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A Modeling Approach to Evaluating Potential Applications of Emerging Fertility Control Technologies in the UK

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ABSTRACT: There is increasing demand for benign approaches to the resolution of conflicts between human interests and wildlife. One non-lethal method to reduce the growth and expansion of overabundant wildlife populations is fertility control. Significant progress has been made in recent years on the development of fertility control agents, culminating in the availability of single-dose injectable immunocontraceptive vaccines that inhibit the fertility of individuals for several years. The potential application of such technology is explored here using the European rabbit, gray squirrel, wild boar, and European badger as examples of species that pose problems of damage to agricultural and forestry interests, disease transmission and threats to biodiversity. A simple model is developed that predicts the likely general population consequences of varying levels of infertility for species with differing demographic characteristics. This suggests that low levels of fertility control will have little impact on population size in species with high reproductive rates and high population turnover rates. Modest levels of infertility can significantly reduce the populations of species with relatively low intrinsic rates of increase. However, these reductions may take longer than those arising from high levels of imposed infertility in species with rapid population turnover rates. The modeling approach, as outlined here, could be used to inform future field studies by identifying suitable target species and making predictions about population responses that can be tested empirically. These studies will be necessary to realize the potential of the emerging fertility control technologies in the form of practical wildlife management applications.

KEY WORDS: fertility control, immunocontraception, population modeling

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INTRODUCTION

Conflicts between wildlife, human activities, and conservation interests often reflect wildlife populations that are expanding or considered overabundant. Non-lethal approaches, such as exclusion by fences or deterrents, are appropriate in some contexts. However, in others the overabundance of the species drives the conflict and problem populations must be reduced in size. It is thus still sometimes necessary to cull such populations. Nevertheless, lethal methods can be ineffective, environmentally hazardous, and uneconomic while also compromising animal welfare (Waddell *et al.* 2001, Fagerstone *et al.* 2002, Delahay *et al.* 2003). At the same time, growing public antipathy towards lethal methods places increasing constraints on management options, particularly for those species which have a high public profile (Jackson 2001, Barr *et al.* 2002, Deigert *et al.* 2003). As an alternative to culling, fertility control has the potential to offer long-term, effective, and humane means of reducing the size and growth of overabundant wildlife populations (Tuytens and MacDonald 1998, Barlow 2000, Smith and Cheeseman 2002). However, potentially effective tools have only recently begun to emerge. In particular, chemical contraceptives such as DiazCon and Nicarbazin hold promise for avian species (Fagerstone *et al.* 2002) while the advent of the "single-shot" immunocontraceptive vaccines, such as Gonadotropin Releasing Hormone (GnRH) vaccine and Porcine Zona Pellucida (PZP) vaccine, offer potential for mammalian species (Miller *et al.* 2000, Curtis *et al.* 2002). The emergence of these vaccines represents a major technological breakthrough as the prospect of

practical wildlife applications becomes realistic. The availability of this technology has reawakened interest in the UK regarding the potential of fertility control to resolve contentious wildlife conflicts. Here, we consider some potential UK target species for this technology and make some preliminary assessments of feasibility.

While many problems can be resolved without recourse to population level management of numbers, for this paper let us consider that population reduction is considered necessary. Exploring whether fertility control is feasible for a specific problem posed by a particular species involves a number of generic questions. Firstly, what proportion of the target population must be rendered sterile to achieve a set reduction in population size or to maintain population growth at zero? For animals that have a lifespan exceeding the duration of the effect of the fertility control agent, an added issue is how often should the agent be applied? Another key question is how long will it take to reduce a population to a target size? Finally, the focus of management might be on reduction of impact rather than population size, therefore what proportion of the population must be rendered sterile to achieve the desired reduction in damage? Answering these complex questions depends on species-specific population parameters as well as the nature of the problem posed by the species. A further complication is that for many species the relationship between population density and level of impact is not linear, so that a reduction in population size is not necessarily followed by a proportional decrease in damage (Hone 1995, 2002).

Our main aim here is to use a range of examples to guide a generic assessment of the feasibility of imposing

sufficient fertility control to meet the management objectives. Mathematical modeling has often been used to deal with the complexities associated with predicting the consequences of imposing fertility control. However, the majority of these models have considered individual species rather than addressing general issues (e.g., Pech *et al.* 1997). Furthermore, where generic approaches have been explored, these have not been directly linked to predicting population consequences of imposing different degrees of fertility control (e.g., Caughley *et al.* 1992; Hone 1992, 1999). However, Hobbs *et al.* (2000) developed a simple, stage-structured population model of fertility control. This assumes a closed population, a constant adult mortality rate that does not vary with age, and density-dependence to operate as linear function of density. A steady-state population size can be derived from the model as a simple function of maximum recruitment rate, adult survival, and a density-dependent function reflecting the carrying capacity of the habitat for that species. We have developed this model, which was initially designed for use with ungulate populations that generally have a maximum annual per capita recruitment rate (number of breeding females recruited to the population per breeding female) of less than 1, into a generic model that allows consideration of more fecund species with higher maximum recruitment rates. This adjusted model is used to predict the population consequences of imposing different levels of fertility control on populations of 4 potential target species in the UK.

A GENERIC MODEL OF FERTILITY CONTROL The Hobbs *et al.* (2000) Model

In Hobbs *et al.* (2000), the population dynamics in the absence of control (either culling or fertility control) are governed by the equation:

$$N_{t+1} = N_t (S + m - \beta N_t)$$

where N_t and N_{t+1} are the numbers of adult females alive at times t and $t+1$ respectively, S is the adult female survival rate, m is the recruitment rate of females to the adult population, and β is the slope of a density-dependent function which reflects the carrying capacity of the population.

A model of population control by culling is given by the equation:

$$N_{t+1} = N_t (S + m - \beta N_t)(1-c)$$

where c is the rate of culling, and it is assumed to occur pre-breeding so that the cull also affects the new adults recruited within the previous year.

The corresponding fertility control models can be categorised into two types: the lifetime model, in which infertile females remain infertile until death, and the fixed duration model in which infertile females experience a fixed period of infertility after which they return to the fertile state.

In the lifetime model we have:

$$\begin{aligned} F_{t+1} &= F_t (S + m - \beta N_t)(1-c) \\ I_{t+1} &= F_t (S + m - \beta N_t)c + I_{t,t} \end{aligned}$$

where F_t and I_t are numbers in the fertile and infertile states at time t , and c is the rate of fertile individuals becoming infertile. The total adult female population size $N_t = F_t + I_t$.

In the fixed duration model, individuals remain infertile for a certain duration τ . The system is now described by the set of equations (using $\tau = 3$ as an example):

$$\begin{aligned} F_{t+1} &= F_t (S + m - \beta N_t)(1-c) + I_{3,t}S(1-c) \\ I_{1,t+1} &= F_t (S + m - \beta N_t)c + I_{3,t}Sc \\ I_{2,t+1} &= I_{1,t}S \\ I_{3,t+1} &= I_{2,t}S \end{aligned}$$

where $I_{i,t}$ is the number of infertile individuals in the i^{th} year of infertility at time t , and $N_t = F_t + \sum I_{i,t}$.

The Adjusted Model

The above model offers an informative first approach to predicting the effects of fertility control, and Hobbs *et al.* (2000) used it successfully to describe the population dynamics of ungulates, which are typically large, long-lived species with relatively low recruitment rates. For smaller, shorter-lived species with higher recruitment rates, the simplicity of the model gives rise to oscillating and even chaotic dynamics at relatively modest values of m greater than 1. Consequently, we propose an amendment to the density-dependent function that allows for larger values for m at low population densities, without the biologically unlikely oscillations and chaos inherent in the simple form of the Hobbs *et al.* (2000) model.

The adjusted model is as above, but also incorporates a density-dependent recruitment rate m^* , such that:

$$m^* = (m_0 - m) \times (\max[(K - F_t)/K, 0]) + m$$

In this equation, m_0 is the recruitment rate at zero population density, while m is the recruitment rate at high population density, and K is the carrying capacity or steady-state population size of the system which is given by $(S+m-1)/\beta$ as in Hobbs *et al.* (2000). Figure 1 shows a comparison of the per-capita population change as a function of density under the two models. Using this formulation for recruitment, we obtain more realistic representations of the biology of shorter-lived species with high maximum recruitment rates, while still being able to make inferences about the population consequences of fertility control.

The model we focus on in this paper is the adjusted 3-year fixed duration model, namely:

$$\begin{aligned} F_{t+1} &= F_t (S + m^* - \beta N_t)(1-c) + I_{3,t}S(1-c) \\ I_{1,t+1} &= F_t (S + m^* - \beta N_t)c + I_{3,t}Sc \\ I_{2,t+1} &= I_{1,t}S \\ I_{3,t+1} &= I_{2,t}S \end{aligned}$$

The 3-year fixed duration model is used because evidence is accumulating that the “single-shot” vaccines offer high levels of infertility for at least 3 years in the majority of females after a single vaccination event (Miller and Killian 2000, L. Miller pers. commun.).

Using this model, we present predictions of the effect of continued infertility treatment administered to a population at a rate c . The initial population is assumed to be fully fertile and at carrying capacity. Furthermore, we assume that individual animals can be identified thus “already-infertile” animals are not revaccinated and therefore their infertility cannot be prolonged (i.e., no transitions from I_2 to I_1 , or I_1 to I_1 are allowed). Individuals in I_3 can potentially be revaccinated immediately on regaining their fertility and as such transitions are permitted between states I_3 and I_1 . Case studies of 4 potential target species in the UK have been considered using this model.

Figure 1. The y-axis shows the per capita annual population change given by the Hobbs *et al.* (2000) model ($S + m - \beta N_t$) (solid line) and by the adjusted model ($S + m^* - \beta N_t$) (broken line) in the absence of control (models parameterised with $S = 0.5$, $m = 0.8$, $\beta = 0.003$, and $m^* = 3$).

CASE STUDIES

European Rabbit (*Oryctolagus cuniculus*)

Rabbit damage is now re-established as the most important economic threat posed by wildlife to agricultural and forestry interests in the UK. Before the arrival of the disease myxomatosis in 1953, there were estimated to be up to 100 million rabbits in the UK (Rees *et al.* 1985). Myxomatosis killed an estimated 99% of the UK population, so that by 1955 the rabbit was no longer considered to be a major problem (Lloyd 1970). Subsequently, the reduced pathogenicity of the disease, derived from the co-evolution of rabbits and the myxoma virus, has led to the gradual recovery of the rabbit population, so that by the 1980s there were an estimated 20 million rabbits causing about \$US 190 million of agricultural damage annually (Rees *et al.* 1985). It has been estimated that the population has continued to grow at an average rate of just over 1% per year (Trout *et al.* 2000). However, although by 2002 the population had thus approximately doubled since the mid 1980s, the value of crops had decreased, giving an estimated annual loss to

rabbit damage of around \$US 220 million (Smith *et al.* 2006). Nevertheless, this is a substantial and increasing problem, and ways of locally reducing overabundant populations are required. There are no legal ways of using poison baits against rabbits in the UK, and the availability of burrow fumigants is becoming restricted. Hence, alternative approaches are required, which might include fertility control if suitable technology becomes available.

The population biology of the wild rabbit in the UK is well understood, with high annual productivity (Brambell 1944, Lloyd 1970, Trout and Smith 1995) offset by high juvenile mortality (>90%) and annual adult mortality of 40-60% (Cowan 1987). Density-dependent processes can influence both fecundity and mortality rates (Smith 1997). From these published data, we parameterized the adjusted model, which was then run for 20 years, imposing varying degrees of infertility ranging from 10% to 90% of breeding females (Figure 2). This predicts that low levels of fertility control have minimal impacts on population size, and that at least 80% infertility is required to drive the population down towards extinction. However, the downward responses of populations to high levels of imposed infertility are rapid.

Figure 2. Changes in the size of the adult female population predicted by the adjusted model, parameterised using data on European rabbit population biology ($S = 0.5$, $m = 0.8$, $\beta = 0.003$, and $m^* = 3$), with varying degrees of fertility control imposed ranging from 10% to 90% of fertile adult females vaccinated each year.

Gray Squirrel (*Sciurus carolinensis*)

The Eastern American gray squirrel was introduced to the UK in the late 19th century and subsequently expanded its range, so that by the end of the 20th century it was present across much of the country. This has had major negative consequences, particularly for forestry interests (Mayle 2005). In addition, the advance of the gray has played a major role in the decline of the native red squirrel (*Sciurus vulgaris*), this probably being at least partly driven by disease in the form of a parapox virus, carried by gray squirrels acting as a reservoir of the disease, to which red squirrels are particularly susceptible (Rushton *et al.* 2000).

The population biology of the gray squirrel in the UK is well defined. Productivity is not as high as that of rabbits, with 2 litters of 2 to 4 young being born per adult female, although yearlings generally produce only one litter (Shorten 1954). Population turnover rates are consequently somewhat slower for gray squirrels than for rabbits. Complete population turnover takes around 6 years (Gurnell 1983). However, mortality rates are still relatively high compared to larger mammals. About 75% of juveniles disappear during the first winter, but thereafter annual survival improves to around 50%. Mean life expectancy is greatest for females at 6 months (4-5 years) and for males at 18 months of age (2-3 years) (Gurnell 1987). These data provided estimates of the parameters for the adjusted model, which was run for 20 years with varying degrees of fertility control imposed (Figure 3). The model suggests that, as with the rabbit, low levels of infertility have little impact. However, if levels of 70% infertility or more can be achieved, then fertility control apparently can drive populations down to probable extinction.

Figure 3. Changes in the size of the adult female population predicted by the adjusted model, parameterised using data on gray squirrel population biology ($S = 0.5$, $m = 0.7$, $\beta = 0.002$, and $m^* = 2.1$), with varying degrees of fertility control imposed ranging from 10% to 90% of fertile adult females vaccinated each year.

Wild Boar (*Sus scrofa*)

Wild boar have been extinct in the UK since the 17th century. However, a number of populations have recently become established in southern England as escapes and releases from wild boar farms. These populations can potentially impact on a variety of human interests, ranging from damage to crops, disease reservoirs, damage to livestock production, and vehicle collisions (Goulding *et al.* 2003, Wilson 2004). On the other hand, these populations reflect the reintroduction of a native species, and thus can be viewed positively from a biodiversity perspective, and some of their effects on forest floor ecology might be positive. The management of these populations thus raises complex issues that have yet to be resolved in terms of balancing different interests, and novel approaches, including fertility control, may well be required to meet this challenge.

Our understanding of the population biology of wild boar in the UK is patchy and much less detailed than for continental Europe. Average litter size has been reported as 4.29 (DEFRA 2004) and 4.57 (Wilson 2003). However, litter size in wild boar is known to vary considerably, particularly in relation to autumn food availability (Massei *et al.* 1996). Breeding is seasonal, although females may produce more than one litter per year, again depending on environmental conditions. Thus, the species has a potentially relatively high intrinsic rate of population increase for such a large animal. Mortality rates are highly variable and also reflect environmental conditions, notably food availability (Massei *et al.* 1997). Estimates derived for an English population subject to hunting indicated annual juvenile mortality of 60% to 80% and annual adult mortality of 10-100%, with a rate of 40% measured for tagged animals (DEFRA 2004). These values were used to derive estimates of the parameters for the adjusted model which was run for 20 years with varying degrees of fertility control imposed (Figure 4).

Figure 4. Changes in the size of the adult female population predicted by the adjusted model, parameterised using data on wild boar population biology ($S = 0.6$, $m = 0.7$, $\beta = 0.002$, and $m^* = 1$), with varying degrees of fertility control imposed ranging from 10% to 90% of fertile adult females vaccinated each year.

The model suggests that, compared to the rabbit and gray squirrel, relatively modest levels of infertility will give rise to significant reductions in population size. For instance, a 30% reduction in fertility yields a 50% reduction in population size, while levels of infertility above 50% appear to have the potential to lead to extinction. However, the downward population responses to fertility control are less rapid than for the rabbit and gray squirrel. For example, the effect of 30% imposed infertility may take 4 to 5 years for its effect to be fully established.

European Badger (*Meles meles*)

The European badger has been on the increase in the UK in recent years (Wilson *et al.* 1997, Battersby *et al.* 2005). This species has its own legislation, with full legal protection conferred by Protection of Badgers Act (1992),

UK. However, the Department for Environment, Food and Rural Affairs (DEFRA), UK can grant licences to prevent damage to land, crops, livestock or property. Badgers have colonised a variety of rural habitats, and have now also successfully adapted to urban life and are present in many urban and suburban areas. This has led to increasing conflict with human interests, including agricultural damage (Moore *et al.* 1999), and damage to gardens and property in suburban and urban settings, particularly in the form of sett construction. Furthermore, badgers can be infected with bovine tuberculosis (TB), and cattle are thought to be at risk of infection from environmental contamination by infectious badgers, although the management of this risk by culling is controversial (Delahay *et al.* 2003, Donnelly *et al.* 2006).

In relation to assessing the feasibility of using fertility control to manage badger populations, the demography of the badger in the UK is particularly well understood from long-term studies (Cheeseman *et al.* 1987, Rogers *et al.* 1997). Although mean litter size is around 2.7, average per capita annual birth rate is only 0.29 because not all adult females produce litters. Adult mortality is density-dependent with minimum annual adult mortality of 20%, 29% at carrying capacity, and 33% when above carrying capacity. We thus derived relatively reliable figures for the required recruitment and survival parameters for our adjusted model, and this was run for 20 years with varying degrees of fertility control imposed (Figure 5). This predicts that modest levels of induced infertility might have significant population consequences, although these effects take a relatively long time to emerge.

Figure 5. Changes in the size of the adult female population predicted by the adjusted model parameterised using data on European badger population biology ($S = 0.75$, $m = 0.4$, $\beta = 0.0015$, and $m^* = 0.5$) with varying degrees of fertility control imposed ranging from 10% to 90% of fertile adult females vaccinated each year.

DISCUSSION

The adjusted model developed here successfully accommodates the application of fertility control to the demography of more productive species with faster population turnover rates than those originally intended by Hobbs *et al.* (2000). However, given the simplicity of

the model, it cannot be expected to provide accurate predictions of the precise population reduction resulting from a certain level of fertility control for a given species. In particular, the compensatory responses of populations towards reduced productivity may be more complex than the simple density-dependent processes considered here. Nevertheless, the predictions of the adjusted model provide an indication of the likely general population consequences of varying levels of infertility.

The species considered here as case studies reflect a range of demographic characteristics, thus the predictions made offer some insight into how these characteristics influence population responses to fertility control. The high reproductive rate and rapid population turnover of, in particular, the rabbit but also the gray squirrel, suggest that low levels of infertility have little impact on population size in such species. This is consistent with a large-scale field experiment on the rabbit in Australia using surgical sterilisation of females, where 60-80% of female rabbits needed to be prevented from breeding to achieve a sustained, long-term reduction in rabbit abundance (Twigg *et al.* 2000). The prediction of the adjusted model thus broadly agrees with this evidence from the field. In addition, Twigg *et al.* (2000) reported that the survival of sterilised females was higher than that of unsterilised females, presumably reflecting the costs of reproduction. Higher survival in non-breeding females is widely reported for other species, including badgers (Cheeseman *et al.* 1987), but is not universal; for instance, Saunders *et al.* (2002) did not observe this effect in the red fox (*Vulpes vulpes*). We have not included this variation in our model, but its structure is amenable to further adjustment to assess the impact of enhanced survival of infertile females and duration of infertility on the population consequences of different levels of fertility control.

Several authors (Barlow 1997, Hone 1992, Dolbeer 1998) have suggested that fertility control would be most effective for small-sized, r-selected species, characterised by high productivity and low survival. This position reflects fecundity making a greater proportional contribution than survival to population growth in short-lived species, with the reverse pertaining to long-lived species (Sibly and Hone 2002). However, others have argued that lower levels of infertility are required in longer-lived species with relatively low maximum rates of population increase, to achieve the same population reduction in comparison to shorter-lived species with relatively high population turnover rates (Hone 1999, Hobbs *et al.* 2000). This is because the higher the maximum rate of population increase, the quicker compensatory processes can potentially offset reduced productivity. The results of our adjusted model support this general premise, with relatively high levels of infertility predicted to be necessary for the rabbit and gray squirrel. This has practical consequences, because in order to vaccinate the necessarily high proportions of target populations of these species, an oral vaccine delivered via bait would be required. However, an effective oral immunocontraceptive has yet to be developed. Furthermore, if one does become available, the current technology suggests that this is unlikely to be species-specific. Therefore, species-

specificity will need to be achieved via the baiting system. This would be challenging, although a feeding hopper exists for the gray squirrel that may afford a high degree of specificity.

Whether fertility control could be used to intervene effectively in the interaction between gray and red squirrel populations in the UK remains uncertain. This is complicated by the need to consider the epidemiology of the parapox virus implicated in the decline of the red (Rushton *et al.* 2000). More sophisticated models are thus required, although while Rushton *et al.* (2002) do not identify any significant advantage of fertility control over culling, they do acknowledge that immunocontraception might play a role in an integrated management strategy.

The adjusted model's predictions suggest that fertility control is a potentially feasible means of reducing and managing wild boar populations. It is relatively easy to trap this species (DEFRA 2005). Hence, managing local populations through capture, parenteral vaccination, and release may be a realistic possibility. However, the demographic data used to parameterise the model for this species are relatively weak, and thus the inferences drawn must be treated with caution. Nevertheless, the finding that equivalent population reduction takes somewhat longer than in the rabbit and gray squirrel is probably correct and is due to the moderately lower wild boar population turnover rate. The maximum rate that fertility control can reduce a population will depend on population turnover rate; the slower the turnover rate, the longer it will take for the population to be reduced through natural mortality (Hone 1992). However, several authors suggest that for species and contexts where an immediate reduction of population size is required, culling could be used initially to bring the population down to the target density, followed by fertility control to hold density at the reduced level (White *et al.* 1997, Merrill *et al.* 2003). The closed population assumption of the model may be realistic for the discrete wild boar populations currently found in the UK, but this is not the case for the rabbit and grey squirrel, where immigration is likely from areas outside those subject to fertility control.

The adjusted model suggests that relatively modest levels of infertility are necessary to reduce badger populations significantly. However, it is uncertain how this might help resolve conflicts involving this species. It has recently been demonstrated that bovine TB incidence can be reduced in areas where badgers are culled, but incidence increases in areas adjoining those where badgers are culled (Donnelly *et al.* 2006). A suggested reason for this increase is that social perturbation due to culling disrupts the social organisation, with consequent increased movement and contact between individuals resulting in increased risk of disease transmission (Cheeseman *et al.* 1993, Woodroffe *et al.* 2006). Fertility control would, in principle, cause less social perturbation than culling (Tuytens and MacDonald 1998). However, assessing whether fertility control could play a role in managing badger populations in the context of bovine TB would again require a more sophisticated modelling approach than that considered here. For instance, this would need to include spatial aspects of disease epidemiology. Nevertheless, it has already been

suggested that fertility control might form part of an integrated approach alongside culling or disease vaccination (White *et al.* 1997, Smith and Cheeseman 2002).

The other potential context for fertility control in this species concerns problems posed by badgers in urban and suburban areas. These are becoming more common, with increasing numbers of licence applications being made annually under The Protection of Badgers Act (1992), UK. Such problems can become intractable and locally devastating to property being undermined by badger activity, primarily through digging and sett construction. We are beginning to learn more about badger behavioural ecology in these settings. For instance, home ranges are generally small, movements are restricted, foraging is concentrated in gardens, and there is limited direct contact between social groups (J. Davison, pers. commun.). Small, isolated populations may thus be causing intense local problems and, interestingly, long duration fertility control has a high probability of extinction for small, closed populations (Hobbs *et al.* 2000).

The prediction of Courchamp and Cornell (2000) that immunocontraception could eradicate feral cats on oceanic islands is based on a similar premise. Fertility control might thus offer a relatively benign but effective solution for some intractable badger problems in urban and suburban settings. However, not all female badgers produce cubs each year (Cheeseman *et al.* 1987). The presence of non-breeding females, and the possibility that breeding is suppressed by socio-sexual behaviour, means that ideally the socio-sexual behaviour of vaccinated animals should be unaffected, given the potential for subsequent compensatory breeding by unvaccinated non-breeders. In extreme cases, such compensatory breeding could give rise to the perverse outcome of fertility control leading to increased productivity (Caughley *et al.* 1992), although this process may already be partially or fully accounted for in the density-dependent functions included in the adjusted model. Nevertheless, a key potential advantage of fertility control over culling is that infertile animals remain in the population, thus contributing to density-dependent feedback that constrains recruitment and survival (Knipling and McGuire 1972, Shi *et al.* 2002). If this feedback is lost, for instance if rendering dominant females infertile means that they no longer suppress the productivity of subordinates, then this potential advantage of fertility control would be at least partially undermined. Any evaluation of fertility control in badgers would thus need to focus on the response, if any, of non-breeding, unvaccinated females.

There is still some way to go before the emerging fertility control technology leads to practical applications. Nevertheless, progress and encouraging results are being obtained as individual based studies are made under field conditions (Miller *et al.* 2000, Rudolph *et al.* 2000, Walter *et al.* 2002, Merrill *et al.* 2003). The next challenge will be proof of concept in large-scale field studies, with population change as the outcome variable. The modelling approach, as outlined here, may help inform such studies by identifying suitable target species and making predictions about population responses that

can be tested empirically. It is through such studies that the potential of novel fertility control techniques will be realised, perhaps initially to complement existing management approaches but ultimately offering major changes in wildlife management practice.

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LITERATURE CITED

- BARLOW, N. D. 1997. Modelling immunocontraception in disseminating systems. *Reprod. Fertil. Devel.* 9:51-60.
- BARLOW, N. D. 2000. The ecological challenge in immunocontraception: editor's introduction. *J. Appl. Ecol.* 37:897-902.
- BARR J. J. F., P. W. W. LURZ, M. D. F. SHIRLEY, AND S. P. RUSHTON. 2002. Evaluation of immunocontraception as a publicly acceptable form of vertebrate pest species control: the introduced grey squirrel in Britain as an example. *Envir. Manage.* 30:342-351.
- BATTERSBY, J. (EDITOR) AND TRACKING MAMMALS PARTNERSHIP. 2005. UK mammals: species status and population trends. First Report by the Tracking Mammals Partnership. JNCC/Tracking Mammals Partnership, Peterborough, UK.
- BRAMBELL, F. W. R. 1944. The reproduction of the wild rabbit *Oryctolagus cuniculus* (L.). *Proc. Zool. Soc. Lond.* 114:1-45.
- CAUGHLEY, C. R., P. PECH, AND D. GRICE. 1992. Effect of fertility control on a population's productivity. *Wildl. Res.* 19:623-627.
- CHEESEMAM, C. L., P. J. MALLINSON, J. RYAN, AND J. W. WILESMITH. 1993. Recolonisation by badgers in Gloucestershire. Pp. 78-93 in: T. J. Hayden (Ed.), *The Badger*. Royal Irish Academy, Dublin.
- CHEESEMAM, C. L., J. W. WILESMITH, J. RYAN, AND P. J. MALLINSON. 1987. Badger population dynamics in a high density area. *Symp. Zool. Soc., Lond.* 58:279-294.
- COURCHAMP, F., AND S. J. CORNELL. 2000. Virus-vectored immunocontraception to control feral cats on islands: a mathematical model. *J. Appl. Ecol.* 37:903-913.
- COWAN, D. P. 1987. Patterns of mortality in a free-living rabbit (*Oryctolagus cuniculus*) population. *Symp. Zool. Soc., Lond.* 58:59-77.
- CURTIS, P. D., R. L. POOLER, M. E. RICHMOND, L. A. MILLER, G. F. MATTFELD, AND F. W. QUIMBY. 2002. Comparative effects of GnRH and porcine zona pellucida (PZP) immunocontraceptive vaccines for controlling reproduction in white-tailed deer (*Odocoileus virginianus*). *Reproduction* 60:131-141.
- DEFRA. 2004. The ecology and management of wild boar in southern England – Project VC0325. Report to the Dept. for Environment, Food and Rural Affairs, UK.
- DEFRA. 2005. Investigating capture and removal strategies for wild boar at low density – Project WM0308. Report to the Dept. for Environment, Food and Rural Affairs, UK.
- DEIGERT, F. A., A. E. DUNCAN, K. M. FRANK, R. O. LYDA, AND J. F. KIRKPATRICK. 2003. Immunocontraception of captive exotic species. III. Contraception and population management of fallow deer (*Cervus dama*). *Zoo Biol.* 22:261-268.
- DELAHAY, R. J., G. WILSON, L. M. ROGERS, AND C. L. CHEESEMAM. 2003. TB and the badger: culling as a method to control a wildlife disease reservoir. Pp.165-171 in: F. H. Tattersall and W. J. Manley (Eds.), *Conservation and Conflict: Mammals and Farming in Britain*. Linnean Society Occas. Publ. Series, Westbury Press, Smith Settle, Otley, UK.
- DOLBEER, R. A. 1998. Population dynamics: the foundation of wildlife damage management for the 21st century. *Proc. Vertebr. Pest Conf.* 18:2-11.
- DONNELLY, C. A., R. WOODROFFE, D. R. COX, F. J. BOURNE, C. L. CHEESEMAM, R. S. CLIFTON-HADLEY, G. WEI, G. GETTINBY, P. GILKS, H. JENKINS, W. T. JOHNSTON, A. M. LE FERVE, J. P. MCINERNEY, AND W. I. MORRISON. 2006. Positive and negative effects of widespread badger culling on cattle tuberculosis. *Nature* 439:843-846.
- FAGERSTONE, K. A., M. A. COFFEY, P. D. CURTIS, R. A. DOLBEER, G. J. KILLIAN, L. A. MILLER, AND L. M. WILMOT. 2002. Wildlife fertility control. Technical Review 02-2, The Wildlife Society, Bethesda, MD.
- GOULDING, M. J., T. J. ROPER, G. C. SMITH, AND S. J. BAKER. 2003. Presence of free-living wild boar *Sus scrofa* in southern England. *Wildl. Biol.* 9 (Suppl. 1):15-20.
- GURNELL, J. 1983. Squirrel numbers and the abundance of tree seeds. *Mammal Rev.* 13:133-148.
- GURNELL, J. 1987. *The Natural History of Squirrels*. Christopher Helm, London. 201 pp.
- HOBBS, N. T., D. C. BOWDEN, AND D. L. BAKER. 2000. Effects of fertility control on populations of ungulates: general, stage-structured models. *J. Wildl. Manage.* 64:473-491.
- HONE, J. 1992. Rate of increase and fertility control. *J. Appl. Ecol.* 29:695-698.
- HONE, J. 1995. Spatial and temporal aspects of vertebrate pest damage with emphasis on feral pigs. *J. Appl. Ecol.* 32:311-319.
- HONE, J. 1999. On rate of increase (r): patterns of variation in Australian mammals and the implications for wildlife management. *J. Appl. Ecol.* 36:709-718.
- HONE, J. 2002. Feral pigs in Namadgi National Park, Australia: dynamics, impacts and management. *Biol. Conserv.* 105:231-242.
- JACKSON, D. B. 2001. Experimental removal of introduced hedgehogs improves wader nest success in the Western Isles, Scotland. *J. Appl. Ecol.* 38:802-812.
- KNIPLING, E. F., AND J. U. MCGUIRE. 1972. Potential role of sterilization for suppressing rat populations: a theoretical appraisal. USDA, Agricultural Research Service Technical Bulletin No. 1455, Washington, DC. 27 pp.
- LLOYD, H. G. 1970. Post-myxomatosis rabbit populations in England and Wales. *EPPO Publications (A)* 58:197-215.
- MASSEI, G., P. V. GENOV, AND B. W. STAINES. 1996. Diet, food availability and reproduction of wild boar in a Mediterranean coastal area. *Acta Theriol.* 41:307-320.
- MASSEI, G., P. V. GENOV, B. W. STAINES, AND M. L. GORMAN. 1997. Mortality of wild boar in a Mediterranean area in relation to sex and age. *J. Zool., Lond.* 242:394-400.
- MAYLE, B. A. 2005. Britain's woodlands under threat: grey squirrels and the risk they pose to European woodlands. *Trees, J. Int. Tree Found.* 65:9-11.
- MERRILL, J. A., E. G. COOCH, AND P. D. CURTIS. 2003. Time to reduction: factors influencing management efficacy in

- sterilizing overabundant white-tailed deer. J. Wildl. Manage. 67:267-279.
- MILLER, L. A., B. E. JOHNS, AND G. J. KILLIAN. 2000. Immunoneutralization of white-tailed deer with GnRH vaccine. Am. J. Reprod. Immunol. 44:266-274.
- MILLER, L. A., AND G. J. KILLIAN. 2000. Seven years of white-tailed deer immunoneutralization research at Penn State University: a comparison of two vaccines. Proc. Wildl. Damage Manage. Conf. 9:60-69.
- MOORE, N., A. WHITEROW, P. KELLY, D. GARTHWAITE, J. BISHOP, S. LANGTON, AND C. L. CHEESEMAN. 1999. Survey of badger *Meles meles* damage to agriculture in England and Wales. J. Appl. Ecol. 36:974-988.
- PECH, R., G. M. HOOD, J. MCILROY, AND G. SAUNDERS. 1997. Can foxes be controlled by reducing their fertility? Reprod. Fertil. Devel. 9:41-50.
- REES, W. A., J. ROSS, D. P. COWAN, A. M. TITTENSOR, AND R. C. TROUT. 1985. Humane control of rabbits. Pp. 96-102 in: D. P. Brit (Ed.), Humane control of land mammals and birds. Universities Federation of Animal Welfare, Potters Bar, England, UK.
- ROGERS, L. M., C. L. CHEESEMAN, P. J. MALLINSON, AND R. S. CLIFTON-HADLEY. 1997. The demography of a high-density badger (*Meles meles*) population in the west of England. J. Zool., Lond. 242:705-728.
- RUDOLPH, B. A., W. F. PORTE, AND H. B. UNDERWOOD. 2000. Evaluating immunoneutralization for managing suburban white-tailed deer in Irondequoit, New York. J. Wildl. Manage. 64:463-473.
- RUSHTON, S. P., J. GURNELL, P. W. W. LURZ, AND R. M. FULLER. 2002. Modeling impacts and costs of gray squirrel control regimes on the viability of red squirrel populations. J. Wildl. Manage. 66:683-697.
- RUSHTON, S. P., P. W. W. LURZ, J. GURNELL, AND R. FULLER. 2000. Modelling the spatial dynamics of prapoxvirus disease in red and grey squirrels: a possible cause of the decline in the red squirrel in the UK? J. Appl. Ecol. 37:997-1012.
- SAUNDERS, G., J. MCILROY, M. BERGHOUT, B. KAY, E. GIFFORD, R. PERRY, AND R. VAN DE VEN. 2002. The effects of induced sterility on the territorial behaviour and survival of foxes. J. Appl. Ecol. 39:56-66.
- SHI, D. Z., X. R. WAN, S. A. DAVIS, R. P. PECH, AND Z. B. ZHANG. 2002. Simulation of lethal control and fertility control in a demographic model for Brandt's vole *Microtus brandti*. J. Appl. Ecol. 39:337-348.
- SHORTEN, M. 1954. Squirrels. Collins, London, UK. 212 pp.
- SIBLY, R. M., AND J. HONE. 2002. Population growth rate and its determinants: an overview. Philosoph. Trans. Royal Soc. Lond. Series B-Biological Sci. 357:1153-1170.
- SMITH, G. C. 1997. An analysis of the form of density dependence in a simulation model of a seasonal breeder undergoing control. Ecol. Model. 95:181-189.
- SMITH, G. C., AND C. L. CHEESEMAN. 2002. The control of diseases in wildlife populations: culling, vaccine and fertility control. Ecol. Model. 150:45-53.
- SMITH, G. C., D. G. GARTHWAITE, AND A. J. PRICKETT. 2006. Rabbit control in Great Britain. Pp. 165-174 in: C. J. Feare and D. P. Cowan (Eds.), Advances in Vertebrate Pest Management IV. Filander Verlag, Fürth, Germany.
- TROUT, R. C., S. LANGTON, G. C. SMITH, AND R. H. HAINES-YOUNG. 2000. Factors affecting the abundance of rabbits (*Oryctolagus cuniculus*) in England and Wales. J. Zool., Lond. 252:227-238.
- TROUT, R. C., AND G. C. SMITH. 1995. The reproductive productivity of the wild rabbit (*Oryctolagus cuniculus*) in southern England on sites with different soils. J. Zool., Lond. 237:411-422.
- TUYTTENS, F. A. M., AND D. W. MACDONALD. 1998. Sterilization as an alternative strategy to control wildlife diseases: bovine tuberculosis in European badgers as a case study. Biodivers. Conserv. 7:705-723.
- TWIGG, L. E., T. J. LOWE, G. R. MARTIN, A. G. WHEELER, G. S. GRAY, S. L. GRIFFIN, C. M. O'REILLY, D. J. ROBINSON, AND P. H. HUBACH. 2000. Effects of surgically imposed sterility on free-ranging rabbit populations. J. Appl. Ecol. 37:16-39.
- WADDELL, R. B., D. A. OSBORN, R. J. WARREN, J. C. GRIFFIN, AND D. J. KESLER. 2001. Prostaglandin F-2 alpha-mediated fertility control in captive white-tailed deer. Wildl. Soc. Bull. 29:1067-1074.
- WALTER, W. D., P. J. PERKINS, A. T. RUTBERG, AND H. J. KILPATRICK. 2002. Evaluation of immunoneutralization in a free-ranging suburban white-tailed deer herd. Wildl. Soc. Bull. 30:186-192.
- WHITE, P. C. L., A. J. G. LEWIS, AND S. HARRIS. 1997. Fertility control as a means of controlling bovine tuberculosis in badger (*Meles meles*) populations in south-west England: predictions from a spatial stochastic simulation model. Proc. Royal Soc. Lond. Series B-Biological Sci. 264:1737-1747.
- WILSON, C. J. 2003. Distribution and status of feral wild boar *Sus scrofa* in Dorset, southern England. Mammal Rev. 33:302-307.
- WILSON, C. J. 2004. Rooting damage to farmland in Dorset, southern England, caused by feral wild boar (*Sus scrofa*). Mammal Rev. 34:331-335.
- WILSON, G., S. HARRIS, AND G. MCLAREN. 1997. Changes in the British badger population 1988-1997. People's Trust for Endangered Species, London, UK.
- WOODROFFE, R., C. A. DONNELLY, D. R. COX, F. J. BOURNE, C. L. CHEESEMAN, R. J. DELAHAY, G. GETTINBY, J. P. MCINERNEY, AND W. I. MORRISON. 2006. Effects of culling on badger *Meles meles* spatial organization: implications for the control of bovine tuberculosis. J. Appl. Ecol. 43:1-10.