UNIVERSITY OF SOUTHAMPTON

FACULTY OF MEDICINE, HEALTH AND LIFE SCIENCES

School of Biological Sciences

Field test of impacts of intraguild predation on a mammalian prey population: the badger *Meles meles* and hedgehog *Erinaceus europaeus*

by

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Thesis for the degree of Doctor of Philosophy

December 2005

UNIVERSITY OF SOUTHAMPTON

Abstract

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Field test of impacts of intraguild predation on a mammalian prey population:

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Intraguild predation (IGP) is a common interaction in ecosystems which is thought to strongly influence the population dynamics and behaviour of prey, though few manipulative field experiments have been conducted to test its effects on mammalian prey populations. An opportunity to carry out such an experiment was provided by the Randomised Badger Culling Trial, a field trial to investigate the effect of culling Eurasian badgers (*Meles meles*) on the incidence of bovine TB in cattle. The badger is a predator of western European hedgehogs (*Erinaceus europaeus*) but both species also potentially compete for similar invertebrate food and may thus be engaged in IGP.

Previous work indicated that badger predation may regulate hedgehog populations and predicted that in areas where badgers are abundant, predation pressure would exclude hedgehogs from their preferred agricultural habitats. Surveys of hedgehogs in rural areas of England, carried out in the present study, confirmed this prediction and identified a negative spatial relationship between badger density and hedgehog occurrence and abundance in suburban micro-habitats, which are thought to provide hedgehogs with spatial refuges from predation. When badger abundance was reduced by culling, hedgehog population density in suburban micro-habitats doubled, while remaining unchanged in controls.

The growth rate of hedgehog populations appeared to be negatively related to indices of badger abundance, indicative of top-down control by predation. There was evidence that hedgehog population growth rates were density dependent, potentially leading to two stable states of abundance according to the magnitude of predation. In the control treatment, a lower equilibrium population size indicated regulation by predators, whereas in areas where badgers were culled, an equilibrium population size some three times the density was observed. Predation risk may have influenced habitat use by hedgehogs. After badger culling, pastoral habitats were used more and suburban habitat less, although the effect was marginal. In combination with previous results, this study has provided evidence that predation by badgers determines the distribution and abundance of hedgehog populations and that spatial refugia, in the form of suburban micro-habitats, allow predator and prey to co-exist at a landscape scale.

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Acknowledgements

I thank my supervisors, Patrick Doncaster and Richard Delahay, for all their invaluable advice throughout this PhD; from the initial design to the completion of the thesis. I am grateful for all the challenges and guidance they provided me, which ensured I could not have wished for a better training in research.

I acknowledge all my colleagues at Woodchester Park, with whom I worked so closely with during my time there, but in particular I again thank Richard Delahay, but also Chris Cheeseman and Lucy Rogers, for creating the opportunity for me to carry out the PhD. Neil Walker and Guy Forrester deserve thanks for their statistical advice and help. I am very grateful to the 'EcoCon' team for all their efforts in the field during the hedgehog surveys, in particular Mark Claridge, Richard Yarnell and Iain Adderton. I must specially thank Gavin Wilson, John Davison and Iain Trewby for being good friends as well as colleagues and for their ever valuable help and support. Tim Hounsome deserves individual recognition, for getting me the job at Woodchester Park of course, but most of all for being a great friend who inspires me to think of the 'big picture' but also 'not to worry too much'.

I would like to thank John Fa who trusted me enough to complete this PhD to offer me a fantastic job, when there was still much work to do.

I dedicate this thesis to Susie, who has been alongside me every step of the way, providing unflagging support and encouragement and never letting me doubt my ability to finish this thesis, even during the often unpleasantly busy last year. Also, I thank you for our little creation that I hope will ensure life is just as busy after this PhD than during the write-up! Finally, I thank my parents, for everything. They deserve all my gratitude for developing me into a person capable of taking on this PhD and enjoying the challenges that it is has offered.

Chapter 1: Introduction

This research thesis aims to experimentally investigate intraguild predation (IGP) and its effect on the abundance and behaviour of a prey population in a terrestrial mammal system. IGP describes predatory interactions between potentially competing species and is hypothesised to have direct and indirect effects on populations and community structure that may be more complex than the effects of either competition or predation alone (Polis, Myers & Holt 1989). IGP is common in many ecosystems and is of increasing interest to ecologists, as its potential influence on animal behaviour and the abundance and distribution of animal populations is recognised (Heithaus 2001). The effects of IGP on mammalian prey populations have rarely been experimentally investigated (Litvaitis & Villafuerte 1996). The Eurasian badger (*Meles meles*) is both a predator of and potentially a competitor for food resources with the western European hedgehog (*Erinaceus europaeus*) (Doncaster 1992). A framework to facilitate an experimental investigation of the effects of IGP on prey populations was provided opportunistically by a manipulation of predator populations during a badger removal operation carried out by the Department for Environment Food and Rural Affairs of the UK Government (DEFRA). The removal operation is part of a controlled experiment to test the effect of culling badgers on the incidence of bovine TB (*Mycobacterium bovis*) in cattle (Krebs 1997). This provided a unique opportunity to test hypotheses regarding the effects of an intraguild predator on the abundance and behaviour of a prey species in a terrestrial mammal system.

This introductory chapter will briefly discuss the theory of population dynamics, including limitation and regulation, the effects of predators on prey populations and the various methodological approaches used to investigate the population dynamics of predation. Also discussed are more complex predator prey interactions, particularly when predation and interspecific competition interact, and the consequences for prey populations and indirect effects observed in communities. A review of the theoretical and empirical evidence of IGP to date will summarise the potential implications of IGP for animal behaviour, populations and community structure. The effect of IGP on prey behaviour and populations in terrestrial mammal systems and the IGP relationship between badgers and hedgehogs will be discussed in more detail along with the background ecology of these two species. Finally, the

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experiments and surveys designed to explore the effects of IGP by badgers on hedgehogs are described and the main objectives of the thesis are outlined.

1.1 Population dynamics and predator-prey interactions

A central focus of animal ecology is the study of the mechanisms that determine the abundance and distribution of animal populations (Begon, Townsend & Harper 2005). This is important at a conceptual level but also because of a pressing need to understand and predict the consequences of anthropogenic perturbation of populations and ecosystems to inform wildlife management and biodiversity conservation. Population dynamics is the study of how populations change in time and space. Four processes determine changes in population size: births, deaths, immigrations and emigrations. The fundamental equation of population change is given by,

$$N_{t+1} = N_t + (\text{births} - \text{deaths}) + (\text{immigration} - \text{emigration})$$

where the population size at time $t+1$ (N_{t+1}) is determined by the population size at time t (N_t) plus births and immigrants minus deaths and emigrants. With unlimited resources populations with positive growth would grow exponentially. However as was first pointed out by Malthus (1798) populations do not grow without limit; individuals within populations compete for resources and as abundance increases resources become more limited, which reduces the fecundity and survival rates of these individuals. Such competition can occur through either exploitation (where individuals are affected by the extent to which resources have been depleted by others) or interference (individuals interact with each other, and prevent one another from exploiting resources). Intraspecific competition for resources leads to logistic population growth where recruitment into a population is small at both low density, when few individuals are available to give birth, and at high density when competition for resources becomes intense, and is at a peak at intermediate densities. Therefore, the population increases most rapidly at intermediate density but slows down and reaches an asymptote at high density, when birth rates are equal to death rates. The population size at which this occurs is known as the carrying capacity, K. Populations above K are likely to decline in size and populations below K are likely to increase. Therefore in the logistic model, the growth of a population depends on its own density, a mechanism known as density dependence. In reality the carrying capacity is very unlikely to be a single level but more likely a range of density as a result of variation in fecundity and survival rates. Intraspecific competition therefore should

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lead to the narrowing of the range of densities the population achieves at carrying capacity i.e. populations are regulated or bounded within limits. However, this does not necessarily mean that the population size is stable, as a time-lag in the response of the population to changing resources, known as delayed density dependence, should lead to cycles in population size. Changes in the strength and/or type of the intraspecific competitive process can lead to a range of population dynamics including stable equilibria, damped oscillations, stable limit cycles and chaos. Thus a model built around a density-dependent, regulatory process of intraspecific competition can lead to a very wide range of population dynamics.

In real populations, however, individuals are not just affected by intraspecific competition. Predators, parasites, disease, prey and interspecific competition can affect individuals' fecundity or survival and these effects are cascaded to the population level. Competition for resources between individuals of different species can affect populations of both competing species. The Lotka-Volterra model of interspecific competition (Volterra 1926; Lotka 1932) has provided insights into the circumstances that permit the co-existence of competitors and those that lead to competitive exclusion. It is an extension of the logistic equation used to model the effects of intraspecific competition. In general, strong interspecific competitors outcompete weak competitors and can exclude them. The model predicts that if interspecific competition is more important than intraspecific competition then the outcome of the interaction depends on the species' starting densities. If interspecific competition is less important than intraspecific competition then the species are predicted to coexist. However, the outcome of interspecific competition can be strongly influenced by heterogeneous environments which are thought to facilitate co-existence between species even of different competitive abilities. As mentioned earlier, badgers and hedgehogs can be considered as interspecific competitors for invertebrate food resources.

Predation is an interaction that affects the population dynamics of prey as well as the predator. It is evident from the literature that a large range of dynamics can occur, ranging from predators having an extremely detrimental impact on the abundance of their prey to predators apparently having no effect at all (Begon *et al.* 2005). Other examples reveal predators and prey linked together by coupled oscillations in abundance or more frequently predator and prey populations fluctuating in abundance seemingly independent of one another. The direct effect of

predation on prey is a numerical reduction in their abundance through mortality. In this thesis the definition of a predator follows that of Begon *et al.* (2005); a consumer that kills its prey more or less immediately after attack. Badgers are thought to kill and consume hedgehogs relatively quickly following the initial attack.

To help understand predator-prey dynamics, theoretical models such as the differential equation model of Volterra (1926) and Lotka (1932) have been developed. The model dictates that the effect of predation on prey depends on the encounter rate between predators and prey. Encounters will increase with the abundance of both predators and prey but the exact number of prey consumed by the predators depends on the searching and attacking efficiency of the predator, and these factors combined determine the consumption rate. The effect of prey on the predator depends on the efficiency of the predators turning food (i.e. prey) into their offspring. The Lotka-Volterra model points to a tendency for predator-prey interactions to generate fluctuations in the prey population that are tracked by fluctuations in the predator population, in coupled oscillations. Put simply, when the abundance of prey increases, predators also increase in number, which leads to an increased predation pressure on prey and thus a decrease in prey. This in turn then leads to a food shortage for predators and a decrease in predator abundance which relaxes predation pressure and prey abundance increases and the cycle continues. The time-lag in the numerical response in the predator population (i.e. the time it takes to reproduce or to move) to changes in prey abundance is a mechanism known as delayed density dependence (as it depends on past density), and this drives the population cycles. Delayed density dependence of a predator-prey interaction should tend to regulate a population, however, as it acts strongly on large populations and weakly on small populations. The nature of the delays and strengths of the different numerical responses dictate the type of oscillations. Population cycles have been observed in nature (e.g. snowshoe hare; Krebs *et al.* 1995; microtine rodents, Hansson & Henttonen 1985; red grouse, Moss & Watson 1991) although they do not necessarily provide direct evidence for this predator-prey model.

The early Lotka-Volterra predator-prey models made simplistic assumptions (which have been refined in later models) about the behaviour of predator and prey. For example they assumed a linear increase in consumption rates of prey with predator abundance. This is unrealistic due to intraspecific competition between predators which leads to defending of food resources (mutual interference). The

effect of prey abundance on the consumption rate of predators is also important, which is known as the functional response (Solomon 1949). Two main types of functional response are thought to occur most frequently in predator-prey interactions: type II and type III (Holling 1959). The type II functional response describes a decelerating rise with prey density in the rate of prey consumption per predator, which eventually asymptotes when prey density saturates the predator. Saturation occurs because the handling time of the prey (i.e. hunting and consuming) limits the number of prey eaten per unit time. The type III functional response is similar to the Type II response at high density, but at very low densities prey are avoided and therefore their population growth occurs irrespective of predator abundance. However, as prey increases under the type III functional response there is a more than linear increase in consumption rate. This can occur when predators switch between prey or when the searching efficiency of prey increases with prey density. Different functional responses by predators are thought to have different effects on population dynamics. A type III response leads to predators regulating the prey at a low and stable level of abundance. The effect of the type II response depends on the efficiency of the predator but in theory it can destabilise population dynamics leading to oscillations in both predator and prey populations.

A further important factor that has been shown to affect the population dynamics of predation is environmental heterogeneity and the subsequent responses of predators and prey (Huffaker 1958). Patchiness of habitat quality is common place in nature and therefore both prey and predators tend to aggregate in patches of high food density. Incorporating spatial heterogeneity, for example prey refuges or partial refuges, into the Lotka-Volterra model appears to stabilise predator-prey dynamics, although this process is complex and depends on the biology and behaviour of predator and prey, amongst other factors. However, it is clear that predator-prey interactions can generate spatial as well as temporal patterns in populations. In landscapes where habitat is patchy the populations of prey (and predators) are often not one single population but a collection of localised populations. A metapopulation describes a population of subpopulations occupying discrete habitat patches that interact by dispersal of individuals across a matrix of unsuitable habitat (Hanski & Gilpin 1991). Metapopulation dynamics is a key component of conservation management due to increasing rates of anthropogenic fragmentation of habitat. The relative probability of extinction and recolonisation of the subpopulations is central to

metapopulation dynamics (Hanski & Simberloff 1997). Persistence of a metapopulation is predicted to occur when overall colonisation rates exceed extinction rates, assuming that the subpopulations fluctuate asynchronously, despite the fact that individual subpopulations are relatively unstable. If certain habitat patches have positive population growth rate they represent 'sources' and those with negative population growth are referred to as 'sinks' (Pulliam 1988). Populations with positive growth will tend to lose more individuals through dispersal than they gain, whereas populations declining in abundance will gain more than they lose. Therefore, dispersal and asynchrony give rise to density dependent net migration rates, which in theory stabilize population dynamics of the overall metapopulation. Predator-prey interactions that would be otherwise prone to extinction have been shown to persist through metapopulation processes (Bonsall, French & Hassell 2002).

Two key questions are frequently asked in the study of predator-prey dynamics; whether predators limit prey populations or whether they regulate prey populations. Limitation is defined as a process that sets the population equilibrium and regulation is the process by which a population returns to its equilibrium when perturbed (Sinclair 1989). The position of the equilibrium point can be set by both density-dependent and density-independent factors (e.g. weather) (Sinclair 1989). By definition, regulation can only occur as a result of one or more density-dependent processes that act on rates of birth, death and/or movement to maintain a population within upper and lower limits, through a negative feedback mechanism (Sinclair 1989). Limiting or regulatory factors can be intrinsic to the population; e.g. social, physiological or genetic, or extrinsic; e.g. predation, food supply, disease, parasites, weather or landscape (Krebs 2003). Predation has been shown theoretically and empirically to produce a range of effects on prey populations (Sinclair & Pech 1996). As predation inherently increases the mortality rate of the prey, predation can be said to be always limiting to some extent (Sinclair 1989). Predators can regulate their prey populations through density dependence where prey mortality rates increase with increasing density (Sinclair 1989). Predators have been shown to have depensatory effects on their prey through inverse density dependence, where mortality rates increase with decreasing prey abundance, and this can lead to extinction of prey populations (Sinclair & Krebs 2003). Alternative stable states (or multiple equilibria) have been observed in predator and prey populations where prey species escape the regulatory effects of predation so that they outbreak in population size and achieve

another stable equilibrium at higher abundance (Sinclair, Olsen & Redhead 1990). This most frequently occurs after a perturbation (e.g. predator abundance decreasing) or sudden change in the environment (e.g. heavy rains) but is theoretically possible through the interaction itself (e.g. a slight delay in the predator response to an increase in prey). At high prey density, the predators no longer regulate their prey, which are now regulated by intraspecific competition for food resources. Other more complex predator-prey interactions exist including the influence of habitat refuges and the presence of alternative prey on population dynamics (Sinclair & Krebs 2003) and some of these are discussed briefly in the next section.

In reality, the abundance of most populations across a period of time and space is likely to be affected by a range of biotic and abiotic factors, including fluctuations in the natural environment. The relative importance of biotic, density dependent interactions compared to abiotic, density independent interactions in determining population abundance has been the subject of a long-standing debate in ecology between two conflicting schools of thought which still persists to some extent today (e.g. Sinclair 1989; Krebs 1995; Sinclair & Pech 1996; Berryman 2002, 2004; Murray 1999; White 2001; 2004). One school of thought, which can be linked back to Nicholson (1954), concentrated on the stability in populations and argued that density-dependent interactions played the main role in determining population size, although density-independent processes exerted influence from time to time. The contrasting argument, first presented by Andrewartha & Birch (1954), focused on fluctuations in populations and suggested the most important factor determining population size is the shortage of time when population growth is positive, i.e. populations undergo a series of setbacks and recovery after stochastic environmental fluctuation. It seems apparent now that the first argument concentrated on what regulates populations and the second argument with what limits populations. Recent consensus is that a clear understanding of patterns in abundance is likely to require the incorporation of both density-dependent, biotic effects and the density-independent, often stochastic effects of weather (Begon *et al.* 2005).

However, it is indisputable that for populations to persist in the long term density dependent processes must operate at some stage (Sinclair 1989). Sinclair & Krebs (2003) proposed some general rules of the factors that determine population growth. They suggested that food supply is generally the most important factor determining population growth rate in animal populations. Nevertheless, top-down

processes from predators, social interactions within species and stochastic disturbances can override or modify the bottom-up control of food supply. Interactions between these four controls generate the range of complex effects on population growth and patters in abundance that we see in nature. Sinclair & Krebs (2003) also provided some generalisations of the primary controls of populations, although they stressed these represent hypotheses for future testing. Fish populations and many invertebrates seem to be affected by stochastic disturbances affecting recruitment through food limitation. Bird populations appear driven by food limitation coupled with social interactions over territories. Food supply appears to drive large mammal populations and predation infrequently intervenes. Small mammals however may tend to be affected by top-down processes, such as predation, coupled with social interactions and are rarely limited by food resources. If this latter generalisation is valid, hedgehog populations may be expected to be determined by badger predation rather than food limitation.

If population ecology is a predictive science that is useful to wildlife management and conservation, it is vital to understand how populations are controlled and to develop generalised rules to remove the need to carry out separate studies of every single population (Sinclair & Krebs 2003). Three general approaches are used to investigate questions about the determination and regulation of populations: the 'demographic', 'density' and 'mechanistic' paradigms (Sibly & Hone 2003). Population growth rate, given as $r = \log_e [(N_{t+1})/N_t]$, is often used in these approaches and is the summary parameter of trends in population abundance as it combines the effects of birth, death and movement on abundance.

Firstly, the demographic paradigm focuses on the relationship between population growth rate and age-specific fecundity and survival (Sibly & Hone 2003). Various approaches (e.g. key factor analysis, population projection matrices, λ - contribution analysis) can be used to investigate the relative contributions of survival and fecundity to population growth. Secondly, the density paradigm looks at the relationship between population growth rate and density (Sibly & Hone 2003). Population regulation can be considered to occur if population growth rate is negatively density dependent (Sinclair 1989). The demographic components that relate to density and the extrinsic or intrinsic factors that cause changes in these demographic components (i.e. mortality, reproduction or movement) can then be identified (Krebs 2003). Density dependence is frequently investigated in populations

that undergo phases of sustained population growth as part of large density fluctuations or cycles, as it is often possible to see density dependent declines of population growth rates at high densities (Krebs 2002). This typically involves the time series analysis of census data from long term studies. However, this approach can only suggest hypotheses about population regulation and limitation, whereas experimental studies are required to test them (Sinclair 1989).

Thirdly, the 'mechanistic paradigm' proposed by Krebs (1995) focuses directly on the relationships between population growth rate and ecological mechanisms of regulation, such as food availability, disease or predator abundance. Krebs (1995) argued that seeking density dependence in populations is not a useful approach as a predictive science of population dynamics cannot be founded on describing relationships between vital rates and population density, without specifying the ecological mechanism driving these rates and therefore population change. However, despite the advantage of focusing on one particular factor of interest, this approach may lead to losing sight of the relative importance of that factor compared to others. Determining the factors that prevent population growth rate is the classic question of regulation and is arguably the most valuable single piece of information on any population (Krebs 2002). In applied ecology it is essential to know what factors can be manipulated to stop growth of over abundant populations or to increase the population growth of endangered species (Krebs 2002). It is argued that the mechanistic approach is more utilitarian and predictive than the density or demographic paradigms as it can provide a better understanding of the ecological mechanisms behind population dynamics in the field (Krebs 1995). Additionally, this paradigm permits shorter manipulative experiments to test specific hypotheses regarding regulatory mechanisms, which provide the strongest evidence of the extent to which prey populations are limited or regulated by predation (Sinclair 1989).

However, perturbation experiments involving higher vertebrates such as mammals or birds are problematic and thus rare (Sinclair 1989). As a result of this, and because of an interest in biological control, insects have been the most studied taxonomic group and are fundamental to the understanding of population ecology. The majority of evidence for predator regulation in vertebrates is correlative, resulting from the search for density dependence in patterns of predator abundance (numerical responses) and diet (functional responses) during fluctuations in prey densities (Banks 2000). Only for a few population systems have predictive relationships between

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population growth rate and ecological mechanisms been investigated using an experimental approach (Krebs 2003). This thesis includes such a perturbation experiment; badger abundance was manipulated and the response of hedgehog abundance and thus population growth rate monitored.

1.2 Complex predator-prey interactions

In the previous section population interactions between two species were discussed; predators and prey, or two competitors. However in reality predator-prey interactions necessarily involve further species as they are always part of a larger food web. For example, the interaction is likely to be affected by the dynamics of the food supply of the prey, competitors of the prey or predator species, or alternative prey consumed by the predator. Therefore predator-prey interactions are often highly complex and are capable of generating indirect effects in food webs. Examples of such interactions are reviewed here.

Early empirical evidence of the indirect effects produced by a predator was provided by Paine (1966), in a pioneering experiment looking at the influence of a top predator on the structure of a community on the Pacific shores in North America. The carnivorous starfish (*Pisaster ochraceus*) was removed from plots in a marine rocky intertidal system and the abundance of intermediate predator and prey species monitored over subsequent years. The starfish preys on filter-feeding barnacles (*Balanus glandula*), mussels (*Mytilus californicus*) a carnivorous whelk (*Thais emarginata*) and a number of browsing species of limpets and chitons. Four species of algae and a sponge were also monitored. In the absence of the top carnivore, the barnacle initially dominated but was subsequently superseded by the mussel. Three species of algae and a browser species disappeared as they were outcompeted for either space or food. The exclusion of the starfish resulted in species diversity of the food web falling from fifteen to eight. Predation, by the starfish, kept the abundance of competitively dominant species sufficiently low to allow subordinate competitors enough space and food to coexist, a process known as predator-mediated coexistence. The term 'keystone predator' is now used to describe a species that promotes species co-existence and richness in a community by decreasing competitive interactions between prey species through predation (Henke & Bryant 1999). This experiment showed how predation and interspecific competition interacted to produce 'indirect' positive effects on community diversity. Most studies of the effects of species interactions such as predation and competition have emphasised the 'direct' effects of these interactions (Sih *et al.* 1985). Predation was traditionally thought to act between trophic levels and competition within levels and this led to a conventional approach of investigating predation and interspecific competition as isolated processes (Kotler &

Holt 1989). However, frequently the effects of predation and competition are inseparable and often interact (Kotler & Holt 1989).

Trophic cascade (Paine 1980) is a process whereby a predator reduces the abundance of its prey and this effect cascades down to the trophic level below so that the food resources of the prey increase in abundance. For example, in a predator-herbivore-plant system, trophic cascade is the indirect effect of carnivores on plants mediated by a reduction in herbivore abundance. Conversely, in a system with four trophic levels, the predator can reduce the abundance of an intermediate predator, which in turn allows a herbivore to increase in numbers leading to a decrease in plant abundance. Evidence for trophic cascades has tended to come from relatively simple aquatic systems, which has led to some debate whether this process is important in more species-rich terrestrial systems (Polis *et al.* 2000; Shurin *et al.* 2002). However, this may reflect the practical difficulties of carrying out experimentation to investigate trophic cascades in terrestrial systems.

One aspect of trophic cascades, known as mesopredator release (Soule *et al.* 1988), has received particular attention from the field of biodiversity conservation. Top predators, and mammalian carnivores in particular, are prone to extinction or depletion in numbers through habitat fragmentation and persecution, and their disappearance is thought to lead to increased numbers of intermediate predators, or mesopredators, which in turn has negative impacts on their prey species, such as birds and other small vertebrates (Crooks & Soule 1999). Mesopredator release has been implicated in the decline and extinction of prey species, and has been incorporated into many conservation programmes, despite receiving little empirical evaluation (Crooks & Soule 1999). The effects of mesopredator release have also been modelled for island systems where exotic predators have been introduced and are predating indigenous prey which has led to counter-intuitive management recommendations on the control of invasive predators (Courchamp *et al.* 1999). For example on islands where both domestic cats *(Felis domesticus)* and rats *(Rattus* spp.) have been introduced, mesopredator release predicts that removal of the top predator, in this case cats, without the simultaneous control of rat populations, would lead to more detrimental effects on indigenous prey species than if no action was taken at all (Courchamp *et al.* 1999). The model predicted that without cat predation rat populations would increase in abundance to such an extent as to drive the indigenous prey species to extinction.

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Investigation of trophic cascades has led to wider questions about how communities are structured, particularly whether they are dominated by top-down processes via predation or from the bottom-up through intraspecific competition for food resources. The 'Green World' view of Hairston *et al.* (1960) proposed that the most important force was top-down through the impact of predation on herbivore populations which enhanced plant community productivity and biomass. Others (Pimm 1991) have suggested that as plants have evolved chemical and physical defences, herbivores are limited by competition for available food and in turn predators compete for a limited availability of herbivores and therefore bottom-up controls dominate. The level of primary productivity may dictate whether top-down or bottom-up controls predominate in communities by modifying the lengths of food chains (Chase 2003). However, most communities are probably organised by a combination of biotic and abiotic forces, including competition, predation, disturbance and recruitment, although understanding patterns of top-down and bottom-up controls in communities remains a future challenge (Begon *et al.* 2005).

One specific example of a complex predator-prey interaction, with relevance to the study of badgers and hedgehogs in this thesis, is apparent competition (Holt 1977). This interaction involves one prey species exerting a negative effect on the population growth rate or abundance of another prey species mediated through the action of a shared predator (Morris, Lewis & Godfray 2004). Put simply, in a system of two prey species and a shared predator, if the abundance of prey A increases, the numerical response of the predator increases predation pressure on prey B which leads to a decrease in their population size. This process can result in a decrease in the population growth of two prey species that do not compete for the same resource but do share the same natural enemy. However, the two prey species could be alternatively considered to be engaged in interspecific competition for 'enemy free space', as suggested by Jeffries & Lawton (1984). Recent theoretical and empirical support has shown that apparent competition is likely to be important in structuring species assemblages (Bonsall & Hassell 1997; Bonsall & Holt 2003). Badgers are predators of both hedgehogs and invertebrates. Therefore an increase in invertebrate prey abundance is likely to lead to badgers also increasing in number which consequently would reduce hedgehog population size. However, badgers and hedgehogs are also potential competitors for the same invertebrate food resources, which adds another level of complexity to the interaction.

Intraguild predation (Polis *et al.* 1989) involves the direct interaction of interspecific competition and predation which can produce indirect effects on populations and communities. In intraguild predation, a predator consumes a prey species but both species compete for a shared food resource. It is considered an important force in structuring communities (Polis *et al.* 1989) and is discussed in detail in the next section.

1.3 Intraguild Predation

1.3.1 Theoretical and empirical evidence

In intraguild predation (IGP) a predator kills and consumes a prey species that is also a potential competitor for a shared food resource. Polis *et al.* (1989) consider a guild as the "taxa in a community that use similar resources (food or space) and thus may compete". The resource for which two species compete in IGP is referred to as the 'basal resource' (Heithaus 2001). IGP is distinguished from the traditional concepts of competition by the direct energetic benefit for the predator and from predation because the predatory act reduces potential competition. IGP is considered as an extreme form of interference competition.

Polis *et al.* (1989) presented a framework for describing the many different configurations of IGP. They classified forms of IGP according to symmetry and age-structure. Asymmetrical IGP occurs when one species always predates another (e.g. badger and hedgehog; Doncaster 1992) whereas symmetrical IGP occurs where there is mutual predation between two competitive species (e.g. lion *Panthera leo* and spotted hyena *Crocutta crocutta*; Schaller 1972). Age structure can be important as IGP sometimes only occurs at certain stages of development of either the prey or predator (e.g. adult rattlesnakes prey on eggs and nestlings of burrowing owls but not the adults; Polis 1991). Asymmetrical IGP has long been considered in basic food-web ecology where it is generally termed 'omnivory'. IGP is a form of omnivory, which is defined as feeding on resources at different trophic levels. Most predators eat prey items in a particular size range regardless of the trophic level of the prey (Polis *et al.* 1989). Thus larger species are frequently omnivorous both on a resource and on smaller consumers of that resource.

Asymmetrical IGP is therefore a common feature of many ecosystems and is thought to be a central process in the structure and functioning of many natural communities (Polis *et al.* 1989). IGP has been recorded in a variety of systems including freshwater, marine and terrestrial and occurs both within and between taxa (see Polis *et al.* 1989 for review). Examples of IGP can be found in numerous taxa, including: protozoa (Diehl & Feissel 2001); jellyfish (Purcell 1991); a range of arthropods (Moran & Hurd 2000; Wise & Chen 1999) including, crustaceans (MacNeil & Prenter 2000), scorpions (Polis & McCormick 1987), insects (Lucas, Coderre & Brodeur. 1998) and spiders (Okuyama 2002); fish (Winemiller & Ponwith

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1998); reptiles (Gerber & Ecthernacht 2000); amphibians (Walls & Williams 2001); birds (Jaksic 1982); rodents (Stapp 1997); and mammalian carnivores (Mills & Gorman 1997). IGP can also occur between taxonomic groups and has been recorded between species in different phyla. The wolf spider (*Gladicosa pulchra*) for example predates ground skinks (*Scincella lateralis*), and both consume similar leaf-litter invertebrates (Rubbo *et al.* 2001). IGP between mammals and fish has been studied in Zimbabwe, where Cape clawless otters (*Aonyx capensis*) predate African mottled eels (*Anguilla bengalensis*) who both compete for freshwater crabs (Butler & Marshall 1996).

Despite the ubiquity and importance of IGP, little formal theory and few mathematical models have been formulated to help understand it as a regulatory mechanism in populations and communities (Holt & Polis 1997). Holt & Polis (1997) produced a theoretical framework for such work by generalising a number of multi-species competition and predator-prey models to include IGP. These models predict a number of outcomes including coexistence or exclusion of either the IG predator or prey. They predicted that IG predators and prey can only coexist if the former is inferior to the latter at exploiting the basal resource. If the IG predator is a superior competitor, even in a system without IGP, the IG prey will be outcompeted and excluded. Even species roughly equal in competitive ability are unlikely to coexist, if one species predates another.

The models formulated by Holt & Polis (1997) also predict that environmental productivity will affect the outcome of IGP. At low productivity, when resources are scarce, the IG prey can exclude the IG predator via exploitative competition for a limiting basal resource (i.e. the competition element outweighs the effects of predation). At high productivity, the IG predator may exclude the IG prey via the combined effects of apparent and exploitative competition (i.e. abundant resources sustain the IG predator at sufficiently high numbers to exclude the IG prey). Coexistence is most likely at intermediate levels of productivity when the negative effects of competition and predation offset each other. The importance of productivity and asymmetry of resource utilisation to IGP is supported by empirical evidence from experimental food webs containing two freshwater protists, *Colpidium striatum* (IG prey) and *Blepharisma americanum* (IG predator) (Lawler & Morin 1993; Morin 1999). *Colpidium* competitively excluded *Blepharisma* at low

productivity levels but co-existed at intermediate levels for many generations. At higher productivity levels the IG predator was able to exclude the IG prey.

The same models also predict that IGP can generate dynamic instability in a system in which IG predator and prey coexist (Holt & Polis 1997). Consider a food chain without IGP: following a perturbation the prey increases or decreases followed by a lagged response in the predator population. The system returns to equilibrium with damped oscillations as in traditional predator-prey dynamics. In a system with IGP, following a decrease in the IG prey, the decline of the IG predator is slower because it utilises the basal resource. Therefore, as the IG prey declines to low numbers, high predation rates persist due to the relatively high densities of IG predators. The net effect is that IG prey populations are driven to even lower densities and will recover more slowly than in a system without IGP. Extended phases of low population densities can increase the risk of localised extinction due to stochastic events. The IG prey can only recover when the IG predator population has declined sufficiently due to over consumption and subsequent reduction of the basal resource. When IG prey increases it can do so rapidly as the basal resource has had sufficient time to recover.

Thus, theoretical studies suggest that IGP has major implications for IG predator, prey and basal resource populations and consequently for community structure. Communities with IGP are susceptible to the exclusion of species, particularly in productive environments. Despite these predictions, empirical studies have shown that coexistence of IG predator and prey in high productivity habitats is common in nature (Polis *et al.* 1989). Holt & Polis (1997) recognise that their models fail to explain this and they suggest factors that could foster coexistence such as adaptive behaviour and alternative prey. For instance, effective predator avoidance behaviour can allow the IG prey to persist (Lima & Dill 1990). Alternatively, the IG predator could switch between consumption of the basal resource and the IG prey, depending on the relative abundance of these species. This would theoretically stabilise the IGP interaction and allow coexistence. Additionally, alternative prey exclusively available to the IG prey can encourage their persistence. Spatial heterogeneity in an environment can also provide conditions for coexistence. Many examples of IGP seem to involve spatial refuges for the IG prey (Diehl 1993) and the importance of enemy free space to the persistence of prey species is well documented (Jeffries & Lawton 1984).

Holt & Polis (1997) suggest these mechanisms need more study to provide a further understanding of IGP. Individual behavioural decisions regarding habitat use are important in determining both population dynamics and community structure and may also influence the spatial nature of IGP amongst mobile species (Heithaus 2001). Heithaus (2001) argued that despite the ubiquity of IGP in natural communities, and the importance of individual behavioural decisions, IGP has received almost no attention from behavioural ecologists. Heithaus (2001) modelled habitat use under the conditions of asymmetrical IGP using a framework of ideal free distribution (IFD). The IFD (Fretwell & Lucas 1970) has been used extensively to study how competition and predation influence the distribution of animals among habitats (e.g. Doncaster 2000). The model predicted how IG predators and prey should distribute themselves across two habitats based on a number of factors including, habitat productivity, inherent habitat riskiness and the presence and productivity of an alternative resource for IG predators. When the diet of IG predators is restricted to IG prey and the basal resource, this model confirms that co-occurrence is only stable when dietary overlap is low and productivity of the basal resource is not high. It predicts that IG prey will select the least risky habitat and thus can be excluded from productive habitats. IG predators will be distributed roughly proportional to basal resource productivity. Alternatively, if one habitat has higher basal resource productivity and has a lower predation risk, all IG prey will congregate in this habitat.

However, if alternative resources are available for IG predators then this may facilitate coexistence under many conditions. In reality, IG predators probably consume at least some alternative resources and this may help to explain the ubiquity of co-existing IG predators and prey in a variety of systems. If IG predators use substantial alternative resources, the Heithaus (2001) model predicts the distributions of both IG predators and prey will change. In such a case, IG predators will be distributed proportional to alternative resource availability rather than the basal resource. Variation in alternative resource productivity produces a continuum of IG prey distributions, from one matching the safest habitats to one balancing predation risk and basal resource productivity.

1.3.2 Intraguild predation in terrestrial mammal systems

IGP is common in terrestrial mammal systems and may account for up to 68% of known mortality in some species (Palomares & Caro 1999). Medium and large

carnivores are most frequently the IG predators in this system, preying on smaller mammal species in both related and unrelated taxa. IGP is particularly prevalent amongst mammalian carnivores. Examples of IG predator and prey relationships include lions (*Panthera leo*) and cheetahs (*Acinonyx jubatus*) (Laurenson 1994); lions and wild dogs (*Lycaon pictus*) (Mills & Gorman 1997); Eurasian lynx (*Lynx lynx*) and red fox (*Vulpes vulpes*) (Sunde, Overskaug & Kvam 1999); and Iberian lynx (*Lynx pardinus*) and Egyptian mongoose (*Herpestes ichneumon*) (Palomares *et al.* 1995). The role of IGP in mammalian carnivore populations is of particular interest to ecologists, as reduction of top predator populations (e.g. through persecution) is thought to allow smaller predators to increase, which in turn has serious implications for lower trophic levels in a community, i.e. mesopredator release (Crooks & Soule 1999; Henke & Bryant 1999). For instance Crooks & Soule (1999) found that where coyotes are absent, or at low density, smaller mammalian predators are more abundant which in turn has deleterious consequences for their avian prey.

The majority of empirical studies that have contributed to the understanding of the role of IGP in regulating animal behaviour and populations have used manipulative experiments of invertebrates, frequently as part of biological control studies. Larger vertebrates, such as mammalian carnivores, are not suitable for such manipulations due to their cryptic behaviour, scarcity and high mobility (Fedriani *et al.* 2000). These experiments are also financially and ethically problematic (Crooks & Soule 1999). Consequently, few attempts to experimentally evaluate the importance of intraguild predation have been made in terrestrial mammal systems (Litvaitis & Villafuerte 1996). Most studies of IGP in mammalian carnivores therefore rely on descriptive data to investigate relationships between species. For example, Fedriani *et al.* (2000) used descriptive data to seek correlations between coyote (*Canis latrans*) and gray fox (*Urocyon cinereoargenteus*) populations in California. Both species predominantly prey on small mammals and seven out of twelve recorded gray fox deaths were due to coyote predation, suggesting IGP between these species is important. Fedriani *et al.* (2000) found a significant negative relationship between the abundance of coyotes and gray foxes that suggested foxes avoided habitats of high predation risk. They proposed that coyotes could limit the number and distribution of their IG prey to the extent of locally excluding gray foxes.

Other studies have presented circumstantial evidence to suggest IG predators can limit the abundance and distribution of IG prey. Lindstrom *et al.* (1995)

opportunistically used a decline in red fox (IG predator) numbers in Scandinavia, due to an outbreak of sarcoptic mange, to investigate the effects on pine marten (*Martes martes*) (IG prey) abundance. An increase in pine marten numbers was observed concomitant with the fall in fox numbers. Lindstrom *et al.* (1995) argue this 'natural experiment' suggested that IGP by red foxes limits pine marten populations. Red foxes are also thought to suppress the abundance of the endangered arctic fox, and in regions at the limit of their range cause local extinctions (Hersteinsson & Macdonald 1992).

These studies, however, can only confirm that IGP occurs between species, by investigating predation events and dietary overlap. They do not provide evidence of the importance of IGP as a limiting or regulatory mechanism in terrestrial mammal populations or a determinant of behaviour. Controlled manipulative experiments would be required to demonstrate the properties of IGP. Palomares *et al.* (1995) described IGP between the Iberian lynx and Egyptian mongoose, two competing predators of rabbits (*Oryctolagus cuniculus*). Their surveys found a negative correlation between lynx and mongoose population size in comparable habitats. They argue that the Iberian lynx limits the abundance and distribution of Egyptian mongoose populations through IGP. An alternative explanation offered by Litvaitis & Villafuerte (1996), suggests that the habitat characteristics of the study sites were not comparable. They argue that the differences in lynx and mongoose density can be explained by the presence of human altered habitats. Mongooses are often successful in these habitats whereas lynx suffer high levels of mortality. This illustrates how apparent correlations between IG predator and prey abundance and distribution do not necessarily indicate a cause and effect relationship, as other factors may be involved.

However, an experimental manipulation of hedgehogs (IG prey), in comparable habitats of varying badger (IG predator) density in southern England, provides evidence that IGP can influence the distribution of mammal prey populations (Doncaster 1992) (see below for more detail). Doncaster (1992) also showed that in some areas badgers, supported by high basal resource productivity, achieved densities high enough to exclude local populations of hedgehogs by a combination of predation and behaviourally-mediated effects. This supports predictions from theoretical studies that IGP in productive habitats can lead to local exclusion of prey species.

Theoretical studies also predict the potential instability of IG predator and prey populations. Empirical investigation of population instability requires IG predator

and prey abundance to be quantified over a number of generations. This is problematic for mammals due to long generation times and therefore little is known about the possible long-term effects of IGP on population dynamics of mammalian species. Equally, little is known about the ecological consequences of perturbing these systems. Perturbations, such as changes to fauna and landscape, are commonplace in terrestrial environments and may affect the relationship between predatory and prey species (Reynolds & Tapper 1996). Anthropogenic changes to factors such as basal resource productivity within habitats (e.g. through changes in land use), relative competitive ability, or behaviour and abundance of IG predators and prey (e.g. through wildlife management or predator control) are likely to produce a range of responses in IGP systems.

Despite the theoretical predictions of species exclusion under a range of conditions, coexistence is often observed between mammalian IG predator and prey species (e.g. Palomares & Caro 1999). As mentioned earlier, the disparity between these predictions of coexistence in IGP systems and empirical studies, suggests that other mechanisms may be important. Changes in habitat selection (e.g. use of less risky habitats and predator free refuges), predator avoidance and prey switching behaviour, greater movement of prey species and use of alternative resources by predators may help to promote co-occurrence of species of varying competitive abilities, along a gradient of basal resource productivity (Heithaus 2001). Most terrestrial mammals are highly mobile and display complex behaviours, which may moderate the effects of IGP.

To illustrate this, Heithaus (2001) argued that the interaction between lions and wild dogs provides qualitative support of how changes in habitat selection can allow co-occurrence of IG predator and prey in a system where IGP is substantial. Lions are significant predators of wild dogs, accounting for 43% of adult and 39% of pup deaths in Kruger National Park (Mills & Gorman 1997). Wild dogs primarily eat impala (*Aepyceros melampus*) and other ungulates. Lions do eat these species and kleptoparasatise wild dog kills, but their primary prey species are wildebeest (*Connochaetus taurinus*), buffalo (*Synercus caffer*) and zebra (*Equus burchelli*). Lions are therefore common predators of wild dogs but they have a low dietary overlap. Lions are distributed in habitats in which their primary prey is most common. These habitats also have the highest productivity of the prey species of most importance to wild dogs, but the latter avoid them, preferring habitats of lower

productivity. Consequently, there is a negative correlation between lion and wild dog abundance, which appears to fit the predictions of the model presented by Heithaus (2001) of IG predator and prey distribution.

1.3.3 Summary

In summary, both theoretical and empirical studies have shown that IGP has profound implications for individuals, populations and communities. IGP is now an important research topic in areas such as ecology, biological control and conservation biology (Muller & Brodeur 2002). It can produce a range of alternative stable states in populations, ranging from coexistence to exclusion. Theoretical models predict that co-existence can only occur if the IG prey is more efficient at competing for the basal resource relative to the IG predator. Productivity of the basal resource can influence IGP, with exclusion of IG prey likely if productivity is high, and coexistence of IG predator and prey predicted at intermediate levels of productivity. Communities with substantial IGP are susceptible to the exclusion of species, particularly in productive environments. IGP can generate unstable dynamics in both predator and prey populations, resulting in extended phases of low prey population densities and consequently an increased risk of localised extinction.

Contrary to the predictions of IGP models, numerous examples of coexistence in natural communities with IGP can be found. This suggests that other mechanisms, such as predator avoidance behaviour, use of alternative resources and spatial refuges, facilitate the co-occurrence of IG predators and prey. This can lead to IG prey distributions ranging from matching habitat safety to one that balances predation risk and utilising the basal resource. These behavioural mechanisms need more empirical investigation, particularly within terrestrial mammal systems, as species are capable of exhibiting complex behavioural responses and high mobility.

IGP in terrestrial mammal systems has frequently been revealed through qualitative rather than quantitative methods. Therefore, future efforts should concentrate on determining to what extent various densities of IG predators alter the abundance and behaviour of IG prey (Fedriani *et al.* 1999). To understand the consequences of IGP, an experimental manipulation of IG predators combined with quantitative data predator and prey populations is required.

1.4 Intraguild predation between badgers and hedgehogs

1.4.1 Background ecology

Badgers and hedgehogs are two mammal species involved in IGP. Badgers are medium sized carnivores that occur throughout the UK and Europe. They are associated with mixed pasture and arable agricultural areas, but they are most abundant in habitats comprising a mix of woodland and pastoral dominated farmland, typical of southern England (Neal & Cheeseman 1996). In this region, two localised, intensive studies have estimated badgers at densities as high as 38 individuals km^{-2} (Macdonald & Newman 2002) and 25.3 individuals km^{-2} (Rogers et al. 1999). These populations have risen drastically over the last two decades, undergoing a three to four fold increase, which is consistent with the increase in badger numbers seen across much of the UK (Wilson et al. 1997). The Badger Act 1973, Wildlife and Countryside Act 1981 and Protection of Badgers Act 1992, have afforded badgers high levels of protection from persecution, and are likely to have facilitated this rise in population size (Cresswell, Harris & Jeffries 1990; Wilson, Harris & McLaren 1997).

Badgers den socially in setts, often in hedgerows and woodland, but forage individually, both in wooded habitats and frequently in open farmland. Badgers have a very omnivorous and adaptable diet but earthworms (*Lumbricus terrestris*) are overwhelmingly their most important food item in the UK (Neal & Cheeseman 1996). However, during the summer and early autumn months, conditions are often too dry for foraging for worms, and cereals and fruits become of major significance. Insects are also an important food source, including, dung beetles (Scarabeidae), ground beetles (Carabidae), caterpillars of moths (Noctuidae) and crane-fly larvae (Tipulidae). Although mammals do not appear regularly in badger diet, they may be significant due to their energetic content. Rodents, especially short-tailed voles (*Microtus agrestis*), moles (*Talpa europea*), rabbits and hedgehogs are the most frequently taken species. The importance of hedgehogs in the diet of badgers is unclear. Neal & Cheeseman (1996) suggest they are eaten occasionally but a badger killed near Oxford was found with four hedgehogs in its stomach (Middleton 1935 in Neal & Cheeseman 1996). Dietary studies show that hedgehogs occur infrequently in the diet of badgers (Kruuk et al. 1979; Roper 1994). One adult hedgehog represents most of a night's food requirement and therefore may be more important than the frequency of occurrence data suggest (Doncaster 1994). However although

hedgehogs may be unimportant in the diet of badgers, in the sense that they are rarely eaten, their distributions may be strongly influenced by badgers because of their sensitivity to the real threat of predation on the occasions that badgers encounter them.

Hedgehogs are insectivorous mammals, generally abundant across their western European distribution. In England they are present in nearly all lowland habitats where there is sufficient cover for nesting, required both as summer day-nests and winter hibernacula (Morris 1991). They are traditionally thought to favour habitat types where badgers are also most abundant (i.e. pastoral dominated farmland mixed with woodland). In general, they concentrate in grassland rather than arable habitats (Doncaster 1992). Hedgehogs are also very abundant in suburban habitats of gardens, parkland and amenity grassland (Reeve 1994), which badgers tend to avoid due to human disturbance (Doncaster 1992). However, in the absence of systematic monitoring, the status of hedgehog populations in the UK is uncertain, both in terms of long term changes in abundance and distribution across different habitats.

The vast majority of hedgehog diet is ground-living invertebrates. Ground and dung beetles are the most numerous prey items, followed by caterpillars, earthworms and earwigs (Yalden 1976; Wroot 1984 in Reeve 1994; Dickman 1988). Hedgehogs are also known to eat mammals, usually carrion, and birds' eggs (Jackson & Green 2000). Dietary studies probably underestimate soft-bodied prey items in favour of the more indigestible species with exoskeletons, such as beetles (Reeve 1994). However, despite this bias, Wroot (1984, in Reeve 1994) found earthworms in 95% of hedgehog droppings, equal to 34% of the total energy intake, which makes this food item the most important in terms of energy. There is therefore a large dietary overlap between badgers and hedgehogs, specifically earthworms and to a lesser extent beetles and caterpillars. These invertebrate species represent the basal resource over which these guild members potentially compete.

Hedgehogs possess a specialised morphological adaptation to defend themselves against predators (Reeve 1994). Their dorsal surface is covered by sharp spines that, when the hedgehog rolls into a ball, present an impenetrable exterior. This provides good protection from most nocturnal predators, including owls and to a large extent foxes. The latter are thought to occasionally predate hedgehogs but do not represent a significant predator (Doncaster 1993). Hedgehog remains were present in less than 1% of fox faeces, collected from areas where both species were

abundant (Doncaster, Dickman & Macdonald 1990). However badgers are strong and dextrous enough to be able to unroll the hedgehog to expose its unprotected underbelly, in order to kill them (Neal & Cheeseman 1996). Neal & Cheeseman (1996) provide a detailed eyewitness account of a badger predating an adult hedgehog: "When the hedgehog was on its back with the 'join' between head and hindquarters uppermost the boar made one swift movement of its left paw and ran the claws straight down and into the 'join'. Then the right paw descended on the 'join' which was now open and raked sideways along the belly of the prey. The hedgehog was now opened flat and pinned at both ends by the formidable claws. The boar then lowered its head and began to eat." The boar badger ate the whole hedgehog with only "a flat skin with spines and a tiny piece of head" remaining. The tendency for badgers to eat all the hedgehog, leaving only a cleaned skin and spines behind as evidence of the predation event, is confirmed by other anecdotes documented by Neal & Cheeseman (1996).

The frequency of predation is not clear but where they coexist the badger appears to be a major predator of the hedgehog. For example, seven of 30 hedgehogs, released into a habitat of high badger density, were predated by badgers in rural habitats of Oxfordshire (Doncaster 1992). In another manipulative study in the same habitat, three of 12 hedgehogs were killed and eaten by badgers within two months (Doncaster 1993). However, rates of predation within resident, unmanipulated hedgehog populations are unknown and are likely to depend on many factors, including the density and behaviour of predators and prey, distribution of food resources and habitat structure.

Although there is substantial dietary overlap between badgers and hedgehogs, there may be little competition between these species during summer months when invertebrates can become extremely abundant in open grassland habitats and therefore not a limiting resource. However, the possibility of badgers and hedgehogs sharing the same resource (i.e. being engaged in IGP rather than traditional predator-prey dynamics) has important consequences for hedgehog dynamics. Firstly, in contrast to traditional predator-prey dynamics, there should be no numerical response in the badger population to declining hedgehog numbers, as badgers are likely to be supported by plentiful invertebrate food resources. Therefore, as numbers of IG prey (hedgehogs) decline their per capita mortality rates will increase through constant predation pressure, which can easily lead to the exclusion of the IG prey. Secondly,

insofar as they eat the same foods, badgers and hedgehogs will have similar foraging strategies and schedules which will lead to high encounter rates between IG predator and prey in areas where they co-exist, all else being equal (Doncaster 1992). Both hedgehogs and badgers are nocturnal and frequently forage on short grass pastures where invertebrates are abundant and easily accessible and they have even been observed foraging simultaneously on the same fields (Doncaster 1994).

However, hedgehogs have a keen sense of smell and therefore are likely to use olfactory cues to avoid predators (Ward, Macdonald & Doncaster 1997). Enclosure and field experiments showed that hedgehogs avoid areas tainted with badger faeces and reduce foraging effort in response to badger faecal odour (Ward *et al.* 1996, 1997). Badgers have a highly developed olfactory communication system and use specialised scent glands to scent mark territories as well as regularly using latrines (Neal & Cheeseman 1996). Thus, habitats used intensively by badgers are well scent marked, and this is likely to elicit a strong predator avoidance response from hedgehogs. Nevertheless, at a home range scale, Doncaster (1993) found that foraging hedgehogs did not demonstrate any response to predators. Despite a significant predation risk from badgers, they did not use cover more than expected at random, and frequently foraged on open pastures.

1.4.2 Empirical evidence of Intraguild predation

One of the few manipulative experiments to investigate the effects of IGP on IG prey populations and behaviour in a terrestrial mammal system was conducted by Doncaster (1992). IG prey populations were manipulated to seek the effect of badger density on hedgehog distribution by quantifying response variables such as survival, habitat use and movement. Hedgehogs were translocated into an area where a population was known to persist and into an area where they were absent. The two sites had very similar availability of preferred habitat but a marked difference in badger density. Survival of hedgehogs in the high badger density area (predator rich) was lower than in the area of low badger density (predator scarce), due mainly to predation by badgers. Hedgehogs introduced into the predator rich area dispersed twice as far as those animals in the predator scarce area. There were also differences in habitat use whilst animals were present at the sites. Hedgehogs in the predator rich areas strongly preferred suburban microhabitats, which badgers avoid. Growth rates of hedgehogs were similar in both sites, which may indicate that food resources in this

habitat are not limiting. This is an example of IGP regulating an IG prey species distribution both through predation and behaviourally-mediated effects. Hedgehogs were excluded from areas by IGP because of high predator activity, either being predated or moving away from this habitat to enemy free refuges.

Doncaster (1994) also conducted a manipulative experiment to identify factors regulating local variations in population abundance of hedgehogs. A low abundance population was artificially increased in numbers and a high density population was reduced. An intermediate density population was manipulated but kept at its original level to act as an experimental control for the stress effects of translocation. All three sites had different levels of badger abundance: the expanded population was at high badger density; the experimental control at low badger density; and the depleted population had no badgers present in the area. Mortality was significantly higher in the expanded population than in the control due mainly to predation by badgers. Hedgehogs in the expanded population dispersed further and faster and had stronger preferences for suburban microhabitats than hedgehogs in the control site. This was explained by differences in badger abundance and therefore a varying risk of predation. The expanded population returned to its original size within 2 months. The effects on survival and dispersal were not as extreme as those detected by transplanting hedgehogs into an area where hedgehogs were absent (Doncaster 1992). However, this experiment is more powerful because the treatment site (the expanded population) naturally supported hedgehogs, albeit at a low density. It was high predation rates by badgers that were responsible for keeping the hedgehog population below the level achieved at the control site. In addition, weight gains of hedgehogs at the control site were significantly less than hedgehogs in the expanded population. This indicates the control site was much nearer carrying capacity than the expanded population site. This is therefore strong evidence to support the prediction that IGP can regulate IG prey abundance in terrestrial mammal systems, both through predation and behaviourally-mediated effects.

The effect of shared food resources (basal resource productivity) as well as IG predator activity on the pattern of hedgehog abundance and distribution was investigated using descriptive data from a large scale survey (Micol, Doncaster & Mackinlay 1994). The abundance of hedgehogs, a measure of badger activity and food resource availability (indices of earthworm availability), were estimated at a range of suburban and rural sites across the same agricultural landscape in

Oxfordshire used in the experimental manipulations. Other factors, such as fox abundance, habitat characteristics and distance to town (as a measure of distance to predator free refuge) were simultaneously quantified. Relationships between these factors and variations in hedgehog abundance were investigated. Analysis showed badger activity, food resources and distance to town correlated with hedgehog abundance. Hedgehogs occupied both rural sites (pasture fields) and suburban sites (amenity grassland fields). Hedgehogs in rural sites were distributed according to the level of food resources and badger activity. Sites combining the richest food resources and lowest predator activity were most likely to support hedgehogs. The vast majority of suburban sites supported hedgehogs (25 of 31 playing fields), with hedgehogs mainly distributed in relation to predator activity. Six sites that did not support hedgehogs were very close to the nearest badger activity. Distance to town was also independently important but food resources, much more available in this habitat, were of little consequence to hedgehog abundance. All playing fields were relatively close to town (i.e. near a predator free refuge), often far from badger activity and have a greater availability of food resources, resulting in higher hedgehog abundance than in pasture fields. Densities of 1.8 hedgehogs per hectare were estimated on playing fields compared with 0.2 hedgehogs per hectare on pasture fields in areas where badgers were relatively abundant.

These experimental and survey data reveal implications of IGP for IG prey behaviour and populations in terrestrial mammal systems. A range of distributions of hedgehogs can occur, dependent on the level of badger abundance and therefore predation risk. Co-existence occurs at low badger densities in pastoral habitats, with the distribution of hedgehogs balanced between predation risk and shared food resources. However, at higher badger densities, increased rates and risk of predation lead to hedgehogs being excluded from pastoral habitats persisting only in enemy free refuges of suburban habitat. At a landscape scale, individual decisions regarding habitat use allow the coexistence of IG predator and prey species as predicted by Heithaus (2001). However, if hedgehogs are distributed as a network of localised populations they may be subject to metapopulation processes and if so successful movement between populations will be vital to the persistence of hedgehogs at the landscape scale (Micol *et al.* 1994). Doncaster, Rondini & Johnson (2001), using an experimental manipulation of hedgehogs, investigated the environmental correlates of dispersal. Manipulated hedgehogs were able to disperse relatively far, up to a

maximum linear distance of 3.8km, which would allow all populations in their study area to be connected. However, these are artificial dispersal events and natural dispersal distances of this magnitude were rare in this region (Doncaster *et al.* 2001).

Micol *et al.* (1994) found that hedgehog abundance varied in direct inverse relation to badger sett density and exclusion of hedgehogs in rural habitats was predicted above a threshold of 2.3 badger main setts $10km^{-2}$. Main sett density can provide a broad measure of badger activity and is used as index of badger abundance at large scales (Wilson *et al.* 1997). A density of 2.3 main setts $10km^{-2}$ is not uncommon in the UK and does not represent a particularly dense badger population. In a national sett survey, Wilson *et al.* (1997) found mean main sett densities above 2.3 main setts $10km^{-2}$ in the following regions of the UK: south west, southern, and south east England; central and west midlands; and Wales. Scotland, northern and eastern England supported mean main sett densities below this figure. The threshold value of main sett density for hedgehog persistence needs more critical evaluation however as it is based on data from a single survey in one region of southern England. Therefore, further investigation of the spatial relationship between hedgehog populations and badger abundance and distribution on a larger scale is required.

The empirical studies reviewed here provide strong evidence that the effects of IGP by badgers have serious consequences for hedgehog populations and behaviour. Micol *et al.* (1994) argue that an increase in badger numbers in the UK may have serious consequences for the survival of hedgehogs in rural areas. Therefore recent increases in badger abundance (Wilson *et al.* 1997) are likely to have caused declines in hedgehog population abundance and distribution in many areas of the UK. Investigators have anecdotally observed a marked decline in hedgehog numbers in rural areas (Doncaster 1999; Mammals on Roads Survey; N. Reeve, pers. comm.). However, without a systematic national monitoring programme, or a long term study of hedgehog populations, it is not possible to quantify potential changes in hedgehog abundance.

1.4.3 Summary

Empirical investigation of the factors that influence and regulate hedgehog populations revealed badgers as a significant predator of hedgehogs (Doncaster 1992, 1994; Doncaster *et al.* 2001). Field experiments, involving manipulations of hedgehogs, found IGP by badgers can limit hedgehog distribution and regulate

abundance through predation and behaviourally-mediated effects (Doncaster 1992, 1994).

A field survey of hedgehog populations found that at low badger densities the distribution of hedgehogs in rural habitats is balanced between predator activity and shared food resource availability (Micol *et al.* 1994). However, in areas where badgers are supported by abundant invertebrate food sources (high basal resource productivity) they can achieve sufficiently high densities to exclude hedgehogs. Suburban habitats, avoided by badgers, act as enemy free space and contain abundant food resources, which support hedgehogs in dense, isolated populations. Therefore, selection of less risky habitats by hedgehogs facilitates co-existence of both IG predator and prey at a landscape scale.

Hedgehog abundance has a negative association with badger main sett density and exclusion of hedgehogs is predicted from rural habitats above a relatively low threshold of main sett density (Micol *el al.* 1994). This may have serious consequences for hedgehog populations in many rural areas of the UK. Persistence of the rural hedgehog metapopulation relies on the ability of hedgehogs to move between isolated populations (Doncaster *et al.* 2001; Rondini & Doncaster 2002).

Future work to improve our understanding of the interaction between hedgehogs and badgers and how IGP influences hedgehog populations is required. This should include: quantification of hedgehog and badger abundance and distribution across a number of replicated sites; seeking spatial correlations between the two populations; and an investigation of behavioural mechanisms, such as habitat selection, predator avoidance and dispersal of hedgehogs, that are likely to affect the IGP relationship. An experimental manipulation of badgers to test hypotheses about the effect of IGP on IG prey abundance and behaviour should prove profitable, the design of which is discussed in the next section.

1.5 The Randomised Badger Culling Trial

Terrestrial mammals, particularly carnivores, are often not suitable for field manipulations due to behavioural, financial and ethical problems (Crooks & Soule 1999). However, a large-scale experimental removal operation of badgers in the UK (1999 - present date) provides a unique opportunity to empirically investigate IGP in this system. This field trial is a predator removal experiment of an unprecedented scale and is being carried out by the Department for Environment, Food and Rural Affairs (DEFRA) as part of a research programme to investigate bovine TB in cattle. Bovine TB, caused by the bacterium *Mycobacterium bovis*, is a disease in cattle that has significant economic and welfare consequences to agriculture. A body of indirect and correlative evidence suggests that badgers are a significant source of infection in cattle (reviewed by Krebs 1997). Krebs (1997) recommended a Randomised Badger Culling Trial (RBCT) to test the effect of badger culling on the incidence of bovine TB in cattle.

The RBCT comprised a randomised block experimental design (see Fig. 1.) with ten matched 'triplets' each consisting of three 100 km^2 areas, randomly receiving one of the following treatments: 'proactive' culling of all badgers; localised 'reactive' culling following the identification of bovine TB in cattle; and 'control' where no culling takes place (Donnelly *et al.* 2003). Recently the initial results of the RBCT have been published which revealed that reactive culling led to a slight increase in the incidence of TB in cattle and therefore this strategy was deemed not to offer a management solution to the bovine TB problem (Donnelly *et al.* 2003). The trial of the proactive culling strategy in the incidence of TB in cattle is ongoing at the time of writing.

The treatment areas were delineated up to one year before any culling took place, which allowed data collection on hedgehog populations both before and after the cull in all treatment areas, thus providing a spatial and temporal control. Treatments were unknown until culling began. As part of the trial, DEFRA carried out full field surveys of badger sign, including all setts and latrines across all treatment areas. This represents a uniquely large-scale dataset on badger activity, which is available to this research project and allows the quantification of distribution and indices of badger abundance.

Fig. 1. Randomised block experimental design of the Randomised Badger Culling Trial. Only the left-most branch of each tree is shown for this balanced design

Triplet: A_1 A_2 A_3 A_4 A_5 A_6 A_7 A_8 A_9 A_{10}

Treatment area: Proactive B_1 Reactive B_2 Control B_3
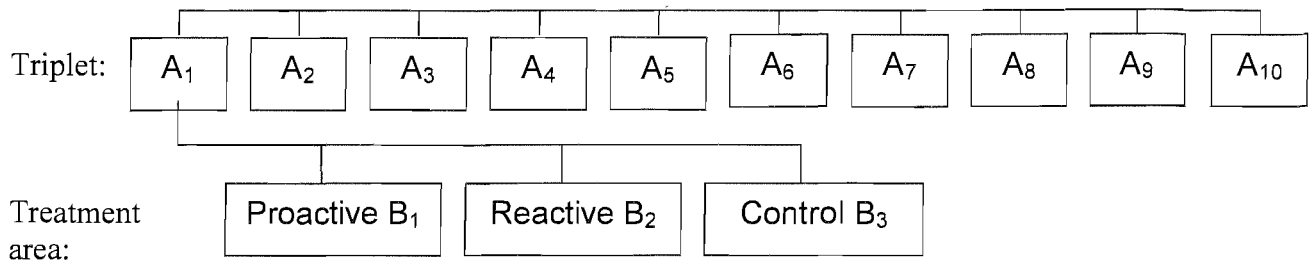
In summary, the RBCT provided a manipulation of IG predator density within a replicated randomised block design and a comprehensive dataset on the abundance and distribution of an IG predator. This provided a framework for testing hypotheses regarding the effect of IGP on the population abundance and behaviour of an IG prey species in a terrestrial mammal system.

1.6 Objectives of the research

The aim of this research project was to conduct a controlled replicated experiment to investigate whether IGP by badgers determines the abundance and distribution of hedgehogs and strongly influences their behaviour. This was achieved by testing the following hypotheses:

1. The density and distribution of hedgehog populations are inversely correlated with badger abundance

2. Hedgehog populations will increase in size after badgers are reduced in abundance through culling

3. Growth rates of hedgehog populations are correlated with the abundance of badgers

4. Use of rural habitats by hedgehogs will increase after predation risk is reduced through badger culling

5. Hedgehogs will forage further from cover after predation risk is reduced through badger culling

The data needed to test these hypotheses were collected during the following programme of fieldwork:

- The abundance and distribution of hedgehogs in rural and suburban habitats was quantified in the proactive and control treatment areas of five RBCT triplets, before and for four years after culling

- In these sites, badger distribution and indices of abundance in each year of the experiment were quantified to seek spatial and temporal correlations between hedgehog and badger populations

- Habitat selection and patterns of movement by hedgehogs were estimated in the proactive and control treatment area of the RBCT Gloucestershire Triplet, before and after culling

These research objectives will contribute to a better understanding of IGP by providing experimental evidence of the extent to which badger predation is capable of regulating or limiting hedgehog abundance and distribution. Through the perturbation of predator abundance, the potential for different stable states in hedgehog populations can be investigated. The research will also allow the empirical

investigation of spatial refugia as a stabilising factor in predator-prey interactions; this is hypothesised to be an important mechanism that facilitates the co-existence of IG prey and IG predators, which otherwise is not predicted to occur in habitats of high productivity. Patterns in the distribution of hedgehogs and their relationship with the abundance of their IG predators will be investigated, in order to describe the implications of this IGP interaction for prey populations at a regional scale.

Chapter 2: Spatial variations in hedgehog abundance in relation to badger density and distribution

2.1 Introduction

Predation and competition frequently interact to produce indirect effects that can have a strong influence on animal behaviour and population dynamics (Sih *et al.* 1985). Asymmetrical intraguild predation (IGP) is such an interaction, where predator and prey are also potential competitors for a shared food resource (Polis, Myers & Holt 1989). The impact of IGP on prey populations is more complex than predation and competition alone, as the act of predation reduces future competition for food resources as well as providing direct energetic benefits to the predator (Polis *et al.* 1989). IGP can shape the abundance and distribution of predator and prey species and generate unstable dynamics in both populations (Holt & Polis 1997). Theoretical studies have suggested that ecological communities with IGP are susceptible to the exclusion of prey species, particularly in productive environments where abundant food resources sustain high predator numbers (Holt & Polis 1997). Despite these predictions, empirical studies have shown that intraguild predator and prey commonly coexist in many ecosystems, even in highly productive habitats (Polis *et al.* 1989; Palomares & Caro 1999). It has been suggested that behavioural mechanisms, such as adaptive foraging (Holt & Polis 1997), the use of spatial refugia by prey (Holt & Polis 1997) and the availability of alternative food resources to predators (Heithaus 2001) facilitate the co-occurrence of intraguild predators and prey. In particular, the use of spatial refugia (i.e. the selection of less risky habitats) by terrestrial mammals and birds is likely to be an important mechanism as these species tend to be very mobile and can move easily between habitats (Heithaus 2001; Sergio, Marchesi & Pedrini 2003). The importance of spatial refugia to the co-existence of intraguild predator and prey has been confirmed by empirical studies (e.g. Durant 1998; Kamler *et al.* 2003; Sergio *et al.* 2003). IGP theory predicts that the distribution of intraguild prey species can vary from one that is restricted to the safest habitats only, to one that balances predation risk and food availability (Heithaus 2001). Theory also predicts that changes in the productivity of a habitat can have a major impact on the equilibrium between intraguild predator and prey populations, which profoundly affects their abundance and distribution (Holt & Polis 1997).

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In the UK, the Eurasian badger (*Meles meles* L.) is a predator of the western European hedgehog (*Erinaceus europaeus* L.) (Doncaster 1992) and these species are also potential competitors for the same invertebrate prey, particularly earthworms (*Lumbricus terrestris*) and beetles (Scarabeidae and Carabidae) (Neal & Cheeseman 1996; Reeve 1994). Experimental manipulations of wild hedgehog populations revealed that predation by badgers was a regulatory factor in the abundance and distribution of hedgehogs through increased mortality and by stimulating changes in hedgehog behaviour (Doncaster 1992, 1994). Badger predation also strongly influenced patterns of hedgehog dispersal (Doncaster *et al.* 2001). Hedgehogs have a keen sense of smell and will avoid areas tainted with badger odour (Ward *et al.* 1996; Ward, Macdonald & Doncaster 1997). During manipulations of hedgehog populations, individuals reduced their risk of predation by moving faster and further away from areas of higher badger density (Doncaster 1992, 1994). Hedgehogs also reduced the risk of predation by selecting suburban habitats, such as villages and farms, where badgers tend to be less active (Doncaster 1992; Doncaster *et al.* 2001). Such experimental evidence of the importance of IGP on intraguild prey in terrestrial mammal systems is rare, as it is often impossible to manipulate either the predator or prey populations because of logistical, financial or ethical reasons (Crooks & Soule 1999).

In Oxfordshire, UK, a survey of hedgehogs revealed a strong negative spatial correlation between badger activity and hedgehog distribution (Micol, Doncaster & Mackinlay 1994). The probability of occurrence of hedgehogs in both rural and suburban habitats increased significantly with greater distance to the nearest signs of badger activity. Hedgehog abundance was also positively correlated with earthworm availability and therefore hedgehog distribution in rural habitats was likely to be the result of a trade-off between food availability and predation risk. Furthermore, hedgehog numbers were negatively correlated with badger main sett density (an index of badger abundance). This relationship predicted that hedgehogs would be excluded from rural habitats that support more than 0.23 main setts km^{-2} (0.001 to 0.72 main setts km^{-2} at 95% confidence limits) and would only survive in isolated populations in suburban habitats, which act as predator-free spatial refugia. In the mid 1990s, average main sett densities in rural habitats of southern England, central and west Midlands and Wales exceeded this predicted threshold for hedgehog occurrence (Wilson, Harris & McLaren 1997).

Coexistence of hedgehogs and badgers in rural habitats therefore can only be expected at low badger densities (Micol *et al.* 1994). In areas where badgers are supported at higher densities (through abundant invertebrate food resources in productive habitats) a high predation pressure on hedgehog populations is sustained and this is likely to have serious consequences for the persistence of hedgehog populations in rural habitats (Micol *et al.* 1994). Increases in badger abundance between the mid 1980s and the late 1990s have been observed at small-scale sites in southern England (Macdonald & Newman 2002; Rogers *et al.* 1997), and the same trend was detected across the majority of the UK (Wilson *et al.* 1997). Hedgehogs have been traditionally considered to be an abundant species and present in all lowland habitats in the UK where sufficient cover exists for summer day-nests and winter hibernacula (Morris 1991). However, in the absence of long term systematic monitoring, the current status of hedgehog populations in the UK is uncertain.

The objective of the present study was to estimate the abundance of hedgehogs in both rural and suburban habitats and to investigate the use of spatial refugia by hedgehogs in relation to indices of badger density and distribution. We set out to test the prediction of Micol *et al.* (1994) that in rural landscapes supporting badgers at high density (above 0.23 main setts km^{-2}) hedgehogs will be absent from pasture grassland and restricted to isolated spatial refugia in suburban habitats. The study was carried out in areas where the Department for Environment, Food and Rural Affairs (DEFRA) has conducted large-scale surveys of badger activity as part of the Randomised Badger Culling Trial (RBCT) (Krebs 1997). This provided an opportunity to investigate the spatial relationship between hedgehogs and badgers at a much larger scale than has been carried out previously.

2.2 Materials and Methods

2.2.1 Study sites

Ten treatment areas used in the RBCT were surveyed for hedgehogs, during the summers of 2000 and 2002, in the following regions of England: the Cotswolds region of Gloucestershire (2 study sites); Wiltshire (1 study site); the Forest of Dean region in Gloucestershire (1); Somerset (3); and Staffordshire (3) (Fig. 2.1).

Fig. 2.1. Location of the ten treatment areas
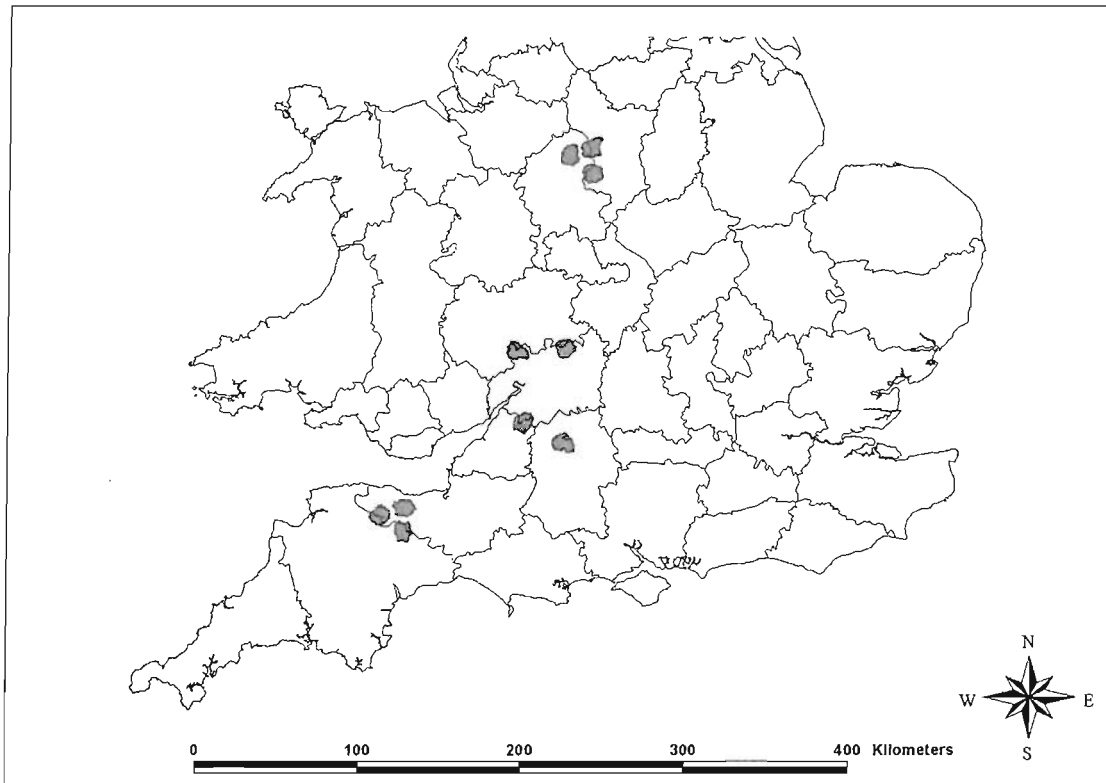
Each treatment area (henceforth referred to as study site) was approximately 100 km^2 in size and comprised of mixed farmland dominated by pasture, interspersed with patches of suburban habitat, such as small villages and farm buildings, and woodland (see Fig. 2.2 for the percentage cover of different land use types in the study sites). No badger culling as part of the RBCT had taken place in the study sites prior to the hedgehog surveys.

Fig. 2.2. Percentage cover of different land use types in the 10 study sites (data from Land Cover Map 2000, Centre for Ecology and Hydrology, Monks Wood, UK)
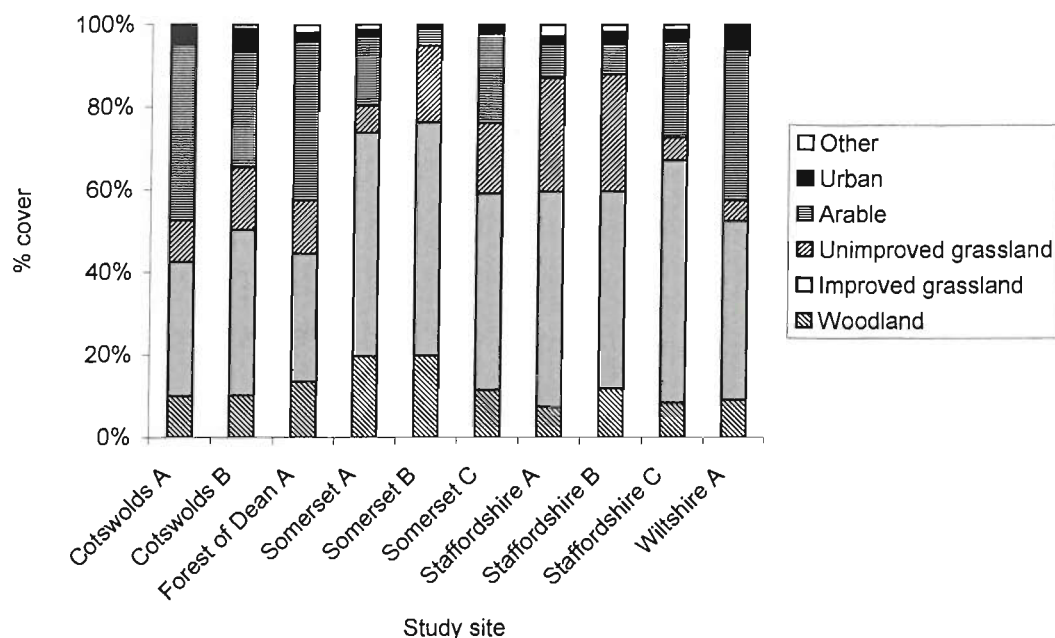
Hedgehogs tend to forage on short grassland where invertebrates are easily accessible, and these habitats are considered to be their preferred type. They include amenity grassland in suburban areas (e.g. playing fields, parks etc), and short grazed pasture fields in rural areas (Doncaster 1992). The term 'preferred habitat' is used in this thesis to refer to habitats that are used more frequently than would be expected at random. The survey was stratified by habitat type so that approximately three amenity grassland fields and nine pasture fields were surveyed per study site. Typically there were between five and seven villages within each 100 km^2 study site from which three villages were selected at random, ensuring each village was a minimum of 1.5 km from the edge of the study site. One amenity grassland field was surveyed per village. Amenity grassland fields tended to be situated on the edge of villages or within approximately 100 m of the village boundary. Three pasture fields were selected randomly from all pasture fields available within a 1.5 km radius of each village. Villages tended to be no further than 3 to 4 km apart and therefore very few pasture grassland fields within the study sites were unavailable for sampling. A total of 23 amenity grassland fields and 82 pasture fields were sampled across the ten study sites. All fields were a minimum of 500 m apart in an attempt to achieve independence in terms of hedgehog abundance. This distance is greater than the

circular diameter (391 m) of an average male hedgehog's home range of 12 ha (Morris 1991), thus minimising the likelihood that an individual animal would be observed in more than one field.

2.2.2 Hedgehog surveys

Each field was surveyed over three separate visits between mid June and mid September and between the hours of 23:00 and 03:00 using methods similar to those of Micol *et al.* (1994). Amenity grassland and pasture fields were surveyed for hedgehogs by two fieldworkers using red-filtered spotlights (1.2 million candle power, Optronics, Oklahoma, USA). Each field was systematically searched from the perimeter inwards. On average, it took 20 ± 1 (s.e.) minutes to complete the survey of one field.

All hedgehogs observed at a site were captured and examined to determine weight, sex and age class (adults > 1 year, juveniles < 1 year). Hedgehogs were uniquely marked by attaching eight heat-shrink plastic tubes (RS Components, Northamptonshire, UK) over individual spines. A portable soldering iron was used as the source of heat to shrink the tube onto the upper half of the spine, in order to avoid burning the skin. By applying different coloured heat-shrink tubes in discrete groups in various positions on the dorsal coat of spines, individuals could be uniquely marked. The reliability of this marking system was validated on radiotagged individuals during a study of hedgehog behaviour carried out concurrently with the surveys in three of the study sites (Chapters 4 & 5). Hedgehogs were released within 10 minutes of capture. The total number of hedgehogs caught at each site over the three repeat visits provided an estimate of relative abundance and was divided by the area of the field to calculate relative density.

2.2.3 Badger surveys

During the hedgehog survey, the number of badgers observed in each field was recorded. In addition, a daytime survey of each field was also conducted to record signs of activity, including droppings, setts, runs and other field signs (e.g. tracks and hair caught on fences), in order to establish whether badgers were active in a field. Data on the location of badger setts and latrines across the study sites were provided from DEFRA badger surveys. These surveys were carried out no more than one year previous to the hedgehog surveys. DEFRA badger surveys were carried out by teams

of trained surveyors according to standard field protocols (Independent Scientific Group 1998). Farmland habitats were surveyed by walking all linear features, such as hedgerows, ditches and fence lines, searching for badger activity. Woodland was surveyed by walking transects or by a line of surveyors walking in parallel across the area of interest. The locations of all setts, latrines, tracks and runs were recorded on 1:10,000 scale survey maps before being digitised. Setts were classified as active or disused and either as a main or subsidiary sett. Substantial variation occurs in badger social group size between active setts (Wilson *et al.* 2003). However, the physical characteristics of badger setts are poor indicators of group size (Wilson *et al.* 2003) and therefore it was not possible to quantify group size at setts given the resources available. Therefore, in this study we treated sett density as an index of badger abundance that provided a broad picture of how badger abundance changed across relatively large scales rather than an accurate measure of badger numbers. Sett density has been used previously to quantify badger numbers at localised scales (Micol *et al.* 1994) and at the national scale (Wilson *et al.* 1997).

The badger activity data from DEFRA were analysed in a GIS (ArcView 3.2, Esri, California, USA). The number of active main and subsidiary setts around each field was counted at two different spatial scales. These two scales were chosen to reflect (1) the average diameter of a badger home range of 500 m in a high badger density area (Rogers *et al.* 1997) and (2) the average dispersal distance of hedgehogs in rural areas of 2 km (Doncaster *et al.* 2001; Chapter 5). The area of land surveyed by DEFRA within these two radii was also measured. Indices of badger density were calculated at these two spatial scales by dividing either (a) the number of main setts or (b) the number of all setts, by the area of land surveyed. Sett density at these two spatial scales will be referred to hereafter as 'local sett density' (within 500 m radius) and 'regional sett density' (within 2 km radius). The proximity of each field to badger activity was calculated from the DEFRA survey data as the distance from the edge of the field to the nearest badger activity (i.e. sett or latrine).

2.2.4 Data analysis

The study of hedgehog behaviour did not find any individual home range overlapping with more than one field (Chapter 4 & 5). Hence, fields were treated as independent sampling units. The dependency in hedgehog occurrence (presence/absence) to habitat type, indices of badger abundance, proximity to badger activity and distance to

nearest suburban habitat, was analysed by logistic regression in a generalised linear model (GLM). In order to select an optimal statistical model for the above explanatory variables, both a backward and forward stepwise selection procedure was performed. The variables retained in this procedure were then entered into a generalised linear mixed model (GLMM). Village nested in study site nested in region were entered as random effects in the model.

The relationship between hedgehog numbers in amenity grassland fields and sett density in the surrounding area was examined using a GLM. Due to a high frequency of zeros in the observed hedgehog density, the count of individual hedgehogs over three visits was treated as the response variable and modelled with a negative binomial distribution and a logarithm link function. The area of amenity grassland fields was log-transformed and entered as an offset into the GLM to take account of the variability in field size (i.e. survey effort). A linear regression was conducted to investigate the relationship between mean hedgehog density in amenity grassland habitat and badger sett density at the study site scale. Hedgehog abundance in amenity grassland habitat was normally distributed. The linear regression was weighted by the number of amenity grassland fields that were surveyed in each study site to take account of varying sample effort between sites. All statistical analyses were conducted using GenStat 6.2 (Lawes Agricultural Trust, Rothamstead, UK).

2.3 Results

2.3.1 Hedgehog abundance and distribution

Hedgehogs were extremely scarce in pasture fields (Fig. 2.3), with only six individuals captured in three of 82 fields sampled (4% of fields). The relative density of hedgehogs varied from 0 to 0.79 ha^{-1} between study sites with a mean of 0.09 ± 0.07 ha^{-1}. This mean was raised however by a pasture field in one of the Cotswolds study sites supporting a high relative density of 5.52 ha^{-1}, probably as a result of immigration from a large population in an amenity grassland field 500m away. Hedgehogs were more abundant in amenity grassland habitat (Fig. 2.3), with a total of 44 individuals observed in 14 of 23 amenity grassland fields (61 %) resulting in a mean relative density of 1.54 ± 0.44 ha^{-1}.

Fig. 2.3. Mean $\pm$ SE relative density of hedgehogs in amenity grassland (no shading) and pasture fields (grey shading) in each region
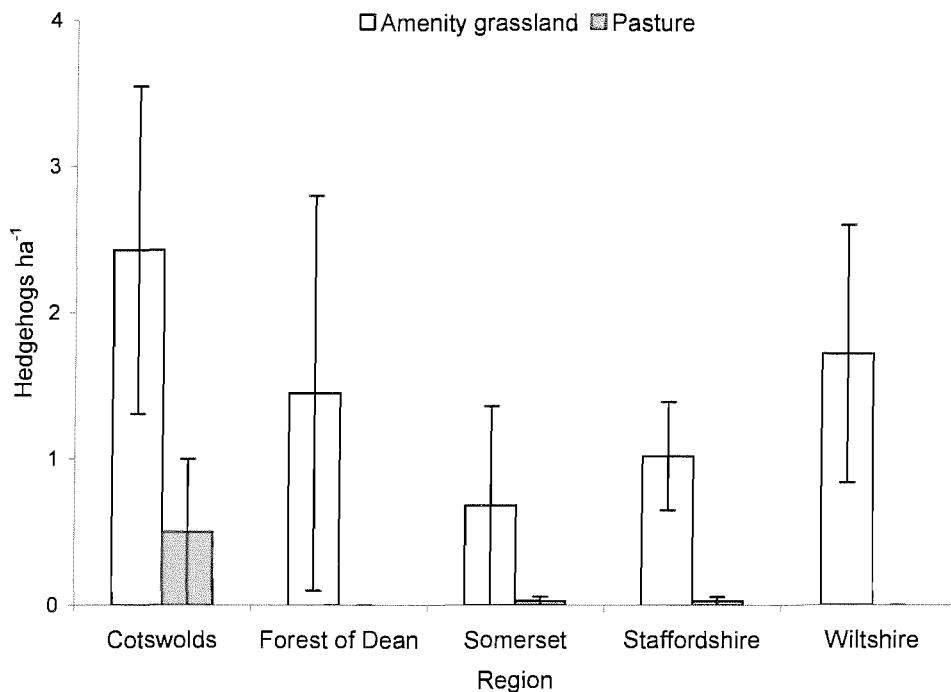
2.3.2 Indices of badger abundance and activity

Average regional main sett density was 0.81 (range 0.35 – 1.37) and 0.72 (range 0.24 – 1.02) main setts km^{-2} around amenity grassland and pasture fields respectively (Table 2.1). Mean regional density of all setts (i.e. main and subsidiary) was 6.19

badger setts km^{-2} (range 4.00 - 11.68) around amenity grassland fields and 6.56 badger setts km^{-2} (range 3.60 - 8.26) around pasture fields (Table 2.1).

Table 2.1. Number of amenity grassland and pasture fields surveyed and the mean sett density and main sett density (km^{-2}) for each habitat type in the study sites. The overall mean ± SE is given for the 10 study sites

Study site	Amenity grassland			Pasture		
	n	Setts km^{-2}	Main setts km^{-2}	n	Setts km^{-2}	Main setts km^{-2}
Cotswolds A	3	4.95	0.91	4	5.26	0.89
Cotswolds B	3	7.01	1.07	7	5.13	0.87
Forest of Dean A	5	4.13	0.35	5	3.60	0.24
Somerset A	1	11.68	0.91	10	8.00	0.66
Somerset B	1	4.00	0.43	11	5.25	0.45
Somerset C	0	-	-	11	8.26	0.57
Staffordshire A	2	5.47	0.72	10	6.18	0.92
Staffordshire B	3	9.69	1.37	8	8.11	1.02
Staffordshire C	2	5.73	0.94	9	6.59	0.92
Wiltshire A	3	6.22	0.72	7	6.87	0.64
Total	23	6.19 ± 0.66	0.81 ± 0.08	82	6.56 ± 0.35	0.72 ± 0.04

There was no difference in regional sett density around fields between habitats taking into account the effect of study site ($F_{1,94}$ = 0.31, P = 0.579). Nearest badger activity was significantly further away from amenity grassland fields (277.0 ± 36.0 m) than pasture fields (160.3 ± 15.5 m) including the effect of study site ($F_{1,94}$ = 5.09, P = 0.026).

Table 2.2. Indices of badger density and activity and distance to nearest suburban habitat in fields (both habitat types) with and without badger activity. Mean values are given ± SE

Badgers	Number of fields	Distance to nearest badger activity (m)	Regional sett density (km^{-2})	Local sett density (km^{-2})	Regional main sett density (km^{-2})	Local main sett density (km^{-2})	Distance to suburban habitat (m)
Absent	60	205.9 ± 17.3	6.04 ± 0.36	4.57 ± 0.51	0.74 ± 0.05	0.57 ± 0.10	457.9 ± 57.7
Present	45	139.7 ± 25.3	7.06 ± 0.52	8.88 ± 1.09	0.74 ± 0.05	0.87 ± 0.16	490.6 ± 88.7
Student's t		2.23	-1.67	-3.58	-0.09	-1.57	-0.31
P		0.028	0.097	< 0.001	0.930	0.121	0.758

2.3.3 Correlates of hedgehog occurrence

Both backward and forward stepwise selection in a GLM retained habitat type (pasture or amenity grassland) and regional sett density in the optimal model as the best explanatory variables of hedgehog occurrence ($F_{3,101}$ = 14.73, P < 0.001). There was no interaction between habitat and regional sett density (t_{101} = 1.24, P = 0.216). As mentioned earlier, there was a strong preference for amenity grassland fields (t_{101} = -3.17, P = 0.002) with a mean predicted probability of hedgehog occurrence in this habitat of 62% and only 4.4% in pasture fields. There was a negative association between the occurrence of hedgehogs and regional sett density (t_{101} = -2.30, P = 0.021). Badger activity, local sett density, local main sett density, distance to nearest badger activity and distance to suburban habitat were not selected for inclusion in the model.

The relationship between the predicted probability of hedgehog occurrence, estimated from the GLM, and regional sett density in both amenity grassland and pasture habitats is shown in Fig. 2.4. The probability of occurrence was low for pasture habitat even when badger sett density was low. For example, at sett densities of less than 2 setts km^{-2}, the model predicted that there was only a 10% probability of hedgehog occurrence. This declined with increasing sett density and above 7 setts km^{-2} the probability of occurrence was near to zero. In amenity grassland fields, in areas of low sett density, the model predicted that the vast majority of sites would be

occupied. However, the probability of occurrence declined sharply as sett density increased. For example, in high sett density areas of over 10 setts km^{-2}, hedgehog occurrence in amenity grassland fields was predicted to be only 33%.

Generalised linear mixed modelling, controlling for the effects of region and study site, also revealed that habitat (Wald statistic = 25.30, df = 1, P <0.001) and regional sett density (Wald statistic = 6.35, df = 1, P = 0.018) were significant explanatory variables of hedgehog occurrence. There was no interaction between habitat and regional sett density (Wald statistic = 2.98, df = 1, P = 0.084).

Fig. 2.4. Generalised linear model of estimated mean probability of hedgehog occurrence in amenity grassland (black line) and pasture fields (grey line) (with 95% confidence limits) in relation to badger sett density. The presence or absence of hedgehogs is given for individual fields
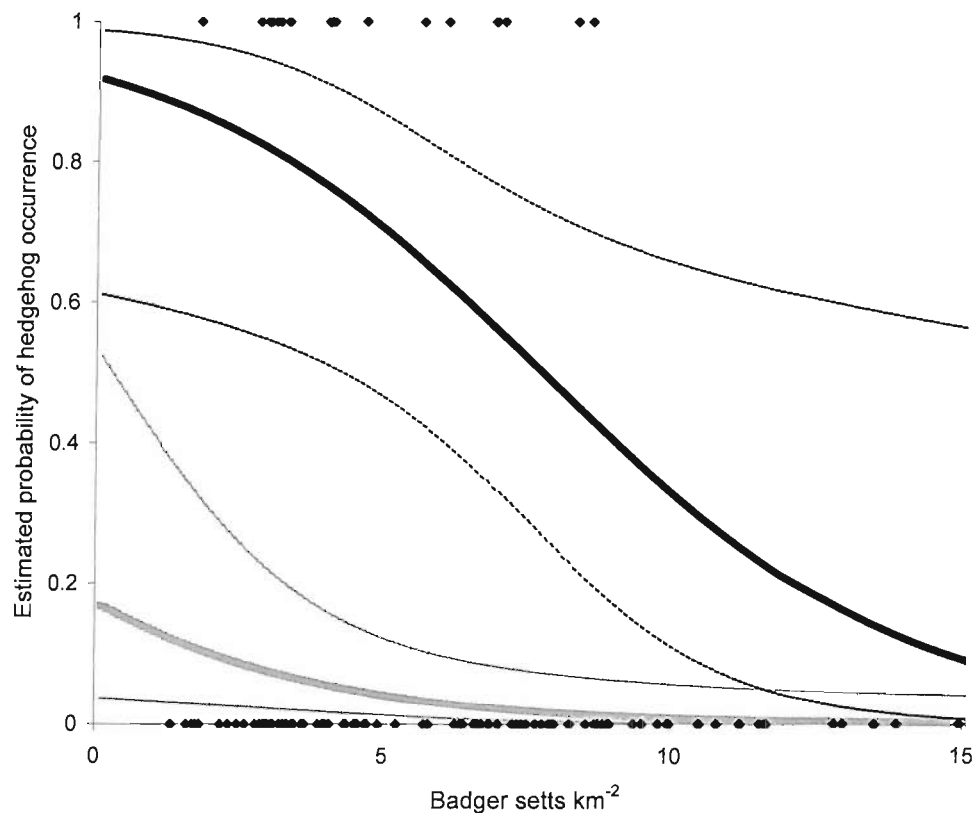
2.3.4 Hedgehog abundance and sett density

Hedgehog abundance in amenity grassland fields decreased as regional sett density in the surrounding area increased ($F_{1,21}$ = 4.03, P = 0.045). The relationship between the predicted abundance of hedgehogs, estimated from the GLM, and regional sett density

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is shown in Fig. 2.5. It is predicted that at very low sett densities, hedgehog density would be greater than 3 hedgehogs ha^{-1}. At high sett densities, above 10 setts km^{-2}, the negative binomial regression model predicted that hedgehog density would fall to less than 0.5 hedgehogs ha^{-1}. The relationship between hedgehog abundance and badger sett density in pasture habitat was not investigated due to the lack of fields (n = 3) supporting hedgehogs.

Fig. 2.5. Generalised linear model of predicted hedgehog density in amenity grassland fields (with 95% confidence limits) in relation to badger sett density. The relative density of hedgehogs is given for individual amenity grassland fields
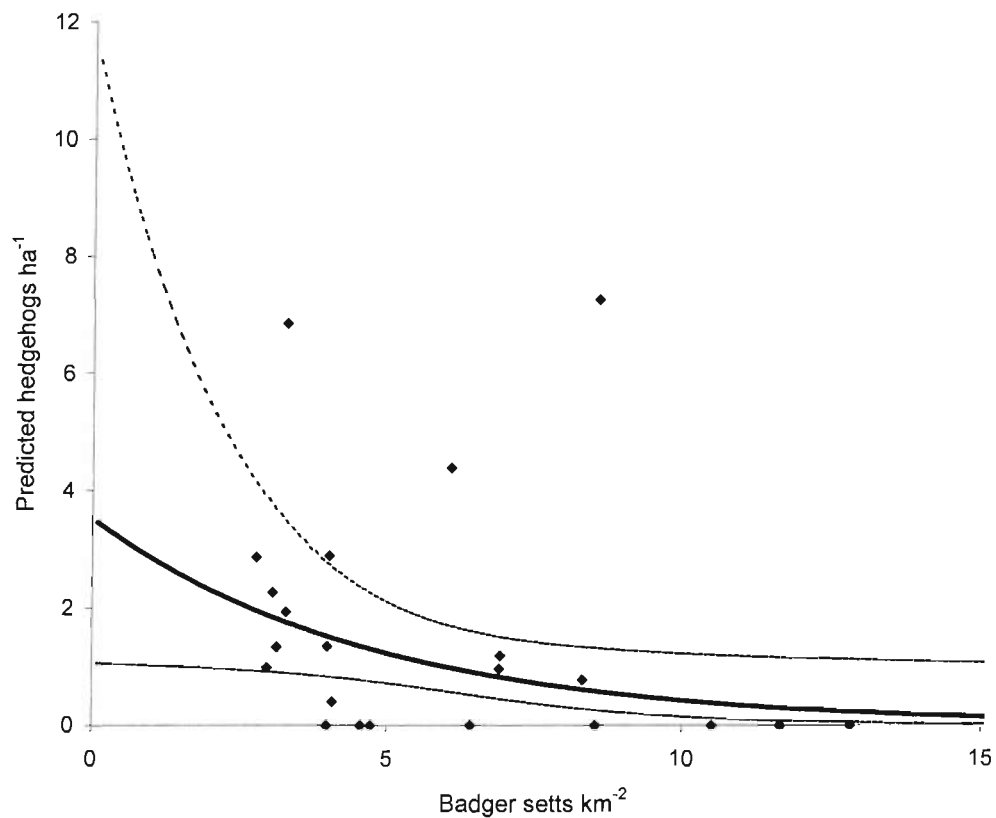
There was no relationship between mean hedgehog abundance and sett density at the study site scale (equation: mean hedgehog density = 3.218 - 0.270 × sett density, $F_{1,7}$ = 4.72, P = 0.066). However, the probability value was very close to significance. Badger sett density explained 31.8% of the variation in hedgehog abundance. At very low sett density, hedgehog density was predicted to be greater than 3 hedgehogs ha^{-1} (Fig. 2.6). This is in agreement with the negative binomial

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regression model. In areas supporting badger sett densities above 11.8 setts km^{-2}, the linear regression model predicted that hedgehogs would be completely absent from amenity grassland fields in suburban habitats (Fig. 2.6).

Fig. 2.6. Weighted linear regression model of predicted mean hedgehog abundance in amenity grassland habitat in relation to badger sett density (with 95% confidence limits), including values for each study site
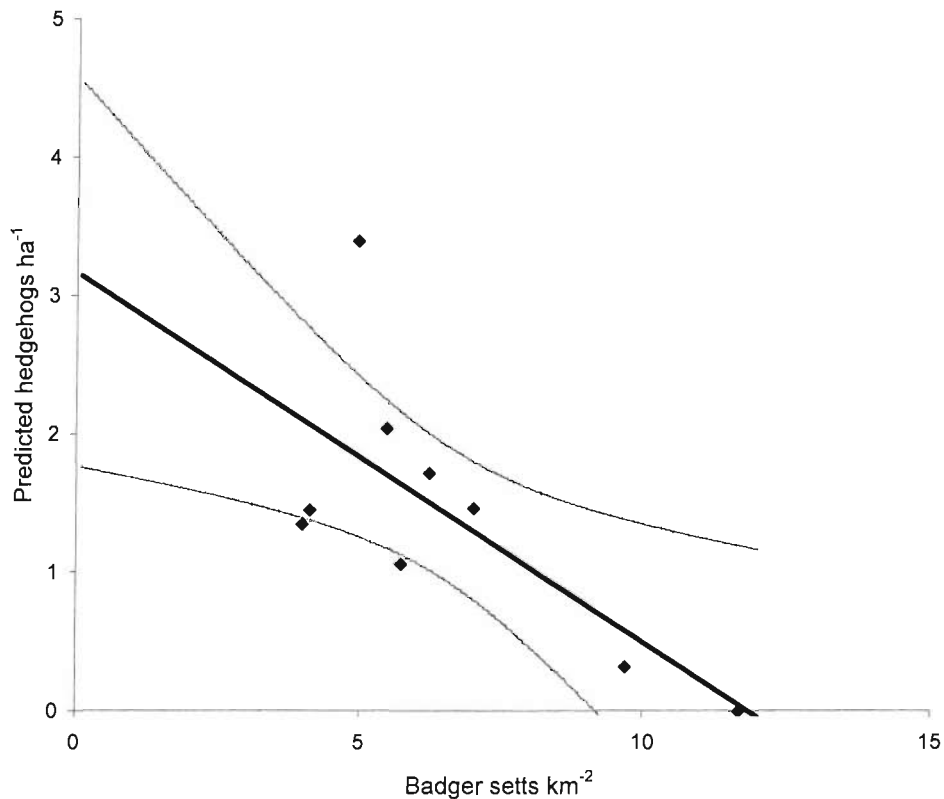
2.4 Discussion

Pastoral dominated agricultural habitats in southern England are productive and can support very high badger densities of up to 30-40 badgers km^{-2} (Macdonald & Newman 2002; Rogers *et al.* 1997). All the study sites supported badger main sett densities that were higher than the threshold for hedgehog occurrence predicted by Micol *et al.* (1994) of 0.23 main setts km^{-2}. Average main sett densities around both amenity grassland and pasture fields were equal to or higher than the upper 95% confidence limit of this predicted value (0.72 setts km^{-2}) (Table 2.1). Badger activity occurred in close proximity to both habitat types. For example, the average distance to nearest badger activity from pasture fields was 160.3 m ($\pm$ 15.5 m). In comparison, Micol *et al.* (1994) recorded the average distance to nearest badger activity to be 678.4 m from pasture fields where hedgehogs were absent and 1480.0 m from fields where they were active. The high levels of badger abundance and close proximity to badger activity in these study sites suggest that predation pressure was likely to be far greater than in the study areas of Micol *et al.* (1994).

Hedgehogs were at very low density in rural habitats (Fig. 2.3), being found in only 3.7% of pasture fields. This is less than 10% of the distribution recorded by Micol *et al.* (1994), where 41 hedgehogs were caught in 40% of 58 pasture fields and mean density was 0.29 hedgehogs ha^{-1}. No historical data on hedgehog populations in the current study sites exist and therefore it is impossible to directly determine if hedgehogs have declined in abundance or were always very scarce. However, habitat within the study sites is very similar in composition to the Oxfordshire study area where hedgehogs were relatively abundant (Micol *et al.* 1994). Field experiments (Doncaster 1992, 1994) have provided strong evidence that badgers can regulate the abundance and distribution of hedgehogs in localised areas of pastoral dominated agricultural habitat. In areas of high badger density, hedgehogs moved from pastoral grassland and used suburban habitats more frequently. Hedgehogs also suffered from higher mortality through predation in high badger density areas than in areas of the same habitat where badgers were less abundant. Average growth rates of hedgehogs in both high and low badger density areas were similar, suggesting food availability was not an important factor. The present study has revealed that in large areas in the Midlands and Southwest regions of England, hedgehogs exist at very low densities or are completely absent from pastoral habitats. This is therefore in agreement with the

prediction that hedgehogs would be absent in rural habitats supporting high badger numbers.

Hedgehogs were almost completely limited to suburban habitats, although they were slightly less abundant and were present at a lower proportion of sites than recorded by Micol *et al.* (1994). Amenity grassland has greater earthworm availability than pasture habitat and consequently is able to support hedgehogs at higher density (Doncaster 1994). It was thought that due to human disturbance badgers tend not to be as active in suburban habitats, which act as a refuge for hedgehogs from badger predation (Micol *et al.* 1994). Spatial refugia therefore appear to facilitate the coexistence of hedgehogs and badgers at the rural landscape scale. These results are in agreement with a number of previous studies of terrestrial vertebrates (e.g. Mills & Gorman 1997; Durant, 1998, 2000; Fedriani *et al.* 2000; Sergio *et al.* 2003) that have identified spatial refugia as a vital mechanism in alleviating the effects of IGP on prey populations.

However, both the probability of occurrence (Fig. 2.4) and hedgehog abundance (Fig. 2.5) in amenity grassland fields declined as regional badger sett density in surrounding areas increased. In areas of high badger sett density, the likelihood of hedgehogs occurring in these sites was predicted to decline towards zero. This was not expected as it was assumed that suburban habitats would be relatively free from the effects of predation. Badger activity was recorded in nine of 23 amenity grassland fields (compared to only one of 31 fields recorded by Micol *et al.* 1994), which suggests that they are more active in this habitat than was previously thought. Hedgehogs have been shown to demonstrate predator avoidance behaviour by avoiding localised areas tainted with badger odour (Ward *et al.* 1996; Ward *et al.* 1997). However, the presence of badger activity was not related to hedgehog occurrence, which indicates that hedgehogs do not necessarily avoid amenity grassland fields where badgers are active. Local sett density and distance to nearest badger activity, which were the best indicators of badger activity in both habitat types (Table 2.2), were also not related to hedgehog occurrence. This was also unexpected, as it seemed probable that the localised abundance of badgers around a site and the proximity of a site to badger activity would determine predation risk and therefore affect the occurrence of hedgehogs at a particular site. Some amenity grassland fields provide very abundant and accessible food resources (i.e. earthworms), which may be preferentially used by hedgehogs in spite of the presence of badgers. The highly

fragmented structure of suburban areas (e.g. gardens), surrounding or near to the amenity grassland fields, provide hedgehogs with more cover which may reduce the risk of predation in this habitat.

It was the index of badger density on the scale of hedgehog dispersal (i.e. 2 km) around amenity grassland fields that was associated with hedgehog occurrence and abundance, rather than local badger density or proximity to badger activity. A likely explanation for this relationship is the effect of high badger density and subsequent predation pressure on the ability of hedgehogs to move between patches of suburban habitats. Hedgehog populations in suburban habitats were spatially discrete and likely to constitute a metapopulation. Hedgehogs have been recorded to disperse up to distances of 3.8 km (Doncaster *et al.* 2001) and patches of suburban habitat were rarely farther apart than this in the study sites and therefore likely to be connected by dispersal. Mortality during dispersal can affect the dynamics of fragmented populations and metapopulations (Hanski & Gilpin 1991). Hedgehogs are vulnerable to predation by badgers whilst moving through areas of high badger density (Doncaster 1992). For example, Doncaster (1992) found badgers predated seven of 30 hedgehogs in a period of 10 weeks, after they were released into an area of pasture and woodland habitat supporting approximately 20 badgers km^{-2}. In addition, hedgehogs in rural habitats have been shown to both avoid areas with badger odour through the use of olfactory cues (Ward *et al.* 1997) and to move further and faster from areas where badgers are abundant (Doncaster 1992). Therefore, areas of high badger density could represent a barrier to movement into and from a site (Doncaster *et al.* 2001), which may explain the variations in the occupancy of suitable sites by hedgehogs recorded in the current study.

An experimental approach involving a manipulation of badger density would be required to further investigate and quantify the effect of IGP by badgers on hedgehog populations, in both suburban and rural habitats. The use of spatial refugia by prey species has been previously identified as a vital mechanism to facilitate the co-existence of intraguild predator and prey in terrestrial mammal systems. In the present study, patches of suburban habitat, generally avoided by the intraguild predator, allowed both species to co-exist across the landscape scale. However, the probability of occurrence and abundance of hedgehog populations in their spatial refugia decreased as badger density in surrounding areas increased. The results reported here provide further correlative evidence that IGP can be sufficiently strong

as to exclude intraguild prey from productive habitats but also that IGP may have a major impact on intraguild prey populations occupying spatial refugia. It is likely that the coexistence of badgers and hedgehogs in this landscape will depend on how spatial refugia are distributed with respect to each other and to the abundance of badger populations.

Chapter 3: Does intraguild predation by badgers regulate populations of hedgehogs? Evidence from a field experiment

3.1 Introduction

Knowledge of the extent to which predators determine the growth rates of their prey populations is fundamental to applied ecology as it can inform both the control of over abundant populations and the conservation of endangered species (Sinclair *et al.* 1998; Macdonald, Mace & Barretto 1999). It is also important in a wider context, as researchers strive to understand how populations are controlled and under which circumstances do top-down or bottom-up forces exert the stronger influence (Banks *et al.* 2004). Predation has been shown to affect prey populations in a range of ways, including regulation (through density dependence), limitation (density independence) or through exerting depensatory effects on prey (inverse density dependence) (Sinclair & Pech 1996). Predators have also been shown to generate indirect interactions in communities, such as trophic cascades (Paine 1980), whereby a predator reduces the abundance of its prey and this effect cascades down to the trophic level below so that the food resources of the prey increase in abundance.

Top predators, and mammalian carnivores in particular, are prone to extinction or depletion in numbers through habitat fragmentation and persecution (Crooks & Soule 1999). After predators are reduced in abundance, prey can escape the top-down influence of predation leading to outbreaks in prey populations, which are then controlled from the bottom-up by food limitation, i.e. alternative stable states (Sinclair, Olsen & Redhead 1990). Conversely, the introduction of invasive predators into ecosystems has caused the decline of a large number of indigenous mammal, bird and reptile prey species throughout the world (Sinclair *et al.* 1998; Courchamp *et al.* 1999) and has even induced strong shifts in plant productivity and community structure (Croll *et al.* 2005). Therefore the perturbation of predators or their introduction into communities can have far-reaching consequences for prey populations and community structure and as result a pressing need exists to better understand and predict the population dynamics of predation to inform wildlife management and conservation.

However, providing convincing evidence of the extent to which predation determines the abundance of prey populations is difficult due to the complexity of unravelling these effects from those of other extrinsic factors (e.g. stochastic environmental fluctuations, food availability, disease) and intrinsic factors (e.g. social effects) (Krebs 2003). A number of methodological approaches have been utilised to identify and quantify the processes by which populations are controlled (Sibly & Hone 2003). The 'mechanistic paradigm' proposed by Krebs (1995) is an approach that focuses directly on looking for relationships between population growth rate and ecological mechanisms of regulation, such as food availability, disease or predator abundance. It is argued that the mechanistic approach is more utilitarian and predictive than other approaches (e.g. 'density' or 'demographic' paradigms) as it can provide a better understanding of the ecological mechanisms behind population dynamics in the field (Krebs 1995). Furthermore, the mechanistic paradigm permits shorter manipulative experiments to test specific hypotheses regarding regulatory mechanisms, which provide the strongest evidence of the extent prey populations are limited or regulated by predation (Sinclair 1989). However, there are frequently a number of logistical, financial and ethical problems of carrying out manipulative experiments in mammalian populations (Crooks & Soule 1999) and as a consequence they are rarely undertaken (Sinclair 1989).

The opportunity to experimentally test the effects of predation on a mammalian prey population arose from a field trial, carried out by the UK Government Department for Environment, Food and Rural Affairs (DEFRA), which involved the removal of predators over large scales. The Randomised Badger Culling Trial (RBCT) is a replicated, controlled field experiment, carried out in southern and midlands England, to investigate the effect of culling Eurasian badgers (*Meles meles*) on the incidence of bovine TB (*Mycobacterium bovis*) in cattle (Krebs 1997). In agricultural habitats of this region of the UK, the badger is an effective predator of the Western European hedgehog (Doncaster 1992). Previous studies have used perturbation experiments to investigate factors that affected the abundance (Doncaster 1994) and distribution (Doncaster 1992) of hedgehog populations. Predation by badgers and predator avoidance were the main factors implicated in returning augmented populations to their original level (Doncaster 1994). Hedgehog populations in areas of high badger density were kept below levels they could achieve in other sites of similar habitat, through higher mortality from badger predation and

movement to safer habitats. This provided evidence that badger predation was regulating hedgehog populations. This fits with a general hypothesis that the growth rates of small mammal populations tend to be determined from top down processes, such as predation and disease, and are rarely food limited (Sinclair & Krebs 2003). However, although these prey perturbation experiments are able to identify the mechanisms of regulation they are not able to quantify the extent to which they are regulated below carrying capacity and the potential for alternative stable states in prey populations.

As well as being predator and prey, badgers and hedgehogs are also potential competitors for the same invertebrate food resources and are therefore involved in an ecological interaction known as intraguild predation (IGP) (Doncaster 1992). IGP is a ubiquitous phenomenon in many ecosystems (Arim & Marquet 2004) and is thought to be an important factor in shaping populations and communities (Polis, Myers & Holt 1989; Holt & Polis 1997). As intraguild (IG) predator and prey consume similar food types they tend to have similar foraging behaviours, which therefore can increase the rates of encounter between the two species and consequently the probability of predation for hedgehogs. In this interaction, the predator receives energetic gain from the act of predation as well as removing a potential competitor. In IGP, predators are thought to have strong effects on their IG prey populations as the former can be supported at high density through the shared food resource even as their IG prey declines in number (Polis *et al.* 1989). This is analogous to the effects of predation on a secondary prey species when the predator relies on a more persistent primary prey species (Pech, Sinclair & Newsome 1995). Thus, in habitats where both species co-occur IGP is likely to have a depensatory rather than regulatory effect on prey populations at low density and is capable of generating unstable dynamics in both predator and prey (Holt & Polis 1997). If the IG prey species is also the inferior competitor, then these effects of IGP are reinforced and the IG prey is more likely to be forced towards extinction (Polis *et al.* 1989).

The effects of IGP in areas of high badger density were predicted to be sufficiently strong to locally exclude hedgehogs from their preferred agricultural habitats (Micol *et al.* 1994). A survey of several rural regions of south-west and midlands England, where badgers were abundant, found that hedgehogs were largely absent from agricultural habitats and only persisted in suburban micro-habitats (Chapter 2). These micro-habitats provided abundant food resources and were

thought to offer a spatial refuge from predation and as a consequence supported hedgehogs at higher density than in rural habitats. However, both the probability of occurrence and the abundance of hedgehogs were negatively correlated with badger density. This suggested that badgers may also have a strong effect on the abundance and distribution of hedgehog populations in their spatial refugia.

In the present study we opportunistically used a large-scale predator removal experiment (the RBCT) to test whether badgers determine the population growth rate of hedgehogs in suburban habitats and whether high badger density prevented hedgehogs colonising agricultural habitats. Specifically, we set out to test the hypothesis that hedgehog populations in their spatial refugia would grow when badger abundance was reduced through culling, compared to controls. Further, we hypothesised that if the abundance of hedgehog populations is determined by predation, their population growth rates will be correlated with the relative abundance of badgers, and to hedgehog density if predation is regulatory.

3.2 Materials and Methods

3.2.1 Experimental design

The Randomised Badger Culling Trial (RBCT) comprised a replicated randomised block experimental design (Krebs 1997). Ten experimental blocks ('triplets') each consisted of three plots of 100 km^2 ('treatment areas') with each plot receiving one of the following treatments: (1) 'proactive' culling of all badgers; (2) localised 'reactive' culling following the identification of bovine TB in cattle; and (3) 'control' where no culling takes place. Proactive culling of badgers involved initial removal operations on all areas of land where permission had been given, which was followed up by annual removal operations in the same areas. As landowner participation was voluntary the DEFRA field teams were unable to access some regions of the proactive treatment areas to carry out badger culling. The area of 'landowner non-compliance' varied with triplet but was as high as 38.9% in the proactive treatment area of Triplet H. In some of the triplets there was substantial opposition to the RBCT, including activities such as protestors interfering with deployed badger traps, which in localised areas reduced the trapping efficiency of DEFRA field teams. Although culling was thought to substantially reduce the size of badger populations, these factors resulted in an unquantified number of badgers remaining in the proactive treatment areas during the trial.

Five triplets were surveyed for hedgehogs in the following regions of England: Forest of Dean (A); Wiltshire (E); Staffordshire and Derbyshire borders (G); Somerset and Devon borders (H) and Gloucestershire Cotswolds (I) (Fig. 3.1). Hedgehog abundance was sampled in 'fields' annually, between 2000 and 2004, by carrying out nocturnal spotlight surveys (see 3.2.2 Field Methods) of three amenity grassland and six pasture fields for each treatment area in each triplet. There were no amenity grassland fields available in triplet H. The five triplets were chosen from the ten RBCT areas on the basis of the timing of badger culling operations and logistical considerations. Triplets were delineated approximately one year before initial proactive culling took place, which allowed data collection on hedgehog abundance to be conducted before culling began. However, the type of treatment allocated to each treatment area was unknown to the researchers until after DEFRA carried out the culling operations. Therefore, before the initial removal operation, hedgehog surveys were carried out in all treatment areas, but only in 'proactive' and 'control' treatment

areas in subsequent years. The timing of badger removal operations varied between triplets. Initial badger removal operations were conducted in triplets E, G and H in 2000 and in A and I in 2002. The treatment areas mainly consisted of pasture dominated mixed farmland, interspersed with small villages, farm buildings and patches of woodland (see Chapter 2 for a more detailed description).

Fig. 3.1. Location of the five triplets
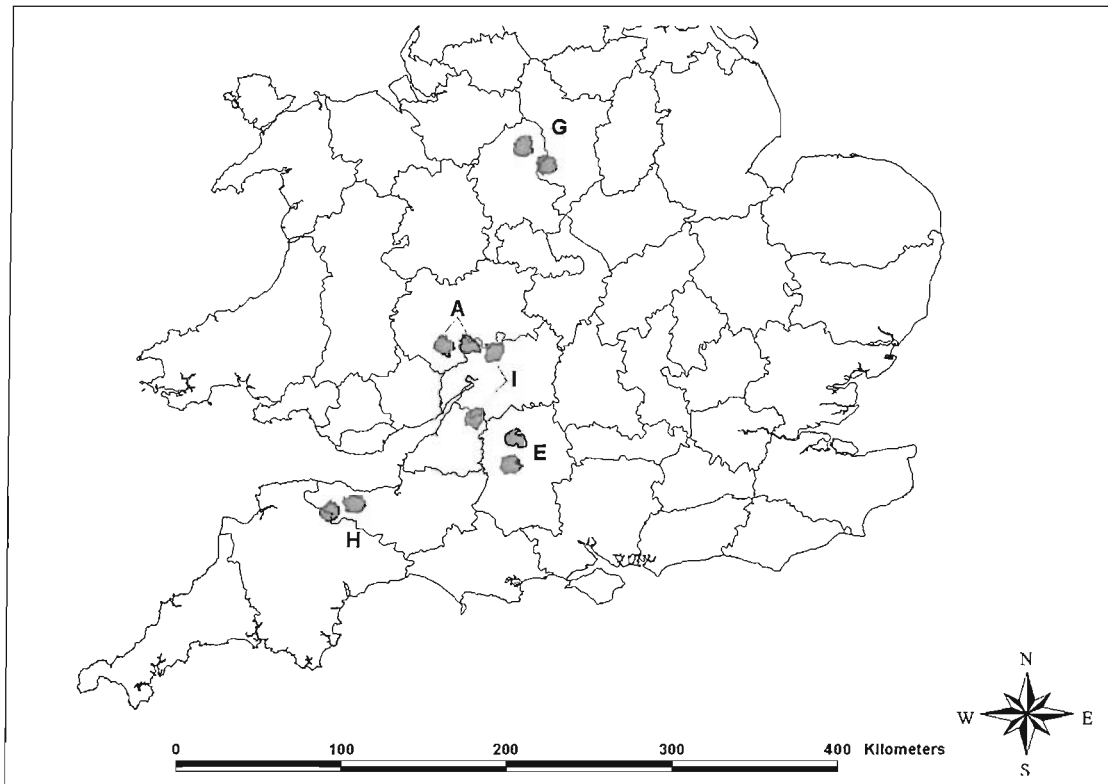
The present field experiment was based on a repeated measures nested analysis of variance design, which is shown in Fig.s 3.2a and 3.2b. The response of hedgehog abundance to badger culling was investigated by the interaction of fixed factors 'time', 'treatment' and 'triplet', with repeated measures random factor 'field' nested within each combination of triplet and treatment, as given by the following statistical model:

Hedgehog abundance = Time | Field (Triplet | Treatment)

The fixed factor treatment of badger abundance had two levels, high density (control) and reduced density (proactive) and time had five levels (0 indicates before

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the initial cull, and 1, 2, 3 and 4 years after culling began). For amenity and pastoral grassland habitat types, triplet had four levels (A, E, G and I) and five levels (A, E, G, H and I) respectively. The effect of interest was the interaction between treatment and time which reflects the response of hedgehogs to badger removal.

Fig. 3.2. Experimental design to investigate the response of hedgehog abundance to badger culling in (a) pasture and (b) amenity grassland. Only the left-most branch of each tree is shown for this balanced design

(a) In pasture
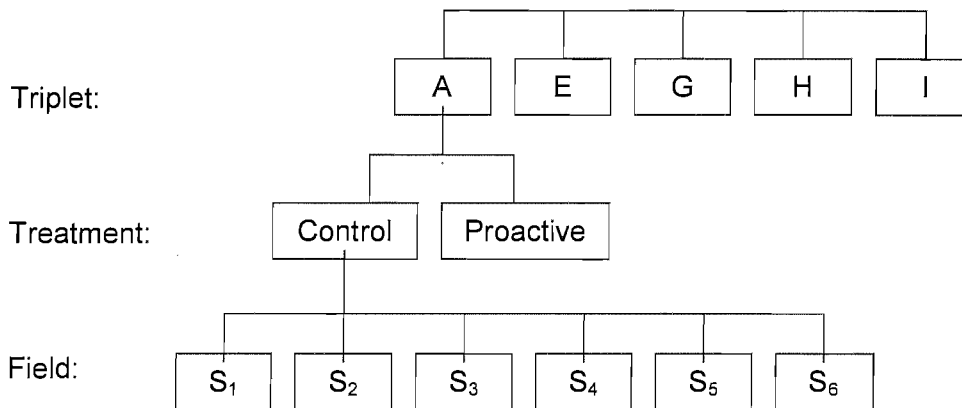
(b) In amenity grassland
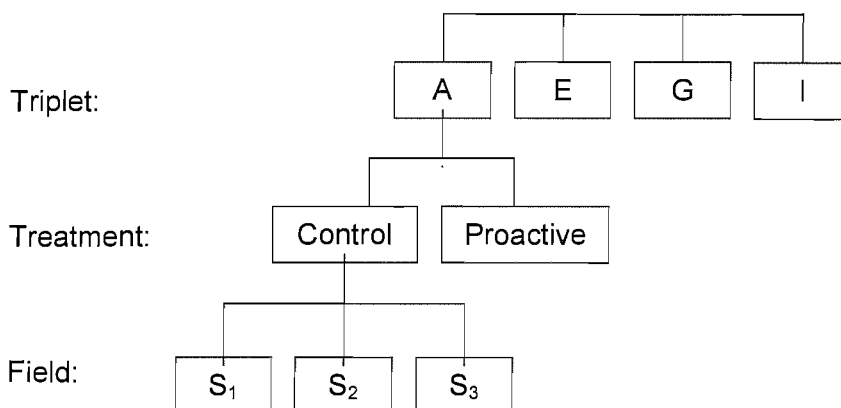
3.2.2 Field methods

Hedgehog surveys were carried out between July and September, when hedgehogs are most active in short grassland habitat types (Doncaster 1994). Within each treatment area, six pasture fields were selected randomly from all fields available within a 1 km radius of a village. Three amenity grassland fields were randomly selected from all

fields available that were in or on the edge of villages. All fields were a minimum of 500 m apart in an attempt to achieve independence in terms of hedgehog abundance. This distance is greater than the diameter (391 m) of an average male hedgehog's home range of 12 ha (Morris 1991), thus minimising the likelihood that an individual animal would be observed in more than one field.

Fields were surveyed over three separate visits between the hours of 23:00 and 03:00, using methods similar to those of Micol *et al* (1994). Each field was surveyed for hedgehogs by two fieldworkers using red-filtered spotlights (1.2 million candle power, Optronics, East Muskogee, Oklahoma, USA) and was systematically searched from the perimeter inwards. On average, it took 21.1 ± 0.7 (standard error) minutes to complete the survey of one field. No animal was seen but escaped capture and it was considered likely that only very few animals avoided detection. On average, the detection probability of hedgehogs was very unlikely to vary systematically with treatment, time or triplet.

All hedgehogs captured were examined to determine weight, sex and age class (adults > 1 year, juveniles < 1 year). Hedgehogs were uniquely marked by attaching eight heat-shrink plastic tubes (RS Components, Corby, Northants., UK) over individual spines using a portable soldering iron. By applying different coloured heat-shrink tubes in discrete groups in various positions on the dorsal coat of spines, individuals could be uniquely marked. Hedgehogs were released within 10 minutes of capture. The reliability of this marking system within a year was validated on 30 radiotagged individuals (Chapter 4 & 5). It was assumed that hedgehogs would lose some or all of their markers between years. The total number of hedgehogs caught at each site over the three repeat visits provided an estimate of relative abundance for each year and was divided by the area of the field to calculate relative density. During surveys of fields, the number of badgers observed was recorded and this encounter rate was used as an index of badger abundance. A daytime visit to each field was also made to record signs of badger activity, including droppings, setts, runs and other field signs (e.g. tracks and hair caught on fences), in order to establish whether badgers were active in a field.

3.2.3 Data analysis

A radiotracking study of hedgehogs carried out concurrently with the surveys in three of the study sites did not find any individual home range overlapping with more than one field (Chapters 4 & 5). Hence, fields were treated as independent sampling units. Due to a high frequency of zeros in the observed hedgehog density variable, modelling as a normal response was deemed invalid. Therefore the count of individual hedgehogs in each field over three visits for a given year was treated as the response variable (hedgehog abundance) which fitted a negative binomial distribution. An Iterative Reweighted Restricted Maximum Likelihood (IRREML) procedure with a negative binomial error structure and a logarithm link function was used to fit a generalised linear mixed model (GLMM) to the response variable. The area of amenity and pasture grassland fields was log-transformed and entered as an offset into the IRREML model, to take account of the variability in field size (i.e. survey effort). The main effects 'treatment', 'time' and 'triplet' and their interactions were entered as fixed terms into the model. 'Field' nested within triplet and treatment was entered as a random term. Testing the effect of the interaction of treatment and time allowed the effect of badger culling on hedgehog abundance to be investigated.

A residual maximum likelihood (REML) generalised linear mixed model, with a binomial distribution and a logit link function, was used to investigate the response of hedgehog occurrence to the manipulation in badger density. The model structure was identical to that outlined above. A REML linear mixed model was used to investigate the effect of the interaction of treatment and time on the weight of hedgehogs. Sex, age and subject (to take account of repeated measures on the same individual hedgehog) nested in field nested within triplet, were included as random terms.

The significance of explanatory terms in the REML and IRREML models were assessed by their Wald statistics, which were distributed as χ^2. The results of these models are presented in tables in the next section (3.3 Results) showing the terms added to the model along with their Wald statistic, degrees of freedom and level of significance under 'model terms'. Interactions between terms are depicted by '*'. The average effects and standard errors of significant interactions of treatment and time are shown under 'minimal model' in the results tables. The average effect of a term shows whether its relationship with the response variable is positive or negative after the lowest value (or the alphabetically first value if text) of that term is set to

zero (Russell *et al.* 2002). The effects of the interactions between treatment and time on hedgehog occurrence and abundance are shown graphically using the average effects of the interaction and the constant to calculate the predicted means for each year of the experiment in both treatment types.

The growth rate, i.e. the per capita growth rate or instantaneous growth rate (r), of hedgehog populations in amenity grassland fields was calculated as $\log_e [(N_{t+1})/N_t]$, where N_t is the density of hedgehogs (hedgehogs ha^{-1}) at time t, and N_{t+1} is the density of hedgehogs in the following year. A REML linear mixed model was used to investigate the relationship between growth rates of hedgehog populations in amenity grassland fields and hedgehog density (N_t) to test for density dependence. Treatment and log of density [$\ln(N_t)$] and their interaction were entered as fixed terms, whilst field nested in triplet was entered as random terms to take account of repeated sampling at sites. Fields that did not support hedgehogs during the experiment were excluded from the analysis.

Observations of badgers in individual fields and treatment areas were too sparse to use as a reliable index of badger abundance and therefore it was not possible to carry out a full analysis of the effects of badger numbers on population growth rates. Consequently, the number of badgers observed in fields (in both amenity and pasture grassland) was averaged across all treatment areas for both proactive and control treatments and this was used as an index of badger abundance for a given year. Hedgehog population growth rate was calculated (as given by the equation above) from annual changes in mean density of hedgehogs in fields (in both habitat types) in proactive and control treatments. Linear regression was used to investigate the relationship between hedgehog population growth rate and mean badger relative abundance. All analyses were conducted in GenStat 6.2 (Lawes Agricultural Trust, Rothamstead, UK).

3.3 Results

3.3.1 Response of hedgehog occurrence

There was a significant positive effect of the interaction of treatment and time on the occurrence of hedgehogs in amenity grassland fields (Table 3.1). After the initial badger cull, the proportion of amenity grassland fields that supported hedgehogs in proactive treatment areas increased by 17% over the duration of the field experiment, whereas in controls it declined by 33% (Fig. 3.3a). In the control areas, the proportion of fields with hedgehogs present in amenity grassland habitat varied widely during the experiment, declining from 60% before the cull to 15% in year 2 and recovering to 40% by year 4.

Table 3.1. REML model showing the treatment effects of badger culling on the occurrence of hedgehogs in amenity grassland fields. Field nested within triplet and treatment was entered as a random term

Model terms	Wald statistic χ^2	d.f.	*P* value
Between fields:			
Treatment	0.07	1	0.795
Triplet	0.38	3	0.944
Treatment*Triplet	0.92	3	0.820
Within fields (repeated measures):			
Time	6.70	4	0.152
Treatment*Time	10.01	4	0.040
Time*Triplet	16.33	7	0.022
Treatment*Time*Triplet	9.12	7	0.104

Minimal model		Average effect		SE
Constant		3.29		123.0
		Proactive	Control	
	0	0.00	0.00	
Treatment*Time	1	-4.46	0.00	43.02
	2	31.86	0.00	
	3	23.45	0.00	
	4	41.93	0.00	

There was also an effect of the interaction of time and triplet on hedgehog occurrence. In Triplets E and I there was an increase in hedgehog occurrence over time until year 3, whereas it remained relatively constant in Triplets A and G during this period.

Fig. 3.3. Change over time in the mean proportion of (a) amenity grassland and (b) pasture fields supporting hedgehogs in proactive (grey shading) compared to control areas (no shading)

(a) Amenity grassland
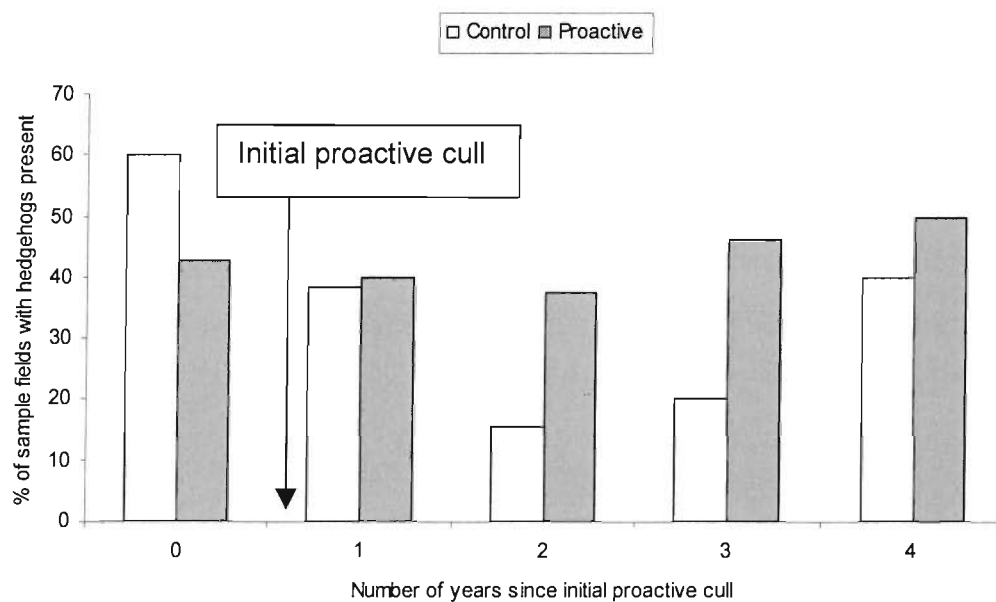
(b) Pasture grassland
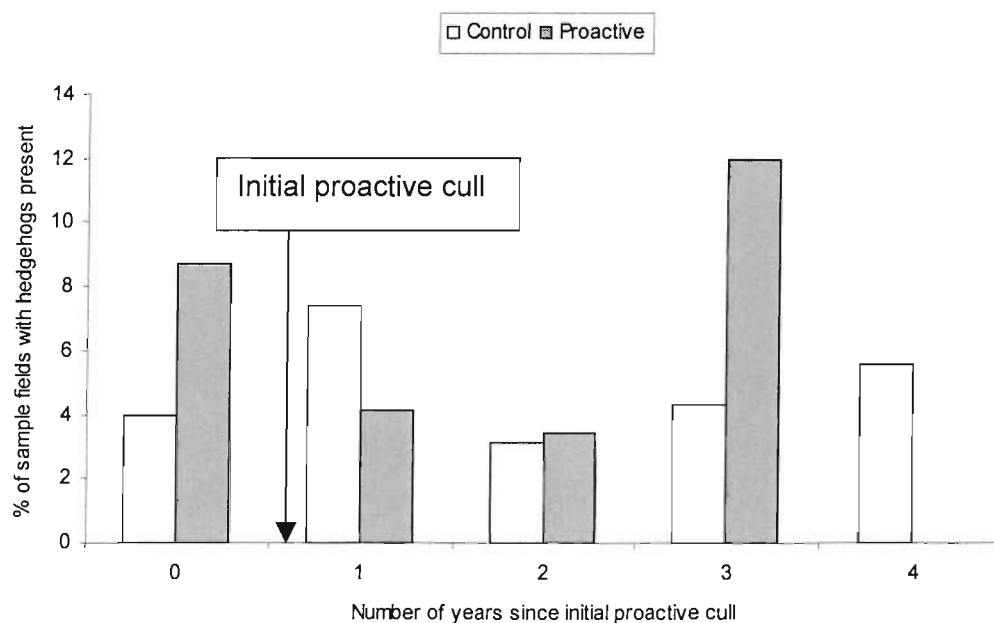
Hedgehogs were very scarce in pastoral grassland habitat in both proactive and control treatment areas throughout the study and were generally found in less than 10% of pasture fields (Fig. 3.3b). There were too few observations to carry out statistical analysis to test the effects of badger removal on the occurrence of hedgehogs in pasture fields. In the proactive treatment in year 3 there did appear to be a slight increase in the proportion of pasture fields supporting hedgehogs. This was due to hedgehogs being found in two pasture fields where they had not been found before. Both fields were at least 800m away from the nearest suburban habitat and this was the only time that hedgehogs were found in pasture fields so far from suburban areas during the study. In all other cases, pasture fields that supported hedgehogs were contiguous with, or very near, villages or large farms. In one of these two fields, the remains of a hedgehog were found which appeared to be the result of badger predation. After this slight increase in hedgehog occurrence, no hedgehogs were found in pasture habitat in the proactive treatment in year 4.

The effect of badger culling on hedgehog occurrence in amenity grassland fields is shown graphically in Fig. 3.4. The REML smoothed model predicted that on average hedgehog occurrence declined in the presence of badgers but remained relatively constant in proactive areas during the course of the experiment.

Fig. 3.4. REML model of the mean predicted response of the occurrence of hedgehogs in amenity grassland fields to badger culling in proactive compared to control areas. Bars are 95% confidence intervals
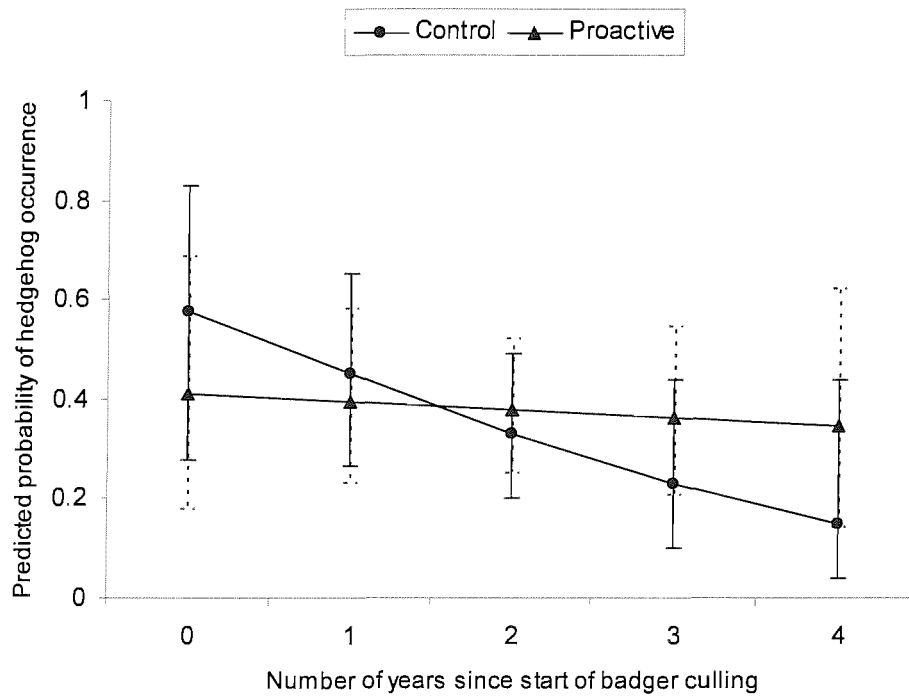
3.3.2 Response of hedgehog abundance

There was a significantly positive effect of the interaction of treatment and time on the number of hedgehogs in amenity grassland fields (Table 3.2). However, the increase in hedgehog numbers was not uniform over the duration of the experiment (Fig. 3.5a). Before the cull, the mean density of hedgehogs in amenity grassland was higher in proactive than in control areas (Fig. 3.5a). A number of fields in the proactive areas supported hedgehogs at high density which elevated the overall mean. Hedgehog density increased by 41% in proactive areas after the initial cull (i.e. in year 1) and then declined markedly in year 2 in both the proactive treatment as well as controls. In year 3, mean hedgehog density in proactive areas increased rapidly but remained relatively unchanged in the control treatment. By the end of the experiment (year 4) mean density was 2.03 hedgehogs ha^{-1} in proactive areas but only 0.41 hedgehogs ha^{-1} in controls. Table 3.3 gives the number of individual sightings of hedgehogs in the proactive and control treatment areas in each year of the field experiment.

There was no clear pattern of change of mean hedgehog density in pasture fields in response to the treatment (Fig. 3.5b). Due to the low number of fields supporting hedgehogs in pasture habitat, mean density tended to be very low but was highest throughout the duration of the field experiment in the proactive areas before the initial badger cull. This was due to one pasture field that supported a very high number of hedgehogs, which resulted in a relatively large overall mean. It was not possible to carry out any statistical analysis on these data due to the large number of zeros in the response variable.

Table 3.2. IRREML model showing the effects of badger culling on the number of hedgehogs in amenity grassland fields. Field nested within triplet and treatment was entered as a random term

Model terms	Wald statistic χ^2	d.f.	P value
Between fields:			
Treatment	0.02	1	0.886
Triplet	1.00	3	0.802
Treatment*Triplet	1.10	3	0.777
Within fields (repeated measures):			
Time	21.04	4	<0.001
Treatment*Time	14.84	4	0.005
Time*Triplet	5.95	7	0.545
Treatment*Time*Triplet	0.26	7	1.000

Minimal model		Average effect		SE
Constant		-1.59		57.95
		Proactive	Control	
	0	0.00	0.00	
	1	6.59	0.00	
Treatment*Time	2	7.36	0.00	63.16
	3	16.85	0.00	
	4	-7.05	0.00	

Table 3.3. Number of hedgehogs observed in control and proactive treatment areas in each year of the field experiment

Treatment	Year 0	Year 1	Year 2	Year 3	Year 4
Control	10	8	9	9	8
Proactive	15	19	9	17	20

Fig. 3.5. Response of mean ± SE hedgehog abundance to badger culling in (a) amenity grassland and (b) pasture grassland, in proactive (grey shading) compared control areas (no shading)

(a) Amenity grassland
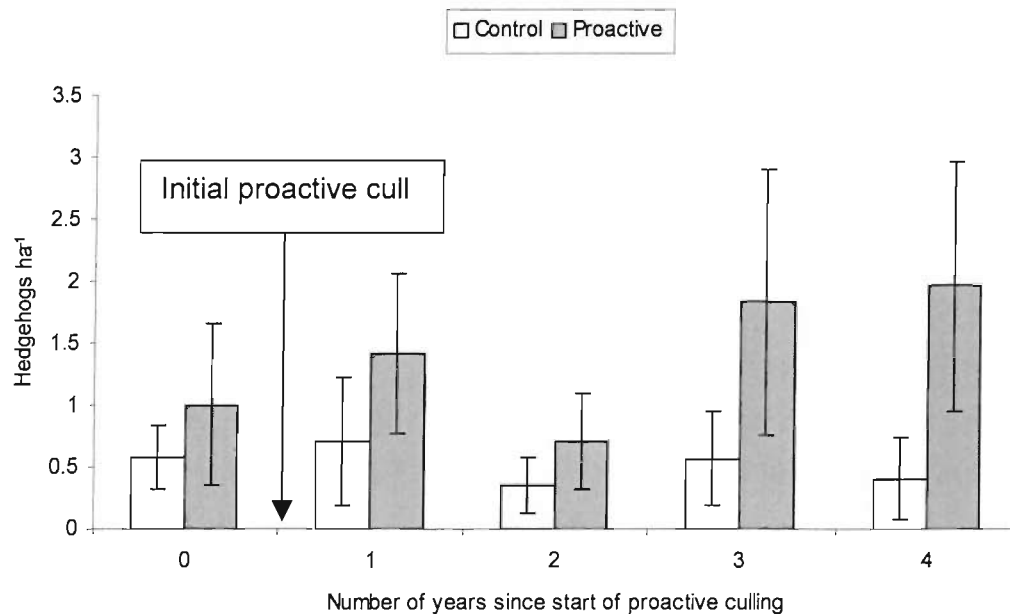
(b) Pasture grassland
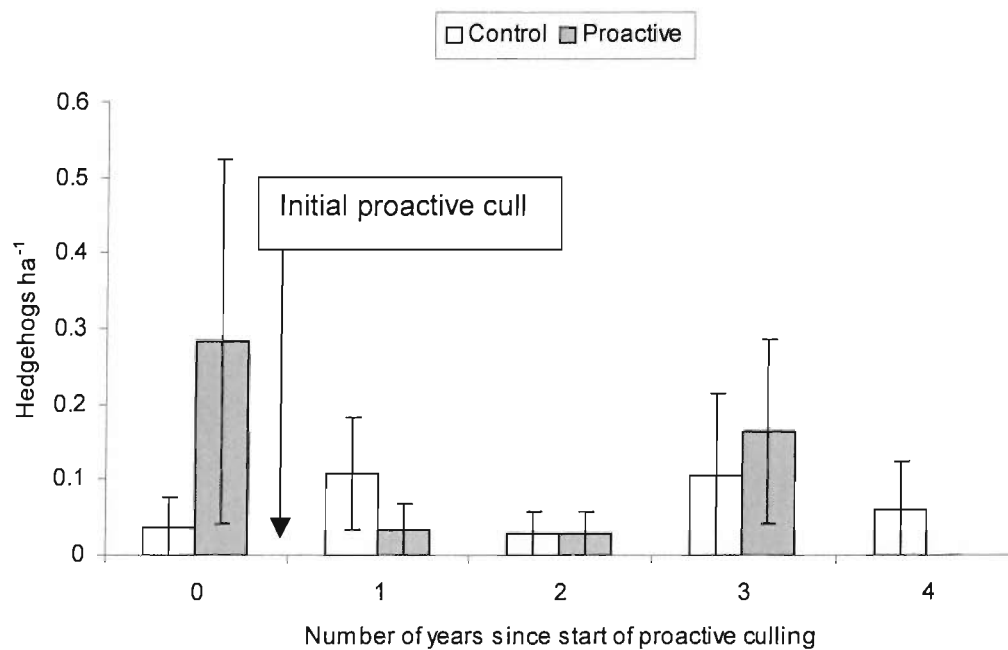
The effect of badger culling on hedgehog density in amenity grassland fields is shown graphically in Fig. 3.6. The IRREML smoothed model predicted that on average over

the duration of the experiment hedgehog density increased by approximately 100% in response to badger culling, whereas it decreased slightly in control areas (Fig. 3.6).

Fig. 3.6. IRREML model of the mean predicted response of hedgehog density to badger culling in proactive compared to control areas. Bars are 95% confidence intervals
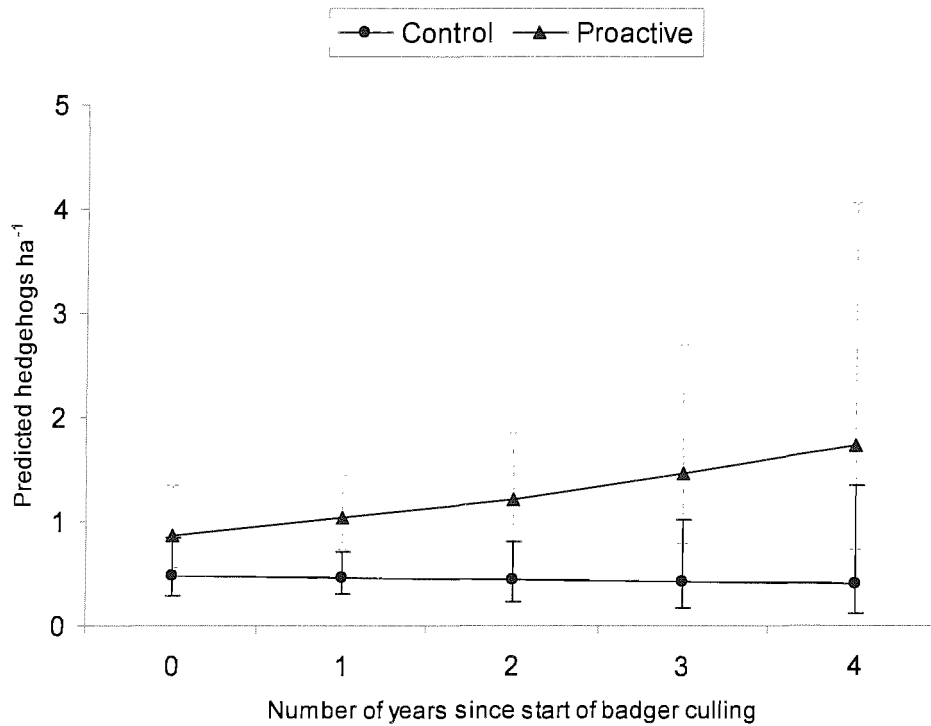
3.3.3 Response of hedgehog abundance by age and sex

The density of adult hedgehogs remained relatively constant in amenity grassland fields in the control treatment throughout the experiment (Fig. 3.7), whereas it varied more widely in proactive areas with an overall increase of 18%. However, there was no effect of the interaction of treatment and time on adult hedgehog abundance (Table 3.4a), although the P-value was very close to significance. The density of juvenile hedgehogs increased markedly in the proactive treatment with an overall increase of 556% between the start and end of the experiment (Fig. 3.7). Numbers of juvenile hedgehogs remained relatively low in the control treatment and juveniles were absent in years 2 and 4.

Table 3.4. IRREML model showing the effects of badger culling on the number of (a) adult and (b) juvenile hedgehogs in amenity grassland fields. Field nested within triplet and treatment was entered as a random term

(a) Number of adults

Model terms	Wald statistic χ^2	d.f.	P value
Between fields:			
Treatment	0.11	1	0.738
Triplet	0.79	3	0.853
Treatment*Triplet	1.09	3	0.780
Within fields (repeated measures):			
Time	14.15	4	0.007
Treatment*Time	9.04	4	0.060
Time*Triplet	6.31	7	0.504
Treatment*Time*Triplet	0.24	7	1.000

Minimal model		Average effect		SE
Constant		-1.53		55.44
		Proactive	Control	
	0	0.00	0.00	
Treatment*Time	1	7.07	0.00	60.20
	2	7.61	0.00	
	3	16.50	0.00	
	4	-7.32	0.00	

(b) Number of juveniles

Model terms	Wald statistic χ^2	d.f.	P value
Between fields:			
Treatment	0.13	1	0.724
Triplet	0.49	3	0.920
Treatment*Triplet	1.42	3	0.700
Within fields (repeated measures):			
Time	91.19	4	<0.001
Treatment*Time	0.90	4	0.925
Time*Triplet	2.07	7	0.956
Treatment*Time*Triplet	2.39	7	0.935

However, there was no effect of the interaction of treatment and time on juvenile hedgehog abundance (Table 3.4b). Examination of the raw data revealed that an increase in the number of juveniles at only two of three sites in the proactive treatment area of the Wiltshire triplet (E) was mainly responsible for the overall increase in mean juvenile density. Additionally, there were a large number of zero counts of juveniles during the survey which is likely to have made statistical analysis problematic. Therefore, given the large increase in mean juvenile density in Fig. 3.7, these results should be interpreted with caution.

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Fig. 3.7. Response of mean ± SE adult (no stripes) and juvenile (stripes) hedgehog abundance in amenity grassland fields to badger culling in proactive (shading) compared to control areas (no shading)
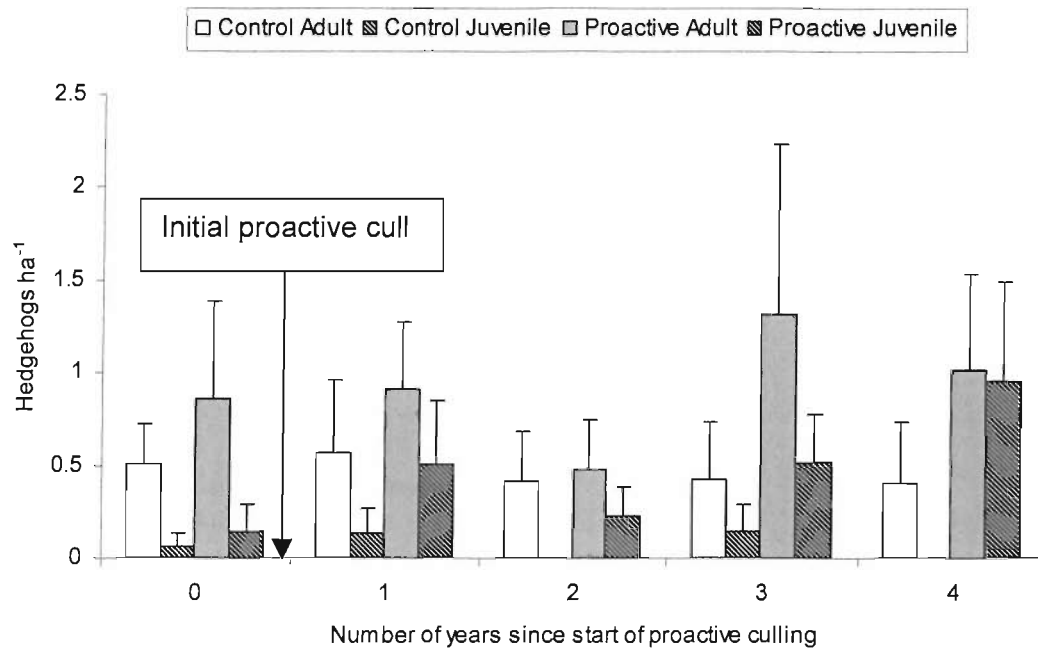
Although male hedgehog density increased in the proactive treatment after badger culling started and remained relatively constant in control areas (Fig. 3.8), there was no effect of the interaction of treatment and time (Table 3.5a). Male hedgehogs were more numerous in proactive areas before the cull than in controls and this ratio did not change markedly during the experiment. However, there was a significantly positive effect of the interaction of treatment and time on female hedgehog numbers (Table 3.5b). In the control treatment, female hedgehog abundance declined slightly whereas in proactive areas it increased by 106% (Fig 3.8).

Table 3.5. IRREML model showing the effects of badger culling on the number of (a) male and (b) female hedgehogs in amenity grassland fields. Field nested within triplet and treatment was entered as a random term

(a) Number of males

| Model terms	Wald statistic χ^2	d.f.	P value
Between fields:			
Treatment	0.03	1	0.864
Triplet	0.68	3	0.877
Treatment*Triplet	0.64	3	0.886
Within fields (repeated measures):			
Time	29.08	4	<0.001
Treatment*Time	0.38	4	0.984
Time*Triplet	0.76	7	0.998
Treatment*Time*Triplet	0.79	7	0.998

(b) Number of females

Model terms	Wald statistic χ^2	d.f.	P value
Between fields:			
Treatment	0.10	1	0.750
Triplet	0.89	3	0.828
Treatment*Triplet	0.79	3	0.852
Within fields (repeated measures):			
Time	10.97	4	0.027
Treatment*Time	10.55	4	0.032
Time*Triplet	8.96	7	0.256
Treatment*Time*Triplet	0.32	7	1.000

Minimal model		Average effect		SE
Constant		-1.84		47.96
		Proactive	Control	
	0	0.00	0.00	
Treatment*Time	1	7.57	0.00	50.76
	2	7.98	0.00	
	3	16.40	0.00	
	4	-6.63	0.00	

Fig. 3.8. Response of mean ± SE male (no stripes) and female (stripes) hedgehog abundance in amenity grassland fields to badger culling in proactive (shading) compared to control areas (no shading)
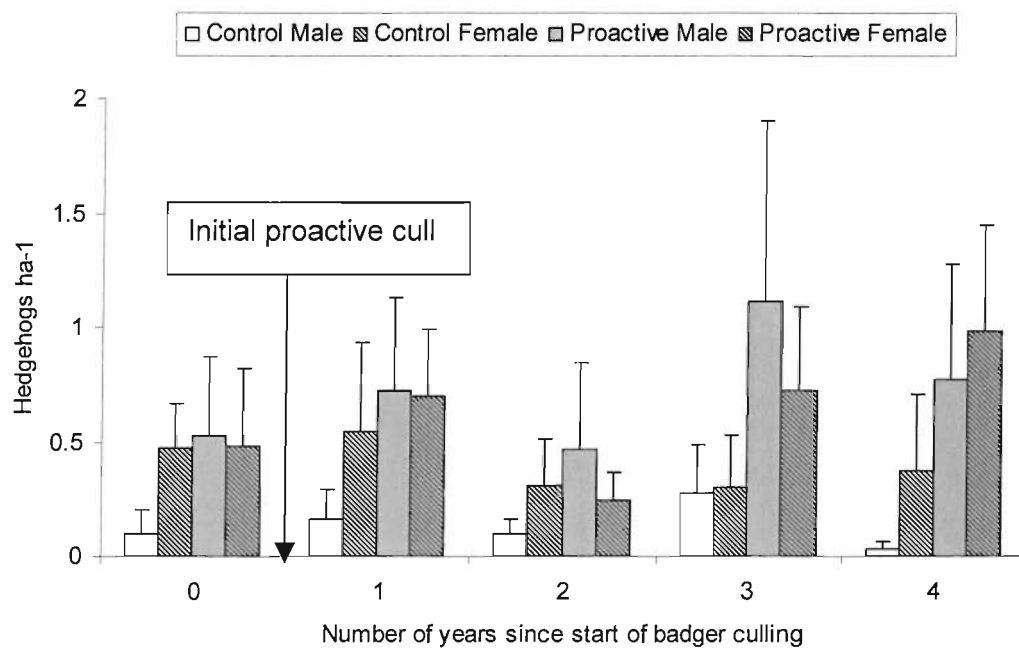
3.3.4 Relationship between the relative abundance of badgers and hedgehog population growth rate

The relative abundance of badgers varied widely throughout the study, including in the proactive treatment after badger culling started. This allowed an investigation of the relationship between an index of badger abundance at time $t+1$, as a measure of predation pressure, and the growth rate of hedgehog populations (Fig. 3.9). Growth rate was calculated from changes in mean hedgehog density in the proactive and control treatments, as opposed to mean changes in density in individual fields, so therefore each of the data points in Fig. 3.9 are calculated from repeated measures on hedgehogs. Growth rates of hedgehog populations (y) declined linearly with the index of badger abundance (x, equation: $y = 0.64 - 3.30x$, $F_{1,6} = 6.42$, $P = 0.044$) (Fig. 3.9). The index of badger abundance explained 43.7% of the variation in hedgehog population growth rate.

Fig. 3.9. The relationship between annual population growth rate, r, of hedgehogs and an index of badger abundance (number of badgers per field) at time $t+1$. Open circles represent the control treatment and closed circles the proactive treatment. Data points are labelled individually with treatment (C or P) and year (e.g. P3 is the mean growth rate in proactive treatment areas in year 3)
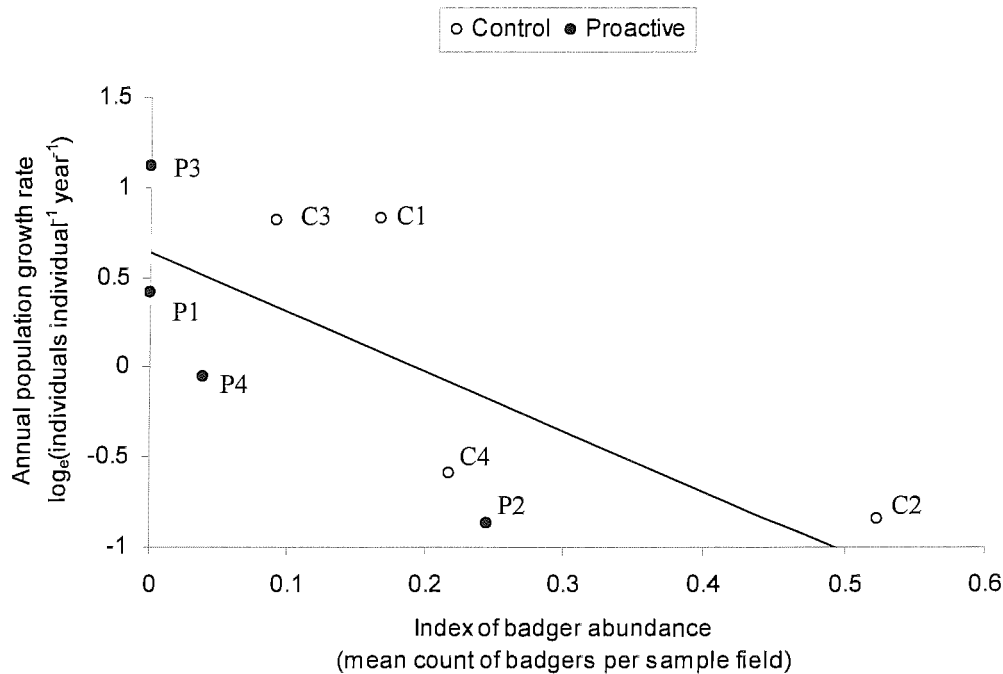
Badgers appeared to be generally less abundant in the proactive treatment than in the control treatment, except in year 2. In this year there was a notable increase in mean badger relative abundance in both the proactive and control treatment. This corresponded with a marked decrease in mean hedgehog density observed in the proactive treatment (Fig. 3.6). There was no relationship between the index of badger abundance at time t and the growth rate of hedgehog populations. This suggests that the effect of badger predation on hedgehog population growth rate occurred without a time-lag.

3.3.5 Density dependent population growth rate

The per capita growth rates of hedgehog populations in amenity grassland fields were related to the log of hedgehog density [$\ln(N_t)$] (Table 3.6). The average effect of log mean density was negative, which provides evidence of density dependence in the rate of population growth. There was no effect of treatment or the interaction of treatment and log mean density on growth rates. A significant interaction would have suggested that density dependent growth rates differed in proactive and control treatments and therefore by the magnitude of predation.

Table 3.6. REML linear mixed model showing the effects of the log of hedgehog density [$\ln(N_t)$] and treatment on the per capita growth rates of hedgehog populations in amenity grassland fields. Field nested within triplet and treatment was entered as a random term

Model terms	Wald statistic χ^2	d.f.	*P* value
Treatment	1.91	1	0.167
[$\ln(N_t)$]	6.77	1	0.009
Treatment*[$\ln(N_t)$]	0.63	1	0.427
Minimal model	**Average effect**	**SE**	
Constant	-5.20	1.56	
[$\ln(N_t)$]	-0.99	0.36	

However, visual inspection of the population growth rates (calculated from changes in mean density in the proactive and control treatments rather than mean changes in density in individual fields) in Fig. 3.10 suggests the possibility of an interaction between treatment and log mean density and the existence of two stable states of density. In the control treatment, where badger abundance was not manipulated, hedgehog population growth rate appeared to decline sharply as log mean density increased. This relationship suggested that population growth rate was stable (i.e. zero) at a density of approximately [$\ln(Nt)$] = -0.7 (or 0.5 hedgehogs ha^{-1} when back-transformed). The slope of the linear regression line was -1.54, which may suggest over-compensating density dependence.

In the proactive treatment in year 2, the observed population growth rate was very low for the given log of mean density. This low growth rate was likely due to

the unexpectedly high badger activity in the proactive treatment in year 2, despite previous badger culling (Fig. 3.9), and was therefore omitted from the analysis. With this data point excluded, the regression line predicted that the population in the proactive treatment reached equilibrium at a higher density of approximately [ln(Nt)] = +0.6 (or 1.8 hedgehogs ha^{-1} when back-transformed). The slope of the linear regression line was -0.88, which suggests slight under-compensating density dependence. The strongest difference in the density dependent growth rates attributable to badgers is their reduction in hedgehog carrying capacity, represented by the displacement of the control line below the proactive line. The equilibrium population size in proactive treatment areas was approximately three times the density of the equilibrium population size in control areas. However, more replicates are required to confirm the effect of the interaction of treatment and density on population growth rates.

Fig. 3.10. Annual population growth rate, r, of hedgehogs in amenity grassland fields in relation to the log of mean population density [ln(N_t)] in control areas (open circles) and proactive areas (closed circles). The closed triangle indicates the population growth rate in proactive areas in year 2
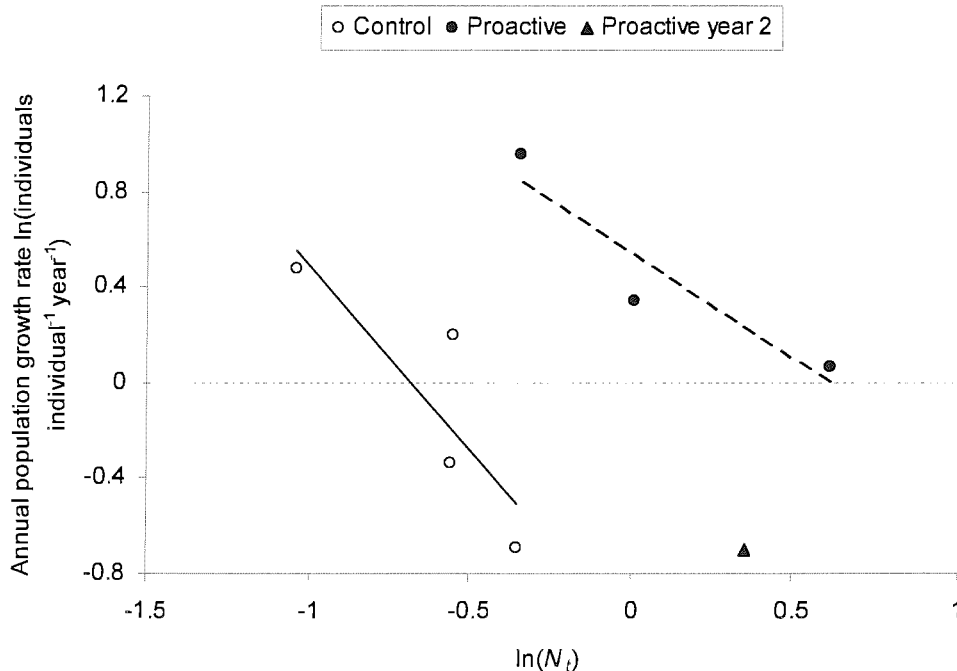
3.3.6 Response of hedgehog weight

There was no effect of the interaction of treatment and time on hedgehog weight, taking into account the effects of sex and age and repeated sampling of individual hedgehogs (Table 3.7). Therefore there was no evidence that mean weight of hedgehogs changed in response to badger culling.

Table 3.7. REML linear mixed model showing the effects of badger culling on the weight of hedgehogs captured in amenity grassland. Sex, age and subject, nested in field nested within triplet, were entered as random terms

Model terms	Wald statistic χ^2	d.f.	P value
Treatment	0.03	1	0.868
Time	8.42	4	0.077
Treatment*Time	2.91	4	0.574

3.4 Discussion

The primary aim of this experiment was to test the hypothesis that hedgehog abundance in their spatial refugia would increase when badger numbers were reduced through culling. Over the five years of the study, mean hedgehog density in proactive areas increased by roughly 100% after badger culling began, whereas there was little overall change in control areas. A significant effect of the interaction of treatment and time on hedgehog numbers allowed the rejection of the null hypothesis and acceptance of the alternative hypothesis that badgers limit the size of hedgehog populations. The response of hedgehog numbers to badger culling varied by sex, with female hedgehogs increasing in abundance whereas males remained unchanged. Females used open amenity grassland habitats more frequently than males (Chapter 4), and also foraged further from cover (Chapter 5), and therefore may be more prone to predation and thus have higher rates of mortality than males.

Juveniles showed no significant response to culling, despite mean juvenile density increasing by nearly 600% in proactive treatment areas after the cull. This average increase for the proactive treatment was largely due to increases at two of three sites in the proactive treatment area of the Wiltshire triplet (E). Given that juvenile numbers remained generally low in control areas, and they were entirely absent in two years, further research is warranted to investigate the possibility that juvenile mortality through badger predation is an important mechanism in hedgehog population dynamics.

There was evidence that badger culling had a positive effect on the occurrence (i.e. presence) of hedgehogs in amenity grassland sites. The REML model predicted that the occurrence of hedgehogs remained stable in areas where badgers were culled but declined in control areas.

These data provide evidence that badgers limit hedgehog abundance but they do not reveal whether they are an important mechanism in determining population growth rate. In order to do this, the mechanistic paradigm advocates seeking predictive relationships between ecological mechanisms and population growth rates (Krebs 2003). Consequently, we hypothesised that if badger predation is an important factor of hedgehog population control, the relative abundance of badgers, as a measure of predation pressure, would correlate with hedgehog population growth rate. The index of badger abundance at time $t+1$ was negatively related with growth rate,

indicative of top-down control of hedgehog populations by badger predation. There was no relationship between these variables at time t however, which suggested that changes in hedgehog abundance were driven by badger predation without a time-lag. This quick response has been seen in other examples of predator-prey dynamics (e.g. barn owls *Tyto alba* and field voles *Microtus agrestis*; Hone & Sibly 2002). This mechanistic relationship predicted that above a predator index of roughly 0.2 badgers per field, the growth rate of hedgehog populations would fall below zero and abundance would decline.

Culling operations reduced badger relative abundance levels in the proactive treatment compared to the control, except in year 2 when there was a notable increase in badger numbers. This increase coincided with a decrease in hedgehog density in proactive areas. In effect therefore the treatment of badger culling was partially reversed. In years 3 and 4 follow-up culls by DEFRA appeared to reduce badger abundance levels in the proactive treatment and a corresponding increase in hedgehog abundance was observed. This result should however be interpreted with caution as the relationship was investigated using population growth rate calculated from annual changes in mean hedgehog density and a mean index of badger abundance across treatments during the experiment rather than using data from individual fields. Thus the analysis did not account for repeated sampling of hedgehogs and badgers in the same sites. Nevertheless, when considered in the context of previous studies (e.g. Doncaster 1992, 1994), which found badgers regulated hedgehog populations in rural areas, these data provide evidence to support the hypothesis that badgers determine hedgehog population growth rates in suburban habitats.

In addition to being their predators, badgers may also compete with hedgehogs for similar invertebrate food resources and therefore a decrease of badger abundance may have lead to increased food availability for hedgehogs in proactive areas. This in turn may have lead to a higher reproductive output of hedgehogs, resulting in population growth. However, there was no increase in the mean weight of hedgehogs in proactive areas over the duration of the experiment, taking into account the effects of sex and age (Table 3.7). Thus, higher food availability is a less plausible explanation than increased survival of hedgehogs, due to reduced predation rates, of the observed rise in hedgehog numbers in proactive areas.

This experiment utilised a mechanistic approach to investigate factors that determine the abundance of hedgehogs and it also provided evidence of density

dependence in their population growth rates (i.e. growth rate was negatively related to log density). When the relationship between log mean density and the rate of hedgehog population growth was investigated separately in control and proactive treatments, there was some suggestion that density dependent growth rates varied according to the magnitude of predation. In control areas, where badgers were unmanipulated, population growth rate appeared to decline rapidly with increasing hedgehog density. The steepness of this slope suggests over-compensating density dependence (i.e. the population is liable to overshoot the equilibrium). In areas where badgers were culled, growth rate appeared to decline less steeply which suggests under-compensating density dependence. These data indicate the existence of two stable states of abundance according to the magnitude of predation. In the control treatment, a lower equilibrium population size (c. 0.5 hedgehogs ha^{-1}) indicated regulation by predators, whereas in areas where badgers were culled, an equilibrium population size more than three times the density was observed (c. 1.8 hedgehogs ha^{-1}). These density dependent relationships fit with type III predation where predators regulate low density prey populations occupying habitat refugia (Sinclair & Krebs 2003). They are similar to the density dependent population growth rates of three species of marsupial in habitat refuges that were observed before and after the abundance of their predators was manipulated (Sinclair et al. 1998). The present experiment therefore has provided evidence that badger predation regulated hedgehog populations in a density dependent rather than depensatory way, contrary to our predictions. In other words, at low hedgehog densities, the per capita predation rate is low but increases as hedgehog density increases, thus regulating the population.

An additional aim of this study was to investigate whether hedgehogs would colonise preferred agricultural habitats they were thought to once occupy, after badger abundance was reduced. Throughout the duration of the study, very few pasture fields were found to support hedgehog populations and there was no evidence that hedgehogs began to colonise these habitats in response to badger culling. However, badgers were still active in agricultural habitats of proactive areas after culling had taken place, as was observed in the index of badger abundance. Furthermore, daytime surveys of badger sign revealed that on average badgers were active in 26% of fields in proactive areas after culling, compared to 36% in control areas. In the Wiltshire proactive area, three years after initial culling activities began, the remains of a hedgehog were found in a pasture field that were indicative of badger predation.

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Landowner participation in the RBCT was on a voluntary basis and consequently there were some regions of the proactive treatment areas that did not receive any culling. As the movements of hedgehogs are likely to be influenced by olfactory cues (Ward, Macdonald & Doncaster 1996, Ward et al. 1997), the presence of residual badger activity may have deterred them from colonising agricultural habitats.

Badgers achieve high population densities in their preferred agricultural habitats, particularly in southern and midlands England (Macdonald & Newman 2002; Rogers et al. 1997). Theory predicts that predators which rely on a persistent primary prey species exert a depensatory (inversely density dependent) effect on the secondary prey population (Sinclair 1989). As one of the factors that determines badger population density is the availability of their primary prey species (i.e. invertebrates), badgers at high density in agricultural habitats are likely to have depensatory effects on hedgehog populations occurring at a range of densities. Badgers are therefore capable of driving hedgehogs to local extinction in these habitats, which are likely to only persist in isolated pockets where badgers occur at a very low density (Micol et al. 1994).

The results of this experiment support the general hypothesis that small mammals tend to be controlled from the top-down and rarely is their population growth limited by food supplies (Sinclair & Krebs 2003). The study has provided evidence that in suburban micro-habitats, in rural regions of southern and midlands England, badger predation determined the rate of population growth of hedgehogs and regulated their abundance. It also demonstrated the utility of a manipulative experiment, as part of the mechanistic approach to population dynamics, for identifying factors that determine population growth rate. Knowledge of the relationship between hedgehog population growth rate and the index of badger abundance could inform the management of hedgehog populations. If hedgehogs were of management concern, badger abundance could be manipulated (e.g. through habitat management) which would lead to a predictable increase or decrease in hedgehog density. Furthermore, knowledge of this relationship provides a tool with which to predict the future dynamics of hedgehog populations according to natural changes in badger density. However, ideally more research is required to investigate the potential existence of alternative stable states in hedgehog populations where their density sufficiently increases to permanently escape predator regulation. In order to

do this the treatment used in this experiment should be reversed and the response of hedgehog populations monitored as badgers are allowed to recolonise proactive areas.

Chapter 4: Field test of the effects of predation risk on habitat selection by foraging hedgehogs

4.1 Introduction

The risk of predation is thought to strongly influence a range of behavioural traits in prey (Lima & Dill 1990). For example, when selecting habitats for foraging, animals are often required to trade-off the availability of food resources against exposure to predation risk (e.g. Sih, 1980; Gilliam & Fraser 1987; Abrahams & Dill 1989; Lima & Dill 1990; Hugie & Dill 1994). The ability to make these behavioural decisions is particularly important when the habitats with high food availability are also the riskiest (Heithaus & Dill 2002). In taxa in which animals tend to be mobile and capable of relatively complex behaviours, the indirect non-lethal effects of predation, such as predator avoidance by prey, may be more important in determining habitat selection than direct mortality (Brown, Laundre & Gurung 1999). Therefore the perceived risk of predation for prey in certain habitats may be high even when actual mortality from predation is low (Lima & Dill 1990). Animals have evolved a number of behaviours to reduce the risk of predation during foraging. Firstly, they may spend less time in risky habitats (Lima & Dill 1990) or avoid them entirely and use spatial refuges from predation (Jeffries & Lawton 1984). Animals often have to accept lower energetic returns in order to forage in safer habitats, as the latter are frequently the poorest in terms of their foraging profitability (Lima & Dill 1990). Secondly, animals in risky habitats may adopt different behaviours to minimise the risk of mortality, for example by forming groups to dilute predation risk (Heithaus & Dill 2002) or by increasing vigilance (e.g. Cassini 1991). Such strategies may have an energetic cost for prey through increased intraspecific competition for food or the loss of foraging opportunities (Banks 2001).

In systems with intraguild predation (IGP), prey species compete with their predators for a shared food resource (Polis, Myers & Holt 1989). Consequently, both species tend to have similar foraging behaviours and habitat preferences, which increases the potential for encounters between predator and prey. Furthermore, in productive habitats, predators can achieve high densities by exploiting abundant shared food resources, and thus exert strong predation pressure on prey species even as prey abundance declines (Holt & Polis 1997). Therefore, in IGP systems, the most

profitable foraging habitats for prey species are frequently the most dangerous, which makes habitat selection a key behavioural decision for intraguild (IG) prey (Heithaus 2001). A number of descriptive studies of habitat selection by mammals have shown that IG prey will select habitats with lower availability of food resources in order to avoid their IG predators (e.g. gray foxes and coyotes, Fedriani *et al.* 2000; wild dogs and lions, Mills & Gorman 1997). The importance of the selection of less risky habitats (i.e. spatial refugia) to the persistence of IG prey populations has been predicted theoretically (Heithaus 2001) and demonstrated empirically (e.g. Durant 1998, 2000; Sergio, Marchesi & Pedrini 2003). Habitat selection has been identified as one mechanism that may partly explain why IGP is so ubiquitous in nature despite theory predicting that it should lead to the exclusion of IG prey (Holt & Polis 1997). However, this subject has received little attention from behavioural ecologists (Heithaus 2001).

In rural areas of the UK, the risk of predation by its intraguild predator is thought to be the most important factor that influences habitat selection by the Western European hedgehog (*Erinaceus europaeus*) (Doncaster 1992). Although the hedgehog is equipped with a substantial morphological defence against predation in the form of its dorsal coat of spines, the Eurasian badger (*Meles meles*) is strong and dextrous enough to overcome this. Both species feed on similar invertebrate prey items, particularly earthworms (*Lumbricus terrestris*), and have similar solitary and nocturnal foraging behaviours (Reeve 1994; Neal & Cheeseman 1996). In areas of low badger density (approximately 5 badgers km^{-2}) hedgehogs and badgers frequently forage in pastoral grasslands, where invertebrates are abundant and easily accessible, and have even been observed foraging for earthworms simultaneously on the same fields (Doncaster 1993). However, hedgehogs have been demonstrated to respond both behaviourally and physiologically to badger odour and avoid areas tainted with badger faeces (Ward *et al.* 1996; 1997). Badgers have a highly developed olfactory communication system and use specialised scent glands to mark territories and regularly use latrines (Neal & Cheeseman 1996). Habitats used intensively by badgers are well scent marked and this is likely to elicit a strong predator avoidance response from hedgehogs.

There is evidence from surveys of hedgehog populations that in pastoral grassland habitats where badgers are at low density, hedgehog distribution reflects a trade-off between food availability and safety (Micol, Doncaster & McKinlay 1994).

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In an area of high badger abundance (approximately 20 badgers km^{-2}), translocated hedgehogs showed strong selection for suburban micro-habitats, which badgers tended to avoid due to human disturbance (Doncaster 1992). Hedgehogs also travelled large distances to suburban areas away from pastoral and woodland habitats where badgers were most active. Habitats, such as gardens and amenity grassland, therefore act as spatial refugia for hedgehogs from the effects of predation in areas of high predation risk. These habitats also have a high availability of food resources and can therefore support hedgehogs at high densities (Micol *et al.* 1994). In rural regions that support abundant badger populations, surveys of hedgehogs have shown that their distribution is almost exclusively restricted to suburban areas (Chapter 2). This is consistent with theoretical predictions, that if one habitat has both a higher foraging profitability and is safer then all IG prey will select it (Heithaus 2001).

Few studies have investigated the effects of predation on prey habitat selection by excluding predators under natural conditions (Banks 2001). The opportunity arose to use an experimental manipulation of badger density to test the hypothesis that predation risk affects habitat selection by hedgehogs. Badgers were culled as part of a large-scale controlled field experiment (the Randomised Badger Culling Trial, RBCT) carried out by the UK Department for Environment, Food and Rural Affairs (DEFRA) to test the impact of badger culling on the incidence of bovine TB (*Mycobacterium bovis*) in cattle (Krebs 1997). In the present study, we estimated habitat selection by foraging hedgehogs in badger culling and control areas of the RBCT and tested whether it changed in response to a reduction of badger abundance. We hypothesised that if habitat use by hedgehogs is determined by the risk of predation by badgers, hedgehogs would use suburban habitats less and increase their use of rural habitats in culling areas compared to controls.

4.2 Materials and Methods

4.2.1 Experimental design

Fieldwork was conducted in the Cotswolds triplet of the Randomised Badger Culling Trial (RBCT) (Fig. 4.1) during 2002 and 2003. The triplet consisted of three plots of 100 km^2 ('treatment areas') and each plot received one of the following treatments: (1) 'proactive' culling of all badgers (I2); (2) localised 'reactive' culling following the identification of bovine TB in cattle (I1); and (3) 'control' where no culling takes place (I3) (Independent Scientific Group 1998). See Chapter 1.5 for more information on the RBCT. Proactive badger culling was carried out by DEFRA in September 2002. As landowner participation was voluntary the DEFRA field teams were unable to access some regions of I2 to carry out badger culling and this resulted in an unquantified number of badgers remaining in the proactive treatment area in 2003.

Fig. 4.1. Map of the three treatment areas in the Cotswolds triplet of the Randomised Badger Culling Trial
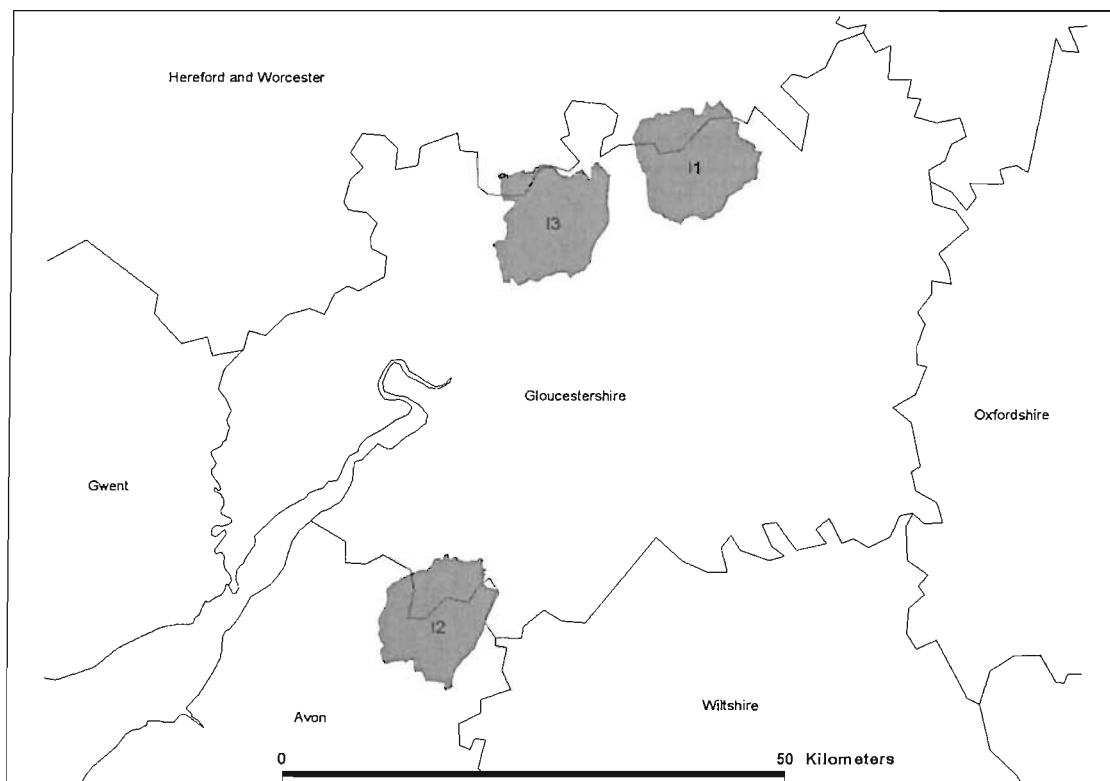
The reactive and proactive treatment areas were located on the western edge of the Cotswolds hills, between 20 m and 270 m above sea level. The control treatment area was west of this range of hills, in the River Severn floodplain area, between 10 m and 78 m above sea level. However, land use was similar in all three treatment areas (Fig 4.2) comprising pastoral dominated mixed farmland, interspersed with patches of woodland and suburban habitat, such as small villages and farm buildings.

Fig. 4.2. Percentage cover of different land use types in the Cotswolds triplet of the Randomised Badger Culling Trial (data from Land Cover Map 2000, Centre for Ecology and Hydrology, Monks Wood, UK)
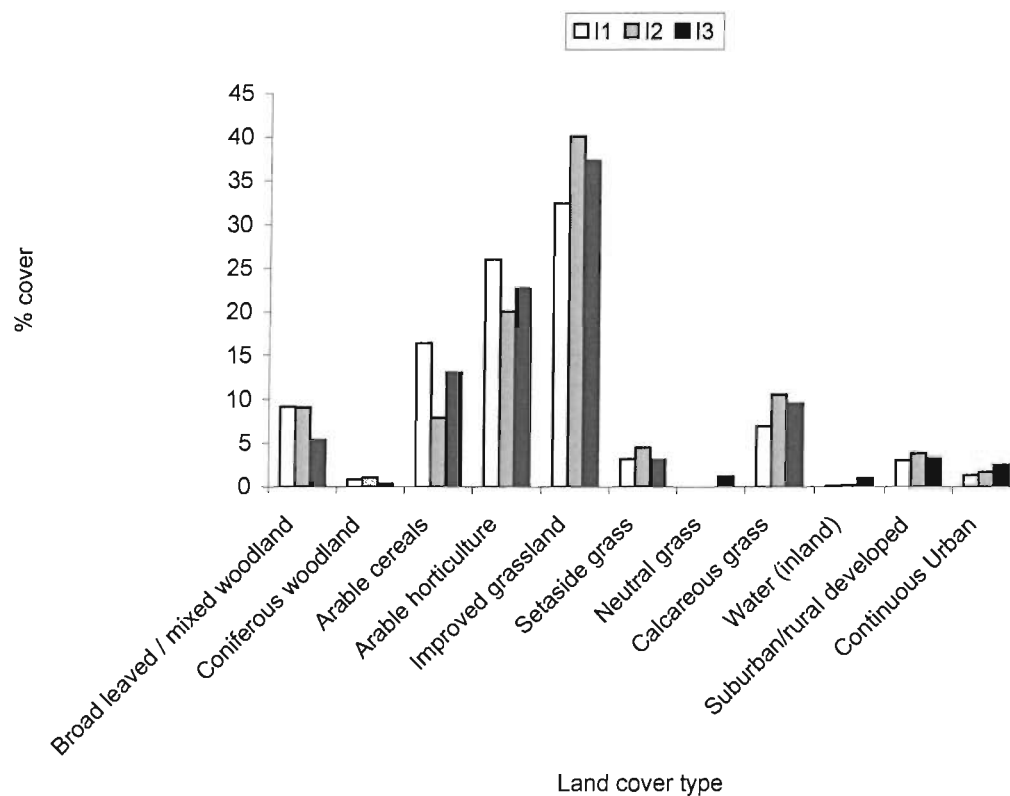
Hedgehogs frequently use amenity grassland fields for foraging (Micol *et al.* 1994) and because they are easily accessible they were used to catch animals for radio tagging. All amenity grassland fields in the study sites were situated on the edge of suburban areas and therefore hedgehogs had both suburban and rural habitats available to them. Suburban areas that contained amenity grassland fields were identified and three of these suburban areas were randomly selected as study sites to sample each treatment area. However only one such area that supported hedgehogs

was located in the control treatment area (I3). Data from the reactive and control treatment areas were pooled as no culling took place in either during the time of the study. Therefore, data were collected in three study sites in the proactive area and four study sites in treatment areas that received no culling which thus acted as controls. The aim of the study was to capture four animals (two adult males and two adult females) in each study site both pre and post badger culling, i.e. different subject animals were studied after the cull compared to before.

This field experiment was based on a nested analysis of variance design as shown by Fig. 4.3. The response of habitat selection by hedgehogs to badger culling was investigated by the interaction of fixed factors 'time' with 'treatment' and 'sex', and the random factor 'study site' nested within treatment, as given by the following statistical model:

Response = Time | Study site'(Treatment) | Sex

The fixed factor treatment had two levels, high badger density (control) and low badger density (proactive), time had two levels ('0' indicates before the badger cull and '1' after the cull) and sex has two levels (male and female). The effect of interest was the interaction between treatment and time which reflects the response of hedgehogs to badger removal.

Fig. 4.3. Experimental design to investigate the response of habitat selection by hedgehogs to badger culling. Only the left-most branch of each tree is shown in full
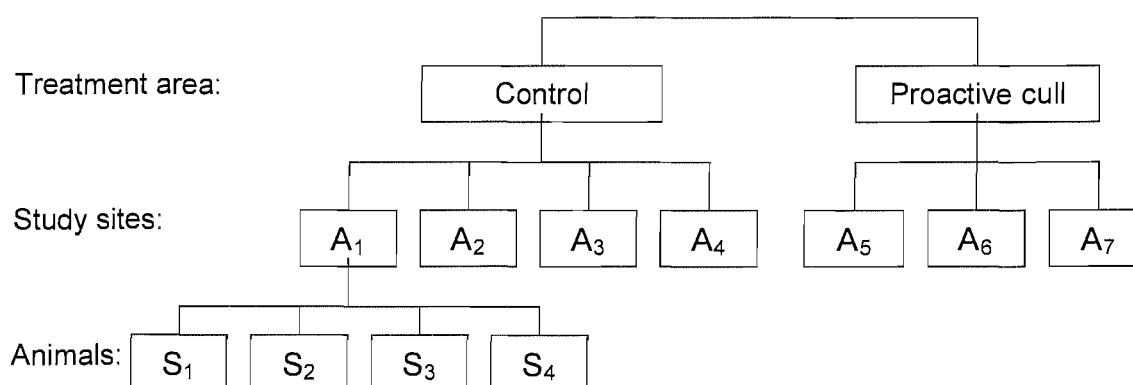
4.2.2 Radiotracking

Hedgehogs caught on amenity grassland fields were fitted with radio transmitters (TW-3, 9g on acrylic mount, Biotrack, Dorset, UK) similar to the technique used by Doncaster (1992, 1993, 1994). After examination to determine sex and weight, a cloth bag was placed loosely over the head of the animal to minimise the disturbance of torchlight and reduce movement. A small patch of spines situated approximately 10-15 cm above the tail of the animal and roughly the area of the base of the transmitter was trimmed by 1 cm in length. Dental acrylic (Biotrack, Dorset, UK) was mixed and applied to the base of the transmitter, which was then placed onto the trimmed patch of spines and held in position for five minutes to allow the dental acrylic to harden. The transmitter was positioned longitudinally along the vertebrae to allow the antenna wire to trail behind the animal. Hedgehog spines were also uniquely marked with heatshrink tubing (as described in Chapter 2). Animals were released back at the site of capture within 20 minutes.

Hedgehogs were relocated, using a radio receiver (TR-4, Telonics Inc., Mesa, Arizona, USA) and antenna (H-Adcock, Telonics Inc., Mesa, Arizona, USA), three times per week at night in order to identify location and habitat. Due to logistical constraints (i.e. travelling time between treatment areas), nocturnal relocations, or fixes, of each animal were made during the same night in each week rather than on different nights. Fixes on individuals were collected at approximately hourly intervals. This sampling regime is bound to have resulted in auto-correlated data and because clusters of observations are separated by long time intervals, this may result in biased home range estimates (De Solla, Bonduriansky & Brooks 1999). In particular, these clusters of sampling will over-sample the probability distribution of an animal in certain areas. This is however considered unimportant as the principal purpose of the study was to observe changes in habitat use. Therefore, the sampling regime was kept constant for all animals to ensure that any potential bias in home range size and shape estimation would also remain constant between treatments and across time.

Radiotracking began a minimum of 1 hour after dusk and ceased no later than 1 hour before dawn, to minimise the effect of the location of nest sites on the samples of locations collected. If possible, hedgehogs were relocated visually. The positions of animals were recorded on a field map with information on time, habitat type and behaviour (foraging/moving/unknown/). However, if the animal was located in an

inaccessible area, its position was estimated by taking a compass bearing in the direction of the strongest radio signal from two different points (i.e. radio fix). The second bearing was made approximately at 90° to the first in order to maximise the accuracy of the triangulation (White & Garrott 1990).

Every two weeks, attempts were made to recapture all radiotagged hedgehogs so that the transmitter could be checked and the individual animal examined and weighed. If necessary, further dental acrylic was applied to strengthen the attachment of the transmitter. An anti-bacterial powder was applied to the area underneath the transmitter in order to minimise the chance of infection occurring at the base of the spines.

Hedgehogs were radio tracked until a minimum of thirty fixes was obtained per individual, following recommendations by Seaman *et al.* (1999) for home range studies using kernel estimates, which took approximately 70-90 days. Animals that shed their transmitters, died or dispersed before this target was achieved were excluded from the habitat selection analysis. Transmitters were removed by cutting the spines beneath the transmitter.

4.2.3 Estimation of home range indices and habitat mapping

A total of 47 adult hedgehogs were tracked during the study, of which sufficient fixes (approximately 30) were collected for 26 animals (15 females and 11 males; 12 individuals before badger culling and 14 after). The mean number of fixes per animal was 33.4 fixes ($\pm$ 1.78 SE). The locations of all visual and radio fixes were mapped in a GIS (ArcView 3.2, Esri, California, USA). The Animal Movement extension (Hooge & Eichenlaub 1997) of ArcView 3.2 was used to calculate two different home range indices for each animal to estimate parameters of animal movement and habitat availability:

(1) A 100% minimum convex polygon (MCP) (Kenward 1987) home range estimator was calculated to encompass all the recorded movements of hedgehogs, except dispersal events, and to allow the comparison of habitat use to the results of other studies. An individual was considered to disperse or attempt to disperse if it moved a linear distance that was greater than the diameter of a mean home range, according to the sex of the individual.

(2) A fixed kernel estimator (with probability densities ranging between 5-95% at 5% intervals) (KHR) (Worton 1989) was calculated to estimate the core

activity areas of active hedgehogs at night. The smoothing parameter was calculated by least squares cross validation (LSCV) as recommended by Seaman *et al.* (1999).

Utilisation plots were used to qualitatively determine core activity areas by plotting the area encompassed by each kernel against the % probability density of the kernel (Fig. 5.5). Utilisation distributions often show a slope discontinuity, as a large percentage of fixes account for a small area (the core activity area), and an inflection point can be identified by eye to determine the kernel that constituted the core activity area (Salz & Alkon 1985). In this case there was a slight discontinuity at 65% kernel and this was used to define the core activity area. The lack of a striking inflection point, and therefore uncertainty over the definition of the core activity area, was considered unimportant as the aim was to investigate treatment effects on habitat use rather than to accurately measure core activity areas.

All habitat types in the study sites were mapped and digitised in the GIS. Five broad habitat categories were used in the study: (1) amenity grassland; (2) suburban; (3) pasture; (4) arable; and (5) hedgerow and woodland. All gardens, buildings, waste ground, allotments and roads within the study sites were classified as 'suburban' habitat. Polygons of home range indices and the locations of fixes were overlaid on the habitat data to calculate the composition of habitat in each home range and core activity area and to assign a habitat type to each fix.

4.2.4 Data analysis

Habitat selection by active hedgehogs at night was investigated at three levels:

(1) A comparison of home range habitat composition to habitat availability in the surrounding area. Habitat availability was defined for each individual by drawing a radius equal to the diameter of an average home range (374 m for males; 296 m for females) around the point of initial capture and calculating the habitat composition within this circle.

(2) A comparison of core activity area habitat composition to habitat availability in the surrounding area (the latter calculated as above).

(3) A comparison of the habitat associated with animal locations (fixes) to home-range habitat composition.

Compositional analysis (Aebischer, Robertson & Kenward 1993) was used to investigate habitat selection, by comparing habitat use with habitat availability. This was carried out at two levels; firstly using rural (pasture, arable and hedgerow and

woodland) and suburban (suburban and amenity grassland) habitat categories only and secondly using all five habitat categories. As the individual proportions of habitats within the range of a given animal sum to 1, they are not independent. Using a log-ratio transformation, they were made independent and approximately normally distributed, based on one of the habitat types as a denominator (Aebischer *et al.* 1993). The choice of habitat type as the denominator in compositional analysis is arbitrary; in this analysis suburban (broad scale) and amenity grassland habitat types (fine scale) were used. Missing values in habitat use (i.e. habitats that were not used) were given a nominal value of 0.001 (Aebischer *et al.* 1993). Missing values for habitat availability were replaced by the mean of all non-missing values for that log-ratio difference, as recommended by Aebischer *et al.* (1993). The difference between the log-ratios of habitat use and availability was calculated for each animal. A Wilk's lambda Λ test was used to determine whether habitat use was significantly non-random, using a chi-square test statistic to calculate the probability value. A matrix of the mean log-ratio differences of all possible pairs of habitat types across all hedgehogs was constructed and habitats ranked according to preference. A Student's *t*-test revealed whether differences between pairs of mean log ratio differences within the matrices were significant.

A residual maximum likelihood (REML) linear mixed model and multivariate analysis of variance (MANOVA) was used to investigate any changes in mean log ratio difference scores of habitat selection in response to badger culling. Treatment, time and sex and their interactions were entered as fixed terms into the model. Study site was entered as a random effect. A REML with the same model structure was also used to investigate treatment effects on the area of habitats used by hedgehogs. A REML generalised linear mixed model (GLMM) with a binomial error structure was used to test changes in the proportion of habitat types used by hedgehogs to the treatment of badger culling. The significance of explanatory terms in REML models were assessed by their Wald statistics, which were distributed as χ^2. Each table presented in the results of the REML models shows the terms added to the model along with their Wald statistic, degrees of freedom and *P*-values under 'model terms'. Interactions between terms are depicted by '*'. The average effects and standard errors of the significant ($P < 0.05$) terms (and terms that approached significance) are shown under 'minimal model' in the results tables. The average effect of a term shows whether its relationship with the response variable is positive or negative after

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the lowest value (or the alphabetically first value if text) of that term is set to zero
(Russell *et al.* 2002). All statistical analyses were conducted using GenStat 6.2
(Lawes Agricultural Trust, Rothamstead, UK).

4.3 Results

4.3.1 Compositional analysis of habitat use

Compositional analysis showed there was significant non-random habitat use in hedgehog home ranges when compared to habitat available in the surrounding area (Wilk's lambda $\Lambda = 0.520$; Chi sq = 17.022, df = 4, $P = 0.002$). A matrix (Table 4.1a) ranked the habitats in the order (>>> indicates a significant difference according to a Student's t-test): amenity grassland > suburban >>> hedgerow & woodland > pasture > arable. As expected there was significantly greater use of the top two ranking habitats, amenity grassland and suburban, than the rural habitat types. Arable was ranked as the lowest habitat type although there were no significant differences between rural habitats.

There was also significant non-random habitat use of hedgehog core activity areas from habitat available (Wilk's lambda $\Lambda = 0.608$; Chi sq = 12.94, df = 4, $P = 0.012$). A matrix (Table 4.1b) ranked the habitats in a similar order: amenity grassland >>> suburban > hedgerow & woodland > arable > pasture.

Finally, compositional analysis of habitat use by foraging hedgehogs within the home range also showed a significant non-random use of habitat types in relation to their availability (Wilk's lambda $\Lambda = 0.248$; Chi sq = 36.29, df = 4, $P < 0.001$). A matrix (Table 4.1c) ranked the use of habitats in the order: amenity grassland >>> suburban > arable >>> hedgerow & woodland > pasture. Hedgehogs again showed the strongest selection for amenity grassland, which was used significantly more than the other habitat types. One notable difference of habitat use by foraging hedgehogs within home ranges, compared to the two previous scales, was that arable habitat was ranked significantly higher than both hedgerow and woodland and pasture.

Table 4.1. Ranking matrices from compositional analysis of habitat selection by foraging hedgehogs. The tables show comparisons of proportional habitat use within (a) home ranges (100% MCP) and (b) core activity areas (65% kernel), with proportions of total habitat availability; and (c) comparisons of the proportion of fixes with the proportions of habitat types within MCP home ranges. A negative value in the matrix indicates that the habitat type in the top row is used more than expected than the habitat type in the left column

(a) MCP home range compared to total study area

	Amenity	Arable	Pasture	Hedgerow & woodland	Suburban	Rank
Amenity		3.209*** ± 0.731	2.147* ± 0.804	1.938*** ± 0.455	0.590 ± 0.596	4
Arable	-3.209*** ± 0.731		-1.394 ± 0.758	-1.758** ± 0.565	-2.305* ± 0.846	0
Pasture	-2.163* ± 0.804	1.317 ± 0.757		-0.400 ± 0.584	-1.917* ± 0.737	1
Hedgerow & woodland	-1.938*** ± 0.455	1.758** ± 0.565	0.400 ± 0.584		-1.517* ± 0.661	2
Suburban	-0.590 ± 0.596	2.305* ± 0.846	1.917* ± 0.737	1.517* ± 0.661		3

$* P < 0.05, ** P < 0.01, *** P < 0.001$ (two-tailed).

(b) 65% KHR core activity area compared to total study area

	Amenity	Arable	Pasture	Hedgerow & woodland	Suburban	Rank
Amenity		2.257* ± 0.918	2.406** ± 0.665	2.130** ± 0.628	1.281 ± 1.250	4
Arable	-2.257* ± 0.918		0.034 ± 0.755	-0.221 ± 0.584	-0.781 ± 1.129	1
Pasture	-2.406** ± 0.665	-0.034 ± 0.755		-0.208 ± 0.547	-1.537 ± 1.115	0
Hedgerow & woodland	-2.130** ± 0.628	0.221 ± 0.584	0.208 ± 0.547		-1.328 ± 1.224	2
Suburban	-1.281 ± 1.250	0.781 ± 1.129	1.537 ± 1.115	1.328 ± 1.224		3

$*P < 0.05, ** P < 0.01, *** P < 0.001$ (two-tailed).

(c) Fixes compared to MCP home range

	Amenity	Arable	Pasture	Hedgerow & woodland	Suburban	Rank
Amenity		1.388*** ± 0.350	4.027*** ± 0.754	3.233*** ± 0.692	0.779** ± 0.278	4
Arable	-1.388*** ± 0.350		2.613*** ± 0.539	1.714* ± 0.679	-0.695 ± 0.407	2
Pasture	-4.027*** ± 0.754	-2.613*** ± 0.539		-0.314 ± 1.096	-3.230*** ± 0.814	0
Hedgerow & woodland	-3.233*** ± 0.692	-1.714* ± 0.679	0.314 ± 1.096		-3.065*** ± 0.713	1
Suburban	-0.779** ± 0.278	0.695 ± 0.407	3.230*** ± 0.814	3.065*** ± 0.714		3

$P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ (two-tailed).

4.3.2. Effects of badgers on habitat use

4.3.2.1. Rural and suburban habitats

There was no effect of badger culling on the log ratio differences between habitat in the home range and the availability of habitat in the study area (log ratio differences; Wald statistic = 0.89, df = 1, P = 0.345; REML). In addition, no effect of the treatment was detected on the log ratio differences between habitat in the core activity area and the availability of habitat in the study area (log ratio differences; Wald statistic = 1.93, df = 1, P = 0.165; REML). Finally, no treatment effect was detected on the log ratio differences between the utilised habitat and the availability of habitat in the home range (log ratio differences; Wald statistic = 0.08, df = 1, P = 0.772; REML).

Examination of the raw data suggested that rural habitats were in greater proportion in the core activity areas in the proactive areas after badgers had been removed compared to controls (Fig. 4.4). However, a generalised linear mixed model revealed that there was no effect of the interaction of treatment and time on the proportion of amenity grassland in core activity area (Table 4.2). There was some evidence of an effect of time, with a higher proportion of rural habitats in core activity areas in both proactive and control treatments in 2003 (Table 4.2).

Table 4.2. REML model showing the effects of badger culling and sex on the proportion of rural habitat in core activity areas. Study site nested in treatment was entered as a random effect

Fixed term	Wald statistic χ^2	d.f.	*P* value
Between sites:			
Treatment	0.41	1	0.522
Sex	0.37	1	0.544
Treatment*Sex	0.26	1	0.612
Within sites (repeated measures):			
Time	3.18	1	0.075
Treatment*Time	1.89	1	0.170
Time*Sex	0.01	1	0.937
Treatment*Time*Sex	0.95	1	0.330
Minimal model	**Average effect**	**SE**	
Constant	-1.50	0.88	
Time (0 < 1)	0.34	0.74	

Fig. 4.4. Mean proportion (%) ± 25% and 75% quartiles of the area of rural habitat types in the (a) home ranges (100% MCP) and (b) core activity areas (65% KHR) of hedgehogs, before (no shading) and after (shading) the badger cull in proactive compared to control areas
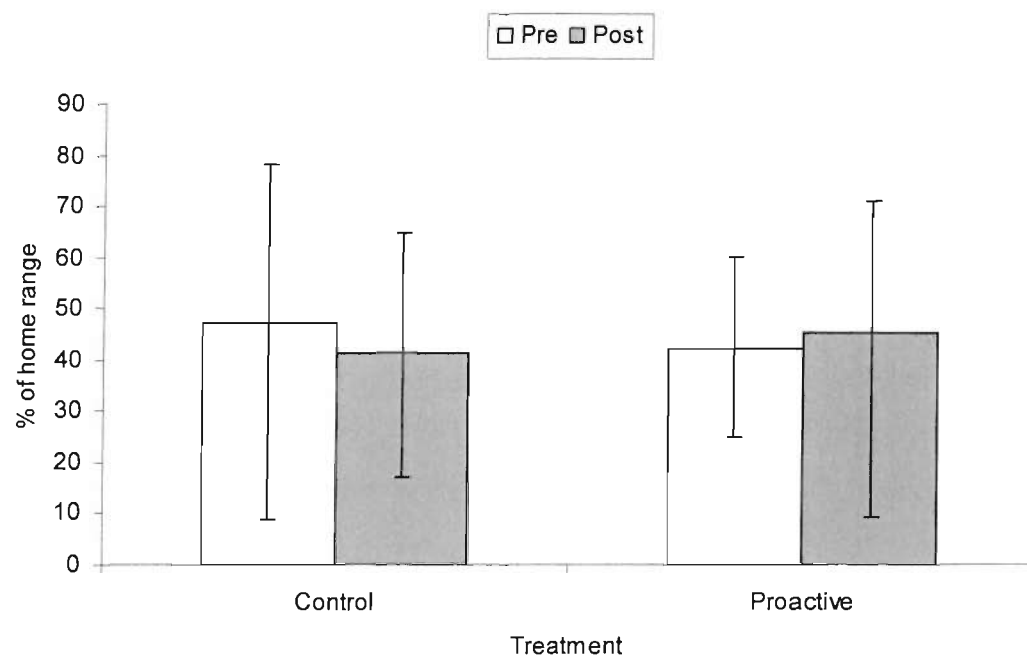
(a) Home ranges

(b) Core activity areas
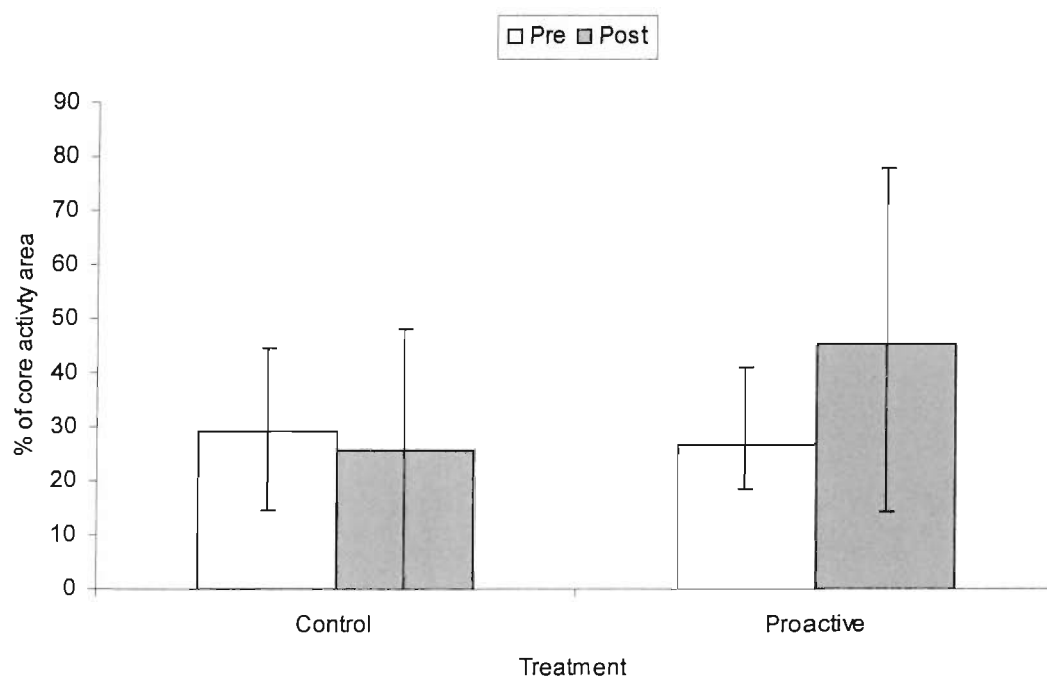
4.3.2.2. All habitats

A MANOVA revealed no effects of the interaction of treatment and time on the habitat use (log ratio differences) of hedgehogs both within the home range (log ratio differences; $F_{4,18} = 0.28$, $P = 0.888$; MANOVA) and comparing the proportion of habitat in home ranges (log ratio differences; $F_{4,18} = 1.23$, $P = 0.333$; MANOVA) and core activity areas (log ratio differences; $F_{4,18} = 0.62$, $P = 0.656$; MANOVA) to total habitat availability.

However, the raw data suggested that the proportion of amenity grassland habitat (the preferred habitat type identified by the compositional analysis) within core activity areas and home ranges decreased markedly in proactive areas after the badger cull but remained relatively constant in control areas (Fig. 4.5). They also suggested that use of suburban and some individual rural habitats increased after the badger cull. The REML model revealed there was no effect of the interaction of treatment and time on the proportion of amenity grassland in both core activity areas and home ranges (Table 4.3). The use of amenity grassland in home ranges varied with sex, with a larger proportion of amenity grassland in the home ranges of females compared with males (Table 4.3a).

There was an effect of the treatment and time interaction on the area of amenity grassland within the core activity areas (Table 4.4b) but not within home ranges (Table 4.4a). On average, hedgehogs used significantly smaller areas of amenity grassland in their core activity area in the proactive treatment after the cull compared to the control.

Table 4.3. REML model showing the effects of badger culling and sex on the proportion of amenity grassland in: (a) home ranges and (b) core activity areas. Study site nested in treatment was entered as a random effect

(a) Home ranges

Fixed term	Wald statistic χ^2	d.f.	P value
Between sites:			
Treatment	0.18	1	0.674
Sex	4.91	1	0.027
Treatment*Sex	0.04	1	0.841
Within sites (repeated measures):			
Time	3.70	1	0.054
Treatment*Time	2.51	1	0.113
Time*Sex	0.65	1	0.421
Treatment*Time*Sex	0.86	1	0.352

Minimal model	Average effect	SE	
Constant	-1.71	0.68	
Sex (females < males)	-0.83	1.44	
Time (0 < 1)	0.32	0.81	

(b) Core activity areas

Fixed term	Wald statistic χ^2	d.f.	P value
Between sites:			
Treatment	0.39	1	0.530
Sex	0.19	1	0.661
Treatment*Sex	0.10	1	0.749
Within sites (repeated measures):			
Time	8.60	1	0.003
Treatment*Time	0.55	1	0.457
Time*Sex	0.14	1	0.707
Treatment*Time*Sex	1.35	1	0.245

Minimal model	Average effect	SE	
Constant	-0.82	0.66	
Time (0 < 1)	-1.33	1.03	

Table 4.4. REML model showing the effects of badger culling and sex on the area of amenity grassland in (a) home ranges and (b) core activity areas. Study site nested in treatment was entered as a random effect

(a) Home ranges

Fixed term	Wald statistic χ^2	d.f.	P value
Between sites:			
Treatment	0.14	1	0.711
Sex	1.42	1	0.233
Treatment*Sex	0.48	1	0.488
Within sites (repeated measures):			
Time	0.12	1	0.728
Treatment*Time	2.48	1	0.115
Time*Sex	0.02	1	0.899
Treatment*Time*Sex	0.06	1	0.813

(b) Core activity areas

Fixed term	Wald statistic χ^2	d.f.	P value
Between sites:			
Treatment	0.91	1	0.339
Sex	1.88	1	0.171
Treatment*Sex	0.07	1	0.796
Within sites (repeated measures):			
Time	2.95	1	0.086
Treatment*Time	4.09	1	0.043
Time*Sex	0.03	1	0.856
Treatment*Time*Sex	0.31	1	0.579

Minimal model		Average effect	SE
Constant		3425	3513.1
Time (0 < 1)		-835.1	4443
Treatment*Time	Control (0 < 1)	0	6888
	Proactive (0 < 1)	-8921	

There was an effect of the interaction of treatment and time on the proportion of pasture habitats in core activity areas (Table 4.5), which increased in the proactive treatment after the cull but decreased in the control (Fig. 4.5b). There were no effects of badger culling on the proportion of pasture grassland in home ranges or on the use of suburban, arable, or hedgerow and woodland habitats in either core activity areas or home ranges.

Table 4.5. REML model showing the effects of badger culling and sex on the proportion of pasture grassland in core activity areas. Study site nested in treatment was entered as a random effect

Fixed term	Wald statistic χ^2	d.f.	P value
Between sites:			
Treatment	0.33	1	0.564
Sex	1.43	1	0.232
Treatment*Sex	2.50	1	0.114
Within sites (repeated measures):			
Time	0.20	1	0.656
Treatment*Time	6.07	1	0.014
Time*Sex	0.00	1	0.974
Treatment*Time*Sex	0.57	1	0.449

Minimal model		Average effect	SE
Constant		-1.80	0.45
Treatment*Time	Control (0 < 1)	0	1.69
	Proactive (0 < 1)	1.58	

Fig. 4.5. Mean proportion (%) ± 25% and 75% quartiles of the area of habitat types in the (a) home ranges (100% MCP) and (b) core activity areas (65% KHR) of hedgehogs, before (no shading) and after (shading) the badger cull in proactive compared to control areas

(a) Home ranges

(b) Core activity areas

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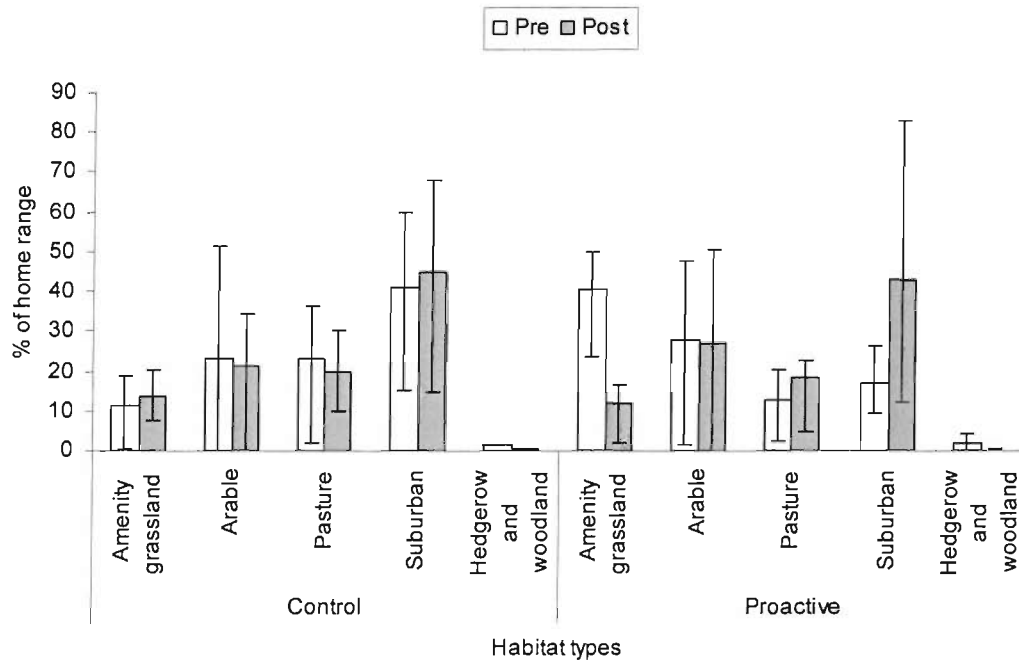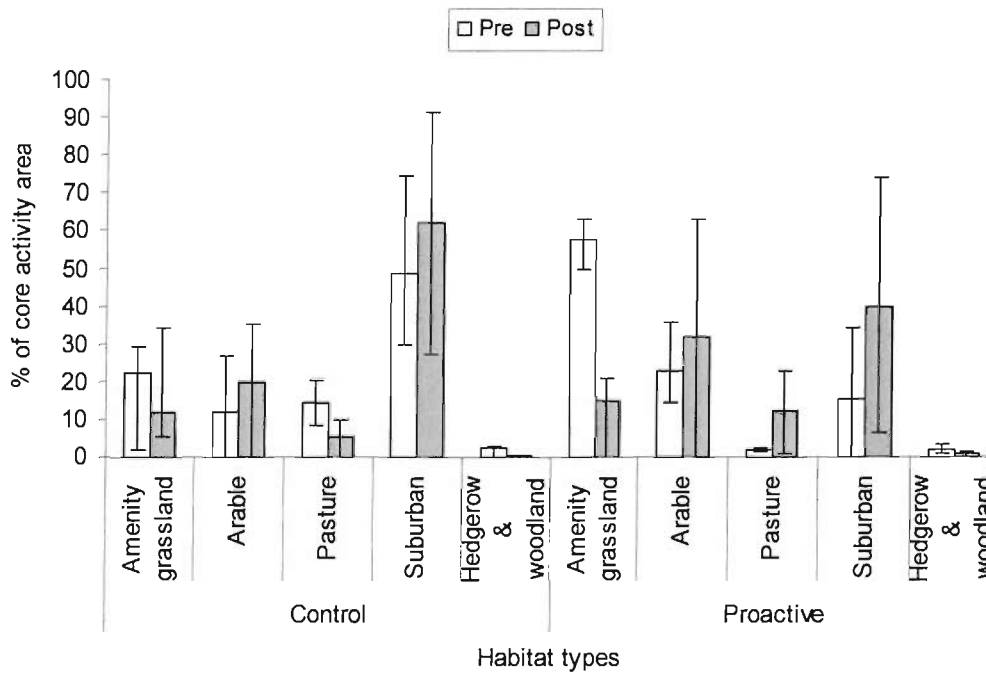
4.4 Discussion

Hedgehogs exhibited non-random use of habitats at all three levels and as expected the preferred habitat types were amenity grassland and suburban. These habitats are most profitable as they provide both higher food availability and a lower risk of predation than agricultural habitats (Micol *et al.* 1994). Within the home range and at the core activity area scale, amenity grassland was significantly preferred over all other habitat types, including suburban, and this therefore appears to represent the primary habitat of hedgehogs in the study areas. There was a higher proportion of amenity grassland in the home ranges of females than males. This sex difference has been observed in a previous study, where adult females spent more time in amenity grassland sites, which supported a high density of earthworms, compared to males and juveniles (Cassini & Foger 1995).

There was considerable variation of habitat use between animals and some individuals in certain study sites used agricultural habitats almost exclusively. Arable habitats ranked as the least and second least favoured habitat at the home range and core activity area scale respectively, but were significantly preferred over both pasture and hedgerow and woodland within the home range. In other studies (Doncaster 1992, 1993) hedgehogs have been observed to avoid arable habitats as they were thought to support low invertebrate food availability compared to pastoral grassland. Additionally there is likely to be a risk of predation for hedgehogs foraging in arable fields as badgers, which are omnivorous in diet, do regularly forage in arable fields (Roper *et al.* 1995), particularly in the late summer (C. Cheeseman pers. comm.). Therefore arable habitats should not represent a profitable habitat for hedgehogs. However, in the present study arable fields were the most important agricultural habitat for foraging hedgehogs within the home range. In particular oil seed rape was used frequently, although hedgehogs were also observed foraging in maize and wheat fields. This may be because they afford some cover and are therefore less risky than more open habitats (i.e. pasture). As pasture grassland habitat is used very frequently by badgers for foraging for earthworms, particularly in spring and autumn (Neal & Cheeseman 1996), they represent a high level of predation risk. Pasture was the least favoured habitat for hedgehogs. Despite this avoidance, two individual hedgehogs in the control areas appeared to have been predated by badgers whilst using pasture fields (in total three of 26 study animals were predated by badgers). The remains

consisted of a skinned dorsal coat of spines, with all the flesh eaten and in one instance badger hair caught between the spines, indicative of badger predation as has been observed in other studies (e.g. Doncaster 1992).

There were no significant treatment effects of badger removal on habitat use by hedgehogs, as determined by the log ratio difference scores from the compositional analysis. Nevertheless, this field experiment does provide some evidence that the proportions and areas of habitats used by hedgehogs in their core activity areas and home ranges changed in response to the removal of badgers. There was evidence that the area of amenity grassland in the core activity areas of hedgehogs declined in response to the reduction of badger numbers. As the risk of predation declined after the badger cull, hedgehogs appeared to have used the primary habitat less and secondary habitats more. For example, pasture habitat comprised a higher proportion of core activity areas in the proactive areas after the cull whereas it declined in control areas. This provides some support for the *a priori* prediction that preferred rural habitats would be used more frequently after a reduction in badger abundance compared to controls. Pastoral grassland is likely to be a profitable habitat for foraging hedgehogs if there is a sufficiently low risk of predation and previous studies observed a preference for pasture grassland habitats in low badger density areas (Doncaster 1993). However, despite the increase in the proportion of pasture grassland in core activity areas, on average it still comprised only a relatively small percentage of the total area (less than 20%). It is noteworthy that there was no effect of badger culling on the proportion of pasture grassland within the home range. This suggests that hedgehogs did not make large shifts in their home range towards rural habitats in response to badger culling, but may have changed the way they used habitats within the home range. There were no other treatment effects detected on the proportion of individual habitat types within core activity areas or home ranges. Although the raw data suggested that the rural habitats in total represented a greater proportion of hedgehogs' core activity areas in proactive areas after the badger removal operation this was not found to be statistically significant.

There was evidence, however, that badgers were still active in the proactive treatment area after the badger cull and that this activity may have affected hedgehog behaviour. For example, a study hedgehog was predated by badgers in one of the proactive treatment study sites only one month after the culling operations had occurred. The remains of this hedgehog were found in an amenity grassland field

approximately 50m from the edge of a village. Furthermore, badger sign was frequently observed in pasture habitats and occasionally in amenity grassland in the proactive area after badger removal. It is possible badger activity was still sufficiently high to be a major confounding factor in this study. This is likely to have resulted from DEFRA not being able to access some regions of the proactive area, or some individual badgers evading capture at accessible setts, or a combination of both these factors.

In summary, the results of this field experiment provide some support for the predictions of IGP that predation risk is an important factor in habitat selection by hedgehogs and that at high badger density, risky but productive habitats were not selected for foraging. When badger density was reduced, these previously risky habitats comprised a larger proportion of the core activity areas of hedgehogs. However, evidence for a shift in habitat use in response to the predator removal experiment was not conclusive. In addition, there was no replication of treatment areas in this experiment and therefore these results only apply to the Cotswolds region. Other manipulative experiments and behavioural studies have suggested that hedgehogs in high badger density areas are more predisposed to reduce the risk of predation through larger scale movements, rather than localised shifts in the use of feeding patches (Doncaster 1992, 1994; Ward *et al.* 1997). It will be informative for future studies to investigate the role of movement as part of the behavioural response of hedgehogs to predation risk.

Chapter 5: Field test of behavioural responses by hedgehogs to predation risk by badgers

5.1 Introduction

Predation is thought to exert a strong selective pressure on prey species for behaviours that reduce predation risk (Lima 1998a, 1998b). Prey may adapt their behaviour according to the level of predation risk so that they are more difficult to capture, detect, or encounter (Lima 1998b). For example, they may alter aspects of their movement, including: patterns of movement during foraging (Lima & Dill 1990); space use within the home range and home range size (Lagos *et al.* 1995; Borowski 1998); and dispersal (Weisser 2001). For prey species that are capable of perceiving predation risk, including mammals, the threat of predation has been shown to strongly affect foraging behaviour (Lima & Dill 1990). Large mammals will often form groups to dilute predation risk (herbivores: Gerard & Lolsel 1995), increase vigilance by spending more time scanning for predators (Nubian Ibex, *Capra nubiana*: Kotler, Gross & Mitchell 1994) or forage closer to cover in risky habitats (Grey kangaroos: Banks 2001). However, for small mammals that are solitary, or do not exhibit such complex behaviours, changes in movement are likely to be the most effective way of avoiding predation. They have been shown to choose safer micro-habitats, or areas of more complex habitat structure, under the threat of predation (Heteromyid rodents: Brown *et al.* 1988; House mouse, *Mus musculus*: Dickman 1992; Rabbits, *Oryctolagus cuniculus*: Banks, Hume & Crowe 1999). A number of experimental studies have revealed that small mammals use open areas away from cover more frequently, and forage further from refuge, in predator removal sites compared to controls (e.g. Neotropical rodents: Lagos *et al.* 1995; House mouse: Arthur, Pech & Dickman 2004). Open areas are thought to be inherently more risky than areas that provide cover, and therefore the distance that animals forage from refuge is often used as a measure of predation risk.

Home range size and movement within the home range may also be influenced by the level of predation risk (Lima & Dill 1990). For example, the home range size of root voles (*Microtus oeconomus*) was larger in predator removal sites at a lower risk of predation by the weasel (*Mustela nivalis*) than in control areas (Borowski 1998). In areas of high predation risk, the root vole reduced the probability of an

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encounter with a predator by decreasing movement (Borowski 1998). Conversely, another species of small rodent (*Octodon degus*) has been shown to reduce the size of its daily home range in areas after predators were removed (Lagos *et al.* 1995). It was thought that prey individuals in the absence of predators were able to spend more time in food-rich habitats and therefore moved less far (Lagos *et al.* 1995). Male snowshoe hares (*Lepus amerinacus*) in predator removal sites had lower travel rates and smaller home ranges than in control sites (Hodges 1999). However, female snowshoe hares showed no change in home range size or travel rates with the manipulation of predators, suggesting that the effects of predation on movement can vary according to the sex of the prey species. The higher movement rates in risky areas were not expected as most small mammals were thought to reduce movement when predation risk is high (Hodges 1999). In another study of the effect of predation risk on the movement of snowshoe hare home range size did not differ between predator removal and control areas (Beaudoin *et al.* 2004). However, core activity areas were larger in areas of high risk compared to low risk areas after predators were removed (Beaudoin *et al.* 2004). Other studies have observed little response in movement of mammalian prey species to predation risk (e.g. Jonsson, Koskela & Mappes 2000).

A range of approaches has been used to investigate the effects of predation risk on the movement of small mammals. These include seeking correlations between patterns of movement and predator density or habitat type (e.g. Brown & Alkon 1990), experiments using small enclosures to exclude predators (e.g. Stokes *et al.* 2004) or where the sign of predators, such as faeces, is manipulated to mimic various levels of predation risk (e.g. Ward et al. 1997). Experimental studies, where predation risk is directly manipulated through excluding predators under natural conditions are rare (Banks 2001). In this study we investigated movement behaviour of a prey species in response to the experimental removal of its principal predator.

In rural regions of southwest and midlands England, the Western European hedgehog (*Erinaceus europaeus*) persists in sub-populations occupying isolated patches of suburban habitats in a landscape of pasture-dominated agricultural habitat (Chapter 2). The latter habitat is thought to be preferred by hedgehogs but is infrequently occupied due to high predation pressure by the Eurasian badger which often attains high densities in such areas (*Meles meles*) (Doncaster 1994; Chapter 2 & 3). The hedgehog is equipped with a substantial morphological defence against predation in the form of its dorsal coat of spines and a musculature that allows it to

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roll into a tight ball (Reeve 1994). However, the Eurasian badger (*Meles meles*) is strong and dextrous enough to overcome this defence and therefore is an effective predator of hedgehogs (Doncaster 1992).

Hedgehogs have been shown to use olfactory cues to detect predation risk from badgers (Ward *et al.* 1996; Ward, Macdonald & Doncaster 1997). Captive animals exhibited a physiological response to badger odour (Ward *et al.* 1996) and avoided areas tainted with badger faeces whilst foraging (Ward *et al.* 1997). Wild hedgehogs reduced their foraging effort when presented with badger odour, although this behavioural response was short lived, probably due to the cost of lost foraging opportunities (Ward *et al.* 1997). The trade-off between predation risk and the need to forage is particularly important as hedgehogs feed on similar invertebrate prey items to badgers (Reeve 1994; Neal & Cheeseman 1996). A study of hedgehogs in pasture grassland, however, found that foraging individuals did not stay closer to cover than would be expected at random, despite the presence of badgers in the area and a substantial risk of predation (Doncaster 1993). Although badger density was relatively low in this study at 5 badgers km^{-2}, two of the 12 animals were predated during the study. Conversely, hedgehogs appear to respond to the level of predation risk through larger scale movements. For example, in field experiments of the factors that regulate hedgehog distribution and abundance, translocated hedgehogs were found to move further and faster away from areas of high badger density than from areas where badgers were less abundant (Doncaster 1992, 1994). In a study of dispersal, hedgehogs were shown to use habitat edges more frequently than would be expected at random (Doncaster *et al.* 2001), which may be indicative of reducing the risk of predation whilst moving through unfamiliar habitat.

Non-lethal effects of predation are thought to have population level consequences and therefore large impacts on ecological systems, but have not received as much attention as the lethal effects of predation (Lima 1998a). In the present study we used a predator removal experiment, the Randomised Badger Culling Trial (RBCT) (Krebs 1997), to test the hypothesis that predation risk affects the foraging behaviour of hedgehogs. Specifically, we hypothesised that if hedgehogs modify their movement during foraging according to predation risk by badgers, then hedgehogs would forage further from cover after badger culling compared to controls. We also hypothesised that the size of home ranges and core activity areas of hedgehogs would change after badger culling in relation to controls. We additionally

investigated the relationship between different habitat types within the home range, and home range size. Finally, we monitored any dispersal events that occurred during the study to evaluate whether hedgehogs were capable of dispersing sufficient distances to move between suburban habitat patches.

5.2 Materials and Methods

5.2.1 Experimental design

Fieldwork was conducted in the Cotswolds Triplet of the Randomised Badger Culling Trial (RBCT) (Fig. 5.1) during 2002 and 2003. The triplet consisted of three plots of 100 km² ('treatment areas') and each plot received one of the following treatments: (1) 'proactive' culling of all badgers (I2); (2) localised 'reactive' culling following the identification of bovine TB in cattle (I1); and (3) 'control' where no culling takes place (I3) (Independent Scientific Group 1998). See Chapter 1.5 for more information on the RBCT. As landowner participation was voluntary the DEFRA field teams were unable to access some regions of I2 to carry out badger culling and this resulted in an unquantified number of badgers remaining in the proactive treatment area in 2003.

Fig. 5.1. Map of the three treatment areas in the Cotswolds Triplet of the Randomised Badger Culling Trial
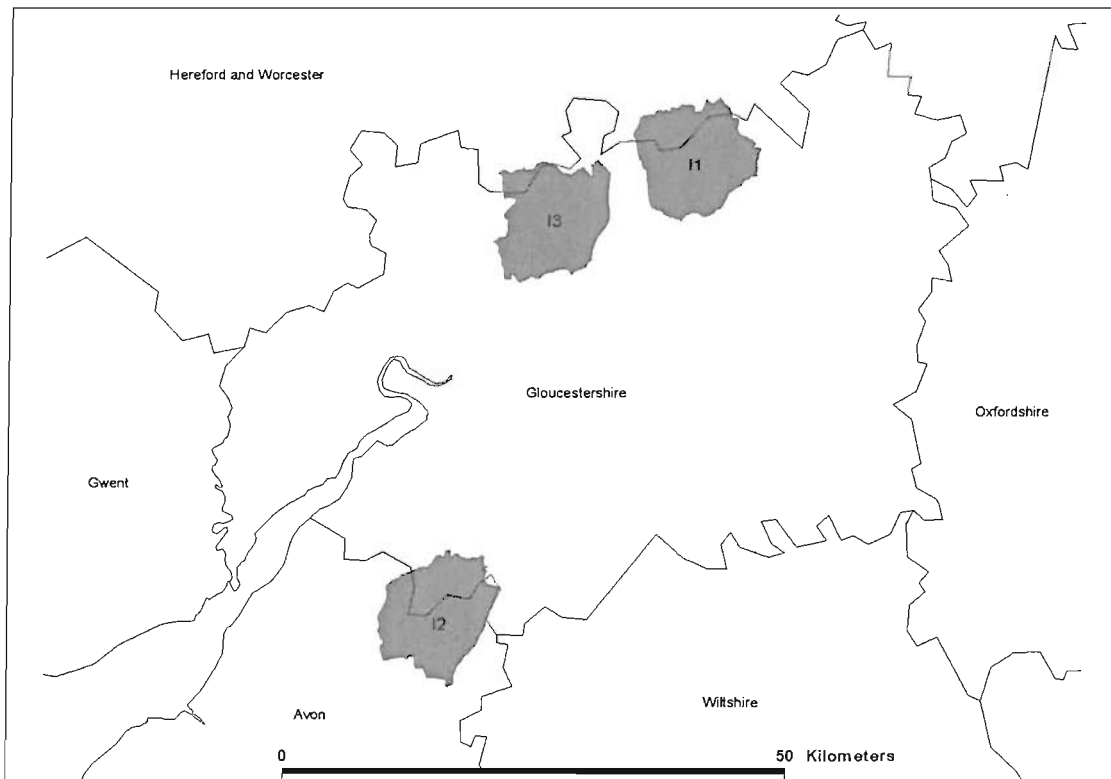
Proactive badger culling was carried out by DEFRA in September 2002. The reactive and proactive treatment areas were located on the western edge of the Cotswolds hills, between 20 m and 270 m above sea level. The control treatment area

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was west of this range of hills, in the River Severn floodplain area, between 10 m and 78 m above sea level. Despite these differences in height, land use was similar in all three treatment areas (Fig 4.2) comprising pastoral dominated mixed farmland, interspersed with patches of woodland and suburban habitat, such as small villages and farm buildings.

Hedgehogs frequently use amenity grassland fields for foraging (Micol *et al.* 1994) and these habitats were used to catch animals for radio tagging because of their high visibility here. All amenity grassland fields in the study sites were situated on the edge of suburban areas and therefore hedgehogs had both suburban and rural habitats available to them. Suburban areas that contained amenity grassland fields were identified and three of these suburban areas were randomly selected as study sites to sample each treatment area. However only one such area that supported hedgehogs was located in the control treatment area (I3). Data from the reactive and control treatment areas were pooled as no culling took place in either during the time of the study. Therefore, data were collected in three study sites in the proactive area and four study sites in treatment areas that received no culling which thus acted as controls. The aim of the study was to capture four animals (two adult males and two adult females) in each study site both pre and post badger culling, i.e. different subject animals were studied before the cull and after.

This field experiment was based on a nested analysis of variance design as shown by Fig. 5.2. The response of distance to cover of foraging hedgehogs to badger culling was investigated by the interaction of fixed factors 'time', 'treatment' and 'sex', and the repeated measures random factor 'subject' nested in 'study site' and treatment, as given by the following statistical model:

Distance to cover = Time | Subject'(Study site'(Treatment) | Sex)

Subject was included to take account of repeated sampling of the same individual. The investigation of the response of the size of home ranges and core activity areas to badger culling used the same design but omitted this repeated measures term, as given by the following statistical model:

Hedgehog movement = Time | Study site'(Treatment) | Sex

The fixed factor treatment had two levels, high badger density (control) and reduced badger density (proactive), time had two levels ('0' indicates before the badger cull and '1' after the cull) and sex has two levels (male and female). The effect of interest was the interaction between treatment and time which reflects the response of hedgehogs to badger removal.

Fig. 5.2. Experimental design to investigate the response of movement by hedgehogs to badger culling. Only the left-most branch of each tree is shown in full

Treatment: | Control | | | | Proactive cull |

Study site: A_1 A_2 A_3 A_4 A_5 A_6 A_7

Subject: S_1 S_2 S_3 S_4
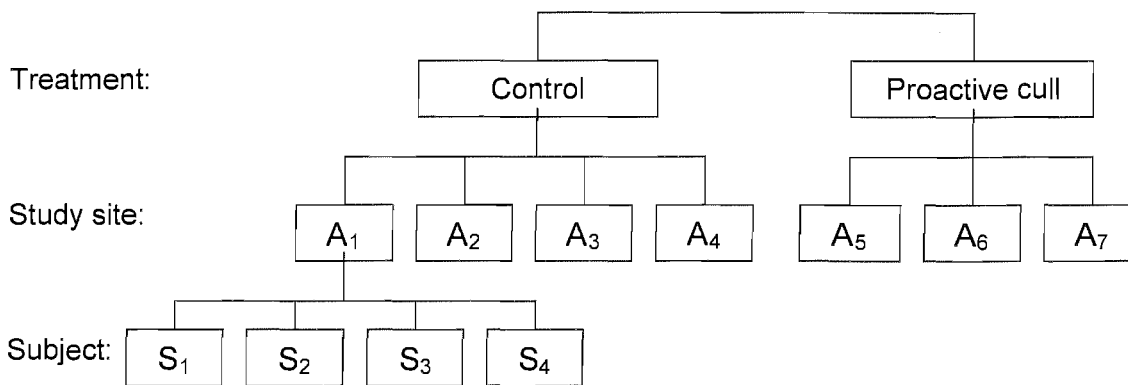
5.2.2 Radiotracking

Hedgehogs tended to become active in late March or early April after hibernation and remained so until early November. Data collection on the movement by hedgehogs was therefore carried out between early April to mid September in 2002 and 2003. Hedgehogs were caught on amenity grassland fields and fitted with radio transmitters (TW-3, 9g on acrylic mount, Biotrack, Dorset, UK) similar to the technique used by Doncaster (1992, 1993, 1994). After examination to determine sex and weight, a cloth bag was placed loosely over the head of the animal to minimise the disturbance of torchlight and reduce movement. A small patch of spines situated approximately 10-15cm above the tail of the animal and roughly the area of the base of the transmitter was trimmed by 1cm in length. Dental acrylic (Biotrack, Dorset, UK) was mixed and applied to the base of the transmitter, which was then placed onto the trimmed patch of spines and held in position for five minutes to allow the dental acrylic to harden. The transmitter was positioned longitudinally along the vertebrae to allow the antenna wire to trail behind the animal. Hedgehog spines were also uniquely marked with heatshrink tubing (as described in Chapter 2). Animals were released back at the site of capture within 20 minutes.

Hedgehogs were relocated, using a radio receiver (TR-4, Telonics Inc., Mesa, Arizona, USA) and antenna (H-Adcock, Telonics Inc., Mesa, Arizona, USA), three times per week at night in order to identify their location and habitat. Due to logistical constraints (i.e. travelling time between treatment areas), nocturnal relocations, or locations, of each animal were made during the same night in each week rather than on different nights. The locations of individuals were recorded at approximately hourly intervals. This sampling regime is bound to have resulted in auto-correlated data and because clusters of observations are separated by long time intervals, this may result in biased home range estimates (De Solla, Bonduriansky & Brooks 1999). In particular, these clusters of sampling will over-sample the probability distribution of an animal in certain areas. This is however considered unimportant to the principal purpose of the study, to observe changes in parameters of movement. Therefore, the sampling regime was kept constant for all animals to ensure that any potential bias would remain constant between treatments and years.

Radiotracking began a minimum of one hour after dusk and ceased no later than one hour before dawn, to minimise the effect of the location of nest sites on the samples of locations collected (Rondini & Doncaster 2002). If possible, hedgehogs were relocated visually. The positions of animals were recorded on a field map with information on time, habitat type and behaviour (foraging/moving/unknown). However, if the animal was located in an inaccessible area, its position was estimated by taking a compass bearing in the direction of the strongest radio signal from two different points (i.e. radio location). The second bearing was made approximately at 90° to the first in order to maximise the accuracy of the triangulation (White & Garrott 1990).

Every two weeks, attempts were made to recapture all radiotagged hedgehogs so that the transmitter could be checked and the individual animal examined and weighed. If necessary, further dental acrylic was applied to strengthen the attachment of the transmitter. An anti-bacterial powder was applied to the area underneath the transmitter in order to minimise the chance of infection occurring at the base of the spines.

Hedgehogs were radio tracked until a minimum of 30 locations were obtained per individual, following recommendations by Seaman *et al.* (1999) for home range studies using kernel estimates, which took approximately 70-90 days. Animals that shed their transmitters, died or dispersed before this target was achieved were

excluded from the habitat selection analysis. Transmitters were removed by cutting the spines beneath the transmitter.

5.2.3 Estimation of movement parameters

A total of 47 adult hedgehogs were tracked during the study, of which sufficient locations to estimate home range size (i.e. approximately 30) were collected for 26 animals (15 females and 11 males; 12 individuals before badger culling and 14 after) and these were the animals included in this study. The mean number of locations per animal was 33.4 locations ($\pm$ 1.78 SE). The locations of all visual and radio locations were mapped in a GIS (ArcView 3.2, Esri, California, USA). Patches of suburban habitat, woodland and hedgerows were considered as cover and were digitised in the GIS. The distances between the locations of foraging animals in amenity grassland and rural habitats, and the nearest cover were measured using the Nearest Features v. 3.6c extension of ArcView 3.2. If animals were located in a patch of habitat that represented cover, e.g. in a hedgerow, the distance was 0m.

The Animal Movement extension (Hooge & Eichenlaub 1997) of ArcView 3.2 was used to calculate two different home range indices for each animal. A 100% minimum convex polygon (MCP) (Kenward 1987) home range estimator was calculated to encompass all the recorded movements of hedgehogs except dispersals (see below). Secondly, a fixed kernel estimator (with probability densities ranging between 5-95% at 5% intervals) (KHR) (Worton 1989) was used to calculate both a 95% kernel home range (95% KHR) of foraging hedgehogs at night and a core activity area. A 95% kernel was chosen as it is a commonly used estimator of home range, although its precise value is not crucial to the aim of the study, to test for changes in home range size in response to badger culling. The smoothing parameter was calculated by least squares cross validation (LSCV) as recommended by Seaman *et al.* (1999). An utilisation plot was used to qualitatively determine the size of core activity area by plotting the area encompassed by each kernel against the % probability density of the kernel (Fig. 5.3). Utilisation distributions often show a slope discontinuity, as a large percentage of locations account for a small area (the core activity area), and an inflection point can be identified by eye to determine the kernel that constituted the core activity area (Salz & Alkon 1985). In this case there was a noticeable discontinuity at 65% probability density and this was used to define the core activity area (Fig. 5.3).

An animal was considered to disperse or to attempt to disperse if it moved a linear distance that was greater than the diameter of a mean home range, according to the sex of the animal. The dispersal distance was quantified as the distance between the centre of the home range and the furthest recorded location during the dispersal event.

5.2.4 Data analysis

Distance to cover was not normally distributed and was square-root transformed in order to achieve normality. Due to the difficulty of capturing the pre-determined number of male (n=2) and female hedgehogs (n=2) at each site in proactive and control areas, both before and after badger culling, the design was consequently highly unbalanced. Therefore the flexible residual maximum likelihood (REML) linear mixed model was used to investigate whether hedgehogs foraged further from cover in response to badger culling, instead of using an analysis of variance. Treatment, time and sex and their interactions were entered as fixed effects into the model. Subject nested in study site was entered as a random effect. A REML linear mixed model was also used to determine if the size of home ranges (100% MCP and 95% KHR) and core activity areas (65% KHR) changed in response to badger culling. Model structure was the same as outlined above except the repeat measures term subject was omitted.

The significance of explanatory terms in the REML models was assessed by their Wald statistics, which were distributed as χ^2. Each table presented in the results of the REML models shows the terms added to the model along with their Wald statistic, degrees of freedom and P-values under 'model terms'. Interactions between terms are depicted by '*'. The average effects and standard errors of the significant ($P < 0.05$) terms (and terms that approached significance) are shown under 'minimal model' in the results tables. The average effect of a term shows whether its relationship with the response variable is positive or negative after the lowest value (or the alphabetically first value if text) of that term is set to zero (Russell et al. 2002). A linear regression was used to investigate any relationship between home ranges size and the proportion of suburban or rural habitat within the home range. All statistical analyses were conducted using GenStat 6.2 (Lawes Agricultural Trust, Rothamstead, UK).

5.3 Results

5.3.1 Effects of badgers on distance to cover

There was no effect of the interaction of treatment and time on distance to cover (Table 5.1). Hedgehogs foraged further away from cover after the badger cull in both proactive and control areas (Fig. 5.3) as shown by the effect of time (Table 5.1). There was also no effect of sex on the mean distance to cover (Table 5.1), although the P-value approached significance. The raw data suggested that on average males foraged approximately 10m closer to cover than females (Fig. 5.4).

Table 5.1. REML model showing the effects of badger culling and sex on distance to cover. Subject nested in study site and treatment was entered as a random effect

Model terms	Wald statistic χ^2	d.f.	P value
Between sites:			
Treatment	0.77	1	0.380
Sex	2.94	1	0.086
Treatment*Sex	0.63	1	0.427
Within sites (repeated measures):			
Time	4.60	1	0.032
Treatment*Time	0.02	1	0.893
Time*Sex	0.53	1	0.469
Treatment*Time*Sex	1.20	1	0.274
Minimal model	**Average effect**	**SE**	
Constant	5.59	0.68	
Sex (females < males)	-1.89	0.90	
Time (0 < 1)	0.50	0.80	

Fig. 5.3. Mean distance ± SE to cover of foraging hedgehogs (outside of suburban habitats) before (no shading) and after (shading) the badger cull in proactive compared to control areas
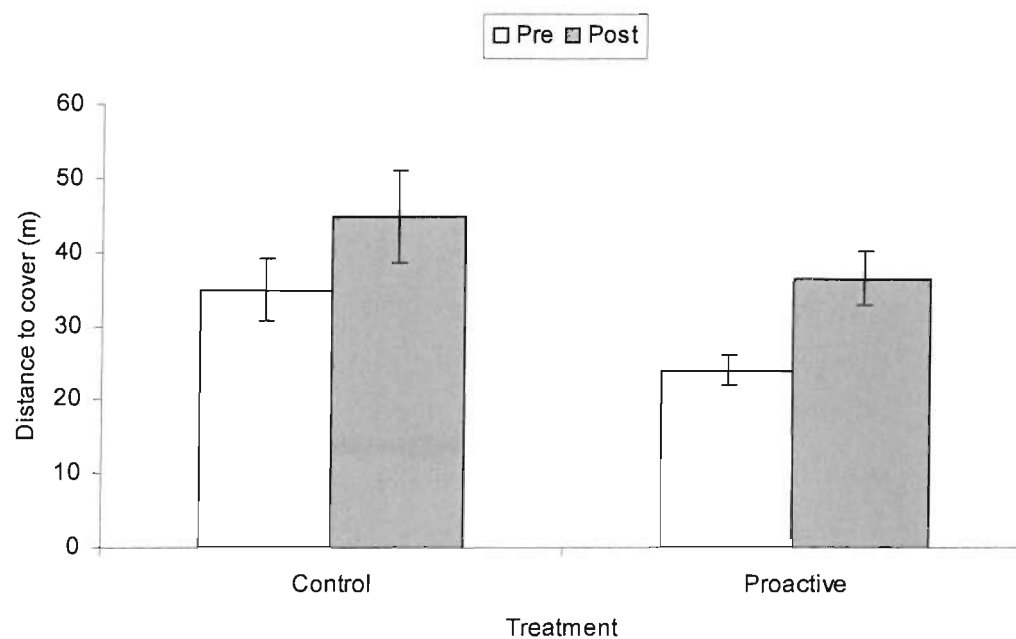
Fig. 5.4. Mean distance ± SE to cover of male and female foraging hedgehogs in amenity grassland and rural habitats
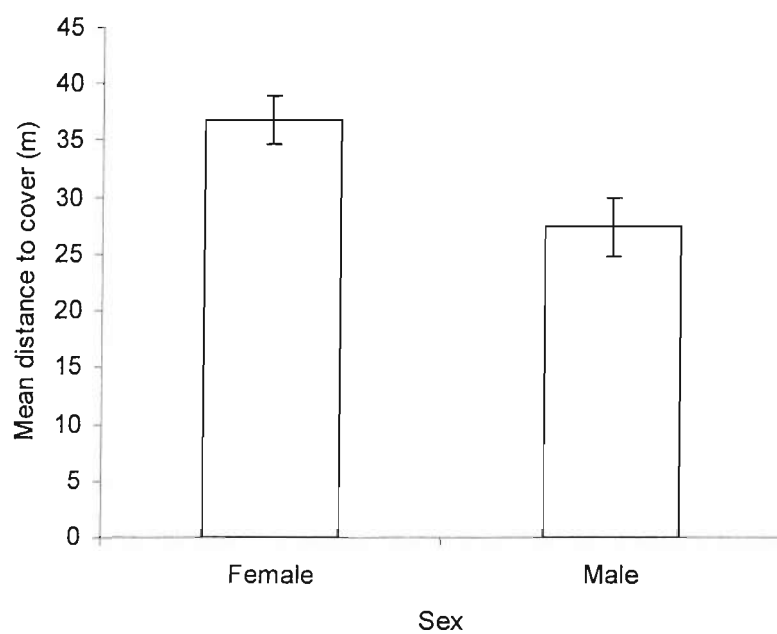
5.3.2 Core activity areas

In the utilisation plot of mean kernel area and % probability density (Fig. 5.5), a slight inflection point was noted at 65% probability density. This was used to delineate the mean core activity area of hedgehogs. The lack of a striking inflection point, and therefore uncertainty over the definition of the core activity area, was considered unimportant as the aim was to investigate treatment effects on the size of core activity areas rather than to accurately estimate core activity areas *per se* .

Fig. 5.5. Utilisation plot of mean kernel area (ha) of animals and % probability density. A noticeable inflection point can be observed at 65% probability density. Error bars are 95% confidence intervals
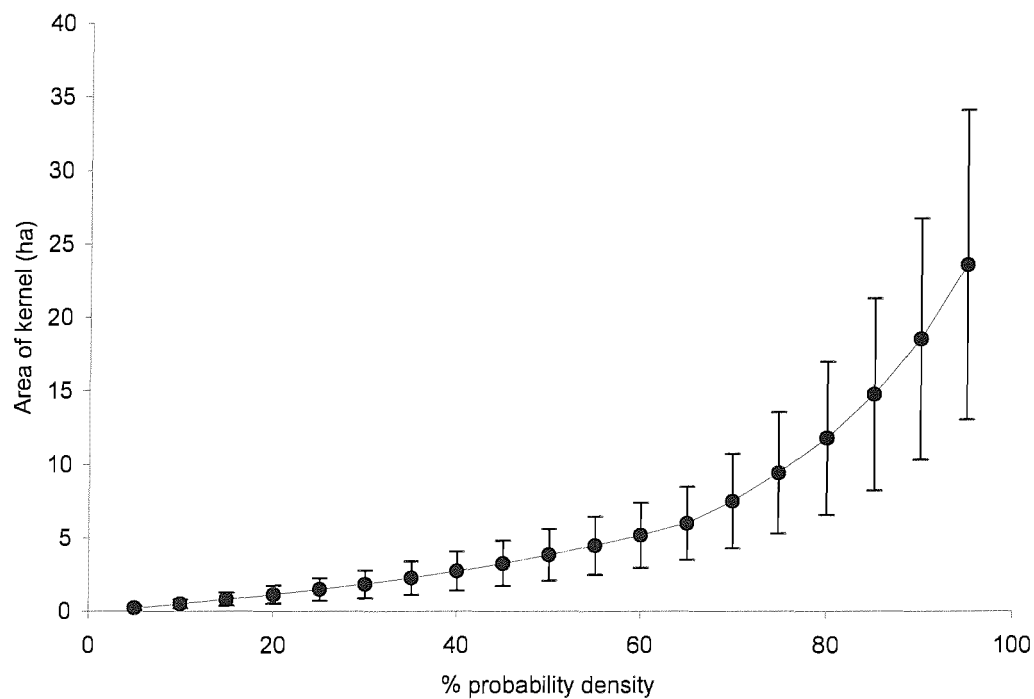
5.3.3 Effects of badgers on the size of home ranges and core activity areas

There was no effect of the interaction of treatment and time on the size of home ranges (100% MCP and 95% KHR) or on the size of core activity areas (65% KHR) (Table 5.2; Fig. 5.6). There was an effect of sex on the size of 100% MCPs (Table 5.2a); the mean home range size of males (11.5 ha) was approximately 70% larger than of females (6.8 ha) (Fig. 5.7). The size of 95% KHR and 65% KHR did not vary

with sex (Table 5.2b and 5.2c), although the *P*-value for the latter response variable was nearly significant.

Table 5.2. REML model showing the effects of badger culling and sex on the area of (a) 100% MCP, (b) 95% KHR and (c) 65% KHR of hedgehogs. Study site nested in treatment was entered as a random effect

(a) 100% MCP

Model terms	Wald statistic χ^2	d.f.	*P* value
Between sites:			
Treatment	1.25	1	0.264
Sex	3.92	1	0.048
Treatment*Sex	0.00	1	0.973
Within sites (repeated measures):			
Time	0.54	1	0.461
Treatment*Time	0.21	1	0.648
Time*Sex	0.23	1	0.632
Treatment*Time*Sex	0.59	1	0.441
Minimal model	**Average effect**	**SE**	
Constant	8.37	3.27	
Sex (females < males)	2.14	5.84	

(b) 95% KHR

Fixed term	Wald statistic χ^2	d.f.	*P* value
Between sites:			
Treatment	0.68	1	0.408
Sex	2.46	1	0.117
Treatment*Sex	0.28	1	0.600
Within sites (repeated measures):			
Time	0.17	1	0.684
Treatment*Time	0.23	1	0.631
Time*Sex	0.04	1	0.845
Treatment*Time*Sex	0.68	1	0.409

(c) 65% KHR

Fixed term	Wald statistic χ^2	d.f.	*P* value
Between sites:			
Treatment	0.05	1	0.816
Sex	3.19	1	0.074
Treatment*Sex	0.01	1	0.908
Within sites (repeated measures):			
Time	0.19	1	0.661
Treatment*Time	0.01	1	0.904
Time*Sex	0.48	1	0.490
Treatment*Time*Sex	1.17	1	0.280
Minimal model	**Average effect**	**SE**	
Constant	2.79	1.51	
Sex (females < males)	2.99	2.58	

Fig. 5.6. Mean area ± SE of the home ranges (100% MCP and 95% KHR) and core activity areas (65%KHR) of hedgehogs before (no shading) and after (shading) the badger cull in proactive compared to control areas
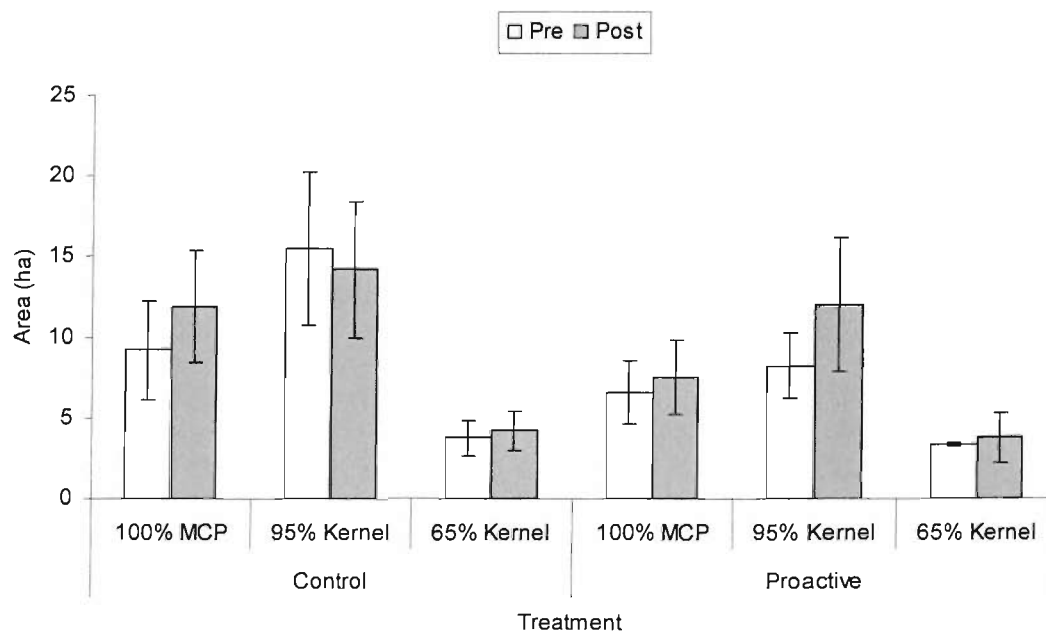
Fig. 5.7. Mean area ± SE of the home ranges (100% MCP and 95% KHR) and core activity areas (65% KHR) of male (no shading) and female (shading) hedgehogs
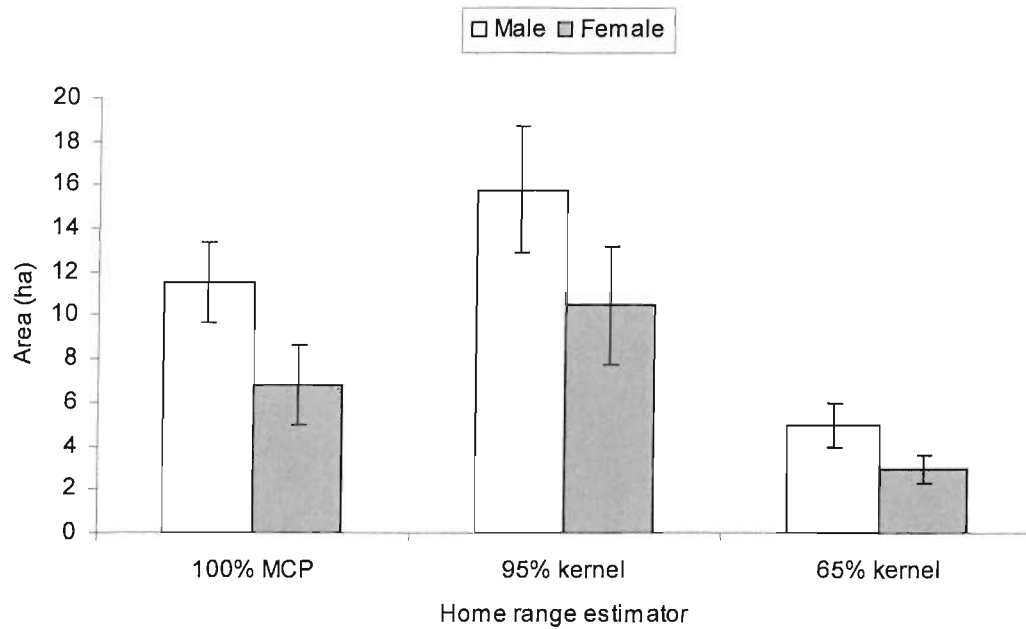
5.3.4 Dispersal

Only five dispersal and attempted dispersal events were recorded during the study and therefore it was not possible to examine any effects of predation risk on dispersal rates or distance (Table 5.3). Three males were observed to make a permanent dispersal away from their home range. They were tracked for at least two weeks after dispersal and did not return to their original home range. Two of these animals appeared to settle in an area of farm buildings and one in the middle of a small village. The mean distance between the furthest recorded location during the dispersal period and the centre of the original home range was 2.50 ± 0.55 km (SE). One female and one male returned to their home range after a period of approximately one week after making the initial movement. The female hedgehog was recorded using an area of farm buildings before being observed back in the original home range. The male hedgehog was last recorded in an arable field before returning to its home range. No dispersal or attempted dispersal events were recorded in the proactive area after the badger cull.

Table 5.3. Dispersal and attempted dispersal events of hedgehogs during the field experiment

Hedgehog ID	Sex	Treatment	Pre/Post culling	Distance (km)	Type of movement	Habitat
A3	Male	Control	Pre	1.92	Dispersal	Village
GO10	Male	Control	Post	1.98	Dispersal	Farm
W2	Male	Proactive	Pre	0.80	Attempted	Arable field
W4	Male	Proactive	Pre	3.61	Dispersal	Farm
W9	Female	Proactive	Pre	1.01	Attempted	Farm

5.3.5 Relationship between home range size and habitat

There was a negative relationship between the log of home range size (100% MCP) and the arcsine transformed proportion of suburban habitat (including amenity grassland) within the home range ($F_{1,24} = 31.42$, $P < 0.001$) (Fig. 5.8). The proportion of suburban habitat explained 56.7% of the variation in home range size. In other words, as the proportion of suburban habitat in the home range decreased, and thus the proportion of rural habitat increased, home range size increased.

Fig. 5.8. Relationship between home range (100% MCP) size (log transformed) and the proportion of suburban habitat in the home range (arcsine transformed) ($F_{1,24} = 31.42$, $P < 0.001$)
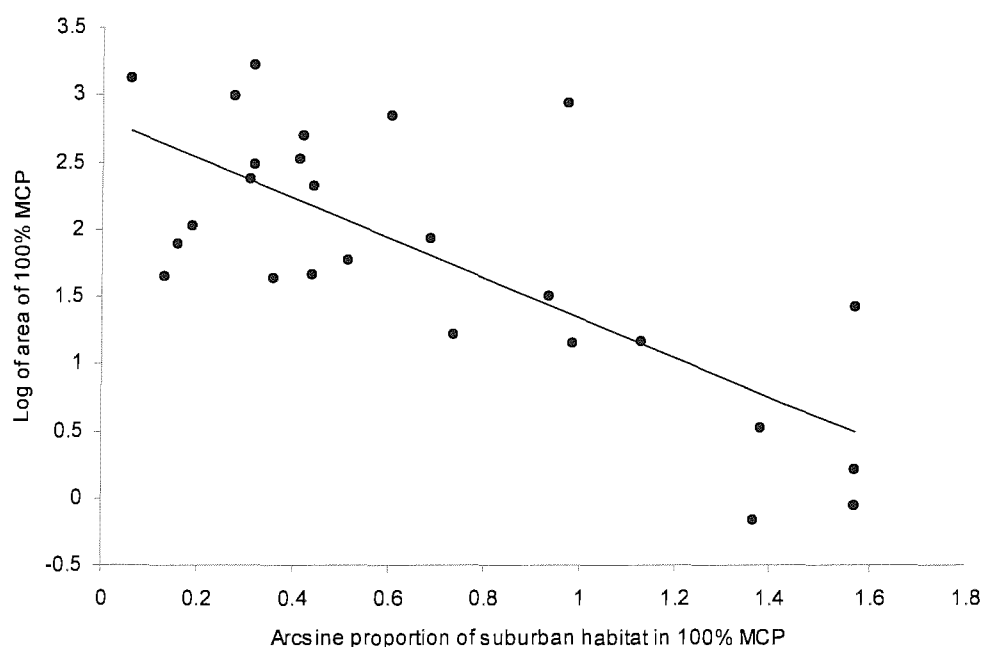
5.4 Discussion

The main objective of this field experiment was to investigate whether hedgehogs adapted their movement during foraging in relation to the level of predation risk. Predation risk was manipulated by the reduction of badger abundance through culling. Although hedgehogs foraged further from cover in proactive areas after culling, this also occurred in control areas and thus there was no effect of the interaction of treatment and time. Therefore, there was no evidence that hedgehogs foraged further from or closer to cover in response to varying predation risk from badgers. However, it is noteworthy that despite intensive culling operations in the present study, a number of badgers were still active in the proactive areas in the second year of the experiment (Chapter 4). This is likely to have resulted from DEFRA being unable to access some regions of the proactive area to carry out culling operations, or some individual badgers evading capture at accessible setts, or a combination of both these factors. One of the three (of a total of 26) radiotagged hedgehogs predated by badgers during the field experiment occurred after the badger cull in the proactive area.

The lack of response in distance to cover accords with a previous descriptive study (Doncaster 1993) which observed that hedgehogs did not forage further from, or closer to, cover than would expected at random despite a high risk of predation. The evolution of a morphological defence (i.e. dorsal coat of spines) may have resulted in a lack of anti-predator behaviours in hedgehogs. However, correlative evidence exists that other morphologically adapted mammals do exhibit a behavioural response to predation risk. For example, the Indian crested porcupine *Hystrix indica* preferred to forage in areas providing cover, presumably to seek protection from predators (Brown & Alkon 1990). A previous study of hedgehogs during dispersal after artificial translocation, observed that individuals were more attracted to habitat edges than at random expectation in unfavourable habitat (higher badger density) than in favourable habitats (lower badger density) and in control sites (Doncaster *et al.* 2001). Dispersal is thought to be particularly risky as animals are required to move through unfamiliar terrain, which may explain this observation (Doncaster *et al.* 2001). During the present study, when hedgehogs were approached they tended to move to cover if relatively close to a habitat edge but if they were far from cover they would remain stationary and assume a defensive posture in the open (pers. obs.). Doncaster (1993) hypothesised that the reactions of hedgehogs disturbed in the open suggested the

utility of cover may be a complex function of perceived chances of pre-empting and escaping attack.

The reason hedgehogs foraged further from cover in both control and proactive areas after the badger cull than before is not certain. The spring and summer in 2003 was generally dryer and hotter than in 2002 (UK Met Office), which may have resulted in lower food availability in short grassland habitats. Animals therefore may have been forced to forage further from cover to find food than in 2002. There was some evidence of an effect of sex on the distance hedgehogs foraged from cover; on average males appeared to forage approximately 10 m closer to cover than females. Assuming hedgehogs do use cover to seek refuge from predators, this difference suggests that females take more risks during foraging and therefore may be more susceptible to predation from badgers than males. This may provide some explanation why female hedgehog population growth was more strongly affected by predation than male hedgehogs (Chapter 3), i.e. females may have higher mortality rates through badger predation than males.

Hedgehogs have well developed olfaction and have been shown to use olfactory cues to perceive and avoid predators (Ward et al. 1996, 1997). In areas of reduced badger abundance it was hypothesised that hedgehogs would move further to utilise food rich patches under low predation risk, particularly in productive agricultural habitats, and therefore have larger home ranges. However, there was no effect of the interaction of treatment and time on the size of home ranges. Alternatively, if hedgehogs trade-off foraging with predation risk, then we expected hedgehogs to utilise food rich patches for longer periods of time in areas of reduced badger abundance, which would result in enlarged core activity areas. There was also no effect of the interaction of treatment and time on the size of core activity areas.

There was an effect of sex on home range size (100% MCP) as has been noted by a number of previous studies (see Reeve 1994 for a review). On average, the home ranges of males were approximately 70% larger than those of females. However, home range size was very variable, with the 100% MCPs of females ranging from 0.94 ha to 25.0 ha and males between 0.85 ha and 20.0 ha. There was a near significant effect of sex on the size of core activity areas (65% KHR); males appeared to use larger areas than females. There was a strong negative relationship between the proportion of suburban habitat and home range (100% MCP) size. As the proportion of suburban habitat in home ranges decreased, and consequently the proportion of

rural habitat increased, the size of home ranges increased. Suburban habitats are thought to support more abundant food resources for hedgehogs than rural habitats (Micol *et al.* 1994) and therefore hedgehogs are likely to be required to move further in rural habitats in order to obtain sufficient food. This strong relationship suggests that food availability is more important than predation risk in determining the home range size of hedgehogs.

Three of 26 animals in this study were observed to disperse permanently away from their home range. Although no clearly defined dispersal phase is recognised in hedgehogs, anecdotal evidence suggests that dispersal is predominantly by juveniles before the first winter hibernation or in the following spring (Reeve 1994). To the best of the authors' knowledge, this is the first study to observe natural dispersal events in adult hedgehogs. Two other individuals were observed to move away from their home range but returned after a period of approximately two weeks, which was assumed to be a failed attempt to disperse. Of the five individuals recorded to disperse, four were males and one was female, which, despite being a small sample, is consistent with the tendency of male biased dispersal in mammals (Greenwood 1980). This number of observations of dispersal events during the study was insufficient to investigate the effect of badgers on the rates and scale of hedgehog dispersal. Understanding the effects of predation risk on dispersal for species in fragmented populations is very important as their persistence relies on the ability of individual animals to move between sub-populations that occupy favourable habitat patches (Lawton & Woodroffe 1991). Predation is thought to influence a number of aspects of dispersal, including, whether an individual leaves its natal population, the habitat to which an individual disperses, and the survival of dispersing individuals (Weisser 2001). It can therefore affect the dynamics of metapopulations and the distribution of prey species (Banks *et al.* 2004).

In particular, estimating the rate and scale of dispersal is essential for predicting the dynamics of fragmented populations (Telfer *et al.* 2003). The average distance of the three dispersal events in the present study was 2.50 km with a maximum dispersal distance of 3.61 km. In a manipulative experiment, translocated hedgehogs were observed to move up to between 3.0 and 3.6 km from the release point (Doncaster 1992, 1994). As patches of suburban habitat in the present study sites were often between 3 and 4 km apart, this evidence suggests that hedgehogs are capable of moving between sub-populations. However, a study of genetic

differentiation among hedgehog populations in Oxfordshire revealed that dispersal only occurred rarely and another factor other than distance between populations affected rates of dispersal (Becher & Griffiths 1998). It was not clear whether this was due to low dispersal rates in the species or the result of barriers that reduce dispersal success. High badger density in agricultural habitats is likely to represent a substantial barrier to dispersal, which could reduce the rate of dispersal of hedgehogs between suburban habitat patches.

In summary, this study suggested that predation risk does not have a strong effect on patterns of movement during foraging and the size of home range and core activity areas of hedgehogs. The strong relationship between the amount of suburban, and therefore rural habitat, and home range size suggested that food availability rather than predation risk is more important in determining movement of hedgehogs. In areas where both hedgehogs and badgers co-exist, they often use similar habitats for foraging (e.g. short grassland fields) (Doncaster 1993). Therefore the lack of observed anti-predator behaviours in the present study, despite a high risk of predation, suggests that hedgehogs are likely to be very susceptible to predation during foraging. In order to understand the effects of predation risk on dispersal in hedgehogs, an investigation of both adult and juvenile dispersal should be pursued. This would also provide valuable information on the role of dispersal in hedgehog metapopulation dynamics. However, despite technological advancements such as radio-telemetry, monitoring dispersal in mammals through behavioural observations of un-manipulated populations is very difficult as these events occur usually once in an individual's lifetime and consequently often requires a prohibitive amount of time and resources. Further, empirical estimates of the rates and scale of dispersal, from radiotracking or mark recapture, are typically imprecise and often negatively biased compared to molecular approaches (Telfer et al. 2003). A combination of behavioural observations and a molecular approach should therefore prove productive.

Chapter 6: General discussion

In this general discussion chapter, the effects of badger predation on hedgehog populations and behaviour are discussed, followed by a consideration of the implications of the research for the management of hedgehog populations. The wider implications of the study's findings to the understanding of IGP predator-prey dynamics are then discussed. Firstly, however, information is provided on how this research fits into a larger project, the logistical constraints of conducting the field experiment within the framework of the RBCT and the resulting potential confounding factors.

6.1 Research project

The research documented in this thesis comprised part of a larger DEFRA funded project to investigate the 'ecological consequences of removing badgers from the ecosystem'. The project, which began in March 1999 and is due to finish in March 2006, aims to examine the effects of badger culling on various aspects of the ecology of foxes, rabbits, hares, ground nesting birds and earthworms as well as hedgehogs. Data collection on behalf of this PhD thesis was carried out by me but also by colleagues from the Central Science Laboratory. Data on hedgehog abundance were collected in RBCT areas in 2000 and 2001 before I registered for a PhD with the University of Southampton in September 2001, and these have been included in this PhD thesis. During this period, and up until December 2004, I worked as an ecologist for the Central Science Laboratory and was entirely responsible for the hedgehog related research as part of the Ecological Consequences project, including experimental design, implementation of the fieldwork, data analysis and interpretation. I also designed the study to investigate the effect of badger culling on hedgehog behaviour and solely carried out data collection.

Using the RBCT as the basis for the experimental design of this research presented a number of difficulties to the organisation of data collection which potentially represented confounding factors and therefore are documented here. Firstly, landowner participation in the RBCT was voluntary which resulted in the DEFRA field teams being unable to access regions of the proactive treatment areas to carry out badger culling where landowners did not subscribe to the trial. The area of 'landowner non-compliance' varied with triplet but was as high as 38.9% in the

proactive treatment area of Triplet H. Secondly, in some of the treatment areas there was substantial opposition to the RBCT. This included activities such as protestors interfering with deployed traps at badger setts, which in localised areas reduced the trapping efficiency of DEFRA field teams. Both these factors resulted in an unquantified number of badgers remaining in the proactive treatment areas during the trial. Therefore the culling operations were only able to reduce badger abundance rather than remove all of them, which was confirmed by the observations of badgers and their sign in proactive areas after the culling operations started. This has had consequences for the interpretation of results in this thesis, particularly the investigation of the impact of badgers on habitat use and movement by hedgehogs. It was difficult to ascertain if the lack of any major behavioural response of hedgehogs to badger removal was a real effect or because badger activity was still sufficiently high to prevent any change in behaviour. There were no other sources of data available at the time of writing (apart from the badger activity data documented in Chapter 3) to quantify how much badger abundance was reduced during the RBCT in proactive treatment areas. Another factor that affected culling operations arose in February 2001 when DEFRA announced restrictions on access to the countryside due to the outbreak of Foot and Mouth Disease in the UK. These restrictions rendered the study sites inaccessible between January and July 2001 and although this did not directly impact fieldwork (as this was carried out from July to September 2001), it did result in the suspension of badger culling by DEFRA. Consequently, no badger culling was carried out between late 2000 and May 2002, which may have contributed to an increase in badger activity in proactive treatment areas during this period (as has been discussed in Chapter 3).

6.2 The effects of badger predation on hedgehog populations

The evidence presented in this thesis lends strong support to a study by Micol *et al.* (1994) in which a negative spatial relationship between badger and hedgehog abundance was reported (Chapter 2). This relationship was shown to exist at a larger scale than previously recorded, indicating that badgers may have an impact on hedgehogs across large parts of their range. The current study confirmed the prediction of Micol *et al.* (1994) that hedgehogs would be at extremely low density or absent in rural habitats supporting high badger density. Hedgehogs appeared to use suburban microhabitats as spatial refugia from high predation pressure which facilitated their persistence at the landscape scale. However, the current study found that hedgehog abundance and occurrence in this habitat was inversely related to badger density in the surrounding agricultural area, suggestive of an effect of predation on prey populations in their spatial refugia.

The field experiment provided strong evidence that badger predation restricted the growth of hedgehog populations in amenity grassland fields, with hedgehogs doubling in density after badger culling (Chapter 3). At the beginning of this study, suburban microhabitats were thought to provide hedgehogs with spatial refugia from predation. However, three of the 26 radiotagged hedgehogs that were caught initially in amenity grassland fields were predated by badgers and this represented the most important mortality factor amongst these individuals (Chapter 5). The majority of radiotagged hedgehogs also used rural habitats to some extent which is likely to increase the risk of badger predation (Chapter 4). Hedgehogs also used other micro-habitats in suburban areas, particularly gardens, where they may be less prone to predation. However, a recent national survey of wildlife in gardens indicated that there was a negative relationship between the occurrence of badgers and hedgehogs in gardens (P. Baker, pers. comm.), which suggests that badger predation in this habitat is more frequent than was thought hitherto.

Due to the logistical difficulties of culling badgers, and possibly due to the suspension of culling operations as a result of the FMD outbreak, the relative abundance of badgers varied in proactive treatment areas during the course of the field experiment. Furthermore, a marked increase in badger activity in the second year of the experiment in effect represented a reversal of the treatment of badger culling which coincided with a decrease in hedgehog abundance. Utilising the

approach advocated by the mechanistic paradigm (Krebs 1995) the relationship between the hypothesised mechanism of population determination, in this case predator abundance, and the population growth rate of hedgehogs was investigated. There was an overall negative relationship between the growth rate of hedgehog populations and the mean index of badger abundance at $t+1$. This suggested that predation by badgers is an important determinant of the population growth rate of hedgehogs but also that predation acts on the hedgehog population without a time-lag. However as discussed in Chapter 3, these results should be interpreted with caution.

The fact that badgers determine the abundance and distribution of hedgehogs in rural habitats was revealed in previous studies which used an experimental manipulation of hedgehog populations (Doncaster 1992, 1994). Mortality from badger predation and movement away from high predation risk areas were the key factors. In the present study, however, no response of hedgehog abundance in pasture grassland to the experimental manipulation was detected (Chapter 3). There was some suggestion that hedgehogs caught in suburban areas used adjacent pasture grassland habitats more frequently in proactive treatment areas after culling compared to controls (Chapter 4). However, very few hedgehogs were observed in surveys of pasture grassland fields (Chapter 3), although colonisation of these habitats is a process that may not have been detectable within the timescale of this experiment.

When the response of hedgehogs in amenity grasslands to badger culling was investigated by sex, the largest increases in abundance were observed in females (106% increase) (Chapter 3), which suggested they have higher mortality rates through predation than males. Females foraged further from cover than males (Chapter 5) and were also observed to have a higher proportion of amenity grassland habitats in their home ranges (Chapter 4) and therefore may be at a higher risk of predation. Juveniles are likely to be more vulnerable to predation than adults due to their smaller size and a large increase in mean juvenile abundance was observed in proactive areas (556% increase) compared to control areas, although the effect of badger culling on juvenile populations was not significant. Nevertheless, these data suggest that juvenile mortality through badger predation may be an important demographic component of hedgehog population growth rates and may represent a productive avenue of future research.

This experiment provided evidence that population growth rates of hedgehogs in amenity grassland fields declined with increasing hedgehog density, i.e. growth rate

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was density dependent and therefore hedgehog populations were being regulated (Chapter 3). The nature of this density dependent population growth appeared to be different in areas with badgers than in areas where badgers had been reduced in abundance through culling. This indicated the existence of two different stable states of abundance; a lower population equilibrium at approximately 0.5 hedgehogs ha^{-1} in the presence of predators and a higher population equilibrium at roughly 1.8 hedgehogs ha^{-1} in areas with reduced predator abundance. In control areas, the steepness of the slope of this relationship indicated over-compensating density dependence. The advantage of the approach used in this experiment (i.e. manipulating predator populations) over the perturbation of prey populations carried out previously (Doncaster 1992, 1994), is the ability to investigate the potential of prey populations achieving different stable states and the extent to which they are regulated by their predators. The density of hedgehogs at the higher stable state is very similar to the level of hedgehog abundance observed by Micol *et al.* (1994) (1.8 hedgehogs ha^{-1}) in amenity grassland fields in areas of low badger density in Oxfordshire, which suggests that this is an accurate estimate of the carrying capacity of amenity grassland habitats in agricultural landscapes. Badgers appeared to regulate hedgehog populations by restricting them to spatial refugia and holding their abundance at a level substantially below the carrying capacity of the habitat. Whether hedgehog populations are kept at such a low level that they are susceptible to decline through demographic and environmental stochasticity is unclear. After the RBCT has been completed it would be extremely informative to monitor hedgehog populations as badgers recolonise culled areas to investigate if they permanently escape regulation by badgers (i.e. the existence of alternative stable states).

The overall impact of predators on prey populations (i.e. the total response) depends on both the numerical and functional (behavioural) response of predators (Solomon 1949). Predator-prey theory predicts that a Type III functional response should result in regulation of prey populations as prey are not predated at low density, or their habitats are avoided, but consumption rate increases rapidly with increasing prey density (Sinclair 1989). The nature of the negative density dependent growth rates of hedgehogs observed in suburban habitats is consistent with such a Type III predator-prey interaction. A very similar pattern was observed in the population growth rates of Australian marsupials under predation by red foxes where the prey used refuges to reduce predation risk (reviewed by Sinclair *et al.* 1998 and Sinclair &

Krebs 2003). It appears that suburban habitats provided hedgehogs with a sufficient refuge from predation to induce a Type III response from badgers, which stabilised the predator-prey interaction resulting in regulation of the prey population. Little is known about the efficiency of badgers in predating hedgehogs and hence their consumption rate; it is assumed that rather than actively seeking hedgehogs, badger predation is opportunistic whilst they are foraging for invertebrates. One possible explanation of how this Type III interaction arose is that amenity grassland fields that support rich food resources for periods of time are actively used by both badgers and hedgehogs leading to frequent encounters and thus high predation rates. Conversely amenity grassland fields with low food availability for periods of time are avoided by badgers, easing predation pressure on hedgehogs, but they are profitable to a small number of hedgehogs as they have lower energetic requirements than badgers. If this is the case, the functional response of badgers is driven by the availability of their primary prey of invertebrates (or the basal resource) rather than by hedgehogs.

In contrast, it would appear that in rural habitats that support high badger density, hedgehogs are unable to withstand the magnitude of predation pressure and no lower stable population equilibrium exists. This high predation pressure is likely a function of high predator density and increased encounter rates as IG predator and prey have similar foraging behaviours. Hedgehogs and badgers have been observed foraging simultaneously in the same pasture field in areas of low badger density (Doncaster 1994). The dynamics of badgers are likely to be independent of hedgehogs and may be driven by the distribution and abundance of invertebrate food resources (Kruuk & Parish 1982) and den sites (Doncaster & Woodroffe 1993), and limited by territoriality (Macdonald 1983) which precludes a numerical response to declining hedgehog density. Thus badgers are able to exert a constant predation pressure which results in increasing per capita mortality rates in hedgehogs with declining prey density (i.e. inverse density dependence). Therefore badgers at high density appear able to exert depensatory effects on hedgehogs, driving populations to localised extinction. This IGP interaction is similar to the effect of predators on prey when their dynamics depend on some other primary prey, resulting in a Type II interaction which tends to be destabilising (Sinclair & Krebs 2003). Further, it is analogous to the harvesting of wildlife populations by humans who can maintain hunting pressure even as prey density declines and thus producing inversely density dependent mortality which extirpates populations. As colonisation of rural habitats is

likely to occur over a longer time frame than this study, a profitable direction of research would have been to translocate hedgehogs into these habitats in both control and proactive areas and to monitor movement patterns and mortality rates. This would allow a direct test of the hypothesis that badger predation is sufficiently high to eliminate hedgehogs in rural habitats.

The ability of the prey to evade predation is an important factor that affects predation, or killing rates. The investigation of the behavioural responses of hedgehogs found little evidence that they adapted their movement or habitat use to reflect variations in predation risk (Chapters 4 & 5) although it is unclear if the presence of badger activity remaining in proactive areas after culling may have confounded this conclusion. Hedgehogs have been shown to display behavioural and physiological responses to badger odour although these responses were found to be relatively short-lived (Ward *et al.* 1996, 1997). Additionally, hedgehogs translocated into rural areas moved further and faster from areas where badgers are abundant than where they were scarce and they also used suburban micro-habitats more frequently (Doncaster 1992, 1994). This was strongly suggestive that hedgehogs were able to perceive predation risk and respond through large scale movement. However, another study of foraging hedgehogs at the scale of their home range found that they did not forage closer to cover than would be expected at random, despite high predation pressure (Doncaster 1993). Therefore this evidence, combined with the results from the present research, suggests that hedgehogs respond to badgers through large scale movements away from areas of high predation risk but do not demonstrate strong predator avoidance behaviour when moving within their home range.

6.3 Implications of the research for the management of hedgehog populations

Anecdotal evidence from researchers and wildlife managers, combined with results from recent surveys of numbers of hedgehogs killed on roads (Mammals on Roads Surveys, Mammals Trust UK), have raised concern that hedgehogs are undergoing a national population decline. The 2001 Mammals on Roads Survey revealed a 30% national decrease in the number of hedgehogs killed on roads between 1991 and 2001. More recently, the 2004 Mammals on Roads Survey revealed a decline of approximately 20% since 2001. There are regional differences in these trends, with the biggest declines observed in eastern England, although the frequency of hedgehogs on roads was lowest overall in south-west England. However, it must be noted that the relationship between the trend in the frequency of hedgehogs killed on roads and that in the wider population is not known.

In the present study, surveys suggested that hedgehogs are extremely rare or absent from pasture grassland across approximately 1000 km^2 of agricultural landscape in the southwest and midlands of England. Badger numbers have increased nationally over the past twenty years with large increases observed in regions both within and outside of south-west and midlands England (Wilson *et al.* 1997), and the upward trend may be continuing (Battersby 2005). The evidence from this field experiment and previous studies (Doncaster 1994; Micol *et al.* 1994) suggests increasing badger abundance will have serious consequences for the persistence of hedgehogs in rural habitats in many areas of the UK, which is therefore likely to raise further concerns for the conservation status of hedgehogs. However, whether the increase in badger numbers is responsible for the apparent national decline in the frequency of hedgehogs killed on roads is not certain. The intensification of agriculture, leading to a decrease of food resources and loss of habitat for nest sites, has been hypothesised as an important factor in the decline of hedgehog populations and is subject to research efforts elsewhere. Clearly a robust national monitoring programme of hedgehogs is required to have a better understanding of the long term population dynamics in both rural and suburban habitats.

In suburban habitats in agricultural landscapes that support high density badger populations, hedgehogs appeared to be regulated at a stable equilibrium and so therefore they are unlikely to be extirpated from these habitats by badgers (Chapter 3).

However populations held at this lower stable state may be subject to stochastic demographic or environmental processes that could result in localised extinction. In recent years, badgers are thought to be increasingly using suburban areas (R. Delahay pers. comm.), which may destabilise this interaction by increasing predation pressure in suburban hedgehog refugia. If the network of hedgehog populations in suburban habitat patches represents a metapopulation (i.e. unstable localised populations stabilised by density dependent movement) then the ability of hedgehogs to disperse between patches will be vital to their persistence (Hanski & Gilpin 1991). Badgers could disrupt hedgehog metapopulation dynamics directly through predation during dispersal but also possibly by dampening fluctuations in population size in suburban habitats which can lead to changes in density dependent patterns of dispersal (e.g. effects of mink on vole metapopulation dynamics; Banks *et al.* 2004). Evidence from molecular studies suggests dispersal of hedgehogs between suburban habitat patches in agricultural landscapes is very infrequent (Becher & Griffiths 1998). However, three dispersal events of adult hedgehogs were recorded in the present study, including one of 3.6 km which suggests a scale of hedgehog dispersal sufficient for suburban sub-populations to be linked (Chapter 5). The magnitude of the scale of dispersal is in agreement with the findings of a manipulative study of dispersal in hedgehogs (Doncaster *et al.* 2001). However, neither this nor the present study investigated dispersal by juveniles, which is thought to comprise the majority of movement between hedgehog populations. In order to understand the effect of badger predation on the persistence of hedgehog metapopulations, it would be informative to investigate the rates and scale of juvenile and adult dispersal and how they are related both to hedgehog density and badger abundance.

This field experiment provides strong evidence that reducing badger numbers leads to increased population growth of hedgehogs in suburban habitats, which may in turn lead to rural habitats being recolonised. Knowledge of the relationship between hedgehog population growth rate and the index of badger abundance could inform the management of hedgehog populations in suburban habitats. Furthermore, knowledge of this relationship provides a tool with which to predict the future dynamics of hedgehog populations according to natural changes in badger density. If hedgehogs were considered to be threatened, badger abundance could be manipulated leading to a predictable increase in hedgehog density. However, evidence from previous studies (Micol *et al.* 1994) suggests that badger populations in high density areas, such as the

south-west of England, would need to be reduced drastically from current levels to allow the co-existence of badgers and hedgehogs in rural areas in this region. Such manipulation of badger populations over large scales is likely to be very difficult to implement. For example, long term management of badger populations through culling would require substantial resources as well as being ethically, politically and legally problematic. A potential longer term solution would be to promote co-existence between the species through reducing environmental productivity in order to lower IG predator abundance, as predicted by theoretical models of IGP dynamics (Holt & Polis 1997; Heithaus 2001). This is likely to include the reduction of the area of pasture grassland and some arable habitats in order to diminish the availability of the primary food sources of badgers. However this would require substantial changes in land use planning and agricultural management which is liable to be very difficult to coordinate over large areas.

6.4 Wider implications of the research

Understanding the determinants of population growth rates is fundamental to wildlife management and biodiversity conservation (Krebs 2003). In the present study, the use of an experimental manipulation of predator populations allowed a test of the hypothesis that predation determined the population growth rate of prey populations. By seeking mechanistic differences (i.e. by monitoring levels of predator numbers) between experimental and control populations this study provided evidence of a causal relationship between prey population growth rates and predator abundance. This field experiment therefore has underlined the utility of the mechanistic paradigm by providing data within a relatively short time scale that can inform the management of wildlife populations. However, in this study the demographic rate which had the greatest effect on hedgehog population growth rates was not directly investigated. Sibly & Hone (2003) proposed an approach to provide a fuller understanding of the controlling mechanisms of populations by using an experimental study that combines aspects of the mechanistic and demographic paradigms.

This is one of only a few studies of IGP in mammals that has used an experimental approach and it has provided strong empirical evidence of the effects of IGP on prey populations. IGP was found to regulate hedgehog populations in their spatial refugia where they can escape predation at low density (i.e. a type III interaction) and this appeared to stabilise the intraguild predator-prey interaction at the landscape scale. This resulted in hedgehogs being regulated at a density substantially below the carrying capacity of the habitat, but after the predators were reduced in abundance they appeared to move to a higher population equilibrium. To the best of the author's knowledge this is the first time that this pattern of predator-prey dynamics has been observed in an IGP interaction in mammals. As in many examples of IGP, the dynamics of badgers are independent of hedgehogs. In rural habitats they can exert a strong predation pressure even as hedgehogs decline in abundance and produce depensatory effects through inverse density dependent mortality. Therefore, this study lends strong empirical support to the theoretical predictions that IGP in productive environments leads to exclusion of IG prey but that spatial refugia stabilise the IGP interaction and allow co-existence of IG predator and prey to occur (Polis et al. 1989; Holt & Polis 1997; Heithaus 2001). It has also provided evidence to support the hypothesis of Sinclair & Krebs (2003) that small

mammals tend to be regulated by top-down processes such as predation, rather than from the bottom-up by intraspecific competition for food supplies.

Finally, the patterns of badger-hedgehog dynamics documented here may be an example of the product of a complex indirect effect of predation on communities, namely meso-predator release. In the UK, badgers have been released from historical predation through the extinction of top carnivores and therefore are able to achieve high densities, particularly in anthropogenic habitats that provide abundant food resources. This has resulted in high predation pressure on hedgehog populations in agricultural landscapes, holding them substantially below carrying capacity in suburban micro-habitats, and excluding them from rural areas.

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