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Applying quantitative methods to conservation planning

Population dynamics of the Eurasian otter in Ireland.

Doctor in Philosophy

2008

Lughaidh Ó Néill



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SUMMARY

As appears typical in the field of conservation biology, the current study has parallel aims. The first is to improve both the limited toolbox and the biological information available for the conservation of a vulnerable species. The second is to compare and contrast the integrative, systematic and objective approach idealised by conservation biology with the traditional simplistic, or even ad hoc, approaches to conservation that persist for economically unimportant taxa. This thesis involves the gathering of information on the basic biology of otters and its synthesis into a logical modelling framework relating otter populations to the Irish landscape so as to optimise conservation measures. The thesis is presented as a series of published papers and manuscripts.

Otters have been extremely difficult to capture and mark efficiently and humanely and research on some aspects of their biology was impeded as a consequence. I present and evaluate a novel trapping technique involving Global System for Mobile communication (GSM) trap alarms coupled with padded leghold traps. The trapping method was highly efficient compared with the most popular trap currently in use. Stress and trauma were minimised by removing animals from their traps within a matter of minutes. I show that functioning alarms can greatly reduce the injuries suffered to a level consistent with one or two broken nails or claws. I tested a number of alternative methods for attaching radio-transmitters to otters and concluded in favour of intra-abdominal implantation. I implanted radio-transmitters in the field without complication, following the approach of North American researchers of river otters. This approach has not been used for Eurasian otters. The whole implantation procedure lasted less than 3 hours from capture to release such that long-term stress was avoided, almost all animals stayed within their territories and pups were not abandoned. These methodologies allow highly efficient and humane capture and marking of animals and should facilitate the collection of improved field data for otters.

Otters are secretive and nocturnal and difficult to observe and most radio-tracking studies relied on small samples of dispersed individuals. There is a reasonable body of data available on individual spatial requirements but little on the spatial structure of populations. Radio-tracking of 20 individuals revealed exclusive intra-sexual home-ranges on mesotrophic freshwaters. Information had been lacking for this common habitat in temperate regions. The aquatic area within adult male home-ranges was greater than that of adult female home-ranges and male home-ranges were heavily influenced by con-

specifics such that population perturbation occurred rapidly. Adult female home-ranges were inversely related to river width and were far smaller than those in oligotrophic systems. These observations were consistent with the classical food-based home-ranges of female mustelids (Powell 1979). By establishing the spatial structure of populations, the many estimates of individual spatial requirements could be converted to the habitat specific densities that are often a foundation of effective species conservation.

I integrated quantitative biological information, such as density and demography, into objective conservation planning. Density and demography had not been studied in Ireland previously. I determined the extent of aquatic habitat in Ireland and classified water-features according to width, productivity, altitude and geology. I estimated the potential population of otters based on habitat-specific density data and took account of declining habitat quality by correcting for the change in otter status since 1982. The corresponding estimate for the number of adult females on the island was 6, 421 (95% confidence intervals: 5,659-7,769)). I identified age-specific mortality and fecundity rates for Ireland from 78 otters gathered from 1996-2007. The deterministic rate of increase (λ) of the population was 1.07 (SD = 0.054). These data are fundamental to understanding and predicting how the Irish otter population will respond to environmental change.

The near-threatened status of the otter has led to over 14,000km of Irish watercourses being designated as candidate Special Areas for Conservation (cSAC) under the EU Habitats Directive (1992). The role of the cSAC network is to ensure the favourable conservation status of otters. The process of cSAC designation was based on expert opinion alone. I developed a spatially explicit population model, incorporating variable landscape permeability and environmental and demographic stochasticity, to investigate the ability of Ireland's cSAC network to ensure favourable conservation status for otters. I examined the extent to which favourable demographic conditions would have to be maintained or generated within cSACs to buffer the population's distribution against the effects of declining habitat quality in unprotected areas. Focusing management on the cSAC network proved little or no more efficient than simply managing the landscape homogeneously, particularly where cSACs were restricted to realistic growth rates (1.0<λ<1.1). Replacing certain cSACs with new SACs in vulnerable areas has the potential to greatly improve the network's performance. I advise that either the landscape be managed homogeneously or the cSAC network be modified. Sensitivity analysis indicated that conservation should be focused primarily on reducing mortality of adult females and juveniles. These findings have been contributed to national policy as outlined in the otter Species Action Plan (2008).

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Applying quantitative methods to conservation planning: population dynamics of the Eurasian otter in Ireland

CHAPTER 1

Introduction

INTRODUCTION

1.1 - CONSERVATION BIOLOGY

There is a growing consensus that the rate of extinction of species has increased a thousand-fold compared with pre-industrial times (Ulfstrand 1996) and is likely to increase by a further order of magnitude over the next 100 years (Lawton and May 1995, Lawton 1997). The need to moderate the impact of anthropogenic pressures on species and ecosystems has been enshrined in international law through agreements such as the Principle of Sustainable Development, the Convention on Biodiversity (UNCED 1992) and the Kyoto Protocol (UNFCCC 1997). At the national level, most countries have passed conservation legislation and designated protected areas for vulnerable species or ecosystems. However, as Lawton (1997) pointed out, 'conservation action without good science to underpin it is like alchemy, or faith healing: both sometimes produce desirable results, but you have no idea why, and mostly they do not'.

At its heart, conservation is not a scientific activity (Lawton 1997). The very establishment of conservation programs is not in itself a scientific process. Science may help to inform the process, but the decisions are ultimately political, ethical, aesthetic, even

religious, and embrace much more than just scientific information (Lawton 1997). Consequently, scarce resources and competing land-use goals necessitate efficient conservation measures to provide the ecological requirements of target species (Lomolino 1994, Jiang et al. 2007).

From the beginning, in the 1970s, conservation biologists had a common mission of slowing species loss (Noss 1999), both by highlighting the need for conservation and by providing the efficient tools it needed. Conservation biology has been described as a 'crisis discipline' (Soule 1985) and indeed some anti-conservationists dismiss it as religion rather than science (Noss 1999). Either way, conservation biology is not a cosy, academic game (Lawton 1997).

The biogeographical theory of MacArthur and Wilson (1963, 1967) was the primary stimulus for the development of modern conservation biology. The theory was rapidly interpreted in terms of reserve design (Terborgh 1974, Diamond 1975) and ensuing controversy captured the attention of natural scientists and awakened their interest in conservation (Noss 1999). Island biogeography was interesting to biologists because it was theoretical, testable, and applicable to real-world problems (Noss 1999). It led directly to the concepts of minimum viable population (MVP) and population viability analysis (PVA) which defined the new field of conservation biology (Noss 1999).

Population modelling has become one of the most powerful tools in conservation biology for comparing alternative management actions or conservation programs (Marshall and Edwards-Jones 1998, Gough and Rushton 2000, Reed et al. 2001, Lurz et al. 2003, Nilsson 2003, Bonesi et al. 2007). Modelling synthesises knowledge of a system into a logical and transparent framework and allows the examination of that system at otherwise unfeasible spatial and temporal scales (Gough and Rushton 2000, Kramer-Schadt et al. 2004, Linnell et al. 2007). Simulation models can optimise environmental decision making without the ecological and economic costs of trial and error (Kingsland 2002, McIntire et al. 2007). If used properly, they can guide conservation efforts even where data are scarce (Kramer-Schadt et al. 2004, 2005).

However, population models are not a panacea for population ecologists (Dunnings et al. 1995). They require data that are often difficult and expensive to obtain (Ruckelshaus et al. 1997, Akçakaya and Sjögren-Gulve 2000, Reed et al. 2001). For example, demographic parameters are typically plastic to temporal or spatial variations in climate, food, population density and management actions (Saether et al. 1998, Mech and Boitani 2003, Linnell et al. 2007, Sulkava et al. 2007). Similarly, dispersal is extremely

difficult to study and the limited availability of empirical information has also attracted much criticism of population models (e.g. Lima and Zollner 1996, Beissinger and Westphal 1998, Dunnings et al. 1995, Macdonald and Rushton 2003).

The results of properly constructed models are often subject to wide confidence intervals because they take full account of the uncertainty in the information they are based on (Akçakaya and Sjögren-Gulve 2000, Reed et al. 2001). The information required to forecast actual numbers for even the simplest of systems is usually lacking and population modelling should be regarded as a qualitative tool (Dunnings et al. 1995, Beissinger and Westphal 1998, Akçakaya and Sjögren-Gulve 2000, Reed et al. 2001, Lindemmayer et al. 2007). Their validity depends on the appropriateness of the data used and model output must be compared with observed patterns (Dunnings et al. 1995, Rushton et al. 1997, Lindenmayer et al. 2000, McIntire et al. 2001, Reed et al. 2001, Todd et al. 2001, Carroll et al. 2003). Nevertheless, spatially-explicit simulation models are virtually the only means to examine population development under different landscape and demographic scenarios (Kramer-Schadt et al. 2004).

There are significant costs involved with modelling, not only with preparing the model itself, but also with gathering expensive field data for their parameterisation. Conservation practitioners may defer these costs by relying on empirical generalisations, principles or indeed ad-hoc management. However, all rules of thumb have exceptions (Noss 1999), and in conservation biology exceptions occur to the extent that some ecologists have insisted that 'the world is all special cases' (e.g. Shrader-Frechette and McCoy 1993). Generalisations and principles must be interpreted and applied to particular cases cautiously and only by competent biologists familiar with the region and taxa involved. Simplistic and uncritical application of general principles can lead to flawed advice (Noss 1999). The criticisms levelled at population models apply to other decision making approaches that do not attempt to integrate the complex interactions of species and environment. Often these 'simpler' approaches ignore uncertainties and make hidden assumptions and as a consequence are highly subjective (Akçakaya et al. 2004). Indeed, in situations that incur a direct economic cost from flawed advice, such as fisheries management, the need for advice based on empirical data and objective modelling approaches haves been widely acknowledged, whereas in situations where the cost is purely or largely ecological, as in conserving carnivores, ad hoc management is predominant (Chapron and Arlettaz 2006).

Conservation biology as a discipline requires increased emphasis on broad and rigorous science, the basic field data necessary to construct and validate models, compelling applications of conservation biology on the ground in land management, and increased influence in the policy are:na (Noss 1999). The current thesis regards the conservation of the near-threatened Eurasian otter (*Lutra lutra*) (IUCN red-list 2008) in Ireland as a suitable case study for contrasting this idealised approach to conservation with traditional ad-hoc management.

1.2 - SPECIES DESCRIPTION

The Eurasian otter (*Lutra lutra*) belongs to the Lutrinae sub-family of the Mustelidae. There are 13 members of the Lutrinae but the Eurasian otter is the only species found in Europe (Wilson and Reeder 2005). Its historic range encompasses Eurasia with the exception of most south-east Asian islands (Ruiz-Olmo 2001, Kruuk 2006).

The otter is a semi-aquatic carmivore that exploits still and running freshwaters of all types (Chanin 2003). They also occur in coastal areas, provided they can maintain the water resistance of the fur by bathing frequently in freshwater (Beja 1992, Kruuk 1995). Adult males weigh 7-12kg and measure 100-120cm, while adult females are smaller at 5-8kg and 95-110cm (Ruiz-Olmo et al., 1998). Their elongated body and short legs are typical of mustelids and are well suited to an amphibious lifestyle. The eyes and nostrils are displaced to the upper part of the cranium, allowing the otter to breathe, see and hear while hardly removing its head from the water (Ruiz-Olmo 2001). Further adaptations to water include long whiskers, webbedl toes, a long flat tail and dense fur. The fur has exceptional thermal insulation and watter resistance and was highly prized by the fur trade (Saavedra 2002, Gorgadze 2004). It is generally a lustrous dark brown with slightly lighter ventral fur.

Compared with European populations, Irish otters have a darker pelt, a distinct cranial form and conspicuous throat-patches. Consequently it has been suggested that Irish otters deserve the sub-specific status of *Lutra lutra roensis* (Lynch and O'Sullivan 1993, Lynch et al. 1996). This classification has been challenged (Mason and Macdonald 1986), and recently the Irish population was found to be genetically undifferentiated from most European populations (Randi et al. 2003).

1.2.1 - DIET

The otter is an opportunistic predator that exploits prey in proportion to its availability in the environment (Erlinge 1968a, Jenkins 1980, Breathnach and Fairley 1993, Ottino and Giller 2004). A review of 37 dietary studies revealed that otters tend to act as highly specialised piscivores in temperate freshwaters which have a reasonably stable water regime, whereas in southern locations with dry seasons they behave as more generalist predators (Clavero et al. 2003).

Diet is almost exclusively of aquatic origin in Ireland and the British Isles (Chanin 2003, Bailey and Rochford 2006, Preston et al. 2006). In freshwater areas of Ireland, diet is dominated by salmonids, eels (*Anguilla anguilla*), frogs and cyprinids (Bailey and Rochford 2006), while crayfish (*Austropotamobius pallipes*) can be a dominant prey species locally (McFadden and Fairley 1983). Terrestrial prey is taken infrequently, with birds occurring in just 3% of spraints and mammals occurring even more rarely (Bailey and Rochford 2006). Otter diet has not been studied on a national basis for coastal areas, but a survey on Inis Mór found that rockling and wrasse (Labridae) dominated the diet, while eel, sea scorpion (Cottidae), blenny (Blenniidae) and molluscs were also important (Kingston et al. 1999).

There are significant energetic costs associated with fishing in cold water and cost-benefit analysis has indicated that otters are frequently living close to the limits of possible existence (Kruuk 2006). Indeed, food availability often limits otter populations by affecting numbers, timing of reproduction, breeding success and mortality (Kruuk et al. 1987, 1991, 1993, Kruuk and Conroy 1991, Heggberget and Christensen 1994, Beja 1996, Ruiz-Olmo et al. 2002, Sulkava et al. 2007).

1.2.2 - HABITAT

Otters exploit a narrow strip of habitat that bridges the interface of water and land. They spend approximately three quarters of their lives on land and one might expect the structure of the riparian habitat to be important (Kruuk 2006). Yet, while riparian cover can be of some importance, factors relating to prey density are far more so (e.g. Jenkins 1980, Macdonald and Mason 1983, Mason and Macdonald 1986, O'Sullivan 1993, Prenda

and Granado-Lorencio 1996, Durbin 1998, Madsen and Prang 2001, Chanin 2003, White et al. 2003). Re-introduced otters in under-populated conditions are a good model for determining habitat preferences and they focus almost exclusively on high productivity areas (Sjöåsen 1997, White et al. 2003).

Otters can occur in almost all aquatic habitats provided there is sufficient food (Robitaille and Laurence 2002, Kruuk 2006). Nevertheless, breeding females and their young cubs are likely to be more susceptible to disturbance and have more stringent riparian habitat requirements (Liles 2003). Declines in otter populations have been related to human disturbance and the recovered cadavers of many cubs display bite wounds from dogs (Kauhala 1996, Simpson 2006). Suitable breeding sites for otters must be undisturbed, have a good food supply nearby and not be at risk from flooding (Liles 2003, Durbin 1996a, Ruiz-Olmo et al. 2005).

1.2.3- DEMOGRAPHY

Although otters sometimes show preferences for breeding in certain months (Erlinge 1967, Kruuk et al. 1987, Hauer et al. 2002, Ruiz-Olmo et al. 2002), in general they are far less synchronised in their breeding season than other carnivores (Stephens 1957, Harris 1968, Corbet and Harris 1991). They can mature during their second year, but rarely mate until the following year (Hauer et al. 2002). Average litter sizes for otters range from 1.4-2.8 cubs depending on both food availability and population density (Wijngaarden and Peppel 1970, Mason and Macdonald 1986, Kruuk et al. 1987, 1991, Kruuk 1995, Sidorovich 1997, Hauer et al. 2002, Sulkava et al. 2007). The cubs are dependent on the mother for 12-14 months and the proportion of adult females that breed in a given year displays great temporal and spatial variation (Hauer et al. 2002b, Sulkava et al. 2007).

Given the low reproductive output of otters, one might expect them to have a high rate of survival and a long life-expectancy. Many studies have examined the age structure of otter populations and their findings are surprising in that regard. While potentially living for up to 16 years in the wild, their average life-expectancy is just 3 to 4 years (e.g. Heggberget 1991, Kruuk and Conroy 1991, Gorman et al. 1998, Ruiz-Olmo et al. 1998, Hauer et al. 2000).

Demographic parameters can vary markedly between populations and years depending on climate, food supply, population density, local adaptations and management actions (Saether et al. 1998, Mech and Boitani 2003, Linnell et al. 2007). For example, estimates of juvenile survival in European populations vary from 60% to 80% (Heggberget 1991, Kruuk and Conroy 1991, Gorman et al. 1998, Ruiz-Olmo et al. 1998, Hauer et al. 2000). Nevertheless, otter populations generally possess similar rates of recruitment and mortality, making them vulnerable to detrimental changes in either (Kruuk 2006).

1.2.4 - POPULATIONS

Classically, female mustelids occupy food-resource based territories, while male territories are determined by the dispersion of females, at least during the breeding season (Powell 1979). Exceptions to the classical model can occur even within species, as mating systems result from individual strategies rather than being an evolved feature of the species (Clutton-Brock 1989, Johnson et al. 2000). The social structure of otter populations remains largely unknown (Chanin 2003, Kruuk 2006).

Methodological issues confounded most attempts to investigate otter social structure (Kruuk 1995, Chanin 2003). Otters were difficult to capture and mark efficiently and safely, and radio-tracking studies of native populations were limited to small, dispersed samples of otters (e.g. Mitchell-Jones et al. 1984, Jeffries et al. 1986, Durbin 1993, Kruuk et al. 1993, Kranz 1995, Polednick 2005, Kruuk 2006). The social and spatial structure of an established otter population was identified on just two occasions, where researchers could either observe otters directly or track them in snow (Erlinge 1967, Kruuk and Moorhouse 1991). Resource dispersion is fundamental to the spacing and structure of carnivore society in that it may set the limits to group size and territory size (Macdonald 1983). Females appeared to vary their social structure in response to food-resource dispersion, occupying exclusive intra-sexual group territories in a coastal habitat with rich but patchily distributed resources (Kruuk and Moorhouse 1991), and fully exclusive intra-sexual territories in a highly productive freshwater environment (Erlinge 1967). Adult male territories covered several females and expanded where neighbouring males died (Erlinge 1967, Kruuk and Moorhouse 1991).

Much information is available on the range sizes of otters because this does not require tracking multiple individuals within the one area. The most striking feature to arise from these studies is the size of otter home-ranges. In coastal areas, female ranges covered

4-14km of coastline (Kruuk and Moorhouse 1991), while in freshwater areas, they ranged over 15-30km of watercourse (Erlinge 1967, Green et al. 1984, Jefferies et al. 1986, Kruuk et al. 1993, Durbin 1998, Saavedra 2002, Kruuk 2006). However, most freshwater studies were carried out in oligotrophic upland environments or in under-populated conditions following re-introductions or translocations. In Mediterranean areas, densities on oligotrophic rivers ranged from 0.05-0.20 otters/km, while those on more productive rivers ranged from 0.20-0.90 otters/km (Ruiz-Olmo 2001). Ecological studies of established populations in rich lowland rivers are lacking for north-western populations (Chanin 2003).

Consistent with their wide ranging behaviour, otter population densities are generally low. Densities ranged from 0.01-0.33 otters/km in Scottish fresh-waters (Kruuk et al. 1993), and 0.16-1.09 adult-females/km in coastal areas (Kruuk and Moorhouse 1991, Yoxon 1999). Although highly variable, otter densities are low compared with terrestrial species of similar size. This low density derives from the dispersion of their habitat and the low profit margin associated with their foraging strategy.

1.2.5 - VULNERABILITY

As a specialised predator of aquatic prey, the otter is highly susceptible to accumulating toxins. They are also highly sensitive to changes in prey availability, occur at low population densities and have low survival and fecundity rates, making the otter a naturally vulnerable species. Consequently, increased anthropogenic pressures caused populations across Western Europe to collapse during the latter half of the last century (e.g. Jefferies 1989, Foster-Turley et al. 1990, Macdonald and Mason 1992, Conroy and Chanin 2001, Elmeros et al. 2006, Prigioni et al. 2007). The pervasive impact of human presence on otter populations across Europe is illustrated by higher human density and road density in areas where otters are absent (Robitaille and Laurence 2002). The dominant pressures responsible for the decline were contaminants such as organochlorines and mercury that directly affected otter survival and fecundity or pollutants that affected fish-populations (Hamilton and Rochford 2002, Heggberget and Myrberget 1979, Jefferies 1989, Murk et al. 1998, Kruuk and Conroy 1991, Mason 1989, Mason and Macdonald 1986, Roos et al. 2001). Anthropogenic mortality and habitat change are also a significant concern for some populations (e.g. Sidorovich and Luazel 1992, Strachan and Jefferies 1996, Philcox et al. 1999, Chanin 2003). Owing to environmental improvements and focused conservation efforts, widespread healthy populations now occur in a third of European countries (Conroy and Chanin 2001). However, in a fifth of European countries, otters remain threatened, declining, rare or extinct (Conroy and Chanin 2001).

The first Irish otter survey recorded signs of otters at 88% of 2,042 sites (Chapman and Chapman 1982). A smaller follow-up survey of 246 sites, carried out a decade later, found a highly significant 13% decrease in otter presence (Lunnon and Reynolds 1991). The most recent otter survey in the Republic of Ireland, carried out 14 years later, searched 525 sites and found that otter presence had declined by a further 5% to just over 70% (Bailey and Rochford 2006). This trend was paralleled by a 10% decline in otter presence in Northern Ireland over the same period (Preston et al. 2006). There has been little spatial variation in the decline in either jurisdiction, suggesting a general decline in the density of the island's otter population (Bailey and Rochford 2006, Preston et al. 2006).

The cause(s) of the Irish decline remains unclear. The contaminants primarily responsible for the widespread collapse of otter populations in Europe were not a significant concern in southern Ireland in the early 1990s (Mason and Macdonald 1986, O'Sullivan et al. 1993, Jefferies and Hanson 2002, Kruuk 2006). Water quality declined substantially between 1980 and 1995 due to organic enrichment and poor water quality has been related to sites that proved negative for otter signs in some, but not all, surveys (e.g. Lunnon and Reynolds 1991, Hamilton and Rochford 2000, Stapleton et al. 2000, Bailey and Rochford 2006). Most recorded otter deaths arise from anthropogenic causes, yet the impact of this pressure has not been quantified because 'natural' deaths are less likely to be detected (O'Sullivan and FitzGerald 1995, Poole 2007).

1.2.6 – LEGISLATIVE PROTECTION

In response to the otter's dramatic decline and its natural vulnerability, national and international legislation was passed granting it strict protection from disturbance and exploitation (Wildlife Act 1976, 2000, CITES 1979, Council of Europe 1979, Wildlife Order 1985, Conservation Regulations 1995). The European Union (EU) requires member states to designate a coherent, trans-boundary network of Special Areas for Conservation (SAC) to ensure the favourable conservation status of otters (EU Habitats Directive 1992). The conservation status will be taken as favourable when population dynamics data indicate that it is maintaining itself on a long-term basis as a viable component of its

natural habitats, and there is, and will probably continue to be, a sufficiently large habitat to maintain its populations on a long-term basis, and the natural range of the species is neither being reduced nor is likely to be reduced for the foreseeable future (EU Habitats Directive 1992). The Habitats Directive was transposed into national legislation and 40 candidate SACs have been designated for the otter in Ireland (Conservation Regulations 1995, Natural Habitats Regulations 1997).

The preamble to the Habitats Directive explicitly states that the improvement of scientific and technical knowledge is essential for its implementation (EU Habitats Directive 1992). This is certainly true in Ireland's case. Owing to the methodological issues discussed above, research has been largely dominated by spraint surveys. Consequently, there is a reasonable understanding of diet, distribution and trends in the otter population (Chapman and Chapman 1982, Lunnon and Reynolds 1991, Hamilton and Rochford 2002, Bailey and Rochford 2006, Preston et al. 2006). There have also been several studies examining the effects of contamination and pollution (e.g. Mason and O'Sullivan 1992, 1993a, 1993b, Mason 1993, Hamilton and Rochford 2002). Nevertheless, important factors affecting otter vulnerability, such as demography and density, have received little attention (figure 1.1).

The criteria for the selection of SACs require an understanding of;

- the size and density of the population both on the site and nationally
- the quality of the habitat
- the degree of isolation of the site in relation to the range of the species
- the value of the site for conservation of the species (EU Habitats Directive 1992)

The integration of a firm understanding of the first three criteria with population demography is required to assess the value of the site and the network for ensuring favourable conservation status.

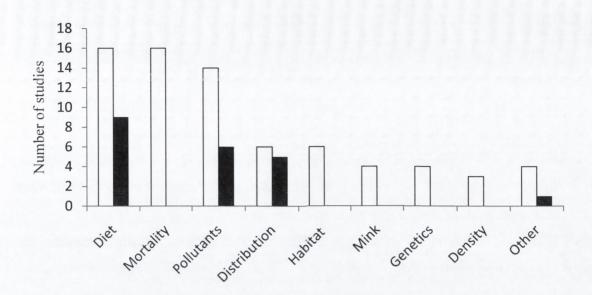


Figure 1.1. Relative intensity of research carried out on various aspects of otter biology in Great Britain (white columns) and Ireland (black columns). Numbers are based on records returned by the 'google scholar' search engine (http://scholar.google.com/schhp) on 18 March 2008 for titles containing the words 'Lutra lutra' and either of the words 'Ireland', 'Irish', 'Britain', 'British', 'Scotland', 'Scottish', 'Wales', 'Welsh', 'England', 'English' and 'UK'. Duplicate records were removed. Numbers are not absolute.

1.3 - AIMS AND OBJECTIVES

As appears typical in the field of conservation biology, the current study has parallel aims. The first is to improve both the limited toolbox and the biological information available for the conservation of a vulnerable species. The second is to compare and contrast the integrative, systematic and objective approach idealised by conservation biology with the traditional simplistic, or even ad hoc, approaches to conservation that persist for economically unimportant taxa.

This thesis involves the gathering of information on the basic biology of otters and its synthesis into a logical modelling framework relating otter populations to the Irish landscape so as to optimise conservation measures. The thesis is presented as a series of published papers and manuscripts.

 In chapters 2 and 3, I use the widespread and apparently common Irish population to develop field techniques to overcome the methodological impediments that have limited research.

- In chapter 4, I examine the spatial and social structure of otter populations in rich lowland rivers.
- In chapter 5, I estimate the size of the Irish otter population.
- In chapter 6, I determine the demography of the Irish otter population and identify lifehistory transitions that are of particular importance to the population.
- In chapter 7, I integrate information on population density, demography and behaviour into a spatially-explicit population model, and apply scientific method to evaluating and improving Ireland's approach to otter conservation.
- Finally, in chapter 8, I discuss the thesis and provide recommendations for conservation and research.

Applying quantitative methods to conservation planning: population dynamics of the Eurasian otter in Ireland.

CHAPTER 2

Minimizing Leg-Hold Trapping Trauma for Otters With Mobile Phone Technology

The data relating to the 10 otters trapped in Latvia was provided by de Jongh, Ozoliņš and de Jong. All other work was carried out in Ireland by myself.

MINIMIZING LEG-HOLD TRAPPING TRAUMA FOR OTTERS WITH MOBILE PHONE TECHNOLOGY

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ABSTRACT

We present and evaluate a protocol for the capture of otters (*Lutra lutra*) using padded leg-hold traps coupled with Global System for Mobile communication (GSM) trap alarms. The trapping method was highly efficient, capturing 46 otters at 6.9 trap-nights each. Functioning alarms allowed us to remove 36 otters from their traps within 22 (SD = 14) minutes of capture. We caught 10 otters in trap sets with malfunctioning trap alarms and retrieved them the following morning, after \leq 24 hours. Functioning alarms reduced the injuries suffered from an average cumulative score of 77.7 to just 5.5 on the International Organization for Standardization 10990-5 trauma scale (Z = 5.074, P =

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0.001). As a result, we strongly encourage the use of GSM trap alarms under the principle of refinement in animal experiments. (JOURNAL OF WILDLIFE MANAGEMENT 71(8):2776–2780; 2007)

2.1 – INTRODUCTION

The Eurasian otter (*Lutra lutra*) received a lot of research attention because of its high priority for conservation (Council of Europe 1979, EU Habitats Directive 1992, IUCN 2006). Its threatened status also focused attention on research protocol, and animal welfare considerations favoured the use of box traps in live-trapping studies (Reuther 1991, White et al. 1991, Harris et al. 2005). Regrettably, box traps were inefficient and consistently resulted in poor sample sizes ($n \le 5$; e.g. Durbin 1993, Kranz 1995, 1996b, Poledník 2005). Hancock traps were used occasionally (Green et al. 1984, Mitchell-Jones et al. 1984) but remained unpopular due to safety concerns for both humans and animals (Kruuk 1995, 2006, Blundell et al. 1999). The inefficiency of the available humane traps resulted in a meagre understanding of Eurasian otter social structure and spatial requirements (Chanin 2003, Kruuk 2006).

Leg-hold traps, although highly efficient and safe to humans (Blundell et al. 1999, Fernández-Morán et al. 2002, International Association of Fish and Wildlife Agencies [IAFWA] 2006), were more stressful and traumatic to animals than box traps (White et al. 1991, Harris et al. 2005). Prolonged retention by leg-hold traps caused frequent bone fractures or joint luxations, although padded jaws significantly reduced this risk (Olsen et al. 1986). Padded leg-hold traps, however, had poorer retention rates and caused more dental damage than nonpadded traps (Blundell et al. 1999).

Minimizing the time spent in traps could potentially reduce or eliminate the flaws of leg-hold traps and provide us with a valuable management tool. Trap alarm systems have generally involved emitting or changing the frequency of a radio signal when a trap was activated (Hayes 1982, Nolan et al. 1984, Marks 1996, Proudfoot and Jacobs 2001). Because researchers had to monitor the signals manually from nearby, Blundell et al. (1999), for example, could only reduce the maximum time spent by otters in leg-hold traps to between 8 hours and 10 hours. Larkin et al. (2003) introduced alarm systems that used the Global System for Mobile communication (GSM) network to notify researchers remotely the instant an animal entered a trap. Unfortunately, these alarms were not evaluated in terms of their effect on trauma or trapping yields. We developed a protocol for the timely release of otters from padded leghold traps using GSM trap alarms similar to

those developed by Larkin et al. (2003). We aimed to determine the impact of GSM alarms on trap-related trauma, trapping yield and the rate of retention of captured animals.

2.2 - MATERIALS AND METHODS

2.2.1 - STUDY AREA

We trapped otters in Ireland and in Latvia to provide individuals for an ecological study of social structure and for a reintroduction program, respectively. The most recent Irish national otter survey indicated a widespread distribution (Bailey and Rochford 2006). The Irish study areas included the Boyne, Nore, and Liffey river systems (figure 2.1a). All 3 systems had otter densities of roughly 0.3–0.5 otters/km of river (see chapter 4). The rivers were lowland limestone systems, dominated by brown trout (Salmo trutta) and crayfish (Austropotamobius pallipes). They also included stocks of pike (Esox lucius), perch (Perca fluviatilis), eels (Anguilla anguilla), stickleback (Gasterosteus aculeatus), and minnow (Phoxinus phoxinus).

A standard survey of otter distribution had not been carried out in Latvia, but records of otter presence indicated a widespread distribution (Ozoliņš and Rantiņš 1992). We conducted our study on the Tirza, Lieda, Kuja, and Aiviekste catchments that drained abandoned lowland agricultural land with almost 50% forest coverage (figure 2.1b). Almost all watercourses were dredged during the Soviet era but most were not maintained and reverted to a more natural state. The rivers were fed to a large extent by waters from drainage pipes, ditches and small streams rising in swamps and raised bogs. The waterways were distinguished by richness of beaver (*Castor fiber*) activity, including burrows, lodges, dams, and felled trees. Cyprinids dominated the fish fauna, although brown trout (*Salmo trutta fario*) occurred in some stretches.

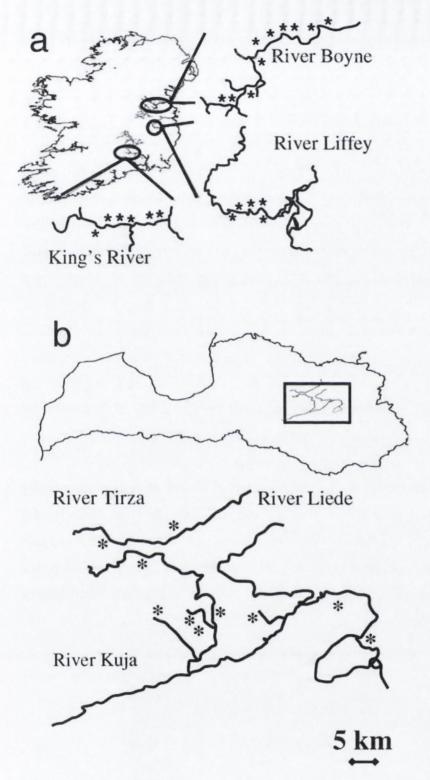


Figure 2.1. We trapped Eurasian otters from rivers in Ireland (Apr 2005–Jul 2006; a) and Latvia (May 2004; b). All trap site locations (*) were within 5 minutes walk of suitable parking on a road.

2.2.2 - TRAPPING

Alarm systems.—Larkin et al. (2003) developed an alarm system where each individual trap was fitted with a motion-sensitive very high frequency radio alarm that, when moved, caused a nearby cellular telephone to notify the researcher through the GSM network. The system was designed for use with traps set in a star formation around a central call-out station. Spacing each trap set several km apart was a more appropriate configuration for trapping riverine otters. Accordingly, we developed a simplified alarm unit that sensed the trap activation directly and placed the call to the researcher's phone. In this simple homemade Mark-I system. Phonetracker® microcontrollers (Berolina Elektronik GmbH, Berlin, Germany) caused a mobile cell phone to contact a nominated number when a circuit was closed (figure 2.2a). We incorporated a reed switch into a simple circuit that allowed us to break the circuit by placing a magnet alongside it. Removal of the magnet closed the circuit and activated the alarm. We could, therefore, monitor the trap set with a single alarm. We housed the system in a waterproof tube, glued the reed switch to the bottom of the lid, and armed the system by placing a magnet on top of the lid above the reed switch. Finally, we increased the active life of the system by adding a battery pack of 8 rechargeable AA batteries. Phonetracker microcontrollers were designed to notify the nominated number when battery power became critically low.

Owing to faults with the Mark-I system, we adopted a more generic, professionally produced, Mark-II alarm system (CatchAlert[®], Mereltron B.V., Zutphen, Netherlands) similar to that of Larkin et al. (2003). The radio alarm part of the system was again activated by removing a magnet from a reed switch so that we could fit each trap set with a single alarm (figure 2.2b). The Mark-II system also notified us remotely when battery power was low.

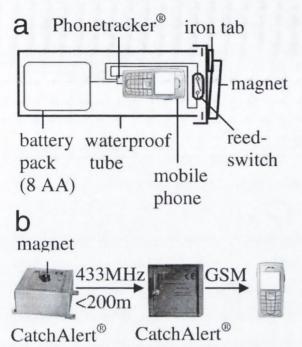


Figure 2.2. We used homemade Mark-I (a) and professionally produced Mark-II (b) Global System for Mobile communication (GSM) trap alarm systems (CatchAlert®, Mereltron B.V., Zutphen, Netherlands) while trapping Eurasian otters in Ireland (Apr 2005 - Jul 2006) and Latvia (May 2004). Following removal of the magnet from the trap alarm, both systems called the trapper's phone. The Mark-I system used a mobile phone within each trap alarm to make the call. In the Mark-II system, the trap alarms emitted a very high frequency signal to a central relay station that made the call to the researcher's phone. One relay station serviced any number of trap alarms within 200 m and identified the activated trap alarm.

Trap and alarm set-up.—We live-trapped otters in Latvia (May 2004) and in Ireland (Apr 2005–Jul 2006) using Victor SoftCatch® number 3 coyote-size leg-hold traps in their off-the-shelf state (Snare Shop, Carroll, IA, USA). Removing scent or darkening traps proved unnecessary. Initially, we replaced the rubber pads once every 2-3 months. Later on, we replaced them more frequently to increase the trap-retention rate. Otherwise, we employed standard preparatory methods (IAFWA 2006). We laid trap sets following Blundell et al. (1999), except that we trapped otter pathways rather than latrines. We took particular care that trap jaws were almost bare when set and avoided setting traps beside dens or on a slope. Trap sets consisted of 2 or 3 leg-hold traps each.

We placed one trap alarm alongside each trap set, beyond the reach of a captured animal (figure 2.3). We then placed a magnet on top of the trap alarm and connected it

independently to each trap with a length of 2kg monofilament. To ensure that animals pulled the magnet off the alarm we positioned the trap alarm and the trap anchor on opposite sides of the trap set and kept the monofilament as short as possible. We responded to trap alarm alerts immediately and checked each trap daily between 0700 hours and 0900 hours.

Immobilization.—Ketamine with medetomidine has been used without complication on otters that were removed from leg-hold traps several hours after their capture (Fernández-Morán et al. 2001). However, this drug combination is extremely dangerous for use on otters within minutes of capture when they are highly stressed (T. de Jong and A. de Jongh, Dutch Otterstation Foundation, unpublished data). To sedate otters fully, for example, when attaching external radiotransmitters, we administered an intramuscular injection of ketamine (Vetalar[®], Pfizer Animal Health, Cork, Ireland) and midazolam (Hypnovel[®], Roche Products Ltd., Welwyn Garden City, England) at 10mg/kg body-weight and 0.25mg/kg body-weight, respectively (Spelman et al. 1993). When partial sedation was sufficient, for example, to facilitate the transferal of animals from traps to transport boxes, we reduced the dosage by 66% (see chapter 3).

The Bio-Resources Unit of Trinity College (No. 201005) and the Department of Health and Children (No. B100/3735) ethically approved the trapping program in Ireland. We received trapping licenses from the National Parks and Wildlife Service (1/2005, 9/2005, C15/2005, C68/2005, C69/2005). We carried out our trapping in Latvia under license from the Nature Protection Board at the Ministry of the Environment and the State Forest Service (No. 76-34 2004).

2.2.3 - ASSESSMENT

The International Organization for Standardization 10990-5 'Methods for testing restraining traps, Annex C, C.1 Trauma scale' (www.iso.org), as adopted by the IAFWA (2006), presented the best criteria for assessing the humane use of restraining traps (Harris et al. 2005). The scale designated a score and a severity class for all injuries, so that loss of a claw was mild trauma scoring 2 points, and digit luxation was moderate trauma scoring 30 points. We recorded the incidence of moderate trauma or worse and calculated the cumulative trauma score for each individual. United States best management practice (BMP) criteria for animal welfare required an incidence of moderate to severe trauma of <30% and an average cumulative trauma score <55 points (IAFWA 2006). We used the

Mann—Whitney U-test to determine the effect of trap alarms on leg-hold trapping trauma by comparing the scores for the animals caught with functioning alarms against those caught with malfunctioning alarms. We assessed the efficiency of the trapping protocol by determining the average number of nights until a trap set successfully captured an otter (trap-nights/otter). By taking account of the number of trap sets laid every night by each researcher, we calculated the average number of otters caught by each researcher each night (otters/researcher-night). Finally, we determined the trap retention rate as the percentage of traps activated by otters that successfully restrained them (Serfass et al. 1996).

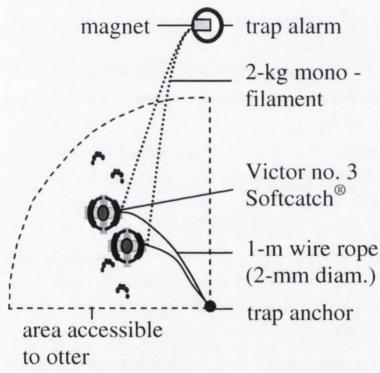


Figure 2.3. The layout of our sets of leg-hold traps (Victor SoftCatch®, Snare Shop, Carroll, IA, USA) and Global System for Mobile Communication trap alarms for trapping Eurasian otters on rivers in Ireland (Apr 2005–Jul 2006) and Latvia (May 2004). We connected each trap to a single magnet with a length of monofilament. We laid the trap alarm beyond the reach of a captured animal and armed it by placing the magnet above the reed-switch trigger. The captured animal's struggles removed the magnet and activated the alarm.

2.3 - RESULTS

Mark-I trap alarms proved unreliable due to numerous malfunctions including false alarms, missed alarms, and failure to alert when battery power was low. Because of these

faults, we retrieved 10 of the 32 otters caught in traps coupled with Mark-I alarms the following morning. The Mark-II system allowed us to capture 14 animals without complication, although it did malfunction occasionally in hard freezing conditions (\leq 4°C). The difference in reliability between the Mark-I and Mark-II alarms was highlighted by their respective trauma scores of 25.2 and 5.9 ($Z_{32,14} = -1.8$, P = 0.075).

The shorter retention time for otters trapped with functioning alarms (22 min, SD = 14 min, n = 36) compared with malfunctioning alarms (≤ 24 hr, n = 10) reduced the trauma score from 77.7 points to 5.5 points ($Z_{10.36} = -5.074$, $P \le 0.001$). A trauma score of just 5.5 was consistent with minor trauma, whereas a score of 77.7 ranked between moderately severe and severe trauma. Of the 36 cases where the alarms successfully alerted us, 5 otters suffered minor damage to gums or nails and 2 suffered moderate trauma. Conversely, of 10 otters retrieved in the morning following alarm malfunction, 1 died with severe capture myopathy, 1 died from cold exposure, and 5 suffered moderately severe to severe trauma such as dental damage, digit dislocation, or serious ocular injury (figure 2.4). Therefore, the incidence of moderate trauma or worse was just 5.6% where trap alarms functioned properly, compared to 70% where trap alarms failed to alert us $(Z_{10,36} = -4.8, P \le 0.001)$. Functioning trap alarms reduced the average cumulative trauma score and the incidence of moderate to severe trauma to just 10% and 20%, respectively, of the United States BMP criteria for animal welfare, and retention for ≤24 hours greatly exceeded both criteria (IAFWA 2006). We released all injured otters without keeping them in captivity for treatment as we did not perceive their injuries to be life-threatening.

The trapping rate throughout the study was 6.9 trap-nights per otter. By laying and servicing 4.5 trap sets each per night, we caught 46 otters, including 2 recaptures, at a rate of 0.65 otters per researcher-night. We observed an overall trap retention rate of 77%. This average was heavily influenced by escapes that occurred before we realized how frequently the rubber pads needed replacing. We increased the trap retention rate to 88% over the last 16 otters caught by replacing the rubber pads once per fortnight and by making sure that the jaws of the traps were practically bare when set.

We caught 28 medium to large-sized nontarget mammals (2 domestic dogs, 1 beaver, 2 badgers [Meles meles], 1 red fox [Vulpes vulpes], 1 raccoon dog [Nyctereutes procyonoides], 2 pine martens [Martes martes], 3 feral cats, and 17 American mink [Mustela vison]). We released them all uninjured, apart from 2 mink that drowned and 1 mink that suffered minor dental damage. We encountered less success in avoiding injury to smaller animals. Of 9 birds and small mammals (4 brown rats [Rattus norvegicus], 1

moorhen [Gallinula chloropus], 3 wood pigeons [Columba palumbus], and 1 mallard [Anas platyrhynchos]), all but 2 died or required euthanasia.

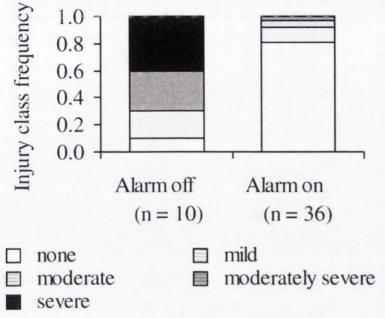


Figure 2.4. A comparison of the injuries suffered by Eurasian otters caught in alarmed and unalarmed leg-hold traps in Ireland (Apr 2005–Jul 2006) and Latvia (May 2004). We classified injuries according to the International Organization for Standardization 10990–5 Methods for testing restraining traps, Annex C, C.1 trauma scale.

2.4 - DISCUSSION

Our objective was to determine the impact of GSM alarms on trap-related trauma, trapping yield, and the rate of retention of captured animals. Clearly, the reduction of retention time, allowed by GSM alarms, minimized the injuries caused by leg-hold traps. Perhaps unsurprisingly, the reliability of the alarm system impacted greatly on animal welfare and the work involved in fixing or responding to malfunctioning alarms.

Our aim of removing otters from traps within half an hour of capture limited us to 4 or 5 trap sets per researcher. To compensate, we selected only particularly good trap sites and removed unsuccessful traps rapidly. This allowed us to record a high trapping rate (6.9 trap-nights/otter) in comparison with other studies (20.8 trap-nights [Blundell et al. 1999], 60.3 trap-nights [Serfass et al. 1996], or 159 trap-nights [Fernández-Morán et al. 2002]). This trapping rate provided us with 0.65 otters per researcher-night, whereas 0.33 otters were caught each night by a team setting 100 leg-hold traps in regions of high otter density in Spain and Portugal (D. Saavedra, Fundacio Territori i Paistage, personal communication).

Following fine-tuning of our protocol we achieved a trap retention rate of 88% over the last 16 otters caught. This rate was far better than the 60% previously recorded for similar traps without alarms (Serfass et al. 1996, Fernández-Morán et al. 2002) and similar to the 84.6% recorded by Blundell et al. (1999) using non-padded traps. In arriving at their figures, Blundell et al. (1999) and Serfass et al. (1996) excluded escapes resulting from the otter triggering the trap with its chest. We made no such exclusion, and so our relative trap retention rate was probably better still.

In conclusion, GSM trap alarms minimized leg-hold trapping trauma and reduced escapes without compromising trapping yield, making their combination an attractive livetrapping option.

2.5 - MANAGEMENT IMPLICATIONS

The GSM trap alarms allowed us to refine our live-trapping by greatly reducing retention time and trauma for captured animals. Nevertheless, researchers must allow for the possibility of alarm failure and set and monitor their traps accordingly. Given our success with leg-hold traps and otters, the use of GSM trap alarms for refining live-trapping with other traps and taxa should be explored.

Applying quantitative methods to conservation planning: population dynamics of the Eurasian otter in Ireland

CHAPTER 3

Field Techniques for Handling, Anaesthetising and Fitting Radio-Transmitters to Eurasian Otters (*Lutra lutra*)

FIELD TECHNIQUES FOR HANDLING, ANAESTHETISING AND FITTING RADIO-TRANSMITTERS TO EURASIAN OTTERS (LUTRA LUTRA)

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ABSTRACT

Thirty-four highly-stressed Eurasian otters (*Lutra lutra*) were restrained with ketamine and midazolam within minutes of capture, to fit externally-mounted transmitters or to transfer them to transport boxes. Eleven otters were fitted with harness mounted radio-transmitters, 2 were fitted with glued-on radio-transmitters and 15 were surgically implanted with intra-abdominal radio-transmitters in the field. The intra-abdominal transmitters were implanted under isoflurane anaesthesia within an hour of initial sedation. I experienced no complications with this anaesthetic regime. The abdominal cavity was accessed by a lateral approach. All surgeries were successful and I recorded no serious post-operative complications. The implantation procedure lasted less than 3 hours from capture to release such that almost all animals stayed within their territories, and pups were

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not abandoned. However, following their release, animals were sensitive to directed disturbance and could easily be forced to disperse. (EUROPEAN JOURNAL OF WILDLIFE RESEARCH. 54(4): 681-687)

3.1 - INTRODUCTION

The near-threatened status of Eurasian otters (*Lutra lutra*) focused attention on research protocol (Council of Europe 1979, EU Habitats directive 1992, CITES 1979, IUCN 2006), such that the understanding of certain aspects of their socio-biology remains meagre because otters could not be captured and marked efficiently and humanely (Chanin 2003, Kruuk 2006). Newly captured animals suffer short-term traumatic stress associated with capture and long-term fatiguing stress associated with confinement and transportation (Nielson 1999). In chapter 2 I have described a highly efficient trapping protocol involving trap alarms that minimises short-term stress by allowing one to capture, mark and release animals within a matter of minutes (see chapter 2: Ó Néill et al. 2007). However, the similar circumferences of the otter neck and head make it unsuited to standard collar mounted transmitters that can be attached rapidly in the field (Melquist and Hornocker 1979, Kruuk 1995, Zschille et al. 2007). Consequently, the major methodological issue for tracking studies of otters is identifying a transmitter attachment procedure that minimises long-term stress and population perturbation.

Several studies of native populations of the North-American river otter (*Lontra canadensis*) support implanting otters with radio-transmitters in the field without any period of retention in captivity (e.g. Melquist and Hornocker 1979, Blundell et al. 2002, Bowyer et al. 2002, Gorman et al. 2006). Nevertheless, I and other European researchers have found it difficult to receive the necessary permissions to follow this promising approach on the highly protected Eurasian otter (Hans Kruuk, Institute of Terrestrial Ecology Banchory, personal communication). I, therefore, tested two alternative methods of external attachment: harness mounted radio-transmitters (Mitchell-Jones et al. 1984) and glued-on radio-transmitters as used for other semi-aquatic mammals (e.g. seal spp. [Fedak et al. 1983] and platypus *Ornithorhynchus anatinus* [Gardner and Serena 1995]). Based on my findings, I received permission to implant otters with radio-transmitters in the field following the North American approach. I report on experiences with anaesthetising exceptionally stressed Eurasian otters just after their capture and attempts at limiting long-term stress and population perturbation associated with attaching radio-transmitters.

3.2.1 - STUDY SITE AND CAPTURE

The study was conducted on the Liffey, King's and Boyne rivers in the east and south east of Ireland (figure 2.1a). I captured otters with padded leghold traps fitted with trap-transmitters that alerted me as soon as an animal was caught and I arrived on site in a mean time of 22 (SD = 14) minutes. The trapping technique is described and evaluated in Chapter 2. The Bio-Resources Unit of Trinity College Dublin (201005) provided ethical approval for the research program and the Department of Health and Children (B100/3735) licensed me to implant otters with intra-abdominal radio-transmitters. Further trapping and tagging licenses were issued by the National Parks and Wildlife Service (1/2005, 3/2005, 8/2005, 9/2005, C15/2005, C68/2005, C69/2005).

3.2.2 – SEDATION AND HANDLING

I needed a chemical restraint that was safe to use on otters that had stepped on traps just minutes earlier and were clearly highly stressed. Ketamine with medetomidine, an intra-muscular anaesthetic combination used for sedating wild-caught otters (Fernández-Morán et al. 2001), was lethal for such highly stressed otters (T. de Jong and A de Jongh, Dutch Otterstation Foundation, unpublished data) and so I used ketamine with midazolam (Spelman et al. 1993). For sufficient immobilisation to attach an external transmitter, I administered this drug combination at a dosage of 10mg/kg and 0.25mg/kg respectively (Spelman et al. 1993). When an animal was to be operated upon, I administered a lower dosage of 3mg/kg and 0.08mg/kg, respectively, to facilitate its transferral from the trap to the transport-box. Later in the study I adopted the lower dose even for animals being fitted with external transmitters because of the potential to administer multiple injections without exceeding guide levels.

To administer the intra-muscular injection I physically restrained the otter with a handling tongs (figure 3.1). These wooden tongs were 1m long and the closed jaws encompassed a 12cm diameter opening that was lined with soft rubber. I placed the tongs around the otter's thorax and injected the sedative to the gluteal mass when under control. Body temperature was measured rectally as soon as possible and hyperthermia (>40°C) was relieved by partially immersing the otter and massaging its fur to aid water penetration. This is of critical importance as all otters struggled vigorously in the traps. I

then fitted the animal with an externally mounted radio-transmitter or transferred it to a sturdy clear plastic 'transport' box (0.8 x 0.3 x 0.3 m). To induce light surgical anaesthesia 4% isoflurane was introduced to the transport box at a rate of 10l/min 100% oxygen for 6 minutes using a portable anaesthetic machine with a precision vaporiser (O'Neill Medicalia Ltd., Liverpool, UK). When the otter lost its ability to right itself, I administered 1.5% isoflurane at a rate of 2l/min through a facemask. I monitored muscle response to surgical manipulation throughout the surgery and varied the concentration of isoflurane as necessary to maintain light surgical anaesthesia.



Figure 3.1. Otter handling tongs. The otter is clamped around the thorax just behind the forelegs. When under control, an intramuscular chemical restraining agent is administered to the gluteal mass.

3.2.3 – EXTERNAL ATTACHMENT OF RADIO-TRANSMITTERS

I fitted radio-transmitters (15g backpack TW-52 high power twin 10-28 cells, Biotrack Ltd., Peterborough, U.K) externally to 11 otters with harnesses following the approach of Mitchell-Jones et al. (1984). I also attempted to glue radio-transmitters directly to the fur of 2 otters using a thick flexible cyano-acrylate (Loctite Contact[®] 4860, Radionics, Dublin, Ireland). I coated the transmitter in glue and stuck it to the fur between

the otter's shoulder blades with the aerial oriented towards the tail. By parting the fur the transmitter was buried as deeply as possible and the surrounding fur was wrapped over the radio-transmitter.

3.2.4 – SURGICAL IMPLANTATION OF RADIO-TRANSMITTERS

All surgeries were performed by L. Ó Néill under the supervision of P. Wilson (MRCVS). The preferred surgical theatre consisted of a clean room within 30 minutes of the trap site, but when necessary a van fitted with a dedicated surgical table was used as a mobile theatre. Otters were prepared for surgery outside the theatre. A 6X6cm patch on the upper flank was shaved midway between the last floating rib and the hip bone, and clipped guard hairs from the surrounding 2-3cm. The surgical site was scrubbed with 98% alcohol and disinfected with sterile disinfectant swabs. The otter was placed upon the surgical table in lateral recumbence and covered with a cloth drape followed by a sterile disposable surgical drape with a slightly narrower aperture (6cm diameter) to prevent contamination by wet fur. All instruments and gloves and gown were sterile. The radiotransmitters were encased in silicone and polycarbonate tubes (28g, 8.5cm long, 2cm diameter, TW-5FT high power twin cell with 1/2 AA, Biotrack Ltd. Peterborough, U.K.). I cleaned the tubes thoroughly and steeped them in 98% alcohol for at least 72 hours prior to implantation.

I made a 3.5cm dorso-ventral incision through the skin in the centre of the surgical site and separated the underlying tissue layers by splitting muscle fibres along their axes and by tearing fat layers dorso-ventrally (Melquist and Hornocker 1979, Hernandez-Divers et al. 2001). I pierced the peritoneum with a fine-forceps and opened a 3.5cm tear. I placed a stay suture through the transverses abdominis and the peritoneum as the introduction of the transmitter often forced the innermost muscle layer and the peritoneum down and made it difficult to appose the peritoneal edges. I closed the muscle layers separately with 3 or 4 interrupted sutures (3-0 Monocryl, Ethicon, Johnson and Johnson, Belgium). I closed the skin layer for the first 2 otters with a continuous horizontal mattress, while for the remaining 13 otters I used 4 or 5 interrupted sub-cuticular sutures (3.0 Polysorb, USSC Auto Suture Company, France). I released the animal from the transport box when it began moving incessantly and scratching in a determined manner. I then prevented the animal from accessing the water manually by calmly placing myself in its path. When the animal was sufficiently coordinated to pass me in spite of my efforts I

considered it sufficiently coordinated to be released safely. The animals did not appear unduly stressed by this.

3.3 - RESULTS

3.3.1 - SEDATION AND ANAESTHESIA

Values are given ± standard deviations. Exertion associated with attempting to escape the trap and avoid the tongs meant that 11 of 36 animals were hyperthermic with temperatures ranging from 40-43°C. Early on in the study one hyperthermic (≥41°C) animal died under sedation due to inefficient monitoring of rectal temperature and a second died when its airway was partly blocked by ingested vegetation and its neck extension was not properly preserved. The mean induction time for the high dose of ketamine and midazolam was 4 ± 2 minutes (n = 10). I apparently failed to administer the first injection properly on two occasions and had to deliver a second full dose. Animals given the high dose of ketamine and midazolam remained unconscious for 39 ± 17 minutes and had become coordinated enough to be released 91 ± 19 minutes after recovery (n = 8). The lower dose was designed to allow for brief handling of conscious but uncoordinated and non aggressive animals. The level of sedation was subjectively and conservatively assessed and the recorded induction times varied considerably (10 \pm 7 minutes) with 7 animals losing consciousness (n = 26). No complications ensued for any animal sedated with the lower dose including those animals that required two (n = 5) or three (n = 2)additional injections at the same dosage. In general, I concluded that the booster injections were necessary where the initial injection was improperly administered because of the animal's struggles.

Only those otters that had been given the low doses of ketamine and midazolam were anaesthetized with isoflurane. The induction time for the sedation with isoflurane in the transport box was 6 ± 2 minutes (n = 15). Induction proceeded smoothly and without complication in all cases. The isoflurane afforded excellent control of the degree of anaesthesia. In one case I resolved the onset of irregular breathing by stopping administration of isoflurane and allowing the otter to breathe 100% oxygen for one minute. Otters had regained consciousness 7 ± 3 minutes after the flow of isoflurane was stopped. The otters were sufficiently coordinated to be safely released 37 ± 9 minutes following recovery of consciousness.

3.3.2 – EXTERNAL ATTACHMENT OF RADIO-TRANSMITTERS

Harness mounted radio-transmitters were retained by animals for 18 ± 15 days (n = 11). Five harnesses were retrieved from submerged snags upon which they had become entangled. The carcass of an animal (SAF5) that was recovered as a road traffic victim after 45 days, revealed an open sore on the inside of one foreleg caused by abrasion with the leather strap of the harness. The harness leather was substantially weakened after 4 weeks. Glued-on radio-transmitters were fitted to 2 animals and remained attached for 15 and 17 days. As far as I could determine, all animals fitted with external transmitters remained in home-ranges surrounding the trap site.

3.3.3 - INTRA-ABDOMINAL RADIO TRANSMITTER IMPLANTATION

All surgery was successfully performed without serious complication. From time of primary incision to wound closure, surgery lasted 55 and 60 minutes for the first 2 otters. Placing the stay suture through the transverses abdominis and peritoneum prior to the insertion of the radio transmitter reduced operating time to 41 ± 6 minutes (n = 13). Slight bleeding occurred twice when small blood vessels in fat layers were ruptured, but I observed no other significant bleeding.

No animal exhibited post-operative complications that could be detected (table 3.1). The first otter operated on was killed in a road traffic accident 12 days later. A post-mortem found that the cuticular edges of part of the surgical wound were slightly apart owing to failure of the continuous horizontal mattress subcuticular suture. Consequently, a more secure discontinuous suture pattern was adopted for the other 14 animals. In spite of the failure of the sutures, the wound was sealed, secure, showed no clinical evidence of infection, and was healing normally. The skin layer displayed satisfactory progression in secondary healing. There were no adhesions between the transmitter and the omentum or the peritoneum. Professor P. Wilson (MRCVS) concluded from the necropsy that the animal was uninfected and that its death was unrelated to the surgery. I recaptured a second otter (AF10) after 13 days. This otter showed no clinical evidence of infection and the skin layer appeared fully healed.

Following this recapture I lost contact with this otter most probably because she dispersed. I lost contact with two other individuals that were caught in the same trap and were very probably mother and cub. Contact was lost with the juvenile (SAM3) immediately, even though I was still in contact with his mother (AF9). I then lost contact

with the mother nine days later following disturbance as I tried to investigate apparent inactivity.

I searched the region intensively (radius of 20 km from trap site) for several weeks without detecting either animal. I walked all streams from the bank and detected no signal though I was easily capable of detecting signals for nearby otters diving to depths of 2m. I detected otters with implanted transmitters on $94.7 \pm 4.6\%$ of occasions prior to loss of contact (217 fixes for 14 otters) and I attributed most failures to receiver faults. This indicates that otters were detectable in the vast majority of holts. One of the transmitters from the same batch as the three missing animals failed several days after activation while it was still in my possession. I am confident that either the transmitters failed or the animals dispersed. Excluding these 3 animals, all other individuals remained within the vicinity of the trap site and adults occupied exclusive territories with stable borders. Overall, three sets of instrumented lactating females and dependent offspring returned to each other following release and one further case remains inconclusive (AF9 and SAM3 above).

Table 3.1. Summary details for the 15 otters intra-abdominally implanted with radio-tags on the King's and Liffey rivers in the Republic of Ireland in 2006.

Name	Sex	Weight (kg)	Tracking per	riod (d) Fate
AM5	3	8.5	167	Alive Oct 2006
AM6	8	8.0	164	Death (illegal snare)
AM1	8	8.0	150	Alive Oct 2006
YAF1	\$	5.4	150	Alive Oct 2006
SAF3	2	5.0	150	Alive Oct 2006
AF2	2	5.8	90	Alive Oct 2006
SAF2	9	4.0	90	Alive Oct 2006
SAM1	3	5.3	90	Alive Oct 2006
YAM1	3	7.0	80	Contact lost
AF3	9	7.0	62	Contact lost
SAF4	9	4.8	60	Contact lost
AF9	9	6.5	10	Dispersed *
AF10	9	6.0	13	Dispersed*
AM8	3	8.5	12	Death (RTA)
SAM3	3	4.5	0	Contact lost

^{*} dispersal in direct response to anthropogenic disturbance.

3.4 - DISCUSSION

I experienced no significant complications associated with the surgical implantation procedure, though it clearly entailed greater complexity and risk than external attachment. The harnesses I used remained attached for shorter and more variable periods than those achieved by Mitchell-Jones et al. (1984) who developed the method. This probably reflects their having practiced on captive animals. Indeed, the retention of harnesses improved somewhat as the study progressed, though not significantly so. The harnesses could cause considerable discomfort and were often retrieved from under-water snags. This may present a risk of drowning, although all my animals successfully escaped from the harness. The glued-on radio-transmitters involved negligible risk or, presumably, discomfort to the animal but the retention time was too short. I agree with the general consensus that surgical implantation is the best approach for tracking studies of otters (see e.g. Kruuk 2006).

Instrumented otters were released within three hours of entering the traps. The short duration of the procedures meant that almost all animals occupied ranges including the trap site for several weeks following capture and dependent offspring and their mothers returned to each other. Three instrumented lactating females successfully raised at least a single and two pairs of instrumented cubs respectively. It appears therefore, that these procedures followed could be safely used on all classes of individuals, apart from heavily pregnant females or extremely juvenile individuals, without perturbing the population structure. However, otters were sensitive to directed disturbance during the weeks following capture.

Periods of captivity for semi-aquatic mammals (e.g. a minimum of 72 hours) can help deal with complications such as wound failure (Hernández-Divers et al. 2001, Fernández-Morán et al. 2002, 2004, Zschille et al. 2007). Studies of native populations of Eurasian otters have kept animals in captivity for several days following surgery (e.g. Durbin 1996, Kruuk et al. 1993, König and König 1998, Kruuk 2006, but see also Arnemo 1991) as have studies of reintroduced Eurasian otters where the animals had to spend time in captivity in any event (Sjöåsen 1997, Saavedra 2002, Fernández-Morán et al. 2002, Niewold et al. 2003). Hertweck et al. (1998) observed the death of a female otter following suture failure 3 days post-release. Zschille et al. (2007) suggest that such a death and the death of one of their captive male mink within 24 hours of surgery supports prolonged retention. I argue that the stress caused by captivity is unwarranted if the animal

is likely to die in spite of being kept in captivity as in Zschille's case. Fernández-Morán et al. (2002) observed 9% of otters dying due to captive management though they observed no surgical complications. Furthermore, behavioural and hormonal signals indicated that captive wild otters were highly stressed or approaching that state for 2-5 days following capture (Fernández-Morán et al. 2004) and territories of dead (i.e. removed) otters are usurped rapidly (Erlinge 1967), even within a matter of days (see chapter 5). Finally, prolonged captivity must increase the likelihood of dependent offspring being abandoned.

Nevertheless, animal welfare considerations might require close observation and appropriate euthanasia if the risk of painful complications such as evisceration is high. Evisceration is a likely result of suture failure where the abdomen is accessed by an incision through the linea-alba (e.g. Zschille et al. 2007, Melquist and Hornocker 1979). This risk is decreased by accessing the abdomen through a para-lumbar incision and muscle-split techniques (Melquist and Hornocker 1979, Hernandez-Divers et al. 2001, Bowyer et al. 2003, Blundell et al. 2002). This approach reduces the risk of behaviourally induced suture failure (Melquist and Hornocker 1979) and makes evisceration a less likely consequence because the muscle layers slide over each other and misalign the openings so that the sutures of the inner muscle layers and peritoneum cannot be accessed. Following this approach combined with a relatively small incision (3.5cm) I observed satisfactory secondary healing where the cuticular sutures had failed, reassuring greatly as to the safety of the method. The risk of evisceration is not sufficient to necessitate the stress and population perturbation caused by keeping animals in captivity.

3.5 - MANAGEMENT IMPLICATIONS

- 1. Ketamine and midazolam should be used to sedate highly stressed otters.
- 2. Isoflurane provided great control of anaesthesia and was safe to use on otters restrained 20 to 30 minutes earlier with ketamine and midazolam.
- 3. Implanted radio-transmitters were superior to external transmitters both for the data they allowed us to gather and for the comfort and safety of the otters.
- 4. A lateral or para-lumbar approach resulted in a secure wound that did not require the otter to be kept under observation.
- 5. Capturing, marking and releasing the animals within 3 hours avoided population perturbation.

Applying quantitative methods to conservation planning: population dynamics of the Eurasian otter in Ireland

CHAPTER 4

Ranging Behaviour and Spacing of Eurasian Otters (*Lutra lutra*) on Lowland Mesotrophic River

RANGING BEHAVIOUR AND SPACING OF EURASIAN OTTERS (LUTRA LUTRA) ON LOWLAND MESOTROPHIC RIVER SYSTEMS.

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ABSTRACT

I examined the spatial structure of a native wild population of Eurasian otters (*Lutra lutra*) on mesotrophic rivers in a mild temperate climate. Radio-tracking of 20 individuals revealed exclusive intra-sexual home-ranges. Adult female home-ranges (7.5km, SD = 1.5km, n = 7) were inversely related to river width ($R^2_{adj} = 0.68$, $F_6 = 13.5$, P = 0.014) and so appeared to be based on food resources. The aquatic area within adult male home-ranges (30.2ha, SD = 9.5ha, n = 5) was greater than that within adult female's (16.8ha, SD = 7.0ha) ($t_{10} = 2.437$, P = 0.035), though this result is inconclusive because some males were tracked on oligotrophic rivers. One adult male expanded its range from 10.2km to 19.3km within 5 days of the death of the neighbouring male, suggesting that male home-

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ranges were heavily influenced by con-specifics. (European Journal of Wildlife Research – In Press).

4.1 - INTRODUCTION

In spite of its high priority for conservation (CITES 1979, Council of Europe 1979, EU Habitats Directive 1992, IUCN 2006), the socio-biology of the Eurasian otter (*Lutra lutra*) remains largely unknown (Chanin 2003, Kruuk 2006). On only 2 occasions have researchers identified the spatial structure of a native otter population (Erlinge 1967, Kruuk and Moorhouse 1991). Adult male territories were mate-based (Erlinge 1967, Kruuk and Moorhouse 1991) and heavily influenced by topography and the occurrence of other dog otters (Erlinge 1967). Female spatial structure appeared to rely on resource distribution with exclusive communal ranges in a coastal area of heterogeneous resources (Kruuk and Moorhouse 1991) and exclusive individual territories in a highly productive freshwater area (Erlinge 1967). Therefore, both studies were consistent with the resource dispersion hypothesis and the classical mustelid model (Powell 1979, MacDonald 1983).

Otters in the freshwater system studied by Erlinge (1967) occupied large annual ranges of around 20-30km. Equally large home-ranges were consistently observed in other studies of native freshwater otter populations involving small samples of dispersed individuals (e.g. Green et al. 1984, Durbin 1993, 1996a, Kruuk et al. 1993, Kruuk 2006, Poledník 2005). Translocated or reintroduced populations have also been monitored following their release and were again found to occupy similarly large ranges, even where river systems were highly productive (Jefferies et al. 1986, Saavedra 2002).

Otters in freshwater systems appear characterized by large and fairly constant linear spatial requirements. Nevertheless, rich lowland rivers have received little attention in north-western Europe (Chanin 2003), although higher densities were observed in such systems in Mediterranean areas (Ruiz-Olmo 2001). The classical mustelid model predicts female home-ranges based on food resources (Powell 1979, Johnson et al. 2000) that should, therefore, be shorter on more productive rivers and on wider sections of autochtonous systems. I aim to identify the spatial structure of otter populations in a simple mesotrophic system to augment the limited knowledge of otter socio-biology and to facilitate the interpretation of fragmented data or data from complex environments.

4.2 - MATERIALS AND METHODS

4.2.1 - STUDY AREA

In contrast with most other European populations (Macdonald and Mason 1994), Irish otters remained widespread during the 20th century (Chapman and Chapman 1982, Lunnon and Reynolds 1991, Bailey and Rochford 2006). Ireland has a mild, temperate, oceanic climate. In the east and south-east, where this study was conducted, mean monthly temperature varies from 5-15°C, mean monthly rainfall from 50-70mm, and snow persists past 09.00 hr in lowland areas for 5-6 days per year (Met Éireann – Irish Meteorological Service 2006). Three alkaline, calcium-rich rivers were chosen for this study; the River Boyne, the River Liffey and the King's River (Figure 2.1). The Boyne and King's are mesotrophic (0.04-0.06mg orthophosphate per I) (EPA 2006). The fish communities are dominated by brown trout (Salmo trutta) and salmon (Salmo salar), but include pike (Esox lucius), perch (Perca fluvialtilis), eel (Anquilla anquilla), stickleback (Gasterosteus aculeatus), and minnow (Phoxinus phoxinus), with crayfish (Austropotamobius pallipes) also present (Reynolds 1998, Demers et al. 2005). The section of the Liffey within the study area was oligotrophic (0.01mg orthophosphate per 1 [EPA 2006]) and was again dominated by salmonids and crayfish (W. Champ, Eastern Fisheries Board, Dublin unpublished report).

4.2.2 - BIOTELEMETRY

Details of the trapping and tagging program were presented in chapters 2 and 3. The trapping technique yielded a remarkably high trapping rate of 8.4 trap-nights per otter, or 1.7 (SD = 0.9) nights per capture at successful sites. Initially, I fitted 13 individuals with externally mounted radio-transmitters (TW-5 high power twin cell tags with 2 10-28 cells, Biotrack Ltd., Peterborough, UK), 11 with harnesses (Mitchell-Jones et al. 1984) and 2 with glue. Highly variable and generally short retention of these transmitters led me to use intra-peritoneal implants on a further 15 individuals (TW-5 high power twin cell with ½ AA, Biotrack Ltd., Peterborough, UK) (see chapter 3).

I captured and radio-tagged 12 otters on a 30km stretch of the King's River. I estimated maturity based on genitalia and body-size. One young male was tracked in 2005, while the remainder were tracked concurrently in 2006, although the tag failed

almost immediately for one larger adult male (AM3) (figure 4.2a). Only one animal escaped from a trap in this study area and I determined from its prints that it was a small sub-adult. I continued to trap the King's River study area for 21 unsuccessful trap-nights following the last capture. Based on the efficiency of the trapping technique, I was confident that all individuals commonly using the area were trapped. I captured 13 otters on the River Boyne but the data-set was fragmented by escapes, radio-transmitter failures and the death of adult females AF6 and AF7 (figure 4.2b,c). Finally, I captured 6 otters on the River Liffey, but equipment failures and the death of one adult male again fragmented the data set.

Receiving equipment consisted of a Sika[®] receiver and a flexible three-element Yagi[®] antenna (Biotrack Ltd.). Owing to safety concerns my surveying was largely limited to daylight hours following the procedure of Melquist and Hornocker (1983). Individuals with external radio-transmitters were tracked to source daily as the expected retention time was short, whereas individuals with implants were located once or twice a week. No more than one location per day was included in the analysis of home-ranges.

4.2.3 - HOME-RANGE ANALYSIS

I calculated Kernel density contours (95%) with least squares cross validation smoothing from the distribution of fixes for each individual (Arc View 3.2, Animal Movement SA v.2.04 beta) (Seaman and Powell 1996, Gorman et al. 2006). Least Squares Cross Validation (LSCV) smoothing can result in excessive fragmentation of kernels and underestimate [discontinuous] linear home-ranges (Blundell et al. 2001). Nevertheless, I used LSCV smoothing because I did not observe much fragmentation of continuous riverine home-ranges, and because fixed-kernels with reference smoothing (Blundell et al. 2001) extended too far beyond the apparent boundaries of territories. I measured homeranges as the length of river or lake-shore bounded by the 95% contour (Blundell et al. 2001) because the contours included a high proportion of unused terrestrial habitat. I estimated the average channel width of the river section contained within each home-range from 3 evenly spaced measurements per km made at straight sections of watercourse. I calculated home-range aquatic area as the product of the watercourse width and the homerange length. It is important that any home range estimate remains stable with increasing numbers of radio locations (Aebischer et al. 1993). Individual home-ranges were accepted as stable when 5 successive partial home-range estimates varied by less than 5%. To establish the minimum number of fixes required to estimate home-ranges for the population I calculated the difference between successive partial home-ranges for each individual i.e. the difference between the home-range calculated from 7 fixes and that calculated from 8 fixes etc. The differences were normalized as a proportion of the final home-range. Stability was satisfactory where the mean absolute difference between successive partial home-ranges approached 0 with a standard deviation less than 0.05, leading to 95% confidence intervals of 10% around the home-range estimates. After accepting a home-range as stable, I corrected any fragmentation by including intervening stretches between fragments in the final home-range estimate.

4.3 - RESULTS

4.3.1 – HOME-RANGE STABILITY

For those animals with at least 15 fixes, excluding lactating females that required extended or intensive monitoring, I found that home-range estimates became stable after 13 locations (n = 16) (figure 4.1). I accepted home-range estimates for 20 animals as stable (table 4.1). Various equipment failures limited the usefulness of the data from the other otters. Fluctuating signals indicated that otters were active on 21% (SD = 6.8%) of occasions (358 fixes, n = 20). Based on an average of 14.1 (SD = 4.0) fixes where the otter was inacitve, I recorded 7.0 (SD = 1.9) separate resting sites each (n = 20). This is a conservative estimate based on a limited number of fixes and no distinction of nearby resting sites (<80m apart).

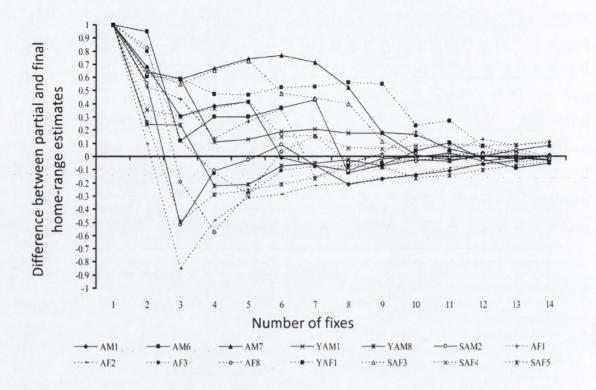


Figure 4.1. The difference between the size of partial and final home range estimates (95% kernel density) for 14 otters as the number of fixes is increased (i.e. $(HR_n - HR_i)/HR_n$.

Table 4.1. Summary of the 20 individuals for whom enough data was gathered to make stable estimates of home-ranges. Large signal fluctuations prior to loss of contact with implanted individuals suggested tag failures. Missed fixes were mostly attributable to faulty antenna connections. (Table continued overleaf...)

	tagging method	tracking period (d)	fixes	fix success rate	fate	home-range (km)
AF1	harness	17	15	100%	tag loss	10.4
AF2	implant	90	19	100%	<u>-</u>	6.8
AF3	implant	62	16	84%	contact lost	7.9
AF4	harness	40	29	100%	tag failure	5.9

	tagging method	tracking period (d)	fixes	fix success rate	fate	home-range (km)
AF5	harness	14	13	100%	tag loss	6.2
AF8	harness	24	17	100%	tag failure	8.3
AM1	implant	150	19	86%	-	14.0
AM2	harness	14	13	100%	tag loss	8.7
AM5	implant	167	19	100%	-	$10.2/19.3^{\dagger}$
AM6	implant	164	15	100%	death	17.4
AM7	harness	30	24	100%	tag loss	7.0
YAF1	implant	56	21	100%	-	5.1
YAM1	implant	80	20	100%	dispersed	6.0
SAF2	implant	60	15	100%	-	4 .0
SAF3	implant	93	22	93%	dispersed	7.8
SAF4	implant	150	19	90%	-	6.7
SAF5	harness	52	28	100%	death	7.2
SAM1	implant	90	16	89%	-1	3.5
SAM2	harness	16	15	100%	tag loss	13.3
SAM8	harness	22	15	100%	tag failure	8.0

[†] expansion following a neighbour's death

4.3.2 - FEMALE SOCIAL STRUCTURE

The data collected for the King's River allowed me to determine the spacing pattern of family groups consisting of mother and offspring (figure 4.2a). Crucially, this data set showed adult females occupying exclusive intra-sexual home-ranges. The ranges of advanced dependent or newly independent offspring (SAF3, SAF4, YAF1, SAM8) approximated the resident adult female home-ranges (AF2, AF3, AF8). Although the fragmented data-set for the Boyne is not suitable for determining spacing patterns on its own, the home-range boundaries of adult and sub-adult females are not inconsistent with evenly spaced exclusive female home-ranges (figure 4.2b,c).

Observations of pre-dispersal range restriction supported exclusive intra-sexual home-ranges by suggesting that mature or maturing individuals were not tolerated within the resident adult female's home-range. Juveniles were initially limited to a range spanning 1-2km of the maternal range (n = 2). Dependent sub-adults covered the maternal range in the company of their mother (n = 5). Finally, just before dispersing, females became restricted to the edge of the resident adult female's home-range (n = 3) (figure 4.3). When I caught YAF1, an adolescent or young adult female, the larger resident adult female was lactating. YAF1 covered the full home-range of the resident adult female AF2 but seemed to avoid the area surrounding the holt containing AF2's cubs (based on 18 fixes over 32 days). YAF1's range eventually became confined to the edge of AF2's home-range (based on 11 fixes over 43 days) before I lost contact, probably because of dispersal. The genetic relationship between YAF1 and AF2 was unknown. A similar pattern was observed for sub-adult female SAF3 who was almost certainly AF3's daughter. Initially I located her in the company of AF3 on 8 of 12 occasions covering a period of 50 days. I then found her alone on 6 consecutive occasions over a period of 30 days while continuing to use AF3's full home-range. Finally, I found her within a small area at the edge AF3's home-range on 4 occasions over 12 days before losing contact, probably following dispersal. I also observed this pattern of range restriction in a sub-adult female where the resident adult female died. I saw SAF5 following a slightly larger otter on 2 occasions. Twenty-five days following her capture I found the fresh cadaver of an adult female from within SAF5's home-range. SAF5 continued to cover her home-range as before until day 30 (18 fixes in total) when she became confined to a resting-site 200m away from the main river. She remained at this location for 7 days (5 fixes) before dispersing downstream (5 further fixes). SAF5's cadaver was eventually retrieved as a

road-traffic victim on day 52. I consider it likely that the range restriction and subsequent dispersal were caused by a new adult female entering and occupying AF3's home-range.

Further support for exclusive, intra-sexual territoriality was provided by the trapping data. Traps remained within every captured otter's home-range for 10-15 days. The extremely high efficiency of the traps meant that I was confident that resident animals were either captured or had escaped from traps. Gradually moving the traps upstream resulted in otters being caught as soon as the traps entered their home-ranges. Sixteen of the 20 otters whose home-ranges I identified were caught towards the edges of their home-ranges. Adult females represented 15 of 36 captures overall. I plotted home-ranges for 6 adult females and none of the 12 additional animals caught within these ranges were conspecific.

The spatial structure of female home-ranges appears to be determined by the resident adult female. Therefore I used only the home-ranges of the adult females, or a well developed resident sub-adult where data was lacking for the resident adult female, to estimate the relationship between home-range size and river width (AF1, AF2, AF3, AF4, AF5, AF8, and SAF5). I found that their home-ranges were inversely related to river width $(\bar{x} = 7.5 \text{km}, \text{SD} = 1.5 \text{km}, \text{n} = 7, \text{R}^2_{\text{adj}} = 0.68, \text{F}_6 = 13.5, \text{P} = 0.014)$ (figure 4.4). In terms of aquatic area, adult female home-ranges averaged 16.8ha (SD = 7.0ha).

4.3.3 – MALE SOCIAL STRUCTURE

Adult males were tracked on both mesotrophic (n = 3) and oligotrophic (n = 2) rivers whereas the females were all tracked on mesotrophic rivers. The adult male ranges (30.2ha [SD = 9.5ha] or 13.2km [SD = 5.3km], n = 5) were quite variable and appeared to be influenced by the presence of con-specifics. Two animals occupying adjacent homeranges, AM6 and AM5, were tracked on the Liffey. When AM6 was killed in an illegal snare, AM5 expanded his range from 10.2 km (based on 16 fixes over 80 days) to 19.3 km within 5 days (based on 3 additional fixes). Adult male home-range aquatic area was larger than female's ($t_{10} = 2.437$, P = 0.035).

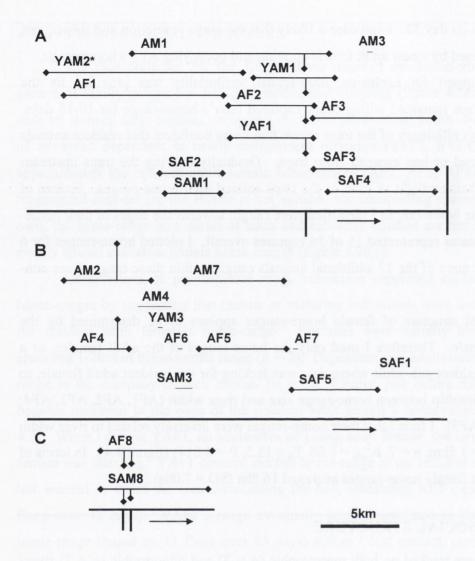


Figure 4.2. The spatial structure of otter populations on (A) the King's River (7 to 20 m wide), (B) the lower River Boyne (30 to 40 m wide), and (C) the middle River Boyne (20 to 25 m wide). Thick lines represent simplified water-courses. Lines without stoppers indicate incomplete home-ranges based on less than 13 fixes. Individuals are classed as males (M) or Females (F) and Adult, (A), Young-Adult (YA), or Sub-Adult (SA). Family range boundaries are indicated with a broken line. YAM2 was tracked 11 months prior to the others in the King's River data set.

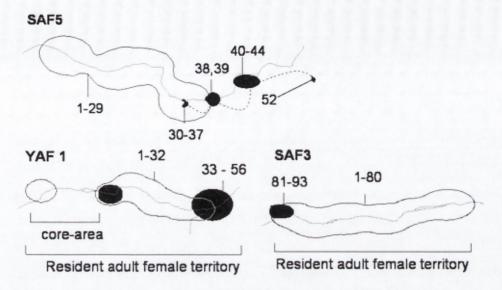


Figure 4.3. The behaviour of otters immediately prior to dispersal. The contours represent 95% kernel density contours for the period indicated. SAF5 appeared to be forced to disperse following the death of the resident adult female on day 25. On day 30 she suddenly became confined to a holt 200m away from the main river. Seven days later she dispersed downstream and was ultimately recovered as a road traffic victim on day 52. When we caught YAF1 the resident adult female was already lactating with a new brood. YAF1 was apparently tolerated within the resident's territory but not in the core area. YAF1's range gradually declined until she eventually became confined almost exclusively to the edge of the territory. SAF3 was semi-independent of her mother when captured. She gradually became fully independent and used the full range of her mother before becoming confined to a small area at the extreme edge of her mother's range.

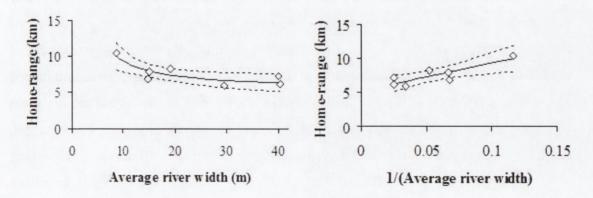


Figure 4.4. Family group home-ranges are inversely related to the average width of the watercourse ($y = 40.42x^{-1} + 5.284$, $R^2_{adj} = 0.68$, $F_6 = 13.5$, P = 0.014). Open symbols represent family-group home-ranges and broken lines indicate 95% confidence limits.

4.4.1 – METHODOLOGICAL ISSUES

The quality of my data may be challenged in 2 ways: I tracked animals over relatively short periods averaging less than 3 months and I based my analysis of homeranges on daytime fixes. I am confident from my analysis of homerange stability that I identified the area 'normally traversed by the animals' (Burt 1943) for the periods studied. I expect that the otters would disperse or otherwise change their home-ranges if social or environmental conditions warranted. Therefore a longer term study might identify a larger range consisting of several temporally distinct home-ranges. In this sense, my data should be viewed as a snapshot of otter space use over a few months. Seasonality in precipitation and temperature is remarkably moderate in the study area and therefore I suspect that ranging behaviour should not display great temporal variability. I tracked animals in all life-stages; lactating females, non-lactating females with cubs, adult females without cubs, adult males, and juvenile and sub-adult individuals. Therefore, I believe that my data describes the ranging behaviour of otters in the study area in general, although there is certainly scope for longer term study.

Health and safety considerations limited my surveying to the daytime. Daytime locations have been used to analyse ranging behaviour in nocturnal North American River Otters (Melquist and Hornocker 1983) and re-introduced Eurasian otters (Sjöåsen 1997) but it is possible that unrecorded nocturnal movements were more expansive. The many resting sites used by the otters should represent a reasonable proxy for the extent of foraging movements if cover or disturbance are not limiting. My subjective assessment of cover and disturbance in the study area was that they were at favourable levels and indeed otters were frequently active during the daytime. I trapped intensively along the main rivers and did not catch animals outside of the area later identified as their home-ranges, suggesting that excursive nocturnal movements were not common. If unrecorded foraging on small tributaries was common I would expect great variation in the home-ranges arising from the unequal distribution of such tributaries. Furthermore, Green et al. (1984) recorded many resting sites on small tributaries and so I should have found the otters resting on such streams in the daytime also. If the otters were moving up tributaries at night I would expect the neighbours on the tributaries to make reciprocal nocturnal

movements down onto the main river and consequently to have been caught in my traps. I conclude that the methodology was sufficient to identify the areas that were of importance to our study animals in the study area. Studies that calculated home-ranges from continuous tracking data and hence included the full extent of excursive movements may give rise to more precise home-range estimates than mine (e.g. Green et al. 1984, Kruuk et al. 1993, Durbin 1996).

4.4.2 - BIOLOGICAL SIGNIFICANCE

Male home-ranges appeared to be intra-sexually exclusive to some degree but I did not track enough neighbouring pairs to determine the degree of overlap. Males had larger home-ranges than females though this result is confounded by 2 males being tracked on an oligotrophic river. Male home-ranges expanded remarkably rapidly following the removal of a neighbouring con-specific. The range of adult male home-ranges (7-19km, n = 5) were of a similar size to those recorded in a Swedish freshwater environment (10-21km, n = 8) (Erlinge 1967) and in a Scottish coastal environment (7-19km, n = 5) (Kruuk and Moorhouse 1991).

Adult females occupied intra-sexually exclusive territories that were inversely related to river width. Females shortened the length of their home-ranges as the width of the foraging habitat increased and this relationship suggests that the home-ranges were food-resource based as predicted by the classical model of mustelid social organisation (Powell 1979, Johnson et al. 2000). In a productive freshwater environment, Erlinge (1967) observed females ranging over annual ranges that were several times larger than those I recorded. However, these females seasonally switched from 2-3km radius home-ranges consisting of lakes and streams, to stream-only home-ranges averaging 5km of stream length when lakes froze. Following Burt's (1943) definition of home-ranges, these otters can be regarded as having occupied 2 home-ranges each year, both of which were of a similar size to those identified in my study.

Home ranges averaging 18.6km (SD = 3.5km, SE = 1.1km) were recorded for females in Scottish oligotrophic river systems (0.0-0.02 mg/l orthophosphate) (n = 10) (Green et al. 1984, Kruuk et al. 1993, Durbin 1996, Kruuk 2006). As expected for foodbased ranges in a less productive environment, these home-ranges were much larger than the 7.6km (SD = 1.1km, SE = 0.6km) I observed on mesotrophic rivers (0.04-0.06 mg orthophosphate per l). The low resources in the riverine part of the oligotrophic habitat

were highlighted in one study by frequent crossings of watersheds, the maintenance of exclusive cores of non-riverine habitat, and just 14-29% of home-range area consisting of riverine habitat (Green et al. 1984). Interestingly, the values for the Scottish female homeranges were unrelated to river width (Green et al. 1984, Kruuk et al. 1993, Durbin 1996) and appeared to arise from otters selecting a length of terrestrial-riverine interface (Durbin 1996). I feel that the lack of relationship with river width in the Scottish data reflects the origin of the river's productivity. In allochtonous, oligotrophic systems fish productivity relies primarily on terrestrial input and hence the terrestrial-riverine interface. A given length of a wide stream has an equal amount of this interface as a narrow stream, resulting in a sharp decrease in the density of aquatic biomass on wider rivers as observed by Kruuk et al. (1993). In such systems otter home-ranges include enough of this interface (channel length) to supply their needs, and females concentrate on small streams where biomass density is greater (Kruuk 2006). Conversely, as in-stream productivity increases and rivers become autochtonous, biomass density is expected to be more constant as the river widens, leading to home-ranges inversely related to river width. Hence, the relationship between female home-ranges and river width across mesotrophic and oligotrophic systems is consistent with food-resource based home-ranges.

My trapping results also support the importance of trophic status. Trapping rates on the oligotrophic river Liffey averaged 25.0 trap-nights/otter (n=6), while on mesotrophic rivers they averaged just 5.1 (n=30). The importance of the trophic status of fresh-waters for otters has also been demonstrated by higher densities of otters in rich rivers in Spain and by re-introduced Swedish otters focusing almost exclusively on freshwaters with orthophosphate levels above $0.02 \, \text{mg/l}$ (Sjöåsen 1997, Ruiz-Olmo 2001).

Recently translocated populations on resource-rich systems displayed far greater and more variable ranges than the native populations in a similarly rich system that I studied, averaging 30km and varying from 3-85km (Saavedra 2002, Jefferies et al. 1986). Saavedra (2002) recorded a female occupying a 5km home-range for several months around parturition, although she ranged over 85km during the year following her release. The static territory was similar to those observed in this study and by Erlinge (1967). In an under-saturated system, there is less incentive to maintain a static territory, except when burdened with non-mobile young. In light of the results, and my interpretation of Erlinge's (1967) results, data from unstable under-saturated systems are inappropriate for estimating otter spatial requirements.

Most previous studies of established otter populations were carried out on oligotrophic or complex systems. I observed higher otter densities in simple mesotrophic river systems. While for these systems, rivers supported greater female densities than streams, the length of their home-ranges became roughly constant as rivers widened beyond 15m. For an autotrophic system this suggests that otters could not efficiently exploit the additional mid-stream habitat available.

An understanding of habitat-specific population density is often considered critical to conservation planning (EU Habitats Directive 1992). This understanding has proven elusive for otters owing in large part to difficulties associated with their capture or observation (difficulties dealt with in Chapters 2 and 3). As a consequence, conservation planning has relied heavily on qualititative scientific advice based on presence-absence data from spraint surveys (e.g. the Special Areas for Conservation network designation in Ireland).

Estimates of otter populations have been attempted occasionally (Harris et al. 1995, Heggeberget 1995, Prigioni et al. 2006) but are often based on dubious assumptions e.g. sprainting intensity can be converted to a number of otters (Kruuk 2006). The current study has improved this situation in two ways. Firstly, it has shown that adult female otters occupy exclusive home-ranges in lowland mesotrophic rivers in North Western Europe. This understanding of spatial structure facilitates the interpretation of the relatively large body of work for that region that has determined individual home-ranges without determining spatial patterns (as described above). Adult females appear to be the dominant unit in determining overall otter density, and as such are the most appropriate life-class for use in extrapolating habitat specific density data over large areas. The work presented in this paper makes an extrapolation of female spatial requirements possible. Secondly, the study has determined otter spatial requirements in rich lowland rivers and increased the information available for relating otter density to habitat. This progress will be employed in Chapter 5 where a preliminary estimate of the Irish otter population will be made using all available habitat specific density data. The size and distribution of a population determine its vulnerability in general and indeed the population-level response to spatially heterogeneous environmental change. Indeed, the information derived from the work presented in this chapter will be fundamental to determining the response of the Irish otter population to environment change and/or management actions as explored in Chapter 7.

Applying quantitative methods to conservation planning: population dynamics of the Eurasian otter in Ireland

CHAPTER 5

The size of the Irish otter population

THE SIZE OF THE IRISH OTTER POPULATION

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ABSTRACT

I used digitised maps at a scale of 1:50,000 to determine the extent of aquatic habitat in Ireland and classified water-features according to width, productivity, altitude and geology. I estimated the potential population of otters based on habitat-specific density data and took account of declining habitat quality by correcting for the change in otter status since 1982. The corresponding estimate for the number of adult females on the island was 6,421 (95% confidence intervals: 5,659-7,769). The decline in status between 1982 and 2005 occurred predominantly in densely populated regions and the resulting population decline was more drastic than indicated by the surveys alone. (MANUSCRIPT).

5.1 - INTRODUCTION

The Eurasian otter (*Lutra lutra*) is a high-priority species for conservation within the European Union (EU) and member states must designate and protect a network of Special Areas for Conservation (SAC) for otters (EU Habitats Directive 1992). One of the key criteria for evaluating potential SACs requires knowledge of the national population and the numbers present on the site (EU Habitats Directive 1992). An understanding of how population density varies across habitats is critical for species conservation (Kruuk 2006).

Otter density is difficult to assess. They can be visually counted where they are active during daylight hours (Kruuk and Moorhouse 1991, Yoxon 1999, Ruiz-Olmo et al. 2001). However, the species is generally secretive, nocturnal and sparsely spread (Kruuk 2006). Otters can be counted indirectly by identifying individuals from their footprint morphology, from their spraints using genetic techniques, or from the number of active holts (Erlinge 1967, Kruuk et al. 1989, 1993, Yoxon 1999, Hung et al. 2004, Ottino and Giller 2004, Prigioni et al. 2006). Alternatively, studies can estimate density by revealing the spatial structure of populations and the habitat specific spatial requirements of individuals (see chapter 4, Erlinge 1967, Kruuk and Moorhouse 1991). These techniques are highly labour intensive and are suitable for small study areas. Estimating populations over large areas requires extrapolation (Harris et al. 1995, Heggeberget 1995, Prigioni et al. 2006). A complicating factor for such extrapolations is the tendency of intensive studies to focus on relatively high-quality habitat (Kruuk 2006). Population estimates based on extrapolated data must take account of the range of habitat available and the variation in its quality for them to be acceptable (Kruuk 2006).

Otter densities have been examined in the most common habitats of Ireland and the British Isles (see chapter 4, Yoxon 1999, Kruuk 2006). In coastal areas, densities range from 0.16-0.09 adult-females/km, depending on the geology of the coastline (Yoxon 1999). The carrying capacity of freshwater areas are largely determined by nutrient status, watercourse size and altitude (see chapter 4, Ruiz-Olmo 1998). In oligotrophic and mesotrophic freshwater systems, densities average 0.05 adult-females/km and 0.13 adult-females/km respectively (see chapter 4, Green et al. 1984, Kruuk et al. 1993, Durbin 1996b, Kruuk 2006). Adult female density is positively related to river width in mesotrophic systems but not in oligotrophic systems (see chapter 4). Otter density drops off steeply at altitudes above 500m (Ruiz-Olmo 1998).

Large-scale data on the Irish population is limited to the results of national, standardised spraint surveys where a large number of randomly selected stretches of watercourse are examined for signs of otter presence (Chapman and Chapman 1982, Lunnon and Reynolds 1992, Bailey and Rochford 2006, Preston et al. 2006). Certain authors have considered sprainting intensity to be related to otter density (Conroy and French 1987, Madsen and Gaardmand 2000, Ruiz-Olmo et al. 2001, Mason and Macdonald 2004). Consequently, sprainting intensity has been used to estimate otter numbers (Harris et al. 1995, Prigioni et al. 2006). However, this approach is somewhat controversial (e.g. Kruuk and Conroy 1987, Kruuk 2006). It is generally accepted that spraint surveys are appropriate for determining large-scale trends in a population based on otter presences or absences (e.g. Mason and Macdonald 1986, Kruuk 2006). Otter signs were detected at 88% of the sites visited in 1982, but the rate of detection declined by approximately 18% since then (Chapman and Chapman 1982, Lunnon and Reynolds 1992, Bailey and Rochford 2006, Preston et al. 2006). Because the distribution of the population remained unchanged these results were interpreted as indicating a general decline in habitat quality and, consequently, otter population density (Preston et al. 2006).

I aim to estimate the population of otters in Ireland, the degree by which those populations have declined since 1982 and the proportion contained within Ireland's candidate SAC (cSAC) network. These data form much of the basis of Ireland's Species Conservation Assessment (2007).

5.2 - METHODS

5.2.1 – HABITAT EXTENT

All calculations were carried out using ArcView3.2 Geographical Information Systems software. I used Ordnance Survey of Ireland (OSI) and Ordnance Survey of Northern Ireland (OSNI) 1:50,000 vector water-features layers to estimate the extent of otter habitat. Water bodies were classified as rivers, streams, lakes and coast. The width of the river and stream classes were calculated by using the ground-truth data gathered in the various national surveys (Chapman and Chapman 1982, Bailey and Rochford 2006, Preston et al. 2006). The ground-truth data graded river width as <2m, 2-5m, 6-10m, 11-20m, >20m. For example, using mid-range values (1m, 3.5m, 8m, 15.5m, 30m), I estimated the average width of river and stream features as classified by the OSI to be 12.9m (n = 893) and 4.2m (n = 955) respectively. Similar calculations were performed for

the various OSNI fluvial habitat classifications (n = 6). I measured rivers and streams as the length of one bank. On rivers wider than 80m I measured both banks because otters do not forage beyond 80m from the shore (Kruuk and Moorhouse 1991). Similarly, lake or coastal shores within 80m of each other were treated as co-incident because they give access to the same foraging habitat.

5.2.2 - HABITAT TYPE

I classified all rivers, lakes and streams according to their trophic status (0.00-0.02, 0.02-0.04 and >0.04 mg/l orthophosphate) by intersecting the habitat layers with a Kriging interpolation of the Environmental Protection Agency and Environments Agency median orthophosphate measurements from over 700 survey locations (ArcView3.2 – Spatial Analyst Extension) (figure 5.1). I also classified water features according to altitude (< 500m, 500-1000m and >1000m above sea level) using OSI and OSNI 1:50,000 altitude contours. Finally, I classified the coastline according to the underlying geology (Geological Survey of Ireland – All Ireland Bedrock Map, ArcView3.2).

5.2.3 - HABITAT QUALITY

In 1982, Irish rivers were in near-pristine condition and otter survey results were near-optimal (Chapman and Chapman 1982, Stapleton et al. 2000). I took account of declining habitat quality by adjusting all population estimates by the change in the status of otters since 1982 (Chapman and Chapman 1982, Bailey and Rochford 2006, Preston et al. 2006) (figure 5.2). The change in status was regarded as directly proportional to the change in otter populations at the River Basin District (RBD) scale. Status was calculated for 2006 as the proportion of sites visited found to have positive signs, standardised against the 1982 survey results. Confidence intervals for the difference between the two proportions (proportion of sites positive in 1982 and 2006) were calculated using the standard z-test formula. These confidence intervals were then applied to the estimated status for each RBD to account for survey intensity (figure 5.2).

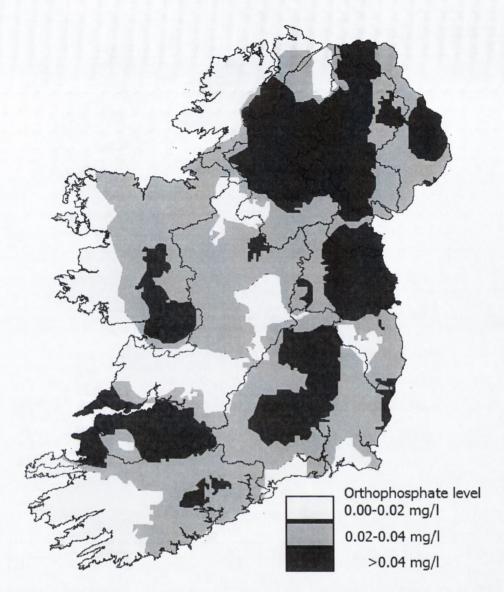


Figure 5.1. Isoclines of orthophosphate levels in Irish freshwaters. Map is based on a Kriging interpolation of median orthophosphate levels measured at over 700 locations by the Environmental Protection Agency and the Environments Agency (ArcView3.2 – Spatial Analyst Extension).

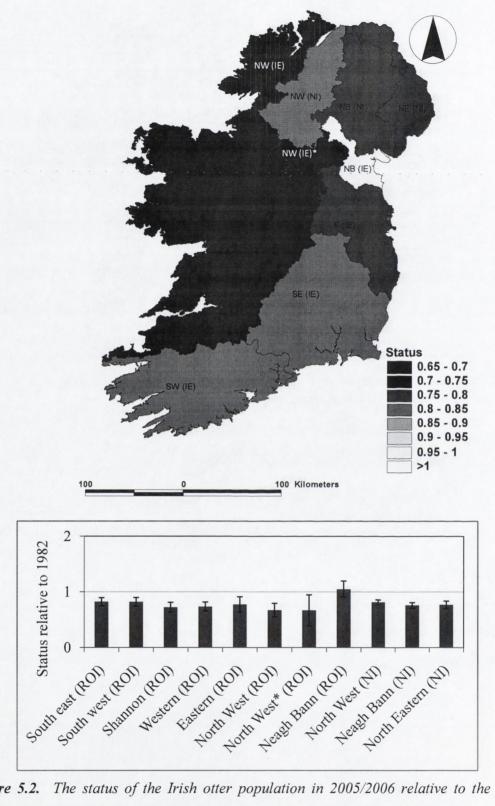


Figure 5.2. The status of the Irish otter population in 2005/2006 relative to the 1982 baselines survey (Chapman and Chapman 1982, Bailey and Rochford 2006, Preston et al. 2006). The proportion of sites found to have positive signs of otters was assumed to be a direct measure of otter status at the RBD scale. Error bars: 95% confidence intervals.

5.2.4 – POPULATION ESTIMATION

I estimated raw numbers of otters based on the habitat specific density estimates described in Table 5.1. I took account of altitude by reducing the density of high altitude areas by the proportion identified by Ruiz-Olmo (1998). Each habitat based population estimate was multiplied by the appropriate RBD specific status to account for changing habitat quality between 1982 and 2006. The uncertainties in both the habitat-specific densities and the change in status were integrated in the final population estimate by generating 1,000 stochastic calculations of the product of the two measures. Each parameter was randomised around its estimated mean and standard deviation. Because the uncertainty regarding habitat densities was asymmetric, the positive and negative deviations were calculated separately.

Table 5.1. Adult female density per km for the various habitats common in Ireland. For freshwaters, densities are related to watercourse widths and estimated for each GIS layer classification through ground-truth data on their average river widths. Habitat layer names are derived from the nomenclature employed by the Ordnance Surveys of Ireland and Northern Ireland as appropriate. OP represents orthophosphate. 95%ci represents 95% confidence intervals.

			Lower	Upper
GIS hab	oitat layer	Estimat	e 95%ci	95%ci
Lake (OSI/ OSNI)	0.00-0.02 mg/l OP ^l	0.05	0.05	0.06
Lake (OSI/ OSNI)	$0.02 \text{-} 0.04 \text{ mg/l OP}^{\dagger}$	0.09	0.05	0.21
Lake (OSI/ OSNI)	0.04 - $0.06 \text{ mg/l OP}^{II}$	0.17	0.15	0.21
OSI 'River'	0.00-0.02 mg/l OP ¹	0.05	0.05	0.06
OSI 'River'	$0.02 \text{-} 0.04 \text{ mg/l OP}^{\dagger}$	0.08	0.05	0.14
OSI 'River'	0.04-0.06 mg/l OP ^{II}	0.12	0.11	0.14
OSI 'Stream'	0.00 - $0.02 \text{ mg/l OP}^{\text{I}}$	0.05	0.05	0.06
OSI 'Stream'	$0.02 \text{-} 0.04 \text{ mg/l OP}^{\dagger}$	0.06	0.05	0.10
OSI 'Stream'	$0.04 \text{-} 0.06 \text{ mg/l OP}^{\text{II}}$	0.07	0.05	0.10
OSNI river 'All'	0.00-0.02 mg/l OP ^l	0.05	0.05	0.06
OSNI river '0'	$0.02 \text{-} 0.04 \text{ mg/l OP}^{\dagger}$	0.06	0.05	0.11
OSNI river '0'	$0.04-0.06 \text{ mg/l OP}^{II}$	0.07	0.06	0.11
OSNI river '7'	$0.02 \text{-} 0.04 \text{ mg/l OP}^{\dagger}$	0.07	0.05	0.11
OSNI river '7'	$0.04 \text{-} 0.06 \text{ mg/l OP}^{\text{II}}$	0.07	0.06	0.11
OSNI river '13'	$0.02 \text{-} 0.04 \text{ mg/l OP}^{\dagger}$	0.07	0.05	0.12
OSNI river '13'	$0.04 \text{-} 0.06 \text{ mg/l OP}^{\text{II}}$	0.10	0.08	0.12
OSNI river '26'	$0.02 \text{-} 0.04 \text{ mg/l OP}^{\dagger}$	0.08	0.05	0.13
OSNI river '26'	$0.04 \text{-} 0.06 \text{ mg/l OP}^{\text{II}}$	0.11	0.10	0.13
OSNI river 'Scalar'	$0.02 \text{-} 0.04 \text{ mg/l OP}^{\dagger}$	0.08	0.05	0.15
OSNI river 'Scalar'	$0.04 \text{-} 0.06 \text{ mg/l OP}^{\text{II}}$	0.13	0.12	0.15
High water mark	Paleozoic ^{III}	0.43	0.38	0.49
High water mark	Carboniferous ^{††}	0.43	0.38	0.49
High water mark	Devonian [‡]	0.10	0.09	0.11
High water mark	Igneous III	0.10	0.09	0.11
High water mark	Mesozoic ^{III}	0.66	0.58	0.75
High water mark	Pre-cambrian ^{III}	0.18	0.16	0.20
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The Green et al. 1984, Kruuk et al. 1993, Durbin 1996, Kruuk 2006; Iló Néill chapter 4; Ill Yoxon 1999; †estimated as intermediate between lower and higher trophic status with most extreme confidence intervals; ††I assumed that Carboniferous limestone was similar to the predominantly limestone Cambrian rock studied by Yoxon (1999); †otter density is low on Devonian rock (Kruuk 1995, Yoxon 1999, H. Kruuk personal communication 2007).

5.3 - RESULTS

I estimated the size of the adult female otter population within Irish RBDs in 1980/1981 (table 5.2) and 2004/2005 (table 5.3) (figure 5.3). The population of adult females has declined by 22.3% from 8,261 to 6,421 since 1982.

I estimate that cSACs contain 1,442 adult females (95%ci: 1,251-1,792), representing approximately 20% of the current otter population. If SACs are returned to their 1982 state, as targeted in the Republic of Ireland's (ROI) Species Conservation Assessment (2007), the total population will increase by 454 individuals or 6.7%. Because SACs are biased towards the ROI, the population within that jurisdiction would increase by a slightly higher 8.1%.

Adult females represented approximately 37% of 36 captures from the wild Irish population (see chapters 2 and 4). I can thereby provide a rough estimate for the total population at between 16,000 and 22,000 otters (excluding juveniles under 4 months).

Table 5.2. The estimated number of adult females in Irish River Basin Districts in 1981/1982.

	# adult females	lower 95%ci	upper 95%ci
South east (ROI)	1024	918	1295
South west (ROI)	1204	1121	1384
Shannon (ROI)	1515	1401	1779
Western (ROI)	1784	1664	2073
Eastern (ROI)	552	497	684
North West (ROI)	766	708	891
North West* (ROI)	161	142	215
Neagh Bann (ROI)	121	107	153
North West (NI)	469	435	554
Neagh Bann (NI)	434	407	514
North eastern (NI)	231	207	285
Total	8261	7609	9826

Table 5.3. The estimated number of adult females in Irish River Basin Districts in 2005/2006.

River basin district	# adult females	lower 95% ci	upper 95%ci
South east (ROI)	856	712	1110
South west (ROI)	1010	864	1206
Shannon (ROI)	1123	949	1369
Western (ROI)	1347	1155	1621
Eastern (ROI)	437	309	595
North West (ROI)	524	410	660
North West* (ROI)	109	41	187
Neagh Bann (ROI)	129	89	179
North West (NI)	380	330	458
Neagh Bann (NI)	329	279	405
North eastern (NI)	177	141	229
Total	6421	5659	7769

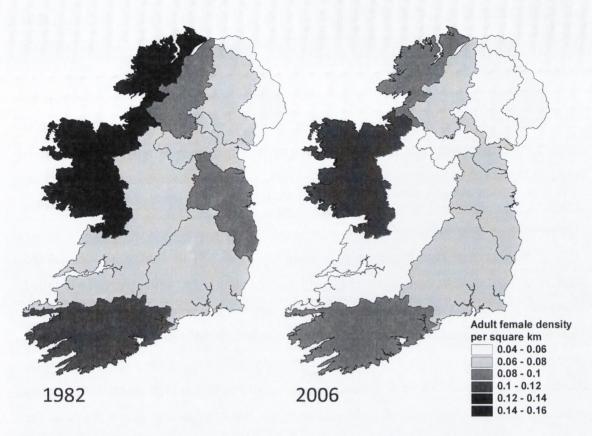


Fig 5.3. Change in the density of adult female otters in Irish River Basin Districts.

5.4 - DISCUSSION

The widespread presence of otters in 1982 led to the population being considered internationally important (Chapman and Chapman 1982, Whilde 1993). My findings support this consideration, estimating a current population of 5,659-7,769 adult females or approximately 16,000-22,000 otters. Although otter population estimates are not commonly available, it is clear that Ireland holds one of the largest populations in Western Europe. Norway holds an estimated 10,000-15,000 individuals on its coast (Heggberget 1995) and Scotland contains roughly 6,600 otters (Harris et al. 1995), with a further 230 individuals on Skye (Yoxon 1999) and 700 to 900 individuals on Shetland (Kruuk et al. 1989). Other strong populations are believed to exist in Portugal and eastern Germany (e.g. Conroy and Chanin 2001, Hauer et al. 2000). Significant populations also occur in Eastern Europe with an estimated 7,000 otters in Byelorussia, for example (Sidorovich and Lauzhel 1992). However, otter populations have been decimated in most of the rest of Europe since the 1950s (Mason and Macdonald 1986, Foster-Turley et al. 1990, MacDonald 1991, Macdonald and Mason 1994, Jefferies and Hanson 2000, Kruuk 2006).

England and Wales, for example, contained a mere 750 individuals in the mid-1980s (Harris et al. 1995), while the Italian population remains at just 230 to 260 animals (Prigioni et al. 2006).

Although still among the largest in Europe, the Irish population has declined by 22% since 1982. The population decline was more pronounced than the survey results indicated because the decline in status occurred predominantly in densely populated RBDs (figures 5.2 and 5.3). A population decline of 1% per annum over 23 years is a serious concern and has necessitated an unfavourable conservation assessment (Species Conservation Assessment 2007).

The causes of the decline have not been identified. Some studies have correlated poor water quality with sites that proved negative for otter signs, while others have failed to do so (Chapman and Chapman 1982, Lunnon and Reynolds 1991, Hamilton and Rochford 2000, Bailey and Rochford 2006). Declining prey resources have also been suggested as a cause (Preston et al. 2007). In addition, anthropogenic mortality, disturbance and loss of riparian habitat are thought to contribute (see appendix I: Species Action Plan 2008). My findings highlight the urgent need to quantify the pressures on the population and to determine whether the population continues to decline (see appendix I: Species Action Plan 2008). I attempt to address the latter concern by examining otter demography in chapter 6.

Applying quantitative methods to conservation planning: population dynamics of the Eurasian otter in Ireland

CHAPTER 6

The demography of the Irish otter population

THE DEMOGRAPHY OF THE IRISH OTTER POPULATION

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ABSTRACT

I identified age-specific mortality and fecundity rates for Ireland from 78 otters gathered from 1996 to 2007. The age structure was similar to apparently healthy and widespread European populations and significantly different to recovering or declining populations. The deterministic rate of increase (λ) of the population was 1.07 (SD = 0.054). This supports the tentative suggestion, based on spraint survey results that the rate of decline of the Irish population has slowed since 1992 (Bailey and Rochford 2006). Survival was estimated to be of more importance to the growth rate of the living population whereas a more precise estimate of maternity was of was of far greater importance to reducing uncertainty in λ . (MANUSCRIPT).

6.1 - INTRODUCTION

Population demography is critical to predicting the fate of populations and identifying the pressures acting upon those populations. Demographic information can contribute to conservation planning by identifying the key life-stages and life-history transitions requiring management action. Temporal trends in demography can also provide relatively rapid post-evaluation of management measures. Unlike most aspects of otter biology, population demography is relatively easily studied and much research attention has focused upon it (Kruuk et al. 1987, Kruuk and Conroy 1991, Sidorovich 1991, Gorman et al. 1998, Heggberget 1991, 1998, Ruiz-Olmo et al. 1998, Hauer et al. 2000, 2002a, 2002b). However, demographic parameters can vary across years and populations depending on climate, food supply, population density, local adaptations and management actions (Saether et al. 1998, Mech and Boitani 2003, Linnell et al. 2007, Sulkava 2007). For example, estimates of annual juvenile mortality across Europe range from 20-40% (Gorman et al. 1998, Heggberget 1998, Ruiz-Olmo et al. 1998, Hauer et al. 2000, Kruuk 2006), while estimates of average litter sizes range from 1.55-2.8 (Wijngaarden and van Peppel 1970, Mason and Macdonald 1986, Kruuk et al. 1987, 1991, Sidorovich 1997, Sulkava 2007).

Otters are a naturally vulnerable species that are susceptible to dramatic declines and slow recovery (see chapter 1). In spite of the high level of protection afforded the species since the 1970s and 1980s (e.g. Wildlife Act 1976, Council of Europe 1979, Wildlife Order 1985), the otter population declined by 23% since 1982 (see chapter 5). Even though the basic biology of otters makes them likely to be sensitive to changes in mortality and fecundity (see chapter 1), demographic information is wholly lacking for the Irish otter. Identifying the age-structure of a population is fundamental to estimating age-specific measures of reproduction, growth and survival (Bodkin et al. 1997) and these measures are often a prerequisite for the design of correct management policies (Kruuk et al. 1987, Beissinger and Westphal 1998, Gough and Rushton 2000, Akçakaya 2004). These measures may identify life-history transitions that are of particular importance to the growth rate of the population and indicate whether the population is in a state of deterministic growth or decline (Leslie 1945, 1948).

There is some suggestion that the rate of decline of the Irish otter population has slowed in recent years (Bailey and Rochford 2006). However, confidence in this result is

limited by the temporal coarseness of the survey program and the relatively small sample of the intervening 1991 survey (Lunnon and Reynolds 1991).

I calculated fecundity and age-specific mortality rates for the Irish otter population and constructed Leslie matrices to estimate the deterministic rate of change of the population (λ) and identify the relative importance of each demographic transition.

6.2 - MATERIALS AND METHODS

I gathered a sample of 74 otter cadavers found in Ireland between 1996 and 2007. Cadavers were donated by National Parks and Wildlife rangers, members of the public and other researchers. Most cadavers were road traffic victims (86%), with fish-traps and natural mortality accounting for the remainder (7% each). Because, the majority of cadavers were in poor condition, weight and length estimates were inaccurate and are not considered here.

A number of mammalian structures respond to changes of physiological condition of an organism by changing their morphological characteristics as they grow (Klevesal 1996). Periodic increments within these structures can indicate the age of an animal. For otters, counting annual incremental rings in the teeth is the most accurate approach (Heggberget 1984). Each cadaver was aged to the nearest year by counting rings in a cross section of the dentine of the root of the canine or, where necessary, incisor tooth (Heggberget 1984, Kruuk and Conroy 1991). The age of each animal was estimated 3 times by one researcher using a double blind approach. Incremental rings are often indistinct and counts actually represent an index of age. The age-structure was calculated as the average for the 3 counts.

To estimate the survival rates for each age class (S_x) , I assumed that the distribution among the ages of the collected sample was the same as in the living population. I calculated age-specific mortality as the number of otters of year-class 'i', divided by the number of otters in the sample assumed to have entered year-class 'i' (i.e. the total number of deaths in the sample of aged carcasses, minus the number of deaths of otters less than 'i' years old) (Kruuk and Conroy 1991). Chi-squared tests were used to compare the age structure of our sample with those of European populations.

Litter sizes can be estimated by examining the uterus for the presence of embryos or placental scars (Hauer et al. 2002b). I recorded the presence and number of uterine scars and calculated the proportion of females with intact uteri that displayed them. The poor quality of the cadavers limited detection of other signs of pregnancy. The ratio of

uterine scars to other signs of pregnancy should be constant. I estimated the proportion of females that breed each year based on the ratio determined in a large study of over 1,000 otters that could examine all signs of pregnancy (Hauer et al. 2002b). The sample of cadavers could not include otter cubs that died within the natal holt and these deaths were not included in my calculation of age-specific mortality rates. Therefore, maternities (M) based on uterine scars would overestimate the growth rate of the population. Instead, I based my calculation of maternities on observations of family groups consisting of mother and cubs up to 12 months old. Sightings were subjectively vetted to exclude fleeting observations that might miss otter cubs. Family groups were observed by L. Ó Néill (n = 6), National Parks and Wildlife Service rangers (n = 6), wildlife photographers (n = 4), and other ecological researchers (n = 4) from 2004-2007. To estimate litter size at emergence from the natal holt, I assumed that the ages of the cubs and the likelihood of dying were evenly distributed across ten months and corrected for the number of otters that were likely to have died in the sample since emergence.

Fecundities (F_x) were calculated as the product of the likelihood of surviving to the next time step (S_x) and the maternity (M_x) in terms of female offspring:

$$Fx = Sx. Mx.$$

Where x corresponds to the age class in question. It was assumed that the maternity rate was constant for all mature age classes (2+ years) (i.e. $M_x = M$).

The standard errors (se) for each demographic rate (e.g. age specific survivals, litter sizes and the proportion of females breeding in a year) were calculated using the equation for the standard error of a proportion (P) where appropriate i.e. $(\sqrt{(P(1-P)/n}))$ or otherwise simply $(\sqrt{(sd)/n})$. The standard error for maternity and fecundity were slightly more complex as they were the product of several parameters. Maternity was a product of litter size and the proportion of animals breeding each year, whereas fecundity was a product of maternity and survival. In both cases the appropriate uncertainty was assessed by allowing each of the parameters involved in the calculation to vary randomly and independently around its mean and standard deviation and repeating the calculation 300 times. The resulting set of solutions was used to determine the standard deviation of the product (i.e. maternity or fecundity) which is equivalent to the standard error of the parameter estimate.

6.2.1 - THE POPULATION PROJECTION MODEL

I constructed a series of age-based female-only Leslie matrix for a post-breeding census (Leslie 1945, 1948). The model only considered females and so assumed that sex ratios in the field were even. A population structured as 6 age classes (including 0 and 5+ age classes) at time t can be represented as:

$$N(t) = \begin{pmatrix} N_{0(t)} \\ N_{1(t)} \\ N_{2(t)} \\ N_{3(t)} \\ N_{4(t)} \\ N_{5+(t)} \end{pmatrix}$$

In an age-structured model, individuals are grouped by their age; those that are the same age are assumed to have the same survival and fecundity rates. These rates may differ between ages, however, between age classes. The survival rate S_x is the proportion of x-year old individuals that survive to be x+1 years old one time step later. The fecundity, F_x , is the average number of offspring censused at the next time step per individual of age x alive at a given time step (Akcakaya 2005). Fecundity is calculated as the product of the average maternity and the age specific survival of the mother i.e. potential mothers must survive and then breed. These parameters are combined to form a Leslie matrix, which for an age structured population with 6 classes would take the form:

$$L = \begin{pmatrix} F_0 & F_1 & F_2 & F_3 & F_4 & F_{5+} \\ S_0 & 0 & 0 & 0 & 0 & 0 \\ 0 & S_1 & 0 & 0 & 0 & 0 \\ 0 & 0 & S_2 & 0 & 0 & 0 \\ 0 & 0 & 0 & S_3 & 0 & 0 \\ 0 & 0 & 0 & 0 & S_4 & S_{5+} \end{pmatrix}$$

Note that this is an extended form of the Leslie matrix because there is a non-zero value at S_8 that assumes survival is similar for all ages at or above 5 years old. Note also that while F_0 and F_1 are included in the model for clarity the value of these parameters is zero for otters where breeding occurs only among animals of 2 years and older. Projections of the population size can be made by multiplication with a Leslie matrix. The distribution of abundances in the next time step is given by:

$$N(t+1) = L.N(t)$$

Repeatedly multiplying an age distribution by a Leslie matrix with constant elements tends to lead it to a stable age distribution. Once the stable age distribution has been reached the proportion of individuals in each of the age classes remains the same. At

this point, multiplying the age distribution by the Leslie matrix is the same as multiplying it by a scalar number which is the population growth rate λ , where $\lambda = e^r$ and r is the per capita rate of increase.

The effect of a small change in specific vital rates on λ determine the sensitivity of the population's growth rate to those parameters. Sensitivities are calculated analytically as the relative size of the change in λ to the small change in the relevant matrix element (a_{ij}) .

sensitivity
$$s_{ij} = \frac{\partial \lambda}{\partial a_{ij}}$$

The proportional sensitivity, or elasticity, is the proportional change in λ caused by proportional change in the cell. The elasticity is an important measure for guiding conservation or management measures in that it indicates the elements that have the largest relative impact on population growth.

elasticity
$$e_{ij} = \frac{a_{ij}}{\lambda} \cdot s_{ij}$$

For this analysis there was no demographic stochasticity, density dependence or spatial structuring of the population. Ignoring demographic and environmental stochasticity means that the population growth rates estimates may be higher than in the living population.

To account for the uncertainty in the estimates of maternity and the age-specific survival rates (i.e. M, $S_0...S_{5+}$), I constructed 50 Leslie matrices by randomly varying each parameter value around the corresponding distribution of uncertainty. λ was calculated for each matrix. I used standardised linear regressions between parameter values and estimates of λ to determine the relative sensitivity to the uncertainty in the parameter values (McCarthy et al. 1995, Saltelli et al. 2000, Frieberg and Jenkins 2005, Nilsen et al. 2007). I fitted regression models through data scaled to have a mean of zero and a standard deviation of unity (Saltelli et al. 2000). If parameters are not strongly correlated, the sensitivity of model prediction to a parameter is the square of the regression estimate for that parameter (Saltelli et al. 2000). This technique results in unit-less coefficients representing the relative importance of the uncertainty in the different parameters (Frieberg and Jenkins 2005).

6.3 - RESULTS

The 3 replicate counts for each tooth varied by an average standard deviation of 0.75 and there was no relationship between count variance and the average age estimate ($R^2 = 0.046$). However, the incremental rings became difficult to distinguish for animals over 6 years old. We therefore grouped these individuals into a single composite class for comparison with other populations. The age structure of the population was significantly different to that of Shetland, Spain, England and Wales, and Norway (Ruiz-Olmo et al. 1998, Gorman et al. 1998, Heggberget 1998), but was similar to Scotland and eastern Germany (Kruuk 2006, Gorman et al. 1998, Hauer et al. 2000) (table 6.1). Age-specific mortality rates increased linearly following the first year until the seventh year ($R_{adj}^2 = 0.88$, $F_4 = 31.6$, P = 0.011) (figure 6.1, table 6.2). The average life expectancy at birth was estimated at 2.9 (SE = 0.7) years.

Table 6.1. Comparison between the age-structure we identified for the Irish otter population based on 74 cadavers and those of other European countries. Non-significant P-values indicate that the observed differences in the age structures are consistent with chance variation.

	N	X^2	P	Author
Eastern Germany	1028	7.79303	0.254	Hauer et al. 2000
Spain	79	18.11463	0.006	Ruiz-Olmo et al. 1998
Shetland	146	33.58138	0.000	Kruuk 2006
Scotland	148	6.800809	0.340	Gorman et al. 1998
England and Wales	97	39.97852	0.000	Gorman et al. 1998
Norway	2030	82.45632	0.000	Heggberget 1998

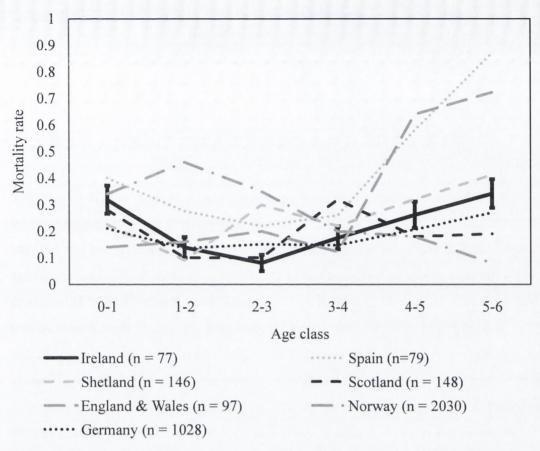


Figure 6.1. The variability of age structures among European otter populations. Agespecific mortality rates from the Irish sample (± 1SE) are compared with rates for other European populations (Gorman et al. 1998, Heggberget 1998, Ruiz-Olmo et al. 1998, Hauer et al. 2000, Kruuk 2006). Significant P-values (and grey lines) indicate populations that a Chi-Squared test has shown are significantly different to the Irish population.

Litter sizes based on uterine scars averaged 2.1 (SD = 0.78, n = 9), while those based on otter cub sightings averaged 1.95 (SD = 0.82, n = 20) suggesting that 7% of cubs died before emerging from the natal holt. Uterine scars were evident for 9 of the 20 females with intact uteri that were above 2 years old, indicating, by comparison with Hauer et al. (2002b), that 74% (SE = 11%) of females breed each year. Maternity was therefore calculated as 0.72 (SE = 0.10) female-offspring/adult-female/yr (table 6.2).

Table 6.2. Estimated demographic parameter values for the Irish otter population.

Age class	Survival (se)	Maternity (se)	Fecundity (se)
0-1	0.68 (0.05)		
1-2	0.86 (0.04)		
2-3	0.92 (0.03)	0.72 (0.1)	0.66 (0.1)
3-4	0.82 (0.04)	0.72 (0.1)	0.59 (0.09)
4-5	0.74 (0.05)	0.72 (0.1)	0.53 (0.09)
5-6	0.66 (0.05)	0.72 (0.1)	0.47 (0.08)

The deterministic growth rate of the population (λ) was calculated in the absence of density dependent effects and with the assumption of a stable age-distribution. Under these conditions, the estimates in table 6.2 would give rise to a growth rate of $\lambda = 1.07$ (sd = 0.054). The uncertainty in λ was estimated by deriving its value for 50 matrices whose elements were varied randomly around the distribution indicated in table 6.2. This growth rate must be regarded as an approximate estimate because λ was calculated without account of demographic or environmental stochasticity. The effect of the uncertainty in the demographic parameters is such that the growth rate cannot be said to be significantly greater than 1.

I analysed the relative importance of the various parameters to the growth rate by deriving an analytical solution for the elasticity and sensitivity of the baseline Leslie Matrix (table 6.2). The population growth rate is most highly influenced by changes in survivorships. The total sensitivity for survivorship is approximately 4 times greater than that for fecundity. It is likely therefore that the living population is a great deal more sensitive to survival than fecundity. However, the sensitivity of λ to the actual level of uncertainty in the parameter estimates shows an opposite result. In this case, the coarse estimate of maternity accounted for 75% of the uncertainty in the final lambda estimate.

Table 6.2. Analytical solutions for the sensitivity and elasticity of the matrix elements in the baseline model.

	Analytical solutions for base model				
	Elastic	ities	Sensitiv	vities	
Age classes	Survivorship	Fecundity	Survivorship	Fecundity	
0	0.21		0.33		
1	0.21		0.26		
2	0.14	0.07	0.16	0.11	
3	0.09	0.05	0.12	0.09	
4	0.06	0.04	0.08	0.07	
5+	0.09	0.06	0.15	0.13	

Table 6.3. Sensitivity to uncertainty in parameter values. Results are derived from standardised linear regressions between 50 sets of independently randomised parameter values and model predictions. Parameter values were randomised around their corresponding estimated distributions. In this case the sensitivity of model prediction to a parameter's uncertainty is the square of the regression estimate for that parameter (Saltelli et al. 2000).

	Bayesian solution for model uncertainty		
Parameter	Age classes	Sensitivity (β^2)	
Maternity	2+	0.54	
Annual survival	0-1	0.088	
	1-2	0.015	
	2-3	0.015	
	3-4	0.022	
	4-5	0.028	
	5+	0.01	

6.4 - DISCUSSION

6.4.1 - METHODOLOGICAL ISSUES

The modest sample size of this study led to a large degree of uncertainty for each parameter estimate and for the deterministic rate of increase (λ). I pooled males and females to calculate demographic rates. The degree of bias introduced by pooling these results can vary from none (Gorman et al. 1998) to slight but significant (Hauer et al. 2000, 2002a). Any bias will tend to increase estimates of mortality for the young age classes and

decrease estimates of adult mortality (Hauer et al. 2000). Based on my analysis of the relative importance of age-specific mortality, this may cause slight overestimation of λ .

6.4.2 – SIGNIFICANCE OF RESULTS

My sample differed markedly and significantly from populations in Shetland, Norway, Spain and England and Wales. The Norwegian population increased by around 58% from 1990 to 1995 (Heggberget 1998a). In Spain, the population had declined or become extinct in much of its range since the 1950s and the sample was collected from across the country from 1969 to 1996 (Ruiz-Olmo et al. 1998). The decline and gradual recovery of otter populations in England and Wales have been widely documented (e.g. Crawford 2003). In contrast, the age structure of my sample was similar to that calculated for mainland Scotland and eastern Germany where populations remain widespread and apparently common (Green and Green 1997, Hauer et al. 2000, Kruuk 2006). It would appear that the age structure of the Irish population may be characteristic of a healthy and relatively stable population.

The finite rate of increase for the population (λ) suggests that, in the absence of demographic or environmental stochasticity, the population has the potential to grow. However, this result is not significant and also ignoring demographic and environmental stochasticity and spatial structuring of the population may overestimate growth rates. Nevertheless, it is unlikely that the population was in general decline during the period 1998 to 2007. This supports the findings of the national otter surveys of Lunnon and Reynolds (1991) and Bailey and Rochford (2006). The population appears to have stabilised to the factors that caused the decline between 1982 and the mid 1990s. Nevertheless, the uncertainty associated with my estimate of λ and the importance of this statistic for predicting population dynamics (see Chapter 7) strongly encourages the continuation and intensification of demographic studies on the Irish otter. Interestingly, although the analytical solution for the sensitivity and elasticity of the baseline Leslie matrix (representing the best estimates for parameter values) suggest that survival rates are of more importance to the growth rate of the living population than fecundity, it is clear that research should focus on maternities if increased precision of the growth rate estimate is required. Thus, in the short term at least, management and research should focus on mortality and fecundity respectively. Until a more precise estimate of fecundity is achieved it will prove difficult to relate management measures to changes in growth rate.

Applying quantitative methods to conservation planning: population dynamics of the Eurasian otter in Ireland.

CHAPTER 7

Quantitative integration of biological data into conservation planning: do Ireland's Special Areas for Conservation work for otters?

QUANTITATIVE INTEGRATION OF BIOLOGICAL DATA INTO CONSERVATION PLANNING: DO IRELAND'S SPECIAL AREAS FOR CONSERVATION WORK FOR OTTERS?

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ABSTRACT

Over 14,000km of Irish watercourses have been designated as candidate Special Areas for Conservation (cSAC) under the EU Habitats Directive (1992). I developed a spatially explicit population model, incorporating variable landscape permeability and environmental and demographic stochasticity, to investigate the ability of Ireland's cSAC network to ensure favourable conservation status for otters. Favourable conservation status requires that the population's distribution remains above its 1992 level for the foreseeable future. I examined the extent to which favourable demographic conditions would have to be maintained or generated within cSACs to buffer the population's distribution against the effects of declining habitat quality in unprotected areas. Focusing management on the SAC network proved no more efficient than simply managing the landscape homogeneously. I evaluated the relative contribution of the individual cSACs to maintaining favourable conservation status and found that the network could be reduced by 17.6% without materially affecting its performance. Nevertheless, this reduced network

was still only marginally more efficient than simply managing the landscape homogeneously. Conversely, replacing the inefficient cSACs with new SACs in vulnerable areas has the potential to greatly improve the network's performance. I advise that either the population be managed homogeneously throughout the landscape or that the SAC network be modified. Sensitivity analysis indicated that conservation should be focused primarily on reducing mortality of adult females and juveniles. Systematic collection and analysis of cadavers would allow improved precision of estimates for parameters that dominate model sensitivity. Quantification of the impact of management actions on those vital rates should be a conservation priority. (MANUSCRIPT).

7.1 - INTRODUCTION

Scarce resources and competing land-use goals necessitate efficient conservation measures to provide the ecological requirements of target species (Lomolino 1994, Jiang et al. 2007). Conservation programs developed ad hoc have been frequently criticised for their lack of efficiency (Rebelo and Siegfried 1992, de Vires 1995, Lombard et al. 1995, Bulte and Van Kooten 2001, Araújo et al. 2007, Stewart et al. 2007). Consequently, a great deal of research, money, and effort has been put into developing theory and techniques to make conservation more efficient (Stewart et al. 2007, Prendergast et al. 1999). Sophisticated approaches that apply scientific ideas and methods to reserve design have developed over the last few decades (Caughley 1994, Kingsland 2002).

Population simulation modelling, in particular, has become one of the most powerful tools in conservation biology for comparing alternative management actions or conservation programs (Marshall and Edwards-Jones 1998, Gough and Rushton 2000, Reed et al. 2001, Lurz et al. 2003, Nilsson 2003, Bonesi et al. 2007). It provides a rigorous, objective and transparent methodology that integrates available data, uncertainty and natural variability in predicting biological responses (Akçakaya and Sjögren-Gulve 2000, Gough and Rushton 2000, Kramer-Schadt et al. 2004, Chapron and Arlettaz 2006, Linnell et al. 2007).

It has been noted that objective and systematic tools are used infrequently by those charged with managing landscapes (Pressey 1994, Prendergast et al. 1999). Although commonly used in fisheries, managers have been slow to adopt the use of population modelling for managing carnivores (Chapron and Arlettaz 2006). Non-quantitative approaches often continue to be employed because population modelling requires data that

are often difficult to obtain and predictions for individual cases may generate large confidence intervals (Lima and Zollner 1996, Ruckelshaus et al. 1997, Beissinger and Westphal 1998, Akçakaya and Sjögren-Gulve 2000, Gough and Rushton 2000). Alternative forms of decision-making are at least equally imprecise, although this is rarely acknowledged when solutions are provided that ignore uncertainty or make hidden assumptions (Akçakaya et al. 2004). Preparing population models and in particular gathering the data to parameterise them incur a significant that is avoided (or at least postponed) if decisions are based on expert opinion for example. However, as noted in chapter 1, it is telling that where there is a direct economic cost associated with management decisions, as in fisheries, modelling approaches are used.

Non-quantitative approaches were employed in the design of Ireland's protected area network for otters (*Lutra lutra*) (Bailey and Rochford 2006). The otter's European distribution collapsed during the latter half of the last century (Mason and Macdonald 1986, Foster-Turley et al. 1990). The European Union's (EU) response was to create a coherent, trans-boundary, ecological network of protected areas, termed Special Areas for Conservation (SAC), to ensure the favourable conservation status of otters within its jurisdiction (EU Habitats Directive 1992). Favourable conservation status requires that the distribution of the species is unlikely to drop below its 1992 level for the foreseeable future, provided this reference range is sufficient for the species' long term survival (EU Habitats Directive 1992).

Between the Republic of Ireland (ROI) and Northern Ireland (NI) over 14,000km of watercourses, representing 13.7% of all aquatic habitats, have been designated as candidate SACs (cSAC) for otters (figure 7.1). The potential contribution of this cSAC network and its components to maintaining a favourable conservation status for otters is unknown, even though this knowledge was explicitly cited as a site selection criterion in the EU Habitats Directive (1992).

Favourable conservation status in Ireland is based on the 1982 National Otter Survey that found otters at over 90% of locations (Chapman and Chapman 1982, Species Conservation Assessment 2007). Subsequent declines in habitat quality caused the otter population to drop by 22% (see chapter 5). There is a clear need for conservation action but it is unclear if focused management of a protected area network, the design of which was informed by expert opinion rather than quantitative information, is the proper vehicle for its delivery.

7.2 - AIM

The aim of the current paper is to develop a population model to evaluate the performance of protected area networks for the conservation of a wide-ranging species given unforseen changes to the landscape. My approach will be to simulate the fate of populations under an exhaustive set of conditions where protected areas act as population sources of various strength (i.e. net exporters of individuals) and unprotected areas act as population sinks of various strength (i.e. net importers of individuals). This leads to the range of conditions where the conservation target can be met for a given network of protected areas. The best network is that which achieves the conservation target under the widest range of conditions. I will use this approach to evaluate the subjectively designed cSAC network for the Eurasian otter in Ireland in ensuring favourable conservation status.



Figure 7.1. The distribution of the candidate Special Areas for Conservation for otters in Ireland.

7.3.1 - BASIC MODEL STRUCTURE

I built a stage-structured, stochastic, spatially-explicit, sub-population based model for the population of female otters in Ireland. The typical otter mating structure is polygyny with a single male overlapping several females (Erlinge 1968, Kruuk and Moorhouse 1991, Johnson et al. 2000). Male home ranges expand dramatically when neighbours are absent and can be several times larger than female home-ranges (see chapter 4, Erlinge 1967, Durbin 1998). Often a single dominant male occupies an extremely large area and covers all the females in that area (Koelewijn 2007). I excluded males from the analyses because they are highly unlikely to be the limiting sex and their inclusion would have unnecessarily complicated the model.

In conditions of low population density, female otters have been observed to range over up to 80km of watercourse (Saavedra 2002). The Irish network of waterways and coastal shore was divided into 375 coherent sub-catchments each containing an average of 73.8km (SD = 30.0km) of river, lake-shore or coast, along with associated streams (figure 7.2a). Shores within 80m of each other were considered co-incident because otters commonly forage up to this distance from the shore (Kruuk and Moorhouse 1991).

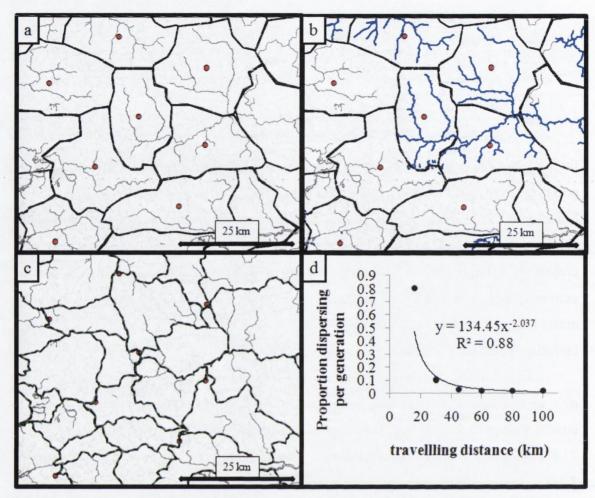


Figure 7.2. The landscape template for the spatially explicit population model. (a) Polygons (black lines) were drawn around sub-catchments encompassing roughly 80km of rivers, lake shore or coast (dark grey lines) along with associated streams (light grey lines). (b) Population sizes were estimated for each sub-catchment and the proportion protected within Special Areas for Conservation (blue lines) was calculated. (c) The 'otter distance' between each sub-catchment centroid (red dots) was calculated using least cost paths (green and black lines). (d) The degree of connectivity between each sub-catchment was based on a distance related dispersal function observed for 104 North American river otters (adapted from Blundell et al. 2002).

Population growth, density dependence, emigration and imigration were modelled within and between each sub-catchment. Hence, the population in subcatchment i the following year $(N_{i,t+1})$ results from the effect of its specific rates of fecundity (F), juvenile survival (S_{juv}) , sub-adult survival (S_{sa}) , and adult survival (S_{ad}) on the population the

preceding year $(N_{i,t})$, combined with the net effect of emigration (E) and immigration (I) and the carrying capacity of subcatchment $i(K_i)$ (equation 7.1).

$$\begin{bmatrix} N_{juv.i.t+1} \\ N_{sa.i.t+1} \\ N_{ad.i.t+1} \end{bmatrix} =$$

$$\begin{cases}
\begin{bmatrix}
0 & 0 & F_{i} \\
S_{juv.i} & 0 & 0 \\
0 & S_{sa.i} & S_{ad.i}
\end{bmatrix}_{I} \begin{bmatrix}
N_{juv.i.t} \\
N_{sa.i.t} \\
N_{ad.i.t}
\end{bmatrix}_{II} + \sum_{j=1}^{n} \begin{pmatrix}
I_{juv.j.i} \\
I_{sa.j.i} \\
I_{ad.j.i}
\end{pmatrix} - \begin{pmatrix}
E_{juv.i.j} \\
E_{sa.i.j} \\
E_{ad.i.j}
\end{pmatrix}_{III}$$

$$\times \left(\begin{bmatrix}
\frac{N_{ad.i}}{K_{i}}
\end{bmatrix} if N_{ad.i} > K_{i} \right)_{IV}$$

I – demographic rates, *II* – population structure, *III* – movement, *IV* – density dependence

POPULATION STRUCTURE

Although capable of breeding in their second year (Kruuk 2006), only one of several hundred individuals did so in a German study (Hauer et al. 2002b). I therefore limited reproduction to individuals more than 2 years old. I did not impose a maximum age for reproduction because the range of mortality rates included in the model allowed aproximately 4% of individuals to survive to 16 years, an age at which reproduction has been observed in the wild (Hauer et al. 2002b).

Juvenile (0-1 years), sub-adult (1-2 years) and adult (≥2 years) stages were included in the model. Although evidence for age-specific mortality of adult otters was found in chapter 6, I simplified the model to a single adult stage. Patterns of age-specific morality rates are inconsistent and sometimes not evident in studies across Europe (see chapter 6). The model examines the cSAC network's performance over a wide range of hypothetical demographic conditions that are not limited to the conditions currently observed in Ireland.

DEMOGRAPHIC RATES

Otters reintroduced to protected areas in the Netherlands suffered high levels of mortality by ranging outside of the protected area (VanLiere and VanLiere 2005). I assumed that otters could not distinguish between protected and unprotected areas so my analysis investigated the effects of threats which otters cannot detect, such as road traffic induced mortality. In under-populated conditions, otters spread out throughout a catchment and occupy large annual ranges (Mitchell-Jones et al. 1984, Saavedra 2002). Consequently, all individuals within a sub-catchment had identical vital rates based on the proportion of protected and unprotected areas within the sub-catchment. The population size within each sub-catchment and the proportion of that population that was protected within cSACs was estimated as described in chapter 5 (figure 7.2b).

Demographic stochasticity was modelled by sampling survivals and migrations from a binomial distribution and births from a Poisson distribution at each time-step of the simulations (Akçakaya 1998). I modelled environmental stochasticity by drawing survival and fecundity values from a set of lognormal distributions whose parameters reflect the average value and temporal variability of each demographic rate. Multi-annual census data suitable for estimating the degree of environmental stochasticity was unavailable. Instead, I used the variability of the demographic rates between those populations not significantly different to the Irish population as a surrogate for the year-to-year environmental variability in Ireland (see chapter 6). Lognormal distributions are useful where the demographic rates are close to zero or one in order to avoid biases caused by truncating biologically impossible values (i.e. negative fecundity or survival greater than one) (Akçakaya 1998, Bretagnolle et al. 2004). The long period of parental care for sub-adult otters makes it likely that breeding success and adult survival are highly correlated and I therefore assumed that the values of fecundity and survival of a population for a given year were perfectly correlated.

I constructed 16 post-breeding Leslie matrices by varying the demographic parameters around the ranges recorded among populations that were not significantly different to the Irish one (see chapter 6) (Leslie 1945, 1948). The λ varied between 1.0 and 1.2 for these matrices. I then investigated a range of scenarios involving increased mortality in non protected areas that reduced λ to between 0.9 and 1.0 for these areas. All models were analysed by Monte Carlo simulation using Ramas Metapop (Akçakaya 1998). I performed 100 stochastic replications for each of 80 scenarios and recorded the occupancy of each sub-catchment after 50 years in each case. I interpreted the 'foreseeable

future' (sensu EU Habitat's Directive 1992) as a 50 year time horizon. Population models that emphasise short-term projections are generally more successful (Beissinger and Westphal 1998). I believe that forecasting over a longer time horizon is unwarranted owing to expected climate change and because landscapes are unlikely to remain static over longer periods. I ran the same set of simulations at 0.75 and 1.25 times relative dispersal to account for uncertainty regarding this parameter. The populations within each subcatchment were at carrying capacity with a stable age distribution at the beginning of each simulation. I plotted λ in protected areas as y-values, λ in unprotected areas as x-values and the size of the population's range after 50 years as z-values. I then calculated isoclines representing the range of demographic conditions resulting in favourable conservation status with a Spline interpolation (ArcView3.2 - Spatial Analyst Extension) (figure 7.3).

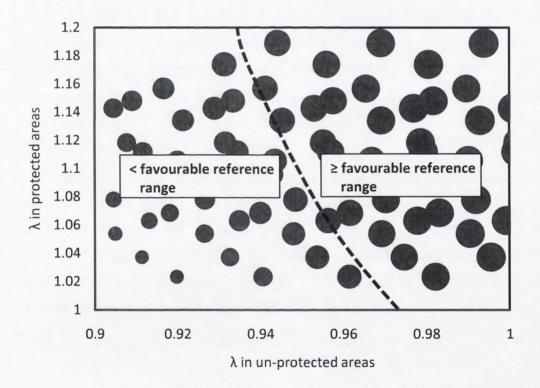


Figure 7.3. The range of conditions (represented by the isocline) in which a hypothetical protected area network could preserve a population at or above a given conservation target; in this case a favourable reference range. The size of each point represents the results of a scenario examining the projected range of a population under the relevant demographic conditions.

MOVEMENT

Spatially-explicit models are generally highly sensitive to the details of dispersal behaviour (Ruckelshaus et al. 1997). Models based on cost-weighted distance take account of variable landscape permeability and provide better agreement with observed patterns for riparian animals than Euclidian or geographic distance (Jansens et al. 2006, Bunn et al. 2000, Bosschieter and Goedhart 2002). I measured approximate least cost paths between each sub-catchment centroid (ArcView3.2) (figure 7.2c). The cost of travelling across land was six times greater than travelling along watercourses (Saavedra 2002, Williams et al. 2002, Janssens et al. 2006). I treated open water similarly to dry land because North American river otters (*Lontra canadensis*) travel distances of up to 13km across open water between islands (Blundell et al. 2002).

There has not been a systematic survey relating Eurasian otter dispersal with travel distance, although it has been reported that there is little gene flow over distances greater than 100-150km (Dallas et al. 1999, Kruuk 2006). Reintroduced otters have been tracked following their release and their movements are considered somewhat analogous to natural dispersal (Sjöåsen 1997). Based on 36 released yearlings, 67% travelled a geographic distance of less than 20km from the release site and 100% travelled less than 40km. Similarly for 104 individuals from a native wild population of river otters in Canada, 56% dispersed a geographic distance of less than 15km and 100% travelled less than 50km (Blundell et al. 2002). Consequently, river otter dispersal appears to be a reasonable surrogate for that of Eurasian otters. The main advantage of the river otter data is that it also relates dispersal to the actual distance travelled. The river otters displayed equal rates of natal dispersal for males and females (Blundell et al. 2002). Pooling Blundell et al.'s (2002) natal dispersal data for males and females reveals a power function describing the proportion of individuals per generation dispersing (Ψ) to a certain distance in km (D) by the most likely travel path (equation 7.2) (figure 7.3d).

Equation 7.2
$$\Psi = 134(D)^{-2.04}$$

I estimated the proportion of individuals dispersing out of a sub-catchment per generation (Ψ°) using the average travel distance to the two nearest neighbouring subcatchments in place of 'D' in equation 7.1. By averaging between two neighbours I achieved a better approximation of the size of the source sub-catchment and hence the

proportion of animals that were likely to leave it. I converted the proportion of individuals dispersing out of a sub-catchment per generation (Ψ°) to the proportion dispersing per annum by dividing by the average life-expectancy of otters, which is 2.9 years in Ireland (see chapter 6). The likelihood that a dispersing individual from catchment 'i' would arrive in catchment 'j' was weighted by the likelihood of dispersing the relevant distance (Ψ_{ij}) and the area of catchment 'j' (A_j) compared with the total area accessible at that distance (πD_{ij}^2) i.e. ($A_j/\pi D_{ij}^2$). The dispersing individuals from catchment 'i' ($\Psi^{\circ}_{i}/2.9$) were allocated between the potential recipient catchments in proportion to their relative weightings (equation 7.3).

Equation 7.3
$$P_{ij} = \frac{\psi^{\circ}_{ij}}{2.9} \left[\frac{\psi_{ij} \left(\frac{A_j}{D_{ij}^2} \right)}{\sum_{1}^{n} \left\{ \psi_{in} \left(\frac{A_n}{D_{in}^2} \right) \right\}} \right]$$

DENSITY DEPENDENCE

Intra-specific competition has been clearly shown to occur among otters (Sulkava et al. 2007). Adult females formed the basis of density dependence because of their territoriality (see chapter 4, Erlinge 1967, 1968b, Sjöåsen 1997). Each sub-catchment was assigned a carrying capacity for the number of adult female otters present within the sub-catchment (see chapter 5). Where the number of adult females exceeded this ceiling the whole sub-population was truncated by the proportion required to return adult females to their carrying capacity (Akçakaya 1998). This simple ceiling density dependence model is suitable for territorial species with a long period of parental care (Erlinge 1967, Kruuk 2006).

7.3.2 – MODEL VALIDATION AND SENSITIVITY TESTING

Spatially explicit population models can be highly sensitive to the details of basic biology or parameter values (Ruckelshaus et al. 1997, Todd et al. 2001) and their validity depends on the appropriateness of the data input (Reed et al. 2001, Lindenmayer et al. 2000, Todd et al. 2001, Dunnings et al. 1995, Carroll et al. 2003). Model validation generally compares modelling results with observed patterns, such as population expansion given recorded mortality and fecundity (Rushton et al. 1997). The validity of the dispersal sub-model was tested by constructing 200 scenarios where a random 80-90% of the

island's sub-catchments were depopulated at the outset. I allowed a population with the same demography as the best estimate for the Irish otter population to recover over a period of 50 years. I recorded the rate of expansion of the population in each case and compared it with empirically observed rates of expansion of several European populations.

Sensitivity analysis involves performing multiple simulations to determine if the specific value used for a given parameter has a disproportionate impact on model results (Dunnings et al. 1995). I used standardised linear regressions between parameter values and model predictions to determine prediction sensitivity to parameter values (McCarthy et al. 1995, Saltelli et al. 2000, Frieberg and Jenkins 2005, Nilsen et al. 2007). Parameter estimates were varied normally around their distributions in the literature or where unavailable around a co-efficient of variation of 25%. Fifty sets were drawn at random from these distributions and the stochastic model was run 100 times for each set of parameters. Each of the 100X50 simulations were run for 50 time steps with population distribution reported for the final time-step. I then calculated the mean area occupied by the population for each set of parameter values. Using the area occupied by the population after 50 years as the dependent variable, I fitted regression models through data scaled to have a mean of zero and a standard deviation of unity (Saltelli et al. 2000). If parameters are not strongly correlated, the sensitivity of model prediction to a parameter is the square of the regression estimate for that parameter (Saltelli et al. 2000). This technique results in unit-less coefficients representing the relative importance of the different parameters (Frieberg and Jenkins 2005). If demography within cSACs remained as estimated for Ireland (see chapter 6), favourable conservation status would be preserved provided the level of increased mortality in unprotected areas remained below 17.5%. I selected this level of increased mortality in unprotected areas for my sensitivity testing.

7.3.3 – RANKING CANDIDATE-SACS AND OPTIMISING THE NETWORK.

I ranked the importance of each individual cSAC by recording the effect its removal had on the population's distribution. I performed 500 stochastic replications for each cSAC removal. I then removed the least efficient cSAC from the network and tested the sensitivity of the model to removal of each of the remaining cSACs. Again, I removed the least effective SAC and repeated the process until I had optimised the cSAC network. Finally, I tested the performance of a modified network where the inefficient cSACs were replaced with new SACs in vulnerable areas.

7.4.1 – SENSITIVITY ANALYSIS AND MODEL VALIDATION

Sensitivity analysis showed that the distribution of the population is dependent primarily on adult survival, followed by juvenile survival and fecundity, with little sensitivity to dispersal or carrying capacity (table 7.1). My analysis examined the effect of varying demographic parameters on population distribution. Therefore, the sensitivity of the model to these parameters does not effect my confidence in the results. Survival rates for otters in their second year of life are relatively high, such that model sensitivity was low for this parameter.

The estimates I used for the carrying capacity of sub-catchments were reasonably coarse, the total ranging from 5,659-7,769 adult females (chapter 5). The model output was insensitive to variation in population size because the populations within sub-catchments seldom achieved carrying capacity where population sources were surrounded by population sinks. I conservatively based the evaluation of the network on the lower limits of the population estimates.

Dispersal is not well studied for Eurasian otters and I based its simulation on the ecologically similar North American river otter. To validate the use of this data I examined the rate of expansion of the otter population in the model. The average rate of expansion was 1,010km² (SD = 100km²) per annum equivalent to 10.1 (SD = 1.0) new 100 km² grid squares per annum. Recovering populations of otters in several European countries occupied 11.3 (SD = 3.7) new 100 km² grid squares per annum ([Denmark] Madsen et al. 1992, [Wales] Andrews et al. 1993, [England] Strachan and Jefferies 1996, [Scotland] Green and Green 1997, [Poland] Romanowski 2006). My simulation of otter dispersal was accurate and the model output proved insensitive to this parameter (table 7.1).

Table 7.1. Prediction sensitivity to parameter values based on standardised linear regressions between parameter values and model predictions. The sensitivity of model prediction to a parameter is the square of the regression estimate for that parameter (Saltelli et al. 2000).

description of parameter	$(\beta)^2$	<i>p</i> -value	r^2	M
fecundity (female cubs/female/annum)	0.112	0.015	0.118	98 -
juvenile survival (0 - 1 years)	0.152	0.006	0.152	
sub-adult survival (1-2 years)	0.012	0.446	0.012	
adult survival (>2 years)	0.327	< 0.001	0.328	
relative dispersal	0.025	0.282	0.025	
carrying capacity	0.032	0.218	0.032	

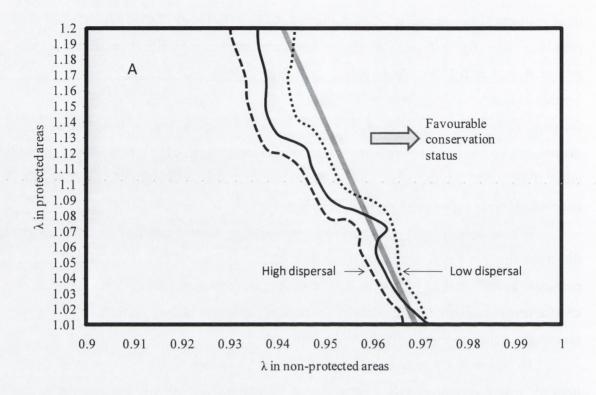
7.4.2 – EVALUATION OF THE CANDIDATE SAC NETWORK

The cSAC network makes a modest contribution to maintaining otter distribution above the favourable reference range (figure 7.4a,b). One can calculate the expected performance of an equivalently sized SAC network that is exactly as cost-efficient as managing the whole landscape homogeneously by assuming a constant cost per unit area for increasing λ. If the protected area comprises, say, 10% of the landscape, the cost of increasing lambda by 'x' in the protected area is assumed to be equal to the cost of increasing lambda throughout the landscape by 0.1 times 'x'. Thus, favourable conservation status is maintained where λ is approximately 0.98 in the absence of any protected area network. Increasing λ from 0.98 to 1.20 within a protected area network comprising 10% of the landscape would cost the same as increasing λ from 0.96 to 0.98 throughout the landscape and so should compensate for a drop in λ in unprotected areas from 0.98 to 0.96. We can compare the isocline describing the range of conditions achieving the conservation target for the target network with the isocline describing the performance of an equivalent network that is exactly as cost-efficient as managaing the whole landscape homogeneously. The currently proposed cSAC network is slightly more efficient than managing the whole landscape homogeneously when very high growth rates are maintained within protected areas ($\lambda > 1.1$) (figure 7.4a,b). However, and more importantly, at more achievable rates of growth (1.0< λ < 1.1) the network is no more efficient than managing the whole landscape homogeneously. The network is slightly

more efficient if the model is based on upper rather than lower confidence intervals for population size (figure 7.4b). This is because there are more individuals available within protected areas to fill unoccupied sink areas. Nevertheless, the improvement in efficiency is modest. Further calculations are performed at baseline dispersal and at the best estimate for population size. The poor performance of the network may arise from the uneven distribution of the cSACs across the island of Ireland (figure 7.1). There are extensive areas of the island that are poorly connected to cSACs and are unlikely to be maintained if unprotected areas act as sinks, regardless of how high λ is within the cSACs.

The sensitivity of the population's distribution to the removal of each cSAC illustrates that there is great variability in their efficiency (figure 7.5). One large cSAC in particular contributes very little to the network's performance. In total we removed 3 cSACs that comprised 17.5% of the network while accounting for just 3.0% of the total sensitivity of the model to individual SAC removal.

To illustrate the potential for modifying the network, I also examined an SAC network where certain cSACs were replaced by alternative SACs in regions that were poorly connected to the network (figure 7.6). This alternative network was by no means globally optimal, but was tested merely to show the potential improvement provided by adding new SACs in vulnerable areas. The alternative network displayed a large improvement over the performance of the original network, particuliarly over the range of achievable growth rates in SACs $(1.0 < \lambda < 1.1)$ (figure 7.7).



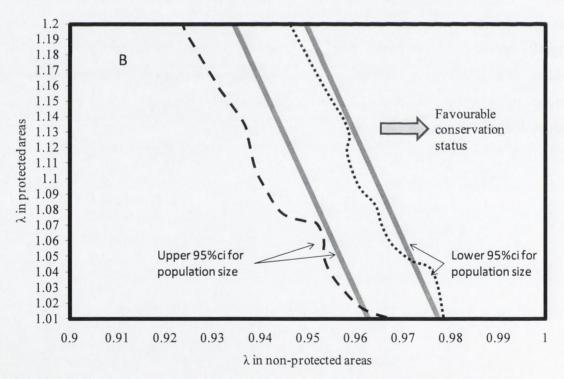


Figure 7.4 – Legend overleaf.....

Figure 7.4. The capacity of the Special Areas for Conservation (SAC) network to maintain otter distribution as the hostility of unprotected areas increases. The black isoclines represent the range of conditions that maintain otter distribution above the favourable reference range for 50 years. (A) The effect of uncertainty in dispersal rate (relative dispersal: 0.75, 1.00, 1.25 left to right). (B) The effect of uncertainty in population estimates (tested at baseline dispersal). Assuming a constant cost per unit increase in λ per unit area, I plot isoclines that represent a network that is exactly as efficient as managing the whole landscape homogeneously (grey lines). Each isocline was calculated from 80 scenarios in which cSACs were treated as population sources of varying strength and non-SAC areas were treated as population sinks of various strength. For each scenario, the average occupancy after 50 years based on 100 stochastic simulations was recorded. Isoclines were calculated as Spline interpolations of the 80 data points with average occupancy as the Z value (ArcView3.2 – Spatial Analyst Extension).

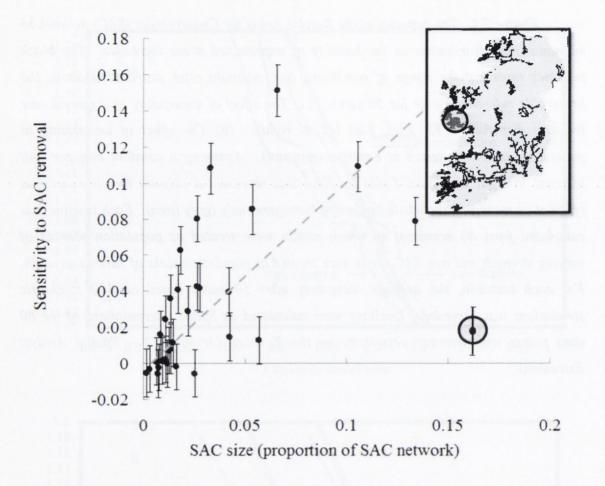


Figure 7.5. The relative importance of each Special Area for Conservation (SAC) to the maintenance of favourable conservation status. Sensitivity was tested at the point above which favourable conservation status would exist if SACs retained vital rates estimated for the current Irish otter population. Each scenario was tested with 500 stochastic replications. Error bars represent standard errors. The circled point represents the particuliarly inefficient Galway SAC. Points above the dotted line indicate SACs that are more efficient than average while points below the line are less efficient than average.



Figure 7.6. An alternative Special Areas for Conservation (SAC) network based on the removal of certain cSACs and the addition of new SACs in areas that are poorly connected to the network. Areas shaded with horizontal lines represent areas in which half the aquatic area is designated as SAC. Black lines represent existing cSACs.

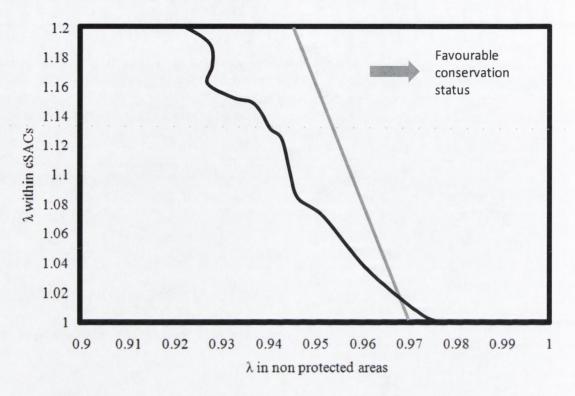


Figure 7.7. The capacity of a suggested alternative Special Areas for Conservation (SAC) network to maintain favourable conservation status for otters in Ireland as the hostility of unprotected areas increases. The black isocline represents the range of conditions that maintain otter distribution above the favourable reference range for 50 years at baseline dispersal and lower limits for population estimates. The isocline was calculated from 80 scenarios in which cSACs and proposed additional SACs were treated as population sources of varying strength and non-SAC areas were treated as population sinks of various strength. For each scenario, the average occupancy after 50 years based on 100 stochastic simulations was recorded. Isoclines were calculated as Spline interpolations of the 80 data points with average occupancy as the Z value (ArcView3.2 – Spatia l Analyst Extension). Assuming a constant cost per unit increase in λ per unit area I plot an isocline that represents the performance of an equivalent network that is exactly as efficient as managing the whole landscape homogeneously (grey line).

7.5.1 - METHODOLOGICAL ISSUES

To evaluate the cSAC network I examined the resistance of the population's distribution to increased mortality in unprotected areas. An important criticism of demographic population simulation models is that they are often based on inadaquate demographic data (Ruckelshaus et al. 1997, Akçakaya and Sjögren-Gulve 2000, Reed et al. 2001, McIntire et al. 2007). Demographic parameters can vary across years and populations depending on climate, food supply, population density, local adaptations and management actions (Saether et al. 1998, Hauer et al. 2000, 2002a, 2002b, Mech and Boitani 2003, Linnell et al. 2007). Uncertainty regarding the vital rates of the current Irish otter population limited me to a rather coarse estimate of the population's intrinsic rate of increase (λ) as 1.096 (SD = 0.056) (see chapter 6). The coarseness of λ severely limits the resolution of analyses comparing the cSAC network with alternatives. Running a set of scenarios produces a more informative output (Chapron et al. 2003a, 2003b, Linnell et al. 2007). I examined the performance of the network under an exhaustive range of demographic conditions that allowed me to identify precisely the range of conditions where a protected area network would maintain a favourable reference range for otters, regardless of uncertainty of the current demography of the Irish otter.

Sensitivity analysis showed that the model output was dominated by adult and juvenile survival, and by fecundity. I was interested in how varying demographic parameters, the only parameters to which the model was sensitive, affected population distribution and, hence, my confidence in model output is high. The population's distribution was insensitive both to the rate of dispersal between sub-catchments and to population estimates, indicating that greater precision in this parameter is not critical to predicting how environmental change may affect otter distribution. While the model is robust to uncertainties regarding parameter values, a number of assumptions require discussion.

Models become less robust as behavioural complexity increases and simple models that data can support are best (Beissinger and Westphal 1998, Akçakaya and Sjögren-Gulve 2000). I chose a simple population-based modelling approach because spatially-explicit individual-based models are extremely data-hungry (Reed et al. 2001) and data are lacking for Eurasian otter dispersal in particular. Population-based models are appropriate when home-ranges are small relative to habitat patches (Macdonald and Rushton 2003).

Otter habitat in Ireland comprises the whole waterways network (Chapman and Chapman 1982, Species Conservation Assessment 2007) and otter home-ranges are therefore small relative to habitat patches. The sub-catchments that were delineated could support an average of 13 female otter home-ranges.

A major factor determining the accuracy of the model output has to be the spatial representation of the landscape (Macdonald and Rushton 2003). The landscape in the model was represented as an array of sub-catchment centroids. The degree of connectivity between each sub-catchment was based on least-cost paths between centroids and sub-population level statistics describing dispersal behaviour. Model validation and sensitivity analyses indicated that the simulation of dispersal between subpopulations was both accurate and robust.

Excluding inbreeding or genetic stochasticity may underestimate the vulnerability of sub-populations (Kramer-Schadt et al. 2004). My simulations began with a very large widespread population and I was interested in the range of conditions resulting in more than 90% occupancy after 50 years. Inbreeding depression is unlikely to constitute a significant concern under these conditions.

7.5.2 – SIGNIFICANCE OF RESULTS

The maintenance of a widely distributed otter population in a landscape of sources (SAC network) and sinks (unprotected areas) is most heavily influenced by variation in the vital rates that determine the instantaneous growth rate of the population (λ). Conservation actions that limit mortality for adult females and dependent (i.e. juvenile) offspring will have the greatest impact in achieving favourable conservation status. There appears to be much scope for modifying these parameters through management actions. Many hundreds of otter cadavers have been collected across Europe over recent decades and the vast majority of deaths were attributable to anthropogenic causes (see chapter 6, Philcox et al. 1999, Hauer et al. 2002a). However, it is difficult to determine the actual proportion of otter mortality caused by human actions because natural deaths are less likely to be detected. Radiotracking studies are as likely to detect natural as anthropogenic mortality and anecdotal evidence indicates that deaths are almost exclusively anthropogenically induced. For example, I recovered 3 dead instrumented otters; 2 suffered road traffic collisions and 1 was killed illegally in a snare (see chapter 4). Certain contaminants may affect vital rates and these were primarily responsible for the dramatic declines in otter populations during the last century (Mason and Macdonald 1986, Foster-Turley et al.

1990, MacDonald 1991, MacDonald and Mason 1994, Jefferies and Hanson, 2000, Kruuk 2006). I suggest that a systematic and intensive program of cadaver collection form the basis of otter conservation so that contaminant concentrations can be monitored and demographic parameters can be precisely estimated and related to the effect of future management actions (see appendix I: Species Action Plan 2008).

The critical result of my work is that focusing resources on the Irish SAC network provides little or no advantage over simply managing the whole landscape homogeneously. Almost all successful reserve networks require management of the surrounding landscape (e.g. Dunnings et al. 1995, Boughton 1999, Lindenmayer et al. 2000, Collinge 2001, Fahrig 2001, Baum et al. 2004, Carroll et al. 2004, Carroll and Miquelle 2006, Linnell et al. 2007). The importance of managing the surrounding landscape is heightened in the Irish case because the conservation target is to preserve the population throughout 90% of the landscape and not just within the reserve network. Given that the likely effect of management actions on λ cannot be quantified at present, there is a clear risk that resources will be overly focused on cSACs and that the global efficiency of management based on the cSAC network will be even lower than our modelling results suggest.

The otter and its habitat are already highly protected throughout the Irish landscape. For example, it is illegal to hunt, disturb or intentionally kill otters (Wildlife Act 1976, 2000). Environmental impact assessments are required for any development schemes that may adversely affect the otter in any way (National Biodiversity Plan 2002). The National Roads Authority has published guidelines to reduce the impact of construction of national road schemes on otters. The Water Framework Directive and associated legislation aims to achieve at least 'good status' in all waters by 2015 (Nitrates Directive 1991, Water Framework Directive 2000). Finally, Farming practices are also being modified to reduce their impact on the aquatic environment (Rural Environmental Protection Scheme, Single Farm Payment Scheme). The additional actions to be carried out within cSACs include identifying and remediating high risk road sections for otter collisions, ensuring that suitable breeding sites are not limiting, and ensuring that fish biomass is monitored and maintained at appropriate levels (see appendix I: Species Action Plan 2008). Owing to the high level of protection afforded to otters throughout the landscape, conservation measures are not in fact heavily focused on cSACs. My findings support this approach and strongly encourage that these measures are applied rigorously throughout the country. However, I advise that the specific actions envisioned for cSACs should also be applied across the landscape, particuliarly regarding remediation of high risk road sections because of its potential impact on the most important parameters in determining the population's distribution.

Augmenting the cSAC network with additional sites in areas that are poorly connected to any existing cSAC will increase the potential of the network to ensure favourable conservation status. Although I have not exhaustively tested the effect of including a range of additional SACs, for illustrative purposes I replaced some cSACs with alternatives within areas poorly connected to cSACs. The alternative network provided a substantial improvement in efficiency.

7.6 - CONCLUSION

The otter cSAC network does not represent a significant improvement over simply managing the whole landscape homogeneously, particularly within the λ range likely to be achievable within the protected areas. The efficiency of the network is improved by removing certain cSACs. Including additional SACs in vulnerable areas substantially increases the performance of the cSAC network. I conclude the cSAC network does not contribute to ensuring the favourable conservation status of otters and that management should either treat the whole landscape homogeneously or revise the cSAC network and add new SACs. The model described in this paper can contribute to that process.

Otter conservation should focus primarily on reducing mortality of adult females and juveniles. Systematic collection of cadavers would allow improved precision and accuracy for the parameter estimates that dominate model sensitivity. Quantification of the impact of management actions on those vital rates should be a conservation priority.

More generally, this study presents a case study where a subjectively designed reserve network has been shown to largely fail to contribute towards the conservation target. The present study has shown that a systematic and quantitative approach can readily improve the performance of the network, rank the individual components of the reserve system, and guide conservation more generally. Population modelling was at an embryonic stage of development for mustelids several years ago (Gough and Rushton 2000). Although, modelling is now commonly used in management of exploited natural resources such as fisheries, it is still not widely used for carnivores (Chapron and Arlettaz 2006). This study supports the conclusion that quantitative and systematic approaches to conservation planning, such as population modelling, should be urgently adopted in order to provide the efficiencies that are necessary to deal with this period of unprecedented species loss.

Population dynamics of the Eurasian otter in Ireland: integrating density and demography into conservation planning

CHAPTER 8

General discussion, recommendations and future work

GENERAL DISCUSSION, RECOMMENDATIONS AND FUTURE WORK

Noss (1999) reviewed the major requirements of the field of conservation biology as: broad and rigorous science, improved basic field data to construct and validate models, compelling applications of conservation biology on the ground and increased influence in the policy arena. This thesis presents significant advances in our capacity to collect basic field data on otters by tackling arguably the major methodological impediments to field research. It has increased our understanding of the basic biology of otters by identifying the spatial structure of populations in riverine systems. It presents basic field data on otter density and demography. Finally, it synthesises these data in models so as to underpin conservation with sound science by identifying the parameters (e.g. life-history transitions) that management and research should focus on and by evaluating alternative management measures. The implications of this research has guided Ireland's approach to otter conservation as outlined in the Species Action Plan for otters (Appendix 1) that I was invited to draft. More generally, this thesis presents a case study showing that a conservation program based on subjective, non-quantitative advice is unlikely to contribute to the conservation target. In this regard, the thesis strongly supports the urgent application of quantitative methods to conservation planning, particularly given the current unprecedented and rapidly increasing rate of species loss.

8.1 - METHODOLOGICAL ADVANCES

This thesis has made an important contribution to overcoming the methodological issues that have impeded research on the Eurasian otter, namely, difficulties associated with capturing and fitting radio-transmitters to otters effectively and humanely (Kruuk 1995, 2006, Chanin 2003). I presented and evaluated a protocol for the capture of otters using padded leghold traps coupled with Global System for Mobile communication (GSM) trap alarms. The trapping method was highly efficient, capturing 46 otters at 6.9 trapnights each. This compares with an average of 200 trap-nights/otter for box traps, the commonly used alternative (Kruuk 1995). Provided reliable alarm systems are used, this

trapping protocol was startlingly effective with almost no discernible trauma. Given our success with leg-hold traps and otters, the use of GSM trap alarms for refining live-trapping with other traps and taxa should be explored.

The trapping protocol greatly limited the short-term traumatic stress associated with capture. Nevertheless, in order to avoid long-term stress and population petturbation, a method for attaching radio-transmitters to otters in the field was necessary. The similar circumference of the otter neck and head make it unsuited to standard collar-mounted transmitters that can be attached rapidly in the field (Melquist and Hornocker 1979, Kruuk 1995, Zschille et al. 2007). Externally mounted radio-transmitters remained attached for highly variable but generally short periods. Surgical implantation of radio-transmitters had been employed in many previous studies of Eurasian otters (e.g. Durbin 1993, Kruuk et al. 1993, Kranz 1995, Sjöåsen 1997, Saavedra 2002, Fernández-Morán et al. 2002, Niewold et al. 2003) where the otters were kept in captivity for prolonged periods to help deal with complications such as wound failure (Hernández-Divers et al. 2001, Fernández-Morán et al. 2002, 2004, Zschille et al. 2007; but see also Arnemo 1991). However, wild otters tend to be highly stressed for the first 2-5 days of captivity (Fernández-Morán et al. 2004). Furthermore, in my radio-tracking work I observed an adult male expanding its range from 10.2-19.3km within 5 days of the death of the neighbouring male, suggesting that population perturbation would be an issue. In North America, river otters are often implanted with transmitters in the field without any period of retention in captivity (e.g. Melquist and Hornocker 1979, Blundell et al. 2002, Bowyer et al. 2002, Gorman et al. 2006). I followed the North American approach and operated on, released and tracked 15 otters without complication.

In combination, these methods allow otters to be captured humanely and efficiently, implanted with radio-transmitters and released, all within 3 hours. Accordingly, almost all animals remained within home-ranges surrounding the trapping site and pups were not abandoned. These methodological advances offer a humane and ethical research approach that will facilitate increased understanding of those aspects of otter socio-biology that remain poorly understood owing to methodological issues (Kruuk 2006).

8.2 - BIOLOGICAL INFORMATION

Density.—An understanding of how population density varies across habitats is necessary to predict how a population will react to changes in a real landscape and, as

such, is critical for species conservation (Kruuk 2006). Indeed, one of the key criteria for evaluating potential Special Areas for Conservation (SAC) of otters requires an understanding of the number of otters present on the site and in the national population. An understanding of the spatial structure of otter populations and the habitat-specific spatial requirements of individuals allows the estimation of otter density over large heterogeneous areas.

Prior to my work, there were only 2 studies that had successfully identified the spatial structure of native otter populations (Erlinge 1967, Kruuk and Moorhouse 1991). Female otters occupied group ranges in Scottish coastal environments (Kruuk and Moorhouse 1991), while in Swedish freshwaters females occupied intra-sexually exclusive territories (Erlinge 1967). I made a concerted effort to capture and track every otter on the stretches of river I studied so that I could determine how home-ranges of con-specifics were arranged. My observations of 20 instrumented otters on mesotrophic rivers in Ireland revealed exclusive intra-sexual home-ranges. Therefore, exclusive intra-sexual territoriality appears typical of riverine populations, at least in Northern Europe. This finding is critically important for the interpretation of the relatively large body of work that examines the spatial requirements of individuals. For example, in Scotland, several studies, involving small samples of otters on oligotrophic rivers, may be combined to show that adult females require approximately 18.6km (SE = 1.1km) of watercourse (Kruuk 2006). Because females occupy exclusive home-ranges, these individual spatial requirements can be converted to densities and used to help direct conservation efforts as illustrated in this thesis.

Information on density or the spatial requirements of individuals had been lacking for lowland mesotrophic rivers in temperate regions (Chanin 2003). I found that adult female home-ranges were several times smaller than those on oligotrophic rivers (7.5km, SE = 0.6km). This finding agrees with work in Spain that found similar differences between oligotrophic and mesotrophic rivers (Ruiz-Olmo 2001). I also found that the lengths of adult female home-ranges were inversely related to river width. Home-ranges were longer on narrower rivers. The classic mustelid model of socio-biology predicts resource-based female home-ranges (Powell 1979, Johnson et al. 2000). Because mesotrophic systems have a relatively high level of in-stream productivity, a given length of a wider river produces more food than a narrower one. Therefore, the relationship of the adult female home-ranges with river width strongly suggests that they were food-resource based. Furthermore, home-ranges of otters tracked in oligotrophic rivers did not show any

relationship with river width and this is consistent with there being little or no in-stream productivity in such rivers.

Following my work examining otter spatial requirements on rich lowland rivers and the work of Yoxon (1999), Kruuk and Moorhouse (1991) and Kruuk (2006), otter densities have been calculated for the most common habitats in Ireland. I determined the extent of aquatic habitat based on digitised maps and classified water-features according to width, productivity, altitude and geology. I was then able to estimate the potential population of otters in any given area. I took account of declining habitat quality by correcting population estimates within each River Basin District by the change in its otter status since 1982. The corresponding estimate for the number of adult females on the island was 6,523 (95% confidence intervals: 4,592-9,870), highlighting the international importance of the Irish otter population (Whilde 1992). However, my calculations of otter density indicated that, because the decline in status occurred predominantly in densely populated regions, the real decline of 22% in the population since 1982 was greater than the 18% indicated by the spraint surveys.

Demography.—Unlike otter socio-biology, population demography is relatively easily studied and it has received much research attention (e.g. Kruuk et al. 1987, Kruuk and Conroy 1991, Sidorovich 1991). However, it varies greatly across populations and years depending on climate, food supply, population density, local adaptations and management actions (Saether et al. 1998, Mech and Boitani 2003, Sulkava 2007). Demographic data do not, therefore, lend themselves to extrapolation from country to country and they were completely lacking for Ireland. I identified age-specific mortality and fecundity rates for Irish otters based on a sample of 78 animals gathered from 1996 to 2007. The deterministic rate of increase (λ) of the population was 1.07 (SD = 0.054). Even though the estimate of λ was extremely coarse, it supports the suggestion, based on spraint survey results, of a slowing in the rate of decline of the Irish population since 1991 (Bailey and Rochford 2006).

8.3 – POPULATION MODELLING: INTEGRATION OF QUANTITATIVE BIOLOGICAL INFORMATION INTO CONSERVATION PLANNING

The science of predicting population dynamics in spatially heterogeneous environments has developed recently (Kingsland 2002, Gough and Rushton 2000, Caddy and Cochrane 2001). It is still not widely used for carnivores (Chapron and Arlettaz 2006)

and it was at an embryonic stage of development for mustelids several years ago (Gough and Rushton 2000). Management programs for terrestrial vertebrates continue to rely principally on expert opinion (Chapron and Arlettaz 2006) and the frequent failure of such advice for fisheries resulted in greater attention being focused on the uncertainty surrounding estimates (Caddy and Cochrane 2001). It is now accepted that decision makers must be provided with a range of options in which the uncertainty is clearly conveyed (Akçakaya and Sjögren-Gulve 2000, Caddy and Cochrane 2001, Reed et al. 2001). There is no logical reason why population modelling should not be applied to terrestrial carnivores (Chapron and Arlettaz 2006).

Expert opinion alone was employed in the designation of Ireland's candidate SAC (cSAC) network and consideration of demography, density and dispersal were treated superficially (Bailey and Rochford 2006). Over 14,000km of Irish watercourses have been designated as cSAC in order to ensure favourable conservation status for otters (EU Habitats Directive 1992). The critical result of my work was that focusing management on the cSAC network proved little or no more efficient than simply managing the landscape homogeneously. The unsophisticated approach followed in the designation of Ireland's cSACs has delivered a network that is unlikely to contribute to achieving the conservation target. Yet, the management plan for cSACs includes such costly actions as monitoring fish-biomass and remediating dangerous road crossings (see appendix I: Species Action Plan 2008). The results show that the cSAC network does not contribute to ensuring the favourable conservation status of otters and that management should either treat the whole landscape homogeneously or revise the network. Models such as the one I have described can contribute to the latter process without the economic and ecological costs of trial and error (Kingsland 2002, McIntire et al. 2007).

One of the advantages of placing the knowledge available on a system into a modelling framework is that one can then determine the relative influence of each parameter towards achieving a conservation or management target (Leslie 1945, 1948, Dunnings et al. 1995, Nilsen et al. 2007). I discovered that the maintenance of a widely distributed otter population in a landscape of sources and sinks is most heavily influenced by variation in adult female mortality, followed by juvenile mortality and fecundity. Local carrying capacity and the connectivity of sub-catchments were far less important. Conservation actions that limit mortality of adult females and dependant offspring will have the greatest impact in achieving favourable conservation status.

8.4 - IMPLICATIONS FOR CONSERVATION POLICY

I was invited by the National Parks and Wildlife Service (NPWS) to draft the otter Species Action Plan (2008) in June 2007 and this presented the opportunity to promote consideration of my findings to national policy. Some of the later results of the modelling could not be included in this document, but they are used here to identify management actions that should be prioritised or modified.

Continually updated population simulation models should be employed in the adaptive management of priority vertebrate species. Population simulation modelling offers a rigorous, logical and objective framework for integrating information from multiple sources. These models can evaluate conservation actions even where data are scarce and identify priority areas for future research.

My findings clearly show that the cSAC network design based on expert opinion is unlikely to fulfil its function of contributing to ensuring the favourable conservation status of otters. I have shown that an effective network can be designed readily through spatially-explicit population simulation modelling. Furthermore, such models can contribute to an adaptive management approach where the impact of environmental change can be quantified. The modelling results strongly suggest that either conservation efforts should not be focused on the cSAC network or the cSAC network should be modified. These results support the conservation actions outlined in the Species Action Plan (see appendix I), the majority of which are not confined to the cSAC network but are carried out on a landscape-wide basis.

My findings highlight the primary importance to the population of mortality of adult and juvenile females and fecundity, compared with dispersal and population size. The NPWS has committed to continuing my cadaver survey by creating a national program of otter cadaver collection by 2009 (see appendix I, point 5.3.2). The ultimate model results strongly support this action because it will deliver the information to which the population is most sensitive.

Actions that limit adult-female and juvenile mortality will have a disproportionate effect on the conservation status of otters. This finding encourages the identification and remediation of high-risk road sections. These high-risk sections can be identified by systematically recording the locations of road-killed otters. This suggestion was adopted for cSACs (see appendix I, point 5.2.6). In light of my unfavourable analysis of the cSAC network, I now suggest that this action should be rolled out across the whole landscape.

Another source of anthropogenic mortality that is likely to be under-reported is illegal persecution. During my field-work, I was contacted on numerous occasions by owners of fish-ponds or fish-farms for whom otters were presenting difficulties. In fact, one of my instrumented otters was caught in an illegal snare in conditions that suggested such conflict. I therefore suggested that the state should have a system in place to address this potential conflict and this has been committed to for 2009 (see appendix I, point 5.3.3).

The use of GSM trap alarms coupled with padded leghold traps overcomes a major impediment to otter research by delivering a highly efficient and humane method of capturing otters. The success of this method is, however, dependent on the use of sedatives that are safe for highly stressed animals. Ketamine and Midazolam (Spelman 1993) was suitable, whereas Ketamine and Dormitor or Medetomidine (Fernández-Morán et al. 2001) was not. The principle of refinement of animal experiments requires that similar trapalarms should be used in all live-trapping studies of otters. The great success of this methodology strongly encourages investigation of its applicability to other traps and taxa.

Coupling rapid release from traps with field surgery minimises disturbance to individuals and populations and avoids the potential for abandonment of dependant cubs. This method, commonly used in North America for river otters, should be employed in studies of native otter populations.

Local otter density, dispersal and the degree of connectivity of river basins were not important to the maintenance of favourable conservation status for Irish otters. Nevertheless, the Irish population is among the largest in Europe and it allowed me to make important advances in both field techniques and in understanding basic otter sociobiology. There is great scope for using the Irish population to examine parameters that may be extremely important in conserving otter populations elsewhere. For example, dispersal has not been systematically studied for Eurasian otters and yet it may be critically important in highly fragmented landscapes. The suggestion that the Irish otter population be used as a research resource has also been adopted in the Species Action Plan (see appendix I, points 5.5.7-5.5.9).

8.5 - CONCLUSION

As discussed at the outset of this thesis, conservation is not a purely scientific activity (Lawton 1997). Although conservation programs may be informed by science, decisions embrace political, economic, ethical, aesthetic and even religious considerations (Lawton 1997). Limited resources and competing land-use goals require efficient conservation measures to provide the ecological requirements of target species (Lomolino 1994, Jiang et al. 2007). Conservation Biology aims to provide managers with the tools they need to be able to conserve species within the social, political or economic constraints they are operating under. An academic criticism of Conservation Biology is that it has limited unifying paradigms, comprising instead a large body of locally specific case studies. Rules of thumb, although cheap and quick to apply and so useful to managers, are liable to give rise to flawed advice. Given the large number of species requiring urgent conservation and the increasing international and national legislation requiring conservation of particular species, managers may be under pressure to develop conservation programs efficiently rather than develop efficient conservation programs. A Conservation Biology approach is more consistent with the latter, as it generally requires additional biological information and preparation of objective systematic tools to apply that information to the conservation objective. The case study presented in this thesis illustrates a non-quantitatively designed protected area network failing to contribute materially to achieving the conservation goal. The protected area network practically might as well not exist. Conversely, a protected area network that would contribute to the conservation goal could easily be designed using the model presented in this thesis. It is no surprise that where the capital lost owing to incorrect decisions is economic, modelling approaches are used (e.g. stock market and fisheries), whereas where it is purely ecological, as in the case of large carnivores, ad-hoc approaches persist. The current study supports Chapron and Arlettaz's (2006) assertion that there is no reason why modelling approaches should not be applied to carnivore conservation, and indeed suggests that there is every reason that it should.

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Population dynamics of the Eurasian otter in Ireland: integrating density and demography into conservation planning

APPENDIX I

Species Action Plan for otters

Draft prepared by L. Ó Néill – June 2007

NATIONAL PARKS & WILDLIFE SERVICE

SPECIES ACTION PLAN

OTTER

LUTRA LUTRA





DEPARTMENT OF THE ENVIRONMENT, HERITAGE AND LOCAL GOVERNMENT

CURRENT STATUS

1

- 1.1 Compared with European populations of *Lutra lutra*, Irish otters have a darker pelt, a distinct cranial form and conspicuous throat-patches. Consequently it has been suggested that Irish otters deserve the subspecific status of *L. l. roensis* (Lynch & O'Sullivan, 1993; Lynch *et al.*, 1996). However, this classification has been challenged (Mason & Macdonald, 1986), and recently, the Irish population was found to be genetically undifferentiated from most European populations (Randi *et al.*, 2003).
- 1.2 The Eurasian otter is a semi-aquatic carnivore that is widespread throughout all Irish fresh-water and most coastal habitats (Chapman & Chapman, 1981; Lunnon & Reynolds, 1991; Bailey & Rochford, 2006). Otters spend three-quarters of their lives on land, so the structure of their terrestrial environment is important (Kruuk, 2006). Otters typically have several resting places within their territories; both above-ground 'couches' and under-ground 'holts'. Holts are most commonly found among tree roots, especially those of Ash and Sycamore, although scrub such as bramble is also important (O'Sullivan, 1993). Suitable breeding sites for otters must be undisturbed, have a good food supply nearby, and not be at risk from flooding (Liles, 2003).
- 1.3 The otter is an opportunistic predator that exploits prey in proportion to its availability in the environment (Breathnach & Fairley, 1993; Ottino & Giller, 2004). In Ireland, as throughout Europe, diet is predominantly of aquatic origin. In freshwater areas, otter droppings, known as spraints, commonly contain stickleback, salmonids, frogs and eels (Bailey & Rochford, 2006), while crayfish can be a dominant prey species locally (McFadden & Fairley, 1983). Terrestrial prey is taken infrequently, with birds occurring in just 3% of spraints and mammals occurring even more rarely (Bailey & Rochford, 2006). Otter diet has not been studied on a national basis for coastal areas, but a survey on Inis Mór found that rockling and wrasse dominated the diet, while eel, sea scorpion, blenny and molluscs were also important (Kingston et al., 1999).
- 1.4 Dramatic declines occurred in many European otter populations during the latter half of the 20th Century (Mason & Macdonald, 1994). Owing to environmental improvements and focussed conservation efforts, widespread healthy populations now occur in a third of European countries (Conroy & Chanin, 2001). In a fifth of European countries otters remain threatened, declining, rare, or extinct (Conroy & Chanin, 2001).
- 1.5 The first national otter sign survey found otters throughout the Republic of Ireland, and recorded signs at 88% of 2,042 sites (Chapman &

Chapman, 1982). A smaller follow-up survey of 246 sites carried out a decade later found a highly significant 13% decrease in otter presence (Lunnon & Reynolds, 1991). The most recent otter survey, carried out 14 years later, searched 525 sites and found that otter presence had declined by a further 5% to just over 70% (Bailey & Rochford, 2006). This trend was corroborated by a 10% decline in otter presence in Northern Ireland over the same period (Preston *et al.*, 2006). There has been little spatial variation to the decline in either jurisdiction (Preston *et al.*, 2004; Bailey & Rochford, 2006) suggesting that there may be a general decline in the density of the island's otter population (Preston *et al.*, 2006).

- In the Irish Red Data book the otter is listed as internationally important (Whilde, 1993). The Eurasian otter is classified as 'near threatened' by the IUCN (2006) and is listed as a strictly protected species under Appendix II of the Bern convention (Council of Europe, 1979). Because it is listed in Appendix 1 of CITES (1979), trade in otter specimens is permitted only in exceptional circumstances.
- 1.7 The otter has been protected in Ireland since 1976 (Wildlife Act 1976). Licenses to hunt otters were issued under this Act until the 1990s. The Wildlife Amendment Act (2000) removed the hunting clause entirely and it is now illegal, to hunt, disturb, or intentionally kill otters.
- Annexes II and IV of the E.U. Habitats Directive (92/43/EEC) list the otter as a species of community interest that is in need of strict protection and for which E.U. nations must designate Special Areas of Conservation (SACs). The E.U. Habitats Directive was transposed into Irish law in the European Union (Natural Habitats) Regulations, (SI 94/1997) and 40 candidate SACs have been designated for the otter in Ireland.

2 CURRENT FACTORS CAUSING LOSS OR DECLINE

Irish rivers were in near pristine conditions when the first national otter survey found otters at 88% of sites (Chapman & Chapman, 1982; Stapleton *et al.*, 2000). Since then the standard of water quality has declined substantially (Stapleton *et al.*, 2000). The EPA reports that oxygen depletion and nutrient enrichment, both of which impact negatively on fish biomass, are largely the result of agricultural runoff and urban waste water discharges (Stapleton *et al.*, 2000). Poor water quality has been related to sites that proved negative for otter signs (Lunnon & Reynolds, 1991; Hamilton & Rochford, 2000). Serious pollution is most frequently caused by sewage discharges (Stapleton *et al.*,

- 2000). The acidification of watercourses, by coniferous forestry for example, decreases prey abundance, and, hence, otter populations (Mason and Macdonald, 1989).
- 2.2 The loss of riparian habitat structure has been reported to be a factor in declines of otter populations throughout Europe (O'Conner *et al.* 1977; Chanin and Jefferies 1978; Macdonald and Mason 1983). Riparian trees and scrub are important for otter breeding and resting sites (O'Sullivan, 1993). Breeding sites require undisturbed areas that are often removed from the main channel (Liles 2003).
- 2.3 Otters are highly sensitive to direct disturbance, and the majority of cub cadavers retrieved in Britain had bite wounds caused by dogs (Simpson, 2006). It is likely that mink hunting with dogs poses a serious disturbance to otters and may prevent otters successfully breeding. Furthermore, where unrestrained dogs are allowed access to long stretches of watercourse they pose a similar risk.
- 2.4 Actions, such as dredging, arterial drainage, and flood defence works, which result in an extensive loss of riparian habitat and decreased fish biomass (O'Sullivan, 1996), are likely to have caused population declines and fragmentation.
- 2.5 Contaminants, such as biomagnified dieldrin, DDT/DDE, PCBs and Mercury, have been blamed for the dramatic decline of otter populations across Europe (Mason & Macdonald, 1986; Jefferies & Hanson, 2000; Kruuk, 2006). Levels of organochlorine pesticide residues and PCBs in otters were not a significant cause of concern in southern Ireland in the early 1990s at least (O'Sullivan *et al.*, 1993); however, there has been no subsequent monitoring.
- 2.6 The vast majority of recorded otter deaths were caused by road traffic accidents (O'Sullivan & FitzGerald, 1995). Where populations have been depleted by other causes, road traffic deaths could pose a local extinction risk or decrease population connectivity.
- 2.7 Fishing gear, such as Fyke nets, has been shown to account for 14-17% of reported mortalities for otters (O'Sullivan & FitzGerald, 1995; Poole *et al.*, 2007). However, there is a clear lack of reliable statistics on any form of anthropogenic mortality of otters. Without these data it is impossible to know whether anthropogenic mortality is a threat to otter populations.
- 2.8 Otters can potentially represent a serious pest of unprotected fish-rearing or fish-holding facilities. Such facilities are become increasingly common, and conflict may be expected to increase accordingly. If unresolved, such

conflict will probably lead to illegal culling of otters, even to levels that would threaten local otter populations.

3 CURRENT ACTION

- 3.1 National otter surveys are being carried out roughly every decade (Chapman and Chapman, 1982; Lunnon and Reynolds, 1991; Bailey and Rochford, 2006). The surveys aim to establish trends in the status and distribution of the Irish otter population. Chanin (2005) has developed a robust, rapid assessment survey for otters and this is now being piloted in Ireland (F. Marnell pers comm.).
- 3.2 There has been significant progress in eliminating pollution from industry, while pollution caused by sewage discharges is being addressed under a major capital investment programme (National Biodiversity Plan, 2002).
- 3.3 The Nitrates Directive (91/676/EEC) and Regulations for Good Agricultural Practices for the Protection of Water (S.I. 378/2006) attempt to avoid input of nitrogen and phosphorus to watercourse through better farming practices, including: limiting the amount, timing, and location of fertiliser application. The Good Farming Practice guidelines also set down obligations relating to the maintenance of protected wildlife habitats, careful use of pesticides and chemicals, and protection of watercourses and wells.
- The Rural Environmental Protection Scheme (REPS) places a particular emphasis on preventing water pollution, and also aims to 'protect wildlife habitats and endangered species'. Subscribers to the voluntary scheme are required to maintain a clear buffer around watercourses of 1.5m for bovids, pesticides, insecticides, and artificial fertilisers, and 10m for slurry and animal manure. However, there is concern that the 1.5m boundary is ineffectually narrow and that the level of monitoring of REPS is inadequate (Feehan, 2002).
- 3.5 REPS provides financial encouragement to farmers, whose land contains a watercourse designated as an SAC, to plant or maintain a ≥10m band of riparian woodland. Furthermore, the Native Woodland Scheme provides grants for landowners to protect and establish native riparian woodland. Such riparian woodland should clearly contribute to otter conservation.
- 3.6 The Single Farm Payment scheme, introduced in 2005, requires farmers to comply with Cross Compliance, i.e. farmers must meet various Statutory

Management Requirements set down in EU legislation on the environment and must maintain their lands in good agricultural and environmental conditions.

- 3.7 The Water Framework Directive (WFD) (2000/60/EEC) presents a major opportunity for strengthened protection of aquatic ecosystems and their associated terrestrial ecosystems. The Directive requires that water quality be managed and monitored in a coordinated fashion by all public authorities on the basis of river basins; an appropriate scale for otter conservation. The integrated monitoring and management system envisaged by the WFD provides a vehicle for the inclusion of considerations for otter conservation to all water management. The Directive aims to achieve at least a 'good status' in all waters, and appropriate standards within all SACs by 2015.
- 3.8 All proposed arterial drainage schemes now require a full assessment of all biodiversity and environmental implications (Planning and Development Act (2000)).
- 3.9 The Planning and Development Act (2000) gives Development Plans mandatory objectives for the conservation of European and nationally important sites.
- 3.10 The Central and Regional Fisheries Boards monitor fish stocks and habitat and perform remediation where necessary. Clearly the protection and enhancement of fish stocks benefit otter conservation.
- 3.11 To reduce the impact of roads on otters, the National Roads Authority published, "Guidelines for the treatment of otters prior to the construction of national road schemes".
- 3.12 Controls for forestry practice are in place that prevents damage to protected areas, whether of European or national origin (National Biodiversity Plan 2002). The "Code of Best Forest Practice" and the "Forest Biodiversity Guidelines" provides for the conservation of biodiversity in all stages of the forest cycle.
- 3.13 A study of the effect of water-pollution on otter presence was carried out with support from the Heritage Council (Hamilton & Rochford, 2002).
- 3.14 The impact of fyke nets on otters was commissioned and published by the National Parks and Wildlife Service (NPWS) (Poole *et al.* 2007).
- 3.15 The Wildlife Ecology Group at Trinity College has set up a national cadaver collection survey, and in 2007 NPWS launched an on-line road-kill survey for otters (www.biology.ie).

3.16 A radio-telemetry study of the social structure and spatial requirements of otter populations on lowland rivers is being carried out by the Wildlife Ecology Group at Trinity College (supported by NPWS and IRCSET).

4 ACTION PLAN OBJECTIVES AND TARGETS

- 4.1 Prevent any further decline in otter status.
- **4.2** Demonstrate a return to the 1982 survey result level of 88% presence in all otter SACs by 2020.

5 PROPOSED ACTIONS WITH LEAD AGENCIES

5.1 Policy and legislation

5.1.1 Ensure that considerations of the habitat requirements of otters are included in future REPS schemes and in all other agri-environmental schemes.

ACTION: Department of Agriculture, Fisheries and Food (DAFF), Forest Service (FS), NPWS, Teagasc.

5.1.2 Ensure that considerations of the habitat requirements of otters are included in the planning process, particularly in relation to operations involving physical alteration of the stream bed or riparian zone.

ACTION: Local Authorities (LAs), An Bórd Pleanála, NPWS, OPW.

5.2 Site safeguard and management

5.2.1 By 2011, in SACs where the otter is not meeting favourable conservation status, identify areas where breeding sites are scarce or absent and provide artificial holts where appropriate.

ACTION: FS, NPWS, LAs.

5.2.2 By 2011, expand the fish biomass monitoring program of the CFB so that biomass estimates are obtained throughout the SAC network to identify areas where fish populations are poor so that remediation can be carried out.

ACTION: CFB.

5.2.3 By 2010, ensure that suitable habitat in all state and semi-state-owned lands is managed in a manner that is beneficial to the conservation of the otter.

ACTION: Coillte, FS, NPWS, Dept. of Defence, DCMNR.

5.2.4 Ensure that designated otter sites are recognised and protected within RBD management plans and in planning authority development plans.

ACTION: DOEHLG, EPA, LAs, NPWS.

5.2.5 Ensure that all operations affecting watercourses, including 'bank improvement' for angling, take account of otters and retain features such as old trees, scrub, and overhanging tree root systems.

ACTION: CFB, FS, LA's, NPWS, RFB's, OPW.

5.2.6 By 2008, identify high risk road sections for otters from the road-kill survey results, and remediate where appropriate.

ACTION: NPWS, NRA, LAs.

5.2.7 By 2009 review the impact of mink hunting on otters.

ACTION: NPWS

5.2.8 By 2009 examine the potential for important breeding sites to be designated as areas where dogs must be kept on a leash.

ACTION: LAs, NPWS.

5.3 Species management and protection

5.3.1 By 2009, examine the potential for an all-island otter forum to co-ordinate conservation, information exchange, publicity and research.

ACTION: CFB, DAFF, FS, EPA, IUCNosg, NPWS, Teagasc, WFD/RBD, Environment & Heritage Service, N.I..

5.3.2 Establish a national program of otter cadaver collection by 2009 to succeed the cadaver survey established in Trinity College.

ACTION: NPWS, WFD/RBD.

5.3.3 By 2009 have a system in place to address the need for compensation and the provision of otter-proof fencing for valuable vulnerable fish ponds.

ACTION: M.I., CFB, DAFF, IFA aquaculture, NPWS.

5.4 Advisory

5.4.1 Ensure that NPWS rangers and Teagasc advisors are trained in the identification of potential breeding holts for otters by 2009.

ACTION: NPWS, Teagasc.

5.4.2 Ensure that REPS advisory talks include information on the otter where appropriate by 2009.

ACTION: DAFF, NPWS, Teagasc.

5.4.3 By 2009, prepare and distribute publications containing information and management advice about otters for distribution to landowners, land managers, farmers etc.

ACTION: ENFO, NPWS.

5.4.4 By 2009, ensure that the 'Guidelines for Drainage and Wildlife' envisaged in the National Biodiversity Plan include specific regard for the conservation needs of otters.

ACTION: Bórd Pleanála, CFB, NPWS, OPW, RFBs.

5.4.5 By 2010, evaluate the effectiveness of the current NRA-recommended mitigation guidelines for otter and ensure that the guidelines are updated as required.

ACTION: NRA, NPWS.

5.5 Future research and monitoring

5.5.1 By 2009, review the results of priority/dangerous substances monitoring under the WFD and assess the likely implications for otter. If appropriate test otter cadavers for these substances and provide feedback to the EPA on any concerns arising.

ACTION: EPA, NPWS, WFD/RBD.

5.5.2 Undertake next national otter survey in 2010 and continue national otter surveys thereafter at 7-10 year intervals. Coordinate with surveys in N.I. where feasible.

ACTION: NPWS, EHS.

5.5.3 Roll out rapid assessment methodology for otters by 2008 and repeat at 2 yearly intervals.

ACTION: NPWS.

5.5.4 By 2009 investigate the level of surveyor error in the national survey results and examine mechanisms for overcoming it.

ACTION: NPWS.

5.5.5 By 2010, consider the development of standardised artificial sprainting sites that can be deployed without introducing significant surveyor bias.

ACTION: NPWS.

5.5.6 Encourage more comprehensive reporting of anthropogenic mortality of otters.

ACTION: CFB, LAs, NPWS, NRA, RFBs.

5.5.7 By 2009, support study of the social structure and density of otter populations in the Irish landscape.

ACTION: NPWS.

5.5.8 By 2009, support study of the genetic structure of the Irish otter population to establish the degree of connectivity of river basin districts.

ACTION: NPWS.

5.5.9 By 2009, encourage and support a study of habitat connectivity for, and dispersal behaviour of, otters.

ACTION: NPWS, NRA, FS.

5.6 Communications and publicity

5.6.1 Public awareness of the presence and needs of otters is often limited by the infrequency with which otters are seen because of their generally cryptic lifestyle. The potential for the development of otter observation sites similar to those on the Isle of Skye should be considered in SACs and National Parks by 2010.

ACTION: LAs, NPWS.

5.6.2 By 2009, increase public involvement in otter conservation by preparing and distributing leaflets on the otter which also provide practical management tips for landowners e.g. the importance of providing areas of scrub and describing the construction of log-pile holts.

ACTION: ENFO, NPWS.

6 LIST OF ABBREVIATIONS

CFB Central Fisheries Board

DAFF Department of Agriculture, Fisheries and Food

DOEHLG Department of the Environment, Heritage and Local

Government

EHS Environment & Heritage Service, N.I.

EPA Environmental Protection Agency

FS Forest Service

IFA Irish Farmers Association

specialist group

LA Local Authority

NARGC National Association of Rifle and Gun Clubs

NPWS National Parks and Wildlife Service

NRA National Roads Authority

OPW Office of Public Works

RBD River Basin District

REPS Rural Environment Protection Scheme

RFB Regional Fisheries Board

SAC Special Area of Conservation

WFD Water Framework Directive

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