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ORIGINAL PAPER

Modeling the eradication of invasive mammals using the sterile male technique

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Abstract Large vertebrates, like the domestic goat (*Capra hircus*), have been transported all over the world and are an ecological disaster to numerous island and mainland ecosystems. Eradication measures for such species are generally centered on lethal methods of removing individuals, an increasingly difficult process as populations become smaller and individual animals become much more difficult to detect. In addition, methods of lethal removal are becoming less desirable in the public eye, prompting the necessity to explore alternatives. Here we investigate the use of the sterile males technique as an effective strategy in the eradication of large mammals. The results of our simulations suggest that the use of sterile males as a single strategy would only be an effective measure to eradicate relatively small (no more than 100 individuals) isolated feral vertebrate populations. However, our results indicate that the technique could be employed as a successful and potentially cost-effective end-point complement to lethal control and/or as a preventative measure against re-invasion.

Keywords Biological control · Contraception · Culling · Islands · Shooting · Vertebrates

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Introduction

Invasive species are important drivers of biodiversity loss (Vitousek et al. 1997). Mammals are specially problematic, being responsible for extensive damage (Lever 1985; Ebenhard 1988), particularly on fragile island ecosystems (Atkinson 2001; Dulloo et al. 2002; Donlan and Wilcox 2008).

Preventing introductions is the best method to avoid biodiversity losses by invasive species (IUCN 2001). Once a species has become established, three general management strategies are available to minimize losses: exclusion, control, or eradication (Bomford and O'Brien 1995). On island ecosystems, eradication (i.e., the removal of all individuals over a specified period of time) is often preferable over exclusion or control (Courchamp et al. 2003). Three types of methods are available to implement eradication programs: physical (e.g., hunting), chemical (e.g., poisoning) and biological (e.g., release of a pathogen, Courchamp et al. 2003). Hunting is generally considered one of the best options for large mammal eradication, as it is very selective and relatively environmentally safe when compared to either poisoning (Gosling and Baker 1989) or pathogen release (Courchamp et al. 2003). The main pitfall associated with hunting, however, is finding individuals at low population densities. On islands, this issue can be aggravated by two circumstances: (1) islands with complex landscapes and inaccessible areas increase the costs of finding the remaining individuals; and (2) hard to reach remote islands often cannot be accessed for sufficient periods to complete the eradication program (Courchamp et al. 2003). In the former case, two methods have been applied to increase the efficiency of hunting on complex landscapes: (1) trained dogs (Cowan 1992); and (2) "Judas" animals (Parkes 1990; Campbell et al. 2005). In the latter, poisoning and self-propagating options (e.g., pathogen release) have been suggested (Courchamp et al. 2003), but the release of sterilized individuals may provide a safer and potentially more effective option.

In contraception/sterilization approaches, it is usual to focus on individuals from only one of the sexes. In large mammals, female hormonal or immunological contraception tends to be favored over male contraception (Fagerstone et al. 2006). Nevertheless, sterile males have been proposed as an effective technique to control invasive species in general (Knipling 1959). In insects, for instance, the sterile male technique (*sensu* Knipling 1959) has been successfully used in controlling invasive species, such as the tse-tse fly (Simberloff 2009). Here, we evaluate the potential of the release of sterilized males as an eradication strategy under different simulated scenarios relative to hunting. In particular, we focus our study on goats (*Capra hircus*), as they are responsible for some of the most extensive damages on island ecosystems (Parkes 1990). We then discuss the advantages of male sterility over female contraception for eradication of large vertebrates from islands.

Model formulation

Hunting and sterile males target survivorship and fertility, respectively. To model these separate effects we used a type II Leslie matrix to simulate female population growth (Case 1999), which allows us to independently manipulate the contribution of fertility and survivorship to the population growth rate (λ). In particular, we were interested in identifying conditions that lead to $\lambda < 1.0$.

Female goats have an average two litters per year, give birth to their first litter sometime before completing 1 year of age, and are fertile on average for an additional 8 years (Watts and Conley 1984). Thus, we considered 18 life stages (0–17), two for the first year of life plus 16 of fertile adult life. We assume that survivorship and fertility are the same from stages 2 to 17. Even though this assumes that there is no upper limit for age, there is a low probability that individuals reach the age of 15+, and therefore substantially alter the results. We also assume an equal sex ratio, with offspring of either sex being born with equal probability. Female goats give birth to an average one and a half (1.5) kids per pregnancy, with an average of two pregnancies per year after the first year of life (Nowak 1999). Thus, we assume fertility to be an average of 0.75 females born per gestation, with the exception of the first stage, where fertility is zero.

We assume that survivorship values are low for stage 0, but increase in later stages ($S0 = 0.5$, $S1 = 0.7$), following survival schedule 7 in Watts and Conley (1984). All other stages were assumed to have a high survivorship ($S2 = 0.9$), which is justified based on a "worst case" scenario commonly found with invasive species lacking predators (Courchamp and Caut 2006). Because our model is structured in 6 months intervals, we transformed the population growth rate obtained into annual growth rates using the rule described in Watts and Conley (1984).

The chosen parameter values yield a $\lambda = 1.28$ (Eq. 1), which is within the range of growth rates estimated for feral goat populations (10–35%, Watts and Conley 1984), and thus we deemed the values an acceptable approximation for the purpose of this study.

$$M = \begin{pmatrix} 0 & 0.525 & 0.625 \\ 0.5 & 0 & 0 \\ 0 & 0.7 & 0.9 \end{pmatrix} \qquad (1)$$

Scenarios

We modeled three different scenarios:

1. *Eradication by hunting*: Is a baseline scenario for comparisons to scenarios 2 and 3.

2. *Eradication by sterile males*: Explores the effectiveness of sterile males in eradicating the population on its own.
3. *Eradication by sterile males and hunting*: Explores how effective sterile males and hunting are when applied together.

Simulations

All simulations were carried out in Mathematica 6.0 (Wolfram Research, Inc., Champaign, IL, USA). The code is available upon request.

Scenario 1: eradication by hunting

Hunting reduces survivorship, and consequently fecundity. The proportional reduction in population due to hunting was used as a weight to reduce survivorship, and fecundity was recalculated accordingly. For example, a reduction of 10% in the female population due to hunting would mean a 10% reduction in survivorship. For simplicity, hunting pressure was kept constant no matter what the population size.

The effect of hunting on survivorship will ultimately depend on the number of man/hours and method used. For instance, Cruz et al. (2009) report a wide range of hunting pressures from relatively low, applied over a long period of time leading to the removal of >12,000 goats in a 2 years period, to high, applied over a very short period of time resulting in a similar number of goats removed over a 3 months period. As such, we sought to examine the whole breadth of possible values of hunting pressure, from no effect on survivorship (i.e., no hunting) to 100% reduction (0–1; Fig. 1), on λ.

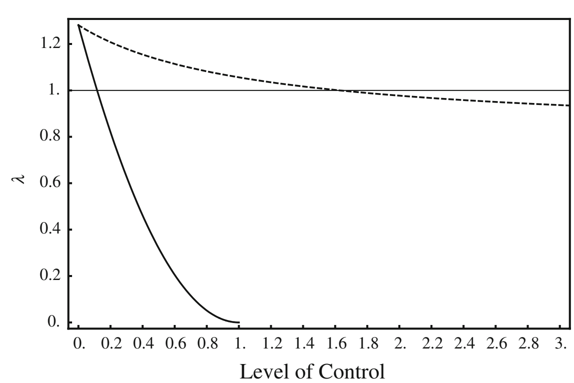

Fig. 1 Plot of variation in population growth rate (λ) for different levels of hunting (*solid line*) and sterile male (*dashed line*) pressure. Hunting pressure is measured as the proportional reduction in survivorship (e.g., 0.1 means a 10% reduction in survivorship in all life stages). Sterile male pressure is measured as proportional reduction in fertile males due to the addition of sterile males to the population (e.g., 1 means that there is a 1:1 ratio of sterile to fertile males in the population, leading to 1/2 reduction in fertility)

The results agree with observed patterns that hunting is an effective manner of eradicating mammals if high pressure can be maintained until the last animal is culled (Smith 1982; de Vries and Black 1983; Schofield 1989; Cruz et al. 2009). In particular, we see a nonlinear decrease in λ with increase in hunting effort, with a decrease in survivorship of ~0.14 resulting in $\lambda = 1.0$.

Scenario 2: eradication by sterile males

Sterile males reduce fertility, and consequently fecundity. Reduction in fertility was based on the assumption that breeding is random. Therefore, fertility was reduced by the proportional reduction in fertile males due to the addition of sterile males in the population. For example, if the number of sterile males is equal to the number of fertile males, then the proportion of fertile males is reduce to 1/2 of the total males, and fertility is consequently reduced by half. This results in an asymptotic decline in fertility towards zero as the proportion of sterile males increases to infinity. This approach assumes that each male has the monopoly of one female to the detriment of all other males—a basic assumption of the sterile males method (Knipling 1955). This assumption may not hold true for goats (Chemineau et al. 2004), however, we shall use it here and discuss later how the method may still be applied to polygynous species.

When sterile males are employed in the eradication of insects, the number of sterile males released is usually much higher than the number of fertile males in the population (Benedict and Robinson 2003). However, to be feasible in large mammal control, the technique should have a significant effect without having to release excessive numbers of individuals—which we arbitrarily define as being no larger than twice the number of fertile males in the population (i.e., a reduction in fertility of 2/3). Thus, we examined values of sterile male pressure resulting in a 0 (i.e., no sterile males) to 3/4 reduction in fertility (i.e., 3 sterile males for every fertile male).

The results are consistent with the observed in other cases of sterile male use (Lance and McInnis 2005), in that a fairly large number of individuals must be released for there to be a significant impact on λ. Nevertheless, a $\lambda = 1.0$ can be obtained with releasing fewer then twice the number of fertile males (1.625 sterile males for every fertile male), which means that for every 50 fertile males approximately 82 sterile males should be released for the population to remain stable (Fig. 1). Therefore, using sterile males as the sole strategy for eradication would only be feasible in relatively small populations, where it would not be too costly to sterilize the necessary number of individuals.

Sterile males can be deployed in two different ways: (1) keeping the proportion of sterile males constant through time; or (2) keeping the number of sterile males constant through time (Knipling 1959). In the first, λ would remain constant, while in the second λ would decrease with the increase in the ratio of sterile to fertile males as the population declines. Therefore, from a management perspective, it would be best to keep the number of sterile males constant. Once eradication is achieved, a portion of these individuals could then be maintained to suppress further invasions. However, if maintaining a stable sterile male population is not a viable option, one can identify the maximum number of sterile individuals that can be deployed at once, and attempt to keep a ratio greater than 1.625 sterile to fertile males in the population.

Scenario 3: eradication by sterile males and hunting

By coupling the effects of sterile males and hunting both fertility and survivorship are reduced. Two methods of deployment can be used: (1) a parallel approach in which sterile males are released simultaneously with hunting; or, (2) a tandem approach in which hunting can be used to suppress the initial population to a level where sterile males become effective given the number of sterile males planned to be released.

If deployed in parallel, $\lambda = 1.0$ can be achieved by releasing as little as 0.12 sterile males for every fertile male and applying a hunting pressure of just 0.1 (Fig. 2). Deployment in parallel has the advantage that sterile individuals can be fitted with radio collars and used as "Judas" animals to facilitate hunting (Campbell et al. 2004). To analyze a deployment in tandem scenario, we calculated how many time steps it would take to reach a target population size under hunting (determined by the sterile males to males proportion), and then calculated the number of time steps it would take for the population to reach one individual under sterile males (assuming that the ratio of sterile males to males remains constant). We then averaged λ of each step weighed by the number of time steps to estimate overall growth rate under different assumptions of hunting and sterile male pressures. In general, the parallel option is much more effective because survivorship and fertility are simultaneously affected, while in tandem, each is targeted separately (Fig. 3). Finally, the results suggest that when combined the strategy is more effective then hunting alone (Fig. 4).

Sensitivity analysis

We use a sensitivity analysis to evaluate the proportional contribution of each element of the Leslie matrix to λ, and therefore the importance of each element in determining population dynamics. In particular, the analysis is important to identify why each control measure might be effective, and to help direct each control measure on the age class in which it will be most effective. According to Cross and Beissinger (2001) the best method for our type of

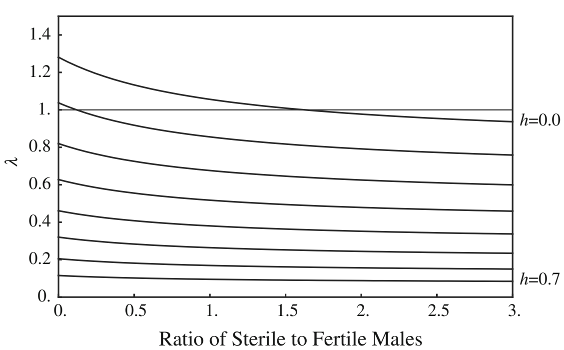

Fig. 2 Population growth rate (λ) as a function of sterile male pressure over different levels of hunting pressure ($h = 0$–0.7) when using these approaches in parallel

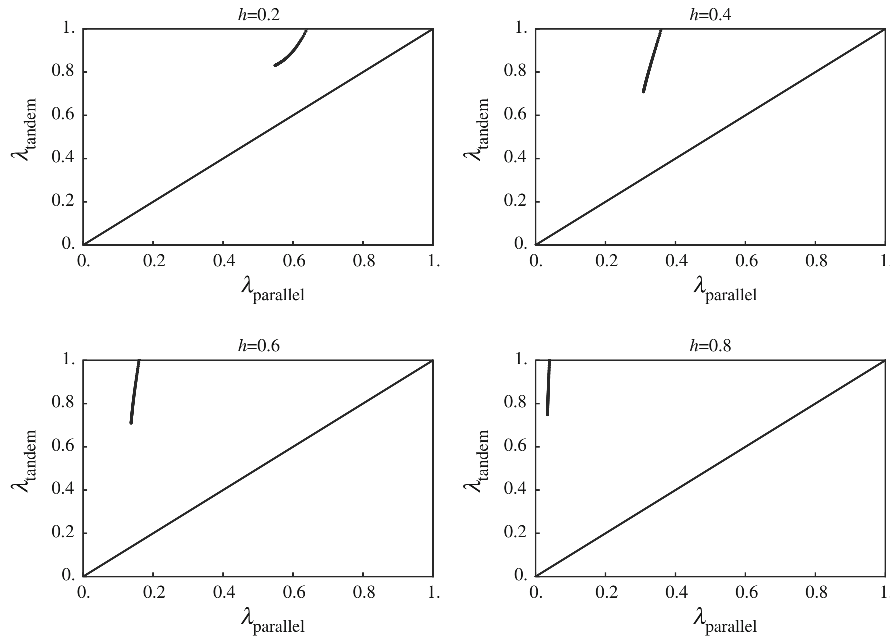

Fig. 3 Difference in population growth rate (λ) between parallel and tandem strategies over sterile male pressure varying from 0 to 10 at 0.1 intervals, and four different levels of hunting (h) pressure

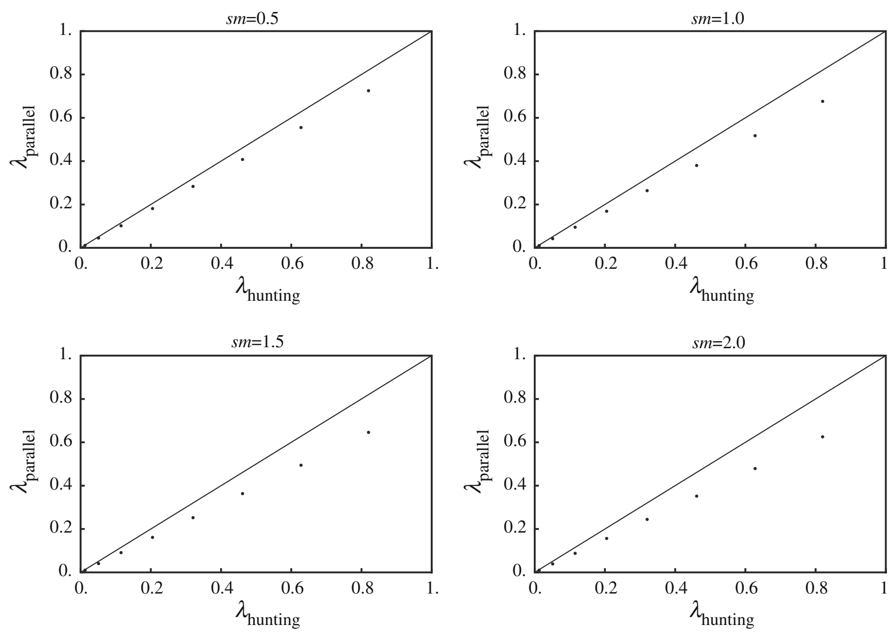

Fig. 4 Difference in population growth rate (λ) between hunting and parallel strategies over four different levels of sterile male pressure (sm)

model is the lower-level elasticity, developed by de Kroon et al. (1986).

The analysis suggests that survivorship during the adult stage (stages 2–17) is the most important factor contributing to population growth, being responsible for approximately 52% of λ (Table 1). The results indicate why hunting is so effective at reducing λ, while sterile males are not as effective on their own. By reducing survivorship across all age classes, hunting can reduce λ by $\sim$82%, while reducing fertility only reduces λ by $\sim$16%. Nevertheless, combining both strategies would affect all growth parameters, and is likely to be more effective.

Table 1 Elasticity values for model parameters

Stages	0	1	2–17
Fecundity (*F*)	0	0.034	0.13
Survivorship (*S*)	0.17	0.13	0.52

Discussion

The use of contraception/sterilization of individuals from invasive species has been advocated as a more humane approach to invasive species eradication (Fagerstone et al. 2006). In general, the approach affords high-specificity, as in other biological control methods, and carries two main advantages over such methods, namely: (1) no new species is being introduced; and, (2) it does not have the same safety and ethical concerns associated with the release of pathogens (Courchamp et al. 2003). In addition, once all reproductive individuals are eliminated, sterile individuals can be kept at relatively low numbers to prevent future introductions, and perhaps more importantly, to guard against possible negative effects associated with the extirpation of a species from the biological community (Taylor 1968; Myers et al. 2000; Mack and Lonsdale 2002). While these are desirable qualities, the first criterion for establishing a successful strategy for eradication is that it leads to a decrease in population size (Bomford and O'Brien 1995).

In general, contraception/sterilization of females, rather then males, is perceived as a more effective strategy for reduction of population growth rate in large mammals (Warren et al. 1995; Fagerstone et al. 2006). However, in the studies that tested sterile males, only a small number of individuals from the actual population were sterilized relative to the population size, and they were sterilized using hormonal or immunological contraceptives that may loose their effectiveness over time. Here, we propose that the release of sterile males into the population, rather then sterilizing individuals within the population, can be an effective tool resulting in a reduction in population growth rates. The release of sterile males has two advantages over sterilizing females within the population that we believe justify their use. First, sterilization by epididymectomy is a relatively simple and cheap permanent sterilization solution (Campbell 2007) that avoids some of the issues associated with the use of controlled sterilization/contraception substances (Fagerstone et al. 2006). Second, release of additional males into the population would skew the sex ratio towards males, which would likely reduce female survivorship (Reale et al. 1996) and male fecundity (Mysterud et al. 2002, 2004), which suggests that sterile males have effects beyond just reducing female fertility (Zhang 2000).

The main disadvantage associated with such a strategy is the number of individuals that have to be sterilized for it to have a significant impact on population growth. However, this is not exclusive to the sterile male technique, but common to any contraception/sterilization strategy and why it is always recommended that such strategies be used in conjunction with a lethal method (Nielsen et al. 1997). In this study, combining the release of sterile males with hunting has significant impacts on population growth even with relatively few released individuals and low hunting pressure. Such a strategy would be particularly useful in the case of hard to access remote islands, helping overcome the limitation of establishing a continuous long-term presence to ensure eradication (Courchamp et al. 2003). Using a similar approach as described in Cruz et al. (2009), a team of hunters could significantly reduce the population size in a short period of time and with the concomitant releases of sterile males, only periodic monitoring would be required. In addition, using released males as "Judas" animals would aid in finding and monitoring the remaining individuals (Campbell 2007). This approach would be highly specific and not likely to significantly affect native species, avoiding one of the principal complications associated with eradication of mammals from islands (Simberloff 2001). Finally, as pointed out by Bomford and O'Brien (1995), costs weigh heavily on the success of any eradication program, and it is important to have the budget available from the onset. Hunting costs grows exponentially as the population declines (Parkes 1990; Cruz et al. 2009), yet sterile males are most cost effective at low population densities. Therefore, the use of sterile males is likely to reduce the overall costs of the eradication program, and thus increase the likelihood of success.

Two main issues remain, though: (1) do sterile males behave as fertile males, and are females equally attracted to them; and, (2) would such a strategy work on polygynous animals. In regards to the first issue, recent work by Campbell (2007) seems to suggest that at least in goats epididymectomy would be an efficient way of sterilization, i.e. males retain their sexual drive and attractiveness to females. In regards to the second, Knipling (1959) suggested that the release of a high proportion of sterile males relative to fertile males is likely to have an impact even in polygynous species beyond what would be expected by the sole removal of individuals. This is justified if we consider the effect of adult sex ratio on demographic parameters in polygynous species (Ginsberg and Milner-Gulland 1994; Le Galliard et al. 2005). By introducing additional competitive males, the technique skews the sex ratio towards males, which would likely negatively impact both survivorship and fecundity beyond what would be expected by sterile males monopolizing females (Reale et al. 1996; Zhang 2000; Mysterud et al. 2002, 2004). Therefore, we posit that a non-monogamous mating system would not invalidate the use of sterile males.

As such, our model may be used as a guide for future work in testing the effectiveness of sterile males in eradication or control of large vertebrates. Parameter values relevant to local populations could be used, and additional modifications could be made to include reduction in survivorship and fecundity associated with skewed sex ratios. In this framework, our model suggests the following guidelines:

1. Reduce populations down to a level at which the application of sterile males can be expected to be economical and effective. If sterile males are used alone, our model suggests a ratio of 1.625 sterile males for every fertile male to obtain a $\lambda = 1.0$; with hunting occurring in parallel, this could potentially be reduced to 0.12 sterile males for every male.
2. Produce “tailor-made” sterile males (e.g., desert-adapted, feral-strain “hybrids” in the case of Galápagos Islands goats), or capture and sterilize males from the existing population, depending upon which type is likely to be the most competitive with fertile males. This is important because it will assist in assuring that the sterile males are competitive when up against a minority of local fertile males. Zoos, with their considerable vertebrate animal breeding and veterinary skills plus their wildlife conservation and animal welfare orientation, might be sympathetic and economical partners in the development of sterile males of numerous taxa for this purpose. Sterile males should be easily identifiable, with a different coat color and/or visible tags in order to prevent hunting-induced mortality among the sterile male population.
3. Maintain some numbers of sterile males present—perhaps in perpetuity—in order to employ an economical “sentry” system against future reintroduction. For instance, given that previous feral goat introductions of known dimension consisted of <5 females (Campbell et al. 2004; Schofield 1989), an effective sentry system might consist of as few as 20 sterile males.

Conclusions

According to Courchamp et al. (2003), “the most appropriate strategy [for control] will be more often the simultaneous use of biological, chemical and mechanical control methods”. Here, we have shown that the sterile male technique has the potential to be an effective method for controlling invasive vertebrate populations particularly if used in conjunction with lethal control, and therefore should be considered as an additional strategy by managers, particularly on remote islands. Combined with hunting, the sterile male technique can act as a two-pronged strategy in which both survivorship and fertility are targeted simultaneously. This, in accordance with the sensitivity analysis, would drastically reduce the population’s growth rate. Furthermore, the sterilized males can be used as “Judas” individuals, and as “sentries” aiding in guarding against further reintroduction and against potential negative effects associated with eradication.

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