Chapter 7
Options for the Control of Disease 2: Targeting Hosts

**Stephen P. Carter, Sugoto S. Roy, Dave P. Cowan, Giovanna Massei,
Graham C. Smith, Weihong Ji, Sophie Rossi, Rosie Woodroffe,
Gavin J. Wilson, and Richard J. Delahay**

7.1 Introduction

Targeting the host has been the most common approach to managing disease in wildlife. This has essentially involved some form of host population reduction, achieved through dispersing, culling, or controlling reproduction.

Dispersion of animals from the site of a disease outbreak has mainly been employed for birds (Wobeser 2007) but has also been attempted for some herding mammals such as bison (*Bison bison*) (Meagher 1989). This works best for non-infectious diseases; otherwise it requires that only susceptible individuals disperse, since the movement of infected animals will increase the geographic spread of disease. Unsurprisingly this method has had little success in practice, and is seldom likely to be of value in controlling infectious disease in wild mammals.

Culling is a long established method of population reduction, for both disease and pest control. This approach assumes that reducing the population size of the targeted species results in a concomitant decrease in the prevalence (and more importantly the absolute number) of infectious individuals. If the aim is to eradicate the pathogen then the number of infectious individuals must fall below a level at which infection can be maintained. However, it may often be sufficient that infection is reduced to a level below which spillover to other host species (e.g. humans, domestic animals, or endangered species) either ceases or is tolerable. Wild mammal populations have most commonly been subjected to culling because they have been perceived as agricultural pests, and less often because they may transmit diseases.

S.P. Carter, S.S. Roy, D.P. Cowan, G. Massei, G.C. Smith, G.J. Wilson, and R.J. Delahay
Central Science Laboratory, Sand Hutton, York, YO41 1LZ, UK

W. Ji
Massey University, Albany, Private Bag 102 904, North Shore Mail Centre, Auckland,
New Zealand

S. Rossi
Unité Sanitaire de la Faune, Micropolis, la Bérardie, Belle Aureille, 05000 GAP, France

R. Woodroffe
Institute of Zoology, Zoological Society of London, Regent's Park, London, NW1 4RY, UK

R.J. Delahay et al. (eds.), *Management of Disease in Wild Mammals,*
DOI:10.1007/978-4-431-77134-0_7, © Springer 2009

Culling can be an effective means of controlling disease in livestock since, generally, all animals can be caught, tested, and if necessary dispatched. As techniques for the management of disease in livestock are well established, these approaches have often been regarded as the first choice for the management of disease in wildlife. Since each animal is only ‘treated’ once, the effect is immediate and permanent, so culling has also often been perceived as a simple and decisive approach with few complications. However, in practice this is seldom likely to be the case where wild mammal populations are concerned. Although there are many challenges associated with the development of non-lethal techniques (e.g. vaccination or fertility control), and their beneficial effects may not be felt immediately, their attractiveness is growing due to increasing evidence of the potential disadvantages, the ecological consequences of culling, and the pressure of public opinion.

Any disease control strategy must have clear objectives; although it is surprising how often this has been overlooked when culling has been employed to control disease in wildlife. The objective should be clearly defined at the outset, and the effectiveness of the intervention measured. Either host eradication or reduction may be considered necessary to achieve the goal of disease control, but neither should be considered as an objective in itself.

Fertility control is emerging as a useful technique for the non-lethal management of wildlife populations, although substantial research will be required before its full potential can be realised (Section 7.4). When used in isolation, fertility control has the potential to reduce population turnover or growth, but in combination with vaccination it could provide a powerful and publicly acceptable alternative to culling. In some circumstances culling is expected to be more effective in controlling disease than vaccination, because of the birth of new susceptible animals (which increases the density of the susceptible population above the threshold required for disease persistence: K_T; see Section 7.3). However, the effectiveness of a vaccination programme could be substantially increased by the addition of effective fertility control to curtail the recruitment of susceptible young animals (Smith and Wilkinson 2003). Furthermore, given the availability of appropriate diagnostic tests, either approach could be combined with selective culling to potentially enhance their effectiveness.

7.2 Host Eradication or Population Control?

There are two basic approaches to non-selective culling of wild mammal populations. One is to attempt to eradicate a species from a defined area, and the other is to maintain numbers below a certain (but seldom specified) level. Eradication may be the favoured option if the host is an exotic introduction, particularly if it is also an economic pest or threatens native ecosystems. A good example is the brushtail possum (*Trichosurus vulpecula*), which was introduced to New Zealand from Australia in 1858 to establish a fur industry. Following their intentional and accidental release, possums have spread throughout New Zealand, severely damaging native ecosystems

(Payton 2000). In addition, they are recognised as the primary wildlife reservoir of bovine tuberculosis (bTB) in the country. Possum management is consequently driven by both conservation and disease control motives. Concerted lethal control campaigns have resulted in the successful eradication of possums from a number of offshore islands (Brown and Sherley 2002). Possum eradication has the advantage of being permanent (barring further deliberate or accidental reintroductions) and the costs, which may be high, are nonetheless seen as a 'one-off' investment.

Mammal eradication programmes are much more likely to succeed on small and remote islands or where the target species has a restricted distribution. For eradication to succeed, removal rates must exceed birth rates, there must be no opportunities for immigration and all individuals must be available to be caught (Bomford and O'Brien 1995; Wittenberg and Cock 2001; Genovesi 2005). Complete eradication of a wild mammal population has not been reported for the specific aim of disease control. However, in Australia, over 7,000 feral Asian water buffalo (*Bubalus bubalis*) were culled from a 389 km^2 area of the Northern Territory between 1982 and 1984 as part of a successful bTB elimination campaign, reducing the estimated population in the region by about 99% (Ridpath and Waithman 1988). Complete depopulation has been proposed as a means of eliminating brucellosis and bTB from bison in Wood Buffalo National Park, Canada. Similarly, the eradication of feral pigs (*Sus scrofa*) has been proposed in the event of a Foot and Mouth Disease (FMD) outbreak in Australia. In the vast majority of cases however, culling has been used as a means of population reduction rather than eradication.

7.3 Culling for Disease Management

Culling is a well-established approach for the management of certain diseases in domestic animal populations. It may be employed when infected animals become an economic liability owing to reduced productivity, or in order to eradicate infectious diseases such as FMD. This can be effective in controlling disease in populations of domestic animals, which are clearly defined and tractable (Ferguson et al. 2001a). Culling wild mammal populations however is an entirely different proposition, as technical challenges and ecological complexities may profoundly influence the implementation and outcome of interventions (see Chapter 2). A wide range of mammal species have been subjected to culling in attempts to either eliminate disease or reduce transmission to a tolerable level. The generally accepted objective is to reduce the host population below some threshold density, K_T, required for the persistence of infection (Anderson 1991), although there is little empirical evidence for disease persistence thresholds in wildlife populations (Lloyd-Smith et al. 2005b) (see Chapter 2). Disease elimination is assumed to occur if the effective reproductive rate of the disease (R) falls below unity, such that on average, each infected animal gives rise to less than one new case (see Chapter 3). In reality, this means that we are not trying to reduce host density below a threshold, but to reduce contact rates below a critical threshold (see Fig. 4.2). Another way to reduce R is through vaccination (see Chapter 6). The choice of whether to cull or vaccinate depends on R_0, host density, and whether density dependence acts on host mortality or recruitment. Culling should be more effective than vaccination when R_0 is high or when host mortality is density dependent, assuming constant host behaviour at different population densities. In contrast vaccination may be more effective when R_0 is low and when density dependence acts on host recruitment, but particularly if transmission does not increase in a linear fashion relative to host density (Barlow 1996; Smith 2005). These differences can be partly explained by recalling that culling removes healthy and infected individuals, who can no longer make a reproductive contribution, and so population size and total productivity are reduced (although in the longer-term compensatory reproduction may occur, see Section 7.3.2). Vaccination on the other hand only 'removes' individuals from the pool of susceptibles (by making them immune), but they continue to contribute to total population size themselves, and to reproduce.

7.3.1 Practical Considerations of Culling

The two most important practical considerations of culling relate to feasibility and cost. When considering culling as a management option, managers must be clear that it is practical to implement in terms of the scale, efficiency and duration required to achieve the objective of disease control. The financial costs of a culling operation can be a significant constraint, as they tend to be expensive to perform and therefore should be examined for the economic return they generate (see Chapter 5).

7.3.1.1 Choosing the Right Method

Issues relating to practical implementation, target specificity, cost-effectiveness, sustainability, humaneness and public perception are of paramount importance when considering culling as an option for disease control. The four main methods used to cull mammals are hunting, trapping (including snaring), gassing and poisoning. There are advantages and disadvantages associated with each, and all have been used in attempts to manage disease in wildlife. The choice of method will be driven largely by the host species in question, although identifying the target may not be as simple as it sounds. Identifying the true reservoir of infection for multi-host pathogens is a persistent problem for wildlife managers (see Chapter 1) and the successful control of an infectious disease usually requires an understanding of the potentially complex reservoir dynamics.

Culling wild mammals by hunting typically involves shooting, either by dedicated teams or by recreational hunters. Hunting has been used for the management of disease in many carnivore and ungulate populations. It has the advantage of being highly species-specific and can sometimes be used to target gender or age classes, or even individuals. Consequently, non-target mortalities are generally low or non-existent. Hunting can also have the added benefit of providing data on the number of animals removed, thus allowing scale and cost-effectiveness to be monitored (see Chapter 5). Disadvantages are that it is labour intensive, requires a high level of skill and may risk dispersing surviving animals more widely. In addition, not all hosts may be accessible to hunters, although dogs *(Canis lupus familiaris)* have been used to track down individuals or find their den sites, restrain them until they could be despatched by hunters, and to catch and kill, where this is legal. For example, trained dogs were used to cull brushtail possums alongside shooting and trapping during their successful eradication from Kapiti Island, New Zealand (Brown and Sherley 2002). Dogs were regarded as essential during the final stages of the operation once the density of possums had been substantially reduced by other means, although this approach has not been widely adopted because of ethical and legal constraints.

Attracting target animals to fixed locations with the use of bait, scent or sound lures can increase hunting efficacy. For gregarious target species so called ‘Judas’ animals have been used to pinpoint herds, especially where culling has been carried out over vast expanses of wilderness or impenetrable terrain. The approach involves fitting a radio-transmitter to a captured animal and releasing it into an area targeted for control. Gregarious species will seek out con-specifics and hence by tracking the ‘Judas’ animal further individuals can be located and culled. This technique has been particularly useful in the eradication and control of introduced goats (*Capra hircus*) and pigs in parts of Australia, New Zealand and some oceanic islands (McIlroy and Gifford 1997; Campbell et al. 2004).

Recreational hunters have frequently been used to conduct or supplement culling operations. However, there may be a dichotomy between the interests of wildlife managers who generally wish to significantly suppress the target population, and sports hunters whose aim may be to maintain a healthy, viable population for future harvesting, through the removal of ‘surplus’ animals. Consequently, hunting pressure may not always be sufficient to reduce population densities to the levels required for disease control. This appears to have been the case in past attempts to control classical swine fever (CSF) in wild boar in Europe (see Box 7.1).

Trapping has typically been the main culling method employed for the management of disease in wild carnivores. The nocturnal or crepuscular habits of carnivores and their occurrence at relatively low densities, compared for example to wild ungulates, may decrease the cost-effectiveness of shooting as a control option. However, the most successful carnivore eradication campaigns have relied on a combination of trapping and shooting (Nogales et al. 2004). Traps essentially consist of devices to either kill or capture the target animal. Animals captured in live traps must be humanely dispatched, typically by shooting or lethal injection. In many countries there is a legal requirement to check traps and snares on a daily basis, regardless of whether they are designed to capture or kill. Consequently, all forms of trapping tend to be labour intensive and expensive. The use of cage traps followed by lethal dispatch is likely to be the most labour intensive method, but it does have the advantage of being highly specific as non-target species can usually be released unharmed.

Box 7.1 The role of hunting in the management of classical swine fever in wild boar

Classical swine fever (CSF) or hog cholera is a highly contagious disease of domestic pigs, which is causing increasing concern in parts of Europe where it is endemic in wild boar (*Sus scrofa*) populations (Artois et al. 2002; Kramer-Schadt et al. 2007). Wild boar may act as a reservoir of CSF, and both analysis of empirical data and mathematical models suggest that the persistence of infection is highly dependent on boar population size (see Fig. 8.2). Culling wild boar to suppress numbers below a critical threshold may therefore appear to be an appropriate tool to achieve disease elimination. Wild boar are already hunted extensively for sport across much of Europe, so an intuitive response to a CSF outbreak might be to consider increasing hunting pressure in the locality of the outbreak. In particular, it has been proposed that selectively targeting young wild boar would yield the greatest benefit as they are more susceptible and this would preserve the older, potentially immune, animals (Zanardi et al. 2003). However, attempts to increase hunting pressure and target piglets in response to CSF outbreaks have had unconvincing results in large wild boar populations (Rossi et al. 2005b). Several factors may help explain this failure. Firstly, hunting pressure was possibly not sufficient to reduce boar numbers below the disease persistence threshold. Indeed, the wild boar population has continued to increase in many European countries since the 1980s in spite of high levels of hunting (Acevedo et al. 2006). This may be related to insufficient targeting of reproductive females and a compensatory increase (see Section 7.3.2 and Box 7.5) in the recruitment of young sows in response to hunting (Rossi et al. 2005b). Secondly, hunting may favour the persistence of pathogens by enhancing the availability of susceptible individuals in seasonal pulses (Guberti et al. 1998; Choisy and Rohani 2006). Furthermore, hunting with dogs may cause wild boar to range further (Maillard and Fournier 1995) and so increase their probability of crossing physical barriers such as motorways (Vassant et al. 1993; Vignon et al. 2002) and hence promote the geographic spread of the virus. A better understanding of the effects of increasing hunting pressure on the demography of the host and the dynamics of disease transmission is therefore required to develop improved approaches to the management of CSF. Other options for disease control such as oral vaccination (Chapter 6) and contraception of wild boar (Section 7.4) are also worthy of further investigation.

Lethal trapping may result in considerable non-target mortality, and although this can be minimised through careful design and deployment of traps and other restraints, it is seldom (if ever) possible to eliminate it.

Capture rates vary widely between species but are often low relative to trapping effort, although this can be improved through the use of scents and lures (Roy et al.

2006). Another common problem is the behavioural avoidance of traps or baits. It is therefore advisable that trapping be carried out in conjunction with an independent means of population monitoring.

The use of snares is likely to be considerably cheaper than traps and in some cases may be more effective (Montague and Warburton 2000) although they arguably require a higher level of operator skill. The biggest drawback of this approach is that snares have been associated with causing significant suffering and so there are strong ethical arguments against their use. As a result, their use is banned or highly restricted in many countries and increasingly they are simply not considered as a realistic management option.

Culling programmes have on occasion taken advantage of the skills of professional and amateur hunters and trappers. One means of encouraging such involvement is by way of a bounty scheme, where individuals are rewarded when they supply an ear, or tail of the target species. Such schemes have been in existence for hundreds of years, and have targeted a variety of mammal species in the interests of 'pest' control, and in some instances for the purposes of disease management. However, this may encourage hunters to only remove 'surplus' individuals or even to import animals, thereby assuring a sustainable yield. Hunters may also tend to neglect populations that are least accessible. Consequently, bounty schemes have not been recorded as making a successful contribution to disease control (Debbie 1991).

Gassing generally involves flooding restricted spaces such as underground den sites or bat roosts with poisonous gas; hence its potential application is relatively restricted. It may be delivered by pumping into a confined space, or deploying a tablet, powder or cartridge, which produces lethal gas when exposed to moisture. A variety of poisonous gases have been used with apparent success in reducing numbers of red foxes (*Vulpes vulpes*) (Müller 1971), striped skunks (*Mephitis mephitis*) (Gunson et al. 1978) and vampire bats (*Desmodus rotundus*) (Fornes et al. 1974) for rabies control. Explosive gases have also been used in attempts to control prairie dogs (*Cynomys* spp.) and other burrowing rodents in the USA, although there are likely to be serious animal welfare concerns associated with such techniques. The use of gas can be target-specific if the restricted space is only occupied by the species of interest, although this is difficult to establish in many circumstances. Another substantial problem with this approach is the challenge of delivering a lethal concentration of gas throughout the enclosed space, particularly in complex burrow systems. In the UK during the 1970s hydrogen cyanide gas was pumped into Eurasian badger (*Meles meles*) burrows (setts) as part of a strategy to control the spread of bTB to cattle. This proved logistically difficult, and was ultimately curtailed on welfare grounds (Dunnet et al. 1986), as sub-optimal concentrations of gas in the further extremities of setts caused serious suffering in some animals.

Poisoning, with toxic baits, is an effective method of culling wild mammals over large areas. Toxic agents can be administered using fixed bait stations or by physically distributing bait in the environment. Baits may be distributed manually over small areas, or from aircraft over large areas and difficult terrain. Culling using poison baits is likely to be less labour intensive than either shooting or trapping unless it is necessary to monitor the fate of deployed baits. Aerial poisoning is the most cost-effective means of reducing brushtail possum numbers in New Zealand, where it has been the main method of control since 1956 (Morgan and Hickling 2000). Six toxicants have been registered for possum control in New Zealand but sodium monofluoroacetate (1080: ten-eighty) has been used most extensively, because of its ability to be degraded by microorganisms (King et al. 1994; Bowen et al. 1995; Eason et al. 1999). However, perhaps the most important challenge when considering using toxic bait on wild populations is to minimise the potential for any impact on non-target species. As 1080 is a broad-spectrum toxin it has the potential to cause secondary poisoning in a wide range of non-target species. Recent research on the development of carnivore-specific toxins (Marks et al. 2006) has been driven by the need to control populations of non-native predatory mammals, but may produce substances suitable for wildlife disease management. Impacts on non-target species can be minimised by tailoring the method of toxin deployment. This was the case when poison was used to control the spread of vampire bat-transmitted rabies in South America. Bats were captured in mist nets, painted with an anticoagulant and released to return to their colony where large numbers of other bats would be killed by ingesting poison during mutual grooming (Lord 1980). In this instance the delivery was highly species-specific, but it is the indiscriminate nature of most poisoning campaigns that is their main drawback. In 1952 an attempt to control the spread of rabies in Alberta, Canada, involved the distribution of nearly 500,000 strychnine baits which killed not only 50,000 foxes, the intended target, but also 35,000 coyotes (*Canis latrans*), 4,200 wolves (*Canis lupus*), 7,500 lynx (*Lynx* spp.) and 1,850 bears (*Ursus* spp.) (Ballantyne and O'Donoghue 1954). It is no surprise therefore that poisoning campaigns have met with most success when used to control introduced pest species on islands devoid of native terrestrial mammals. Examples include the control of black rats (*Rattus rattus*), brown rats (*R. norwegicus*) and Pacific rats (*R. exulans*) on island archipelagos (Howald et al. 2007). However, in some species, prolonged exposure to toxins can result in the development of resistance and aversion to poison baits through the consumption of sub-lethal doses (Leung and Clark 2005) and the selection of behavioural traits such as neophobia (see Section 7.3.2). Despite the proven effectiveness of poisons and continuing development of more environmentally benign formulations, the limited specificity of most existing toxins together with potential risks of environmental contamination and poor public perception, present substantial obstacles to their long-term use.

The concept of biological control involves the introduction of a natural enemy (predator or pathogen) to a population with the intention of reducing their numbers. Unfortunately, this approach has been associated with a catalogue of ecological disasters, which have typically involved the control agent establishing itself as a pest species, or the introduction of novel infections into non-target populations. Bio-control failures include the introduction of stoats (*Mustela erminea*) ferrets (*M. furo*) and weasels (*M. nivalis*) to New Zealand and the small Indian mongoose (*Herpestes auropunctatus*) to several tropical islands. However, target-specific pathogens such as myxomavirus and rabbit haemorrhagic disease (RHD) have been used to successfully control numbers of introduced rabbits (*Oryctolagus cuniculus*) in Australia (Fenner 2002). Such rare successes in using biological agents to control mammal populations are associated with highly species-specific pathogens. An extensive review of diseases in stoats identified potential viral agents for the lethal control of this introduced predator in New Zealand, but the authors advocated a cautionary approach to their development because of the risks posed to non-targets (McDonald and Larivière 2001). Recent advances in biological control include genetically modified organisms and immunotoxins (substances which may cause autoimmune disease), which can interfere with processes such as reproduction, and the use of parasites or viruses as vectors to deliver immunocontraceptives (see Section 7.4.2). However, there are no records of biological control being used to successfully manage a disease outbreak in wild mammals.

7.3.1.2 Selective Culling

So far we have considered culling as an indiscriminate tool for either eradicating, or reducing the size of a wild mammal population. Such approaches will result in the removal of individuals with no regard to their infection status, but opportunities may exist in some instances to target infected animals. This could enhance the efficiency of disease control substantially, particularly in situations where a relatively small number of infectious individuals make a disproportionately large contribution to the spread of disease in a population (see Section 2.2.4).

Selective culling has achieved some success in the control of chronic infections that spread slowly through the host population such as bTB and brucellosis, especially in ungulates that tend to form large aggregations (Tweddle and Livingstone 1994; Cross 2005). In practice this requires the capture and testing of large numbers of individuals to identify those that are infected. This requires considerable effort and, more importantly, is reliant on the availability of a diagnostic test that can be used to rapidly identify infected individuals in the field. A test and slaughter strategy was used to significantly reduce the prevalence of bTB in buffalo herds in Hluhluwe Umfolozi National Park, South Africa (Michel et al. 2006). Once a herd was located they were mustered by helicopters and vehicles and driven into a corral (boma). The construction of the boma allowed the animals to be segregated into smaller groups so that they could be anaesthetised and subjected to a diagnostic skin test. Infected individuals were subsequently shot and uninfected animals released.

A combined approach of culling adult bison and elk (*Cervus elaphus*) testing positive for brucellosis, whilst also vaccinating calves was successful in eradicating the disease from Elk Island National Park, Canada (Tessaro 1986). Nevertheless, test and slaughter is unlikely to be practical for most wild mammal species owing to the difficulty of capturing them in large numbers and the limitations of diagnostic tests. Chronic wasting disease (CWD) has recently emerged as a problem for wild deer in North America, causing considerable concern amongst wildlife managers, biologists and stakeholders (see Box 2.1). Mathematical models suggest that the test and slaughter of infected individuals may be more effective than non-selective culling if the majority of the population can be caught and tested, and if animals can be removed during the early stages of infection (Gross and Miller 2001; Wolfe et al. 2004). Unfortunately, this may not be feasible at the scale of the affected areas. Such problems mean that selective culling may have limited value for disease management in many wild mammal populations. Nevertheless, it may be a more attractive option for the elimination or control of disease in endangered species, where each non-infected individual is extremely valuable and populations are relatively small and potentially isolated (see Chapter 11).

Selective culling may also be directed towards specific age groups or sexes if they are known to be more susceptible to infection and can be identified (see Box 7.1). Conversely, some supposedly non-selective culling methods may inadvertently target some sections of a population over others as a result of inherent bias (Clutton-Brock and Lonergan 1994; Smith et al. 1995), and the subsequent skewing of age and sex ratios may have unpredictable and undesirable consequences for disease control.

7.3.1.3 The Spatio-Temporal Extent of Culling

Clearly, the smaller the geographic range and the shorter the duration of population control, the more feasible and less expensive culling becomes. Consequently, it has been most successful when used to prevent the establishment of an introduced pathogen, or to eliminate or control an existing disease within a restricted range. Both scenarios rely on early detection and diagnosis, and a rapid response, although this may be less important where there is limited scope for disease expansion such as on small, remote islands. The localised culling of carnivores and vampire bats has been successful in preventing epizootic waves of rabies spreading into disease free areas (Wobeser 2007). However, culling is less likely to be successful in the control of a disease that is already established over a wide area, particularly when it influences host behaviour and subsequent transmission rates (see Section 7.3.2 and Box 7.2).

There are few examples where the large-scale culling of a wild mammal population has demonstrated a measurable benefit in the control of disease. Indeed, extensive culling of foxes had no demonstrable effect on the control of rabies across Europe and may have made the situation worse in some areas (Aubert 1994), although it has prevented rabies spread when used in mountain valleys or on an isthmus. In Australia, the systematic culling of the introduced Asian water buffalo made a significant contribution to the eradication of brucellosis and the virtual elimination of bTB from Australian livestock (Cousins and Roberts 2001). The gregarious habits of the buffalo aided the culling approach, which was widely supported because of their exotic ‘pest’ status. However, much of the success of this campaign was also attributed to rigidly enforced cattle

Box 7.2 Positive and negative effects of culling for disease control: lessons from a large-scale field trial

Attempts to eradicate bovine tuberculosis (bTB) from British cattle have been hampered by the presence of persistent infection in badgers (*Meles meles*). For 25 years, cattle-based control measures were supplemented by various forms of badger culling on and around bTB-affected farms. These efforts were not, however, sufficient to prevent a nationwide increase in the incidence and geographical extent of bTB in cattle. An advisory committee of independent scientists therefore recommended that the utility of badger culling be tested in a large-scale randomised field trial (Krebs et al. 1997).

The UK Randomised Badger Culling Trial (RBCT) was conducted from 1998 to 2005 and may constitute the largest ecological experiment ever performed (Independent Scientific Group 2007). Ten 100 km^2 areas, located in areas of high cattle TB risk, were randomly allocated to receive 'proactive culling', that is, annual badger culls conducted on all accessible land. Ten similar areas were randomly assigned to receive 'reactive culling' which consisted of the localised culling of badgers associated with particular cattle TB outbreaks, while a further ten areas received no culling ('survey-only').

Proactive culling caused a substantial reduction in badger abundance inside culled areas (Woodroffe et al. 2008). Badger densities were also somewhat reduced on neighbouring unculled land, presumably as badgers immigrated into the culling areas. In all areas affected by badger culling, their normal territorial organisation was disrupted, with evidence of animals ranging more widely (Woodroffe et al. 2006a). These behavioural changes would have allowed greater contact amongst badgers and probably explain why the prevalence of infection with *Mycobacterium bovis* (the causative agent of bTB) rose among badgers taken on successive proactive and reactive culls (Woodroffe et al. 2006b; Independent Scientific Group 2007).

Proactive culling was associated with a modest (23%) reduction in the incidence of cattle TB inside culled areas (Donnelly et al. 2007). However, on neighbouring lands, and in reactive culling areas, the incidence of cattle TB appeared to show a short-term increase in response to culling, and infection also became less clustered within the cattle population (Donnelly et al. 2007; Jenkins et al. 2007; Jenkins et al. 2008). These changes are all consistent with a hypothesis of transmission from a badger population made more mobile, and more heavily infected, as a result of culling. The overall benefits of proactive culling, after accounting for detrimental effects on neighbouring land, were so small as to be trivial in disease control terms, and were greatly outweighed by the costs of conducting culling (Independent Scientific Group 2007). Localised culling, which was a more palatable policy option in terms of cost as well as numbers of badgers killed, had only detrimental effects (Donnelly et al. 2003). Hence, after extensive consideration of various possible forms of culling, the group overseeing the RBCT concluded that '*badger culling can make no meaningful contribution to cattle TB control in Britain*' (Independent Scientific Group 2007).

movement controls, full support from the farming community for the test and slaughter of domestic cattle, and the absence of other significant wildlife reservoirs. It took 27 years to achieve Australia's 'free from TB' status and a reputed cost of approximately AUS$840 million (Turner 2003). This status has been maintained through ongoing surveillance, followed by a rapid and aggressive response to the detection of bTB in cattle, although infection still occurs in some remaining buffalo herds.

Often, the extent to which a wild mammal population must be reduced in size in order to achieve the required level of disease control is unknown. Computer simulations are useful tools for generating estimates of the magnitude of population reduction required to eliminate or control disease in a wildlife population. For example, for many years the host density threshold required for disease persistence predicted by mathematical models was used to guide the control of brushtail possum populations in New Zealand for bTB reduction (Barlow 1995). Modelling was also used to investigate the importance of previously documented culling-induced changes in the behaviour of badgers in relation to the control of bTB transmission (Smith et al. 2007b). In the absence of replicated experiments or detailed population studies, models can provide valuable information to help inform decisions on the likely success and design of culling programmes. However, even the most complex model may not account for all the significant ecological and epidemiological processes (see Chapter 4), which can be particularly difficult to predict.

There will be a stochastic element to the removal of infected individuals during an indiscriminate culling operation, such that incomplete culling could result in removing none, few, most, or all of the infected animals purely by chance (see Box 4.1). The age, sex and infection status of the remaining animals may influence subsequent rates of disease transmission, immigration and population recovery. Furthermore, the density, demography and disease status of the population prior to culling may determine subsequent social and behavioural responses and their epidemiological consequences (see Section 7.3.2 and Chapter 2).

Simple statistical methods may be useful in determining the optimum duration of a culling operation in terms of removing the majority of the resident population (see Box 7.3), although in many cases it may be necessary to maintain a certain level of control for prolonged periods, or even indefinitely. Annual possum culling in a bTB infected area of central North Island, New Zealand achieved a 92% reduction in infection in the possum population and an 88% reduction in the incidence of disease in six cattle herds over a 10-year period (Caley 1997; Coleman and Livingstone 2000). The control of possums is thought to have reduced bTB infection in cattle and deer herds in New Zealand by over 50% between 1994 and 2000, and maintaining numbers at less than 20% of pre-control levels can lead to elimination of bTB from possum populations (de Lisle et al. 2001). However, such culling programmes are expensive and require sustained financial support. Without continual routine control of possums, bTB infection in cattle can recover to pre-control levels in 5–8 years (Coleman and Livingstone 2000).

Box 7.3 A stopping rule for culling

One potential consequence of culling a wild mammal population is an influx of animals from the surrounding unculled area. The magnitude of this effect will vary between different species and in relation to local densities. During a sustained cull the rate of immigration from outside is likely to increase, as numbers of residents decline (the vacuum effect). These immigrant animals may however not be the desired target of the cull. Hence, it would be useful to determine whether the animals being caught later in a culling campaign were likely to be immigrants from outside the area. Indeed, if the proportion of immigrants rises above some level, this could be used as a rule to determine when to stop culling. The approximate proportion of immigrants trapped on each day of a capture and cull campaign can be estimated using the following approach.

1. Delineate an inner and outer zone within the culling area. Ideally they should be approximately the same area, or initially be expected to contain approximately the same total number of animals. The outer zone should have sufficient width to ensure that any immigrants are likely to be caught before moving to the inner zone.
2. If the two zones are comparable then the capture rates would be similar in each. However, since we cannot be certain of this, it is more appropriate to use the capture rates on the first day(s) of trapping to determine the expected proportion that should be caught in the respective zones on subsequent days.
3. Using the numbers caught in each zone on days one and two we can compare the proportions in each zone. These results can be compared using a 2 × 2 chi-squared test. We can then test to see if the numbers caught in each zone differ over time by comparing day one with day three, and so forth. An increase in the proportion caught in the outer zone would imply that immigrants are arriving and being captured.
4. There are two reasons to combine data from different days. If the capture rate is relatively low and declines slowly in the first few days, it would be valid to combine the first two or three days (if they are not significantly different) when comparing with later captures, as the combined early sample would show less stochastic bias. It may also be necessary to combine later days to ensure that the expected captures in each zone are sufficient for a chi-square test to be valid (i.e. five or greater).

In a worked example, on each of ten days the following numbers of animals were caught in each zone:

Day	Inner	Outer
1	43	59
2	11	22

(continued)

Box 7.3 (continued)

3	11	10
4	5	10
5	5	8
6	4	4
7	5	7
8	4	7
9	2	8
10	1	12

On day two we would run a 2 × 2 chi-squared test comparing numbers caught on days one and two ($\chi^2 = 0.809$, $p > 0.100$). On day three we would compare captures on days one and three ($\chi^2 = 0.739$, $p > 0.100$), and so forth on a daily basis. On day six the expected values are less than five in both areas, so we would combine data from days five and six, and compare them with day one in a 2 × 2 test ($\chi^2 = 0.004$, $p > 0.100$). Similarly we would carry out similar comparisons with data from day one, on day seven with combined data from days six and seven, on day eight with data from days seven and eight, and on day nine with data from days eight and nine. In our example these comparisons yield no significant differences until day ten, when we combine data from days nine and ten and compare with those from day one ($\chi^2 = 6.840$, $p < 0.010$). Consequently, on this day we could be confident that we have more animals than expected in the outer zone, which we can assume are immigrants, and therefore cease culling.

7.3.2 Ecological Consequences of Culling

Wild mammal populations are part of ecological communities, with links to other species, some of which will be their prey, predators or parasites. The nature of these relationships may change as a result of culling, which may in turn affect other organisms in the ecosystem. Some of these effects are obvious and predictable but the complexity of ecological food webs means that many are not.

Culling predatory mammals could result in increases in the density of prey if this releases them from the pressure of predation. This in turn could have knock-on consequences depending on the ecology of the prey species. For example if the prey species is herbivorous, then an increase in their abundance may amplify grazing pressure. When large-scale culling of wild carnivores was employed in an attempt to stop the spread of rabies in Alberta, Canada, it resulted in an increase in deer and moose (*Alces alces*) populations, which gave rise to serious overgrazing and habitat damage (Macdonald 1980). When such chains of effects occur across multiple trophic levels they are known as ‘trophic cascades’.

If the decline or disappearance of a top carnivore leads to increases in the abundance of smaller predators (a process known as meso-predator release) then this can have significant impacts on the prey of the smaller predators. For example, wolves are thought to limit coyote numbers in much of North America. It follows that wolf removal might release coyotes from this source of competition with knock-on effects for prey species like pronghorn antelopes (*Antilocapra americana*) (Berger et al. 2008). It is clear that the ecological consequences of culling can have significant economic and conservation implications. Consequently, these effects should be taken into account when considering population reduction as a disease management tool (see Box 7.4).

Box 7.4 Effects of badger culling on foxes

When badgers (*Meles meles*) were culled in the UK during an extensive field experiment to determine the effect on the incidence of bTB in cattle (see Box 7.2) a concomitant increase in red fox (*Vulpes vulpes*) numbers was observed (Trewby et al. 2008). The badger culling trial provided a rare opportunity to assess experimentally the consequences of culling one wild mammal species on populations of others. Foxes use badger setts (burrows) as breeding dens, share a similar diet and interact directly with badgers (Macdonald et al. 2004). Therefore, it was hypothesised that culling badgers, which are considered to be the dominant species, would result in mesopredator release and hence an increase in fox numbers. Changes in fox numbers may have significant economic, conservation and epidemiological consequences. Foxes kill and eat ground nesting birds (Reynolds and Tapper 1995a), hares (*Lepus europaeus*) (Reynolds and Tapper 1995b) and livestock (Moberly et al. 2003), and are likely to be the principal wildlife vector of rabies in the event of an outbreak in Britain (Smith and Wilkinson 2003).

As part of a project to assess the ecological consequences of badger culling, standardised surveys to estimate fox numbers were carried out prior to intervention in four of the areas where badgers were to be culled, matched with four experimental control areas where no culling was to take place. The surveys were subsequently repeated annually throughout the culling trial. After controlling for patterns of background variation in fox abundance, predicted mean fox densities in areas where badgers were culled were 1.6 to 2.3 foxes per km^2 higher than in the unculled areas (Fig. 7.1). Interestingly, in one area where badger culling was thought to have been less effective (only an estimated 40% removed) fox density did not change.

The results of this study clearly demonstrated that badger culling at the temporal and spatial scales applied in this trial is likely to result in markedly higher fox densities. This has potential implications for the costs of predation on livestock and game, the ecological impact of foxes in conservation terms as predators of ground nesting birds and hares, and risks to public health as potential vectors of rabies. This illustrates why it is necessary to take account of the broader potential ecological consequences when considering culling as an option for wildlife disease management.

(continued)

Box 7.4 (continued)

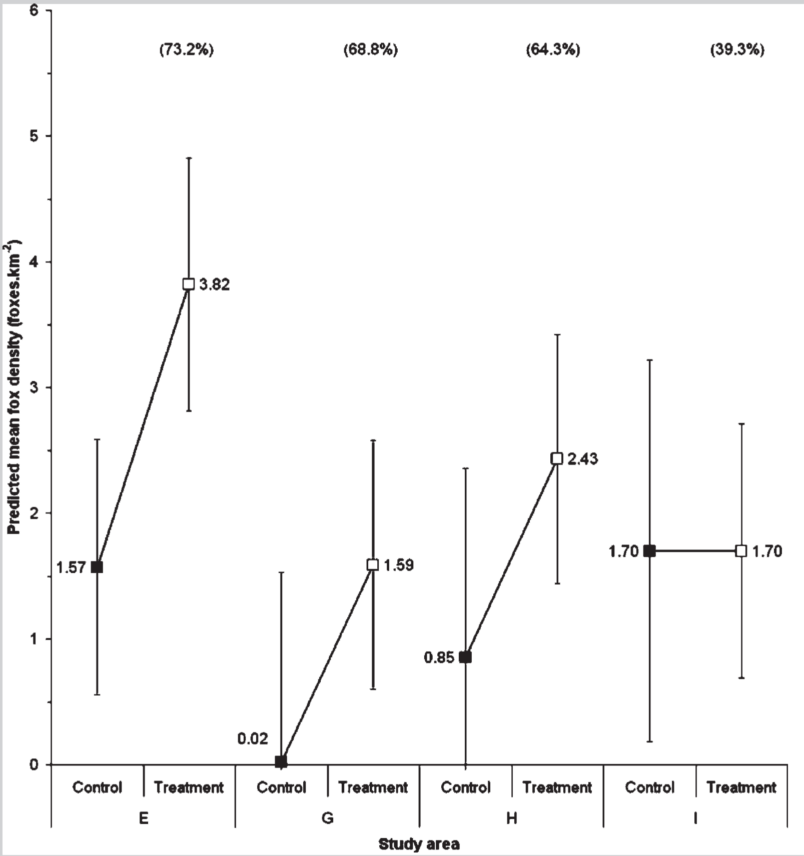

Fig. 7.1 The response of fox populations to badger culling. During the UK Randomised Badger Culling Trial (RBCT) fox density was estimated in culled (treatment) and unculled (control) areas in four locations (E, G, H and I). Predicted mean fox densities (with standard errors) were determined by distance sampling and adjusted for patterns of background temporal and spatial variation. The estimated efficacy of badger removal for the initial cull in each treatment area (Smith and Cheeseman 2007) is shown in brackets

Culling may also invoke behavioural changes in the target species. For example, sustained culling may select for behavioural traits such as neophobia, which results in higher levels of trap or bait shyness, and so reduces the efficacy of control. During a culling operation the population density of the target population declines and consequently the effort required to cull each individual will increase. This effect is likely to be exacerbated by the neophobic behaviour of remaining animals. Using a combination of methods can help to mitigate such effects.

Another behavioural response of wild mammals to culling is compensatory reproduction. Many populations exhibit some level of density-dependent reproduction, such that the production of offspring is greater at lower densities but is curtailed as numbers increase. Consequently, populations subjected to culling may respond by increasing productivity. This phenomenon has been observed in a range of mammal species, including brushtail possums (see Box 7.5) in which it was accompanied by enhanced juvenile survival rates at reduced densities. Enhanced productivity can increase the number (and proportion) of young susceptible individuals in the population, and can have a counter-productive effect on disease persistence.

Culling may also promote increased dispersal by surviving individuals and increased immigration into the culled area. The tendency for immigrants to move into culled areas is often referred to as the vacuum effect, but the extent of potential immigration will vary widely between species and with respect to local conditions. By definition, the distances travelled by dispersing individuals are greater than their typical movement patterns, and so may heighten opportunities for disease transmission. Dispersal is also likely to be a stressful process and so these individuals may be more susceptible to disease owing to poor physical condition or immuno-suppression.

Box 7.5 Possum control and compensatory reproduction in New Zealand

One of the factors that might hinder the desired outcome of culling is the compensatory response of host populations to density reduction. In New Zealand the introduced brushtail possum (*Trichosurus vulpecula*) is a principal source of bovine tuberculosis infection in cattle, and the target of widespread culling. However, brushtail possum populations that have been artificially depleted can recover rapidly because the species has a breeding potential well in excess of the requirements for immediate replacement. Female possums mature at one year and usually give birth to a single offspring each year. However, possums can potentially breed twice in a year with a main breeding peak occurring in autumn and a smaller peak in the spring. Both the proportion of yearling females that breed, and of females with second young were reported to be higher in colonising than in established populations (Green and Coleman 1984; Cowan 1993). Following the removal of 93% and 88% of the original possum populations from two 6 ha areas of native forest remnants in Coatesville and Huapai, North Island, New Zealand (Ji et al. 2004), a higher proportion of females bred, juvenile survival increased, and seasonal body condition fluctuated less in the colonising populations (Fig. 7.2). Two years later possum numbers in these two areas had recovered to 40% and 55% of their respective previous levels. Further evidence of the capacity for possum populations to recover can be found in the results of a 6-year possum eradication programme on Kapiti Island, New Zealand. In this instance, as density decreased, the proportions of young (≤3 years) and old (≥10 years) animals in the population increased. The observed changes in age structure are suggestive of density-dependent survival (Cowan 1993).

(continued)

Box 7.5 (continued)

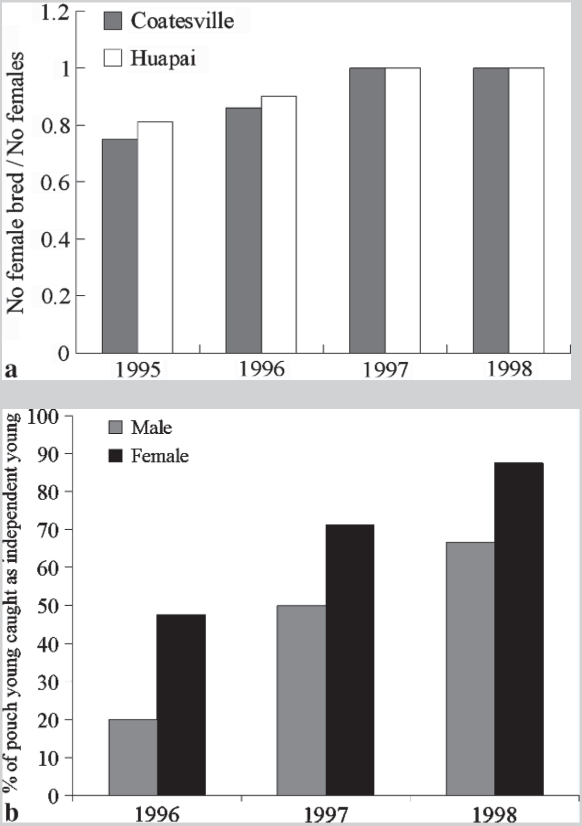

Fig. 7.2 Following depopulation of possums in two native forests in New Zealand, in late 1996, the proportion of females breeding (a) and the survival rate of young animals (≤3 years old) (b) both increased (Ji et al. 2004)

The capacity for disease management interventions to disrupt the social structure of wild mammal populations is increasingly being recognised. For example, the relatively stable social structure of undisturbed high-density badger populations has been shown to mitigate the spread of bTB (Vicente et al. 2007a). Badger culling can disturb this social stability leading to increased movement amongst the remaining and recolonising individuals (Cheeseman et al. 1993; Carter et al. 2007). Evidence from a long-term study showed that increased movement between badger social groups was correlated with increases in the incidence of infectious individuals (Rogers et al. 1998; Vicente et al. 2007a). Furthermore, a large-scale field experiment provided clear evidence that culling resulted in the social perturbation of badger populations and increased the prevalence of bTB in badgers and cattle (see Box 7.2). Evidence for culling-induced social perturbation has also been reported during the control of CSF in wild boar (see Box 7.1) and rabies in red foxes (Macdonald 1995). The combined impact of compensatory reproduction, enhanced immigration into culled areas and increased aggressive encounters (facilitating disease transmission) arising in culled fox populations, is believed to have negated any beneficial effects for rabies control (Holmala and Kauhala 2006).

7.3.3 Public Perceptions of Culling

Culling wild mammal populations often invokes strong reactions from conservationists, the public and other stakeholders. In 1923 public opposition prevented the slaughter of about 7,000 bison in Wainwright Buffalo Park (WBP), Alberta, Canada, and re-stocking with disease-free animals, for the purposes of bTB control. As a result, approximately 17,000 bison were culled between 1923 and 1940 as part of the alternative strategy of annual population reduction, in an unsuccessful attempt to remove bTB from the herd (Fuller 2002). In addition, between 1925 and 1928 nearly 7,000 supposedly "disease-free" bison were translocated from WBP to the newly inaugurated Wood Buffalo National Park (WBNP) on the border of Alberta and the Northwest territories, resulting in a new foci of infection. In 1990 an Environmental Assessment Panel recommended the slaughter and restocking of the entire herd of bison in WBNP, but this again met with public opposition. A 5-year Bison Research and Containment Programme aimed at preventing the spread of bTB and brucellosis to neighbouring uninfected populations, whilst facilitating research into bison disease ecology, was implemented in 1995 followed by the publication of interim measures to contain both diseases in the southwest of WBNP. However, no action was taken, pending the acquisition of stakeholder funding and the results of an extensive public consultation exercise (Nishi et al. 2006).

In the UK, culling badgers for the purpose of controlling bTB in cattle has been the subject of a particularly emotive and contentious debate for decades, resulting in highly polarised views between interested parties. Prior to a large-scale field experiment to assess the contribution of badger culling to the control of bTB in cattle, cage trapping, followed by humane despatch by shooting, was chosen over arguably more efficient methods such as gassing, or snaring and shooting. Prevailing public and political sensitivities associated with these methods, and the expectation that the field experiment would not be completed if either of these approaches were employed, played a large part in reaching this decision (Independent Scientific Group 2007).

Despite efforts to improve the humaneness, specificity and cost-effectiveness of culling, it is still regarded by many as ethically unacceptable, particularly in regard to native species. However, public opinion on culling varies considerably between countries, regions and sectors of society, and is often related to how the target species is perceived. For example, rats have a widespread reputation for disease spread and association with human squalor, and their lethal control is widely practiced and rarely the subject of controversy. In contrast, even when there is a clear case, attempts to control wild mammals with a more positive public image may provoke strong reactions. Hence, proposals to cull hedgehogs (*Erinaceus europaeus*) that had been recently introduced to some offshore islands in the UK sparked a national campaign of protest, even though their presence posed a serious threat to native bird populations (Jackson and Green 2000). Levels of public support for the culling of wild mammals for disease control are also likely to vary in relation to the perceived disease threat to human health, domestic animals or endangered species.

7.4 Fertility Control

As a result of public opposition to culling wild mammals and increasing restrictions on the use of such techniques, there is growing pressure to identify effective and sustainable alternatives. Fertility control has long-been considered by many to have the potential to replace or enhance culling for the purpose of wildlife management (Bomford 1990). However, one likely disadvantage of fertility control is that it will generally take longer to achieve equivalent population reductions simply because infertile animals remain in the population until they die. Nevertheless, in some circumstances fertility control may have some inherent advantages over culling, particularly with respect to disease control. The retention of treated (infertile) animals in the population may for example curtail population recovery through their contribution to density-dependent processes acting on recruitment and survival. Fertility control could therefore be particularly effective at maintaining a population at a lower density after initial reduction by culling (White et al. 1997; Merrill et al. 2003). This approach should be less prone to disruption of host social structures than continued culling, so reducing the potential risk of an associated increase in disease transmission (see above). It could also decrease vertical (i.e. from mother to offspring) transmission, which may be an important component of disease maintenance in a population. Other potential benefits of fertility control include removal of the physiological burden of reproduction and lactation, which may enhance the physical condition of females, and so potentially reduce their susceptibility to disease. Nevertheless, by inhibiting reproductive physiology, fertility control may induce behavioural changes, which could potentially either reduce (Ramsey et al. 2006; Ramsey 2007) or increase (Caley and Ramsey 2001) rates of contact between individuals, and the corresponding opportunities for disease transmission.

7.4.1 Fertility Control Tools

Despite a long-standing interest in the potential of fertility control in wildlife management, only in recent years have tools with real prospects for practical application begun to emerge. These include chemical and hormone agents, surgical sterilisation, intra-uterine devices (IUDs) and immunocontraceptives. The chemical agent with the greatest potential for controlling mammal populations is diazacon, which inhibits cholesterol production and blocks steroid hormone formation (Nash et al. 2007). The effects can last for several months after daily dosing for a 5 to 10 day period, so this approach holds most promise for species with a restricted breeding season. Silicone implants can be used to deliver fertility control agents by slow release, leading to infertility for the duration of the implant. Examples of such agents include progestins (synthetic forms of the hormone progesterone) like levonorgestrel (Sivin 1994), and Gonadotropin Releasing Hormone (GnRH) agonists (Bertschinger et al. 2001; Bertschinger et al. 2006). Implants can confer infertility for up to two years, although they usually only endure for less than 12 months. The main advantage of this approach is reversibility which is often an attractive option for captive wildlife, but seldom likely to be an issue for the management of free-living mammals. The use of such agents is not without risk and negative side-effects are possible (Munson, 2006).

Surgical sterilisation is used extensively around the world for rendering feral cats (*Felis catus*) and dogs infertile. It has also been used in experimental field trials to examine the population level effects of induced infertility, but is unlikely to be cost-effective for the management of most wild mammal populations. IUDs have been developed for use in feral horses (*Equus caballus*) (Daels and Hughes 1995; Killian et al. 2006) and white-tailed deer (*Odocoileus virginianus*) (Malcolm and Van Deelen 2007), offering long-term infertility with limited regulatory issues. However, the considerable effort needed for the capture and anaesthesia of individuals probably renders this method impractical for most wild mammals.

There have been significant recent advances in the development of immunocontraceptive vaccines, which induce the immune system to produce antibodies that interfere with a protein or hormone essential for reproduction. The possibility of using immunisation to control fertility in human and wildlife populations has been explored actively for many years with several sperm, egg or hormonal antigens considered as suitable targets for intervention (Delves et al. 2002). The most promising targets for mammalian vaccines, in terms of safety and effectiveness for a wide spectrum of species, are *zona pellucida* (ZP) protein and GnRH. The ZP vaccine affects female reproduction by blocking sperm penetration of the outer surface (*zona pellucida*) of an ovulated egg, thus preventing fertilisation (Miller and Fagerstone 2000; Dunbar et al. 2002). ZP proteins isolated from the ovaries of domestic pigs (porcine *zona pellucida*, PZP) are the most commonly used antigens and generate infertility in most species tested, although not in rodents (Miller et al. 1997). The GnRH vaccine prevents ovulation, the oestrous cycle, the production of oestrogen and progesterone in females, and the production of sperm and testosterone in males. It is known to be effective in many mammals (Fagerstone et al. 2006). An example of the application of this vaccine for disease management is the potential for reducing transmission of brucellosis in bison, which is primarily through contact with infected aborted foetuses, placentas and associated fluids, by rendering infected females infertile (Miller et al. 2004a).

Until recently, immunocontraceptives required an initial vaccination plus one or two booster doses to induce an immune response sufficient to render treated individuals infertile for one or two years. Consequently, these contraceptives have had limited practical utility for wildlife applications where the recapture of individuals to administer booster doses is often problematic. Recent technological advances have led to the development of so called ‘single-shot’ vaccines capable of inducing long-term infertility from a single dose (Miller et al. 2003; Miller et al. 2004b). This technological breakthrough makes the prospect of practical wildlife applications realistic and potentially cost-effective. The ‘single-shot’ PZP and GnRH vaccines have been shown to induce infertility for three years in a high percentage (>90%) of treated animals with the effect persisting longer in many, and permanently in some (Fraker et al. 2002; Killian et al. 2006). The adjuvant formulation is a key component of the longevity of the response to these single-dose vaccines (Miller et al. 2004b). An alternative delayed release approach to obtaining long-term infertility from a single injection offers two years of infertility with a PZP vaccine formulation (Turner et al. 2007).

7.4.2 Delivery Systems

Injection by hand has been used to deliver some fertility control implants and is currently the standard method of delivering immunocontraceptive vaccines. However, dart and biobullet technologies are improving prospects for remote delivery of vaccines and implants without the need to capture animals. Dart delivery has been used extensively to deliver PZP immunocontraceptive vaccines to feral horses (Kirkpatrick et al. 1990) and booster PZP vaccinations to African elephants (*Loxodonta africana*) (Delsink et al. 2007). The parallel development of automatic marking systems will allow the visual recognition of treated animals. Because immunocontraceptive vaccines can currently only be delivered by hand injection or dart, the potential range of applications for this emerging technology is restricted. The development of an orally effective immunocontraceptive vaccine would offer a far broader spectrum of potential applications. However, although oral delivery is possible for chemical agents of fertility control, such as diazacon, it does not offer the potential for inducing the long-term infertility afforded by immunocontraception.

An alternative approach to delivering an immunocontraceptive vaccine to a high proportion of a target population would be to engineer a biological dissemination agent. The development of such a system, known as Virally Vectored Immunocontraception (VVIC), was explored in Australia as a means to control introduced mammals. It requires the production of a recombinant virus containing an immunogen that renders infected animals infertile. This offers potentially high levels of specificity if the chosen virus only multiplies in the target host. Dissemination of the virus and its immunocontraceptive cargo away from the release site occurs through natural disease transmission processes thereby potentially inducing widespread infertility in the target population. However, such an approach is likely to be technically challenging, and to raise serious concerns over the release of a genetically modified organism (GMO) and the potential for adverse ecological consequences. For these reasons research into using VVIC for the management of wild mammals in Australia was curtailed. The technical feasibility of achieving fertility control in brushtail possums in New Zealand using, for instance, a genetically modified nematode parasite carrying a marsupial *zona pellucida* immunocontraceptive epitope has also been investigated, but this too would need to overcome many technical and regulatory challenges before becoming a viable management tool. Any attempts to develop such systems for the dissemination of fertility control agents will need to also take into account the heterogeneity in patterns of contact amongst individuals within host populations, as this is a major determinant of transmission dynamics (see Chapter 2).

7.4.3 Welfare Implications of Fertility Control

The effect of GnRH vaccines is essentially to revert animals to a sexually inactive state, which is a common feature of the life cycles of many wild mammals. GnRH immunocontraceptive vaccination has been employed in a range of mammal species with no significant welfare concerns recorded. However, there are contraindications for its use in males of species that develop vulnerable secondary sexual characteristics such as antlers in deer, which may fail to harden and remain persistently in velvet, with significant consequences for welfare (Killian et al. 2005).

PZP immunocontraceptive vaccines have a more specific physiological effect than GnRH vaccines and so might present a lower potential risk of inducing negative side effects. However, preventing egg fertilisation in species with a multiple cycling reproductive strategy (e.g. many deer species) has resulted in repeated cycling and an extended breeding season (Curtis et al. 2002). This may lead to a decline in condition, particularly amongst males who may attempt to defend access to repeatedly cycling females, and increase their movement rates with associated risks of enhanced vehicle collisions and disease transmission. Such effects might also occur in these species through the use of IUDs.

The only generic adverse reactions reported for both PZP and GnRH immunocontraceptive vaccines have been injection site granulomas, although these are generally of relatively mild severity (Dalin et al. 2002). Acute reactions have sometimes been reported but these may reflect an inappropriate injection site (Imboden et al. 2006). In assessing the significance of such welfare concerns it is important to make comparison with the negative effects associated with alternative management options.

7.4.4 Disease Management

The use of fertility control for the purposes of disease management in wild mammals raises several important questions. For example, what proportion of the target population must be rendered sterile to achieve a specified reduction in population size, and how long will this take? Also, for animals that have a lifespan exceeding the duration of the effect of the fertility control agent, how often should the agent be applied? As with culling, simulation models (see Chapter 4) have been usefully employed to explore these issues (Hone 1992; Hobbs et al. 2000; Cowan et al. 2006), in some cases with specific regard to disease management (Tuyttens and Macdonald 1998). With few exceptions the results of these modelling exercises generally suggest that fertility control would be likely to yield the most benefit to disease control programmes when employed alongside culling or vaccination, rather than in isolation. In the UK the introduced grey squirrel (*Sciurus carolinensis*) is implicated in the transmission of pox virus to the declining native red squirrel (*S. vulgaris*) population. Mathematical models suggest that when used in isolation, fertility control does not appear to offer any significant advantage over culling as a method of reducing grey squirrel populations, although it may have a role to play as part of an integrated management strategy (Barr et al. 2002). Similarly, it has been suggested that fertility control might be used alongside culling or vaccination, for the management of bTB in Eurasian badger populations in the UK. Fertility control has also been proposed as part of the optimum strategy, including culling and vaccination, to control a point-source rabies outbreak in red foxes. However, one important limitation of these simulation models is that they do not account for other factors such as behavioural changes in individuals subjected to fertility control treatments, which could influence disease transmission rates. Data from long-term field studies will be valuable in refining such models. Results emerging from studies of population-level responses to the injection of multiple and single-shot immunocontraceptive vaccines (Fayrer-Hosken et al. 2000; Turner et al. 2002; Gionfriddo et al. 2008) suggest the potential value of these approaches. There have now been a number of successful demonstrations of the use of immunocontraception alone to reduce populations of white-tailed deer (Rutberg et al. 2004); African elephants (Delsink et al. 2007) and feral horses (Ballou et al. 2008). Whilst the results of these long-term studies are encouraging they have also raised awareness of new issues specific to the fertility control approach that require consideration. Released from the costs of reproduction, infertile animals survive longer than their fertile counterparts, with consequent implications for the magnitude and rate of population reduction achieved. Enhanced longevity may also raise welfare issues associated with an increased likelihood of individuals reaching senescence. Future research will be required to address these new questions as the technology matures from individual based to population level studies of fertility control as a new wildlife management option with potential to contribute to disease control.

7.5 Conclusions

It is frequently assumed that reducing host population density will achieve a reduction in disease incidence. Although this has intuitive appeal and is supported by simple epidemiological models, a growing body of evidence is undermining the generality of this assumption. For example, there is scant empirical evidence for host population thresholds for disease persistence in wildlife (Lloyd-Smith et al. 2005b). In addition, the potential for culling to induce compensatory reproduction and immigration, to increase the proportion of susceptible or infected hosts and to alter host behaviour, means that the outcomes of such interventions can be unpredictable, and potentially counter-productive. Consequently, proposed strategies need to be carefully designed and adaptive in order to respond to any unexpected and undesirable consequences of intervention. It is also important that all the reservoirs of infection are correctly identified and their relative contribution to the maintenance of the disease evaluated.

Outbreaks of particularly virulent diseases in which wild mammals are implicated may represent such an extreme threat to human health or the national economy that there is considerable pressure for immediate action such as culling. In this regard it is useful to note that culling has been demonstrated to be far more successful in preventing the spread or establishment of diseases in wildlife, than as a means of controlling a disease that is already present (Wobeser 2002). Consequently, under certain circumstances culling may be useful as a short-term measure, particularly in response to a localised outbreak (see Chapter 9). However, the use of culling for sustained control or eradication of disease in a wild mammal population is likely to be difficult, protracted and expensive exercise, with unpredictable outcomes. Broad-brush, draconian approaches to disease management such as large-scale eradication and control campaigns are generally no longer regarded as being ethically acceptable or economically sustainable.

Given the potential problems associated with culling, it is likely to be increasingly considered as one component within a wider programme. Culling has been more successful in controlling disease in wild mammal populations when carried out together with other measures such as public education, improved husbandry of domestic livestock, habitat manipulation and vaccination (Rupprecht et al. 2006). In addition, developments in diagnostic testing and greater understanding of the dynamics of disease in wild mammals may enhance opportunities to use culling in a more efficient and targeted manner.

Fertility control offers an attractive alternative to culling. The underlying assumption of both approaches is that reducing host density can diminish the incidence of disease, but fertility control is unlikely to suffer from many of the disadvantages of culling, and is likely to be more publicly acceptable. However, a great deal more research is required before the use of fertility control becomes a practical reality for the management of disease in wild mammals.

There are clearly many factors that need to be addressed when contemplating the management of disease by targeting the wildlife host. To date, most attempts have been fairly heavy-handed, and have either been unsuccessful or impossible to evaluate. The importance of monitoring the success (or failure) of intervention cannot be overstated (see Chapter 10). It is imperative that the ultimate aim of the intervention is clearly defined and the probability of success critically evaluated. In particular, the cost of the intervention, including ongoing maintenance control if disease elimination is not the aim, should be evaluated against the longer-term economic benefit of success (see Chapter 5). Modelling the effect of intervention on subsequent disease prevalence in the targeted host and on any population requiring protection may be useful. However, it is vital that confounding ecological factors such as host ecology and behaviour, compensatory reproduction, social perturbation and the potential for intervention to have unpredictable outcomes are taken into account. Whilst culling may be a useful management option under certain circumstances, and fertility control holds some promise for the future, in general our approaches need to be refined quite considerably to realise their potential. An integrated approach combining conventional methods such as culling with fertility control, vaccination and biosecurity may need to play an increasingly important role in the management of wildlife diseases in order to achieve measurable, cost-effective benefits whilst also preserving biodiversity.