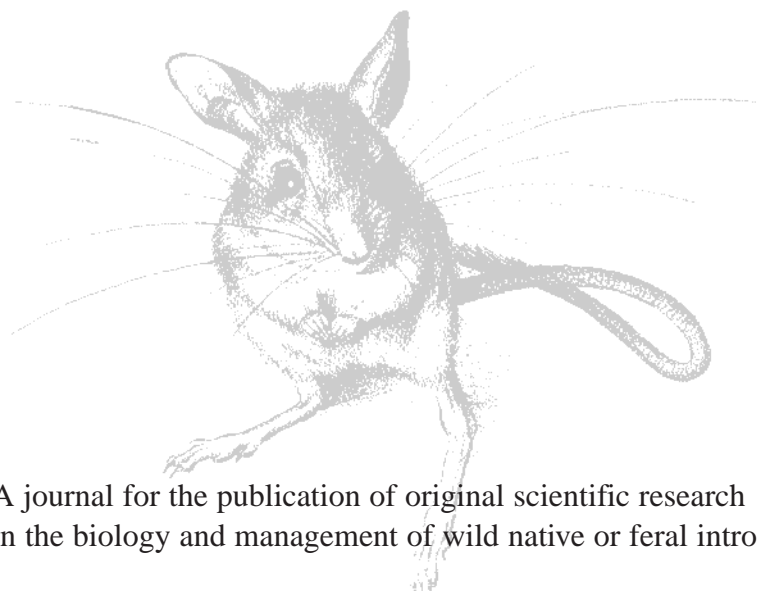

CSIRO PUBLISHING

Wildlife Research

Volume 24, 1997
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Modelling the Relative Efficacy of Culling and Sterilisation for Controlling Populations

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Abstract

Simple logistic models are used to investigate and compare the effects of continuous control by culling or sterilisation on population density. The models consider populations regulated by density-dependent mortality or density-dependent recruitment, with monogamous or polygamous mating systems, and with one or both sexes sterilised. For the first time, an analytical solution is presented for the effect of sterilisation on density-dependent population growth.

The models suggest that the mating system has a considerable effect on the relative efficacy of sterilisation, and that previous models for sterilisation may have overestimated the impact of sterilisation by assuming idealised monogamous mating. In general, and except for populations with monogamous mating or 'harem' systems and both sexes sterilised, culling gives a more rapid reduction in density than does sterilisation. However, the long-term degree of suppression obtained with the same levels of control applied is likely to be similar. Populations with density-dependent mortality will be reduced by sterilisation more quickly than those regulated by density-dependent recruitment, and the effect on the steady-state density of a given proportion that is sterile is greater in the first case than in the second. However, the effect of a given continuous sterilisation rate (e.g. baiting effort) on density is the same in both cases. We compare our model results with those of others and question previous conclusions about the circumstances under which sterilisation is most effective.

Introduction

Few attempts have been made to specifically compare the theoretical effects of sterilisation and culling on wildlife populations. Sturtevant (1970) plotted the theoretical effects of a single 70% cull and 70% sterilisation on a feral pigeon population, while Knipling and McGuire (1972) formulated a difference-equation model for sterilisation of rats, which was subsequently applied to the brushtail possum (*Trichosurus vulpecula*) by Spurr (1981). These and other species-specific studies of sterilisation were reviewed by Bomford (1990). More recent work of this kind includes models for sterilisation of feral horses (Garrott 1991; Garrott and Siniff 1992) and foxes (Saunders and Choquenot 1995).

Stenseth (1981) formulated simple, general mathematical models for birth and death processes in localised populations linked by migration. He used these to predict the optimal control strategy for a population based on its demography, specifically whether it is *r*-selected or *K*-selected. Although not specifically designed to compare culling with sterilisation, Stenseth's models led to the conclusion that a reduction in reproductive potential is likely to be the optimal method of control for populations with a high mortality rate and therefore a high population turnover rate. This was similar to a conclusion of Hone (1992) based on examination of the relationship between the rate of increase of populations and their fecundity and survivorship. Caughley *et al.* (1992) considered the effects of dominance and social structure on the impact of sterilisation of females on the realised productivity of a population. They showed that productivity was generally reduced to a lesser extent than the proportional sterilisation rate, and that in one case sterilisation actually enhanced productivity.

In this paper, we examine the relative effectiveness of sterilisation and culling, but unlike previous studies we consider different assumptions about mating systems and density dependence in the populations. Furthermore, we consider the effects of control not just on the population's rate of increase (e.g. Stenseth 1981; Hone 1992), but, more importantly and of more practical relevance, also on its average abundance. Specifically, we assume the following: (1) that mating systems are represented by polygamy, 'harem' systems or monogamy; (2) that sterilisation is applied to either or both sexes; (3) that linear density dependence acts through mortality or recruitment (defined here as fecundity plus juvenile mortality); (4) that continuous, logistic population growth is modelled by differential equations; (5) that controls are continuous rather than episodic (e.g. trapping or the use of poison, chemosterilant or immunocontraceptive baits, or the use of a micro-organism capable of causing immunocontraception); (6) that sterilisation is life-long and does not affect behaviour; and (7) that all young are born fertile. Results are presented in terms of (1) the extent of control required to achieve a given level of population suppression and (2) the effect of a given level of control on the rate of population decline and final level of suppression. Each of these is assessed for culling and two sterilisation-mating scenarios that give significantly different outcomes, as follows.

- Scenario 1: (i) polygamous mating with females or both sexes sterilised, or
 (ii) monogamous mating and either males or females sterilised, or
 (iii) 'harem' systems, in which a number of females mate exclusively with each dominant male, and either males or females are sterilised;
 Scenario 2: (i) monogamous mating with both sexes sterilised, or
 (ii) 'harem' systems with both sexes sterilised.

The more complex social systems considered by Caughley *et al.* (1992) can be included in the present model by expressing them in terms of the degree of polygamy or monogamy they imply. Thus, family group structures (e.g. foxes and badgers) may be closer to monogamy than to polygamy, whereas the reverse may be true for harem systems with polyoestrous females that breed with subdominant males if the dominant male is sterilised (e.g. feral horses).

An alternative to Scenarios 1 and 2 is polygamous mating and sterilisation of males. However, this is likely to be ineffective in reducing density (see below) and is not considered further in the models.

Solutions were obtained analytically in the case of culling and numerically in most cases of sterilisation. However, we derive for the first time an analytical solution for the effect of sterilisation under Scenario 1, on a population regulated by density-dependent mortality. We also compare our results with those of other models, including a birth-pulse model (e.g. Hone 1992) rather than a continuous-breeding model.

Models

Control by Culling

If we assume that a constant proportion, c , of the population is removed by culling at any instant, then the change in total population density, N , in an environment of carrying capacity K , may be represented by

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - cN \quad (1)$$

based on simple logistic density-dependent population growth, where r is the instantaneous rate of population increase. Equation 1 is appropriate regardless of whether density dependence acts on recruitment or on mortality, and may be expressed more generally as

$$\frac{dN}{dt} = N[f(N) - g(N) - c] \quad (2)$$

where $f(N)$ and $g(N)$ are the recruitment and mortality functions respectively (see below).

Control by Sterilisation

The efficacy of sterilisation as a population-control method is partly dictated by the social structure and mating system of the population (Caughley *et al.* 1992). We consider first a situation involving polygamous mating and either females alone or both sexes sterilised, or monogamous mating with either sex alone sterilised (Scenario 1). In all these cases, the proportion of females not reproducing corresponds exactly or approximately to the probability of sterilisation (whichever sex this applies to). Thus, even if both sexes are sterilised, in the case of polygamous mating the effect of sterilisation of males is small compared with that of the sterilisation of females. For example, if 70% of both are sterilised and a female mates randomly with up to eight males (if not fertilised), there is a 6% chance (100×0.7^8) that she will be non-reproductive because of the sterilisation of males, compared with a 70% chance resulting from the sterilisation of the females themselves. Further justification for ignoring sterilisation of males under Scenario 1 is provided by Caughley (1977, pp. 192, 193), who showed that the male/female ratio had to be reduced very substantially to have an impact on fertility of females, depending on receptivity of the female following mating and the potential number of copulations per male per breeding season.

Under these circumstances, if animals are sterilised at a rate s , the resulting rate of change in the proportion of females not reproducing, Q , is given by

$$\frac{dQ}{dt} = (1 - Q)[s - f(N)Q]. \quad (3)$$

The mathematical derivation of Equation 3 is given in the Appendix, but it reflects the fact that the proportion of females not breeding increases through sterilisation of those currently breeding [$s(1 - Q)$], but decreases through the loss of births to this sector of the population [= birth rate [$f(N)$] \times proportion of the birth rate realised $(1 - Q) \times$ relative size of the sector (Q)].

For sterilisation Scenario 1, the change in total population size is given by the recruitment rate, scaled down by the proportion of females reproducing, minus the mortality rate function, $g(N)$, multiplied by the current population size:

$$\frac{dN}{dt} = N[f(N)(1 - Q) - g(N)]. \quad (4)$$

We now consider the alternative situation of monogamous mating with both sexes sterilised, in which the chance of a female reproducing depends on the fertility both of herself and her partner (Scenario 2). In this case, the recruitment term $f(N)$ must be scaled by a further $1 - Q$, giving

$$\frac{dQ}{dt} = (1 - Q)[s - f(N)Q(1 - Q)] \quad (5)$$

and

$$\frac{dN}{dt} = N[f(N)(1 - Q^2) - g(N)]. \quad (6)$$

Density Dependence

The way in which density dependence acts on the population is reflected in the recruitment and mortality functions, $f(N)$ and $g(N)$, respectively. The models discussed here assume simple logistic density-dependent growth, $f(N) - g(N) = r(1 - N/K)$, with no immigration or emigration. Density-dependent recruitment may be modelled by the following equations.

$$\text{recruitment function} \quad f(N) = a - r \frac{N}{K} \quad (7)$$

$$\text{mortality function} \quad g(N) = b \quad (8)$$

Density-dependent mortality may be modelled by the following equations.

$$\text{recruitment function} \quad f(N) = a \quad (9)$$

$$\text{mortality function} \quad g(N) = b + r \frac{N}{K} \quad (10)$$

where a is the maximum per capita birth rate, b is the minimum per capita death rate, and $r = a - b$. These two density-dependence scenarios represent opposite extremes, and for many populations both recruitment and mortality will be density dependent. The less realistic scenario of density-independent growth is also considered, for which $f(N) = a$ and $g(N) = b$.

Results

Effects of Culling on Population Density after a Given Time

The model for culling, Equation 1, can be solved analytically to give the density at time t given the initial density $N(0) = K$:

$$N(t) = \frac{K(c - r)}{ce^{(c-r)t} - r}. \quad (11)$$

If there is no density dependence in the population, density at time t is simply given by the equation for exponential growth with the intrinsic rate of increase replaced by $r - c$:

$$N(t) = N(0)e^{(r-c)t}. \quad (12)$$

Effects of Sterilisation on Population Density after a Given Time

The model for a population with density-dependent mortality and sterilisation Scenario 1 (Equations 3, 4, 9 and 10) can be solved (see Appendix) with the initial conditions $Q(0) = 0$ and $N(0) = K$ as follows.

$$Q(t) = \frac{se^{(a-s)t} - s}{ae^{(a-s)t} - s} \quad (13)$$

$$N(t) = \frac{bK(r-s)(s - ae^{(a-s)t})}{sa(a-s)e^{bt} - brae^{(a-s)t} - rs(r-s)} \quad (14)$$

It is not possible to obtain explicit solutions for the models with recruitment-regulated populations or those with sterilisation Scenario 2 (monogamous mating and both sexes sterilised), so these cases were solved numerically.

With no density dependence in the population and sterilisation under Scenario 1, the proportion of females not reproducing, $Q(t)$, is the same as before (Equation 13), while the density after time t is given in this case by

$$N(t) = \frac{N(0)[s - ae^{(a-s)t}]}{(s - a)e^{bt}} \quad (15)$$

based on equations A3–A6 in the Appendix with $f = 0$ for density-independent growth. Again, there is no analytical solution for sterilisation Scenario 2.

Effects of Culling and Sterilisation on Long-term Steady-state Densities

For populations with density dependence, sustained control at a per capita rate less than r will give a proportional reduction in steady-state density in the long term equal to c/r for culling and s/r for sterilisation Scenario 1 (see Appendix). In other words, a culling rate of $r/2$ will give a 50% reduction in density to $K/2$ (Caughley 1977), and the same is true for sterilisation (Scenario 1). For sterilisation Scenario 2, the result is more complex and the proportional

suppression, p , depends also on the recruitment function at the steady-state density (N_{ss}). The solution for p , from Equations 25 and 26 below, is

$$p = \frac{s}{r} + \frac{f(N_{ss})}{r} \left(1 - \sqrt{1 - \frac{rp}{f(N_{ss})}} \right). \quad (16)$$

Since p is greater than s/r , mating systems represented by Scenario 2 clearly allow greater suppression for a given effort than those in Scenario 1. If mortality is density dependent, $f(N_{ss}) = a$ and Equation 16 simplifies to

$$p = \frac{a}{2r} \left(1 + \sqrt{\frac{4s}{a} + 1} \right) - \frac{s}{r}.$$

The proportion of females sterile (not reproducing), given a sustained rate of sterilisation s and mating Scenario 1, is s/a for density-dependent mortality and $s/(b + s)$ for density-dependent recruitment (Appendix, Equations A7 and A11), the latter being larger than the former.

Ignoring the rate at which new animals are sterilised (s), the question arises as to the impact of a given sustained level of sterilisation (proportion of females not reproducing = Q) on population density. In this case, the proportional reduction in density is aQ/r for density-dependent mortality and $bQ/[r(1 - Q)]$ for density-dependent recruitment. The former is the greater provided that $Q < r/a$ (i.e. the population is not reduced to zero).

These effects of sterilisation on steady-state population density are summarised in Table 1, in terms of the rate of control applied (s) and the level of sterilisation achieved (Q), where there is density dependence and a mating system corresponding to Scenario 1.

Table 1. Relationships between proportional reduction in population density ($p = 1 - N/K$, where N is the population density and K is the carrying capacity of the environment), instantaneous rate of sterilisation (s) and the proportion sterile (Q = proportion of females not reproducing), for mating Scenario 1 and different types of density dependence

a = maximum instantaneous birth rate, b = minimum instantaneous death rate, r = maximum instantaneous (intrinsic) rate of increase

Variable	Density-dependent mortality	Density-dependent recruitment
Suppression (p) given s	s/r	s/r
Level of sterilisation (Q) given s	s/a	$s/(b + s)$
Suppression (p) given Q	aQ/r	$(a/r - 1)Q/(1 - Q)$
Q for 100% suppression	r/a	r/a
Rate (s) to give suppression p	rp	rp
Level (Q) to give suppression p	rp/a	$rp/(b + rp)$

For density-independent population growth, culling must be at a rate precisely balancing the intrinsic rate of increase (i.e. $c = r$) for a steady state to exist, and the density at time t will be the same as the initial density [i.e. $N(t) = N(0)$, from Equation 12]. For a steady state under sterilisation, the proportion of females not reproducing, Q , must be equal to r/a (from the Appendix, Equation A2 with $dN/dt = 0$ and $rN/K = 0$ for a density-independent steady state). Since Q must also equal s/a for a steady state under sterilisation (from Equation 13 as $t \rightarrow \infty$), for density-independent growth s must equal r and the rate of sterilisation, like the rate of culling, must precisely balance the intrinsic rate of increase.

Effects of Culling and Sterilisation on the Rate at which Populations Decline

The initial impact of sustained control on a population's rate of decline can be estimated by applying the above simple models to a population close to carrying capacity ($N \approx K$). Here natural recruitment and mortality processes are balanced, so any per capita rate of change of density $[(dN/dt)/N]$ will simply reflect the cull rate (Equation 17) or the proportional reduction in recruitment due to sterilisation (Equations 18–20). Thus, setting $f(N) = g(N)$ in Equations 2, 4 and 6 gives

$$\text{for culling,} \quad \frac{dN/dt}{N} \approx -c \quad (17)$$

$$\text{for sterilisation Scenario 1,} \quad \frac{dN/dt}{N} \approx -f(N)Q \quad (18)$$

and for sterilisation Scenario 2 (monogamous mating with both sexes sterilised),

$$\frac{dN/dt}{N} \approx -f(N)Q(2 - Q) \quad (19)$$

and, since $Q \approx 0$,

$$\frac{dN/dt}{N} \approx -2f(N)Q. \quad (20)$$

Q in Equations 18 and 20 is close to zero, so the initial per capita rate of decline is also close to zero whereas for culling it is equal to c (Equation 17). Therefore, culling will cause a greater initial reduction in population density than will sterilisation. Furthermore, comparing Equations 18 and 20 suggests that sterilising both sexes of a monogamously breeding population, or one with a harem system, will cause twice the rate of decline in density as all other sterilisation–mating regimes (except sterilising males alone in a polygamous population, which is assumed to have no effect at all).

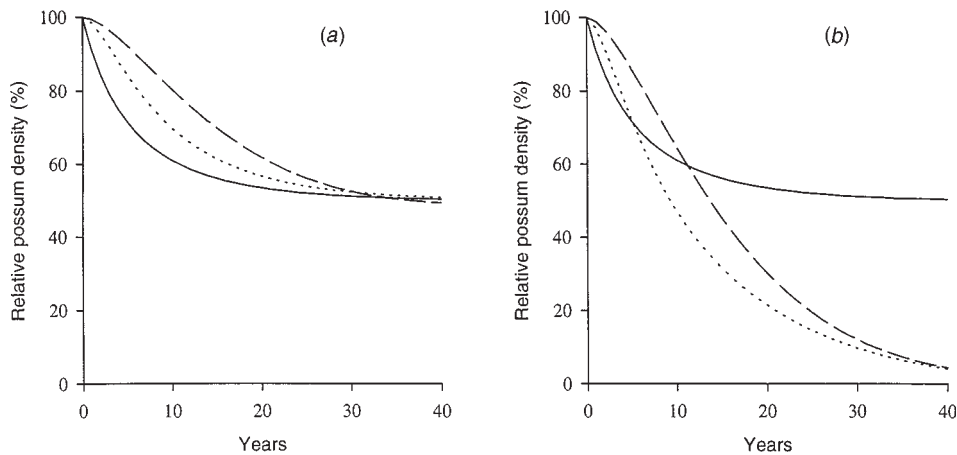


Fig. 1. Effect of continuous control at a rate of 0.1 year^{-1} on densities of brushtail possums over time (Equations 3–6 and 11–14; see text for parameter values). —, culling; — —, sterilisation with density-dependent recruitment; - - -, sterilisation with density-dependent mortality. (a) Sterilisation Scenario 1, most combinations of mating system and sexes sterilised; (b) Sterilisation Scenario 2, monogamous or ‘harem’ mating and both sexes sterilised.

Example Comparison of Culling and Sterilisation

On the basis of Equations 11–14, and numerical solutions for density-dependent recruitment under Scenario 1 (Equations 3 and 4) and for sterilisation Scenario 2 (Equations 5 and 6), Figs 1 and 2 show the predicted impacts of culling and sterilisation regimes on population density over time. For illustrative purposes, we use parameter values for the brushtail possum in New Zealand, namely $a = 0.305 \text{ year}^{-1}$, $b = 0.105 \text{ year}^{-1}$ and $r = 0.200 \text{ year}^{-1}$ (Barlow 1991), and results are given for two levels of control intensity, low (Fig. 1) and high (Fig. 2). In practice, possums are polygamous (King 1990).

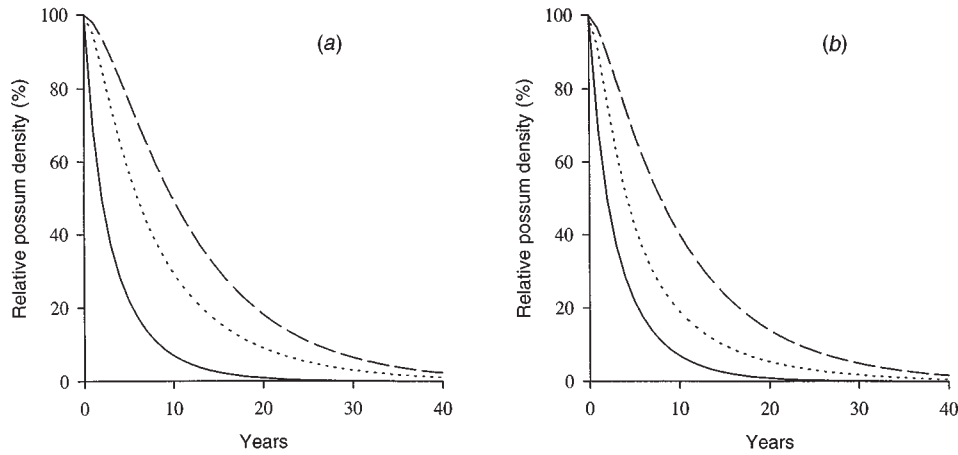


Fig. 2. Effect of continuous control at a rate of 0.4 year^{-1} on densities of brushtail possums over time (Equations 3–6 and 11–14; see text for parameter values). —, culling; — —, sterilisation with density-dependent recruitment; ····, sterilisation with density-dependent mortality. (a) Sterilisation Scenario 1, most combinations of mating system and sexes sterilised; (b) Sterilisation Scenario 2, monogamous or 'harem' mating and both sexes sterilised.

Level of Control Required to Achieve a Given Level of Suppression

The models may be solved algebraically to find the culling effort, c , or sterilisation effort, s , required to maintain the population at a steady-state density, $N_{ss} < K$. Let p denote the proportional reduction in N below K , as above, and Q_{ss} denote the proportion of females not reproducing at the steady-state N_{ss} . Now the general models may be solved for c and s , given $dQ/dt = 0$ and $dN/dt = 0$, and rejecting trivial solutions. From Equations 1 and 2

$$p = (1 - N_{ss}/K) = (dN/dt)/(rN_{ss}) = [f(N_{ss}) - g(N_{ss})]/r. \quad (21)$$

Hence, the rates of control required to suppress a population at K by a proportion p , or maintain an exponentially growing population at constant density, are as follows:

for culling (Equations 2 and 21),

$$c = rp \quad (22)$$

for sterilisation Scenario 1 (Equations 3, 4 and 21),

$$Q_{ss} = \frac{rp}{f(N_{ss})} \quad (23)$$

$$s = rp \quad (24)$$

and for sterilisation Scenario 2 (monogamous mating with both sexes sterilised; Equations 5, 6 and 21),

$$Q_{ss} = 1 - \sqrt{1 - \frac{rp}{f(N_{ss})}} \quad (25)$$

$$s = rp - f(N_{ss})Q_{ss}. \quad (26)$$

The specific forms of Equation 23 corresponding to density-dependent mortality and density-dependent recruitment under Scenario 1 are given in Table 1.

Discussion

Hone (1992) suggested a need to further explore the interactions between fertility control and other control methods. This paper provides a first step, by comparing culling with sterilisation, although it has not addressed their interaction. The reasons for this are, first, that if one strategy is in some way superior to the other it is unlikely that a combination will be superior to both, given the same conditions. Second, effects of both strategies on the rate of increase (r) tend to be linear in our models, and in this sense additive. This contrasts with Garrott (1991) and Hone (1992, 1994), who drew attention to a non-linear relationship between fecundity and r , in the first case from a study of feral horses and in the second from age-specific life-tables approximating those for Himalayan thar and wild pigs. The difference is a simple consequence of the difference in the models. Our models assumed continuous breeding and considered proportional reductions in fertility to apply to the instantaneous birth rate, a , rather than to fecundity at the birth pulse. In contrast, Garrott (1991) and Hone (1992) used birth-pulse models and related r to fecundity. Since r is linearly related to the instantaneous birth rate, a , and since fecundity $= e^a$, then clearly r varies as $\log(\text{fecundity})$. More specifically,

$$r \approx \ln[1 + (1 - Q)F] - b \quad (27)$$

where F is fecundity per head of the population ($= e^a$) per unit time (i.e. per birth pulse), averaged over all ages, and b is the instantaneous mortality rate, again averaged over all ages. Given density dependence, the equation is

$$r \approx \ln[1 + (1 - Q)e^{f(N)}] - g(N). \quad (28)$$

Equation 27 approximates Hone's (1992) detailed age-specific life-tables, although in this case more meaningful values of F and b are obtained by incorporating the substantial first-year mortality [Table 1 in Hone (1992)] within a reduced value of F . In practice, the difference between this birth pulse model and the continuous models used in the present paper is small, particularly for average fecundities less than about 1 per head of the population. For instance, the finite rate of increase (i.e. ratio of densities from one birth pulse to the next) is about 3% greater for a birth-pulse model than for a continuous-breeding model with $F = 0.65$ ($a = 0.5$) and 50% of females sterile or not breeding. The relative difference declines to 2% as the proportion that is sterile increases to 80%.

As a result of the non-linear relationship between r and fecundity, Hone (1992, 1994) suggested that sterilisation would be most effective when r was already low, as in a species with low fecundity or a population that was already being controlled by other means (Hone 1992). While it is true that linear decreases in fecundity give progressively greater linear decreases in r as both decline, a given proportional reduction in fecundity (e.g. due to sterilisation) gives approximately the same linear reduction in r , whatever the initial value of both (e.g. in the examples in Hone's fig. 2), so in this sense the above conclusions do not hold. Moreover, a

greater or lesser effectiveness of sterilisation does not preclude the possibility that culling would be more effective under the same circumstances.

Stenseth (1981) suggested that sterilisation was likely to be an optimum control strategy for populations with a high death rate, as did Hone (1992, fig. 2 and conclusions). Our models indicate a slightly more specific conclusion, that a high death rate relative to birth rate enhances the impact of a given level of sterilisation (Table 1, row 3). The reason is clear from Equation 27 but is most easily visualised by considering an even simpler equation:

$$r \approx a - b. \quad (29)$$

If b is large relative to a , it takes only a small proportional reduction in a to make its value equal b and r equal zero. If a is reduced to zero by sterilisation, the rate of decline is proportional to b and is therefore greatest for species with high death rates. Again, this does not imply that sterilisation is the optimum method of control for species with these characteristics. On the contrary, culling will still give a greater initial rate of decline and the same long-term degree of suppression as sterilisation, for most mating-sterilisation systems (Scenario 1) and irrespective of fecundity or the value of r . The greater impact of culling on the rate of decline is obvious: a 100% cull will instantaneously eliminate a population ($r \rightarrow -\infty$), whereas 100% sterilisation gives a maximum rate of decline equal to $-b$, whatever the mating system.

In terms of the long-term (steady-state) effects of given levels of culling and sterilisation, if the population is to be eliminated, the culling rate c or the sterilisation rate s must exceed r for most mating-sterilisation combinations (i.e. Scenario 1: polygamous mating with females sterilised or monogamous/harem systems with either sex sterilised). For example, intensive trapping at a rate higher than r was successfully used to eradicate brushtail possums from Kapiti Island, New Zealand (Cowan 1993). As Table 1 shows, a given sterilisation rate yields a higher proportion sterile with density-dependent recruitment than with density-dependent mortality, because the lower mortality in the first case means a smaller loss of sterilised animals. However, the effect of a given proportion being sterile on population density is smaller in the first case than in the second (Table 1), because the absolute impact of a reduction in birth rate is discounted by the fact that density-dependent recruitment reduces the birth rate itself (Fig. 3). In spite of this, the proportion sterile required to cause complete suppression is the same whatever the nature of density dependence ($= r/a$). These two opposing effects of density dependence

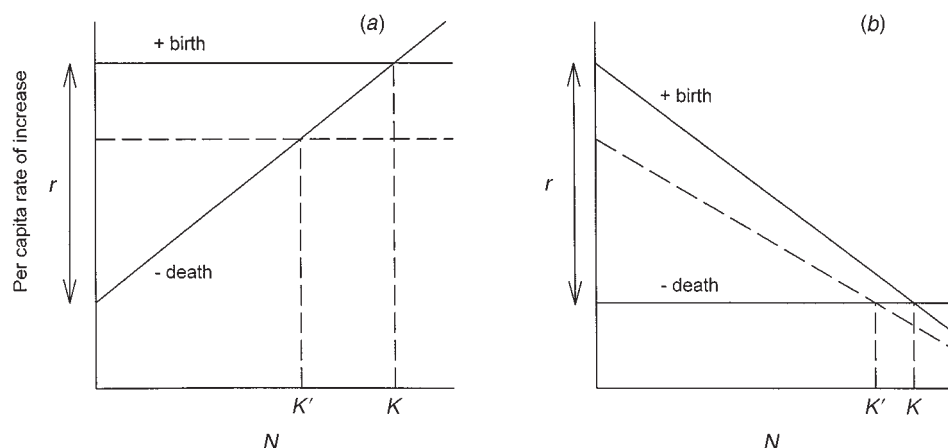


Fig. 3. Comparison of the effect of a proportional reduction in birth rate due to sterilisation on steady-state density, given (a) density-dependent mortality or (b) density-dependent recruitment. In each case, sterilisation reduces the birth rate from the upper solid line to the dashed line and density from K to K' . r is the intrinsic rate of increase.

cancel each other out when considering the effect of the instantaneous sterilisation rate, as opposed to the proportion sterile, on population density. Irrespective of the density dependence, the proportion by which density is reduced is s/r . The models suggest that the critical sterilisation rate for (theoretical) elimination of the population may be less than r for monogamy/harem systems in which both sexes are sterilised (Scenario 2). In this case, too, a control rate of less than r results in a more rapid suppression and greater long-term reduction in density than does culling (Fig. 1).

In terms of the rate of control required to provide a given level of population suppression, the results are again the same for culling or for sterilisation for most mating–sterilisation systems (Scenario 1). For monogamy/harem systems with both sexes sterilised (Scenario 2), the control effort required is less than that for either culling or for sterilisation under Scenario 1, by an amount equal to $f(N_{SS})Q_{SS}$ (Equation 26). This represents an additional ‘intrinsic’ reduction in the birth rate due not to the imposed sterilisation regime but to the proportion of fertile females failing to reproduce because a proportion Q_{SS} of their monogamous partners are also sterile.

Previous sterilisation models have suggested more optimistic results from sterilisation as a method of control than did our model. However, this appears to be due to an assumption of idealised monogamy within these modelled populations (e.g. Sturtevant 1970; Knipling and McGuire 1972). In the case of Knipling and McGuire (1972), the monogamy is not explicit but is dictated by the assumption that mating with a sterile male prevents mating by a fertile one. Our results suggest that such models may considerably overestimate the efficacy of sterilisation for populations that are not strictly monogamous. Alternatively, idealised polygamy, as modelled here, assumes unlimited random matings within the population, a scenario that is as unrealistic as idealised monogamy for most natural populations. On this basis and in agreement with Bomford (1990), we conclude that sterilisation of males alone is likely to be ineffective in reducing population size. Real mating systems can be expected to fall somewhere between these two extremes, so that in practice sterilisation of both sexes may be intermediate in effectiveness between the two sterilisation scenarios illustrated in Figs 1 and 2. However, Caughley *et al.* (1992) demonstrated that most mating systems and social systems involving dominance hierarchies will tend to further reduce the effectiveness of actual sterilisation regimes in comparison with quantitative predictions from simple population models.

Bomford (1990) criticised previous models of sterilisation and culling for not including potential compensatory changes in natality, mortality, immigration and dispersal, following a control operation. Even now, few models of fertility control appear to consider density dependence explicitly, although Saunders and Choquenot (1995) addressed the question in relation to foxes by considering hypothetically the extent to which different forms and degrees of possible compensation in the populations could offset reductions in r due to sterilisation. We have included such changes through density-dependent responses in recruitment and mortality functions. Moreover, the basic models specified in Equations 2–6 are sufficiently general to be applicable to populations with a wide range of density responses, from density independence [in which $f(N) = a$ and $g(N) = b$] to more complex density dependence such as the Θ -logistic response (Gilpin *et al.* 1976). The generalised steady state Equations 22–26, for population suppression given the level of control, or level of control required for a given level of suppression, are valid for this range of scenarios, given that p is defined by $p = [f(N_{SS}) - g(N_{SS})]/r$.

Other forms of compensatory changes are clearly possible, such as increased breeding success of non-sterile animals, or reduced mortality for sterilised individuals. The density dependence may also be more complex. For example, if juvenile survival depends on adult density rather than total density, sterilisation will be considerably more effective since it leaves the adult density unchanged in the short term. So not only are fewer young born but their density-dependent survival remains initially low. Finally, age structure may have a considerable influence on the above conclusions, which are from non-age-structured models (Barlow, unpublished data). These effects will be explored further in slightly more complex versions of the models described here.

In conclusion, the simple population models presented here allow prediction both of the effects of given intensities of sustained culling and sterilisation on population size and of the intensities of control required to achieve given levels of suppression, including analytical solutions for culling and for the most likely mating–sterilisation scenarios. The models suggest that sterilisation is less effective than culling at reducing populations in the short term. In the long term, the effect depends on the sterilisation regime and mating system. In most cases, sterilisation and culling give the same long-term suppression, but for a monogamous population with both sexes sterilised, the level of suppression is considerably greater than that for culling or for other mating system and sterilisation regimes (Fig. 1). In the short term, sterilisation will be more effective in reducing density if populations are regulated by density-dependent mortality than if they are regulated by density-dependent recruitment (Figs 1, 2), whereas the impact of culling is unaffected by the nature of density dependence. A good opportunity to test the quantitative predictions of the sterilisation model (although not the comparison with culling) may be provided by final results from the large-scale sterilisation experiments currently being carried out on rabbits in Australia (Williams and Twigg 1996).

Acknowledgments

This work was funded by the Foundation for Research, Science and Technology, and we are grateful to Nick Caldwell for technical assistance.

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Appendix. Model solutions under Scenario 1

Scenario 1 is that of polygamous mating systems with sterilisation of females only or of both sexes, and monogamous systems with sterilisation of either sex alone (but not both)

Model Solution for Population Density after a Given Time, Assuming Density-dependent Mortality and a Continuous Rate of Sterilisation under Scenario 1

Let S = density of non-reproducing females and v = proportion of females in the population. Then

$$dS/dt = S(-b - rN/K) + s(vN - S)$$

and

$$dN/dt = a(N - S/v) - N(b + rN/K).$$

Further, since $Q = S/vN$ (= proportion of females not reproducing),

$$\begin{aligned} dQ/dt &= [N \cdot dS/dt - S \cdot dN/dt] / N^2 v \\ &= s[1 - S/(vN)] - [aS/(vN)][1 - S/(vN)] \end{aligned}$$

hence

$$dQ/dt = (1 - Q)(s - aQ) \quad (A1)$$

and

$$dN/dt = N[a(1 - Q) - b - rN/K]. \quad (A2)$$

Integrating A1:

$$Q(t) = \frac{[aQ(0) - s] + s[1 - Q(0)]e^{(a-s)t}}{[aQ(0) - s] + a[1 - Q(0)]e^{(a-s)t}}$$

and if $Q(0) = 0$ then

$$Q(t) = \frac{e^{(a-s)t} - 1}{(a/s)e^{(a-s)t} - 1}.$$

To integrate A2, first substitute $Z = 1/N$:

$$\begin{aligned} dZ/dt + [a(1 - Q) - b]Z &= r/K \\ dZ/dt + c(t)Z &= f \end{aligned}$$

where $c(t) = [a(1 - Q) - b]$ and $f = r/K$. Multiplying by the integrating factor $e^{\int c(t)dt}$:

$$\frac{d}{dt}(Ze^{\int c(t)dt}) = fe^{\int c(t)dt}.$$

Integrating:

$$Ze^{\int c(t)dt} = \int fe^{\int c(t)dt} dt + C_1. \quad (A3)$$

The integrating factor is $\int c(t)dt = -bt + \ln\{[aQ(0) - s] + ae^{(a-s)t}[1 - Q(0)]\}$

$$\therefore e^{\int c(t)dt} = \{[aQ(0) - s] + ae^{(a-s)t}[1 - Q(0)]\} e^{-bt} \quad (A4)$$

$$\therefore \int fe^{\int c(t)dt} = (r/K)e^{-bt} \left\{ \frac{ae^{(a-s)t}[1 - Q(0)]}{a - b - s} + \frac{[s - aQ(0)]}{b} \right\} \quad (A5)$$

From A3,

$$N = 1/Z = \frac{e^{\int c(t)dt}}{\int fe^{\int c(t)dt} + C_1}. \quad (A6)$$

Substituting A4 and A5 into A6 gives

$$N(t) = \frac{\{[aQ(0) - s] + ae^{(a-s)t}[1 - Q(0)]\} e^{-bt}}{(r/K)e^{-bt} \{ae^{(a-s)t}[1 - Q(0)]/(a - b - s) + [s - aQ(0)]/b\} + C_1}$$

and, if $Q(0) = 0$ and $N(0) = K$, then

$$N(t) = \frac{bK(r - s)(s - ae^{(a-s)t})}{sa(a - s)e^{bt} - brae^{(a-s)t} - rs(r - s)}.$$

Appendix. continued*Steady-state Reductions in Population Density and Proportions Sterile, under Scenario 1**Density-dependent mortality*

The steady states are given by Equations A1 and A2 above, setting $dQ/dt = 0$ and $dN/dt = 0$, that is

$$Q_{ss} = s/a \quad (\text{A7})$$

and

$$N_{ss}/K = 1 - s/r. \quad (\text{A8})$$

Density-dependent recruitment

In this case the equations for S and N are as follows:

$$dS/dt = -bS + s(vN - S)$$

and

$$dN/dt = (a - rN/K)(N - S/v) - bN.$$

Hence

$$\begin{aligned} dQ/dt &= [N \cdot dS/dt - S \cdot dN/dt] / (N^2 v) \\ &= s[1 - S/(vN)] - [S/(vN)][a - (rN/K)1 - S/(vN)]. \end{aligned}$$

Therefore

$$dQ/dt = (1 - Q)[s - Q(a - rN/K)] \quad (\text{A9})$$

and

$$dN/dt = N[a - rN/K)(1 - Q) - b]. \quad (\text{A10})$$

When $dQ/dt = 0$ and $dN/dt = 0$, $N = N_{ss}$, $Q = Q_{ss}$ and

from Equation A9,
$$Q_{ss} = s/(a - rN_{ss}/K)$$

and from Equation A10,

$$(1 - Q_{ss})(a - rN_{ss}/K) = b.$$

Therefore

$$Q_{ss} = s/(b + s) \quad (\text{A11})$$

and

$$N_{ss} = 1 - s/r. \quad (\text{A12})$$