial scales (frontal, parietals, supra-oculars and prefrontal scales). Both slow-worms and viviparous lizards have less pronounced scales and a combination of cranial and labial (upper and lower labials, pre- and post-oculars loreal scales) scalation and patterning was used to confirm identity. Grass snakes were identified using unique belly patterns located in the anterior third of the dorsal surface.

Post-translocation Monitoring

Following the release of the reptiles, a programme of post-translocation monitoring was undertaken at each receptor site. Where possible, the annual monitoring period was timed to match that of the translocation. The number of years of monitoring and ultimately the number of visits was dependent on the year of the translocation. A minimum of four visits per annum were undertaken at each site, which is considered sufficient to detect a species (if present) with a confidence level of 95% (Sewell et al., 2012).

To maximise the likelihood of detecting reptiles, the survey incorporated two distinct techniques during each visit; namely Visual Encounter Survey and Artificial Cover Object Survey. When used concurrently the combination of these two techniques greatly increases the detectability of native British reptiles (Sewell et al., 2013).

Visual Encounter Survey

A directed transect route was developed for each site, typically following the line of artificial cover objects (see below) but deviating to incorporate suitable habitat foci such as south-facing banks. Although the routes were kept consistent, the order and direction in which they were followed between visits were varied. The length of the transects was determined by the size and accessibility of each site.

Artificial Cover Object Survey

The artificial cover objects (0.5 m^2 pieces of tin or felt) were selectively placed within suitable habitat and, where possible, in close proximity to habitat foci such as south-facing banks, dense patches of scrub or piles of rubble; those placed in large open areas are less effective than those adjacent to patches of cover (Natural England, 2011). Once placed, the artificial cover objects were left to settle in for a minimum of two weeks before the first check in accordance with published recommendations for effective survey (Edgar et al., 2010). The density at which cover objects were installed was noted and in all cases it exceeded 10 per hectare of suitable habitat (Froglife, 1999).

2.3.4 Data Analysis

Individual reptiles were re-identified using a combination of head scalation and colour patterns. Using this process, I was able to determine the number of reptiles and proportion of the population that remained within the receptor site during the post-translocation monitoring.

A Kruskal-Wallis test was used to assess whether the number of recaptures differed between species. This analysis was restricted to slow-worm and viviparous lizard, both of which were recorded from multiple sites. Interactions between the number of animals moved (N), the number recaptured (R) and the size of the release site were tested for using multiple regression.

2.4 Results

Very few translocated individuals were detected after their release (Table 2.2). This trend of low recaptures was consistent across all study sites with little variation. The mean number of reptiles translocated per site was 98 (SE 19.61), of which on average 1.5 (SE 0.72) or 1.6% were recaptured at the receptor sites during the monitoring. No recaptures of any translocated reptiles were made at three of the study sites, which were subject to between four and 12 monitoring visits over the course of the monitoring. The paucity of recaptures precluded the generation of meaningful Capture-Mark-Recapture (CMR) estimates of abundance and of body condition assessments.

Table 2.2: A summary of recapture data by site

Site	Species	N	R (%)	Recapture N			Residents N				Notes
				Year 1	*Year 2*	*Year 3*	*Af*	*Zv*	*Nn*	*Vb*	
Site 1	*Zv*	172	0	0	0	0	0	0	0	0	It was evident that the receptor site was subject to annual flooding. Aquatic plant species were recorded growing on the hibernaculum.
Site 2	*Zv*	102	0	0*	-	-	0	0	0	0	*An average of seven yearling lizards (range 0 – 10), presumed to have been born of translocated females, were recorded per survey visit
Site 3	*Zv*	114	0	0	0	0	9	0	2	3	Viviparous lizards have been recorded in other areas of the site although whether they were translocated is unknown
Site 4	*Zv*, *Af*, *Nn*	45	4 (8.9)	3 (*Af*)	3 (*Af*)**	-	24	3	1	0	The consultant's pre-translocation surveys of the receptor site did not report the presence of reptiles
Site 5	*Zv*, *Af*	111	3 (2.7)	3 (2 *Af*, 1 *Zv*)	0	2 (*Af*)	30	31	0	0	The developer was unaware that reptiles had colonised the receptor site ahead of the translocation
Site 6	*Vb*	45	2 (4.4)	2 (*Vb*)	-	-	0	0	0	16	The consultant's surveys identified a resident population of adders within the receptor site

N – number translocated; R - total number recaptured; *Af* – slow-worm, *Zv* – viviparous lizard, *Nn* – grass snake, *Vb* – adder; ** two individuals - one individual was captured on two occasions

The size of the translocation (N) appears to influence the number of recaptures (R); however, the response is not consistent between species (Figure 2.1). No significant relationships were detected between N, R and the size of the receptor site.

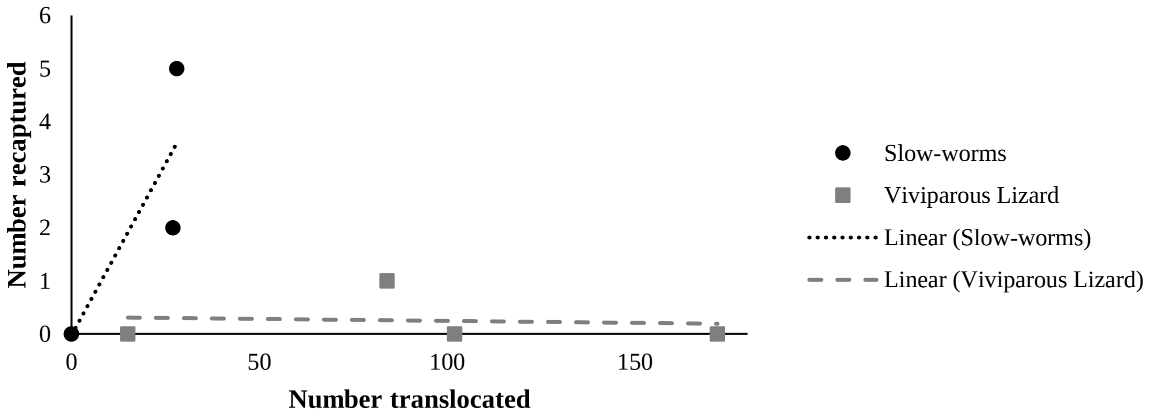

Figure 2.1: The number of recaptures (R) appears to decrease with the number of animals translocated (N)

The observed recapture rates were influenced by species composition (Figure 2.2). The most frequently translocated species was the viviparous lizard, which occurred at five out of six sites. Each translocation of the species averaged 97.4 (range 15 - 172) individuals, of which on average 0.2 (SE 0.2) were recaptured. The second most frequently translocated species was the slow-worm, which occurred at two sites. Slow-worm translocations averaged 27.5 individuals (SE 0.5) with mean recapture rates of 3.5 (SE 1.5) individuals. A Kruskal-Wallis test detected a significant difference between the relative number of slow-worms (range 2 – 4) and viviparous lizards (range 0 - 1) that were recaptured ($H_{(1)} = 4.565$, $P = 0.03$). Slow-worms were more than twice as likely to be recaptured than viviparous lizards. Insufficient translocations of grass snake and adder were undertaken to enable a comparison for these species.

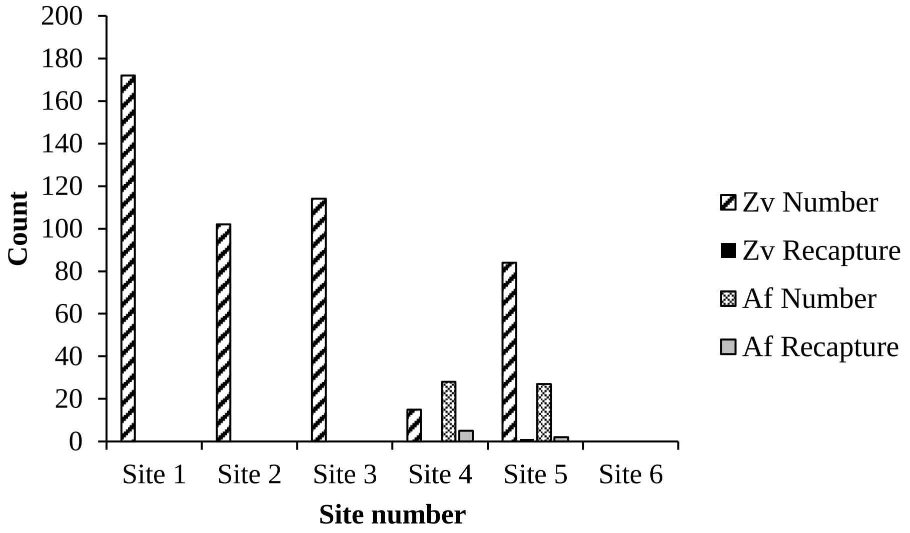

Figure 2.2: The number (N) of animals translocated and subsequently recaptured (R) was influenced by species. A greater number of viviparous lizards were translocated but fewer recaptures were made. *Zv* – viviparous lizard, *Af* – slow-worm

2.5 Discussion

All of the translocations were different in terms of the species and numbers of animals involved, the habitat compositions of both donor and receptor sites and their geographic location. Despite this variation, all were 'typical' examples of mitigation practices in the UK, rather than controlled before-after experiments, which may have improved the design and yielded more consistent results; however, these would not have reflected current practice. All cases involved consultants relocating a population/community of reptiles to a release area to facilitate development. Overall, some 589 reptiles were translocated to the six receptor sites, of which nine animals (1.5%) were subsequently recaptured during three years of post-releasing monitoring. Indeed, no recaptures were made at all at three of the six sites.

There are four possible explanations for the observed recapture rates: 1) the translocated reptiles perished following release (including overwintering mortality); 2) the monitoring failed to detect the translocated individuals; 3) animals were captured but could not be reliably identified; or 4) the reptiles migrated away from the release site (post-translocation dispersal).

Many studies have reported high mortality rates post-translocation (Plummer & Mills, 2000; Germano & Bishop, 2008; Germano et al., 2015). Contributory factors have included an inability to locate suitable habitat features such as hibernacula (Reinert & Rupert, 1999; Plummer & Mills, 2000), overwintering mortality (Reinert & Rupert, 1999), increased persecution (Fischer & Lindenmayer 2000; Nowak et al., 2002) and predation (Lee & Park, 2011). The remains of two juvenile adders were recovered from near the release site on Site 6. The heads and tails had been removed making it impossible to ascertain whether they were part of the translocated population; however, the damage clearly indicated an attack by a mammalian predator. It is highly likely that scavengers would quickly remove evidence of any predation making detection unlikely (Santos et al., 2011).

Reptiles are a particularly cryptic group of animals that can be notoriously difficult to detect in the wild (McDiarmid et al., 2012). It is well known that detectability of reptiles is influenced by a wide range of factors including climate (Kéry et al., 2009; Sewell et al., 2013), population size (Tanadini & Schmidt, 2011) and seasonal variation (Sewell et al., 2012). Lack of observations may therefore be due to either true absence or non-detection of animals that are actually present. Using VES data, Kéry (2002) suggested that 26 visits were required to declare a site free from grass snake with 95% confidence. A more recent model, using detection probabilities generated through both VES and ACO data, has estimated that just five surveys (95% CI: 4.2 – 7.0 surveys) may be required to detect grass snakes. Between one and three visits are sufficient to detect slow-worms (95% confidence), assuming Sewell et al. (2012) detection probability estimates of between 0.83 and 0.91. Given the lower detection probabilities ascertained for viviparous lizards (0.59 to 0.67), a greater level of survey effort (three – four surveys) is required to detect the species (95% confidence). Post-translocation monitoring effort for all sites was sufficient to detect viviparous lizards (if present). Viviparous lizards are likely (95% confidence) to be absent from Sites 1 and 3. Clearly the survey effort required to detect particular individuals of each species is likely to be an order of magnitude higher than the survey effort needed to reliably detect whether the species is present or not.

To date, there have been few studies of how translocation influences individual detectability. Sealy (1997) suggested that translocated timber rattlesnakes (*Crotalus horridus*) were more wary of people, and therefore less detectable, than resident conspecifics. However, this study was based on incidental sightings rather than a standardised comparison of detection rates. No significant differences between the detectability of resident and translocated adders was identified in the current study (see Chapter 3). In the current study, translocated slow-worms were more frequently encountered than viviparous lizards. Whether this was the result of higher detectability of slow-worms (Sewell et al., 2012) or because slow-worm are more sedentary than viviparous lizard is unclear. A slow-worm translocated on Site 5, was recorded during years 1 and 3 of the monitoring but not in year 2. This indicates that translocated reptiles are able to remain undetected within the receptor site for a year or more.

The re-identification of reptiles was based on the comparison of photographs showing the unique scalation and marking patterns (see Section 2.3.3). As the reptiles were released immediately after processing (both during the translocation and monitoring), the inspection of photographs was undertaken at a later time. As such, positive identification was largely dependent on the quality of the photograph. As a small number of the consultant's photographs were of poor quality, it is possible that a correspondingly small number of reptiles were misidentified.

Tomović et al. (2008) describe instability in head scalation patterns that could result in the misidentification of reptiles. Although the study involved *Vipera ursinii*, the authors suggest that the adder's head scales are likely to be subject to oligomerisation (multiple scales fusing into one). However, long-term monitoring of reptiles in the UK does not support this

(Phelps, 2004). Multiple groups of scales were analysed in the current study, reducing the influence of scale modification on individual identification.

Post-release dispersal has been shown to greatly influence the outcome of translocations (Tuberville et al., 2005; Stamps & Swaisgood, 2007; Germano & Bishop, 2008; Knox & Monks, 2014). The paucity of recaptures reported here could be explained by the migration of reptiles away from the release area. Sites 3, 4 and 5 were immediately bordered by suitable habitat and lacked physical barriers to movement. Sites 2 and 6 were situated adjacent to but not directly connected with suitable habitat. Although clearly a plausible explanation for the low recapture rates, there is little direct evidence for post-translocation dispersal here; post-translocation monitoring was extended beyond the receptor site at sites 3 and 5 but no recaptures were observed. However, of the 45 adders translocated from site 6, seven were fitted with a radio tag and tracked for a period of 10 days. All three male adders fitted with a tag migrated away from the release site (see Chapter 3). In contrast, all four translocated females remained within the release area. In 1995, 104 slow-worms were translocated from a development site in Canterbury to Bus Company Island (BCI); see Chapter 4 for further details. BCI is unique amongst the study sites in that it is almost entirely enclosed by a physical barrier to movement - the Great Stour river. High recapture rates (60%) were recorded for several years following the release (Platenberg & Griffiths, 1999). A monitoring survey of the descendants of this founder population has also reported higher recapture rates: of those captured, 50% were caught on more than one occasion whilst 10% were caught on more than three occasions (Chapter 4). In this instance, the presence of physical barriers appeared to have increased site fidelity, which accords with studies of artificially penning translocated reptiles (Knox & Monks, 2014).

Post-release dispersal, like mortality, reduces the number of individuals available for detection within a population. Although the consequences of emigration are varied, they are often negative. Migrating reptiles could be forced to occupy unsuitable adjacent habitats (sites 1 and 2) or sites including those earmarked for future development. At Site 6, two translocated male adders migrated from the release site back to the proposed development. Equally, migrating individuals could settle suitable adjacent habitats (Site 3 for instance). Either way, individuals that migrate away from the release site will not contribute either demographically or genetically to the population (Le Gouar et al., 2012).

Finally, dispersing individuals face higher risks of predation (Bonnet et al., 1999). Post-translocation dispersal ultimately results in smaller populations, which are more likely to become extinct. Two of the study translocations involved relatively small numbers of reptiles (45 individuals); if most of these disperse from the release site then the chances of establishing a population are reduced. Using the criteria contained within the HGBI (1998) guidelines, small and medium populations of slow-worms and viviparous lizards were relocated respectively. If even a small proportion of these populations migrated away from the receptor site, the remaining individuals could be insufficient to maintain a viable long-term population.

Factors influencing post-release dispersal are varied but it has been suggested that habitat quality is a key factor (Griffiths et al., 1989; Owen-Smith, 2003; Nafus et al., 2017). Stamps and Swaisgood (2007) proposed the Natal Habitat Preference Induction (NHPI) hypothesis as a driver of migration. The theory states that animals exhibit strong preferences for habitat types present within their natal home ranges. Once these animals have been translocated, they have difficulty in assessing the quality of unfamiliar habitats, particularly those that lack stimuli encountered within their natal habitat. This uncertainty causes the animals to search for habitats comparable to those of the natal habitat. Although it is difficult to objectively assess habitat quality (Wolf et al., 1998), it is relatively straightforward to assess habitat structure using the JNCC (2010) guidance. None of the purpose-built receptor sites described above replicated the habitat types present within the donor site and this could have contributed to higher levels of dispersal. Data gathered from Site 2 accords with predictions made by the NHPI theory. The translocated population of viviparous lizards included a large proportion of gravid females. No adult lizards were encountered during the monitoring, as would be expected given the contrast in habitats between the donor and receptor sites; however, a large number of (yearling) juvenile lizards were observed. Juvenile lizards are not born with an imprint of their parent's natal habitat and would not be compelled to migrate away from the release site. The success of translocations could be improved through the inclusion of gravid females immediately prior to parturition, or by temporarily confining gravid females until after giving birth. Indeed, it has been suggested that when dealing with species that exhibit strong philopatry, it could be beneficial to release younger individuals (Gill 1979; Bloxam & Tonge 1995; Semlitsch 2002; Tocher & Brown 2004; Germano & Bishop, 2008). It has been demonstrated that juvenile dispersal decreased with increased maternal corticosterone (i.e. stress) levels (Meylan et al., 2001); however, the neonates were significantly smaller. Further studies into effect of stress on unborn young would be required before encouraging this approach. Currently, published guidance discourages the translocation of gravid reptiles (Natural England, 2011).

Another factor that is likely to affect post-release dispersal is competition for resources. Translocated reptiles are typically released at a single point within the receptor site, a hibernaculum for instance. This aggregation would result in high levels of intraspecific competition that would be greatest when large populations are moved. As has been demonstrated above, the larger populations resulted in the fewest recaptures, which would accord with expectations of higher competition. An alternative approach could be to prepare multiple release points spread out across a receptor site.

All of the receptor sites were surveyed by professional ecologists before the translocations. Three of the sites (i.e. sites 1, 4 and 5) were assessed to be free from reptiles entirely; two sites were assessed to be free of the translocated species (i.e. site 2 and 3); and one site (i.e. site 6) was known to support a resident population of the relocated species. However, the observation of unmarked animals at both Sites 4 and 5 indicates either a resident population that was missed and/or rapid natural colonisation at the same time of the translocation. Unless the existing population contains so few animals to be non-viable without supplementation, the introduction of additional animals is likely to have negative effects. Carrying capacities are likely to be exceeded resulting in increased competition for resources. Moving individuals between populations may increase the transmission of diseases and swamp locally adapted alleles if carried out over large distances (Natural England, 2011). In the case of Site 5, a large community of reptiles (n = 111) was introduced to a relatively small and partially enclosed area (< 1 ha). The introduction of these additional individuals is likely to have adversely effected the resident population through an increase on competition for resources.

2.5.1 Future Studies

The greatest difficulty in assessing the effects of translocation is the paucity of detailed, long-term monitoring datasets. Future monitoring programmes should seek to ascertain more than simple qualitative (presence/absence) data. Monitoring needs to be able to differentiate between the relative impacts of natural colonisation versus the translocation, and distinguish between mortality and dispersal. Techniques to re-identify individuals are readily available and should be applied to simple experiments designed to assess movement and distribution. In the absence of radio-telemetry data, such experiments would provide valuable insights to how individuals respond to translocation. However, it is likely that individual recapture rates will be very low and an intensive survey effort would be required to achieve the required levels of detectability.

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Chapter 3: Spatial Ecology of Translocated Adders (*Vipera berus* L.): A Case Study

3.1 Summary

Driven largely by a State's legal framework, the translocation of snakes is both common and widespread. However, the same frameworks often lack legal impetus to record the practice or undertake post-translocation monitoring. This paucity of monitoring has limited our opportunities to examine how snakes respond to relocation.

In 2014, a population of adders was translocated from a development site located in Essex, UK. A subset of the translocated population was fitted with external radio tags and tracked for a period of 10 days in April. A further eight adders, including both translocated and resident individuals, were tracked for 10 days during August. This was coupled with traditional surveys (visual encounter and artificial cover object) in 2015.

Adders, like other viperids, exhibited significantly increased movement and range size post-translocation, although the effect was most pronounced in males. Translocated males (n = 3) undertook long-distance, unidirectional movements away from the receptor site; in contrast, all telemetered females (n = 8) remained within the receptor site. Translocated males maintained home ranges over 16 times larger than resident conspecifics. The core ranges of resident males and both resident and translocated females was aggregated into three discrete groups within the receptor site. Although there was no overlap between the groups, there was considerable overlap within the groups.

When designing receptor sites for adders, it is important to provide sufficient area to account for the increased movements and home ranges. Male adders crossed areas of unsuitable habitat (e.g. grass fairways), which has implications for the siting of receptor sites.

3.2 Introduction

As described in Chapter 2, the practice of translocating snakes in response to human-wildlife conflicts appears to be pervasive. There is no reliable method of determining the annual number of translocations involving snakes; however, a review of the available literature indicates that the practice is both widespread and frequent (Hardy et al. 2001; Nowak et al. 2002; Germano & Bishop, 2008; Lee & Park, 2011; Barve et al., 2013; Germano et al., 2015). The drivers behind this often costly exercise can be broadly categorised into two categories: 1) the removal of 'problem species'; and 2) compliance with national or regional legislation.

Problem species have the potential (or, in many cases, are perceived to have the potential) to cause harm to humans or their livelihood (Plummer & Mills, 2000; Hardy et al., 2001; Butler et al., 2005; Brown et al., 2009). The majority of post-translocation studies relate to problem snake species. Many of these studies originate from areas with burgeoning human settlements that support an abundance of prey species (Barve et al., 2013). Such studies have provided the greatest insight into how snakes respond to translocation on a species, population and individual level.

Many species of snake exhibit clear and predictable annual movement patterns (Plummer & Mills, 2000; Phelps, 2004). This implies that snakes are aware of both the spatial and temporal availability of local resources. Snakes possess a range of sensory systems including visual, chemosensory, thermal, tactile and magnetic (Reinert, 1993). A recent study demonstrated that Burmese pythons (*Python molurus bivittatus*) also possess a 'compass' ability enabling them to home from great distances (Pittman et al., 2014). It is likely that snakes utilise multiple senses concurrently in orientation (Stone et al., 2000). Celestial and compass orientation are clearly more effective over large distances, whilst the recognition of visual and chemical cues are more likely to be utilised within the individual's home range. The absence of well-known landmarks could disorientate the snake forcing individuals to spend a greater proportion of their time searching for resources (Nowak et al., 2002; Hare & McNally, 1997). In a comparison of translocated and resident hognose snakes (*Heterodon platirhinos*), Plummer and Mills (2000) reported similar average daily movements but significantly higher levels of variability in the movements of translocated individuals. Similar erratic movements have been reported for translocated timber rattlesnakes (*Crotalus horridus*) (Galligan & Dunson, 1979; Reinert & Rupert, 1999). Such short, erratic movements have been attributed to exploratory behaviour (Plummer & Mills, 2000).

In addition to increased erratic movements, translocated snakes may range considerably farther than resident conspecifics. Translocated timber rattlesnakes travelled on average three times farther and occupied home ranges ten times larger (Reinert & Rupert, 1999). This pattern of increased movements and extended home ranges following translocation is repeated across a wide range of species including tiger snakes (*Notechis scutatus*) (Bulter et al., 2005), king cobras (*Ophiophagus hannah*) (Barve et al., 2013), Amur rat-snakes (*Elaphe schrenckii*) (Lee & Park, 2011) and western diamond-backed rattlesnakes (*Crotalus atrox*) (Sullivan et al., 2015). Long-distance, unidirectional movements are suggestive of philopatry (Plummer & Mills, 2000; Nowak et al. 2002; Brown et al. 2009). Indeed, homing behaviour is widespread amongst snakes (Butler et al., 2005; Brown et al. 2009; Pittman et al., 2014; Burger & Zappalorti, 2015). Long-distance movements are likely to be more prevalent in species that exhibit strong homing behaviours (Sullivan et al., 2015).

Locomotion is energetically expensive, particularly so when it results in a behavioural shift from foraging to exploration. The combination of increased movements and reduced foraging may result in a decrease in body condition (Reinert & Rupert, 1999). Increased movements have also been associated with elevated risks of mortality (Andren, 1985; Madsen & Shine, 1993; Plummer & Mills, 2000; Butler et al., 2005). Highly mobile individuals are more likely to encounter predators or enter high-risk areas (Andren, 1985; Madsen & Shine, 1993; Shine & Fitzgerald, 1996). In a review involving six species of snake, Bonnet et al. (1999) reported that the highest levels of mortality were in dispersing neonates, males undertaking mate searching and females migrating to egg-deposition sites. Similarly, young adders experienced mortality rates of between 88% and 92% whilst undertaking dispersal (Prestt, 1971; Phelps, 2004). In addition to increased movement, post-translocation monitoring has identified a range of factors that have contributed to increased rates of mortality (Table 3.1).

Table 3.1: Comparative mortality rates of translocated snakes

Species	N	Mortality (%)	Cause(s)*	Source
C. horridus	11	55	Predation (2), overwintering (3), disease (1)	Reinert & Rupert (1999)
H. platirhinos	8	63	Predation (4), unknown (1)	Plummer & Mills (2000)
C. atrox	9	50	Unknown (5)	Nowak et al. (2002)
N. sipedon	10	70	Unknown (7)	Roe et al. (2010)
E. schrenckii	11	27	Predation (2), unknown (1)	Lee & Park (2011)

* The parentheses delineate the number of individuals affected from each study

Many of the above examples describe ‘long-distance translocations’; that is, relocations of animals well beyond the expected ranging distance of the species involved (Hardy et al., 2001). In contrast, ‘short-distance translocation’ is the movement of snakes within their home range. Retaining individuals within their home range should mitigate any increases in movements. To test this, a number of studies have investigated whether the distance moved influences behavioural response (Sealy, 1997; Hardy et al., 2001; Brown et al., 2009). The results of these studies have been mixed and dependent on how success was measured. Sealy (1997) described the application of short-distance translocation to timber rattlesnakes occupying a North Carolinian state park. Snakes were collected from highly populated areas and moved up to 300 m to suitable habitat. Very few of the translocated snakes returned to the point of capture or other highly populated areas. Of those that did return, the snakes appeared to be warier of humans resulting in fewer encounters. Given the reduction in rattlesnake encounters and the apparent absence of adverse effects, Sealy (1997) concluded that short-distance translocation was a beneficial management tool. Further support for short-distance translocation was reported by Hare and McNally (1997) who recorded comparably low recapture rates for tiger rattlesnakes (*Crotalus tigris*). However, both Hardy et al. (2001) and Brown et al. (2009) disagreed with this conclusion, reporting that 39% of black-tailed rattlesnakes (*Crotalus molossus*), 56% of western diamond-backed rattlesnakes and 87.5% western rattlesnakes (*Crotalus oreganus*) returned to ‘conflict areas’. Brown et al. (2009) ascribe Sealy’s (1997) and Hare and McNally’s (1997) low recapture rates to imperfect detection associated with purely observation-based surveys. However, Brown et al. (2009) did record a reduction in the extent of movements when contrasted against individuals subjected to long-distance translocation. As such, both Sealy (1997) and Brown et al. (2009) acknowledge that short-distance translocation would work well as a short-term solution to problem species. Hare and McNally (1997) and Hardy et al. (2001) both refused to endorse short-distance translocation as a management technique with the former reporting higher levels of mortality. Both short- and long-distance translocations have advantages and limitations (Table 3.2).

Table 3.2: A Comparison of short- and long-distance translocations

Advantages	Disadvantages
Short-distance Translocation	
The shorter captivity and transport times will help to minimise stress and associated mortality	There will be fewer potential receptor sites available, which might result in a poorer choice of site
Species with large home ranges are less likely to be displaced	Philopatry could result in animals moving back into areas inappropriately
The risk of disease transmission between populations will be minimised	
Long-distance Translocation	
Greater choice of high quality receptor sites	Reduction in local species populations
Translocations can benefit conservation through targeted (re)introductions	Increase in competitive pressures on species already present at receptor site
Philopatry unlikely to result in inappropriate returns to donor sites	Increased risk of moving species out of their natural range (post-release dispersal)
	Increased stress through longer captivity periods
	Increased risk of disease transmission to new areas
	Loss of locally adapted alleles

Europe does not support the number of problem snake species that are found in the Americas or Australasia. Moreover, current legislative guidance (see http://jncc.defra.gov.uk/page-1359) focuses the need for post-translocation monitoring on EPS (of which very few are snakes). As such, there is a paucity of studies describing how European species respond to translocation. Given that many of Europe's snake species are in decline (Reading et al., 2010) and there is increasing emphasis on conserving the remaining populations *in situ*, understanding the implications of translocations is important. One species in particular, the adder, is frequently subjected to translocation throughout mainland Europe and UK (Kyek et al. 2007; Whiting & Booth, 2012; Herpetologic, 2013). In the UK, the adder is a wide-ranging species and naturally occurs at low population densities when compared to the lizards (HGBI, 1998; Froglife, 1999). As a result, the majority of translocations involve only small numbers of individuals. Current guidance considers the relocation of small numbers of non-

European Protected Species to be a ‘Minor (non-significant)’ adverse effect (CIEEM, 2016), an assessment that rarely requires post-translocation monitoring.

3.2.1 Objectives

Much of our understanding of how snakes respond to translocation originates from studies involving problem species. In contrast, very few studies have investigated how translocation affects the UK’s snakes. To address the continued decline in adder populations (Reading et al., 2010; Wilkinson & Arnell, 2013), it is important to establish how snakes respond to translocation. Within this chapter, I sought to establish whether adders, like other viperids, respond to translocation through:

- An increase in daily movement patterns;
- An increase in the maximum distance moved;
- The maintenance of a significantly larger home ranges; and
- Decreased detectability post-translocation.

3.3 Methods

3.3.1 *Study Site*

The selection of a study site was based on the following criteria:

- The site supported a population of adders with a range of life-history stages;
- The site will be subject to development, either partially or fully, within the anticipated timescales of this study; and
- Access to the receptor site would be permissible following the release of the translocated adders.

Only a single site achieved the above criteria. The site, a disused golf course located in Essex, UK, comprised a mosaic of amenity and rough grassland, scrub, woodland, open water and bare ground. The habitat types present were mapped (Figure 3.1) following the protocols set out by the Joint Nature Conservation Committee (2010).

Figure 3.1: The map depicts the habitat types present prior to development. Although the site has been closed to the public, the habitats continue to be managed as an active golf course.

Planning permission was granted by the District Council for the redevelopment of a 15 ha portion of the 75 ha site (circa 20 %). The approved development plans included the construction of 350 residential dwellings with associated infrastructure (i.e. road upgrades, a cafe, a GP surgery *etc*.). The footprint of the development is focused on the north-east corner of the site; the remaining land is either to be retained as a golf course (14 ha) or re-graded and landscaped to become a country park (46 ha) (see Figure 3.2). Although the principal function of the country park is to provide residents with accessible 'open space', it will also be utilised as a receptor site to accommodate displaced wildlife. Habitat located at the south, farthest away from the residential development, will be less intensively managed to enable a denser and more heterogeneous vegetation structure to develop.

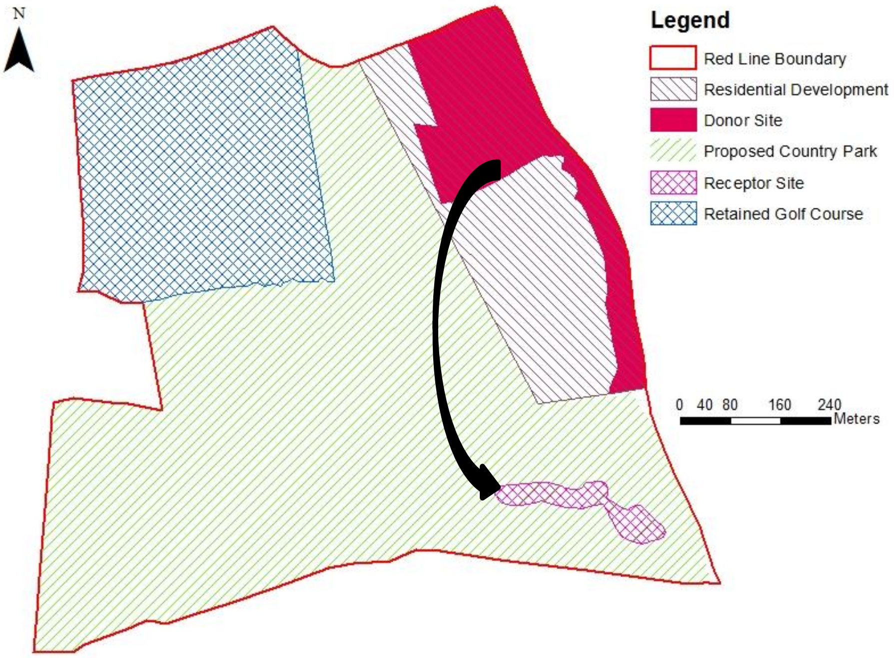

Figure 3.2: Map showing areas to be developed (residential), retained as a golf course and area converted in to public open space (proposed country park). The arrow shows the direction of movement of adders from the donor to the receptor site.

Donor Site

Prior to redevelopment, the donor site comprised a highly disturbed mosaic of rough grassland, bare ground, scrub, earth mounds and open water. Surveys confirmed that the earth banks, which included large south-facing aspects, were utilised by adders as hibernacula. The donor site was well-connected to the wider landscape by both rough grassland and scrub. Predevelopment surveys of the donor site confirmed the presence of a population of adders (a peak count of 24 individuals was achieved in a single survey), principally from within the footprint of the development. The consultant's report suggests that the site supports one of the 10 largest adder populations in Essex (Herpetologic, 2013).

Receptor Site

The receptor site was located between 500 m and 650 m to the south and comprised rough grassland, scattered scrub, tall ruderals and secondary broadleaved woodland. Due to infrequent management, the rough grassland had developed a layer of thatch at its base. The receptor site was connected to the donor sites by contiguous habitat but largely enclosed by amenity grassland. Surveys of the receptor site, undertaken prior to the translocation, identified a resident population of adders. The receptor site was enhanced through the construction of three discrete hibernacula and several piles of brash. Both the hibernacula and piles of brash used vegetation gathered through site clearance operations.

3.3.2 Experimental Design

The translocation commenced in April 2014 and lasted over two months. It was anticipated that, prior to the commencement of the translocation, an exclusion fence would be erected around the boundary of the proposed development. However, the installation of the fence was delayed until August 2014 - several months after the translocation had commenced.

Based on data presented by Phelps (2004), male adders typically range up to distances of 400 m. As the receptor site was situated over 500 m from the donor site, the translocation was assessed to be ‘long-distance’.

Radio Telemetry

Two ten-day blocks of tracking were undertaken; the first during spring (April 2014) and the second during late-summer / early-autumn (August – September 2014).

The incumbent consultants began relocating the adders following emergence from hibernation. During this period, 45 adders of varying life stages were released at the receptor site. A range of morphometric measurements were collected from these adders along with photographs of head patterns and scalation.

Eight of the 45 translocated adders were fitted with a radio tag. Brander & Cochran (1971) and Cochran (1980) recommend that the weight of a tag should not exceed 5% of the total mass of the individual. In this instance, the combined weight of the tag and attachment medium was 2 g. To ensure compliance with this recommendation and to minimise the risk of causing impaired movement, only adders that weighed in excess of 40 g were utilised. Freshly sloughed adders were selected to minimise the risk of the tag becoming dislodged. Prior to the attachment of the tags, each individual was examined for external parasitic loads or recent wounds; those that exhibited injury or poor condition were excluded from the study to prevent further stress. The processing and study of adders was undertaken in strict accordance with the University of Kent’s Ethics Policy, itself compliant with guidance from the Association for the Study of Animal Behaviour (2006).

A Yagi flexible three tier antenna (173 MHz) was coupled with a SIKA radio tracking receiver (138-174MHz). Bespoke 1.1 g PicoPip tags (specification: pulse length 20 ms; 50 pulses per minute, battery life 59 days from production; 10 cm antenna) were utilised. This specification was assessed as appropriate given the adder's terrestrial existence where potential buffers to the signal abound. The tag attachment method was based on Gent and Spellerberg (1993). This approach has been successfully applied to the tracking of adders in Britain and is well-suited to short-duration studies (Ujvari & Koros, 2000).

Adders were placed in long thin plastic tubes to both control the animal and minimise the risk of envenomation. The radio-tag was positioned immediately anterior of the cloaca, on the dorso-lateral surface, slightly offset to the right by 45° from the dorsal surface. The site of attachment was cleaned using standard surgical spirit to remove dirt and loose skin particulates that would compromise the adhesiveness of the tape. Once completely dry, a 4 cm strip of water-resistant surgical tape was applied to the skin. The tape was oriented parallel with the body and covered less than 40% of the circumference to enable the movement of material from the animal's gut to the cloaca. The tag was superglued to this basal layer before a further strip of surgical tape was applied over the tag to minimise drag when moving through dense vegetation (Figure3.3). It has been demonstrated that occasional handling does not affect behaviour (Brown et al., 2009).

Figure 3.3: A tagged adder within a restraining tube

The eight snakes were tracked for a period of 10 days following release. The location of each snake was recorded on three occasions each day: morning (08:00 – 10:00), afternoon (13:00 – 15:00) and evening (18:00 – 19:00). The frequency of sampling was balanced against the risk of causing disturbance; Ujvari and Koros (2000) recommend at least two hours between sampling viper species to allow the resumption of original behaviours. The location of the adders, or point of strongest signal where they were not observed, was recorded to the nearest square meter using a handheld GPS device (Garmin™). The GPS devices were capable of recording with a 4 m^2 resolution.

A further 10-day tracking period was undertaken in late August. Four resident and two translocated adders were tracked in the receptor area as described above. It was hoped that a greater number of translocated adders would be tracked during August.

One hundred and twenty-five artificial refuges (43 ha^{-1}), comprising sheets of tin, felt and carpet, were placed within suitable habitat throughout the receptor site and the surrounding areas. Six checks, using artificial refuges only, were undertaken in 2015 to ascertain which, if any, adders remained within the receptor site.

3.3.3 Data Analysis

A maximum of 30 sample occasions for each animal were recorded; however, several tags detached or malfunctioned resulting in fewer fixes for those individuals. Those adders with fewer than 15 sampling occasions were excluded from range analysis.

Movements were measured as a straight line between successive locations; in reality, these measurements would be underestimates as snakes rarely travel in a straight line (Whitaker & Shine, 2003). Snakes were scored as ‘active’ when the distance moved exceeded 4 m, the minimum resolution of the GPS device. Upon completion of each 10-day study, three measures of activity were calculated: total distance, average distance and maximum distance per sample occasion. Data were log-transformed to meet the assumptions of normality and compared using independent samples *t*-tests.

The 100% Minimum Convex Polygon (MCP) and 95% and 50% harmonic means were calculated using BIOTAS® *v.* 2.0 (Ecological Software Solutions, 2005). The MCP is the smallest possible area that captures all of the recorded locations or survey points and is, therefore, a useful measure of Total Range (Ujvari & Koros, 2000). It does not, however, differentiate between the areas repeatedly utilised by snakes and those passed through on a single occasion. Many species of snake exhibit erratic movements following translocation and the MCP estimate is likely to include ‘outlying’ points (Reinert, 1991; Butler et al., 2005). However, the importance of knowing the total range of adders when assessing the impacts of translocation is clear. Following Butler et al. (2005), the 95% and 50% harmonic means were calculated as a proxy for 'home' and 'core' ranges respectively. Maps were drawn using ArcGIS (*v*.10.3) (ESRI, 2014). I compared the means of MCP, home and core ranges of translocated and resident adders using one-way ANOVA. Where necessary, the data were log-transformed to meet the assumptions of normality.

To supplement the relatively small range datasets, four resident adders from a different site were tracked at the RSPB's Minsmere Reserve, Suffolk, UK. The four adders, comprising two males and two females, were tracked for a period of 15 days in April 2015. The datasets were tested for differences between the two resident populations using an independent samples t-test (t = 1.385; P = 0.398) and subsequently pooled. As the method of data collection was not strictly aligned, data were used for range analyses only.

To test Sealy's (1997) assertion that relocated snakes become warier of people (and therefore less detectable), I compared the frequencies that telemetered resident and translocated snakes were observed. A 'test of equal proportions' was used to test whether the frequency of sample occasions where each snake was observable differed significantly between translocated and resident groups. Data were pooled by status: translocated (Group 1) and resident (Group 2).

$$W = \frac{P_1 - P_2}{\sqrt{\frac{P(1-P)}{n_1} + \frac{P(1-P)}{n_2}}}$$

Where n_x is the number of survey occasions for group x, P_x is the proportion of snakes observed in group x and P is the weighted average of the pooled data. P is calculated as follows:

$$P = \frac{n_1 P_1 + n_2 P_2}{n_1 + n_2}$$

With α set at 0.05, the null hypothesis was rejected when $W < -1.96$ or > 1.96.

The habitat used by telemetered adders was recorded. As snakes select habitat based on structure rather than species composition (Reinhert, 1993), the following broad categories were used:

- amenity grassland (sward length ≤ 10 cm);
- rough grassland (sward length > 10 cm);
- tall ruderals (i.e. tall, non-woody plants);
- scrub (including woody plants); or
- woodland.

The mean proportion of habitat types within the MCP was calculated and compared using a test of equal proportions. The MCP was selected over the home or core range as it represents the areas actually occupied rather than an extrapolation of areas potentially used, which in this instance would include extensive areas of amenity grassland.

3.4 Results

Fourteen adders, comprising ten translocated and four resident individuals, were tracked during 2014. Following a series of tag malfunctions, data were collected from 11 individuals including seven and four translocated and resident adders respectively. A further four ‘resident’ adders were tracked at RSPB Minsmere (range analyses only). Adder AD8 was tracked during both April and August.

3.4.1 Movements

April Study

Adders weighed between 61.6 g and 125.1 g and the transmitter weighed less than 5% of body mass in all cases (Table 3.3).

Table 3.3: Morphometrics collected from translocated adders in April

Adder	Sex	SVL (mm)	Weight (g)	Attachment Weight (%)*
AD1	Male	485.8	109.0	1.83
AD2	Male	465.9	112.1	1.78
AD4	Male	385.3	61.6	3.25
AD5	Female	524.8	125.1	1.60
AD8	Female	366.4	102.9	1.94

* Weight of tag + attachment medium as a percentage of total weight

AD1, the largest male in the study, was translocated 560 m south to the receptor site. Movements were initially frequent, short and erratic. Within five days, AD1’s cumulative movements were 25% higher than the resident male (AD13). A cumulative distance of 259.5 m was recorded within 24 survey occasions (eight days). However, between survey occasion 24 (13:00; 16/04/2014) and 25 (18:00; 16/04/2014), AD1 moved 345 m north (Figure 3.4). To achieve this, AD1 crossed at least one and possibly two 20+ m stretches of amenity grassland. AD1 remained within a mosaic of scrub and grassland for the remainder of the survey in close proximity to a large female adder that had evaded initial capture. The combination of initial exploration and subsequent migration resulted in mean active movement distance (excluding inactive days) of 71.1 m. AD2, also a male, moved from the receptor site immediately upon release to the eastern edge of the site. During this 160 m migration, it appeared that AD2 crossed an area of amenity grassland measuring over 50 m. From here, AD2 moved progressively northwards (c. 100 m) towards the donor site at which point the tag was dislodged. In just six days, average activity equalled 41.1 m resulting in a cumulative distance of nearly 300 m. AD4, a male adder, remained within the receptor site for three survey occasions (one day) post-release before migrating over 100 m south-west (including an 80 m stretch of amenity grassland). The signal was subsequently lost and it is assumed that the radio tag had malfunctioned. Adders AD5 and AD8, both females, remained within the receptor area. Neither animal ventured further than 50 m from the point of release, with AD8 remaining within 25 m. Both animals appeared to set up ranges adjacent to one another with limited overlap. The mean activity distances for translocated females were less than 5 m. AD3, AD6 and AD7 returned too few data points as a result of a tag malfunction and dislodged tags.

August Study

The August tracking survey comprised two translocated and four resident adders (Table 3.4). All recorded activity was confined to the receptor site. Very little range overlap was observed despite the area supporting a high density of adders (c. > 10 ha^{-1}).

Table 3.4: Morphometrics collected from translocated and resident adders in August

Adder	Sex	SVL (mm)	Weight (g)	Attachment Weight (%)*
Resident				
AD9	Female	448.3	108.1	1.85
AD10	Female	472.7	131.2	1.52
AD13	Male	361.5	51.4	3.89
AD14	Female	523.3	174.8	1.14
Translocated				
AD11	Female	444.1	70.0	2.87
AD12	Female	405.8	88.0	2.27

* Weight of tag + attachment medium as a percentage of total weight

AD9, a resident female, exhibited infrequent, short movements (mean 6.6 m) restricted to an area measuring approximately 25 m^2. Comparable activity patterns were also observed for AD10 (resident female), AD11 (translocated female) and AD12 (translocated female). AD11 occupied a 10 m^2 area of rough grassland and scrub, located 40 m to the west of the point of release; movements typically ranged between 4 and 6 m per sample occasion. AD12 was tracked in both April (AD8) and August and like AD10 and AD11, movements were both short and erratic with the exception of a single 45 m movement eastwards across the receptor site. AD12 exhibited a slightly higher (29%) activity movement in August; however, there was no indication that AD12 was attempting to return to the donor site. AD13, the only resident male in the study, exhibited activity movements slightly higher than resident females but lower than translocated males. AD14 initially moved farther than other resident females but movements became short and erratic after one day. This short-term increase in movement, immediately after release, could be the result of elevated stress levels.

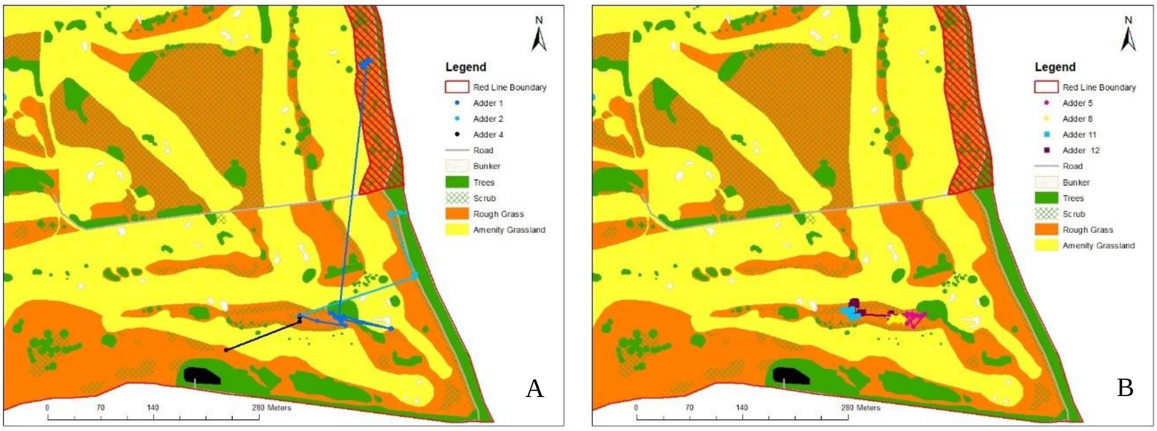

Figure 3.4: A) translocated males (Adders 1, 2 and 4); B) translocated females (Adders 5, 8, 11 and 12). Note that all telemetered males appeared to have left the receptor site by crossing extended stretches of amenity grassland.

Table 3.5: Distance data presented by status (translocated/resident)

Adder ID	Survey Period	N*	Sex	Movements (m)		
				Total Distance	Mean Occasion	Maximum
Translocated Snakes						
AD1	April 2014	30	M	632.2	21.07 (SD 11.6)	344.1
AD2	April 2014	18	M	290.0	17.04 (SD 10.2)	160.0
AD4	April 2014	6	M	116.8	23.36 (SD 13.6)	76.2
AD5	April 2014	27	F	119.2	4.41 (SD 1.4)	24.1
AD8^	April 2014	27	F	100.2	3.71 (SD 0.6)	13.0
AD11	August 2014	12	F	64.2	5.35 (SD 0.9)	13.0
AD12^	August 2014	30	F	137.2	4.73 (SD 1.5)	45.0
Resident Snakes						
AD9	August 2014	30	F	137.9	3.83 (SD 0.5)	13.9
AD10	August 2014	30	F	60.3	2.01 (SD 0.5)	14.3
AD13	August 2014	27	M	270.8	9.03 (SD 1.9)	48.1
AD14	August 2014	27	F	144.1	4.8 (SD 1.0)	25.1

* N = movements; ^ Same individual;

As would be expected, total distance and mean active movements were strongly correlated (Pearson's correlation: r = 0.965; P < 0.001). However, a t-test did not identify and significant differences between the activity of translocated males (defined as the proportion of occasions they moved greater than or equal to 4 m) and resident conspecifics ($t_{(4)} = 0.152$, P = 0.893). Similarly, translocated females were not significantly more active more than resident females ($t_{(5)} = 0.973$, $P = 0.375$).

Translocated males moved significantly greater mean distances than resident conspecifics (t-test: $t_{(4)} = 2.945$; $P = 0.05$) with movements between 1.1 and 2.6 times farther. The translocated males also made the largest unidirectional movements (mean 193.4 vs. 48.1; t-test: $t_{(4)} = 2.810$; $P = 0.048$), resulting in all telemetered individuals leaving the enhanced sections of the release site (Figure3.4). There was considerable variation in the maximum distance moved (SD 137.0). No significant differences between the mean (t-test: $t_{(5)} = 1.284$, $P = 0.255$) or maximum (t-test: $t_{(5)} = 0.495$, $P = 0.642$) distances moved by translocated and resident female adders were detected. Although adders were most active between 12:00 and 18:00, the difference between the three survey periods was not significant.

As would be expected, mean movement distances were strongly correlated with total (Pearson's correlation: $r = 0.987$, $P < 0.001$), home ($r = 0.929$, $P < 0.001$) and core ($r = 0.892$, $P =0.001$) ranges.

3.4.2 Range Analyses

Table 3.6: Home range data by status (translocated / resident) and sex

Adder ID	**Survey Period**	**Sex**	**Range Size (ha)**		
			Total Range	**Home Range**	**Core Range**
Translocated Snakes					
AD1	April 2014	M	2.38	3.02	0.07
AD2	April 2014	M	2.57	6.38	0.35
AD4*	April 2014	M	-	-	-
AD5	April 2014	F	0.04	0.23	0.01
AD8^	April 2014	F	0.02	0.06	0.007
AD11	August 2014	F	0.01	0.03	0.009
AD12^	August 2014	F	0.08	0.15	0.03
Resident Snakes					
AD9	August 2014	F	0.03	0.09	0.008
AD10	August 2014	F	0.006	0.05	0.001
AD13	August 2014	M	0.19	0.52	0.02
AD14	August 2014	F	0.05	0.55	0.02
M1	April 2015	F	0.61	1.44	0.19
M2	April 2015	F	0.80	3.80	0.11
M3	April 2015	M	0.89	2.15	0.312
M4	April 2015	M	0.51	2.66	0.15

* Too few data points; ^ Same individual

Translocated males exhibited larger total ranges than resident conspecifics exhibiting MCPs at least three times greater. Although both the home and core ranges also appeared larger for translocated males (up to16 times greater).

There was no significant difference between the total, home or core range of translocated and resident female adders. In contrast to the males, translocated females held smaller ranges than their resident conspecifics (Figure 3.5).

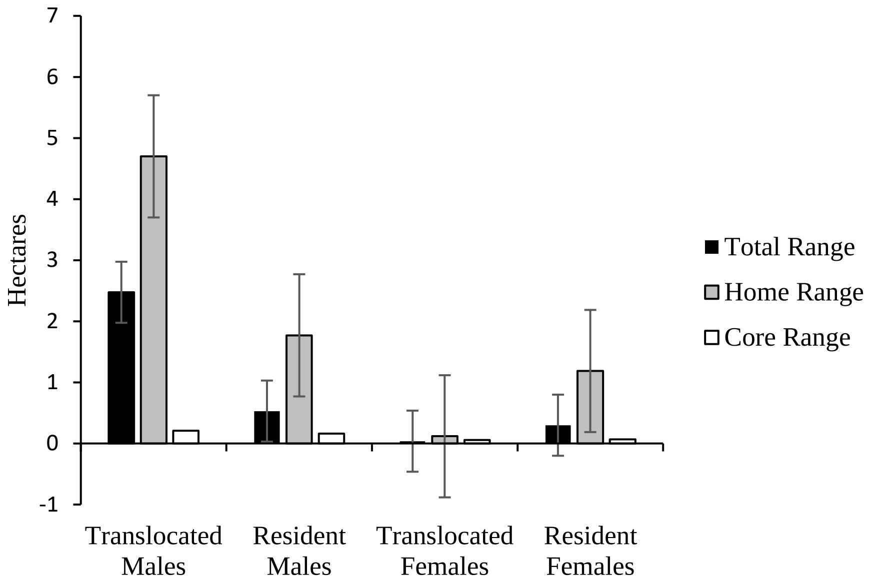

Figure 3.5: Comparison of mean ranges by status (translocated/resident) and sex.

Core ranges, recorded in August, appeared to show an aggregated distribution (Figure 3.6). Eight adders (one male and seven females) occupied three discrete areas. Although there was no overlap between areas, there was considerable overlap within areas.

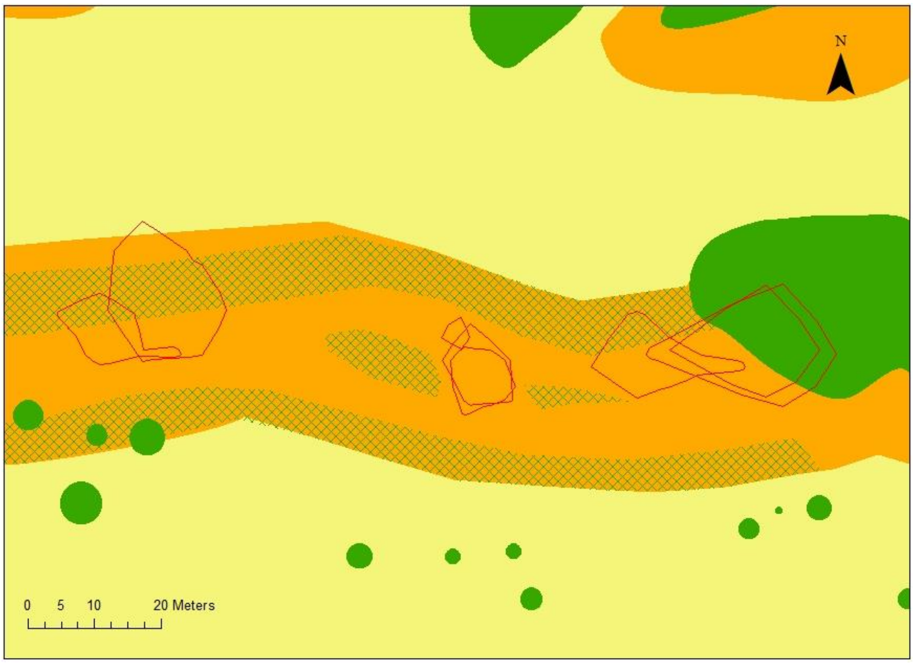

Figure 3.6: The core ranges (red polygons) show a clear pattern of aggregation (August data only).

3.4.3 Detection

Using a standard test of equal proportions, no differences between the detectability of translocated and resident adders (W = -0.19) or between males and females (W = 0.51) were identified. All individuals exhibited comparably low rates of detection (Table 3.7).

Table 3.7: Mean individual detection rates by status (translocated / resident) and sex

Adder	Sex	Detection*
Translocated		
1	M	0.15
2	M	0.00
4	M	0.17
5	F	0.10
8	F	0.10
11	F	0.13
12	F	0.00
Resident		
9	F	0.03
10	F	0.00
13	M	0.14
14	F	0.13

* Mean proportion of sample occasions when the adder was visible.

3.4.5 Habitats

Table 3.8: Comparison of habitat composition and occupancy by total range

Habitat Type	Mean Proportion within MCP		Mean Proportion of Occasions	
	Translocated	*Resident*	*Translocated*	*Resident*
Rough grassland	0.62	0.67	0.64	0.65
Woodland	0.04	0.06	0.12	0.03
Amenity grassland	0.14	0.04	0	0
Scrub / Tall ruderal	0.20	0.23	0.24	0.32

Habitat use by translocated and resident adders is similar, which indicates a strong preference for mosaics of rough grassland and scrub (Table 3.8). The clear exception to this trend is ‘amenity grassland which, although not statistically significant (test of equal proportions: W = 0.10), was nearly four times more frequent for translocated snakes. Although no individuals were recorded within this habitat type, it was evident that the males were crossing the amenity grassland.

Translocated adders occurred more frequently in wooded areas. A closer examination of the data indicates that this skew is likely due to the gender composition of each group. Male adders, irrespective of status, were 27% more likely to occur within a wooded area when compared to females (♂= 0.27; ♀ = 0.01). In contrast, female adders appeared to show a preference for rough grassland; however, it is important to recognise the small sample sizes and limited availability of habitat types and how these could influence any conclusions.

3.4.6 2015 Survey

Surveys undertaken in April 2015, utilising artificial refuges and direct observation survey, identified a total of 18 adders within and around the receptor site; of these, two (4%) were translocated to the receptor site during the previous year. The proportion of sample occasions where the telemetered snake was visible varied between 0 and 0.167; without radio telemetry, individual detection rates are expected to be very low.

3.5 Discussion

Translocated male adders moved, on average, farther than resident conspecifics resulting in greatly enlarged home ranges. All three telemetered males migrated away from the receptor site, crossing areas of unsuitable habitat. Post-translocation monitoring identified just two out of 45 translocated adders (4% of the translocated population) within the receptor site one year after the translocation.

Whether the translocation was a success or not depends on how success is defined. Forty-five adders were removed from the footprint of the development where the risk of harm was considerable; however, previous studies have indicated that the proportion of populations moved in a translocation is typically low (Platenberg & Griffiths, 1999; Germano et al., 2015). Those that remained within the donor site along with those that returned post-translocation are likely to have been harmed through construction-related activities. In this context, for those individuals that were moved and those that did not return to the donor site, the translocation should be considered a success in the short-term at least. Although the current study did not include survival analyses, it is possible to infer increased risks of mortality post-translocation. A clear association exists between increased movements and mortality (Andren, 1985; Madsen & Shine, 1993; Plummer & Mills, 2000; Butler et al., 2005). Male adders, which exhibited both increased mean movements and ranges, would have experienced an increased risk of encountering predators or inhospitable habitat features.

Contrary to published guidance (HGBI, 1998; English Nature, 2004; Natural England, 2011), the translocated adders were released in an area known to already contain adders. The introduction of additional individuals is likely to overload the receptor site’s carrying capacity, thereby increasing density-dependent competitive pressures (to avoid causing disturbance, morphometric measures were not collected here). Reductions in body condition are linked to diminutions in fecundity leading Platenberg & Griffiths (1999) to question the conservation value of translocations. To address restrictions on the carrying capacity, the incumbent consultants augmented the receptor site with three hibernacula and several piles of brash. The hibernacula, like the piles of brash, were constructed of vegetative materials (small stems and branches and grass cuttings) arising from site clearance operations elsewhere on the site. As these materials are likely to rot down, these enhancements are considered to be temporary, particularly so when compared against the donor site hibernacula (earth banks). Furthermore, no actions to immediately bolster the abundance of prey were undertaken, a factor likely to limit the carrying capacity.

A survey of the receptor site undertaken in 2015, one year after the initial translocation, detected just two of the translocated snakes. Low recapture rates are consistent with data provided in Chapter 3 and other studies of translocated snakes (Hare & McNally, 1997; Sealy, 1997); however, there are no data to suggest that the recapture rates of translocated individuals are any different from resident conspecifics. The paucity of recaptures could be explained by 1) high levels of overwintering mortality; 2) low rates of detection; or 3) dispersal into the wider landscape. There is evidence for the latter two theories (see below) but it is likely that all three contributed to the low observed recapture rates. As such, it is unclear as to whether the current translocation was a success or otherwise.

3.5.1 Distances

Translocated males moved greater distances than resident conspecifics, consistent with previous studies (Fitch & Shirer, 1971; Galligan & Dunson, 1979; Hare & McNally, 1997).

Daily movements of translocated males were almost double those of the resident male and over three times that of the females (both translocated and resident). Increased movements may result in higher rates of mortality (Plummer & Mills 2000). Although mortality is unlikely to occur over such limited timescales, adders undertaking increased movements are certain to have incurred higher energy expenditure (Macartney et al., 1988). Increased movements are likely to reflect a reduction in foraging activity (adders are principally ‘sit and wait’ ambush predators) and could lead to reductions in body condition.

Increases in the proportion of time spent on exploratory activity may detract from time available for courtship activities (Wolf et al., 1996). AD1 and AD2 undertook large, unidirectional movements back towards to the donor site and the former was observed in close proximity to a large female. It is not understood why the adders left the receptor site, which contained a high density of females (both translocated and resident), to return to the donor site. Male adders are able to detect females over considerable distances and would have been aware of their presence. Phelps (2004) described the formation of sub-groups within two adder populations across which there was no genetic exchange. If such a sympatric boundary was present, it could explain why AD1, AD2 and AD4 left the receptor site.

Translocated males exhibited the greatest distance moved per survey occasion. All three telemetered males migrated away from the release site, two within 24 hours of release. All three of the telemetered males crossed amenity grassland and in doing so would have exposed themselves to predators. Increased mortality associated with crossing unsuitable habitat was supported by the discovery of two predated adders from adjacent fairways. Whether these adders were captured on the short grass or transported there by predators is unclear. Known drivers behind such high risk movements include philopatry, stress and increased competition.

In contrast to the males, all of the telemetered females remained within 60 m of the point of release. Females did not appear to undertake explorative movements beyond the clear bounds of the receptor site. Although females were capable of moving large distances, the majority of movements recorded were both short and erratic. This behaviour was comparable to males, although to a lesser extent and did not result in females undertaking extensive unidirectional movements.

3.5.2 Ranges

As expected, male adders maintained considerably larger total and home ranges than females. Consistent with previous studies (Reinert & Rupert, 1999; Bulter et al., 2005; Lee & Park, 2011; Barve et al., 2013; Sullivan et al., 2015), the largest ranges were in translocated males. When developing mitigation strategies for adders and, in particular when designing receptor sites, it is important to account for this additional area requirement; however, given the absence of any published values for home ranges of adders in the UK, it is inconceivable that developers or their consultants are incorporating this important metric into mitigation strategies at present.

A study of adders occurring within a subalpine region of the Swiss Alps reported that the median home ranges for males and females were 5.2 ha and 0.76 ha respectively (Neumeyer, 1986). This is a considerably larger value than that reported here and could reflect differences in habitat quality (for instance, animals occurring within lower quality habitat would be expected to have larger ranges). Alternatively, it is possible that the extended duration and greater time intervals in Neumeyer's (1986) survey resulted in proportionately larger home range estimates. A shorter study from Finland reported particularly small home ranges (♂ = 0.002 ha; ♀ = 0.0056 – 0.08 ha); unfortunately, this study did not include habitat details (Viitanen, 1967). Variation could also arise from disparate methods of analyses. Neumeyer (1986) also provided estimates using convex polygon methodology (more comparable to the current study), which returned lower total range estimates (♂ = 0.3 – 3.14 ha; ♀ = 0.02 – 2.33 ha). Neither of the above studies utilised radio telemetry to collect data, which could have exacerbated the effects of imperfect detection (Macartney et al., 1988).

The size of the home range varies throughout the year (Brito, 2003) in response to the availability of spatial and temporal resources (i.e. hibernation, foraging or egg deposition). The home range estimates for male Lataste's vipers (*Vipera latastei*) varied between 0.24 and 1.52 ha in spring and autumn respectively. Male adders are known to undertake annual migrations between hibernation sites and foraging grounds (Phelps, 2004) and it follows that larger home ranges should have been recorded post-breeding (May) and pre-hibernation (September). The range estimates, which did not include peak periods, could be an underestimate.

The core ranges of adders showed a highly aggregated distribution. Within each of the three distinct areas, there was considerable overlap between ranges. In contrast, the core ranges of tiger snakes did not show any overlap and Butler et al. (2005) ascribed this as a competition avoidance mechanism. Phelps (2004) described intra-population segregation, although not on a comparably fine level. The three locations did not correspond with changes in habitat suitability or known hibernacula. Aggregation on this scale has not been reported previously and its biological function is unclear.

There appeared to be differences in habitat use by translocated and resident adders. Although all recorded ranges were dominated by rough grassland and scrub (consistent with Baker et al. 2004), those of the translocated males included a threefold increase in amenity grassland. As no males were recorded within amenity grassland, its prevalence was the result of large unidirectional movements across the habitat type. Amenity grassland is unlikely to provide prey or concealment from predators. During the course of the study, numerous species known to predate upon adders were observed, including carrion crows (*Corvus corone*), buzzards (*Buteo buteo*) and magpies (*Pica pica*), although the severity of predation by aerial predators was unknown. Using plasticine models of adders placed on a plain background, Wüster et al. (2004) demonstrated that many aerial predators actively avoided 'typical' adder patterning. As such, the diversity and abundance of terrestrial predators is likely to exert greater influence on the structure of populations. Two dead adders were recovered from the amenity grassland; both exhibited extensive musculoskeletal damage indicative of large mammals i.e. domestic cats, badger (*Meles meles*) or red fox (*Vulpes vulpes*). As both adders were decapitated, it was impossible to ascertain whether they were part of the translocated population. Whether these adders were attacked on the amenity grassland or were carried there afterwards is unclear. What is clear is that male adders are at greater risk when occupying receptor sites bordered by areas of unsuitable habitat.

3.5.3 Detection

No evidence to support Sealy's (1997) assertion that translocated snakes become warier of people was identified. Very low rates of detection were calculated for both translocated and resident adders alike. Upon release, many of the tagged individuals moved immediately beneath the grass thatch layer where they soon disappeared from view. Individual tag locations frequently moved during the telemetry work, suggesting that the adders were utilising the dense thatch layer to move around undetected. This behaviour was evident in both translocated and resident snakes.

Both translocated and resident adders exhibited low detection rates. Over the course of this study, individual detection rates averaged at 0.09 but dropped as low as zero. There are clear implications for post-development monitoring particularly where it requires individual recapture; as is shown here and also in Chapter 3, the probability of recapturing any one individual adder is exceedingly low. Given the low probability of individual detection, it is difficult to assess which individuals remained within the receptor site and ultimately to determine whether or not the translocation was a success.

3.5.4 Implications for Translocations

Short-distance vs. Long-distance Translocations

Prior to this study, adders were thought to undertake migrations up to 400 m (Phelps, 2004), making the current relocation of over 500 m a long-distance translocation. However, AD1 returned to the donor site and AD2 was moving in that direction when its tag malfunctioned. Clearly, this demonstrates that the species is capable of migrating over much farther distances.

Given the demonstrable response of male adders, consideration should be given to whether short- or long-distance translocation would be the more appropriate technique. To answer this, further studies would be required to ascertain what constitutes ‘typical’ movements and home ranges for adders in the UK. Maintaining adders within their current range has clear benefits, such as the negation of extended movements and associated risks of mortality. Other factors, such as the transmission of disease and the mixing of locally adapted alleles, would also be mitigated. Homing behaviours could be managed through the construction of exclusion fencing (but not habitat manipulation, see below). Conversely, the loss of part or all available habitat (including key features such as hibernacula and corridors) or the introduction of anthropogenic pressures (including domestic pet predation) could result in localised extirpation of retained populations. Any reductions in suitable habitat would correspondingly reduce the carrying capacity and thereby increase competition. Moreover, the introduction of high risks factors, such as a busy road, close to known adder population foci could adversely affect the population; risks such as roads could be addressed through strategically placed fences but this would incur extra costs not only for installation but maintenance.

To determine the most appropriate strategy, a detailed and tailored risk assessment should be developed and implemented along similar lines to the IUCN (2013). The risk assessment should include detailed information on how adders are currently using the landscape throughout the year. Key habitat features should be identified and where possible protected. Where used, *ex situ* receptor sites should be designed to replicate the donor site, thereby alleviating the influence of philopatry (Le Gouar et al., 2012).

Connectivity

Guidance for resolving reptile-development conflicts highlights the need to maintain connectivity both on a site (between features) and landscape (between sites) level. Natural England's now withdrawn 'Reptile Mitigation Guidelines (Natural England, 2011) specifically recommend 'good levels of landscape connectivity' when dealing with the wide-ranging grass snake. The results of the current study indicate that this is appropriate for adders, particularly as isolated populations are significantly more likely to undergo declines than those occupying well-connected sites (Baker et al., 2004). It is also important that receptor sites are designed to accommodate the adder's extensive exploratory movements without exposing them to predators. In the current study, the adders achieved undetected movement by utilising the thick thatch layer; this had the added advantage of supporting a diverse range of adder prey items. Rough grassland, hedgerows and scattered scrub equally could facilitate undetected movement throughout the receptor site.

When considering landscape level connectivity, it is important to consider the influence of philopatry on adders. If the donor site is within migratory-distance (i.e. a short-distance translocation) but it is no longer capable of supporting adders, care should be taken not to deliberately or inadvertently create habitat links. In the current study, two male adders used a strip of rough grassland and scrub to return to the donor site. The route was later severed through the erection of an exclusion fence.

Strategically placed fences or, for more permanent developments, concrete walls (Kyek et al., 2007) appear to be effective at mitigating the effects of philopatry. Similar barriers could also be used to mitigate the propensity of translocated male adders to cross unsuitable and potentially unsafe habitat. However, the purchase and installation of fencing can be costly, extending to many tens of thousands of pounds (Whiting & Booth, 2012; Lewis, 2012). As a cheaper alternative to fencing, developers often intentionally degrade habitat making it unsuitable for reptiles. This 'buffer' is often considered to be sufficient for excluding reptiles from otherwise unfenced development sites. Whereas this approach may be effective for more sedentary species, such as viviparous lizard, the current study has demonstrated that its effectiveness cannot be guaranteed for adders.

3.5.5 Future Studies

Consideration should be given to whether telemetry should be employed at all large linear developments, particularly those that could result in the fragmentation of habitats. Migrating male adders naturally occur at lower densities. The effect of this is two-fold: firstly, the lower densities make it more difficult to detect both the individuals and the habitat corridors that they are using; secondly, consultants are likely to erroneously conclude that because corridors support fewer adders the habitat is of lower importance. The isolation of populations and fragmentation of habitats is considered to be one of the greatest threats to the survival of many species (IUCN, 2016). Radio telemetry would overcome the low rates of detection and provide more useful data to inform approaches to mitigation.

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Chapter 4: Status of a Slow-worm Population 20 Years After Translocation

4.1 Summary

Follow-up monitoring of translocation studies is often not carried out for long enough to determine whether viable populations have become established. This is a particular problem for cryptic species that are difficult to survey and populations that undergo natural fluctuations in relation to environmental factors. Bus Company Island (BCI) is thought to be one of the world’s longest running post-translocation monitoring studies, but no detailed analysis has been performed since the documentation of the original translocation in 1995. BCI is unique receptor site in that it is largely isolated from surrounding habitat by the Great Stour river.

A population of slow-worms continues to persist at BCI two decades after the translocation. The Capture-Mark-Recapture confirmed the presence of a small population of up to 124 individuals. Although individual survival rates were consistently high the population appeared to be declining. Male slow-worms at BCI exhibited higher body condition indices than those at a nearby natural (i.e. control) site; the opposite was true for immature slow-worms. The body condition of both study and control populations decreased over the three-year study and this is possibly related to climate.

The river barrier appeared to minimise both disturbance and post-release dispersal. However, it also precluded the ability to disperse in response to changing conditions. The population of slow-worms at BCI is therefore likely to become increasingly dependent on human intervention. Given the small size and isolated location, the population is unlikely to be either viable or self-sustaining in the long-term.

4.2 Introduction

Translocation is a globally widespread practice used for both conservation and development mitigation alike (Platenberg & Griffiths, 1999; Germano & Bishop, 2008; Germano et al., 2015). Despite its prevalence, there is a clear paucity of post-translocation studies associated with the latter. In the UK, there is no legal imperative or formal mechanism to report translocations involving ‘widespread’ or ‘non-EPS’ reptile species. Consequently, it is difficult to obtain reliable data on the scale of translocations or their ultimate fate.

The principal aim of translocation is the establishment of a viable and self-sustaining population (Griffith et al., 1989). Monitoring should seek to ascertain whether both of these important criteria are met. How long this takes is largely dependent on the longevity and fecundity of the species concerned. The average longevity of slow-worms in the wild is thought to be between 10 and 15 years (Platenberg, 1999; Beebee & Griffiths, 2000); however, they require between three and five years to become sexually mature. To establish whether the offspring of the translocated population are breeding (required to establish the self-sustaining criterion), a monitoring programme of eight years or more might be required (Platenberg, 1999). However, published guidelines for monitoring recommend just five years (Natural England, 2011).

Very few long-term (5+ years) studies of translocated reptiles have been undertaken and published. One such published study is Bus Company Island (BCI), which has now been the subject of intermittent post-translocation monitoring for over 20 years (Platenberg, 1999; Platenberg & Griffiths, 1999). In 1994, planning permission was granted for the construction of a residential development on an area of brownfield located within Canterbury, UK.

Immediately prior to the commencement of construction activities, the developers identified a population of slow-worms. To meet a tight development programme and ensure legal compliance, the developer and their consultants took the unusual step of translocating a population of 134 slow-worms into a temporary holding enclosure (Platenberg, 1999). After one year in the temporary holding pen, 103 slow-worms were captured and translocated 0.8 km to BCI, Canterbury.

Following the relocation of the slow-worms in 1995, two years of intensive post-translocation monitoring were undertaken (Platenberg, 1999; Platenberg & Griffiths, 1999). In total, 62 (60%) of the translocated population were recorded during two years of monitoring. Attempts to generate population estimates using the CMR data were unsuccessful.

No differences in body condition were detected in individuals prior to the translocation and in year 2 of the monitoring; however, a statistically significant decline in body condition was reported in year 1 (the first year after release). Compared to a natural population, the BCI slow-worms exhibited lower body condition scores. The reasons for this are unclear but it could represent differences in habitat quality (Platenberg & Griffiths, 1999), a difference in the demographic groups selected or the direct result of stress. Further to the reductions in body condition, no evidence of breeding was recorded during the two years of monitoring (Platenberg, 1999). Given the barriers to natural colonisation and the anticipated longevity of slow-worms, any animals in the current population are likely to have descended from translocated individuals, indicating that breeding did resume at some point in the past 20 years.

4.2.1 Objectives

For the first time for a known translocated reptile population, I sought to determine the population status 20 years' post-translocation. Using MARK, I sought to ascertain estimates of population abundance, survival and detectability. I also tested whether the present-day body condition of slow-worms were able to return to pre-translocation levels recorded in 1994 and how these compared with a natural (i.e. non-translocated) population.

4.3 Methods

4.3.1 Bus Company Island

BCI is a 1.7 ha island almost entirely enclosed by the Great Stour river (Figure 4.1). Formerly managed as an orchard, BCI was designated as a Local Nature Reserve in 1994; despite this, there is no public access to the site. To maintain the diversity of habitats, the site was subject to monthly habitat management including mowing and selective scrub clearance. Despite ongoing management, much of the site has become inaccessible due to the encroachment of tall ruderal vegetation. This has meant that some open areas previously used for monitoring the site have become shaded and unsuitable for reptiles.

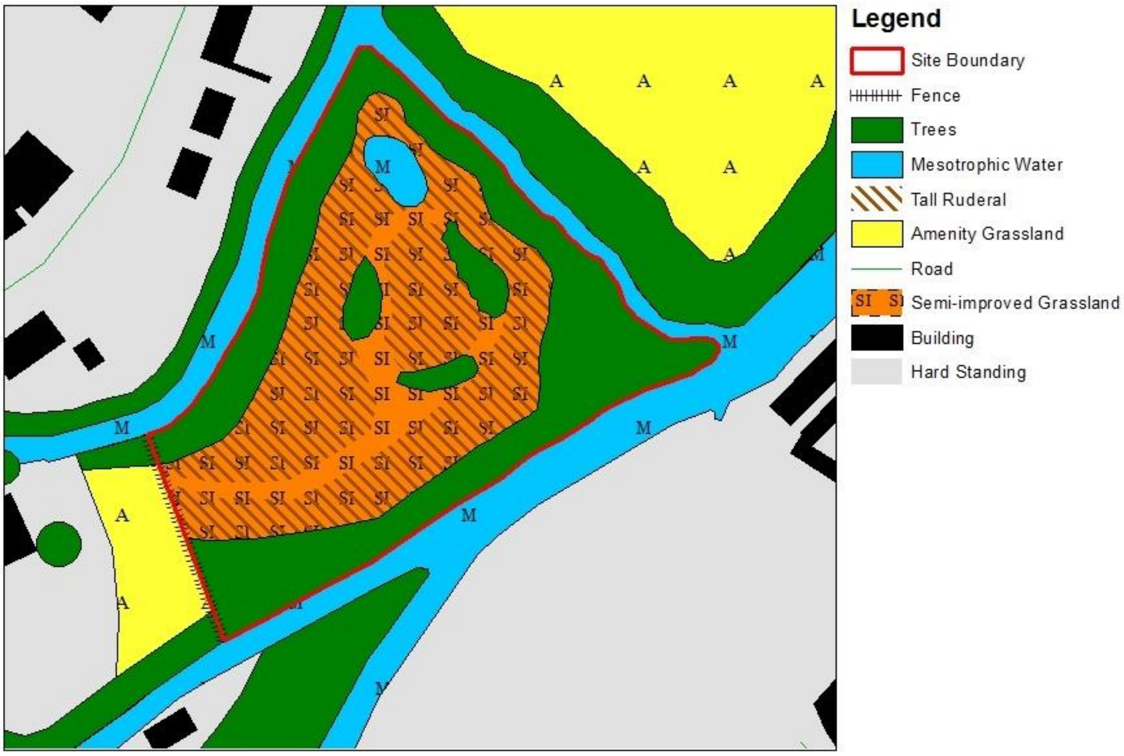

Figure 4.1: A Phase 1 Habitat map of BCI. Although the site is open to the south-west, the shaded woodland and mown-short grassland is assessed as unsuitable habitat for slow-worms.

4.3.2 Field Surveys

The current data were collected between April 2013 and September 2015 (25 visits). On average, two visits per month were undertaken between April and September. As slow-worms typically begin emerging from hibernation in March and go back into hibernation in October, the April – September period was selected as the time when animals would be active. Surveys were timed to coincide with the peak periods for detectability, which include both mornings and late afternoons.

Field surveys comprised Artificial Cover Object (ACO) surveys. Fifty-three ACOs, comprising a mixture of tin, felt and onduline sheets measuring 0.5 m^2, were placed within suitable habitat. The resulting density of ACO was 31 ha^{-1}, well above the recommended density of 10 ha^{-1} advised by Froglife (1999).

Where encountered, slow-worms were captured by hand and processed. A range of morphometric measurements were collected from each individual. Slow-worms have a propensity to lose their tails when stressed so a survey procedure was developed to minimise handling. Body mass was measured using a digital balance; slow-worms were weighed to the nearest 0.1 g. The Snout-to-Vent Length (SVL) was recorded by placing the animal in a custom built squeeze box (Figure 4.2). The squeeze box included a graticule in each corner, which was photographed along with the animal's ventral surface. Computer software (Snake Measurer V1.0: http://serpwidgets.com/main/measure), enabled the standardised measuring of SVL, reducing the natural variability associated with stretching individuals (Rivas et al., 2008).

Figure 4.2: A slow-worm being measured using SnakeMeasurer software

Following Platenberg (1999), size classes were ascribed to individuals as follows:

- Adult > 120 mm SVL;
- Subadult between 100 – 120 SVL; and
- Juvenile < 100 SVL.

The effects of allometry are thought to be greatest in the sub-adult and juvenile groups as it is during this time that individuals develop sexually dimorphic characters (Braña, 1996). As such, these groups were pooled together as 'immatures'.

The identification of individual slow-worms was based on photographs of a combination of lateral (upper and lower labials, pre- and post-oculars, loreal scales) scalation and cranial patterning (see Figures 4.3 and 4.4).

Figure 4.3: Labial scales and patterns

Figure 4.4: Dorso-cranial scales and patterns

As with Platenberg's (1999) study, a comparison was drawn with a control population at Quilter's Wood. Quilter's Wood is a privately owned nature reserve, located 9 km south of Canterbury, Kent. The site comprised three paddocks, which were used intermittently for sheep grazing. Surrounding the paddocks were contiguous areas of rank grassland and ancient woodland. All four widespread reptiles were recorded during field surveys; however, slow-worms were by far the most abundant species. To my knowledge, Quilters Wood has never been the recipient of translocated reptiles, making it a suitable control site.

Morphometric data were collected from individuals at Quilters Wood in an identical manner to BCI. Visits were undertaken on a bimonthly basis between April and September, concurrently with BCI. On an alternating basis, surveys at Quilter's Wood were undertaken either directly before or directly after surveys at BCI. A matrix of ACO were positioned in suitable habitat at a density comparable to that of BCI; the starting point and direction of the survey was varied.

Given the large number of slow-worms present at Quilter's Wood, no effort was made to record photographic identification; this omission precluded a CMR exercise. Effort was instead focused on collecting morphometrics from a range of demographics.

4.3.3 Data Analysis

Capture-Mark-Recapture (CMR)

To establish estimates of survival, detectability and abundance, I constructed a binary encounter history for each individual. To test that the data were appropriate for CMR, encounter histories were tested for Goodness of Fit using 'U-Care' software V2.3.2.

Model selection was largely based on the level of parsimony i.e. the models with the lowest AIC scores and highest model weight and likelihood. However, models that generated non-meaningful estimates of survival and detectability (i.e. 1's or 0's) were rejected and a model with a higher AIC chosen.

MARK software (V8.1) was used to generate estimates of abundance.

Huggins Robust Design Model

To generate estimates of abundance, survival and detectability, a Huggins Robust Design (RD) model was developed (Huggins, 1989; Huggins, 1991). Although the slow-worms at BCI are thought to be a spatially-closed population, it should be considered as 'temporally open' given that data were collected over multiple years. The Huggins RD model accounts for these open and closed aspects (Lefebvre et al., 1982). The model uses primary (in this case years 1-3) and secondary (monthly or bimonthly) sample occasions. As the primary occasions are open, they allow for gains (births and immigration) and losses (death and emigration). The robust design model generates abundance estimates ($\hat{N}$) from the secondary sample data (i.e. short-term); as the study used three years of data, three separate annual estimates were generated for each group (males, females and immatures).

A ‘no movement model’ was generated by fixing γ` and γ`` at 0 and 1 respectively. Gamma prime (γ`) is the probability that an individual was outside of the sample at time $i - 1$ and is also not present in the sample at time $i$ (Cooch & White, 2016). Gamma double prime (γ``) is the temporary emigration vector. The ‘no movement’ model was appropriate given the presence of the Great Stour river, which inhibited movement in and out of the population.

As there are no reports of whether individual slow-worms become trap-prone or trap-shy, the probability of capture fixed as the same as the probability of recapture (meaning that capturing an individual once will not influence the probability of catching it again).

Using MARK software, the Huggins RD model calculated estimates of abundance using the following equation:

$$\widehat{N}_t^s = n_t^{*s} / \hat{p}_t^{*s}$$

Where s is state (observable or unobservable, which in this case was fixed), t is time, n_t^{*s} is the total number of individuals captured in state s during a primary period, and $\hat{p}_t^{*s}$ is the derived probability that an animal is observed on one or more occasion. $\widehat{N}$ is the estimated estimate of abundance (see Cooch & White (2016) for further details).

To develop the most parsimonious model, group estimates of survival (phi) and detectability (P) were allowed to vary over time and between groups (i.e. males, females and sub-adults). The 25 sampling occasions were coded with the corresponding time intervals between visits.

Body Condition

To assess the physical condition of the slow-worms without undertaking invasive or destructive procedures, I utilised two condition indices (CI). The first was a replication of the method used by Platenberg (1999), namely:

$$CI = (M_i/SVL_i^3)10^6$$

where M_i is mass (g) of individual *i* and SVL_i is snout-vent-length (mm) of individual *i*.

This model was used to enable direct comparisons with the data presented by Platenberg (1999). As improved condition indices have been developed in the interim, the Scaled Mass Index model (Pieg & Green, 2009) was also used:

$$\hat{M} = M_i \left[\frac{L_0}{L_i}\right]^{b_{SMA}}$$

where M_i is the mass (g) of individual *i*, L_0 is an arbitrary value (mean SVL in this instance), L_i is the SVL (mm) of individual *i* and b_{SMA} is the scaling exponent obtained from the regression of log mass on log SVL (refer to Pieg & Green (2009) for further details).

Using the SMI, the body condition of adult male and juvenile slow-worms at BCI was compared to a population at Quilters Wood. Females were omitted as their condition is greatly influenced by the effects of parturition, which could skew the results. Independent sample t-tests were used to test for differences in the condition indices of the study and control populations. Data were log transformed to meet the test of normality where necessary. To test whether body condition declined over years, the male morphometrics were pooled together and tested for differences using a one-way ANOVA. This was repeated for immature slow-worms. Where significant differences were detected, *post-hoc* tests (Bonferroni) were undertaken to ascertain where the differences were.

4.4 Results

4.4.1 Encounters

Over the three-year monitoring period, 116 slow-worm encounters were made (Table 4.1). Overall, this equated to a mean of 4.64 individuals per visit, considerably more than the 1.1 - 1.7 reported by Platenberg (1999). However, the number of encounters declined on a yearly basis (one-way ANOVA: $F_{(2, 19)} = 5.143$, $P = 0.0016$) (Table 4.1. A Bonferroni *post-hoc* test confirmed that the differences were between Years 1 and 3 only.

Table 4.1: Summary of BCI capture data. Numbers show mean captures per visit averaged across all sampling occasions within a year.

Year	**Encounters**	
	N	***Per visit (SE)***
2013	71	8.0 (1.46)
2014	35	3.56 (0.94)
2015	10	1.43 (0.53)

Significant differences in monthly encounters were recorded in 2013 and 2015, with more encounters in May than in any other month (2013: $F_{(4, 10)} = 9.5$, $P = 0.002$; 2015: $F_{(5, 12)} = 3.4$, $P = 0.039$); this was also true for 2015. These differences were not influenced by sex or age class indicating a lack of behavioural or trait-specific responses (Figure 4.5).

A

B

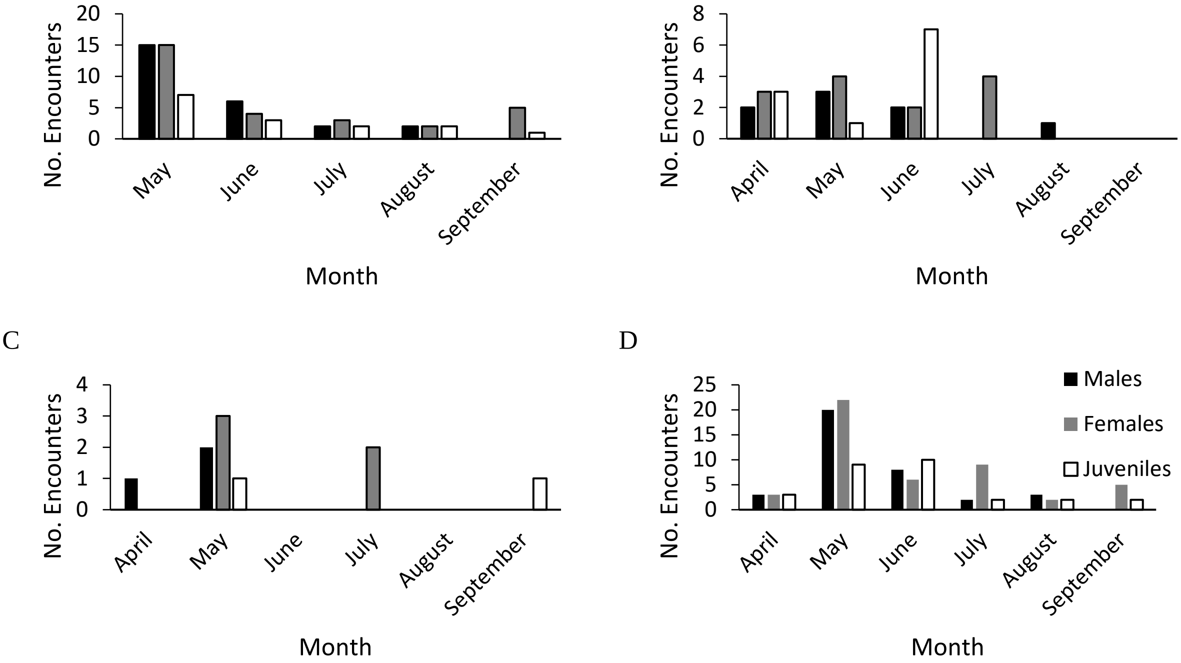

Figure 4.5: Monthly encounter history by sex / age group. A) year 1 (2013); B) year 2 (2014); C) year 3 (2015); and D) cumulative totals

Of the 116 encounters, 59 individually identifiable slow-worms were recorded. Of these, 46 individuals were first recorded in year 1 with an additional 11 and 2 individuals first recorded in years 2 and 3 respectively (Table 4.2). The majority of individuals were caught on a single occasion; however, two individuals were caught on six or more occasions (Figure 4.6).

Table 4.2: Capture history of individual slow-worms over three years.

Group	**Year 1**		**Year 2**		**Year 3**		**Total N**	**Total R (%)**
	N	**R**	**N**	**R**	**N**	**R**		
Male	14	-	3	2	0	2	17	4 (23.5)
Female	21	-	5	6	0	2	26	8 (30.8)
Juveniles	11	-	3	4	2	0	16	4 (25)
Total	**46**	**-**	**11**	**12**	**2**	**4**	**59**	**16**

N – new captures; R - recaptures

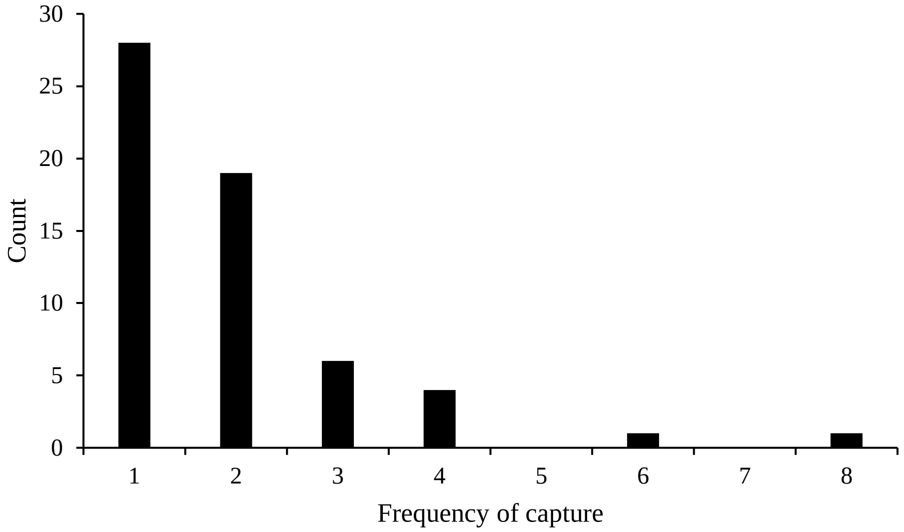

Figure 4.6: Histogram of capture frequencies of individual slow-worms.

4.4.2 Huggins RD Model

Despite a degree of under-dispersal, the goodness of fit test confirmed that the data were appropriate for CMR (ĉ = 0.452; $\chi^2_{(39)} = 17.63$, P = 0.99); ĉ was manually adjusted to 1.0 following Cooch and White (2016).

A range of Huggins RD models were developed and tested to ascertain the best fitting model for the data (see Appendix C). The top three models (i.e. those with the lowest AIC value) all constrained both survival (φ) and detectability (p) over time but not between groups (Table 4.3). Allowing survival and detectability to vary between groups resulted in minor changes (≤ 2 ΔAIC) to the AIC value and, according to Cooch and White (2016), the selection of any of these models could be justified (i.e. the differences were not significant). Model 1 was selected as the best model; however, the deviance was high for all models and this should be considered when assessing the robustness of the model. In Model 1, female and sub-adult vectors for survival and capture/detection were pooled and separated from the males (Table 4.3).

Table 4.3: Huggins RD model selection as generated by MARK software. The models are listed according to AIC value, with the most parsimonious models listed first.

Model	AIC	ΔAIC	Model Weight	Model Likelihood	Parameters	Deviance
1. S(.) γ(fixed) C(.) = P(.) – males separated out for S and P	650.65	0.00	0.48	1.00	8.00	532.88
2. S(.) γ(fixed) C(.) = P(.) – no groups for S, males separated for P	651.26	0.60	0.36	0.74	7.00	535.80
3. S(.) γ(fixed) C(.) = P(.) – no groups for S, all groups separated for P	652.90	2.24	0.16	0.33	10.00	530.36

Survival and Detectability

Table 4.4: Estimates of survival and detectability generated by Model 1 (Table 4.3) using Huggins RD

Group	Estimate	SE	Confidence Intervals	
			Lower	Upper
Survival (males)	0.23	0.10	0.09	0.49
Survival (females and sub-adults)	0.56	0.19	0.22	0.86
Detectability (males) – year 1	0.18	0.04	0.11	0.27
Detectability (females and sub-adults) – year 1	0.09	0.02	0.05	0.14
Detectability (males) – year 2	0.18	0.07	0.09	0.35
Detectability (females and sub-adults) – year 2	0.07	0.02	0.03	0.13
Detectability (males) – year 3	0.27	0.12	0.10	0.56
Detectability (females and sub-adults) – year 3	0.04	0.03	0.01	0.15

The 'female / sub-adult' group had survival rates over double that reported for the males. These differences are likely to have arisen from the fact that proportionately fewer males were recaptured. There is considerable overlap between the respective upper and lower confidence intervals suggesting that this difference in survival is not significant. The mean detectability estimates of the 'male' and the combined 'female - sub-adult' groups were 0.21 and 0.06 respectively. Although there is overlap in the confidence intervals, it is to a lesser extent than reported for survival. Both the survival and the detectability estimates include relatively large standard errors and caution should be used when interpreting the results.

Population Estimate

The RD Huggins model provided annual (or primary occasion) population estimates, split by group, that were allowed to vary between years (Table 4.5). The highest estimates were achieved in Year 1 as a result of the highest number of captures and recaptures; of the 46 individuals identified in Year 1, 20 were captured on two or more occasions. The decrease in recaptures year on year resulted in diminishing population estimates coupled with high mortality rates.

Table 4.5: Annual population estimates of slow-worms based on Model 1 of Table 4.3

Group	$\hat{N}$	SE	LCI	UCI
Year 1 – total of 74 individuals				
Males	17	2.14	15	26
Females	37	8.21	27	62
Sub-adults	20	5.07	14	36
Year 2 – total of 44 individuals				
Males	6	1.35	5	12
Females	23	7.78	15	49
Sub-adults	15	5.53	9	34
Year 3 – total of 20 individuals				
Males	2	0.62	2	6
Females	9	7.76	3	43
Sub-adults	9	7.76	3	43

$\hat{N}$ - abundance estimate; LCI – lower confidence interval; UCI – upper confidence interval

4.4.3 Body Condition Indices

Of the 59 slow-worms identified, 24 (41%) individuals had lost their tail either recently or historically. These individuals were excluded from the body condition analyses. Using the

Platenberg (1999) method, condition indices were calculated for eight individuals that were recaptured over multiple years (Table 4.6).

Table 4.6: Condition indices for recaptured individuals

Individual	**Sex**	**Condition Index (CI)**		
		2013	**2014**	**2015**
BCI-3	Male	4.74	4.33	X**
BCI-6	Immature	5.34	5.85	4.96
BCI-7	Immature	5.21	-	4.62
BCI-27	Immature	6.71	4.41	-
BCI-67	Immature	5.77	5.16	-
BCI-69	Immature	5.20	4.64	-
Mean (SE)		**5.50 (0.28)**	**4.07 (0.85)**	**4.79 (0.17)**

* CI = $(M/SVL^3)10^6$; X** individual encountered but had lost tail

Platenberg (1999) reported a decline in mean male body conditions of 4.6, 4.0 and 3.6 in 1995, 1996 and 1997 respectively. A decline in body condition was evident between year 1 and years 2 and 3; however, no significant differences were identified between years 2 and 3. The small sample size of year could have influenced these analyses.

Scaled mass index values were calculated for slow-worms at both the study and control sites. There were significant differences between the body condition of males occupying the study and control populations (t-test: $t_{(131)} = 4.98$, $P < 0.001$). The males at BCI had a higher mean body condition index (21.37, SE 1.36) than those at Quilters Wood (16.95, SE 0.30). Although male body condition appeared to decline over time for both populations, the difference was not significant (one-way ANOVA: $F_{(1,2)}$ 0.059, $P = 0.809$). A significant difference in the body conditions of immature slow-worms was also detected (t-test: $t = _{(44)} = 10.89$, $P < 0.001$); however, in contrast to the males, the immature slow-worms at the control site (1.93, SE 0.06) had a higher mean body condition than those at BCI (1.25, SE 0.03).

The pooled body condition of both male (one-way AVONA: $F_{(2)} = 3.60$, $P = 0.03$) and immature (one-way ANOVA: $F_{(2)} = 4.21$, $P = 0.02$) slow-worms declined over time. However, post-hoc tests confirmed that this difference was only significant between year 1 (2013) and year 3 (2015) for both groups.

4.5 Discussion

Over 20 years have passed since slow-worms were translocated to BCI and a population continues to persist at the site. Given the presence of the Great Stour river preventing both immigration and emigration and the lack of subsequent translocations, the slow-worms are believed to be direct descendants of the translocated population. Juvenile slow-worms, recorded during the monitoring, were taken as evidence of continued breeding. The presence of slow-worms at BCI could therefore be seen to vindicate the use of translocation in this instance. However, in many respects BCI is not a typical translocation and caution should be used when drawing generalised conclusions. The BCI slow-worm population will almost certainly have benefited from the exclusion of people and domestic animals. The proximity of physical barriers to movement will also have prevented post-release dispersal.

Despite the continued persistence, current population estimates indicate the presence of a small population of slow-worms. A total of 59 individuals were captured over the course of the monitoring. Based on year 1 data, the most robust of the datasets, between 56 and 124 individuals could be present, equating to between 15 and 74 slow-worms per hectare. Although very few studies have investigated slow-worm population densities, those that have place it between 600 and 1,200 ha^{-1} depending on habitat quality (Smith, 1990, Riddell, 1996). This means that either the abundance values are a substantial underestimate, habitat quality is particularly poor or the BCI population supports few individuals. The estimates of abundance do have relatively high standard errors associated with them resulting in some, albeit limited, doubt as to the precision of the models. Furthermore, considerably higher estimates of abundance can be generated by combining estimates of detectability with CMR counts. As such, the actual population size is likely to be closer to the upper confidence interval. The quality of habitats at BCI has changed considerably since the initial translocation. Platenberg (1999) reported a monthly management programme that involved mowing and scrub clearance, which would have resulted in a high level of insolation. Over the currently reported period, habitat management appeared to be considerably less frequent and this is likely to have contributed to the rapid expansion of hogweed (*Heracleum sphondylium*) and stinging nettles (*Urtica dioica*) over the grassed areas (thereby creating shade). Given the adaptability of slow-worms coupled with the wide range of habitats that they occupy (Beebee & Griffiths, 2000), this is unlikely to have resulted in such drastic declines in abundance. Few 'new' captures, as reported for years 2 and 3, typically indicates that the majority of individuals in the population have been identified; however, this is usually supported by a correspondingly high recapture rate. The reduction in new captures and recaptures reported here appears to suggest a declining population. This is supported by the low survival rates reported by the Huggins RD model. The presence of neonates indicates breeding; however, if the birth rate is lower than the death rate, numbers will decline.

The presence of neonate slow-worms confirms that the population is breeding, in contrast to that reported by Platenberg (1999). Stress is known to result in higher levels of corticosterone, a hormone known to inhibit reproduction in some species of reptiles (Moore & Jessop, 2002) and result in smaller offspring in others (Meylan et al., 2001). Stress associated with the translocation could have inhibited breeding within the period monitored by Platenberg (1999).

Initially, 102 slow-worms were translocated into BCI and current population estimates suggest a similar sized population now. It is not clear why the number of slow-worms hasn't increased to the levels reported by Smith (1990) or Riddell (1996) based on the suitability of the habitat, paucity of disturbance or lack of intra- and inter-specific competition. Given the lifecycle and fecundity of slow-worms, sufficient time has elapsed to allow breeding to recommence and the population size to grow. Some unknown factor appears to be capping the population size. Small populations are exposed to proportionately higher risks of localised extinction and the long-term viability of the BCI slow-worm is uncertain. Indeed, of the 59 individuals captured, 11 (19%) were categorised as immature (i.e. non-breeding). Thus, the breeding population comprises just 48 slow-worms (28 ha^{-1}). However, given that slow-worms breed biennially, only half of the females are available to breed in any given year further reducing the breeding population down to 30 individuals (18 ha^{-1}). There are no reported values for the minimum viable population size slow-worms; however, 30 individuals could be below the necessary levels. Franklin (1980) suggested that populations with fewer than 50 individuals were at immediate risk of extinction. Indeed, Reed et al. (2003) suggested that the mean minimum viable population (defined as the number of individuals needed to persist for 40 generations) was 7,316. This study involved 102 species of vertebrates, including 18 species of reptile. No differences in the minimum viable population between taxa were identified. A population viability analysis should be undertaken at BCI to ascertain likely extinction risk.

Small populations have lower genetic variability than large populations (Madsen et al., 1996) and are more likely to suffer from inbreeding depression. Further genetic diversity is likely to be lost through genetic drift (Freeland, 2008) and unequal breeding opportunities. At BCI, this is likely to be exacerbated by the presence of a physical barrier preventing immigration. Low levels of genetic diversity are likely to restrict a population and its constituent member's ability to respond to changing conditions or disease. If the genetic diversity is low, it could cast doubt on the population's long-term viability.

Detectability is likely to be a factor in the low abundance estimates. Indeed, many animals were only recorded on a single occasion. The Huggins RD model points to low individual detectability, particularly for females and sub-adults. There are a number of reasons why detectability should be so low including trap shyness, habitat changes and climatic conditions. Trap shyness, the reluctance of an individual to utilise a trap or feature (or in this case, an ACO), has been demonstrated in skinks (Wilson et al., 2007; Lettink et al., 2011). The highest number of slow-worms was recorded during the first survey after which the number dwindled. Although this is consistent with the effects of trap shyness, no such behavioural response was reported by Platenberg (1999) who undertook a greater number of surveys. The reductions in detectability coincided with changes in the structure of habitats. ACO occupancy was greatest earlier in the year. The vegetation, particularly hogweed and stinging nettle, exhibited vigorous growth beginning in May and continuing through until September. This vegetative growth over-shaded a number of ACO and prevented access to a small number of others (almost certainly reducing detectability). Occupying areas with dappled sunlight reaching the ground enables cryptic species, such as slow-worms, to bask without being detected; indeed, this is a strategy adopted by the smooth snake. Sewell et al. (2012) reported changes to seasonal detectability in UK populations of slow-worm. The detectability peaked in April and September closely followed by May. March, June and July has relatively low detectability. This pattern wasn’t found in the current study but there are some differences in how the surveys were undertaken. The Sewell et al. (2012) study involved a large number of sites (n = 29 in 2009 and 45 in 2010), monthly visits from March to September but excluding August, and comprised 30 ACO. The current survey comprised bimonthly visits between April and September (excluding April in year 1) and 63 ACO. It is conceivable that the effects of these patterns were being masked by other factors influencing detectability, such as the change in habitat composition.

The presence of physical barriers would almost certainly have inhibited post-release dispersal forcing the population to remain *in situ*. Dense woodland and scrub were present at the peripheries of BCI. The encroachment of tall ruderals on the grassland is an example of natural succession. In the absence of management, scrub would follow suit before finally giving way to woodland (the climax state). Given the physical barriers to emigration, the slow-worms are dependent on continued habitat management for their survival. Although all UK populations of reptiles are likely to be dependent on human activities to a certain extent, for the slow-worms at BCI human intervention appears to be essential. As such, they are unlikely to meet Griffith et al. (1989) definition of a self-sustaining population.

The current population of adult male slow-worms at BCI appeared to exhibit higher body condition indices than those reported by Platenberg (1999) or of the control population. The scaled mass index controls for both size and allometric growth, suggesting that the differences are likely to reflect differing energy stores (Pieg & Green, 2009; Pieg & Green, 2010). This indicates that any losses of condition incurred by males following translocation have been recuperated; however, the reason for individuals occupying BCI having higher body conditions than the control unclear. This analysis excludes 41% (n = 24) of the population, which had either recently or historically lost their tails. To place this in context, 50% of translocated slow-worms at Site 4 (Chapter 2) and 26% of those at Site 5 had lost their tails. No external parasites or extensive scarring was observed on BCI slow-worms and they outwardly appeared to be in good physical condition. Conversely, immature slow-worms at BCI had lower body condition indices than the control population. The body condition of juveniles has been linked with that of the mother (Abell, 1999; Olsson &

Madsen, 2001) and stresses incurred during pregnancy (Meylan et al., 2002) in reptiles. Unfortunately, no data relating to the body condition of the females are available.

A trend that concurs with Platenberg's (1999) analysis is a decline in condition over a three-year time frame. This pattern was consistent across both populations and was statistically significant for both males and immature slow-worms (years 1 and 3 only). The reasons for this decline are unclear but are likely to reflect the influence of climatic conditions on the slow-worms. A recent study has shown how climate can greatly influence body condition over relatively short periods of time (Bestion et al., 2015). The authors demonstrated that an increase of just 2°C resulted in higher metabolism, faster growth rates and reduced adult survival in viviparous lizards. One possible reason offered for the reduced adult survival was an inability to feed during periods of induced aestivation. The UK Met Office has confirmed that 2014 and 2015 were two of the hottest years on record in the UK. This increase in temperature coincided with observed declines in the body condition of both populations of slow-worms. Higher winter temperatures are also likely to increase the rate at which energy stores are consumed. In a study of *Vipera aspis*, higher winter temperatures resulted in a marked decrease in body condition resulting from an increased metabolism (Brischoux et al., 2016). The UK Met Office data confirms that the south of England experienced a significantly warmer winter in 1995 but not 1994 or 1996. The elevated winter temperatures experienced in 1995 are likely to have contributed to the drop in the slow-worms observed body conditions in 1996. If increased temperatures are responsible for decreased body condition, it shows a remarkable lack of behavioural and/or physiological adaptability by slow-worms and identifies climate change (prolonged warmer periods) as a real threat to the species persistence. Small populations, with limited genetic variability, are likely to particularly vulnerable to increasing temperatures. The presence of physical barriers prevents the BCI population from being able to migrate in response climate change.

4.5.1 Conclusions

Although the population continues to persist at BCI, its future is far from certain. On the one hand, the barriers have almost certainly prevented post-translocation dispersal thereby enabling the establishment of a population at BCI. The surrounding river would also have inhibited the ingress of domestic pets and other predators. Equally, the barriers have precluded the slow-worms from moving in response to habitat succession or climate change. Indeed, the presence of barriers would also prevent the slow-worms from colonising new areas. Temporarily penning the newly translocated populations may offer a balance between the establishment of a population foci and the sustainable migration of individuals to new areas (see Chapter 4).

The sudden increase in tall ruderal vegetation exposes the slow-worms' dependence on habitat management. Slow-worms also appear to be particularly susceptible to rising ambient temperatures. Maintaining habitats for reptiles in perpetuity is unlikely to be feasible for many commercial developments. This emphasises the need to consider the creation of suitable corridors for movement. As the world experiences the increasing influence of climate change, corridors are likely to become critical to the survival of temperate reptiles such as the slow-worm.

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Chapter 5: Can Penning Improve the Outcome of Reptile Translocations?

5.1 Summary

The translocation of reptiles is widely undertaken for mitigation purposes despite reports that it is prone to failure. One possible cause of failure is post-release dispersal; however, the typically low recapture rates associated with reptile translocations make it difficult to distinguish between the effects of dispersal from increased mortality and reduced detectability. Here I test for post-release dispersal in a population of translocated viviparous lizards (*Zootoca vivipara*) using penned and unpenned release sites.

A translocation of over 1,300 viviparous lizards took place in 2016. The population was equally distributed between two adjacent receptor sites, one enclosed by a reptile-proof fence (i.e. penned) and the other left open (unpenned). Of the 131 adult females released into the penned area, a minimum of 16 (12%) were recaptured during the monitoring. This level of recapture is an order of magnitude greater than previously reported translocations involving viviparous lizards. Moreover, nearly eight times more lizards were seen and/or captured within the penned section compared to the unpenned section. Indeed, no recaptures of released lizards were made in the unpenned area. As estimates of survival and detectability were similar in penned and unpenned area, this disparity in numbers is strong evidence of post-release dispersal. Enclosing the lizards within a penned area appeared to restrict dispersal sufficiently to enable the establishment of a population.

5.2 Introduction

The translocation of reptiles and amphibians is widely undertaken for both conservation and mitigation purposes. Irrespective of motivation, a successful translocation is defined as one that results in a self-sustaining and viable population (Griffith et al., 1989). In a review of reptile translocations, Dodd and Seigel (1991) reported that most (75%) did not meet these criteria for success; indeed, 20% were known to have failed. In a more recent but comparable meta-review, reported success rates were double that described in 1991 but still never exceeded 50% (Germano & Bishop, 2008). Of these, mitigation translocations involving reptiles were the most frequent to result in failure. Both studies questioned the suitability of herpetofauna for translocation.

Amongst the most frequently cited reasons for failure are poor habitat within the receptor site, insufficient numbers released, human collection, predation or persecution, disease, a lack of prey or dispersal from the release site (Dodd & Seigel, 1991; Hare & McNally, 1997; Butler et al., 2005; Germano & Bishop, 2008). The number of failed translocations that cited dispersal from the release site as the principal reason for failure was over three times greater than any other factor (Germano & Bishop, 2008). Post-release dispersal has been shown to greatly influence the success of translocations across a range of taxa (Stamps & Swaisgood, 2007; Le Gouar et al., 2012 and references therein); despite this, post-release dispersal appears to be poorly reported. In a review of over 1,000 published abstracts from studies involving translocated animals (insects, amphibians, reptiles, birds and mammals), just 28% referenced post-release dispersal (Le Gouar et al., 2012). Of the 39 studies that specifically cited post-release dispersal as a factor in the failure of the translocation, two involved reptile species.

Whilst both the causes and effects of post-release dispersal are largely understood (see Chapter 2), relatively few studies have focused on mechanisms to manage it. One proposed solution was to recreate recognisable features (or natal cues) within the receptor site. The Natal Habitat Preference Induction (NHPI) theory states that animals are likely to exhibit strong preferences for habitat types that were present within their natal home ranges as they associate these with survival and resources (Stamps & Swaisgood, 2007). Large disparities between habitats at the capture and release sites can stimulate long-distance migrations (Morris et al., 1993; Stamps & Swaisgood, 2007). If habitats present at the donor site could be accurately recreated within the receptor site, post-release dispersal could be mitigated. However, to what degree the habitats would need to mirror those of the donor site is unknown but is likely to vary according to species.

An alternative method of mitigating post-release dispersal is the soft release of animals into a temporary holding enclosure or pen prior to their full release. Temporary holding areas have ranged from the erection of simple fences around the release site to a full enclosure (Knox & Monks, 2014). This period of captivity prevents post-release dispersal and allows the released animals time to acclimatise to the receptor site (Le Gouar et al., 2012). This approach has been successfully applied to birds (Clarke et al., 2002) and mammals (Stanley Price, 1989; Bright & Morris, 1994). More recently, soft release has also applied to lizards (Knox & Monks, 2014; Fitzgerald et al., 2015) and tortoises (Tuberville et al., 2005). These studies have shown that the presence of physical barriers can inhibit post-release dispersal. Indeed, in all cases involving reptiles, the penned animals exhibited smaller home ranges and increased site fidelity, even after the fence or enclosure had been removed. The duration of the penning ranged from 71 days to 12 months although only Tuberville et al. (2005) tested for the effect of penning duration. Of the three test groups of gopher tortoises (*Gopherus* *polyphemus*) (no pen vs penned for nine or 12 months), those penned for the longest period exhibited the highest levels of site fidelity. Indeed, 92% of the gopher tortoises penned for 12 months established a burrow within 1 km of the core release area, compared to just 62% of those penned for nine months and 23% of those that were unpenned.

Both the act and duration of penning appear to influence site fidelity in reptiles; however, this has never been tested in the UK. A population of slow-worms was translocated to Bus Company Island (BCI) in 1995 (Platenberg, 1999; Platenberg & Griffiths, 1999); although no fences or enclosures were used, the release site was almost entirely surrounded by the Great Stour river. The fast flowing river is likely to have acted as a barrier to dispersal. The slow-worm recapture rates recorded during the two-year post-release monitoring were considerably higher than any reported in Chapter 2. Although not a robust study of penning, the results of BCI do indicate that penning could prove effective at mitigating the effects of post-release dispersal.

5.2.1 Objectives

The aim of this study is to ascertain whether low recapture rates, reported in Chapter 2, were the result of post-translocation dispersal or another factor such as mortality. I examined whether the temporary penning of a translocated population of viviparous lizard resulted in a higher recapture rate. To achieve this I:

- Compared photographic records of translocated animals with those captured during monitoring;
- Compared and contrasted the number of lizard encounters within penned and unpenned release sites;

- Used Capture Mark Recapture (CMR) to generate relative abundance estimates of lizards in penned and unpenned release sites. I also tested for differences in survival and detectability estimates between the groups; and
- Examined whether translocation influences the body condition of viviparous lizards.

5.3 Methods

5.3.1 Donor Site

In 2016, planning permission was awarded for the redevelopment of a now disused research campus in Kent, UK. The campus included 14 ha area of rough grassland with patches of scattered scrub, subdivided into small compartments by a series of drainage ditches. Large vegetated earth mounds were present throughout the area. Although historically the donor site was managed for amenity purposes, the presence of tall shrubs throughout the grassland indicates that no mowing or other habitat management had been undertaken during recent years.

A pre-planning survey was undertaken by an ecological consultant in 2013 to inform an Environmental Impact Assessment. The survey comprised the use of Artificial Cover Objects (ACO) only, involving an unspecified number of felt squares (0.5 m^2) set at an approximate density of 10 ha^{-1}. Seven visits were undertaken between April and July 2013. The survey identified a peak count of between 10 and 18 viviparous lizards (the peak count is the maximum number of individuals recorded on a single visit). Unfortunately, the report does not specify the age class of all captured animals, which is why a range has been provided. Using criteria set out in Froglife (1999), a 'Good' population was recorded.

5.3.2 Release Site

A release site, located approximately 6 km south of the donor site, was selected by ecological consultants. The site comprised a 36 ha parcel of restored land situated within a country park. Formerly, the release site was the site of a coal colliery before being briefly used for agriculture. Within the past 10 years, the habitats in the release site have been allowed to regenerate without human intervention. Habitats found within the release site included a mosaic of rough grassland, scattered scrub, secondary birch woodland and, to a lesser extent, bare ground in the very early stages of succession (Figure 1). The soil was free-draining and the sloping topography meant that there were no ponds or other waterbodies present. The release site was open and received high levels of insolation; however, this same openness also meant that the site was exposed to relatively strong winds. This mosaic was assessed by the ecological consultants as suitable habitat for the viviparous lizard.

Figure 5.1: A plan of the release site showing both the penned and unpenned receptor sites

Prior to the translocation, a reptile survey of the release site and the immediately surrounding land was undertaken by ecological consultants in April and May 2016. The survey comprised seven visits utilising both Visual Encounter Survey and ACO. One hundred cover objects (1 x 0.5 m or 0.5 m^2 pieces of felt) were placed in suitable habitat and checked seven times. No resident populations of reptiles were recorded within the release area; however, a small population of viviparous lizards were recorded 200 m to the north-west within the restored area.

Within the release site, two adjacent areas were selected each measuring approximately 1.5 ha. Each area included a comparable habitat composition of grassland, scrub and bare ground. One of the two areas was randomly selected and enclosed with purpose-built reptile exclusion fencing (Figures 2 and 3). The two receptor sites are referred to as either ‘penned’ or ‘unpenned’. Both the penned and unpenned sites were augmented with comparable enhancements ahead of the translocation. Within each area, the habitat enhancements included the construction of one hibernaculum and four earth banks (for basking).

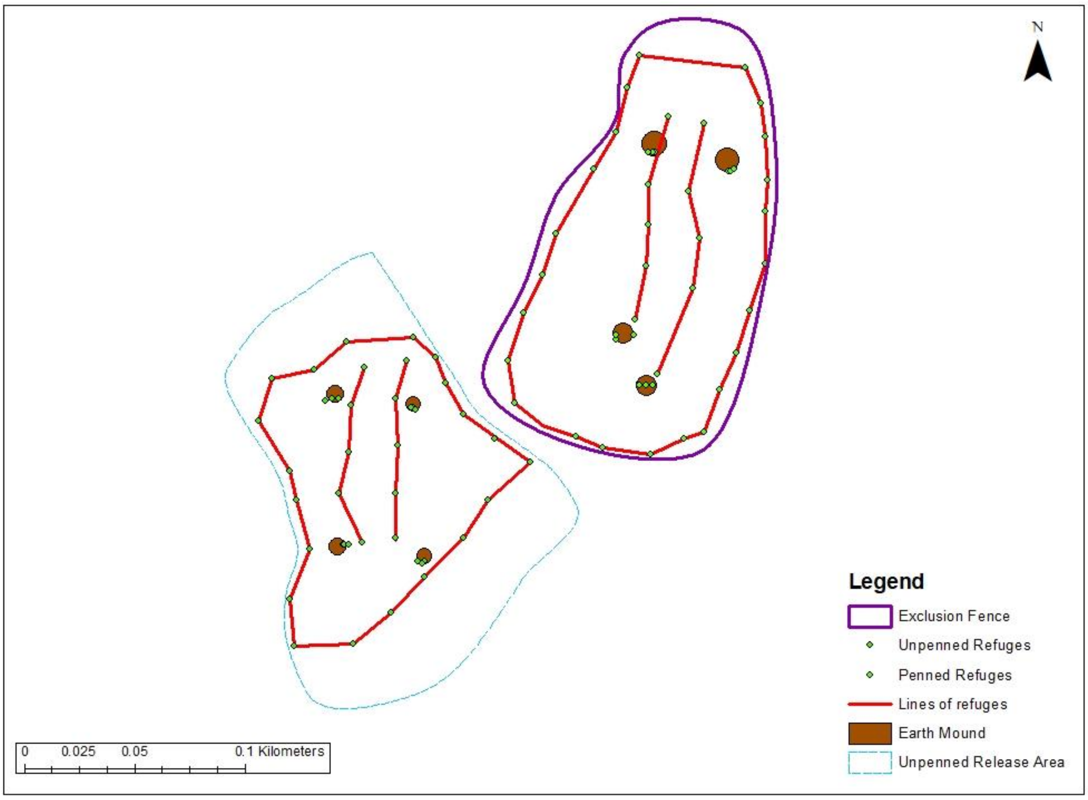

Figure 5.2: The penned and unpenned areas were augmented with comparable habitat enhancements including earth mounds and a hibernaculum. Artificial Cover Objects (refuges) were installed within suitable habitat as follows: two inner rows, an outer row following the actual (penned) or hypothetical (unpenned) fence line. ACO were also installed on the earth mounds. The blue line is the hypothetical boundary of the unpenned area.

Figure 5.3: The reptile exclusion fence prevented the emigration of lizards from the penned site (as can be seen beyond the fence)

5.3.3 Translocation

The capture and translocation of viviparous lizards was undertaken by an ecological consultant. Given the extent of suitable habitat, the donor site was compartmentalised using reptile exclusion fencing and a high number of artificial cover objects were positioned within suitable habitat. The cover objects were checked twice-daily and any reptiles encountered were caught by hand. Morphometric data (body weight and SVL) and identification photographs collected from captured adult lizards only (see below) followed the methods described in Chapters 2 and 3. Other than age class, sex (if known) and tail condition, no data were collected from sub-adults. Viviparous lizards were captured and released on the same day. The translocation commenced on 22nd July 2016 and ended on 17th October 2016, lasting 67 days in total.

The translocated lizards were randomly allocated to the two receptor sites (maintaining a 50:50 sex-ratio where possible). The lizards were divided into three groups depending on their estimated age:

- Adult (≥ 40 mm SVL):
- Sub-adult / juvenile (< 40 mm SVL):
- Neonate: very small and black in coloration (i.e. between birth and first hibernation).

The threshold for adulthood was individuals becoming sexual mature. Huelin (1985) and Bauwens & Verheyen (1987) both reported that sexual maturity was reached at around 40 mm in lowland populations of viviparous lizards. However, as measuring was undertaken by the author retrospectively using photographs taken by the consultant, an estimate of size was also made by the consultant in the field. Where necessary, I amended age classes following analysis.

In total, 1,364 viviparous lizards were translocated, comprising 362 adults and 1,002 unsexed juveniles (Table 5.1). Of these, 695 lizards were released in the penned section and 669 in the unpenned area.

Table 5.1: Translocation data

Group	**Translocated Lizards**	
	Penned	***Unpenned***
N	695	669
Adult males	65	56
Adult females	131	109
Sub-adults	83	83
Neonates	416	421
With lost or damaged tails (%)	157 (23)	161 (24)

5.3.4 Monitoring

Post-translocation monitoring was undertaken by the author between April and May 2017. The monitoring comprised 31 visits utilising a combination of Visual Encounter Surveys and ACOs. Ninety ACO were placed within suitable habitat, 45 in each of the two receptor sites

(c. 30 ha^{-1}). The order in which the penned and unpenned areas were checked was alternated between surveys and the starting point randomised. The ACOs were arranged as follows to test whether the translocated populations were attempting to migrate from the receptor sites (see Figure 2):

- 10 ACO were laid centrally within the fenced area and included the point of release. The cover objects within the inner section were arranged in two rows of five;
- 18 ACO were laid in an outer line, which for the penned area was 5 m inside of the exclusion fencing and for the unpenned area followed the assumed outer boundary; and
- Three ACO were placed on the southern aspect of each of the four purpose built earth mounds found in each receptor site.

Where encountered, viviparous lizards were captured by hand enabling morphometrics and identification photographs to be collected, following methods described in Chapters 2 and 3.

5.3.5 Data Analysis

Recaptures

Identification photographs were collected from all lizards captured throughout the monitoring period. These photographs were compared to those taken of the translocated population to ascertain the number of relocated individuals remaining within the penned and unpenned areas. Given the difficulty of identifying reptiles using photographic identification coupled with the large number of lizards translocated, it was necessary to restrict the analysis of recaptures to a small subset of the available data. Female lizards measuring ≥ 36 mm SVL (the size of the smallest adult female translocated) were selected. As no photographs were taken from translocated sub-adults, no comparisons were attempted here. However, as these sub-adults mature, it will become increasingly difficult to identify recaptures within the population. Individual lizards were identified using chin scalation patterns.

Encounter Frequency

The number of viviparous lizard ‘encounters’ was calculated for both penned and unpenned sites. Encounter rates were calculated as the cumulative total of viviparous lizards caught and those that were seen but evaded capture, divided by the number of visits (31 in this case). It is important to note that ‘encounters’ is not a proxy for abundance as individuals might have been caught on multiple occasions. However, if detectability in the two areas is the same, the number of encounters in penned and unpenned areas do provide an indirect estimate of relative population density.

I tested for differences in encounter rates between the penned and unpenned areas. As the data were non-parametric, a Wilcoxon Matched Pairs test was used to test for differences in whilst controlling for variation between survey dates.

Capture-Mark-Recapture (monitoring data only)

To test whether occupying a penned or unpenned area influenced estimates of survival or detectability, a Cormack-Jolly-Seber (CJS) model (Jolly, 1965; Seber; 1962) was developed using MARK programme (v.8). This was undertaken using monitoring data only and irrespective of data gathered during the translocation in 2016. The two sampling occasions on each day were pooled to provide one sample per day for analysis. Binary encounter histories were constructed for all captured lizards within the penned and unpenned receptor sites. The data were coded according to sex and/or age group (adult male, adult female, sub-adult i.e. < 40 mm SVL). To test that the data were appropriate for CMR, encounter histories were tested for Goodness of Fit using 'U-Care' software V2.3.2.

A range of models was developed and tested; the models are provided in Appendix 4. Vectors of survival and detectability were allowed to vary temporally and between groups. Model selection was largely based on the level of parsimony i.e. the models with the lowest AIC scores and highest model weight and likelihood. However, models that generated non-meaningful estimates of survival and detectability (i.e. 1's or 0's) were rejected and a model with a higher AIC chosen.

An attempt was made to generate estimates of abundance *N* for the penned area; however, very low recapture rates meant the derived parameters and associated confidence intervals were extremely wide and unrealistic. As an alternative, an abundance estimate was generated by multiplying the known number of individuals by the respective mean population detectability rates generated by the CJS model. Although less robust than a Closed Population Model generated in MARK, published studies have validated the accuracy of this method (Wood et al., 1998).

Population-level Morphometrics

To test whether translocation and, in particular penning, affected the body condition of translocated lizards, a Scaled Mass Index (SMI) assessment was undertaken on a subset of the population. This assessment was restricted to adult male lizards with an intact tail as:

- The timing of the translocation meant that the body condition of females is likely to have been affected by parturition;
- Individuals with broken tails exhibit misleading condition indices; and
- Many sub-adults are likely to have developed into adults during the intervening period (Meylan et al., 2001).

The analysis was further restricted to the penned area and compared the mean body condition those animals translocated into the penned area in 2016 to those recorded during the monitoring in 2017. No analysis was undertaken for the unpenned area given paucity of individuals captured and likelihood of encountering a large number of non-translocated (resident) individuals (see below).

The SMI was calculated as described in Chapter 3. An independent samples t-test was used to test for differences in the mean SMI of the penned lizards differed significantly differed from that of the translocated population.

Demographics

To test whether penning influenced demographic structure, a comparison was made between the translocated and both the penned and unpenned areas. A Chi-squared test for differences was used to test for the differences in the ratio of adult males, adult females and sub-adults present.

5.4 Results

5.4.1 Recaptures (2016 – 2017)

One hundred and thirty-one adult female lizards (≥ 36 mm) were translocated into the penned area. The subsequent monitoring identified 39 female lizards, of which 16 were recaptures of translocated individuals. Of the remaining 23 female lizards, five were adult and 18 were sub-adults. The five adult females were either resident lizards, animals that have matured from translocated sub-adults or individuals that cannot be identified due to poor resolution photographs. Given the latter, the five adult female lizards might have been translocated; as such, the recapture rate of translocated animals (12%) is a minimum estimate. No translocated females were encountered in the unpenned area.

5.4.2 Encounter Rates (2017 only)

There was a clear difference in the number of encounters made between the penned and unpenned sections, with nearly eight times more lizard encounters in former (Wilcoxon Matched Pairs: W = 4.0, P < 0.001; Table 5.2).

Table 5.2: A comparison of viviparous lizard encounter histories by area

Group	**Penned**	**Unpenned**
Caught	128	21
Missed	100	8
Total	228	29
Mean encounters per visit (SE)	7.35 (0.91)	0.94 (0.21)

Based on photographic records collected during the CMR (i.e. monitoring data only), the number of individually identified lizards occupying the penned and unpenned areas were 101 and 16 individuals respectively (Table 5.3). Of these individuals, 16% were caught on multiple occasions within the penned area, whilst this number rose to 25% in the unpenned area. The latter value is indicative of a small number of individuals being captured on multiple occasions.

Table 5.3: A summary of viviparous lizard captures by area

Group	**Penned**		**Unpenned**	
	N*	**Proportion**	**N***	**Proportion**
Adult males	27	0.26	7	0.44
Adult females	11	0.11	3	0.19
Sub-adults	63	0.63	6	0.37
Total	**101**	**1.00**	**16**	**1.00**

* N = the number of lizards captured in 2017

During the course of repeated monitoring visits, the number of individuals recognised in the penned area increased rapidly and consistently, in stark contrast to the unpenned area (Figure 5.4). By visit 13, 50% of the identifiable individuals within the unpenned area had been encountered and the population count broadly plateaued after visit 17.

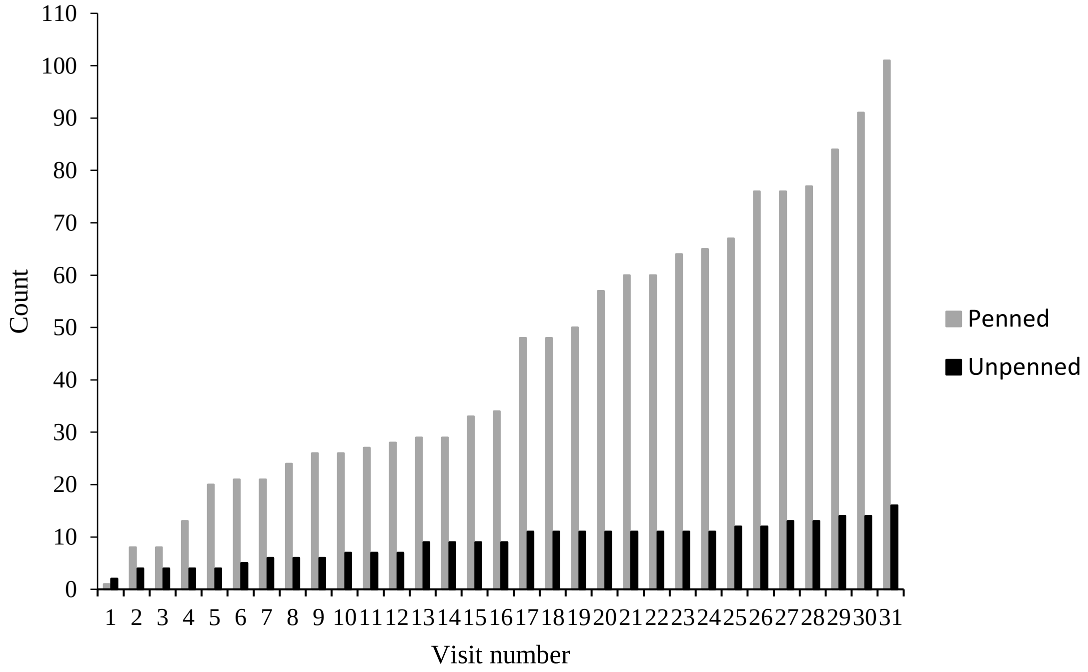

Figure 5.4: The cumulative total of identified lizards increased more rapidly in the penned section when compared to the unpenned section. Furthermore, the increase in numbers reported for the penned section continued to increase throughout the monitoring, which is indicative of a much larger population.

5.4.3 CJS Analysis (CMR data only)

Despite a degree of under-dispersal, the goodness of fit test confirmed that both the penned ($\hat{c} = 0.23$; $\chi^2_{(29)} = 6.57$) and the unpenned ($\hat{c} = 0.96$; $\chi^2_{(1)} = 0.94$) data were appropriate for CMR. Following Cooch and White (2016), ĉ was manually adjusted to 1.0 for both datasets.

Model Selection

A range of CJS models were developed for the penned data, of which the most parsimonious constrained survival (φ) as a constant value and equal between groups (Table 5.4). Given the short timescales involved, it is reasonable to assume constant survival. In contrast, detectability was allowed to vary temporally and between groups. Allowing detectability to vary between groups resulted in minor changes (≤ 2 ΔAIC) to the AIC value, model weight and likelihood; indeed, the use of any of the top three models could be justified. However, Model 1 was the most parsimonious model for the data, confirmed that the detectability of all groups varied equally over time.

Only a single model attracted any support from the unpenned data (Table 5.4). The most parsimonious model was identical to that used in the penned section. As before, survival (φ) was held as a constant value and equal between groups whilst detectability was allowed to alter over time but not between groups.

Table 5.4: CJS model selection showing the top four models for the penned and single model for the unpenned data

Model	AIC	ΔAIC	Weight	Likelihood	Parameters	Deviance
Penned Data						
1. φ(.)p(t) – no groups	220.14	0.00	0.25	1.00	14	141.91
2. φ(.)p(t) - males ‘p’ separated	220.44	0.30	0.22	0.86	18	131.21
3. φ(.)p(t) - females ‘p’ separated	220.54	0.40	0.21	0.82	16	136.93
4. φ(.)p(t) - all groups ‘p’ separated	221.12	0.98	0.16	0.61	20	126.04
Unpenned Data						
5. φ(.)p(t) – no groups	-619.01	0	1.00	1.00	18	23.44

* φ – survival, p - detectability

Using Models 1 (penned) and 5 (unpenned), individual survival and detection rates were derived for lizards occupying respective areas (Table 5.5). Estimates of survival were high in both groups as would be expected for a short duration study. Also in both groups, the 95% confidence intervals of individual detectability varied markedly over time (≤30% penned; 11% unpenned). Detectability was allowed to vary over sample occasions but not between groups. This indicates that some unknown factor, such as ground temperature or wind speed, was influencing the detectability of all groups equally.

Table 5.5: CJS generated survival and detection estimates based on Models 1 and 5 of Table 5.4

Parameter	**Estimate**	**SE**	**95% CI**	
			Lower	**Upper**
Penned				
Survival	0.91	0.02	0.86	0.94
Detectability (mean)	0.14	0.08	0.04	0.36
Unpenned				
Survival	0.99	0.03	0.40	1.00
Detectability (mean)	0.17	0.16	0.01	0.54

Many of the penned and unpenned models generated spurious derived estimates of survival and detectability. It is likely that the models were sensitive to small number of individuals and high proportions of single capture occasions (Figure 5.5).

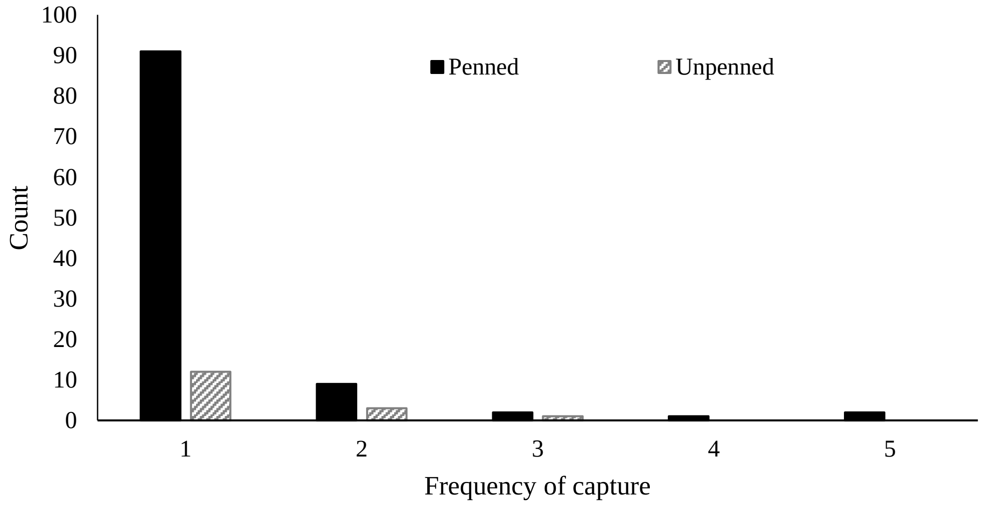

Figure 5.5: A comparison of individual capture frequency in penned and unpenned areas. The frequency of encounters was greater for the penned area and is indicative of a significantly larger population of lizards when compared to the unpenned area.

A broad approximation of abundance was calculated by combining the number of individuals recorded during the CMR (penned = 101, unpenned = 16) with the respective mean detectability estimates generated by the CJS models (penned = 0.14; unpenned = 0.17). The wider confidence intervals reported for the unpenned area indicate a lower level of confidence in the value. Abundance values of 721 (95% CI = 215 – 2,020) and 94 (1 – 333) were achieved for the penned and unpenned sections respectively.

5.4.4 Population-level Morphometrics

Body condition of male lizards (mean SMI = 3.03, SE 0.09) released into the penned area did not differ from that of male lizards (mean SMI = 3.4, SE 0.13) during the monitoring (t-test: $t_{(63)} = 0.62$, $P = 0.537$).

5.4.5 Population Demographics

The pre- and post-translocation populations differed significantly in demographic structure (chi-squared test for differences: penned $\chi^2_{(2)} = 36.642$, $P < 0.001$; unpenned $\chi^2_{(2)} = 27.025$, $P < 0.001$; Table 5.6). The proportion of sub-adults observed declined following the translocation. This shift away from the dominance of sub-adults appeared to be more pronounced in the unpenned population; however, this is likely to be the effect of the smaller numbers involved.

Table 5.6: Population demographics by population and area

Group	Translocated (2016)		Monitoring (2017)	
	N	***Proportion***	***N***	***Proportion***
Penned				
Adult males	65	0.09	27	0.26
Adult females	131	0.19	11	0.11
Sub-adult	499	0.72	64	0.63
Unpenned				
Adult males	56	0.08	7	0.44
Adult females	109	0.16	3	0.19
Sub-adult	504	0.75	6	0.38

5.5 Discussion

In 2016, 695 and 669 viviparous lizards were translocated into the penned and unpenned release sites respectively. Included within the penned subset were 131 adult females. Of these, a minimum of 16 (12%) were recaptured during the subsequent monitoring. As this value of 12% is based on a small subset of the population and given that both survival and detectability are constant across groups, it is possible that 83 (i.e. 12% of 695) translocated lizards were encountered. Within Chapter 2, the highest reported number of recaptured viviparous lizard was a single individual (or 1.2% of the translocated population). Four of the five post-translocation schemes monitored that involved viviparous lizards did not identify any recaptures. Indeed, no recaptures were made in the unpenned area. The presence of an exclusion fence has resulted an increase in recapture rates by an order of magnitude.

The CMR identified 101 individuals within the penned area and 16 within the unpenned. Averaged population estimates indicated abundance sizes of 721 in the penned area and 94 in the unpenned area. Although both estimates have wide confidence intervals, the abundance estimates do broadly accord with respective count and encounter data.

As expected, the exclusion fence appears to have a profound effect on the densities of lizards. The number of lizard encounters (used as a proxy for population density) was significantly greater in the penned area. Assuming the mean penned population of 721, the fenced area could support a lizard density of around 481 ha^{-1}. This figure broadly aligns with the number translocated into the area and falls within the known lizard densities of between 100 and 800 ha^{-1} depending on habitats (Strijbosch & Creemers, 1988). Unfortunately, generating approximate population densities for the unpenned area is more problematic. The absence of physical boundaries and presence of continuous habitat make defining densities more difficult. That said, the low encounter rate of lizards in the unpenned area do indicative lower population density.

Many of the viviparous lizard’s life traits are density dependent, although the nature and extent of these is subject to debate. Both Massot et al. (1992) and San Jose et al. (2016) report increased juvenile mortality rates with increased densities (or specifically adult density in the latter). However, models presented by Mugabo et al. (2013) indicate that yearling survival is density independent whilst juvenile survival actually increases with density. All three studies actively manipulated the density of lizards through translocation. Unlike the other studies, Massot et al. (1992) did not utilise any form of enclosure and post-release dispersal could have influenced their results. The CMR did identify a marked reduction in the proportion of sub-adult lizards in both the penned and unpenned areas from pre-translocation levels. Despite this, the CJS survival rates of both age groups (adult and sub-adult) were consistent during study. It is possible that survival estimates are heterogeneous, and increased mortality rates occurred prior to or during hibernation. High population densities could also result in declines in body condition, typically associated with increased competition. However, no evidence of such declines were identified for the penned population.

Habitats throughout the release site, which included both the penned and unpenned areas, were largely homogeneous; indeed, the release site was selected on this basis. The key difference between the penned and unpenned areas is the presence of an exclusion fence around the former’s periphery. During previous chapters, explanations for the paucity of recaptures of translocated animals included 1) mortality, 2) lack of detection, and 3) dispersal. The use of an exclusion fence in the current study enables these otherwise confounding effects to be teased apart. For instance, if mortality and/or changes in the detectability of translocated animals were the principal causes of the lack of recaptures, both the penned and unpenned populations would be affected in the same way. It is hard to conceive of a scenario in which the presence of an exclusion fence influenced either survival or detectability. The fence would not stop aerial predators nor terrestrial predators such as cats or foxes. The ACOs were positioned a minimum of 5 m from the fence, so not to be affected by its presence (i.e. shading). There is an argument that by preventing the lizards from dispersing, there is an increased chance of detection. The CJS models yielded estimates of detectability for penned and unpenned areas that had widely overlapping confidence intervals, suggesting no difference in detectability between the two populations. The CJS models also indicated that detectability varied temporally but not between groups, suggesting that a common factor is affecting both populations equally. That said, seasonal detection biases have only been reported for slow-worm and not viviparous lizards (Sewell et al., 2012). If either survival and/or detectability were the primary driver behind the paucity of recaptures, the effects would have been the same in both populations.

Populations within both the penned and unpenned areas underwent a significant demographic shift away from being dominated by sub-adults (albeit less so for the penned area). Natal dispersal is known to occur in the juvenile phase in viviparous lizards (Meylan et al., 2001). How natal dispersal interacts with post-release dispersal is unknown; however, the paucity of sub-adults recorded in the monitoring could indicate a synergistic effect. The penned population, in contrast, retained a large proportion of sub-adults, demonstrating that penning can mitigate the effects of both natal and post-release dispersal. The relative importance of penning is likely to be greater if the translocated population includes sub-adult lizards.

In contrast to Platenberg's (1999) slow-worms, the body condition of pre- and post-translocated adult male lizards (penned area only) were not significantly different. There have been no studies investigating how the translocation affects the body condition of viviparous lizards; however, it is clear that the temporary enclosing of a population did not adversely affect the body conditions of those individuals involved.

5.5.1 Conclusions

No adverse effects arising from penning have been reported, either at the population or the individual level. The act of penning lizards appears to have inhibited dispersal, which will increase the likelihood that a population will become established (Tuberville et al., 2005). Where suitable habitat exists, viviparous lizards are able to rapidly colonise new areas assuming suitable habitat (Beebee & Griffiths, 2000). It is expected that once the exclusion fence is removed (see Section 4.6), descendants of the formerly enclosed population will begin the natural colonisation of the remaining release site.

Given the uncertainty of the effects of density, there is a clear need to manage penned populations at levels between those provided by Strijbosch and Creemers (1988). Lizards penned at very high densities are likely to suffer from the effects of increased competition and/or facilitated disease transmission.

Whether penning is an appropriate mitigation strategy should be considered on a case by case basis. A cost-benefit analysis should be undertaken and include consideration of welfare and commercial aspects. When animals are held in captivity, even in a semi-wild state, there is a duty of care on the management to ensure that population is healthy. This should include the provision and maintenance of suitable habitat at an appropriate extent, the control of predators and the limitation (if not preclusion) of anthropogenic disturbance. Species also differ in their suitability for penning. The current study appears to demonstrate that viviparous lizards are appropriate candidates; indeed, data showing poor levels of recapture (presented in Chapter 2) indicate that viviparous lizards may be a particularly suitable species.

Although clearly effective at inhibiting dispersal, penning should not be seen as a panacea for adverse effects arising from translocation. The pre-translocation surveys, undertaken by an ecological consultant in 2013, reported a peak count of between 10 and 18 viviparous lizards. Based on Froglife's (1999) criteria, this is representative of 'Good' population (Table 5.1). The current surveys reported peak counts of seven and two for the penned and unpenned areas respectively. On a single survey visit, the combined peak count was eight. Using the Froglife (1999) guidance, this is assessed as a 'Poor' population. The combined peak counts of viviparous lizards in the penned and unpenned areas were lower than the peak count achieved for the pre-translocation populations. Further work to identify the adverse effects of translocation and methods to mitigate them is still required.

5.5.2 Future Studies

In autumn 2017, the fence will be removed from the penned area releasing the population into the wider release site. The penned population will have been enclosed for a period of 12 months, a period sufficient to alleviate dispersal in gopher tortoises (Tuberville et al., 2005). Further monitoring should seek to ascertain whether a population has become established in the formerly enclosed site.

The use of head scale patterns for large populations and prolonged periods has proved to be problematic. Damage to scales arising from predator attacks and/or fights with conspecifics resulted in scales being damaged or lost. Furthermore, variation in the quality of photographs can preclude the re-identification of individuals. PIT tagging could represent an alternative method enabling the rapid and accurate identification of individuals. However, there are no studies as to the effect of PIT tagging viviparous lizards and it is unclear what, if any, unanticipated effects could arise. Further research into this field could greatly improve the accuracy of monitoring programmes.

Further work to develop spatially explicit CMR is needed to establish the effects of individual response heterogeneity. Incorporating individual responses is an important next step in assessing how populations response to treatments, such as translocation (Chandler & Clark, 2014).

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6.0 Conclusions

The goal of this study was to ascertain the effectiveness of translocation in mitigating the impact of development. It involves the assessment of real world examples of projects and mitigation. The monitoring of six translocated populations of reptiles is reported in Chapter 2. Although the study sites were all different, they were typical examples of mitigation-translocation in the UK. Very few translocated individuals were recaptured during the monitoring; indeed, 50% of the projects had no recaptures at all. There are three possible causes for the lack of recaptures: post-release mortality, imperfect detection or post-translocation dispersal (Dodd & Seigel, 1991; Sealy, 1997; Plummer & Mills, 2000; Butler et al., 2005). Of these, post-release dispersal is the most frequently cited potential cause of failure (Germano & Bishop, 2008). In the absence of recaptures, it is not possible to ascertain the success of the projects. Reptiles could, in theory, establish a population beyond the bounds of the receptor site. This would be dependent on the proximity of suitable habitats; however, these same habitats would lack the legal safeguards afforded to the receptor site and could be subject to development at a later date. Such dispersal would also bring in to question the cost-effectiveness of creating a, potentially, unoccupied receptor site.

Post-release mortality and dispersal both result in populations that are smaller than originally translocated. If reptiles are being moved into hitherto uninhabited areas, they should include sufficient numbers to be viable. This highlights a fundamental issue - how many individuals are needed to form a viable population at a receptor site? Unfortunately, there are no published values for the minimum viable population sizes of widespread reptile species nor any robust guidance on the minimum number of individuals that should be translocated. The values presented in the Herpetofauna Workers' Manual (Gent & Gibson, 2003) are entirely arbitrary and based on ‘best guess’ rather than empirical evidence. Chapter 4 reports on a population of 103 slow-worms that were translocated to BCI over 20 years ago and continue to persist there today. The isolated nature of BCI is likely to have inhibited post-release dispersal; indeed, the results presented in Chapters 2 and 5 suggest that, in the absence of physical barriers, the slow-worms are likely to have dispersed into the surrounding unfavourable habitats. However, assuming that dispersal is controlled, a founder population of around 100 individuals appears to be suitable for slow-worms. The use of population viability analyses could be useful in determining species-specific minimum population viability sizes along with factors that affect them (Lecomte et al., 2004; Bell & Herbert, 2017).

Post-translocation monitoring identified populations of resident reptiles at four of the six study sites including two that were thought to contain no reptiles by the developer. Standard post-translocation monitoring, comprising simple counts, would not have identified these animals as resident; indeed, the presence of these residents would have been (and presumably are being) misinterpreted as evidence of a successful translocation. This highlights the need to collect individual-based monitoring data both before and after mitigation. Simple presence-absence counts alone, as recommended by published guidance (HGBI, 1998; Froglife, 1999; Highways Agency, 2004; Natural England, 2011), are not sufficient to ascertain whether a translocated population has become established. To determine the success of a translocation, it is essential to be able to re-identify individuals post-release. However, until such a time that the published survey guidance includes a need for more detailed data, it is unlikely that it will be collected.

Like many species of snake, the adder exhibits a marked response to translocation (Plummer & Miller, 2000; Butler et al., 2005; Barve et al., 2013); however, in contrast to studies of other species, the effect was most pronounced in males. Translocated male adders significantly increase their movements and home range sizes. They are also capable of undertaking large unidirectional movements back to the donor site, clearly putting themselves at risk from construction-related activities. Whether these increased movements highlight the influence of philopatry or are a behavioural response to translocation is unclear; however, irrespective of this they do confirm post-release dispersal in the species. The adder is unique in so far as it is the UK's only venomous species. Post-release dispersal coupled with the species' willingness to cross areas of unsuitable habitat have clear implications for the siting of receptor sites near human habitation.

Chapter 5 provides unequivocal evidence of the effects of post-release dispersal in viviparous lizards. Translocated lizards were identified within the penned area but not in its unpenned equivalent. The presence of a fence was the only fundamental difference between the sites, which suggests that dispersal – rather than mortality – explains the lack of recaptured lizards in the unpenned area. Sites that lack physical barriers retain very few, if any, translocated animals. Paradoxically, naturally or artificially (i.e. fenced) isolated sites may be more likely to maintain self-sustaining populations, as those with permeable boundaries may allow the founders to become widely dispersed in unsuitable habitat. Evidence from Chapter 5 demonstrates that penning restricts dispersal of viviparous lizards. Results from Chapter 4 suggest that slow-worms can also establish a small population in the long-term if dispersal is restricted by a natural barrier (i.e. a river). Post-translocation penning is not a new idea and it has been successfully applied to reptilian species around the world (Tuberville et al., 2005; Knox & Monks, 2014; Bell & Herbert, 2017). Despite this, none of the published UK survey and assessment guidance documents advocate its use. This is partly the result of outdated current guidance, but could also highlight a disconnect between scientific studies and conservation practice.

There are inevitably additional costs associated with penning, including the purchasing of materials and ongoing maintenance of the fence and habitats. However, these extra costs are relatively minor when compared to the likely overall cost of moving the reptiles (Germano et al., 2015). Furthermore, these additional costs should be balanced against the goal of translocations, which is the establishment of a viable and self-sustaining population of reptiles. The vast sums of money currently being spent have had no demonstrable benefit to the reptile populations involved. Cost reductions could, however, be achieved through the selection of sites that have natural barriers to movement, such as rivers or the bases of cliffs and quarries.

6.1 Concluding Remarks

There is currently no evidence to support the notion that translocating reptiles from development sites provides any tangible conservation benefits. The paucity of recaptures prohibits any meaningful assessment of success. What is equally clear from this study is that post-release dispersal has a profound effect on the outcomes of translocations. To improve the efficacy of translocation, it may therefore be important to restrict dispersal. To this end, penning could prove to be an effective tool. Equally, the selection of receptor sites with natural barriers could inhibit dispersal.

How can mitigation practice be improved within the framework of current legislation and planning regulations? The current legislation protecting widespread reptiles is focused on preventing harm to individual animals rather than the conservation of viable populations. Consequently, there is no legal obligation to ensure that translocated reptiles found a sustainable population, although this is clearly a requirement if there is to be no net loss of populations, and the spirit of ‘Favourable Conservation Status’ – which enshrines the protection of other species – is to be observed. As shown by the current study and previous research (Durso & Seigel, 2015), reptiles have inherently low detectability and this poses challenges for population assessment. Although strengthening the legislation and/or current guidance to ensure that post-translocation monitoring is carried out using individual-based methods would be desirable, clearly this could increase costs, increase delays and increase the need for specialist expertise and training. This is likely to be unpopular with both developers and decision-makers. Alternatively, a more landscape-level approach could be adopted that requires resources to be invested in compensatory activities that strengthen the protection of existing viable populations, rather than moving animals from small, marginal habitats where they may go extinct anyway. Such an approach might embrace habitat banking and offsetting, which are themselves controversial and possibly unproven (Bull et al., 2013). A pilot project is currently underway to test such an approach for great crested newts and the outcome may drive changes to policy and practice for other protected species. Reptiles, with their patchy distribution, could be an attractive model for a similar scheme; however, there are significant gaps in our knowledge of how reptiles respond to such interventions. Prior to undertaking such approaches, effort should be made to ensure such gaps are filled with empirical evidence (Lewis et al., 2017).

6.2 Future Studies

This study provides the first broad-scale quantitative evidence that current mitigation translocations of UK reptiles are not compensating for the loss of populations to development. Rigorous testing and monitoring of translocations are required to make informed decisions over its future use. The first step is to encourage the publication of post-translocation monitoring, even where the outcome is not a favourable one. Learning what doesn’t work is equally as important as identifying what does. The following includes areas highlighted by this study that require further study:

- Grass snakes occur at low population densities, meaning that translocations typically involve few individuals. They are also probably the widest-ranging of British reptiles, with home ranges exceeding 10 ha (Madsen, 1984). It is therefore necessary to investigate the effect of translocation on the ecology and behaviour of this species;
- Design and implement studies to ascertain whether translocation results in changes to individual detectability;
- Investigate whether post-release dispersal is a random process driven by stress and/or disorientation, or whether reptiles orientate themselves by a specific factor or factors; and
- Investigate the physiological and behavioural responses of gravid females and their offspring to translocation.

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Appendix A: Request for Help

Dear XXX,

I'm writing to you to ask for assistance with a Ph.D. research project that I'm currently undertaking. I'm investigating the effectiveness of translocation as a mitigation strategy for reptile-development conflicts. As I'm sure you are aware, a lot of what we (the consultants) and the Statutory Bodies (Natural England, CCW, SNH) endorse as 'appropriate mitigation' has no scientific basis; bat bridges are a recent and fairly high profile example of this (see Altringham, 2013). The use of reptile translocation is a grey area and we are hoping to investigate the longer term effects through the current study.

If you're willing and able to help, your input would be kept to the bare minimum; I expect that the demands on your time are already high. Essentially I need you to collect just a little extra data on top of that which you would normally record during the translocation. By collecting the extra information during this process, we are able to assess the longer term effects using rigorous scientific methods. As individuals are caught, I need you to collect the individual's weight (g) and length (mm) and take an identification photograph. The methods are described in the attached project description sheet along with more information on the background and aims. I've designed the protocol to minimise the additional time required (I appreciate that this is a business) and with a little care each animal can be processed in around one to two minutes.

The receptor site can be either *in situ* or *ex situ* and should involve between ten and 100 animals.

I hope you see the value of this work and if you think that you and (COMPANY) can and would like to help with this, I would be very grateful to hear from you. I'm still several sites short of what is needed and this year is the last year that I can collect meaningful data.

I hope to hear from you soon.

Regards,

Darryn J. Nash
PhD Candidate
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Appendix B: Background Information and Protocols

An Investigation of the Effects of Development-led Reptile Translocation Programmes

SECTION 1: Project Description

Background

Reptile populations occur sporadically throughout the UK where they occupy a broad range of habitats. This patchy distribution is particularly vulnerable to the effects of development, including the direct killing of reptiles or the isolation of populations through habitat fragmentation. All species of native reptile receive legal protection against reckless killing and injury under UK law. In order to prevent an offence occurring, developers frequently commission the trapping and translocation of reptiles to a place of safety outside the development footprint, and occasionally offsite altogether. Although this fulfils the legal obligation of the developer, the long-term future of the translocated population is uncertain. Despite translocation being advocated as a last resort, it continues to be a frequently employed mitigation strategy for reptile – development conflicts.

Translocations are often considered to be a success if the population persists into the following year or show evidence of successful breeding. However, post development monitoring is undertaken sporadically and rarely extends beyond one year. It has been suggested that longer term monitoring programmes may be required to identify significant deviations from typical population trends. There is a paucity of long-term research; however, a long-term study (>10 years) of a population of *Anguis fragilis* indicated that body condition deteriorated following translocation (Platenberg & Griffiths, 1999). Reductions in body condition are typically associated with declines in population fitness and therefore an increased risk of local extinction. If translocations are contributing to increased rates of localised extinction, the continued use of such practices would need careful consideration. However, the *A. fragilis* report is the only long-term study of its kind and further work is needed before making decisions on the appropriateness of using translocation as a mitigation tool for reptile-development conflicts.

Aims & Methods

The overarching goals of this research are to determine both the effects and the effectiveness of reptile translocation programmes through a comparison of pre- (or during) and post-translocated populations and individuals. Reptiles situated on the control sites should not have been subject to translocation previously as they will be compared to those that have recently been moved.

Although each aspect of the research is described separately below, there is likely to be considerable overlap between each of the tasks.

Population Fitness (Control and Study Sites)

Body condition will be used as a proxy for population fitness. Morphometrics, specifically Snout to Vent Length (SVL) and weight, will be recorded from pre- (or during) and post-translocated animals and inputted into a bespoke Body Mass Index (BMI) model. Lengths will be recorded using a bespoke squeeze box, as described in (1) below. The animal will be weighed using digital scales. Identification photograph(s) will be taken for each animal (again see below for details). These photographs will enable the conditions of individual animals to be tracked throughout the study.

Population Viability Analysis (Control and Study Sites)

Demographic data, including age and gender, will be recorded and inputted into statistical models. The model will also include estimates on survival rates, fecundity and the effects of stochastic events to provide long-term viability predictions.

Capture Depletion Modelling (Study Sites Only)

Existing datasets, which include capture totals, will be analysed using advanced statistical modelling. The models will include co-variants including climatic data, surveyor experience and survey effort. Along with data gathered from the study sites, consultants will be asked for access to additional datasets (which will be anonymised prior to use).

Radio Tracking (Study Sites Only)

In order to gain an understanding of how reptiles interact with novel environments, adders (*Vipera berus*) trapped during a translocation programme, will be fitted with a micro-radio transmitter and released at a receptor site. The individuals will be followed for the first 14 days of release to assess how the lifecycle of the individual has been affected (i.e. whether disruption of courtship occurs, for instance). Radio tracking will be undertaken by myself and volunteers.

Destructive Searching (Study Sites Only)

It is unclear how effective destructive searching is. A questionnaire will be provided to consultants that have undertaken such practices. Whether this feeds in to the PhD at this stage is unclear.

Artificial Refuge Distribution (Control and Study Sites)

The success of artificial refuges in detecting reptiles is influenced by a myriad of factors including density, micro-siting, seasonal timing, the species present and even the order in which they are checked. Recording the location, numbers and demographics of each positive refuge, will facilitate the detection of trends such as clustering.

Timescale

The fieldwork is expected to begin in spring 2012 and be completed by September 2016.

Resources

Data will be required from six study (translocation) sites to enable a meaningful analysis. Ideally, each site will be visited approximately eight times during which animals will be captured, recorded and photographed. This is the ideal number and it is accepted that this will not be possible on all sites.

The initial data collection (during translocation) would be undertaken by the respective consultants. All post-translocation monitoring would be carried out by me.

Summary of Requirements

- Reptile translocations should involve between ten and 100 animals and can be *in situ* or *ex situ*;
- The following are required: weight (g), SVL (mm), identification photographs, refuge number / location; and
- Access to the receptor site for approximately four years to undertake monitoring.

An instruction sheet for collecting data can be found on the next page.

Your assistance and continued support for the project is greatly appreciated.

Darryn Nash

Contact details:
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Mobile: 07919 895608

SECTION 2: Instructions to Consultants

Volunteers will be supplied a (bespoke) squeeze box, digital scales and a range of plastic pots; they will need to provide a digital camera. Instructions and recommendations for data collection are described below.

1. Morphometric measurements

Rather than attempting to measure each reptile (which can be time consuming and a large source of error), the animals will be placed in a squeeze box and photographed; computer software will be used to measure the animals based on known squeeze box parameters. Animals that have lost their tail should be noted (so we know what proportion don’t have tails) but do not need to be measured or weighed as they will be excluded from the final analysis.

Squeeze Box Instructions

Place the animal into the open plastic box. Gently but firmly place the foam on top of the animal and invert the box. In the case of adders, the lid should also be placed back on the box prior to inversion. The foam should be held firmly in place (taking care not to injure the animal), or the animal will attempt to correct itself (i.e. rotate itself around to its correct orientation) - photographs of the ventral side (underside) are required for measurements. A second person is useful but not necessary for photographing the animal. It is important that the photographs are as clear as possible and in particular the vent (cloaca) should be visible. The software requires that the box is as flat as possible; photographs taken from an angle will distort the measurements. It is important that either two of the edges of the squeeze box (though must be opposite) or the graticule are visible to provide a frame of reference (for measuring purposes). Where possible, ensure that snakes do not overlap themselves when coiling; if this is not possible (it is difficult with large animals) the cloaca should remain visible.

Weighing

The digital scales should be situated on a flat surface and an appropriately sized pot should be placed on top. The balance should be zeroed (tared) before the animal is added. Remember to add the lid (if used) before zeroing the pot. Try to shield the balance from wind and precipitation.

2. Photographs of individuals

Adder

Adders can be recognised by the unique marking on the head. Identification photographs should clearly show the head pattern, preferably against a plain background. Pictures of adders within white buckets are fine. Note: gloves should always be worn; anyone who does not feel confident should not handle adders.

Grass Snake

Grass snakes have unique belly patterns, particularly on the anterior third of their bodies. Photographs in the squeeze box may be sufficient to re-identify individuals; however, the anterior third must be seen. If necessary, grass snakes can be held in position enabling photographs to be taken.

Slow Worm

A combination of head and labial (lip scale) pictures can be used to identify slow worms. Given the skittish nature of slow worms and their tendency of autonomous limb shedding, particular care must be taken during handling. Always photograph both sides of the head.

Viviparous Lizard

As with the slow worm, the photographs of the top and side of the head will permit identification. Again, always photograph the right side of the head.

3. Age and gender

Estimation of age and gender will be based on size and morphology respectively. Although size varies between individuals and can be affected by a myriad of factors, it is still the best determinant of age. Broad (and somewhat arbitrary) classes will be used for juveniles, sub-adults and adults. Head shape, tail length and coloration will be used to determine gender. As these aspects will be captured during the squeeze box stage, no further measurements are required.

4. Location

Where artificial refuges are used and mapped, the location of captured individuals should be recorded.

Appendix C: Huggins RD Model Selection for BCI

Model*	**AIC**	**ΔAIC**	**AIC Weights**	**Model Likelihood**	**Parameters**	**Deviance**
S(.) γ(.) p(.) c(.): c=p, male separate phi, p and c	650.65	0.00	0.48	1.00	8.00	532.88
S(.) γ(.) p(.) c(.): c=p, male separate p and c	651.26	0.60	0.36	0.74	7.00	535.80
S(.) γ(.) p(.) c(.):c=p, all groups separate p and c	652.90	2.24	0.16	0.33	10.00	530.36
S(.) γ(.) p(.) c(.):c=p, S fixed at CJS values, male separate phi, p and c	668.04	17.38	0.00008	0.0002	6	554.8501
S(t) γ(t) p(t) c(t): c=p, male separate phi, p and c	747.16	96.51	0	0	54	438.086
S(t) γ(t) p(t) c(t): saturated model	943.71	293.06	0	0	19	11691.2

* Movement (γ` and γ``) fixed for no movement; phi – survival; p – detectability; (t) – varies over time; (.) – constant over time;

Appendix D: CJS Model Selection (Chapter 5 – Penned)

Model*	**AIC**	**ΔAIC**	**AIC Weight**	**Model Likelihood**	**Parameters**	**Deviance**
phi(.) p(t): no groups	220.14	0.00	0.25	1.00	14	141.91
phi(.) p(t): male separate p	220.44	0.30	0.22	0.86	18	131.21
phi(.) p(t): female separate p	220.54	0.40	0.21	0.82	16	136.93
phi(.) p(t): all groups separate p	221.12	0.98	0.16	0.61	20	126.04
phi(.) p(t): SA separate p	222.48	2.34	0.08	0.31	19	130.36
phi(.) p(t): female separate phi & p	223.10	2.96	0.06	0.23	17	136.71
phi(t) p(t): all groups separate p	224.53	4.4	0.03	0.11	27	106.79
phi(t) p(t): all groups separate p	233.30	13.16	0.0004	0.001	27	115.56
phi(.) p(.): no groups	239.96	19.82	0.00001	0	2	189.90

* phi – survival; p – detectability; (t) – varies over time; (.) – constant over time; SA – sub-adult

Appendix E: CJS Model Selection (Chapter 5 – Unpenned)

Model*	**AIC**	**ΔAIC**	**AIC Weight**	**Model Likelihood**	**Parameters**	**Deviance**
phi(.)p(t): no groups	-619.01	0.00	1	1	18	23.44
phi(t)p(t): no groups	-51.72	567.29	0	0	31	22.45
phi(.)p(t): male separate p	-48.84	570.17	0	0	35	15.61
phi(.)p(t): SA separate p	-45.78	573.23	0	0	35	18.67
phi(.)p(t): no groups for phi, female separate p	-43.91	575.10	0	0	35	20.55
phi(t)p(t): saturated model	-39.26	579.76	0	0	52	8.68
phi(t)p(t): all group for phi, no groups for p	-36.20	582.82	0	0	46	15.36

* phi – survival; p – detectability; (t) – varies over time; (.) – constant over time; SA – sub-adult

Appendix F: Open Models for removal data

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OPEN MODELS FOR REMOVAL DATA

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Individuals of protected species, such as amphibians and reptiles, often need to be removed from sites before development commences. Usually, the population is considered to be closed. All individuals are assumed to (i) be present and available for detection at the start of the study period and (ii) remain at the site until the end of the study, unless they are detected. However, the assumption of population closure is not always valid. We present new removal models which allow for population renewal through birth and/or immigration, and population depletion through sampling as well as through death/emigration. When appropriate, productivity may be estimated and a Bayesian approach allows the estimation of the probability of total population depletion. We demonstrate the performance of the models using data on common lizards, *Zootoca vivipara*, and great crested newts, *Triturus cristatus*.

1. Introduction. When protected species occur on a site scheduled for development, there may be a legal requirement for them to be relocated to an alternative site before the development can proceed [Germano et al. (2015)]. In the UK, such relocations are often required for amphibians and reptiles. These relocations are typically achieved by conducting regular surveys during which detected animals are relocated to a suitable alternative habitat. We refer to collection and removal as translocation. The duration of the translocation is determined by the predicted size of the community and/or constituent species present. Current guidelines (developed 18 years ago) state that translocations should last between 60 and 120 "suitable" days [HGBI (1998)]. After the prescribed period has elapsed, a minimum of five trap-free days is required before the translocation is considered to be complete. Although it is acknowledged that some individuals may be left behind, this is considered to be a "reasonable effort" in line with current UK legislation. More recent guidance is less prescriptive, but suggests survey effort may need to last for 1–3 years [Natural England/Defra (2015)].

Our proposed methods were motivated by removal sampling data of the kind illustrated in Tables 1 and 2. The species surveyed are respectively common lizards,

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Key words and phrases. Common lizard, depletion, great crested newts, RJMCMC, stopover model.

TABLE 1

Removal sampling: *Counts of common lizards removed in* 2007. *A dash indicates that no sampling took place on that day. Temp denotes the maximum daily temperature* (°*C*) *recorded on each visit to the study site. Here*, *the number of removed individuals*, $D = 213$

Date	**Count**	**Temp**	**Date**	**Count**	**Temp**	**Date**	**Count**	**Temp**	**Date**	**Count**	**Temp**
24-May	0	20	02-Jul	2	15	10-Aug	7	19	18-Sep	6	16
25-May	–	–	03-Jul	7	17	11-Aug	–	–	19-Sep	6	16
26-May	–	–	04-Jul	3	16	12-Aug	–	–	20-Sep	6	14
27-May	–	–	05-Jul	1	15	13-Aug	12	18	21-Sep	4	14
28-May	–	–	06-Jul	1	15	14-Aug	8	20	22-Sep	–	–
29-May	–	–	07-Jul	–	–	15-Aug	1	18	23-Sep	4	14
30-May	–	–	08-Jul	–	–	16-Aug	10	14	24-Sep	1	14
31-May	–	–	09-Jul	1	16	17-Aug	9	16	25-Sep	5	11
01-Jun	0	22	10-Jul	–	–	18-Aug	–	–	26-Sep	5	12
02-Jun	–	–	11-Jul	–	–	19-Aug	–	–	27-Sep	0	12
03-Jun	–	–	12-Jul	2	17	20-Aug	6	17	28-Sep	2	12
04-Jun	–	–	13-Jul	–	–	21-Aug	–	–	29-Sep	–	–
05-Jun	1	21	14-Jul	–	–	22-Aug	–	–	30-Sep	1	14
06-Jun	0	21	15-Jul	–	–	23-Aug	–	–	01-Oct	3	16
07-Jun	2	21	16-Jul	0	18	24-Aug	–	–	02-Oct	0	16
08-Jun	0	23	17-Jul	0	16	25-Aug	–	–	03-Oct	1	16
09-Jun	–	–	18-Jul	3	18	26-Aug	–	–	04-Oct	0	16
10-Jun	–	–	19-Jul	–	–	27-Aug	–	–	05-Oct	0	16
11-Jun	1	26	20-Jul	0	13	28-Aug	–	–	06-Oct	0	16
12-Jun	1	20	21-Jul	–	–	29-Aug	–	–	07-Oct	–	–
13-Jun	–	–	22-Jul	–	–	30-Aug	–	–	08-Oct	0	16
14-Jun	–	–	23-Jul	1	18	31-Aug	–	–	09-Oct	1	14
15-Jun	0	13	24-Jul	–	–	01-Sep	–	–	10-Oct	1	15
16-Jun	–	–	25-Jul	0	16	02-Sep	9	18	11-Oct	1	15
17-Jun	–	–	26-Jul	–	–	03-Sep	–	–	12-Oct	0	16
18-Jun	–	–	27-Jul	–	–	04-Sep	–	–	13-Oct	1	16
19-Jun	–	–	28-Jul	–	–	05-Sep	1	18	14-Oct	–	–
20-Jun	1	18	29-Jul	–	–	06-Sep	8	17	15-Oct	0	16
21-Jun	2	19	30-Jul	–	–	07-Sep	2	18	16-Oct	0	12
22-Jun	3	16	31-Jul	–	–	08-Sep	–	–	17-Oct	0	15
23-Jun	–	–	01-Aug	1	18	09-Sep	11	18	18-Oct	0	15
24-Jun	–	–	02-Aug	0	15	10-Sep	7	18	19-Oct	0	13
25-Jun	2	15	03-Aug	1	15	11-Sep	9	18	20-Oct	–	–
26-Jun	–	–	04-Aug	–	–	12-Sep	1	18	21-Oct	–	–
27-Jun	2	15	05-Aug	–	–	13-Sep	1	17	22-Oct	0	12
28-Jun	2	17	06-Aug	1	16	14-Sep	5	18	23-Oct	0	13
29-Jun	5	18	07-Aug	1	18	15-Sep	–	–	24-Oct	0	9
30-Jun	–	–	08-Aug	4	20	16-Sep	–	–	25-Oct	0	19
01-Jul	–	–	09-Aug	3	20	17-Sep	4	12			

TABLE 2

Removal sampling: Counts of male great crested newts removed in 2010. A dash indicates that no sampling took place on that day. Temp denotes the minimum daily air temperature (°C) recorded on each visit to the study site. Here, the number of removed individuals, $D = 741$. The nine missing covariate values were imputed using the average of the previous and next observed values

Date	**Count**	**Temp**	**Date**	**Count**	**Temp**	**Date**	**Count**	**Temp**
18-Mar	65	7	13-Apr	0	2.8	09-May	1	7.1
19-Mar	115	5.2	14-Apr	0	6.5	10-May	0	9
20-Mar	185	12.4	15-Apr	0	1.1	11-May	0	−0.7
21-Mar	49	6.5	16-Apr	0	–	12-May	0	2.2
22-Mar	64	3.6	17-Apr	0	3.5	13-May	0	13.2
23-Mar	9	2.3	18-Apr	–	–	14-May	1	0.6
24-Mar	38	5.2	19-Apr	–	–	15-May	1	6.9
25-Mar	102	12.4	20-Apr	–	–	16-May	0	1.4
26-Mar	16	5.2	21-Apr	0	−1	17-May	4	1.4
27-Mar	7	2.7	22-Apr	0	−3.2	18-May	0	–
28-Mar	5	3.1	23-Apr	0	−4.2	19-May	1	2.2
29-Mar	8	10.8	24-Apr	0	−4	20-May	1	10.8
30-Mar	22	–	25-Apr	0	6	21-May	0	9.3
31-Mar	0	3.1	26-Apr	16	4.2	22-May	–	–
01-Apr	2	–	27-Apr	2	4	23-May	–	–
02-Apr	–	–	28-Apr	1	7	24-May	1	–
03-Apr	–	–	29-Apr	3	4.3	25-May	0	–
04-Apr	–	–	30-Apr	3	7.7	26-May	0	18
05-Apr	–	–	01-May	4	5.1	27-May	0	10.3
06-Apr	3	–	02-May	1	8.2	28-May	0	–
07-Apr	3	3.7	03-May	0	4.2	29-May	0	15
08-Apr	2	2.1	04-May	0	2.5	30-May	0	11.5
09-Apr	0	1.3	05-May	1	2	31-May	0	–
10-Apr	4	1.8	06-May	1	4.9	01-Jun	0	5.1
11-Apr	0	3.2	07-May	0	3	02-Jun	0	3.9
12-Apr	0	6.1	08-May	0	3	03-Jun	0	3.9

Zootoca vivipara, and great crested newts, *Triturus cristatus*. Both of these are protected species which are frequently removed from the path of development, giving rise to data of the form illustrated.

The original model for removal sampling dates back to Moran (1951) and Zippin (1956). The model is the same as model M_b in the Otis notation for closed population models [McCrea and Morgan (2014), Chapter 3], which allows for behavioural response to trapping with recapture probability constrained to zero. Under this model, expected numbers of individuals decrease geometrically over time as a consequence of the assumptions of closure and constant capture probability. We refer to this as the geometric model. Recent work on removal sampling includes Bohrmann and Christman (2013), who discuss sampling design, and Dorazio, Jelks and Jordan (2005), who present a hierarchical model for when the sample site can be considered to be made up of several distinct subsites distributed spatially, with independent counts taken at each site. In addition, Dorazio, Jelks and Jordan (2005) allow for heterogeneity in capture using a beta-binomial distribution. We note in passing that such an extension to the basic removal model corresponds to models for digit preference in fecundability studies when the total number of individuals in the study is unknown; see Ridout and Morgan (1991). Dorazio et al. (2008) propose a Bayesian nonparametric model for dealing with unobserved sources of heterogeneity and Ruiz and Laplanche (2010) account for the effect of individual variability on population size estimation from removal data.

Existing removal models assume population closure for the duration of the study. However, it is often the case when sampling amphibians and reptiles that the study period encompasses the reproduction period, and hence the population is renewed by the emergence of newborn individuals, violating the assumption of closure. This population renewal is suggested by the data set of common lizards (Table 1) where it can be seen that the number of individuals detected peaks in August, three months after the study commenced. The ecology of the species suggests that this is the result of a renewal of the population due to birth [Avery (1975)]. Motivated by this and similar data sets, we develop a model that allows for a group or groups, of unknown size, of individuals to emerge/arrive at an unknown time while accounting for individuals that may die or permanently emigrate during the study period. In addition, the model estimates the number of undetected individuals, that is, the number of individuals remaining at the site at the end of the study. We note that the number of undetected individuals is the demographic parameter of interest in removal studies. We fit the model using a Bayesian approach to obtain the posterior distribution of the number of undetected individuals. An attractive feature of the Bayesian approach is that it is straightforward to estimate the probability that no animals remain (i.e., that the population is totally depleted). This is analogous to the use of Bayesian methods to estimate the probabilities of bird species being endangered [see Brooks et al. (2008)].

Additionally, when the study takes place at an unfenced breeding site and commences before the start of the breeding season, individuals can migrate into or out of the breeding site, thus violating the assumption of population closure. Populations of great crested newts are a typical example because they are known to migrate to breeding ponds in a staggered manner and then depart at the end of the breeding season. In this case, the number of renewal groups is unknown. We therefore further extend the model to allow for an unknown number of renewal groups and we use a reversible jump [RJ, Green (1995)] MCMC algorithm to fit the model and estimate the renewal pattern and the number of renewal groups.

The model we present responds to a practical ecological need, as data of the type we analyse are often encountered. It provides a completely general modelling framework which extends existing simple models to include features such as survival and recruitment. Conclusions resulting from using rules of thumb or inappropriate model fitting, with no allowance for features such as renewal or variable detection, may be used to conform to current legislative guidelines, therefore it is critical that new statistical approaches are developed so that deleterious effects on protected species can be prevented.

We introduce the model and the parameters in Section 2. We present each motivating example and the results of model fitting in Sections 3 and 4, respectively. Further extensions to the model are discussed in Section 5. Convergence diagnostics, RJMCMC details and simulation results are provided in the supplemental article [Matechou et al. (2016)].

2. Model. We assume that there are T sampling occasions taking place at times $\tau_t, \in \mathbf{R}, t = 1, \ldots, T$ and individuals detected at an occasion are permanently removed from the study site. The data set of a single species, $\mathbf{n}$, is a vector of length T with entry $n_t, t = 1, \ldots, T$ denoting the number of individuals of that species removed at occasion t. The total number of individuals of a species detected and removed from the site is denoted by $D = \sum_{t=1}^{T} n_t$, and the unknown number of individuals that will remain at the site when the study ends by N with $N \geq 0$. The primary aim of sampling is population depletion, and hence the main objective of modelling is to estimate N or its posterior distribution.

Each individual in the population belongs to one of $T + 2$ categories. If an individual belongs to category t, $t = 1, \ldots, T$, then it was removed at sampling occasion t. The N individuals that were never detected and not removed belong to category $T + 1$. The remainder of the individuals, M, left the study site either through death or emigration before being detected and before the study ended.

The probability, γ_t, of an individual belonging to category t is a function of the following parameters:

- $\beta_{t-1}, t = 1, \ldots, T$: entry parameters. The proportion of individuals that became available for detection for the first time at sampling occasion t.

  The proportion of individuals that became available for detection at least once during the study is $\Omega = \sum_{t=1}^{T} \beta_{t-1}$, while the complement of Ω, $1 - \Omega$, is equal to the proportion of individuals that arrived after the end of the study and therefore never became available for detection. It is anticipated that Ω will be close to 1 by study design.
- ϕ_t: survival probability. The probability an individual present at sampling occasion t remains until occasion $t + 1$. The parameter ϕ is used to account for natural mortality and emigration, in addition to the removal process for detected individuals, and therefore denotes apparent survival as it is referred to in the capture-recapture literature.
- p_{t-b}: detection probability. The probability of detecting an individual that is present at sampling occasion t and first became available for detection at occasion b, hence having avoided detection $t - b$ times, at occasions $b, \ldots, (t - 1)$. The parameter p_0 denotes the probability of being detected upon arrival.

Therefore, the probability γ_t can be expressed as

$$\gamma_t = \begin{cases} \sum_{b=1}^{t} \left[\beta_{b-1} \left\{ \prod_{k=b}^{t-1} \phi_k \right\} p_{t-b} \right], & t = 1, \dots, T, \\ \sum_{b=1}^{T} \left[\beta_{b-1} \left\{ \prod_{k=b}^{T-1} \phi_k \right\} \left(1 - \sum_{k=b}^{T} p_{k-b} \right) \right] + (1 - \Omega), & t = T + 1, \\ 1 - \sum_{t=1}^{T+1} \gamma_t, & t = T + 2, \end{cases}$$

where the empty product $\prod_{k=t}^{t-1} \phi_k$ is taken to be unity.

If we denote the vector of model parameters by $\boldsymbol{\theta}$, the data are described by the multinomial distribution,

$$\mathcal{P}(\mathbf{n}|\boldsymbol{\theta}) = \frac{(N + M + D)!}{(\prod_{t=1}^{T} n_t!) N! M!} \left\{ \prod_{t=1}^{T} \gamma_t^{n_t} \right\} (\gamma_{T+1})^N \left(1 - \sum_{t=1}^{T+1} \gamma_t \right)^M. \tag{2.1}$$

Alternatively, conditioning on the event of surviving until detection (or until the end of the study for undetected individuals), we can work in terms of the conditional probabilities,

$$\mathcal{P}_c(\mathbf{n}|\boldsymbol{\theta}) = \frac{(N + D)!}{(\prod_{t=1}^{T} n_t!) N!} \left\{ \prod_{t=1}^{T} \left(\frac{\gamma_t}{\sum_{t=1}^{T+1} \gamma_t} \right)^{n_t} \right\} \left(\frac{\gamma_{T+1}}{\sum_{t=1}^{T+1} \gamma_t} \right)^N. \tag{2.2}$$

Instead of using equation (2.1), we shall follow the conditional approach and use equation (2.2), which is not a function of M, for two reasons: (1) M is of no ecological interest in this case as the aim of sampling is to estimate N and the probability that it is zero, and (2) using the unconditional approach of equation (2.1) results in poor mixing in the MCMC algorithm to be used, especially for parameter M. If M is of interest, then the mixing of the chain can be improved by using more sophisticated proposal distributions that account for the correlations between M and $\{\phi_t\}$ and running the algorithm for longer.

We assume that individuals arriving or emerging into the population do so in groups, called renewal groups, and we model the arrival pattern of these groups using the probability density function (p.d.f.) of a normal distribution. Mixtures of normal distributions have also been used by Matechou et al. (2014) to model emergence of butterfly broods and by Matechou et al. (2015) to model arrival of flocks of birds at stopover sites.

For the data set of common lizards we allow for one renewal group of unknown size, which corresponds to newborn individuals. We assume that the proportion of individuals in this renewal group is equal to π_2, with $\pi_1 = 1 - \pi_2$ denoting the proportion of individuals already present at the start of the study. We further assume that the arrival times of members of the renewal group can be described by a normal p.d.f. with mean μ and variance σ^2 so that the proportion of individuals with arrival time in the interval $(\tau_{b-1}, \tau_b]$ is equal to

$$\beta_{b-1} = \pi_2 P(\tau_{b-1} < X \leq \tau_b)$$

for $b \in \{2, \dots, T\}$ while $\beta_0 = \pi_1 + \pi_2 P(X \leq \tau_1)$, where $X \sim N(\mu, \sigma^2)$.

For the data set of great crested newts, we allow for an unknown number, G, of renewal groups, each of unknown size and unknown arrival/emergence pattern, and each modelled by a normal p.d.f. as explained in the previous paragraph. In this case, π_g, μ_g and σ_g^2, $g = 1, \dots, G$, are respectively population fractions, mean arrival times and variance of arrival times of the G renewal groups, with $\sum_{g=1}^{G} \pi_g = 1$. The proportion of individuals with arrival time in the interval $(\tau_{b-1}, \tau_b]$ is now given as

$$\beta_{b-1} = \begin{cases} \displaystyle\sum_{g=1}^{G} \pi_g P(\tau_{b-1} < X_g \leq \tau_b), & b = 2, \dots, T, \\ \displaystyle\sum_{g=1}^{G} \pi_g P(X_g \leq \tau_1), & b = 1, \end{cases}$$

where $X_g \sim N(\mu_g, \sigma_g^2)$.

We adopt a Bayesian approach for inference and fit the model by using an MCMC algorithm. In the case of an unknown number of renewal groups, we use an RJMCMC algorithm that moves between models with different numbers of groups. The two detailed applications that follow are designed to take into account known features of the studied animals.

3. Common lizards.

To facilitate the redevelopment of a large area of brownfield land in Cumbria, a region in the north of England, a programme of reptile collection and removal was undertaken in 2007. Three areas of land that supported reptiles were enclosed by purpose-built reptile exclusion fencing. Within each of the resulting compartments, artificial refuges (0.5 m^2 sheets of felt and metal) were placed at a density of approximately 50 ha^{-1} within a suitable habitat. These refuges were checked once per day in the mornings only during suitable weather conditions. Common lizards were captured by hand and moved to an ex situ receptor site. The resulting removal data and daily records of temperature (maximum temperature in °C) are presented in Table 1.

Profile likelihood plots for N obtained from fitting the geometric model (which corresponds to the case of $\beta_0 = 1$, $\beta_{t-1} = 0, \forall t > 1$, and $\phi_t = 1, \forall t$) to the data show [supplemental article Matechou et al. (2016), Figure S1(a)] that the maximum-likelihood estimate obtained for N is equal to 903 individuals. This estimate for N is over four times the sample size and the likelihood surface is practically flat over a large range of values for N. The curvature around the maximum likelihood estimate for N is low, resulting in profile likelihood intervals that extend beyond values of N greater than 10,000, 50 times the sample size. The wide profile likelihood intervals are due to the fact that the assumption of population closure is violated because it is evident that a large proportion of the common lizard population actually arrived/emerged long after the start of the study. The result suggests that when there is renewal of the population during a removal study, then a different model from the geometric is needed. For comparison, we also show the profile log-likelihood plot for N obtained from fitting the model presented in Section 2, which allows for one renewal group to demonstrate that the likelihood surface is no longer flat in this case [supplemental article, (Matechou et al. 2016), Figure S1(b)]. Note that we constrain $\phi = 1$ for this illustration.

Based on the literature concerned with the effect of temperature on the detection probability of reptiles [Sewell et al. (2012)], we logistically regress detection probability on maximum temperature and its square, and hence set

$$\log\left(\frac{\eta_t}{1-\eta_t}\right) = \alpha_0 + \alpha_1 x_t + \alpha_2 x_t^2,$$

with x_t the maximum recorded temperature on sampling occasion t and $\alpha_0, \alpha_1, \alpha_2$ the regression coefficients, which gives the following expression for p_{t-b}:

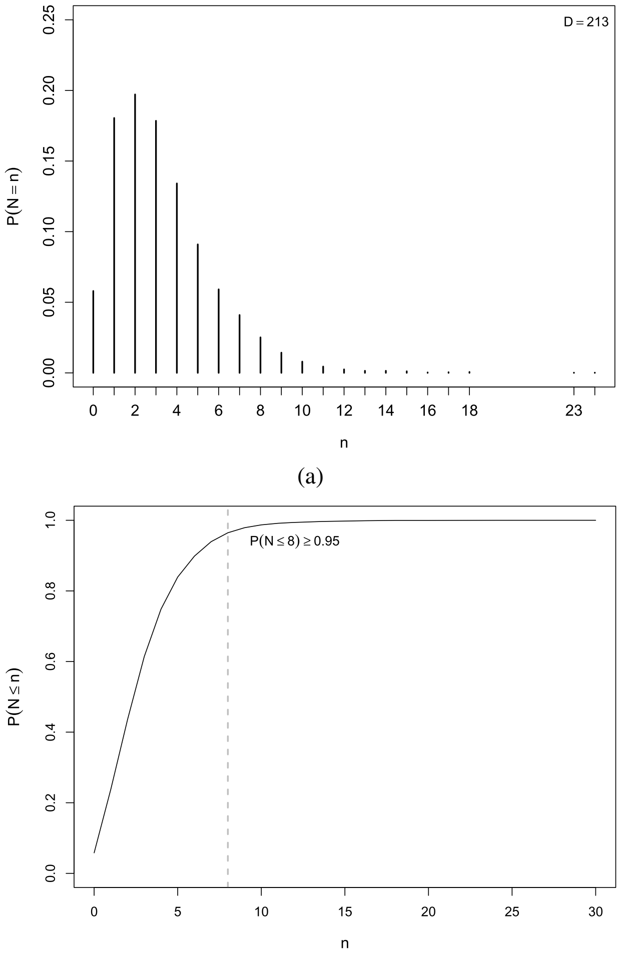
$$p_{t-b} = \eta_t \left\{ \prod_{k=b}^{t-1} (1 - \eta_k) \right\}^{\mathbb{I}(t>b)}, \tag{3.1}$$

where the indicator variable $\mathbb{I}(t > b)$ is equal to 1 if $t > b$ and 0 otherwise.

We chose a Unif[0, 1000] prior for the population size and a Dirichlet(1, 1) for the proportion of N in each group, π_1, π_2. We set the prior for the mean arrival time of the renewal group to be Normal with a mean which corresponds to the end of July – beginning of August, based on the ecology of the species [Avery (1975)] and a standard deviation of roughly one month (30 days). Finally, we chose a half-normal prior for the standard deviation of arrival times of the renewal group with parameter 0.1, a N(0, 1) prior for the coefficients of the covariates in the logistic regression model for detection probability, p, and a Unif(0, 1) prior for ϕ.

We provide the results of convergence diagnostics in Section 1.2 of the supplemental article [Matechou et al. (2016)]. The posterior distribution and cumulative posterior distribution for N are shown in Figure 1. Although the probability that the population has actually been depleted, which corresponds to the probability that $N = 0$, is lower than 10%, most of the posterior distribution mass is concentrated on values that are close to 0. In fact, the model estimates that, with a 95% probability, there were at most eight common lizards at the site after the end of the study. From the observed data, one might have expected that it would be likely that the population was totally depleted at the end of the sampling due to the observed trailing zeros; however, as noted above, the probability of total depletion is actually less than 0.1.

Because in this application the renewal group is thought to consist of juvenile common lizards which are born in the current breeding season, by comparing the



(a)

(b)

FIG. 1. *Common lizard data.* (a) *Posterior distribution, and* (b) *cumulative posterior distribution of N. Also shown in* (b) *is the value of N which corresponds to the* 95% *quantile of the posterior distribution.*

estimated proportion of individuals in each emergence group to the estimated total population, we can also extract information on the number of juveniles per adult (i.e., the rate of productivity). The posterior mean for π_2/π_1 is equal to 3.16 with a 95% posterior credible interval (CI) of (2.20, 4.43). Avery (1975) reports that female common lizards each produce between 3 and 11 juveniles per breeding season, with an average of 7.74. Therefore, assuming an equal sex-ratio of individuals in our study, our estimate of productivity is in close agreement with this previous finding.

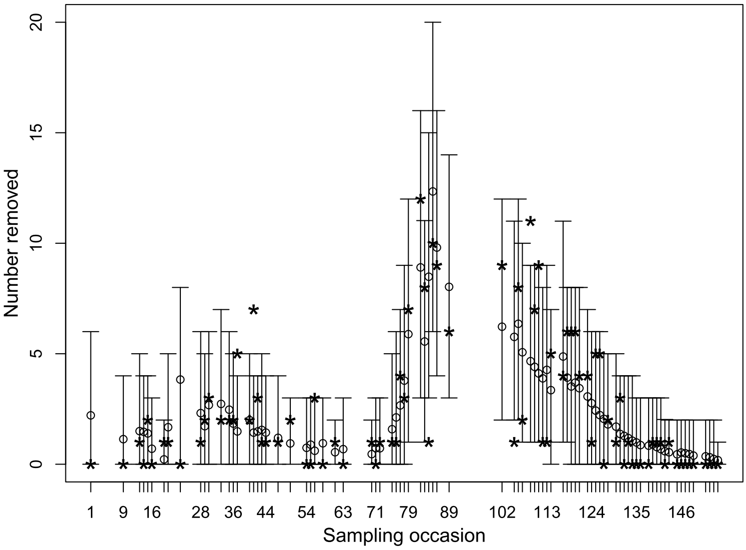


FIG. 2. *Common lizard data: assessment of model fit. The vertical bars show the width of the* 95% *quantile interval of values generated from* 1000 *randomly sampled parts of the chain, the circles show the mean simulated values and the stars the observed values. The gaps in the data correspond to days when sampling was not conducted.*

The mean arrival time of the juvenile renewal group has a posterior mean of 77.89 [95% posterior CI = (76.34, 80.47)], which corresponds to the beginning of August, as would be expected given the northern location of this study site in England [Van Damme, Bauwens and Verheyen (1990)].

The posterior mean of apparent survival probability is 0.997 [95% posterior CI = (0.989, 0.999)], suggesting that the reduction in the size of the population by the end of the study is mostly due to sampling instead of emigration or death.

The fit of the model is assessed by generating data from randomly chosen parts of the chain and comparing them to the true data set in Figure 2, where it can be seen that the model provides a good description of the increase in the number of individuals detected due to population renewal, and the actual numbers of common lizards detected are mostly encompassed by the 95% quantile intervals of the simulated values. The model achieves a good fit to the data despite the sparseness of the data and the fact that no samples were collected during the days when emergence of juveniles peaked.

Finally, the posterior distribution of detection probability as a quadratic function of maximum temperature is summarised in Figure 3. We find that detection probability is at its maximum in mild weather when maximum temperature is roughly equal to 14°C, while it decreases considerably as maximum temperature decreases or increases. Our conclusion regarding the relationship between detection probability and temperature is in agreement with literature on the subject [Gent and

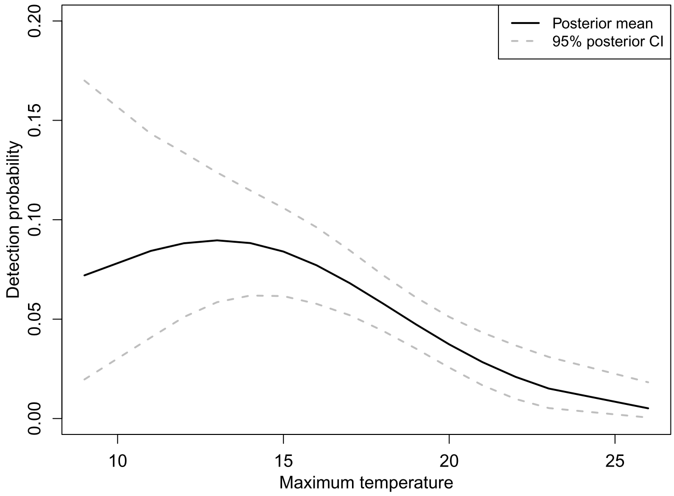


FIG. 3. *Common lizard data. Summaries of the posterior distribution of detection probability as a function of maximum daily recorded temperature. A logistic-quadratic function has been fitted.*

Gibson (1998), Joppa et al. (2009), Reading (1997)]. The large width of the posterior CI at low temperatures is due to the fact that there were very few surveys conducted under these conditions compared to higher temperatures.

4. Male great crested newts. An extensive removal study was conducted at a site in the east of England in 2010 prior to a substantial commercial development project. The areas where great crested newts were most likely to be found were fenced off to intercept the animals coming in from their hibernation areas to the ponds which were in the middle of the site. The trapping consisted mainly of collecting animals from pitfall traps, and this was supplemented by two evenings of sampling using torchlight. The data we consider here consist of removals of adult male individuals. Minimum air temperature was also recorded for most sampling occasions.

An RJMCMC algorithm was used to fit a model with an unknown number of renewal groups assuming constant survival probability, ϕ, and detection probability varying with minimum air temperature at sampling occasion t, x_t, such that

$$\log\left(\frac{\eta_t}{1-\eta_t}\right) = \alpha_0 + \alpha_1 x_t.$$

Missing values for the covariate were imputed using the average of minimum temperatures recorded on the two adjacent sampling occasions.

We used a vague Unif$\{1, \ldots, 20\}$ for the number of renewal groups, G, a Unif$[0, 1000]$ prior for N, a Dirichlet with all concentration parameters equal to 1 for $\pi_g, \forall g$, a Unif$(1, T)$ prior for μ_g to reflect our expectation that individuals are arriving during the study and not before or after, a half-normal with parameter

0.1 for σ_g $\forall g$, a $N(0, 1)$ for the coefficients of the logistic regression model for p and a Unif(0, 1) prior for ϕ.

We present details on the RJMCMC algorithm and the convergence diagnostics used in Section 2 of the supplemental article [Matechou et al. (2016)].

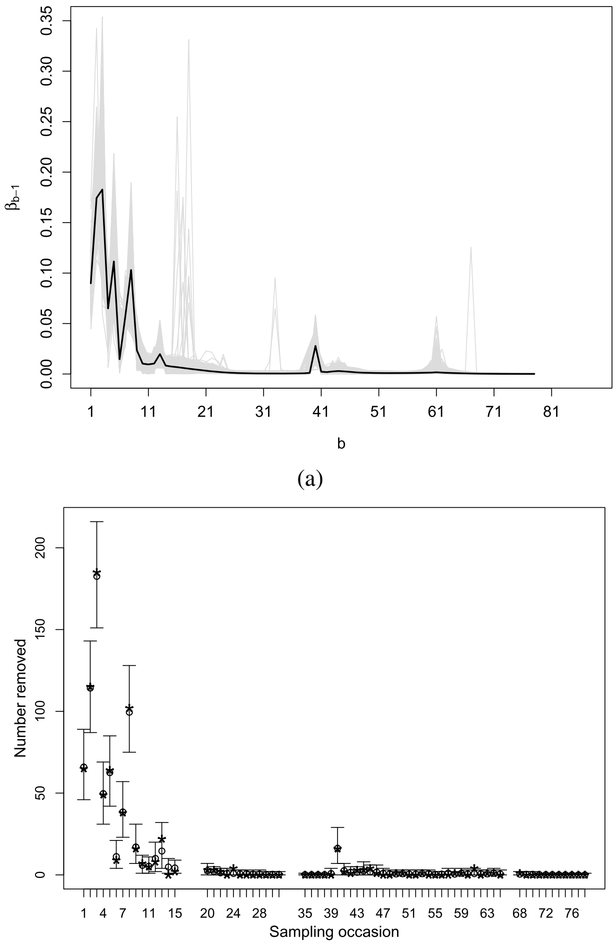
The posterior distribution for G, the number of arrival groups, is mostly (87%) concentrated on the values 7 and 8 [supplemental article, (Matechou et al. 2016), Figure S5(a)]. The posterior distribution for N is mostly (80%) concentrated on 0 [supplemental article, (Matechou et al. 2016), Figure S5(b)], and we estimate that there is a probability of 5% that 2 or more individuals were at the site after the study ended. The low estimated number of undetected individuals is unsurprising, as not only do the data have a large number of trailing zeros at the end of the study, but the estimated mean arrival times of the renewal groups are primarily in the first half of the study (see Figure 4).

Posterior summaries of the probability of detection as a function of minimum air temperature are presented in Figure 5 where it can be seen that, as expected [Sewell, Beebee and Griffiths (2010)], newts are more likely to fall into the traps as the temperature increases. Although the slope of the logistic curve is steep, the 95% posterior CIs are fairly wide. The large width of the posterior CIs is possibly due to a moderate effect of minimum air temperature on detection probability, but it could also be an artefact of the increased uncertainty due to the use of RJMCMC.

The posterior mode for survival probability is around 0.1, with the posterior mean equal to 0.19 (95% posterior CI: 0, 0.6 and 95% HPD interval: 0, 0.5) because the posterior density has a long right tail. This low apparent survival probability in comparison to the common lizard apparent survival probability is likely due to study design. Within the newt study, the traps are outside the ponds, and so newts are able to more easily leave the study area without falling into the traps.

The fit of the model is assessed graphically in Figure 4(b), where it is seen that all of the observed counts lie within the boundaries of the 95% quantile intervals of the counts simulated by the model using randomly chosen iterations of the algorithm.

5. Possible extensions. The effect of unmodelled individual heterogeneity in either detection or survival probability on the estimation of population size has been well documented in the literature [McCrea and Morgan (2014), Chapter 3, and references therein]. Our simulations presented in Section 3 of the supplemental article [Matechou et al. (2016)] suggest that, in the case of removal data, such as those considered in this paper, if there exists heterogeneity in p which the model does not account for, then the posterior for N tends to be concentrated to the left of the true value for N. If N is small, as in the case studies considered in Sections 3 and 4, then the resulting bias is also small. However, when N is large and the population is far from being depleted, then the bias in N can be substantial.



(a)

(b)

FIG. 4. *Male great crested newt data.* (a) *Estimated entry parameters obtained at each iteration of the RJMCMC algorithm, gray lines, together with the mean of all iterations, shown by the black line. The values on the x-axis correspond to sampling occasions.* (b) *Assessment of model fit. The observed counts, stars, lie within the* 95% *quantile intervals of counts simulated from the model, bars, using randomly selected iterations of the algorithm.*

If individuals are expected to exhibit variation in their detectability, then the probability of detection can be modelled as a random variable with a beta-geometric distribution with respective mean and shape parameters η and θ [see Morgan (2009), Section 2.3], which gives

$$p_{t-b} = \eta \frac{\prod_{k=b}^{t-1}\{1 - \eta + (k - b)\theta\}}{\prod_{k=b}^{t}\{1 + (k - b)\theta\}}. \tag{5.1}$$

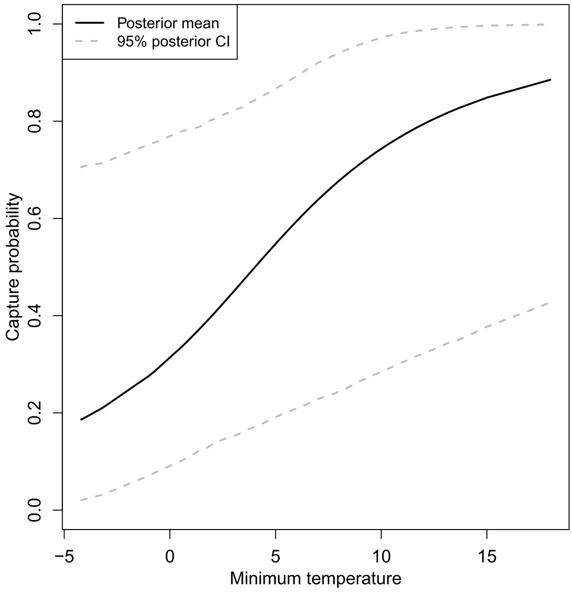


FIG. 5. *Male great crested newt data. Summaries of the posterior distribution of detection probability as a function of minimum daily recorded temperature. A logistic function has been fitted.*

Note that in the case of common detection probabilities between individuals (i.e., when $\theta = 0$) p_{t-b} simplifies to a standard geometric model with probability of success η, and

$$p_{t-b} = \eta \prod_{k=b}^{t-1} (1-\eta) = \eta(1-\eta)^{t-b}.$$

Similarly, if it is anticipated that detection probability depends on covariates, such as environmental factors, as was the case for the applications in Sections 3 and 4, then η can be modelled as a function of these using a logistic regression model. If $\mathbf{x}_1, \dots, \mathbf{x}_q$ are q environmental covariates and $\boldsymbol{\alpha}$ is a set of coefficients of length $q+1$, then

$$\log\left(\frac{\eta_t}{1-\eta_t}\right) = \alpha_0 + \alpha_1 x_{1t} + \cdots + \alpha_q x_{qt},$$

which, for example, in the case $\theta = 0$ gives

$$p_{t-b} = \eta_t \prod_{k=b}^{t-1} (1-\eta_k).$$

It is easy to show that when appropriate the model can naturally accommodate both heterogeneity and environmental covariates, as long as the covariate(s) are discrete or discretised so that the values for all years are not all different. In this discrete case, the recapture probabilities are suitable products of terms of the form illustrated in expression (5.1).

An alternative approach for modelling heterogeneity, both in detection and survival probabilities, is provided by Pledger (2000) via the use of finite mixture models. Finite mixture models have been used extensively in the capture-recapture literature for both open and closed populations, and they provide an effective way to model heterogeneity.

Our presented model assumes that there is no temporary emigration, and hence once an individual has been removed or has departed from the study it does not return. However, amphibians and reptiles have activity patterns that vary according to weather conditions and may become unavailable for detection for a period of time. This issue of temporary unavailability for capture is the equivalent of temporary emigration in the capture-recapture literature; see, for example, Barker (1997), Kendall, Nichols and Hines (1997) and Kendall and Nichols (2002). Although for the data sets considered in this paper we estimated that the population was practically depleted before the expected start of the hibernation period (i.e., end of October [Beebee and Griffiths (2000)]), it is possible that some individuals evaded detection by becoming less active as winter approached. We are currently working on extensions of the models presented in this paper that use a multi-state approach to allow for temporary emigration of individuals, developing methodology from standard capture-recapture literature [Pradel (2005)].

Removal data alone may be insufficient to estimate all parameters of interest; however, models for removal data have survival and detection parameters in common with capture-recapture models. Therefore, it may be possible to perform an integrated analysis—simultaneously modelling removal data and independent capture-recapture data [see Besbeas et al. (2002)]. This integrated analysis would result in generally improved precision of parameter estimates and may overcome challenges such as near-singularity and parameter redundancy of models [Cole and McCrea (2016)].

6. Discussion.

Translocations of protected species from the path of development are widespread in the UK and globally. However, such actions are expensive, often poorly designed and monitored, and undetected animals may comprise a significant proportion of the population left behind at the development site [Germano et al. (2015), Lewis et al. (2014)]. The models we propose here provide a basis for determining the effectiveness of such translocations, and thereby improve policy and guidance for such actions.

We have proposed a new model for the case of removal data when the assumption of population closure is violated because of: (a) individuals emerging/arriving sometime after the start of the study, either through birth and/or immigration, and renewing the population and (b) individuals departing from the study site before being detected through death and/or emigration.

The model allows for either a fixed number of known renewal groups or an unknown number, and estimates their sizes as well as the means and variances of arrival times of the individuals in these groups. The model of this paper responds to a practical need, as the data described are commonly encountered.

We provided two applications:

(i) a data set of common lizards collected during a period that encompassed the reproduction period, and hence there was one renewal group which consisted of juveniles that emerged in late summer. We estimated the probability of population depletion as less than 10%. The ratio of juveniles to adults in the population was also derived as a by-product of the analysis.

(ii) a data set of male great crested newts collected during the time when individuals are migrating to ponds to breed, where we used an RJMCMC algorithm to account for and estimate the number of renewal groups. In this case, the probability of population depletion was estimated at around 80%.

We have also incorporated environmental covariates in the estimation of detection probabilities and, although we have not undertaken a detailed model-selection exercise for our choice of covariates, we have shown using simulation that the model provides a good description of the data. The functional form of the covariate regression used for each application was guided by ecological knowledge. Our results suggest that detection probability of common lizards is lower when the maximum daily temperature is too low or too high, with the optimum being roughly at 14°C. We found that the detection probability of great crested newts varied with minimum air temperature, and as minimum air temperature increased, so did detection probability which is in-line with previous findings relating weather conditions to detectability of these animals [see Sewell, Beebee and Griffiths (2010)].

It is important to note that, while the new model incorporating both arrivals and departures provides good descriptions of the two data sets that we analyse in the paper, if capture probability is high, then there could be difficulties in estimating ϕ: if individuals are removed soon after arrival, then retention due to survival cannot be observed. The model has performed well in both case studies considered, but care should be taken when fitting complex models to sparse data. The diagnosis of possible parameter redundancy of the new model, along with how it might be overcome by combining additional information, is an area of current research.

A great advantage of adopting a Bayesian approach for model fitting is that we can evaluate the probability that more than n individuals remain at the study site for any n. In further work, we plan to investigate the posterior predictive distribution after each sample is collected to use this as a guide for calculating the number of samples still required before total population depletion is achieved.

7. Acknowledgements. We thank Herpetologic Ltd. for providing the great crested newt removal data, particularly Jon Cranfield for helpful information about the sampling protocol. We also thank Cristiano Villa for the discussion about the choice of priors for the parameters. The comments of the Associate Editor and three referees greatly improved the paper.

SUPPLEMENTARY MATERIAL

Supplement to "Open models for removal data" (DOI: 10.1214/16-AOAS949SUPP; .pdf). We provide results of convergence diagnostics, details of the RJMCMC algorithm employed and simulation results.

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