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Effect of Fertility Control on a Population's Productivity

Graeme Caughley, Roger Pech and David Grice

CSIRO Division of Wildlife and Ecology,
P.O. Box 84, Lyneham, Canberra, ACT 2602, Australia.

Abstract

The effect of a sterilising agent upon the productivity of vertebrate pests, such as feral horses, feral dogs, wild rabbits or fruit-eating birds, depends upon the population's social structure and mating system. We investigated the theoretical effect on productivity of three forms of dominance, two effects of sterilisation on dominance, and four modes of transmission. Seventeen of the possible 24 combinations are feasible but lead to only four possible outcomes. Three of these result in lowered productivity. The fourth, where the breeding of a dominant female suppresses breeding in the subordinate females of her group, leads to a perverse outcome. Productivity increases with sterilisation unless the proportion of females sterilised exceeds $(n-2)/(n-1)$ where n (>2) is the number of females in the group. A knowledge of social structure and mating system is therefore highly desirable before population control by suppressing female fertility is attempted or even contemplated.

Introduction

'Increasing community awareness of moral and animal welfare issues associated with conventional pest animal control has focused interest on non-lethal alternatives, such as fertility control' (Bomford 1990). Sterilisation has been used successfully to control some insect pests, particularly the screw-worm fly, *Cochliomyia hominivorax* (Knipling 1959). Its efficacy in *Cochliomyia* control rests on an ability to flood the population with sterile males and on the females mating but once. Such a technique has been tried on rats (Bowerman and Brooks 1971; Kennelly *et al.* 1972) which are more promiscuous breeders, but with limited success. It has been suggested for wild horses where groups of females are accompanied by a dominant male (Kirkpatrick *et al.* 1982; Turner and Kirkpatrick 1982). Bomford (1990) reviewed these and other schemes for reducing the density of vertebrates by sterilising males, concluding that they showed little promise in themselves and were inferior to control systems aimed at sterilisation of females. This investigation is therefore aimed at determining the effect of sterilising a proportion of females, seeking the circumstances in which this would lead to successful population control and the circumstances in which it would not.

Methods

We first catalogued the characteristics of mating systems and the methods of delivering a sterilising agent that might influence the probability that a female would not breed as a consequence of a control operation. The mating systems considered here do not exhaust the possibilities. They do not include, for example, non-linear systems of dominance nor the effect of kinship on the probability of a successful mating.

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Common dominance relationships among females within groups of a gregarious species include:

(A) no dominance, or

(B) linear dominance in the form of a pecking order, or

(C) one dominant and a variable number of subordinates.

The effect of sterilising a dominant female may be to:

(a) have no effect on her dominance (subordinates may or may not mate but if they do mate no offspring survives), or

(b) remove her from the dominance hierarchy (subordinates may then mate and produce viable offspring).

The sterilising agent is assumed to be spread by males acting as carriers, by a virus, or by some other vector. Mode of dispersal of the agent may take one of four forms:

(1) transmission by random contact processes (e.g. airborne or in baits) which act independently of the breeding behaviour of the target species (all females are equally vulnerable and may be sterile prior to mating), or

(2) sexual transmission, where all females in a group are mated by the same male and hence the females in the group are either all fertile or all sterile, or

(3) sexual transmission, where the females of a group may be mated by more than one male and all females are equally vulnerable to sterility, or

(4) sexual transmission, where only the dominant female mates (subordinates cannot be sterilised because they do not mate).

These three groups of factors (A–C, a–b, 1–4) provide 24 combinations which were examined for feasibility. Some combinations are not feasible. For example, one cannot have the combination Ab because A is 'no dominance' and b is 'sterilising a dominant removes her from the dominance hierarchy'.

Having identified the feasible combinations, we derived from first principles the expected number of litters produced per social group of females in the first breeding season following release of the sterilising agent. Additionally, we estimated the mean stochastic outcome of each feasible combination. A total of 500 simulations were run for a population containing 100 groups of females, where the size of each group was one greater than a random draw from a Poisson distribution and where the females to be sterilised were chosen by lot.

Results and Discussion

Theory

The factors defined 24 possible combinations but of these only 17 are feasible. The feasible combinations and the expected number of litters that will be produced in the breeding season immediately after the sterility agent is introduced into the population are listed in Table 1. Each estimate is a function of two variables: p, the probability that a susceptible female will be rendered sterile, and n, the mean number of females per social group.

The three dominance classes (A, B and C) are all known from nature (Emlen and Oring 1977), as are others not characterised here. More than one may manifest within a species according to the level of food supply and shelter to which a population has access. The red fox, *Vulpes vulpes*, provides a clear example of such behavioural plasticity (Macdonald 1979, 1989; Schantz 1984; Voigt and Macdonald 1984).

Table 1. Average number of litters produced per social group in terms of p (the probability that a susceptible female will be sterilised) and n (the number of females per social group) during a single breeding season

See text for explanation of factor coding

Factor combination	Litters
A1	$n(1-p)$
A2	$n(1-p)$
A3	$n(1-p)$
Ba1	$1-p$
Bb1	$1-p^n$
Ba2	$1-p$
Bb2	$1-p$
Ba3	$1-p$
Bb3	$1-p^n$
B4	$1-p$
Ca1	$1-p$
Cb1	$(1-p)(1+np-p)$
Ca2	$1-p$
Cb2	$1-p$
Ca3	$1-p$
Cb3	$(1-p)(1+np-p)$
C4	$1-p$

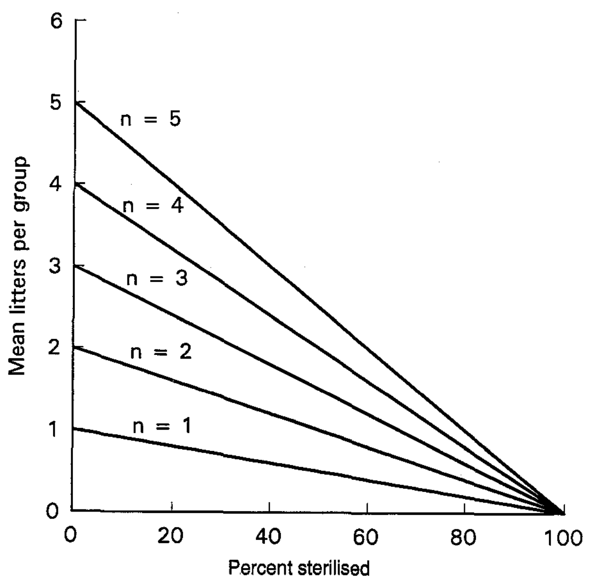

Fig. 1. Mean number of litters produced during a single season of births by a group of n females subject to varying rates of sterilisation. Dominance relationships within a group have no effect on a female's probability of breeding.

An expected $n(1-p)$ litters per group are produced only in the absence of dominance influencing the probability of a female producing a viable litter. The expected outcome (Fig. 1) is the same whether the model is deterministic or stochastic. In contrast, the expectation of $1-p$ litters per group may be realised for either dominance relationship and for all four modes of transmission, depending on the level of the other factors. It is a special case of the other three models, being represented by the line marked $n=1$ in Figs 1–3.

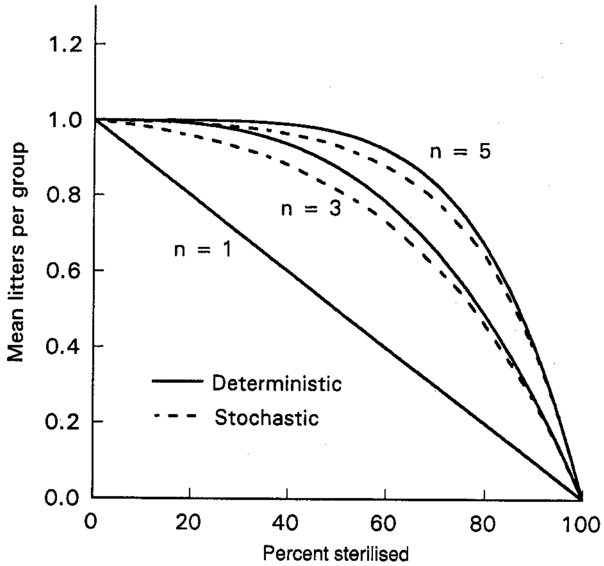

Fig. 2. Mean number of litters produced during a single season of births by a group of n females subject to varying rates of sterilisation. Dominance within the group is linear and only the top dominant breeds. Sterilisation of a female removes her from the dominance hierarchy.

An expected $1-p^n$ litters per group occurs only in special circumstances that include a linear dominance hierarchy disrupted by sterilisation of the top-ranking female. For both the combinations Bb1 and Bb3 (Table 1), a group will produce one litter whenever at least one female is fertile. The effect of the sterilising agent declines progressively as group size increases. The mean of the stochastic outcome differs from the deterministic outcome (Fig. 2) but the deterministic estimate yields an approximation close enough for practical purposes.

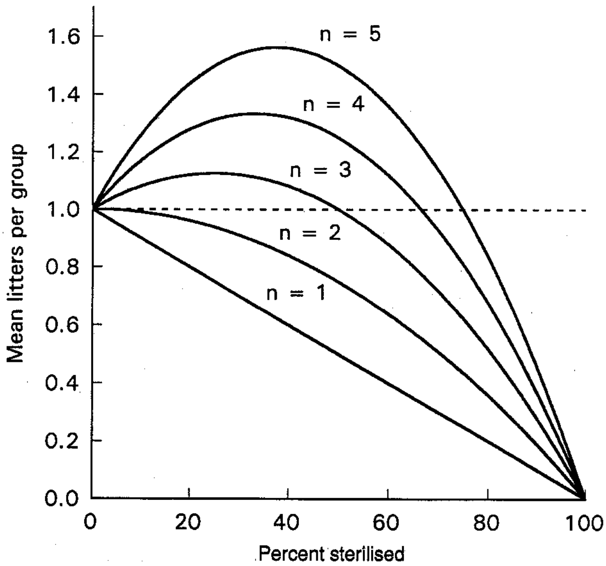

Fig. 3. Mean number of litters produced during a single season of births by a group of n females subject to varying rates of sterilisation. One female is dominant and the others are subordinate to her. Only the dominant female breeds. She relinquishes dominance if sterilised and then subordinates are free to breed.

Each of the above three outcomes describes productivity declining monotonically with rising probability of sterilisation for groups of any size. Not so the fourth. The outcome of an expected $(1-p)(1+np-p)$ litters per group (Fig. 3) obtains in special circumstances which include a single dominant female whose sterilisation releases breeding in the subordinates. For the combinations Cb1 and Cb3 (Table 1) there are two cases. One litter is produced with probability $(1-p)$ if the dominant is fertile. If the dominant is sterile (with probability p), the number of litters produced per group is equal to the number of fertile subordinates, $(n-1)(1-p)$. The total number of litters per group is the sum of the two cases. The effect of introducing a sterilising agent into such a system is to increase productivity for all group sizes greater than two unless the proportion of females sterilised exceeds $(n-2)/(n-1)$.

Management Implications

The analyses and simulations reported here indicate that the effect of a sterilising agent on the productivity of a population is critically dependent on the social behaviour of the target species and on the mode of transmission of the sterilising agent. In most cases a sterilising agent will reduce the productivity of the target population. However, in one case outlined above the effect is to increase productivity unless the probability of a given female being sterilised is very high.

Clearly, one does not knowingly stimulate the productivity of a population one is attempting to control. It is recommended that before a female-sterilising agent is used to control a species it should be used in a small-scale quarantined experiment to determine whether it will in fact work.

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