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Wildlife Contraception, Individuals, and Populations: How Much Fertility Control is Enough?

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ABSTRACT: The resolution of conflicts between human and wildlife interests often involves lethal control to reduce problem wildlife populations. However, lethal control has always had its limitations, the acceptable methods are becoming fewer, and public opposition is on the increase. Fertility control offers a potential alternative approach that is widely regarded as being inherently more benign. Furthermore, in some circumstances fertility control may have specific advantages over culling. The development of "single-shot" injectable immunocontraceptive vaccines that inhibit the fertility of individual animals for several years is leading to practical applications that exploit this novel technology. Further advances can be expected to lead to the emergence of a new generation of wildlife management tools. A key issue in this process is predicting what the population consequences will be for a particular species, given a specific level of induced infertility. Here, we use population modelling techniques to explore how much fertility control is enough to achieve different levels of population reduction, how long it will take to realise these reductions, and to understand how these effects are shaped by the population biology of the target species. This offers some generic conclusions, with low levels of infertility having little impact on species with high population turnover rates, while modest levels of infertility may yield useful population reductions for species with low intrinsic rates of increase, although such effects take longer to be realised in long-lived species. We also observed that there is potential for optimising the intensity of induced infertility, in terms of the proportion of breeding animals rendered infertile, and the frequency of application; so, for instance, biennial application could be more efficient than annual application for some forms of fertility control in certain species. There is increasing evidence from field studies that the survival of infertile animals is enhanced, probably because they do not incur the costs of reproduction. Our model predicts that this effect will be of limited importance for short-lived species with high intrinsic rates of increase, but it is more likely to compromise population reduction in long-lived species. We suggest that the generic modelling approach can help develop an evidence-based platform for discussing when fertility control can be regarded as a feasible, desirable, and sustainable option to manage problem wildlife.

KEY WORDS: Eastern gray squirrel, Eurasian badger, European rabbit, fertility control, immunocontraception, population modeling, wild boar

INTRODUCTION

The resolution of conflicts between human and wildlife interests often involves lethal control to reduce the size of problem wildlife populations. However, lethal control has always had some limitations, the acceptable methods are becoming fewer, public opposition is often pronounced, and this approach can have direct impacts on the conservation of the species concerned (e.g., Fagerstone et al. 2002, Grandy and Rutberg 2002). Fertility control offers a potential alternative to lethal control and would add another method to the toolbox of available approaches to conflict resolution. One potential disadvantage of fertility control, relative to culling, is that it will generally take longer to achieve equivalent population reductions, simply because infertile animals will remain in the population until they die (Hone 1992). Nevertheless, in some circumstances fertility control may have inherent advantages over culling including:

1. Infertile animals remain in the population, thus potentially contributing to density-dependent feedback that constrains recruitment and survival hence slowing population recovery (Knipling and McGuire 1972, Saunders et al. 2002). Fertility control could thus be particularly effective at maintaining populations at an appropriate lower density after initial reduction to that level by culling (e.g., White et al. 1997, Merrill et al. 2003).

2. Culling can increase movement and contact between individuals resulting in increased risk of disease transmission (Donnelly et al. 2006, Woodroffe et al. 2006). Fertility control would, in principle, cause less short-term social perturbation than culling and thus be less likely to increase disease transmission (e.g., Tuyttens and MacDonald 1998).

3. Fertility control could reduce problems specifically associated with breeding activity, such as burrow and nest construction or expansion.

4. Fertility control might encourage long-term dispersal and divorce arising from reproductive failure in species exhibiting site and mate fidelity, thus reducing local breeding populations.

5. Fertility control could potentially reduce vertical transmission of disease (mother to offspring), which might reduce the probability of disease maintenance within a wildlife population (Miller et al. 2004).

6. Fertility control might increase the body condition and general health of infertile animals, thereby reducing their susceptibility to disease and thus reducing disease transmission and incidence.

7. Fertility control can induce behavioural changes in individuals that reduce disease transmission rates (e.g., Caley and Ramsey 2001, Ramsey et al. 2006, Ramsey 2007).

Despite long-standing interest in the potential of wildlife contraception, fertility control tools have only recently begun to emerge with potential for practical application. In particular, immunocontraception, using a vaccine to generate an immune response to some key component of the target's reproductive system, has moved from theory into practice with the development of "single-shot" injectable vaccines (Miller et al. 2000, Curtis et al. 2002). Other contraceptives for potential use in wildlife management now include silastic implants such as levonorgestrel and deslorelin (e.g., Poiani et al. 2002, Herbert et al. 2005), oral chemical contraceptives such as nicarbazin (Bynum et al. 2007) and DiazaCon™ (Nash et al. 2007) and, in the future, oral immuno-contraceptive vaccines may well become available. The emergence of these technologies invites questions about the population consequences of their application to particular species. For instance, how much fertility control will be enough, in terms of the number of animals rendered infertile, to achieve the management goal?

Mathematical modeling is a potentially valuable approach to dealing with the complexities associated with predicting the population consequences of imposing fertility control on a particular species (e.g., Pech et al. 1997, Rushton et al. 2002, Todd et al. 2008). However, the form of imposed infertility can vary, particularly with respect to duration and frequency of application, and the responses of individuals and populations may differ between species. A more generic approach to exploring such variation was developed by Hobbs et al. (2000) in the form of a simple, stage-structured population model of fertility control. This assumed a closed population, a constant adult mortality rate that does not vary with age, and density-dependence operating as a linear function of density. A steady-state population size can be derived from the model as a function of maximum recruitment rate, adult survival, and a density-dependent function reflecting the environmental carrying capacity of that species. Hobbs et al. (2000) designed this model 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. Cowan et al. (2006) developed the model into a more generic form that allows consideration of more fecund species with higher maximum recruitment rates. Here, we use this revised model to explore some generic issues regarding the population consequences of applying fertility control, in terms of variation between species with respect to their demographic characteristics, variation in the duration of induced infertility, variation in the frequency of application, and the potential population level effects of enhanced survival of infertile animals for whom the costs of reproduction no longer accrue (e.g., Turner and Kirkpatrick 2002).

THE MODEL

The model developed by Hobbs et al. (2000) can be categorised into two forms: 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:
$$F_{t+1} = F_t (S + m - \beta N_t)(1-c)$$
$$I_{t+1} = F_t (S + m - \beta N_t) c + I_t S$$
where F_t and I_t are numbers in the fertile and infertile states at time t, c is the rate of fertile individuals becoming infertile at time t (before breeding occurs at time t), 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 that reflects the carrying capacity of the population, and the total adult female population size $N_t = F_t + I_t$.

In the fixed duration model, individuals remain infertile only for a certain duration. The system is now described by the set of equations as follows with a fixed duration of 3 years infertility as an example:
$$F_{t+1} = F_t (S + m - \beta N_t)(1-c) + I_{3,t}S(1-c)$$
$$I_{1,t+1} = F_t (S + m - \beta N_t)c + I_{3,t}Sc$$
$$I_{2,t+1} = I_{1,t}S$$
$$I_{3,t+1} = I_{2,t}S$$
where $I_{i,t}$ is the number of infertile individuals in the ith year of infertility at time t, and $N_t = F_t + \sum I_{i,t}$.

The simplicity of the model as described by Hobbs et al. (2000) gives rise to oscillating and even chaotic dynamics at relatively modest values of m greater than 1. Consequently, Cowan et al. (2006) used an adjustment to the density-dependent function that allows for larger values of m at low population densities, without the biologically unlikely oscillations and chaos. This adjusted model is as above, but it incorporates a density-dependent recruitment rate by replacing m with m*, which is defined as:
$$m^* = (m_0 - m) \times (\max[(K-F_t)/K, 0]) + m$$
where m_0 is the recruitment rate at zero population density, 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). It is this adjusted model that is used here to predict the population consequences of imposing different forms of fertility control on a range of potential target species.

INTER-SPECIFIC VARIATION

We used the model to predict the population level consequences of imposing different degrees of permanent infertility on four potential target species in the UK. These species, selected to offer a range of demographic parameters, were:

a) European rabbit (*Oryctolagus cuniculus*): This species is currently the most important economic threat posed by wildlife to agricultural and forestry interests in the UK, with an estimated annual loss to rabbit damage of around $US 220 million in 2002 (Smith et al. 2007).

b) Eastern American gray squirrel (*Sciurus carolinensis*): The introduction of the gray squirrel to the UK has had major negative consequences, in terms of economic damage to forestry interests (Mayle 2005) and the decline of the native red squirrel (*Sciurus vulgaris*) (Rushton et al. 2000).

c) Wild boar (*Sus scrofa*): Wild boar had been extinct in the UK since the 17th century, but several populations have recently become established in

southern England as escapes and releases from wild boar farms. Although viewed positively by some as the reintroduction of a native species, 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 (e.g., Goulding et al. 2003, Wilson 2004).

d) Eurasian badger (*Meles meles*): The Eurasian badger has been on the increase in the UK in recent years (Battersby et al. 2005), leading to increasing conflict with human interests (Moore et al. 1999). Furthermore, badgers can be infected with bovine tuberculosis (bTB) and thus may act as a source of infection for cattle (Donnelly et al. 2006).

The estimates of the demographic parameters required by the model were derived from the literature for each of these species. Population biology is well understood for the European rabbit in the UK (Brambell 1944, Lloyd 1970, Cowan 1987, Smith 1997) and for the Eurasian badger, at least in rural habitats (Cheeseman et al. 1987, Rogers et al. 1997), and reasonably well known for the gray squirrel in the UK (Shorten 1954, Gurnell 1983, 1987). Our understanding of the population biology of wild boar in the UK is patchy (Wilson 2003, DEFRA 2004), but gaps in this knowledge can be filled with information from continental Europe (Massei et al. 1996, 1997; Geisser and Reyer 2005). The derived parameters are shown in Table 1 with the demography of the European rabbit characterised by a very high intrinsic rate of increase and relatively rapid turnover rate, the gray squirrel by a high intrinsic rate of increase and relatively moderate population turnover rate, the wild boar by a moderate intrinsic rate of increase and relatively moderate turnover rate, and Eurasian badger by a low intrinsic rate of increase and relatively slow turnover rate. The derived parameters were used to populate the model and explore, with the carrying capacity (K) set at 100, changes in population size over a 10-year period following the imposition different forms of fertility control for each of the four target species.

The predictions made by the model for the population consequences in the European rabbit of imposing annually varying degrees of permanent infertility, ranging from 10% to 90% of breeding females, are shown in Figure 1. 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 relatively rapid.

Figure 2 shows the predicted population consequences of imposing varying degrees of permanent infertility for the gray squirrel. This suggests that, as with the European rabbit, low levels of infertility have very little impact. However, if levels of 70% infertility or more can be achieved, then fertility control could populations down to probable extinction.

The predicted population consequences of imposing varying degrees of permanent infertility for the wild boar

Table 1. Population parameters used for the to populate model where S is the adult female survival rate, m is the recruitment rate of females to the adult population at high population density, β is the slope of a density-dependent function that reflects the carrying capacity of the population, and m* is the density-dependent recruitment rate of females to the adult population.

Species	S	m	β	m*
European rabbit	0.5	0.8	0.003	3
Gray squirrel	0.55	0.65	0.002	2.1
Wild boar	0.6	0.5	0.001	1.0
Eurasian badger	0.8	0.4	0.002	0.85
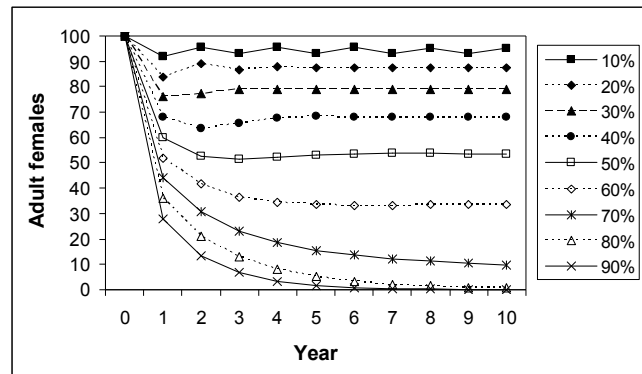
Figure 1. The predicted size of the European wild rabbit adult female population with varying degrees of permanent infertility induced annually in 10% to 90% of fertile adult females each year for 10 years.
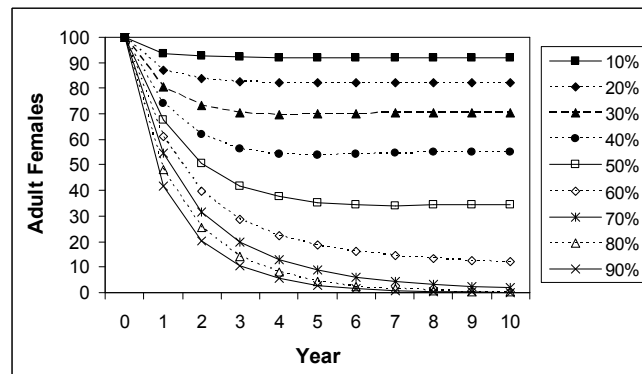
Figure 2. The predicted size of the gray squirrel adult female population with varying degrees of permanent infertility induced annually in 10% to 90% of fertile adult females each year for 10 years.

are shown in Figure 3. This suggests that, compared to the European rabbit and gray squirrel, relatively modest levels of infertility will give rise to significant reductions in population size. For instance, 30% infertility applied annually yields a more than 70% reduction in population size after 10 years. However, the downward population responses to fertility control are less rapid than for the rabbit and gray squirrel.
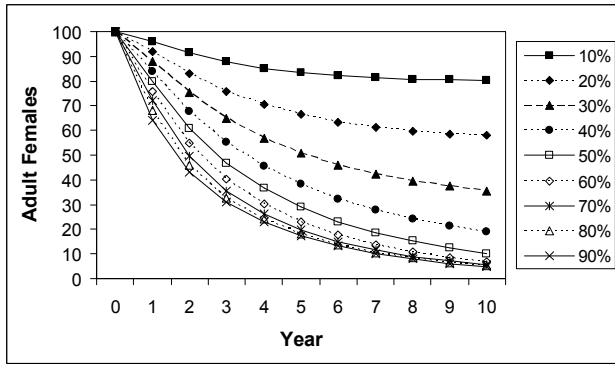
Figure 3. The predicted size of the wild boar adult female population with varying degrees of permanent infertility induced annually in 10% to 90% of fertile adult females each year for 10 years.
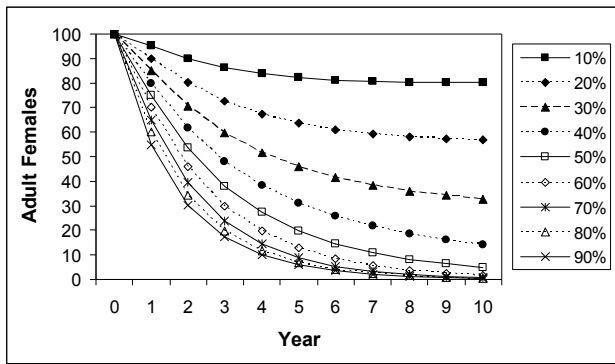

Figure 4. The predicted size of the Eurasian badger adult female population with varying degrees of permanent infertility induced annually in 10% to 90% of fertile adult females each year for 10 years.
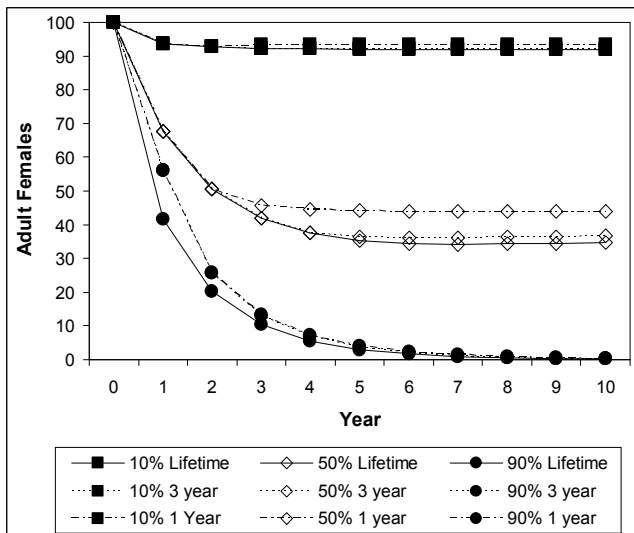

Figure 5. Changes in the size of the gray squirrel adult female population predicted for infertility imposed annually on 10%, 50%, or 90% of breeding adult females for 10 years with lifetime, 3-year, or 1-year duration infertility induced in treated individuals.
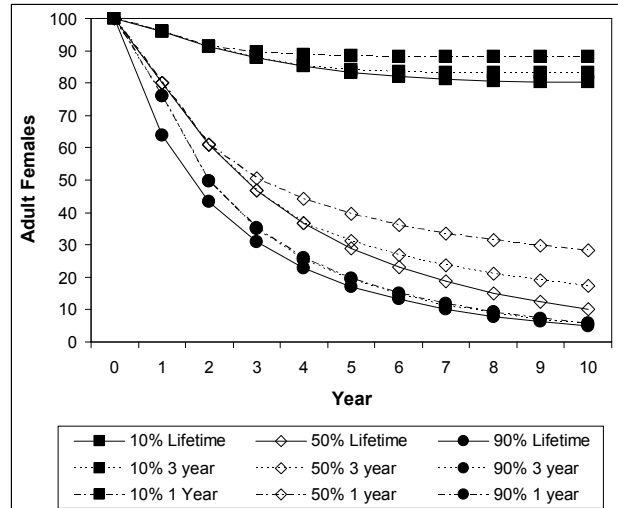

Figure 6. Changes in the size of the Eurasian badger adult female population predicted for infertility imposed annually on 10%, 50%, or 90% of breeding adult females for 10 years with lifetime, 3-year, or 1-year duration infertility induced in treated individuals.

Figure 4 shows the predicted population consequences of imposing varying degrees of permanent infertility for the Eurasian badger. This suggests that modest levels of induced infertility should have significant population consequences, although these effects take a relatively long time to be realised.
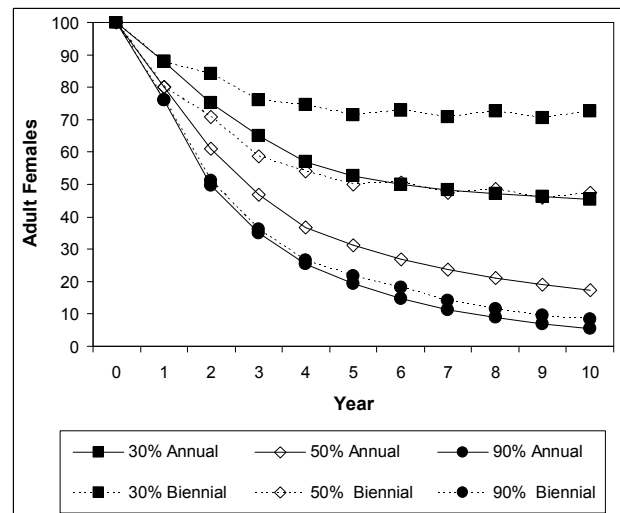
DURATION OF INFERTILITY

The duration of induced infertility in treated animals can vary. Lifetime infertility can be achieved surgically (e.g., Jacob et al. 2004) and maybe sometimes with immunocontraception. However, long-term infertility for 3 years is a more realistic expectation with the "single-shot" immunocontraceptive vaccines (Killian et al. 2008), while for most silastic implants (e.g., Bertschinger et al. 2006) and oral chemical contraceptives, such as DiazaCon™ (e.g., Nash et al. 2007), one breeding season or one year duration infertility would be the maximum expectation. We thus used the model to compare the population consequences of these three different durations of induced infertility.

In the gray squirrel, the responses to both 1-year duration and 3-year duration infertility are similar to those for lifetime infertility with little impact of 10% annually induced infertility on population size, population elimination after around 8 years with 90% annually induced infertility, and 50% annually induced infertility, leading to 55-65% reductions in population size after around 5 years for all three durations (Figure 5).

In the Eurasian badger, the effect of the duration of infertility is minimal if 90% of breeding females are treated annually (Figure 6). However, there are some indications of a greater influence of duration than in the gray squirrel if 50% of breeding females are treated annually, such that 1-year duration infertility leads to a 70% reduction in population size after 10 years, compared to 90% for lifetime infertility.
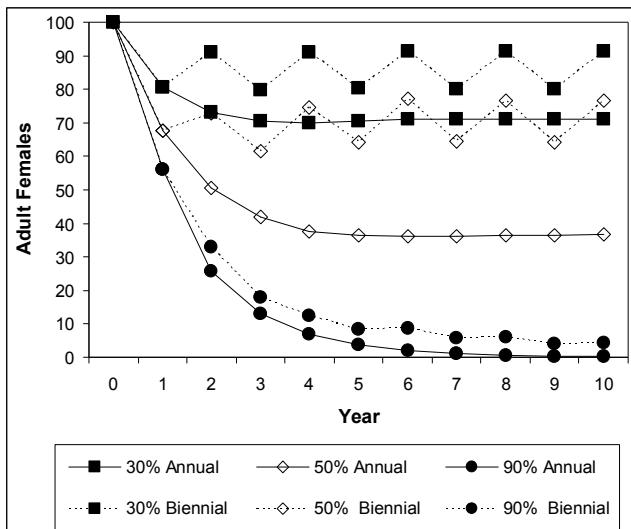
Figure 7. Changes in the size of the gray squirrel adult female population predicted for 3-year duration infertility induced annually or biennially in 30%, 50%, or 90% of fertile adult females for 10 years.

Figure 9. Changes in the size of the Eurasian badger adult female population predicted for 3-year duration infertility induced annually or biennially in 30%, 50%, and 90% of fertile adult females for 10 years.
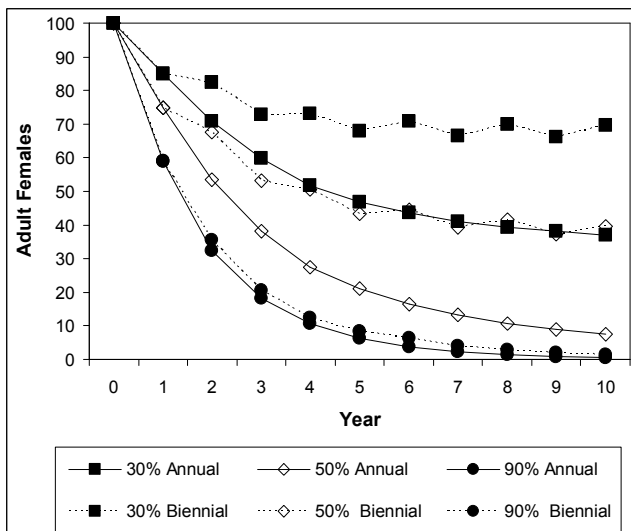
Figure 8. Changes in the size of the wild boar adult female population predicted for 3-year duration infertility induced annually or biennially in 30%, 50%, or 90% of fertile adult females for 10 years.

FREQUENCY OF APPLICATION

A further variation in the way infertility can potentially be induced in a population is the frequency with which application is repeated. We thus examined the predictions of the model for the population conse-quences of repeating annually or every 2 years (biennially) the imposition of 3-year duration infertility on varying proportions of the breeding adult female population. For the gray squirrel, biennial application may preclude elimination of the population even with 90% of breeding females treated (Figure 7). Furthermore, biennial application could compromise the outcome for 50% of breeding females being treated, with the popula-tion oscillating at between 65 and 75% of carrying

capacity, compared to the asymptote of around 40% of carrying capacity achieved with annual application (Figure 7).

The differences between the outcomes for annual and biennial application of 3-year duration infertility are marginal for both wild boar (Figure 8) and Eurasian badgers (Figure 9) if 90% of the breeding females are treated. As with the gray squirrel, there are bigger differences between the outcomes of annual and biennial application to 50% of breeding females. Interestingly, the predicted outcomes are almost identical for biennial induced infertility of 50% of breeding females, and annual induced infertility of 30% of breeding females in both wild boar and the Eurasian badger.
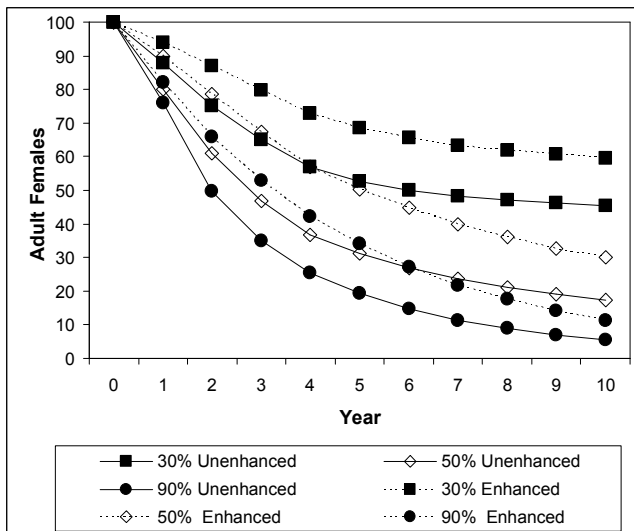
ENHANCED SURVIVAL OF INFERTILE INDIVIDUALS

There is increasing evidence from field studies that the survival of infertile animals is enhanced compared to that of fertile animals (e.g., Twigg et al. 2000, Kirkpatrick and Turner 2007, Williams et al. 2007). This probably reflects the physiological costs of reproduction that are not incurred by infertile animals. In order to investigate the implications of enhanced survival for the population consequences of fertility control, it is necessary to adjust the mortality rate of infertile females. We have done this here by turning off the density-dependent component of mortality (βN_t) in infertile animals, which we argue is a biologically plausible approach. Doing this, it is apparent that with 3-year induced infertility in the gray squirrel, enhanced survival causes a modest increase in the length of time taken to realise the effects, although the eventual outcomes, for given levels of infertility, are very similar (Figure 10).

The effect of enhanced survival is relatively more pronounced in the Eurasian badger (Figure 11). For instance, 30% infertility leads to the population stabilising at less than 45% of carrying capacity in the absence of
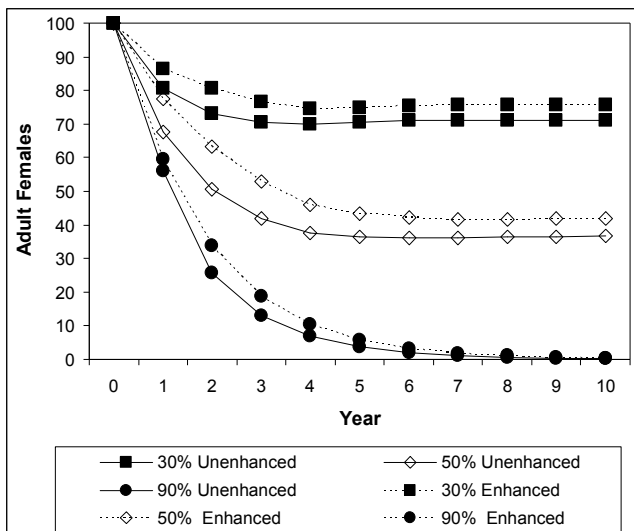
Figure 10. Changes in the size of the gray squirrel adult female population predicted for 3-year duration infertility induced annually in 30%, 50%, or 90% of fertile adult females for 10 years with and without enhanced survival of infertile females through absence of density-dependent mortality.

Figure 11. Changes in the size of the Eurasian badger adult female population predicted for 3-year duration infertility induced annually in 30%, 50%, or 90% of fertile adult females for 10 years with and without enhanced survival of infertile females through absence of density-dependent mortality.

enhanced survival but, in its presence, the population stabilises at around 55% of the carrying capacity. Furthermore, with 90% induced annual infertility, it takes approximately 2 years longer to achieve the equivalent population reductions in the presence of enhanced survival than in its absence.

DISCUSSION

The explorations carried out here demonstrate that the population level effects of fertility control reflect a range of variables with a number of interesting and complex interactions between the population biology of the target species, the specific characteristics of the fertility control application, and the responses of individuals to infertility. Despite this complexity, we suggest that some generic principles are beginning to emerge.

Firstly, in terms of the population biology of the target species, low levels of infertility will have little impact on species with high turnover rates. However, even modest levels of infertility can reduce populations of species with low intrinsic rates of increase, but it may take longer for these effects to be realised in long-lived species. These broad conclusions are consistent with lower levels of infertility being required for species with relatively low maximum rates of population increase to achieve the equivalent population reduction, compared to species with relatively high population turnover rates (Hone 1999, Hobbs et al. 2000). For species with relatively low intrinsic rates of increase, the use of "single-shot" immunocontraceptive vaccines delivered by injection may thus be a viable management tool and, as our model predicts, it is for such species that significant population level effects are beginning to be reported using this type of technology (e.g., Rutberg et al. 2004, Delsink et al. 2006, 2007; Kirkpatrick and Turner 2007, Elhay et al. 2007, Miller et al. 2008, Rutberg and Naugle 2008). For relatively short-lived species, relatively rapid reductions in population size can be achieved because of the high turnover rate, but only if a high proportion of females are rendered infertile which, in practice, makes delivery of immunocontraceptive vaccines by injection unfeasible as a management tool. This view is supported by the surgical sterilisation studies of wild rabbits in Australia, where even 80% female infertility generally failed to reduce subsequent breeding population size (Twigg et al. 2000, Williams et al. 2007). Achieving the high levels of infertility required in this type species is only likely to be feasible using oral delivery of a contraceptive via bait (Cowan et al. 2006). Oral contraceptives are unlikely to be species-specific (e.g., Nash et al. 2007), and thus specificity would need to be achieved through the bait delivery system if viable techniques are to be developed for such species.

With regard to duration of induced infertility, this appears to be relatively unimportant for species such as the gray squirrel, whose demography is characterised by a high intrinsic rate of increase and relatively moderate population turnover rate. This suggests that application of a fertility control agent with single breeding season duration, as potentially offered by DiazaCon™ (Nash et al. 2007), could potentially be useful for this type of demography if it could be delivered to a sufficiently high proportion of the breeding female population. The duration of induced infertility is predicted to have a relatively greater impact on the extent of population reduction in relatively long-lived species such as the Eurasian badger, but only if intermediate proportions of the breeding female populations are treated annually, i.e., around 50%. In longer-lived species, such as ungulates, the difference between single-year and lifetime infertility is more marked (Hobbs et al. 2000, Bradford and Hobbs 2008). The effects of varying the frequency of application are particularly interesting. The equivalence, in

terms of population consequences, of annual treatment of 30% of breeding females and biennial treatment of 50% of breeding females, for both wild boar and Eurasian badger demography, is striking. This indicates that there are considerable opportunities for identifying optimum combinations of intensity and frequency of application to achieve a target population reduction for a given demographic type. For instance, biennial application could be more efficient than annual application, in terms of both reducing the frequency of visits to carry out treatments and the total number of animals treated. The potential use of models to identify the most efficient application strategy has also been recognised elsewhere (e.g., Bradford and Hobbs 2008). This is also an area where model predictions would be particularly amenable to testing and validation through field experiment. Finally, in terms of fertility control-specific population responses, enhanced survival of infertile females is predicted to be of less importance in short-lived species. However, enhanced survival may reduce the effect and increase the time taken for it to be realised if the population turnover rate is relatively low. So, the degree of enhanced survival could be the difference between success and failure for this type of demography. Given that an inverse correlation between reproductive output and lifespan may well be a general phenomenon (e.g., Jewell 1986), it is essential that this is taken into account, particularly for the use of fertility control applications where the duration of induced infertility is significantly shorter than the life expectancy of the target species. Again, this is an area where model predictions can be refined and tested, once more data emerges from empirical studies of fertility control in free-living populations on the degree and variation of enhanced survival.

In conclusion, we suggest that the general principles identified here will help evaluate whether emerging fertility control technologies can be turned into practical applications for particular species. However, further consideration needs to be given to a number of issues. Firstly, given the simplicity of the model, it cannot be expected to provide accurate predictions for a particular species. For this, we need species-specific models that incorporate more detailed information on population biology, including variability of key population parameters. Secondly, we need to incorporate spatially explicit elements into the model that consider dispersal, or at least allow for potentially increased density-dependent immigration of fertile individuals into treated populations. Thirdly, we need to evaluate the model's predictions through testing and validation, using data from the increasing numbers of field studies of fertility control that are taking place around the world. In particular, we suggest that there is considerable potential for optimising the intensity and frequency of fertility control application for particular species, but that our understanding of the population consequences of enhanced survival of infertile animals needs to be increased, particularly for relatively long-lived species. Addressing these issues will help establish an increasingly robust evidence-based platform for discussing when fertility control can be regarded as a viable, desirable, and sustainable option to manage problem wildlife.

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