Wildlife Disease Management

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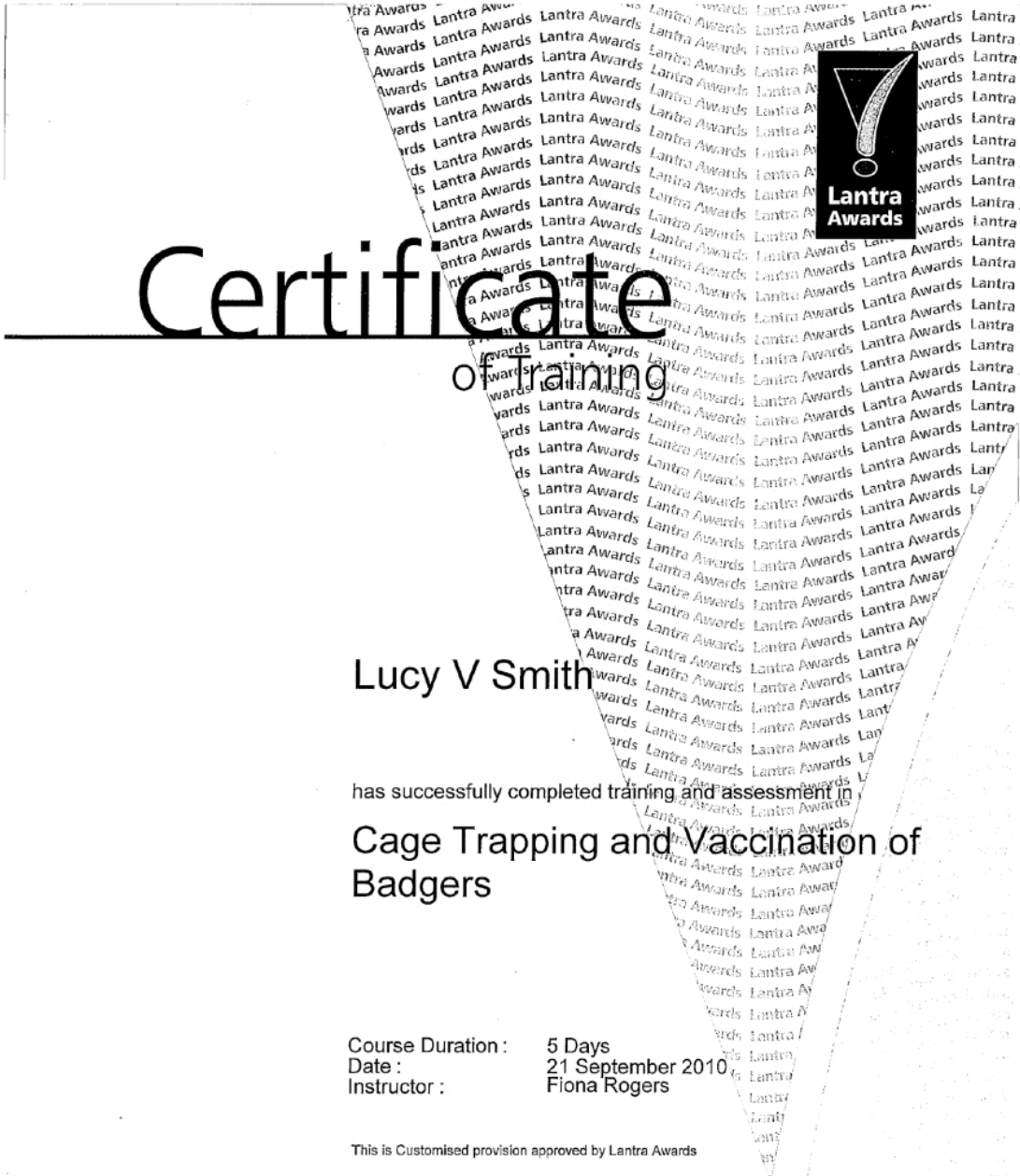
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Section 2.

Literature Review

Managing Wildlife Diseases

Managing Wildlife Diseases

I. INTRODUCTION

Disease is a natural part of any ecosystem; however, it is also a global problem for human health and wellbeing. Characterised as any impairment of normal bodily function, over 1400 diseases have been identified that directly effect humans, 60% of which are known zoonotics (Delahey *et al*. 2009). The cause of disease can come from an external source such as a virus, bacteria, fungi or protozoa or an internal dysfunction such as a cancer. But more diseases can affect humans indirectly, having damaging effects on agriculture, economics and biodiversity. These diseases and those that directly threaten human health become the target of management programmes. During the last century there has been mounting evidence and recognition of the role that wildlife play in the epidemiology of problem diseases, acting as a reservoir, vector or simply a victim (Tompkins & Wilson 1998; Artois *et al*. 2001). Human intervention to manage these issues can be problematic and complicated. This type of human-wildlife conflict is increasingly exacerbated as the world is developed and the interface between humans and wildlife intensifies via urbanisation, agricultural intensification, habitat degradation and the changing climate (Tompkins & Wilson 1998). This review focuses on the various management strategies and considerations for the control of problematic infectious diseases in wildlife with reference to relevant cases.

II. WHY MANAGE WILDLIFE DISEASE?

The decision to intervene with an ecosystem and manage a wildlife disease is made when the cost to the human way of life in considered too high, be this a risk to human health, economic well-being or the threat of loss of biodiversity through species extinction.

(1) Human health

Many diseases are worldwide public health concerns. Those that are zoonotic diseases can be transmitted to humans from domestic or wild animals. Mosquitoes transmit malaria through bites; rabies can be transmitted by domestic dogs and red foxes (*Vulpes vulpes*) amongst others (Lloyd 1976); toxoplasmosis (*Toxoplasma*

gondii) which affects 500 million people around the world is transmitted from felines (Hegab & Al-Mutawa, 2003; Anwar *et al*. 2006). Governments have to act to manage these threats to human health.

(2) Domestic animal health

Animal welfare legislation dictates that animals under our responsibility should be cared for fully, including the treatment and prevention of illness (OPSI 2006). Livestock animals are economically valuable and can be threatened by a number of diseases. This is compounded by animal diseases being regarded as an unacceptable limitation to trade or movement (Thomson *et al*. 2004). Bovine tuberculosis (bTB), though the threat to human health has been solved by pasteurisation of milk products, is still a huge and contentious problem for the cattle industry for both welfare and productivity reasons. The test and slaughter policy of cattle meant that 24,000 cattle were slaughtered in 2004 costing >£36 million in farmer compensation (Delahey *et al*. 2009). Torgerson & Torgerson (2008) claim that the annual Government expenditure on strategies to control bTB in the UK is £74-99 million.

The opportunities for inter-specific pathogen transmission have been increased over the years with the changes in land uses. The modern pastoral farming landscape in the UK has promoted high European badger (*Meles meles*) densities by providing excellent foraging conditions. Both badgers and foxes have adapted to both the agricultural and urban environments that have encroached on their habitats, living ever closer to humans, livestock and domestic animals, increasing transmission possibilities which need to be managed (Delahey *et al*. 2009).

(3) Conservation of species

The safeguarding of healthy ecosystems and their biodiversity are inextricably connected to human well-being for a sustainable future (Chapin *et al*. 2000). Pathogens and infectious diseases are of increasing concern for conservation as they pose a significant extinction risk for a number of endangered species, particularly those in reduced fragmented populations with reduced genetic resistance (Berger *et al*. 1999; Tompkins & Wilson 1998; Woodroffe 1999; Lafferty & Gerber 2002; O'Brien *et al*. 2003; Gaydos *et al*. 2004; Randall *et al*. 2006; Millán *et al*. 2009). The Ethiopian wolf (*Canis simensis*) and African wild dog (*Lycaon pictus*) are but two canid species that are threatened by rabies and canine distemper virus (Randall *et al*.

2006). The Ethiopian wolf has suffered at least two outbreaks of rabies in the last ten years, resulting in >70% mortality during each event, and long term demographic impact (Randall *et al*. 2006). Rabies severely impacted on African wild dogs resulting in their local extinction within the Serengeti-Mara ecosystem of Tanzania and Kenya in 1991 (Vial *et al*. 2006). Spill-over infections are not solely a problem from wild to domestic animals but also have severe consequences from domestic to wild animals. Domestic dogs due to their genetic similarities can carry a number of pathogens that are easily transmitted to wild canid species. In Ethiopia, where rabies is endemic, domestic dogs are accepted as the reservoir for the pathogen transmission to the Ethiopian wolf (Randall *et al*. 2006). Cross-species contact increases disease transmission, this is observed between domestic dogs and other canids (Randall *et al*. 2006; Lafferty & Gerber 2002). The threat of spill-over infections from domestic reservoir hosts to wild species is increasing as global populations of humans and domestic animals grow (Woodroffe 1999).

Diseases can also be a pressing concern for biological conservation when they indirectly threaten ecosystems and habitats. The loss of a predator can have wide-ranging negative effects on the rest of an ecosystem (Estes 1996). The Tasmanian devil (*Sarcophilus harrisii*) is threatened by extinction due to suffering from the Devil Facial Tumour Disease (DFTD), an emerging infectious disease (Hawkins *et al*. 2006). It is believed that the Tasmanian devil has played an integral role in preventing the establishment of red foxes in Tasmania over several incursions. The decline in Tasmanian devil numbers due to DFTD have raised concerns that foxes may settle leading to other species being put under novel pressures that they are not equipped to cope with (Hawkins *et al*. 2006).

Introduced species along with habitat degradation, pollution, exploitation and a changing climate can exacerbate the emergence and transmission of infectious diseases (Epstein 2001; Delahey *et al*. 2009). Usually harmless infections start to cause pathological damage under environmental stress (Lafferty & Gerber 2002).

III. MANAGEMENT CONSIDERATIONS

(1) When to intervene

As pathogens and disease are natural elements of ecosystems, a sufficient reason for intervention is required, as in many cases, doing nothing may be a reasonable decision (Artois *et al*. 2001). Intervention may not benefit wildlife and may result in new

problems or hinder immunological adaptation (Woodroffe 1999; O'Brien *et al*. 2003). The decision will depend on the extent to which the resultant disease disrupts the human way of life by endangering human health, wealth, welfare or biodiversity (Delahey *et al*. 2009). Before intervention to manage the disease can be taken, an assessment of the extent of the pathogen and the likelihood that management would be effective, needs to be assessed (Artois *et al*. 2001). Difficulties arise when stakeholders have opposing perspectives on the extent of the management required. For example, some bird and mammal species that can carry problem diseases are held in great affection by the general public, such as, the Eurasian badger and control of these species can be contentious (Delahey *et al*. 2009). The public may not always be fully informed of the facts involved in managing wildlife which can be antagonised by media attention. Policy makers and politicians need to find a common ground for the basis of intervention (Artois *et al*. 2001).

(2) What to target

  Deciding on which element of the diseases dynamics to focus the management efforts toward is an important one. Whether to target the host/s, the pathogen or the transmission route or all of them needs to be decided. However, Artois *et al*. (2001) suggest that analysis of different available strategies and their possible successes or failures are rarely undertaken. Control of either the host or pathogen can present particular problems when dealing with wildlife populations (Woodroffe 1999). Particularly as some important diseases infect multiple hosts, such as rabies, evoking the necessity for sufficient understanding of the conditions required for the persistence of the pathogen for the selection of the best strategies (Haydon *et al*. 2002). To assume that diseases can be treated in the same manner in wildlife as they are in domestic species would be largely incorrect (Artois *et al*. 2001).

(a) hosts and reservoirs

  The most widely used method to manage disease has been to target the host and reduce the population density. This is usually achieved via culling, fertility control or dispersal through translocation (Delahey *et al*. 2009). Focusing management strategies at a wildlife host or reservoir can be more challenging than focusing on a domestic population as access is limited and signs of infection and disease can be difficult to assess (Artois *et al*. 2001). Long-term monitoring is often needed to gain a

full understanding of population size, rates of morbidity, mortality and population recovery (Randall *et al*. 2006).

To control DFTD the management team decided to segregate young healthy devils from a genetically diverse area, into quarantine centres and trial the culling of sick animals to reduce the transmission to other susceptible devils (Hawkins *et al*. 2006).

(b) pathogen

The most direct strategy for controlling a disease is to eliminate its cause (Wobeser 1994). Techniques can be used to reduce the reproductive rate of pathogens to control disease in wildlife. This can be done by limiting the number of individuals that are susceptible to the pathogen by vaccinating the population or treating infected individuals (Delahey *et al*. 2009). The use of an effective vaccine to combat rabies in Europe resulted in a dramatic decrease in rabies cases but persistence in areas where the vaccine was not used (Artois *et al*. 2001).

A BCG vaccine is being developed for oral bait delivery to tackle the issue of the bTB reservoirs in the European badger and the wild boar (*Sus scrofa*) (Ballesteros *et al*. 2009; Delahey *et al*. 2009).

Treatment of diseased animals has been used in cases for endangered species using antibiotics or anti-parasitic drugs. It is an expensive strategy and one that is only used in rare cases. The Mountain Gorilla Veterinary Project monitors the health and treats illness in individual mountain gorillas (*Gorilla gorilla beringei*) but only after serious consideration of many factors such as age and genetic value to the group (Delahey *et al*. 2009).

(c) transmission route

The environment that a pathogen and host occupy may be open to manipulation as a management tool for disease control. The Brown rat (*Rattus norvegicus*) is known to be the carrier of many zoonotic diseases, such as, toxoplasmosis, hepatitis, leptospirosis, some of these may be passed onto livestock via rat faeces and urine (Webster & Macdonald 1995; Simpson 2002). Rodent proofing farm buildings can reduce direct and indirect transmission and clearing refuse patches and overgrown areas can reduce the local rat population (Delahey *et al*. 2009).

In Australia, increased habitat fragmentation was predicted to result in the extinction of Chlamydia from wild koala (*Phascolarctos cinereus*) populations, however, this

would also increases the risk of extinction for koalas. The delicate balance between agent and host is evolved over time and interfering with this relationship may not always be to the hosts benefit (Augustine 1998; O'Brien *et al*. 2006).

Management of disease through changes in the transmission route can also be achieved through changing behaviours, such as increasing bio-security (Horan *et al*. 2008). White-tailed deer (*Odocoileus virginianus*) are hosts of chronic wasting disease, Lyme's disease and bTB and VerCauteren *et al*. (2006) work on strategies to prevent contact between the deer and domestic livestock for the USDA. A physical barrier such as a fence of the correct design can be a powerful tool in preventing the transmission of diseases between wildlife and domestic animals (VerCauteren *et al*. 2006).

(3) Prevention, control or eradication

Management teams have to decide as to what level they want to manage the target disease, be it the prevention or control, or local or global eradication of the pathogen. Wobeser (1994) stresses the need to define clear differences between these strategies.

Prevention = proactive strategies that are aimed at averting the introduction of a disease into unaffected areas, individuals or populations (Wobeser 1994). Quarantine for domestic dogs travelling between countries has helped keep the UK a rabies free area.

Control = activities designed to reduce or maintain the prevalence of a disease to a tolerable level. This includes finding the balance between cost and benefit to stakeholders with an understanding that some level of disease will persist with the consequence of continuous disease control management (Wobeser 1994; Artois *et al*. 2001).

Eradication = involves the total elimination of a disease, ensuring an absence of continued transmission. This would usually have a time limit and designated area and require extensive resources. For eradication to be a success the correct identification of all sources/reservoirs of infection most be known, which is not always as necessary for prevention or control strategies (Wobeser 1994; Delahey *et al*. 2009).

The choice of management level decided upon will depend on the particulars of each disease problem and more importantly, on the correct identification of the reservoirs of infection and budget available (Delahey *et al*. 2009).

(4) Evidence based action

Sutherland *et al*. (2004) believe that an evidence based approach to conservation biology would guide more productive results and reduce costly mistakes, rather than relying on anecdotal ideas. Many researchers suggest that the discipline if wildlife disease management would also benefit from a similar approach (Woodroffe 1999; Artois et al. 2001; Randall *et al*. 2006; Delahey *et al*. 2009). Randall *et al*. (2006) state that the information required to develop and evaluate sound strategies for wildlife disease management is often lacking. Artois *et al*. (2001) suggest that the deficiency in knowledge may be due to findings not being published in peer reviewed journals.

Wildlife disease managers have not always acknowledged the importance of the need to understand and accommodate the ecological complexities of wildlife within their strategies (Delahey *et al*. 2009). The findings of the Independent Scientific Group (ISG) (2007), in their report on bTB and badgers, demonstrated the fundamental importance of understanding host ecology and social behaviour.

Haydon *et al*. (2002) emphasize the importance of understanding disease dynamics, ecology and behaviour in both the host and target populations and their relative significance to the development and implementation of management strategies. Details of the demographics and epidemiology are crucial but often require intensive, long-term monitoring and identification of individuals but can allow for the assessing of the severity of the disease and population recovery (Randall *et al*. 2006).

Time, however, is rarely a luxury in this discipline and is much more likely to be a limitation. There may need to be a trade-off between gaining a full understanding and the speed of the intervention required. The rapid response required to mitigate the threat of extinction of the Tasmanian devil to DFTD has meant that action has had to be taken before the epidemiology and ecology has been fully understood. (Hawkins *et al*. 2006).

When time is more of a luxury, due to the lack of an immediate danger from a pathogen, a strong preventative management strategy can be developed. In Canada, time was taken to create a policy that was of accord with stakeholders requirements that would prevent any spill-over of bTB from Wood Bison into the cattle industry (Nishi *et al*. 2006).

The monitoring of wildlife populations can be difficult and time consuming, Randall *et al*. (2006) highlight that carcasses are difficult to find, they can disappear quickly or

are too decayed for diagnostic analysis when discovered. Mathematical modelling is emerging as a very powerful tool within wildlife disease management helping to focus attention on the elements which are worthy of consideration over those that are not by predicting likely outcomes of a number of strategies when time constraints on research do not permit field trials (Suppo *et al*. 2000; Caley & Ramsey 2001; Smith & Wilkinson 2003; Macdonald *et al*. 2006; Sterner & Smith 2006; Horan *et al*. 2008). The Ethiopian Wolf Conservation Programme used predictive modelling to evaluate disease risk and to develop their disease management strategies (Randall *et al*. 2006). Plans for the distribution of fox rabies vaccine baits in Ontario were helped by spatial simulation modelling before finalising plans (Artois *et al*. 2001).

Artois *et al*. (2001) and Simpson (2002) suggest that there may be a deficiency in training in wildlife disease, for biologists and veterinarians. Artois *et al*. (2001) found it important to note that within the report from the House of Commons Agriculture Committee in 1999 there was a concern expressed over the attitude of 'veterinary workers' towards the 'scientific approach and science-based policy' and that they should accept 'the limitation of knowledge and the need for scientific underpinning' for policy decisions.

A multi-disciplinary approach to wildlife disease management may facilitate more productive results with more knowledge and expertise (Simpson 2002; Delahey *et al*. 2009). For example, the ISG combined experts in veterinary science, ecology, epidemiology, statistics and economics when investigating the effects of badger culling on the instances of bTB in cattle in the UK.

(5) Politics

Evidence based science is however only part of the battle to manage wildlife diseases. The final decision about which management strategy to use will not be made by wildlife professionals or scientists. Socio-economic and political factors will also drive the decision which will be made by politicians (Artois *et al*. 2001; Nishi *et al*. 2006). The public have quite a sway on decisions in managing wildlife disease. The decision to translocate animals in the fight against bTB in Canada was thwarted by public opposition (Nishi *et al*. 2006). Macdonald *et al*. (2006) highlights that the UK tax-payers, who fund farm payments, would surely have a view on removing badgers from large areas of the countryside. Artois *et al*. (2001) discuss how turning sound scientific evidence into policy can be hindered by the opinions of others. For example,

stakeholders involved in the bTB debate have opposing views, animal lovers will not accept culling on moral grounds and the cattle industry, supported by many veterinarians, see it as a necessity. With this in mind, social factors can have a profound influence on the success or failure of disease management.

IV. MANAGEMENT STRATEGIES

(1) Manipulating host population size

  Reducing infected and susceptible individuals in a population can help with density dependent transmission and contact between wildlife and domestic animal populations (Artois *et al* 2001). This can be achieved by culling or restricting the reproductive rate of the target population through fertility control measures.

(a) culling

  Culling can be achieved by different methods, trapping, shooting, gassing or poisoning of infected domestic animals or wild animals (Artois *et al*. 2001). Culling has been used to attempt to control bTB in badgers in the UK, Rabies in the red fox throughout Europe, rabies in striped skunks (*Mephitis mephitis*) in America and Classical swine fever (CSF) in wild boar in France, Germany and Italy (Wobeser 1994; Artois *et al*. 2001).

  For bTB, lethal controls on wildlife reservoirs have provided some degree of success. In the 1980s the culling of water buffalo (*Bubalus bubalis*) and feral cattle (*Bos taurus*) was an integral component of the eradication programme in Northern Australia (Cross *et al*. 2007). Elsewhere in the world the testing and slaughter programmes in cattle herds have achieved successful control of the infection in most developed countries, though it has proved a persistent problem in parts of the UK, Ireland and New Zealand (McDonald *et al*. 2006), countries which have a persistent wildlife reservoir (Macdonald *et al*. 2006; Delahey *et al*. 2009). In the UK the disease was mostly under control apart from a few localised areas of the south west by the mid 1960. In 1971 a dead badger was found to have bTB and culling via gassing of setts started (Simpson 2002). Due to welfare issues this progressed onto the trapping and shooting of badgers but this has failed to control the disease which has seen an annual increase in prevalence of 18% in cattle (Simpson 2002; Macdonald *et al*. 2006). In England, Scotland and Wales the European badger is protected by conservation legislation, making culling a contentious issue (Cross *et al*. 2007).

However, as a result of the Krebs report in 1997 the Randomised Badger Culling Trail (RBCT) by the ISG took place (Mcdonald *et al.* 2006). Although the culling of badgers successfully reduces bTB in cattle in the areas that are culled, it increases the incidence of bTB in the adjoining areas (Donnelly *et al.* 2006; Independent Scientific Group 2007). Jenkins *et al.* (2010) have revealed however, that this reduction was not a sustainable one in the long term after culling had ceased. Smith *et al.* (2001) found that though culling was successful within their model, vaccination programmes would also work.

  Culling can also have important ecological side effects as removing a carnivore from a food web can induce competitive release resulting in an increase in other carnivores (Cross *et al.* 2007; Trewby *et al.* 2008).

  In New Zealand, poisoning and trapping are used on an on-going basis to control populations of brush-tail possums (*Trichosurus* vulpecula) that act as the reservoir for bTB there, transmitting it to deer and cattle (Cross *et al.* 2007). However, culled brush-tail possums populations recovered via compensatory reproduction and population growth (Delahey *et al.* 2009).

  Using culling to control CSF in Europe was hindered by the effects of hunting. Modelling implied that hunting practise enabled the disease to persist where it would die out should hunting be banned. Hunting promotes dispersal amongst infected herds, increasing transmission rate, it also removes any exposed but immune or vaccinated individuals and promotes compensatory reproduction, bolstering the population with susceptible individuals. With the end of culling and the ban on hunting in the presence of CSF, infected animals would die and immune animals survive sustaining the infection below the threshold required for maintenance (Artois *et al.* 2001).

  The culling of foxes in Europe, in the early 20th century, did not control rabies and the vaccination started to be investigated as an alternative (Lloyd 1976). Caughley and Sinclair (1994) suggested that compensatory reproduction and immigration may thwart a number of culling programs. Reducing the recruitment rate to maintain the population at the desired level could be achieved by fertility control programs and many strategies are moving toward its use (Artois *et al.* 2001)

(b) fertility control

  As a non-lethal technique for managing wildlife populations, fertility control is less controversial than culling although a slower and more lengthy process. While it is used to control pest species and Tuyttens and Macdonald (1998) suggested the sterilisation of badgers for the control of bTB. There is little evidence of fertility control being used as a sole strategy for controlling disease (Jacob *et al.* 2008; Rutberg & Naugle 2008). As fertility control only reduces the number of new individual uptake into a population it does not deal with susceptibility to pathogens, the individuals' already diseased or further transmission. Smith & Wilkinson (2003) use fertility control combined with vaccination within their predictive model for controlling rabies in red foxes against alternative methods of vaccination alone or culling. Vaccination combined with fertility control was found to be more effective than vaccination alone. It is believed that the use of fertility control will increase the effectiveness of vaccination programmes as it restrains the recruitment of new susceptible individuals to the target population (Delahey *et al.* 2009). As a means of reducing population levels, fertility control has advantages over culling as it does not remove individuals from delicate social structures. Fertility control can, however, induce behavioural changes with unknown consequences seen in Caley and Ramsey's (2001) report, their model found a 28% increase in the transmission of leptospirosis in brush-tail possums using female sterilisation.

(2) Immunisation

  Vaccinating individuals within a population also reduces the number of susceptible animals and controls the disease by controlling the threshold population level required for disease persistence (Artois *et al.* 2001). For the strategy to be successful a sufficient proportion of the population need to be vaccinated during a particular period of time. In fox vaccination programs models showed that where there was a sub-optimal number of vaccinated foxes this led to the slowing of natural spread of the infection but extend the duration of infection. In this case, increasing the number of individuals vaccinated would lead to the disappearance of rabies from the area (Artois *et al.* 1997; Tischendorf *et al.* 1998).

  In Ethiopia domestic dogs are the known reservoir for rabies and are the most abundant carnivore, with population levels well above the threshold needed for rabies persistence. Vaccination of the domestic dog population was a management option in

this case but proved problematic due to cultural attitudes of dog handling, a high population growth rate and missing out the families that translocate seasonally, proving the strategy to be logistically and financially difficult (Randall *et al.* 2006). In conjunction with this an emergency vaccination trial in Ethiopian wolves was necessary and restrained the spread of the rabies epidemic. Models suggested that only 20%-40% coverage of vaccination in the wolves would reduce their risk to extinction considerably. This protected individuals and whole packs from rabies infection and stopped the spread of the outbreak (Randall *et al.* 2006). However, failure of a vaccine to protect against rabies has been recorded in wild and captive African wild dogs (*Lycaon pictus*) leading to the hypothesis that booster doses may be required (Randall *et al.* 2006).

 Vaccines for anthrax have been developed for cheetah (*Acinonyx jubatus*), black rhino (*Diceros bicornis*) and roan antelope (*Hippotragus equines*) (De Vos *et al.* 1973; Turnbull *et al.* 2004). The delivery systems for these vaccines involved aerial delivery from a helicopter or sedation of the animals, both of which carrying issues. Trapping is logistically difficult, demanding, expensive, time consuming and involves a potential risk to animals, oral bait delivery is being developed as an alternative method for many vaccines (Randall *et al.* 2006; Cross *et al.* 2007). Considered, less intrusive and more economical, oral bait vaccines are popular but dependent on the development of an efficient immunogen, a suitable delivery system, and a species-specific bait. Rabies persists in different variants and in an array of taxa, this is evidently true for striped skunks for which the current available vaccine is ineffective causing control problems in North America (Cross *et al.* 2007).

 Vaccines are also being developed for bTB and brucellosis to control wildlife reservoirs (Cross *et al.* 2007). However, vaccination of wildlife against brucellosis has not been as successful as rabies vaccination (Davis & Elzer 2002). bTB has spread from African buffalo (*Syncerus caffer*) to lion (*Panthera leo*) populations in the Kruger National Park in South Africa (Michel *et al.* 2006). Vaccination of the buffalo populations has been considered to alleviate the problem in the parks herbivores and lions (Cross *et al.* 2007). It is suggested by Cross *et al.* (2007) that oral vaccination has possibilities in the wildlife disease management for corvids that carry West Nile virus (WNV) in the U.S.A. and migrating anseriforms to control H5N1 avian influenza.

(4) Behavioural modification

The change of behaviour of humans, domestic animals or wild animals can be an effective and less costly strategy than other methods of controlling wildlife diseases. WNV infects humans, domestic animals and a large variety of wildlife. In the United States advice leaflets were distributed to the public with suggestions of precautions that could be implemented to help combat the mosquito born disease. These suggestions included the removal of any standing water to hinder mosquito reproduction (CDC 2009). In the fight against bTB, cattle-to-cattle transmission is a problem and changes in farm management such as bio-security provide an opportunity for solutions to transmission routes (MacDonald *et al*. 2006; Horan 2001). The ISG concluded in their report that bTB could be controlled by more rigid applications of more stringent approaches to cattle testing, diagnostics and movement controls (Independent Scientific Group 2007)

  Changing the behaviour of wildlife can consist of deterring them from areas where they come into contact with other susceptible animals. This could include dispersing animals more widely or using deterrent or scaring devices. In the USA hunters had recently taken to putting out large piles of feed to attract larger numbers of deer, however, in doing so they increased the contact and therefore the transmission of pathogens between the deer (VerCauteren pers. comm.). In response the USDA encouraged hunters to scatter the feed patches and use smaller quantities, to disperse the deer and reduce transmission instances (VerCauteren pers. comm.). Scaring devices can also be employed to deter deer away from cattle ranch feeding areas to reduce species-species transmission of pathogens (VerCauteren pers. comm.).

(5) Combining strategies

The methods mentioned within this review all have their limitations and a number of wildlife disease management teams and researcher are now suggesting that integrated management strategies would be much more effective (Suppo *et al*. 2000; Artois *et al*. 2001; Smith *et al*. 2003; Hawkins *et al*. 2006). Kaden *et al*. (2000) successfully combined oral vaccination alongside the culling of young on controls on CSF in wild boar in Germany. The Ethiopian Wolf Conservation Programme took a multi-disciplinary approach which resulted in an integrated disease management strategy. The programme used long-term population monitoring and disease surveillance,

modelling, a domestic dog vaccination programme and a rabies vaccination trial on Ethiopian wolves during an epidemic (Randall *et al*. 2006).

(6) Monitoring

Surveillance of disease in wildlife is poorly developed in most countries with few currently having their own wildlife disease surveillance network (Artois *et al*. 2001; Delahey *et al*. 2009). It is often the people on the ground, such as hunters or wildlife conservationists who report cases and remove sick animals (Artois *et al*. 2001).

The monitoring of disease in wildlife can encompass the use of sentinels. In the USA, wildlife surveillance programs identified relatively high disease prevalence in coyotes (*Canis latrans*), highlighting them as a potential sentinel species for detecting bTB prevalence in white-tailed deer (Atwood *et al*. 2007). Corvids and chickens have been used as sentinels for monitoring the progress of WNV across the United States (Komar *et al*. 2003; Brault *et al*. 2004).

The Devil Disease Project Team intends to monitor six sites including areas that are non-diseased, recently diseased and long term diseased. They will also monitor regions near the disease frontline with the aid of camera traps (Hawkins *et al*. 2006). The Ethiopian Wolf Conservation Group intend on monitoring disease in the species by radio collaring one wolf in each of the packs, ensuring the rapid detection of any outbreaks by observation of clinical signs and discovery of carcasses (Randall *et al*. 2006).

Epstein (2001) and Simpson (2002) maintain that global climate change will have implications for ecosystems and their pathogens, increasing the chances of emergence and re-emergence of pathogens and their vectors in new geographic areas and hosts.

It is widely believed that a system for the routine monitoring of wildlife needs to be in place as an essential tool for future wildlife disease management with greater co-ordination between national agencies (Krebs *et al*. 1997; Artois *et al*. 2001; Simpson 2002; Delahey *et al*. 2009).

IV. CONCLUSION

With the recognition of the role that wildlife can play in problem disease transmission has come a change in the understanding of the essentials of disease management. An in-depth understanding of the epidemiology of the pathogen and all the reservoir hosts and their related ecology are now accepted as requirements for

successful management and the selection of the correct strategies. Scientific evidence and lessons should be shared to assist the management of diseases now and in the future. Assumptions and anecdotes can cost a lot in time, money and sometimes in the welfare of humans and animals. Modelling is proving to be an invaluable tool to aid knowledge and decision making by researchers and managers.

With an increased likelihood of further emerging and re-emerging diseases coming with the change in global climate, there needs to be better and more co-operative surveillance and monitoring of pathogens and their related diseases. Wildlife disease management needs to move from a reactive crisis discipline to one of proactive planning. The knowledge divide between different disciplines (veterinarians, biologists, ecologists, statisticians, economists, modellers) needs to be mitigated by using integrated groups for disease management problem solving in the future, such as with the ISG.

Ultimately, the final decisions on wildlife disease management are made by politicians and policy makers.

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Section 3.

Research Project

Investigating territoriality and movement in *Meles meles*, in the context of wildlife disease management.

Investigating territoriality and movement in *Meles meles*, in the context of wildlife disease management.

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Summary

1. Badger movement may be of major significance to the spread and control of bovine tuberculosis in cattle. Fragmentation of social groups' structure in response to culling may exacerbate disease spread. Understanding the reasons why social group cohesion and territoriality may break down naturally and what the consequences are for rates of badger movements, may provide useful information in the context of natural social perturbation.

2. Bait-marking and live trapping data were used to investigate demographic factors that may influence movement or territorial changes at both population level and territory level.

3. There were more territories and more cross-boundary movements with increasing density. Males move across boundaries more than females, but female movement was more closely correlated with population density. Badgers moved more between setts when there was no territory boundary present compared to when there was.

4. Understanding what changes occur in the demographic constitution of social groups before territorial boundaries break down would be highly relevant to badger TB management in the context of when perturbation is triggered. The difference between the types of movement expressed within badger populations need to be taken account of and partitioned accordingly within investigations.

Key-words: bait-marking, bovine TB, dispersal, European badger, extra-group mating, *Mustelidae*, population size, ranging behaviour

Introduction

Over recent years, wildlife has been increasingly implicated in the epidemiology of persistent and emerging infectious diseases (Artois *et al.* 2001). Wildlife disease

managers have not always acknowledged the importance of the need to understand and accommodate the ecological complexities of wildlife within their strategies (Delahay, Smith and Hutchings 2009). Tompkins and Wilson (1998) did recognize that the study of wildlife diseases is relevant to a wide range of disciplines, including ecology, conservation biology and evolutionary biology. Understanding disease dynamics, ecology and behaviour in wildlife populations, and their relative significance to the development and implementation of management strategies has been emphasized by, amongst many others, Haydon *et al*. (2002) and Vicente *et al*. (2007). The findings of the Independent Scientific Group (ISG) (2007), in their report on bovine tuberculosis (bTB) and Eurasian badgers *Meles meles* L., demonstrated the fundamental importance of understanding host ecology and social behaviour, alongside the need to make efficient and effective management decisions.

Although many species carry diseases of importance to humans (Simpson 2002), some have more impact than others. Globally, bTB has been a problem for many countries (Caley and Ramsey 2001; Michel *et al*. 2006; Nishi, Shury and Elkin 2006). In the UK, bTB in cattle is a very serious economic and political issue, particularly in the South West regions (Krebs *et al*. 1997; Macdonald, Riordan and Mathews 2006). While bTB is carried by a broad range of mammalian hosts (Ragg, Moller and Waldrup 1995; Böhm *et al*. 2007; Delahay *et al*. 2007), robust evidence of the role that *M. meles* plays in transmission of the disease to cattle in the UK has been extensively reported (Donnelly *et al*. 2006; Macdonald, Riordan and Mathews 2006; Woodroffe *et al*. 2006; Mcdonald *et al*. 2007).

In much of the UK badger populations are arranged as large social groups, whereas elsewhere, individuals may live in pairs or even solitarily (Johnson, Macdonald and Dickman 2000). In Britain badgers display a high level of social organisation, mutually defending their group territories (Neal & Cheeseman 1996). Dispersal rates are considered to be low as groups are believed to be made up primarily of natal individuals with relatively few dispersals occurring between neighbouring groups (Kruuk and Parish 1982; Woodroffe, Macdonald and da Silva 1993; Rogers *et al*. 1998; Macdonald *et al*. 2008).

Rogers *et al*. (1998) found that an increase in the movement of individual badgers between groups was followed by a rise in the incidence of the disease in badgers of an undisturbed population. The possibility that badger movement may be of major significance to the spread and control of the disease has been highlighted by ISG

(2007) and Vicente *et al.* (2007). The perturbation of badgers from social groups that were subjected to culling in the ISG study, increased disease spread through wider ranging behaviour and increased animal to animal contact (Woodroffe *et al.* 2006; Donnelly *et al.* 2006). The fragmentation of social groups in response to culling practices has also been documented in wolves and dingo (Haber 1996; Wallach *et al.* 2009). Understanding the reasons why social group cohesion and territoriality break down naturally, and what the consequences of this are for rates of badger movements, may provide useful information in the context of natural social perturbation. The territoriality of badgers could therefore be an important factor in mitigating bTB spread through populations and is an important area of consideration in the management of badger populations for bTB control.

The movement of badgers between social groups and breakdowns in territorial boundaries and the consequent changes in territory number can be seen in the long-term wild badger study population of Woodchester park. Woodchester Park has the highest known badger density anywhere at 25.3 adults per km^2 in 1993 (Rogers *et al.* 1997). The study there also indicates that some territorial boundaries are stable over several years whereas others are not so stable, with territories varying between being highly defined and separate, to there being little evidence of territorial defence against neighbouring groups and seemingly becoming one larger merged group. Territorial changes have also been documented in an area of the South Downs over a 20 year period, but this study did not monitor the social groups yearly but only in 1970 and then 1990 and so observations of mergers or territory growth were not observed in between these years (Ostler and Roper 1998). The possible ecological and demographic triggers to territorial changes were not examined. Little other published data on this subject can be found.

Throughout its range, territoriality in badgers seems to become more defined as population density increases (Kruuk 1978a; Revilla and Palomares 2002; Kowalczyk 2004; Palphramand, Newton-Cross and White 2007). This may be due to increasing competition for limited resources. The high-density Woodchester Park population may therefore show heightened evidence for territoriality with increasing population size. It might also be biologically intuitive to suggest that the population size of the social groups may have an influencing factor on the need to expand the territory in some way, particularly under the belief that dispersal of individuals is low. Similarly, other demographic characteristics such as the number of males and females in the

group or the number of cubs to adults may influence this also. The movement levels of badgers may increase prior to social group merger or with increased population size. We might also expect to see increased movement between the setts in what were two clearly defined, separate group territories, when these territories become merged, and the field evidence of territorial defence disappears.

An investigation into factors that may influence territory boundary cohesion or breakdown and its relationship to badger movement in natural circumstances would clearly be important in understanding badger ecology for the purpose of disease management. Utilising 27 years of existing live trapping and bait marking data for the Woodchester Park badger population in Gloucestershire, this study aims to gain some inference to the underlying mechanisms that drive territorial changes by investigating group characteristics such as population size, sex ratio and the degree of movement at population and territory level.

Materials and methods

STUDY AREA

The data were collected from Woodchester Park, located in the Cotswolds in South West England. The area of study was approximately 7 km^2 and made up of mixed woodland, grassland and arable. Central to the study area was a steep sided wooded valley which was surrounded by agricultural grassland. The resident badger population occupied main setts that were relatively regularly spaced throughout the study area (Fig. 1).

BADGER TRAPPING AND PROCESSING

Data for this study comprised trapping records for intensively and consistently studied social groups at the study area from 1982 – 2008 inclusive.

Badgers were trapped under United Kingdom Home Office and Natural England Government licenses. Each social group was trapped four times per year, once per season. Trapping was suspended between late January and April to avoid disturbance during the final two trimesters of gestation and during the period when newborn, highly dependent young were present. Badgers were trapped using steel mesh box traps baited with peanuts and set after 4-8 days of pre-baiting. Traps were located at
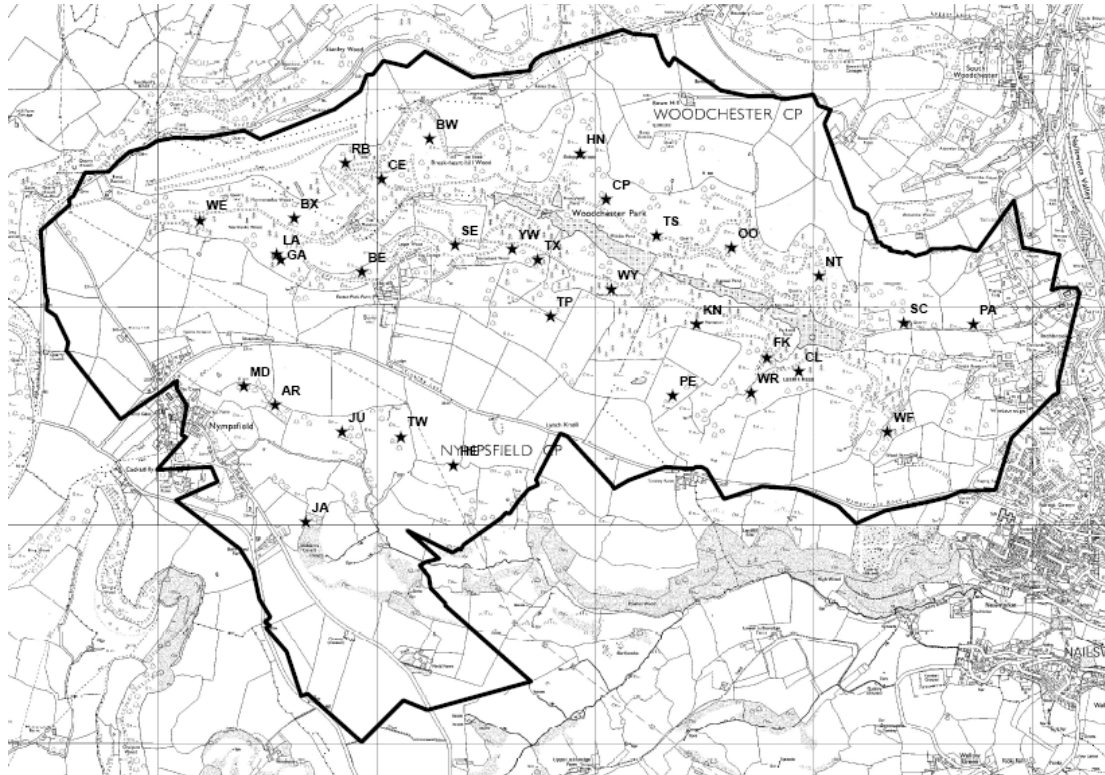
Fig. 1. Map of Woodchester Park, Gloucestershire showing the boundary of the study area and the main badger setts in 2008 (★).

the active setts in each territory. Trapped badgers were transferred from the traps into holding cages and transported to the sampling unit on site where they were anaesthetized for sampling and processing (See De Leeuw *et al*. 2004 for details). On first capture each badger was given a unique identifying tattoo on the belly. For each capture event, the location, sex, body weight, body condition, tooth wear, and the age class (<1 year = cub, 1 year ≥ adult) were recorded. Samples for laboratory studies were also taken. After a period of recovery all trapped badgers were re-released at the point of their capture the following day.

SOCIAL GROUP TERRITORY DEFINITION

The configuration of badger social group territories was determined in late February-April each year by bait-marking (Kruuk 1978a; Delahay *et al*. 2000). These months coincide with the spring peak in boundary marking behaviour (Roper, Shepherdson & Davies 1986). The only exception to this rule was in 2001 which was conducted in the autumn due to disruption from the foot and mouth outbreak. Bait-marking involved distributing a palatable bait of peanuts and golden syrup laced with small coloured plastic pellets for 10 days at the main sett of each social group. The pellets were harmless and indigestible and were passed in the faeces of badgers that consumed the

bait and subsequently identified in dropping latrines around the study area. Each social group main sett was fed pellets of a different colour and shape to identify the location that the bait had been consumed at. Boundaries between adjacent social group territories were characterised by the presence of latrines with droppings containing pellets fed to both or more groups. Extensive field surveying of the study area was carried out to record the locations of the deposits of the coloured pellets in the badger latrines. The distribution of plastic pellets at latrines and survey records of clear boundary runs for each year were digitised in the geographical information system, ArcView 3.2 and were used to define the best possible fit for the social group territories. An exclusive territory was considered present when there was strong evidence of territorial behaviour. This included bait returns in latrines on boundaries shared with neighbouring groups, evidence of visibly worn boundary runs indicating regular patrolling by badgers and minimal overlap of bait returns with neighbouring groups. Each year a small number of bait returns were excluded from delineated home ranges. These were single bait returns that were located deep within the territories of other social groups with no further evidence that the area was a shared territory between badgers from more than one sett (Delahay *et al*. 2000). Social groups were considered to be merged when the bait marking returns from each groups significantly overlapped, there were no or few shared latrines with badgers from the neighbouring sett and there was an absence of boundary runs. Bait-marking has been shown to present a good approximation of territories of badgers estimated from radio-telemetry (Kruuk 1978a; Delahay *et al*. 2000).

DATA ANALYSIS

Analyses were initially conducted at population level for years 1982-2008 to gain an overview of any demographic factors that may influence movement or territorial changes. As some areas of Woodchester Park are more prone to territorial mergers than others, further investigational analyses were conducted at territory level for years 1998-2008 to ascertain influencing factors. As merger was represented as a binomial response (merger = 1, non merger = 0) within the territory level analyses, too many non-merger years may have lost signal within the data. As the Woodchester Park population had had a relatively stable social structure up until the late 90's Data from 1982-1997 were excluded from the territory level analysis. Data from and inclusive of 1998 was used, this incorporated two years prior to the first observed merger year

(2000) within the selected years (1998-2008). Statistical analyses were conducted within R (version 2.6.2).

Population Level Data and Analysis

A number of GLM analyses were conducted in R. The numbers of territories and the amount of movement seen within the population were used as the response variables in separate models. Two-way interactions were included in the maximal models and model simplification by the removal of non-significant terms was conducted. Population size, sex ratio, adult/cub ratio were used as explanatory variables along with territory number and movement index scores in the models in which they were not the response variable. Data for population size, sex ratio and adult/cub ratio were taken from calculations for previous studies with the Woodchester Park data (N. Walker, *pers.comm*.). Population size was estimated using the POPAN procedure in Program MARK (White & Burnham 1999) version 6. Population size is estimated as a function of trap probability and number of animals trapped. This was done on a yearly basis giving annual population size estimates. The ratio of females to males was estimated by considering the number of females as a proportion of the total number of badgers within the core area. Adult/cub ratio was calculated in the same way and presented as the percentage of adults. Territory number was a count of the number of territories within the database within the study area for each year. Where merged social groups were present; these were considered as one territory.

Movement indices for each year were calculated using the trap data for individual badgers. Each badgers first capture was excluded as it was not possible to determine at what sett they had previously been. Individual scores were allocated at each trap event for each badger according to whether it was captured in a territory that was different to its previous capture (score=1) or not (score=0). The movement index was calculated as the percentage of movements within all captures for each year (movement index = total movements/captures x 100). All capture events were used to calculate the movement indices rather than just recapture events as these two different methods produced data that were correlated ($R^2 = 0.95$) and the use of all capture events took into account all trapping effort. Movement indices were then also calculated separately for males and for females for each year.

Time lags in the response variables of the GLM models were investigated at year *t*-1 and year *t*-2 in response to the explanatory variables. This was to examine any

possible biological delay in response to demographic factors in the two years prior to the response year.

Territory Level Data and Analysis

Based on the results of the social group territory definition methodology, using bait-marking maps from 1998-2008 and the evidence of boundary runs, seven pairs of social groups were identified as having historically merged territories for at least one year during the period (Table 1).

   GLMM analyses were conducted within R with binomial response variables of merged or not merged for each group throughout 1998-2008. Group and year were included as random effects. Two-way interactions were included in the maximal models and model simplification by the removal of non-significant terms was conducted. Adult sex ratio, group size and movement index scores were used as the explanatory variables. The data sets were formulated for the paired groups from the live trapping data. Group size was estimated from the number of individual badgers caught within each of the paired groups (e.g. Yew and Top setts) each year as a proxy for the population size of the paired groups. Adult sex ratio was calculated as the percentage of females in the group (based on captures) in relation to the total number of adults caught within each group each year. Movement indices values were calculated in the same way as for the population level analysis using data only from the traps at the appropriate paired social groups' setts for each year.

Table 1. Paired social groups, based on historic bait-marking maps and field observations.

Group	Social Group 1	Social Group 2	Year/s of territory merger between 1998 - 2008
1	Arthurs	Junction	2000
2	Cole Park	Honeywell	2006 & 2008
3	Kennel	Peglars	2008
4	Kennel	Wych Elm	2001
5	Old Oak	Nettle	2006
6	Peglars	Pontins	2002
7	Yew	Top	2004 - 2008

Results

BAIT MARKING MAPS AND TRAPPING

Bait-marking maps for 1998-2000 are supplied as examples within the supplementary material for this paper. The results of the bait-marking maps for 1998-2008 were used to compile the paired groups for the territory level analysis.

During the years 1982-2008 the number of badger territories identified in the study area fluctuated between 19 and 25. During the study a total of 13219 individual capture events took place involving 2658 individual badgers.

POPULATION LEVEL ANALYSIS

The movement indices for the whole population showed that movement varied over time, but that male movement did not vary in a pattern consistent with female movement (Fig. 2). Between some years there is a clear parallel increase, for example, years 1986 to 1987 and 1997 to 1998. However, during most of the period investigated male and female movements do not mirror each other, with a number of years showing opposing trends (1990-1991 and 1996-1997) (linear regression, $F_{1,25}=2.75$, $P>0.1$). There also did not seem to be a time lag response by either sex to the movement levels of either sex.
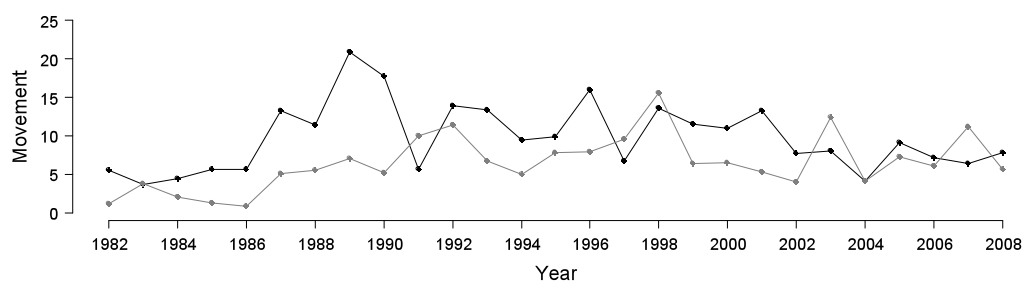

Fig. 2. The movement indices for males (black) and females (grey) for the whole population of Woodchester Park between 1982 – 2008 (including cubs).

An increase in the number of territories found in Woodchester park was positively correlated with an increase in the population size (ANOVA, $F_{25,26} = 20.6$ $P< 0.0001$) (Fig. 3).

Increased movement of badgers between territories was positively correlated with increased population size (ANOVA, $F_{24,25}=14.4$, $P<0.0019$). When the movement of males and females was analysed separately, this positive correlation remained but had higher significances for the movement of female badgers than for male badgers

(ANOVA, $F_{24,25}$=15.2, P=0.0006. ANOVA, $F_{24,25}$=7.7, P=0.01 respectively) (Fig. 4) with additional factors of sex ratio for females and adult/cub ratio for males, (ANOVA, $F_{24,25}$=6.0, P=0.02. ANOVA, $F_{24,25}$=6.2, P=0.019).

The investigations into possible lags in the reaction of the response variables to the explanatory variables can be seen in Table 2. Territory number seemed to continue to be influenced by population size for at least 2 years prior to the response year. These were all positive correlations.

Movement continued to be influenced by population size, though to a lesser degree each year, for 2 years prior year t. Male movement has a more significant positive correlation with population size in year t-1 than in year t, with no significant factors for year t-2. Whereas with female movement, population size drops below being a significant factor in year t-1, but then becomes significant again at year t-2.

TERRITORY LEVEL ANALYSIS

The movement indices for the paired groups within the territory level investigation again showed a lack of cohesion between male badger movement and female badger movement (Fig. 5 a-g). Some groups have a higher instance of movement by females than by males and other groups, vice versa. The movement patterns for the paired group Yew and Top, the only group that was recorded to have stayed merged for more than one consecutive year, shows a very different pattern again. Rather than the sharp peaks and troughs of movement seen in most of the groups, Yew and Top show continuous movement between the paired social groups' setts during the period when the territories were considered merged.

The GLMM with binomial errors (merged = 1 and non-merged = 0) found movement to be a significant factor (Chi = 9.8899, P = 0.0016) with a positive correlation suggesting that movement is increased when territories are merged. No other significant associations were found. Fig. 6 shows the model run without the random effects and with 5 outliers removed. Over-dispersion was tested for and not found. The fit of this model suggests that there are likely be other influencing factors determining the merger of social groups that were not included within this study.
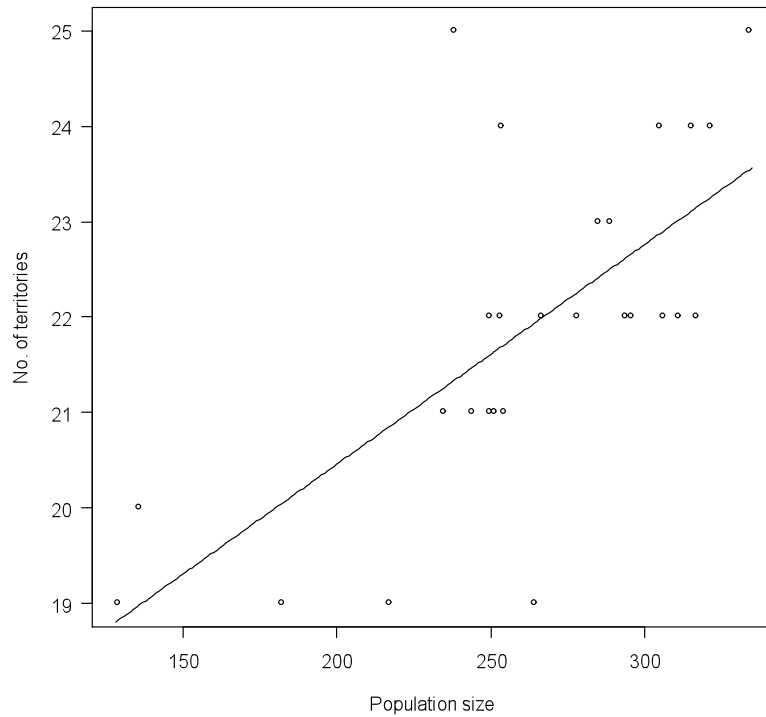
Fig. 3. Correlation between the population size of the study area of Woodchester Park and the number of territories observed there, n=27 years).
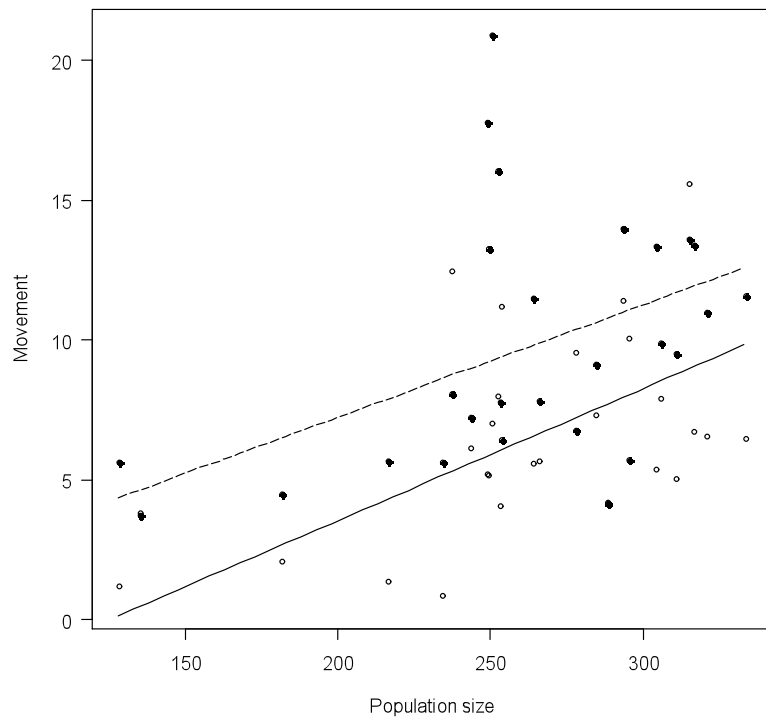

Fig. 4. Correlation for female badger movement between territories and population size ($\circ$,—) ($F_{24,25}$=15.2, P=0.0006) and the positive correlation for male badger movement between territories and population size ($\bullet$,----) ($F_{24,25}$=7.7, P=0.01) of the core area of Woodchester Park, n=27 years.

Table 2. Results from the GLMs to investigate possible explanations for the number of territories or amount of movement by badgers between territories, with the response variables lagged by 0 (year *t*), 1 (year *t*-1) and 2 (year *t*-2) years to examine any delayed responses to triggers in the previous years.

Minimum adequate model			d.f.	Model estimate	*F*-value	*P*
No. of territories (year *t*)	~	Population size	25,26	0.023	20.61	0.00012***
No. of territories (year *t*-1)	~	Population size	24,25	0.021	20.17	0.00015***
No. of territories (year *t*-2)	~	Population size	23,24	0.02	18.56	0.00026***
Movement (year *t*)	~	Population size	25,26	0.034	11.99	0.00193**
Movement (year *t*-1)	~	Population size	24,25	0.033	11.75	0.00222**
Movement (year *t*-2)	~	Population size	23,24	0.026	7.13	0.01367*
Male movement (year *t*)	~	Population size	24,25	0.04	7.7	0.0105*
		Adult/cub ratio	24,25	25.33	6.22	0.0199*
Male movement (year *t*-1)	~	Population size	24,25	0.042	8.29	0.0082**
Male movement (year *t*-2)	~	Population size	23,24	0.023	2.07	0.1636
Female movement (year *t*)	~	Population size	24,25	0.047	15.28	0.00066***
		Sex ratio	24,25	48.32	6.01	0.02188*
Female movement (year *t*-1)	~	Population size	24,25	0.025	4.09	0.05427
Female movement (year *t*-2)	~	Population size	23,24	0.028	5.68	0.02576*

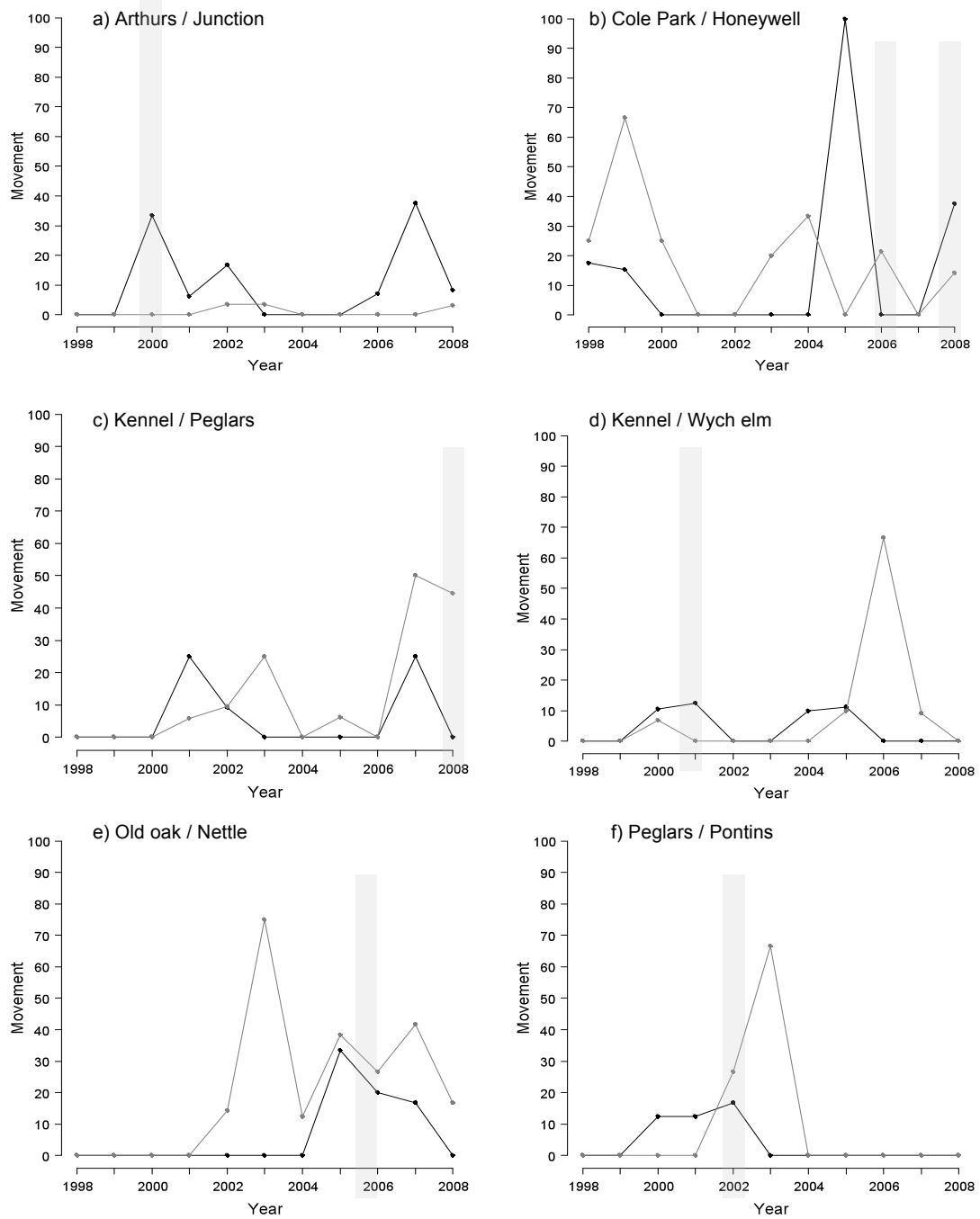* P < 0.05, ** P < 0.01, *** P < 0.001, **** P < 0.0001

Fig. 5. The movements between the paired social groups, males (black) and females (grey) with year/s of merger shaded in light grey.

a) Arthurs / Junction, 2000 merger

b) Cole Park / Honeywell, 2006 and 2008 merger

c) Kennel / Peglars, 2008 merger

d) Kennel / Wych Elm, 2001 merger

e) Old Oak / Nettle, 2006 merger

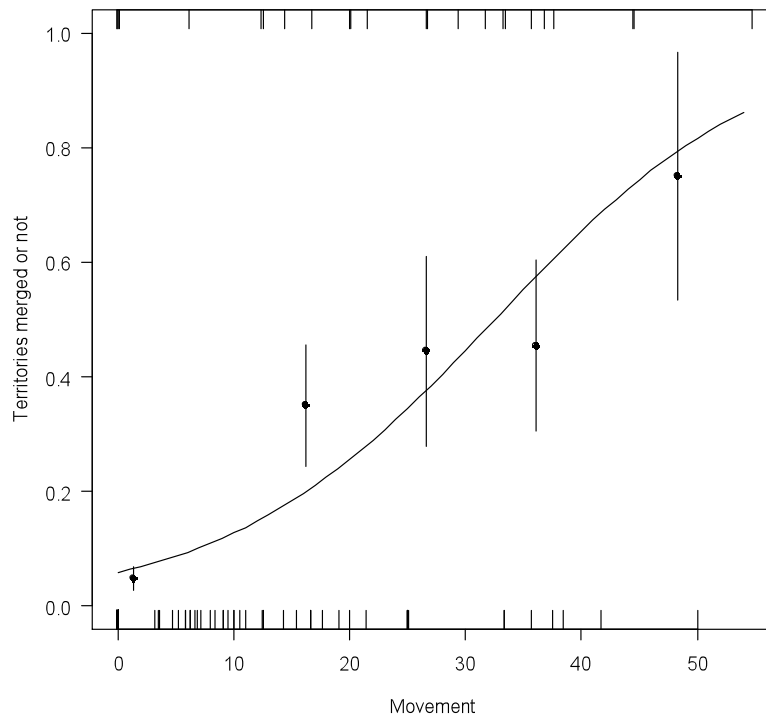f) Peglars / Pontins, 2002 merger

g) Yew / Top, 2004 – 2008 merger

Fig. 6. The correlation between the amount of movement between the setts in the paired social groups when the territories were merged (= 1) or not merged (= 0), fitted without the random effects and with five outliers removed, with the models empirical probabilities plotted along with their standard errors.

Discussion

The current study of a high-density badger population focused on identifying the main factors which may be associated with territorial changes and badger movements and investigate any relationship that there may be between them. In this study population size influenced the number of territories and the amount of movement seen within the whole of the study area. The movement levels seen in males and in females were significantly different to one another, were associated with the population size to differing levels and were further influenced by the factors of adult/cub ratio and sex ratio respectively. This clear distinction between the differing influences on the movements of the sexes could complicate the use of badger movements in any management or monitoring strategies. Further to this, it was found that movement between social group setts was greater when there was no evidence of territorial defence between the territories.

At the population level investigation, both territory number and movement rates between territories increased with population size. It might be expected therefore that the increase in the number of territories provides more opportunity for movement between territories, however, an increase in territory number did not correlate with an increase in movement and no interactions were found. This may highlight that an increase in movement is not due to an increase in the number of territories available to move between, but may be due to the rise in population size simply providing more individuals that have the potential to move. Nevertheless it is clear that an increase in population triggers more movement between territories. The increase in territories and therefore territorial behaviour could be in response to the increase in population as pressure for resources is increased. The positive correlations with population size remained when the response variables of number of territories and movement were lagged for year t-1 and year t-2. In both cases the response variables maintained significant associations with population size with the significance decreasing as the years were lagged. This suggests a steady relationship between the response variables and population size.

When the movements of badgers were looked at separately for males and females, differences between male and female movement were apparent and were suggestive of differences in the motivation of movement for the sexes. Fig. 2. shows more movement between territories by the males than the females of Woodchester Park with only five years showing higher movement by females than males. Despite this, female movement is much more strongly associated with population size than male movement in a given year. However, interestingly the strong association between female movement and population size ceases to be significant in year t-1 and becomes significant again in year t-2. It could be speculated that this is revealing of some sort of cyclic relationship between female movement and population levels that may be worthy of further study. It would be interesting to see if there is a cycle within cub production and if this is associated with female movement. For example, if there is a year of low cub production does this have an association with higher movement of females in the following year that are seeking mating opportunities? If this were the case it would suggest that population size is actually acting as a proxy for cub production. Male movement again sees a different result to that of female movement, in that, in year t-1 the significance of population size has increased and in year t-2 it ceases to be significant at all. This suggests that there may be a delayed response by

males to the increase in population size in the previous year (year *t*), possibly suggestive of a cascading effect of some kind.

In year *t* female movements were also positively correlated with sex ratio as well as population size whereas male movements correlated positively with adult/cub ratio along with population size. As sex ratio was represented as the percentage of females, an increase in the density of females resulted in an increase in the movement of females. Macdonald *et al*. (2008) found that females were more likely to disperse to groups with fewer females in them. The current studies results are suggestive that this may also be the case in Woodchester Park, as an increase in females may trigger the need to find a new territory containing fewer females. Kruuk and Parish (1987), backed up by Cresswell *et al.* (1992), states that reproduction is usually monopolised by one or two older members of each sex within a social group. Consequently competition for breeding rights is likely to be high and has been observed in female badgers in captive and wild populations (Kruuk and Parish 1987; Cresswell *et al*. 1992). Bite wounds in females are believed to peak in April and in November and December, these months coincide with lactation and implantation respectively and could be due to harassment from other females in an attempt to induce failed implantation, abortion or cub deaths (Cresswell *et al*. 1992; Roper 2010). In their observations of captive badgers Kruuk and Parish (1987) observed a female kill the cubs of her sister when she had a litter of her own, subsequently killing the sister and breeding for six years afterwards with a number of non-breeding females in the group. On occasion females have been observed to breed soon after joining a new group (Woodroffe, Macdonald and da Silva 1993). However, dispersal by females does not necessarily equal the chance to breed (Macdonald *et al*. 2008).

It is likely that male movement is also dictated by the drive to reproduce. Adult/cub ratio was the secondary factor in explaining male movement and was represented as the number of adults. Consequently, an increase in the density of adults at population level was associated with an increase in the movement of males between territories. This could have been a reaction to there being more competition for mating and/or there being more opportunity for mating. Woodchester Park was believed to have a female biased adult population in the Rogers *et al*. study in 1997. It has also been hypothesised that the use of latrines by females for scent marking may not be for the purpose of warning off outsiders but actually for the purpose of advertising their breeding availability to passing males (Roper 2010). If an increase in adults alongside

an increase in the population triggers increased movement in male badgers and Woodchester Park tends to have more females to males overall, it could be fair to speculate that this increase in male movement may be in response to an increase in breeding opportunity. Rogers *et al.* (1998) similarly suggested that male movement may be motivated by the availability of reproductively mature females. However, this scenario should also prompt an association with sex ratio and this was not seen in this study. Therefore, the males may simply be reacting to an increase in competition for mating opportunities. It might be of interest to break the population level analysis down into monthly data points as opposed to yearly data points. This may provide a more in-depth understanding of the movement patterns and their potential drivers, for example does male movement correlate more strongly to population size and adult/cub ratio during the mating seasons of spring and autumn (Cresswell *et al.* 1992)? There is evidence of a bimodal pattern of road mortalities of badgers at these times of year (Davies, Roper and Shepherdson 1987) presumably as a result of increased movement.

As reflected in the interpretation of the results for this study the movement indices used did not differentiate between the different types of movement that badgers may be displaying. For example female movement having an association with sex ratio has been interpreted as females moving to groups containing fewer females than their previous group, thus moving permanently as dispersals. However, the interpretation of male movement having an association with adult/cub ratio attributed these movements to only temporary visits to neighbouring groups for mating opportunities. It is documented that males and females will both visit neighbouring social groups and both disperse (though to varying levels) (Woodroffe, Macdonald and da Silva 1993; Rogers *et al.* 1998). Badgers are known to take night foraging visits into other social groups territories and it may be that some of the capture events included in the movement indices figures may have been badgers exhibiting this behaviour and getting trapped at the neighbouring sett. Rogers *et al.* (1998) used a system of 'occasional movers', 'permanent movers', 'frequent movers' and 'non-movers' to classify the types of movement seen in badgers. Further investigation into the triggers of badger movements may benefit from a similar type of categorisation system to help differentiate between visits to neighbouring setts for foraging or mating, and visits with intent to disperse or that result in full dispersal. Carpenter *et al.* (2005) found that around 50% of cubs in Woodchester Park are fathered by extra-group males,

suggesting that there is far more movement occurring between social groups than is detected in the trapping record. To get a more accurate measure of fine-scale movements, whether temporary or part of dispersal, methods such as radio-tracking studies would have to be implemented as in Roper, Ostler and Conradt's study (2003).

The analysis of the data for the territorial level investigation did find that increased movement was correlated with merged territories as expected. If two social groups have become one then there should be free movement between those social groups' setts within the one territory, represented as an increase in the movement indices. This result is less clear when looking at the movement indices for each of the paired groups. It was expected that there would be a pattern of increased movement during the years of merger and possibly the years either side as the merger developed and waned. Yet this is only seen in two of the seven groups, Old oak/Nettle and Yew/Top (Fig. 5.e. and 5.g. respectively). In general, looking at the movement indices figures for each paired group, no clear pattern of activity of one kind or another around the years classed as mergers can be seen, except for these two groups. As previously mentioned at population level, males do seem to move more in general though movement itself is sometimes female biased and sometimes male biased within any one year. There are studies that show sex bias movement for both sexes (Woodroffe, Macdonald and da Silva 1993; Rogers *et al.* 1998). It might also be expected that in years of merger that both sexes would be moving freely between the two setts. With this in mind the movement indices (Fig. 5) may be more in accordance with the years classified as mergers. Peglars/Pontins only have one year where both sexes are moving, 2002, their merger year. Cole Park/Honeywell see movement from both sexes in 2008, a merger year but not in 2006, their other merger year, but also in 1998 and 1999, non-merger years. Whereas, Kennel/Peglars and Kennel/Wych Elm have movement from both sexes in the year prior to their mergers (2007 and 2000 respectively) but also in the non-merger years of 2001 and 2002; and 2005 respectively. Least in accordance were Arthurs/Junction that were merged in 2000 but only show movement by both sexes in 2002 and 2008. Looking at it in this way suggests that there may be some undetected years of merger or at least a closer relationship between some social groups than previously thought. It is previously suggested that the fit of this model in Fig. 6 may be due to there being other influencing factors determining the merger of social groups that were not included within this study. However, the interpretation of badger runs as boundary runs

alongside the bait-marking returns require highly skilled staff to decipher the territorial boundaries and remains a subjective process (Delahay *et al*. 2000). It may be that as part of the process of categorising social groups as merged involves some subjective opinion, all be it from very experienced field team members, that some mergers in some years may have been misclassified. Alternatively, the patterns seen in the groups movement indices could be due to a large amount of noise from various other factors. It may be good practice for the research team at Woodchester Park to review the merged/non-merged status of some of the groups for years where high/low levels of movement or movement by both sexes is observed in the movement indices used in this study. Certainly, any misclassified years could have influenced the results for this part of the study as merged/non-merged was used as the response variable. In the years where the movement indices corresponds most with the current classifications of merged/non-merged years female badgers seem to be moving more than males (Fig. 5.e,f,g.). Perhaps, the inclusion of the level of movement by both sexes, with emphasis on females, between the social groups might be included alongside the bait-marking maps and trap data to help determine the merged/non-merged status of neighbouring social groups in the future.

An alternative or inclusive explanation for the fit of the model could be that there may be some noise in the data created by the lack of differentiation between a move that is just a night foraging/breeding affair or a move that is indeed due to social group territorial merger. Movement may not necessarily indicate merger. Again, as with the population level investigation, breaking the movement indices down into months would help to know when the moves were happening and if they were related to mating behaviour or indeed if they were close to the end of a year that was not classed as a merger year and the following year was, based on bait-marking implemented in February.

There are two further limitations to the study undertaken at territory level due to the time constraints of this project certain variables were calculated in a less complex manner than would have been the ideal. Due to the way that adult sex ratio was calculated for the territory level investigation, the data set included figures of 100 percent females. It is clearly not realistic for a group to be without any males for a whole year, as represented in this data set, particularly in such a high-density population and this could have created bias in the data and influenced the resultant model. Secondly, group size was estimated from the number of individual badgers

caught within each of the paired groups (e.g. Yew and Top setts) each year as a proxy for the population size of the paired groups. This was a much cruder calculation than that used for the population level data and it does not account for trap shy badgers or visiting individuals. This crude measure of population may have affected the results seen in this analysis. If time had not been a constraint then these variables would have been better calculated in the same manner as that in the population level analysis data set.

If time were not a constraint on this study further analysis of the demographic make-up of the social groups that undergo changes could also have been implemented. The breakdown or re-appearance of territorial boundaries between social groups may be influenced by the presence of older, dominant boar badgers. Adult males are known to patrol the territorial boundary runs (Kowalczyk 2004) and to utilise the boundary latrines more than latrines situated further within their territory and more than females (Roper 2010). Alternatively, a dominant sow in a neighbouring group may have died allowing a take-over by females from the other social group (Woodroffe, Macdonald and da Silva 1993). Analysing the age classes and changes to it may give further understanding as to the triggers of territory mergers and splits. Adding to this data for 2009 and 2010 could also aid the understanding of this process as the paired group Yew/Top that were merged from 2004 to 2008 in this study, remained merged in 2009 but split up into separate groups again in 2010 (K. Palphramand, *pers. comm*; see supplementary material for territory maps).

Although the data treatment and model in these analyses did not take account of how many times an individual badger was caught, for the purpose of this study it was assumed that the animals caught and the level of movement recorded was a good representation of the whole populations trappability and moveability.

It may not be realistic to try to compare the two different levels of analysis undertaken in this study as one included the social groups from the whole study area and looked at movements between territories and the other focused on selected groups of interest and the movements within territories. It may perhaps be revealing to include paired social groups from Woodchester Park that have never had a merger within the territory level analysis. These may act as control groups within the analysis which would be important in ensuring that what is seen in the territory level results is actually due to merger and not simply a characteristic of these particular social groups. At population level, badgers may put more effort into territorial marking

behaviour when population increases. But at territory level, occasionally, individual territory boundaries breakdown and when that happens, badgers do move between the setts more than when there is evidence of territorial defence.

What is clear is that there are movements between social groups throughout Woodchester Park as has been seen in previous studies (Rogers *et al*. 1998; Vicente *et al*. 2007). Even though the bait-marking results are just a snap shot in time taken only once in the whole year; they undoubtedly serve to give a better picture of group mergers than the all year round trapping data (see supplementary material). Badger ranging behaviour is not necessarily an indicator of a territory merger. Studies have shown that badgers venture into neighbouring groups territories for foraging excursions (Roper 2010). But what makes this particularly interesting is the fact that these visits into a neighbour's territory are not met with aggression from the badgers whose territory it is that has been encroached upon (Roper 2010). Roper (2010) has observed badgers of both sexes foraging peacefully within the territory of a neighbouring group in the presence of members of that group without any challenges. The home ranges of individual badgers from the same social group have been shown to overlap extensively (Roper 2010) but also overlap to some extent into other groups territories (Garnett, Delahay and Roper 2005). Palphramand, Newton-Cross and White (2007) have shown that the home ranges of individual badgers change size seasonally, as do that of group ranges (Roper *et al*. 2001). Palphramand, Newton-Cross and White (2007) showed that home ranges were largest in autumn followed by the summer and spring and were in line with the seasonal availability of food. The home ranges were smallest in winter, when badgers are relatively inactive. Further to this Roper (2010) states that extra-territorial excursions for foraging purposes were rare in spring. This could be due to spring encompassing the breeding season when it is believed that there is more latrine use and heightened territorial behaviour (Cresswell *et al*. 1992; Roper *et al*. 1993). Roper (2010) concludes from this that territoriality is seasonal. Stating that it is a relaxed system with extra-territorial excursions permitted in summer and to some extent in autumn. If this is the case then this would potentially put badger movements at least in summer if not also in the autumn under different scrutiny to movements observed in the spring. The fact that territorial boundaries do not seem to be strongly maintained outside of the mating season makes determining how movements relate to territorial changes or mergers much more complicated. It also highlights the question of what time of year territorial

changes may occur. For example, changes may start to occur during the relaxed periods with confirmation of changes being communicated in the spring peak of latrine use. Badgers may take advantage of any opportunities observed during the relaxed period of boundary defence. Or indeed, as latrines are used most just after the mating period, perhaps dominant males establish their territories according to their mating successes of within group and neighbouring females.

Nevertheless, the maintenance of territorial boundaries in the mating season does not seem to deter moves into neighbouring territories completely. Cheeseman *et al.* (1988) found that males would travel into neighbouring territories during the main mating season of January to March. Further to this, bait-marking studies usually implemented during the spring season of activity, often find bait returns located deep within the territories of other social groups with no other evidence that they are part of a territory merger (Delahay *et al.* 2000; Roper 2010). Woodroffe, Macdonald and da Silva (1993) supposed that these transient excursions were associated with breeding. Indeed, these bait returns are believed to indicate excursions into neighbouring territories by badgers of both sexes in search of mating opportunities (Woodroffe, Macdonald and da Silva 1993). Carpenter *et al.* (2005) discovered that roughly half of the paternities that they could identify were attributed to males from outside the cubs' social groups in a Woodchester Park study. With further investigation into this with a different high-density population, Dugdale *et al.* (2007) revealed a polygynandry mating system with multiple paternity litters. Some litters had paternity from both within-group and extra-group males. This type of mating system has also been found in red foxes (*Vulpes vulpes* L.) in the UK (Baker *et al.* 2004), a species also subject to disease monitoring and management. Clearly the evolution of such a system prevents inbreeding and requires that individuals encounter members from other social groups for mating purposes. Roper (2010) suggests that the movement behaviours seen in badgers during the mating season have evolved as an inbreeding avoidance mechanism. These movements not only help to avoid inbreeding but are also for the purpose of increasing the individuals' chance of reproduction. As previously discussed, breeding within social groups is usually monopolised by one or two badgers of each sex, usually older members meaning that younger members have to wait for their chance to reproduce. However, individuals may use differing strategies to ensure reproduction. Carpenter *et al.* (2005) found that some males appeared to

father all their cubs in the group that they lived in; some fathered cubs solely in other groups and others had mixed strategies.

It has been suggested that movements in the form of permanent dispersals may allow badgers to queue jump for breeding rights within a group (Rogers *et al.* 1998). However, Macdonald *et al.* (2008) found that dispersal to a new group did not affect the likelihood of those females reproducing. Furthermore, females that have successfully bred in their natal group have been observed dispersing from that group (Roper, Ostler and Conradt 2003). Dispersal is considered infrequent and unpredictable with the majority of badgers never dispersing at all and remaining in their natal groups (Rogers *et al.* 1998). Even so, some of the moves recorded in this present studies movement indices may well have been part of dispersal behaviour. The Rogers *et al.* (1998) study at Woodchester Park reported a dispersal rate where approximately 56% of badgers were never observed outside of their natal group. Whereas Macdonald *et al.* (2008) found this to be just 35% at a different study site. Dispersers can be either sex or any age, but the majority are sexually mature badgers (Cheeseman *et al.* 1988). Roper, Ostler and Conradt (2003) reports the movements of badgers as they disperse to neighbouring groups, describing the process as prolonged and complex having observed five badgers move from one group to another over a period of nine months. The dispersals started with night time visits and after weeks of this the bagders started to spend longer periods at the new setts, progressing to day time sleeping and using outliers as temporary stopping posts, with the eventual incorporation into the new groups. This highlights that movements that may at first seem like night foraging visits could actually be part of a longer strategy of dispersal.

There have been many studies that have accessed the differences in dispersal rates for the sexes (Kruuk and Parish 1987; Cheeseman *et al.* 1988; Woodroffe, Macdonald and da Silva 1993; Christian 1994; Rogers *et al.* 1998; Macdonald *et al.* 2008). However, they have rarely found the same results. Some found that males were more likely to move than females (Kruuk and Parish 1987; Cheeseman *et al.* 1988; Rogers *et al.* 1998) whereas others found the reverse (Woodroffe, Macdonald and da Silva 1993; Christian 1994). Conversely, Macdonald *et al.* (2008) found no difference in the dispersal rates of the sexes. Though this present study could not determine dispersal rates, female movements seemed to be associated with the number females in a group and suggested the inclusions of some dispersal events within the movements. Woodroffe, Macdonald and da Silva (1993) found that male dispersals

declined when population density increased, though there was no effect on female dispersals. This current study similarly found that male movement was less associated with population size than female movement, but no inference can be made about dispersals due to all movements being treated in the same way. The consensus within the literature however, does seem to be that dispersals are not common place.

The use of boundary latrines by badgers seems to functions to mark the territory boundary and to potentially communicate information (Davies, Lachno and Roper 1988; Palphramand and White 2007). However, this behaviour does not occur in low density populations in the UK and bait-marking is not used in studies in Europe due to the lack of territorial behaviour and boundary latrine usage in badgers there (Revilla and Palomares 2002; Kowalczyk 2004). In High-density populations Roper, Shepherdson and Davies (1986) theorised that latrine use by badgers related to the defence of oestrus females within the territory. Cresswell *et al.* (1992) however, highlights inconsistencies in this theory as they observed that latrine use peaks in April and October, occurring after the main mating periods of January and August. Roper (2010) maintains that deposits of anal secretions at latrines are for the purpose of mate defence or attraction. That neighbouring social groups share boundary latrines is evidence however that latrines are used for some level of communication between badgers within and outside of the social group. Furthermore, Stewart *et al.* 2002 found that badgers visiting latrines would defecate on about 50% of the visits and the other 50% of the visits they would spend time sniffing defecation sites, urinate or deposit secretions, presumably a signal of further communication.

Very few observations of the establishment of new territories have been documented. (Ostler and Roper 1998) found in their study that new territories had emerged from 1970 to 1990 on a site in Sussex. More territories at smaller sizes were found with nearly twice as many social groups than 20 years previously. Roper (2010) documents the emergence of a new territory which was lead by a female taking up residence in an outlier on the edge of her original group territory and two other territories. A year later bait-marking revealed that it had become an established territory and had pushed back the boundaries of the neighbouring groups. This sett went on to become a breeding sett. No further explanation is given by Roper (2010) as to how territories may emerge or breakdown. With the setts Yew and Top at Woodchester Park having now, in 2010, split up again after six years of merger (K. Palphramand. *pers.comm.*), further investigation into how this might occur could be

investigated. Was this also led by a female re-establishing an old territory and boundary by establishing a new breeding sett or did a dominant male take up residence with a female using that sett and start to establish a boundary to attempt to defend the female from other potential mates? Unfortunately, purely trap records may not be able to answer these questions.

Determining what might drive this territorial behaviour may help in understanding how or why territorial changes occur. There are a number of theories suggested but none seem to explain the whole story. It was suggested by Kruuk (1978b) that territoriality was ultimately about the defence of food resources. This was further developed into the Resource Dispersion Hypothesis (RDH) by Macdonald (1983). Alternatively, Roper, Shepherdson and Davies (1986) suggested that territoriality was more to do with reproduction than food resources with the Anti-Kleptogamy Hypothesis (AKH). This proposed that territoriality was a mainly male activity to prevent other males from accessing the females in the group for breeding. This was prompted by the observation that latrine use peaks in spring and autumn, the main mating seasons (Roper, Shepherdson and Davies 1986; Delahay *et al*. 2000). However, AKH only accounts for territoriality in males. Females in other mustelid species are territorial (Johnson, Macdonald and Dickman 2000) and Roper *et al*. (1993) found that females scent mark more in latrines close to the sett than at boundary latrines. The main sett is a breeding resource for which there is competition within the group already, so it would make sense to defend it against intruding females. Alternatively, offspring-defence hypothesis has been suggested as an explanation for territoriality in female mammals (Wollf and Peterson 1998). Infanticide amongst female badgers is briefly mentioned by Roper (2010), although he states that evidence is sparse. Non-mobile, dependent young that are deposited in a protected den site, as seen in badgers, is found to be a common trait of species with female territoriality (Wollf and Peterson 1998). Wollf and Peterson (1998) found that the timing of female aggression and territoriality appeared to be more closely associated with lactation than with food resource availability. This is in line with the findings of Cresswell *et al.* (1992) that aggression between female badgers is highest in April.

Whereas one theory alone does not fully explain the movements and territorial behaviour of badgers, there are likely to be different drivers on the activity of males and females, this is suggested in the results of this study. Where males may be

concerned with the acquisition of mates, females may mainly be concerned with the defence of offspring and breeding resources (the sett). Food resources are likely to be defended by both sexes, particularly females as food is important for reproduction and rearing.

Additionally to these theories is the observation that territoriality does not seem to occur in lower density populations (Cresswell *et al*. 1992). Cheeseman *et al*. (1993) observed the re-colonisation of an area cleared of badgers and the defence of territories only seemed to occur once a population reached a certain density. Suggestive that territorial behaviour may also be in response to heightened competition for resources.

Research done by Vicente *et al*. (2007) supports the idea that a stable social structure in badgers mitigates against new incident cases of bTB. Rogers *et al*. (1998) found that infection status was not important in determining which badgers moved and when but that variation in the frequency of movement between social groups may be linked to transmission of bTB between social groups. A correlation between bTB excretion status and ranging behaviour has been found by Garnett, Delahay and Roper (2005) who found that tuberculous badgers were likely to extend their ranging into a neighbouring area by four times that of an uninfected badger.

It has been shown that local reductions in badger density, via culling, can cause rapid changes to badger ranging behaviour (Cheeseman *et al.* 1993).

This study has gone some way to investigate associations with the natural movement of badgers, in a high-density population. There were more territories with increasing density and more cross-boundary movement with increasing density. Particularly revealing were the differences between the movement of males and females and the potential causes of those differences. Males seemed to move across boundaries more than females, but female movement was more closely correlated with population density. In the paired social group territories, badgers moved more between setts when there was no territory boundary present compared to when there was. This indicates that the bait-marking results illustrate something about badger territoriality.

The question as to why territories may sometimes seemingly merge or split has not been sufficiently answered within this study and numerous suggestions have been made that may help in further investigation into this complex matter. Most importantly the difference between the types of movement expressed within badger

populations need to be taken account of and partitioned accordingly within investigations. Understanding what changes occur in the demographic constitution of social groups before territorial boundaries break down would be highly relevant to badger TB management in the context of when perturbation is triggered. As avoiding the exacerbation of this movement could mitigate increases in disease spread through future badger control strategies.

It is hoped that this study further highlights the complexities in and the importance of the understanding of wildlife ecology in the management of wildlife diseases.

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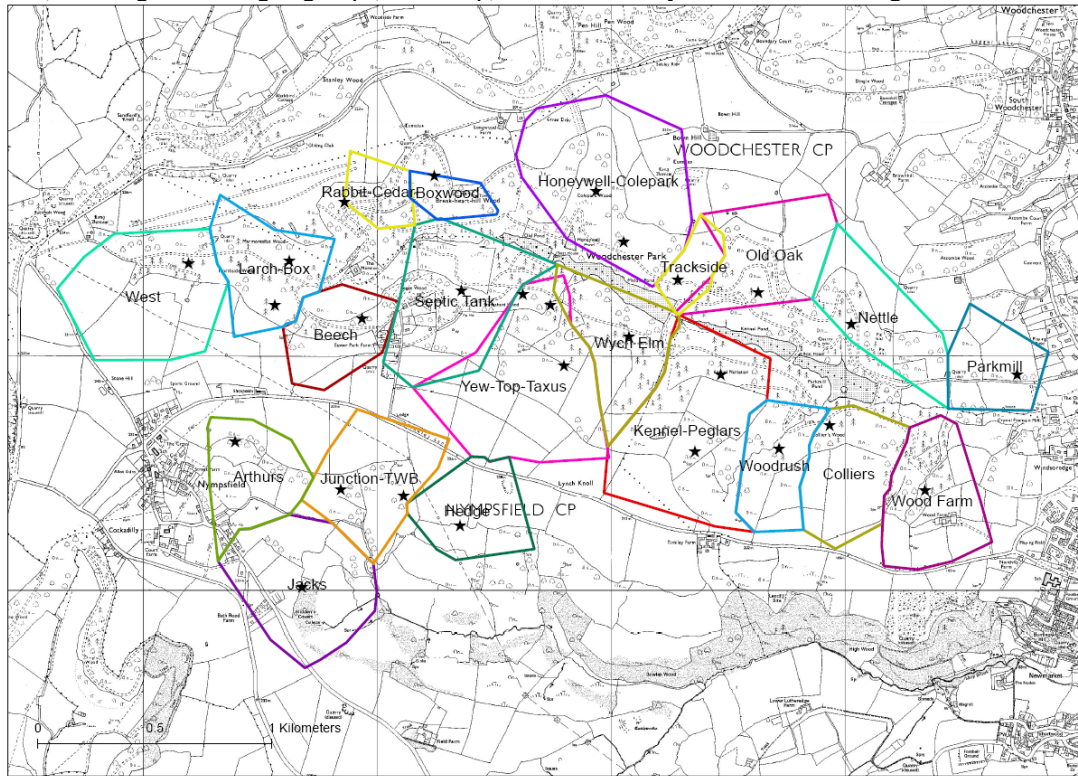
Supplementary material

Example of bait-marking maps 1998, 1999 and 2000, showing the bait return spooks from the main sett to the latrines where the returns where found.
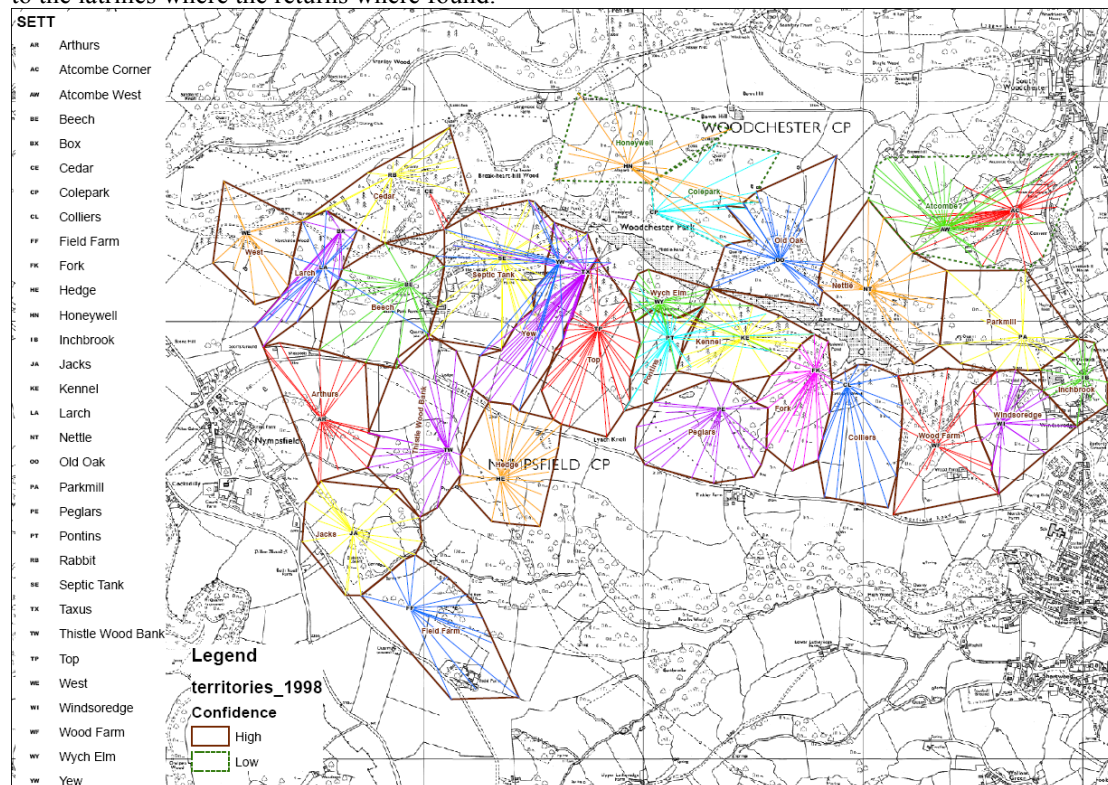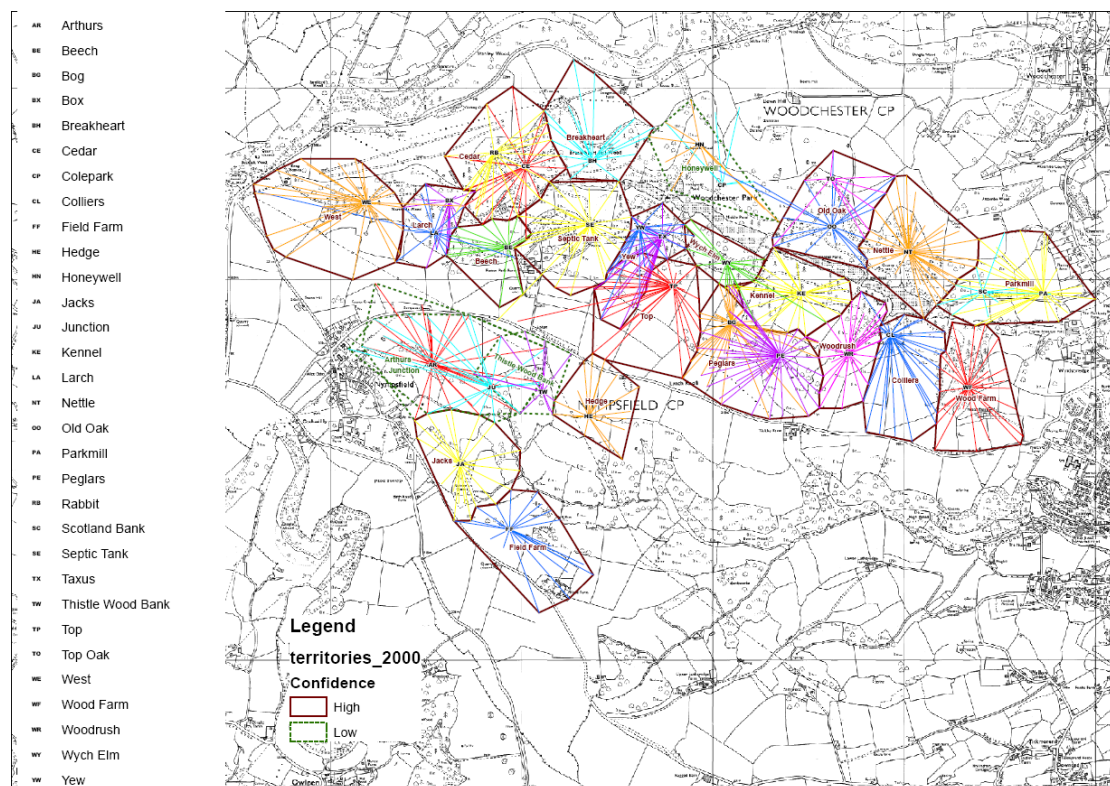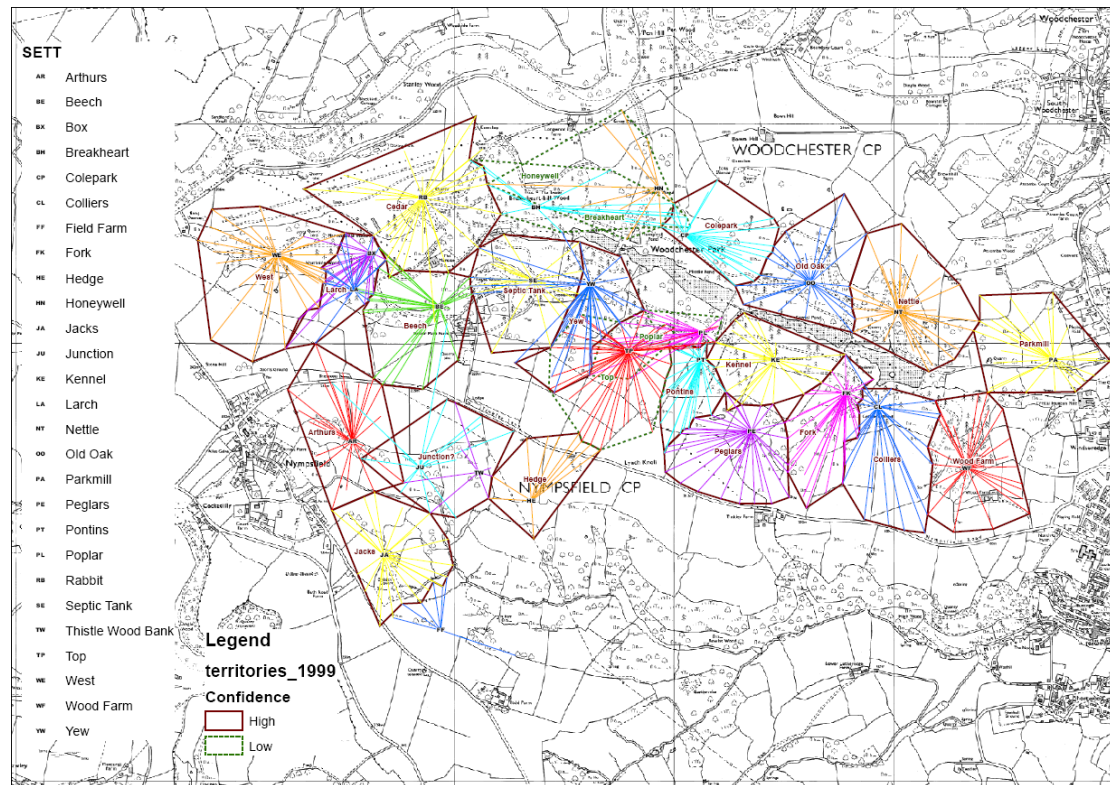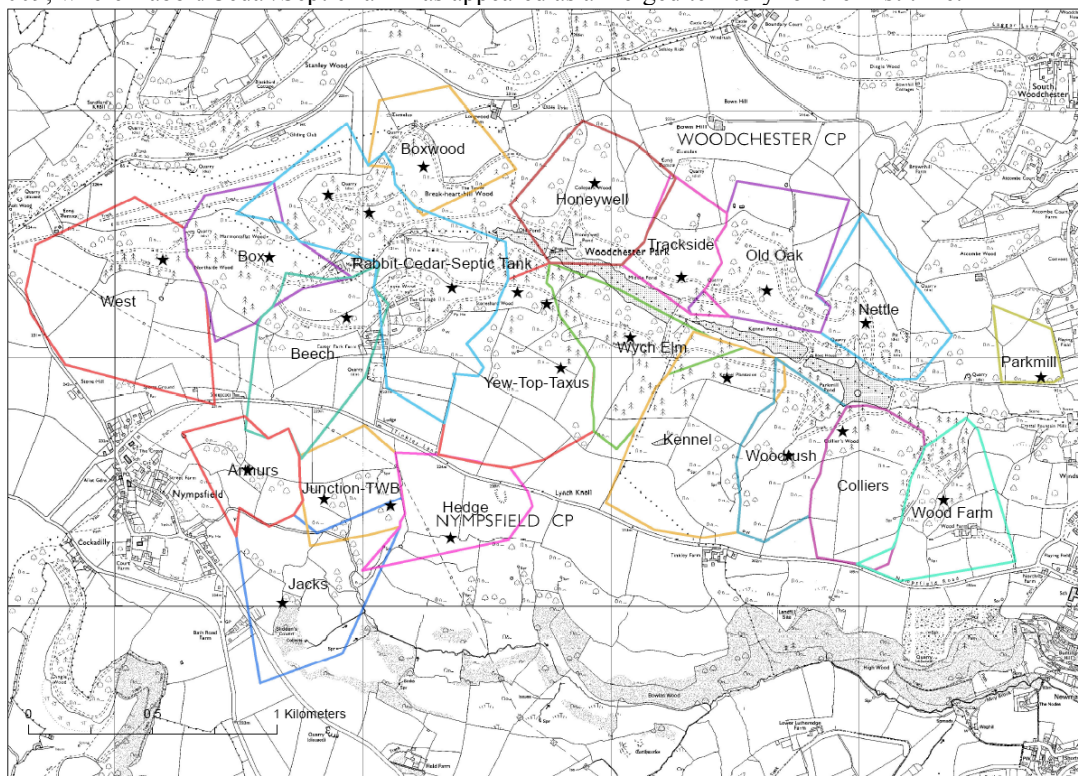
Territory maps based on the bait-marking data for 2008-2010 showing just the territory outlines.

2008, showing three merged groups, Yew/Top, ColePark/Honeywell and Kennel/Peglars

2009, where Rabbit/Cedar/SepticTank has appeared as a merged territory for the first time.

2010, Yew/Top have split up and Rabbit/Cedar/SepticTank from 2009 has split up and Yew/SepticTank has become a new merged group.