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Title

The effect of fertility control in the population dynamics and behavior of brushtail possums (Trichosurus vulpecula) in New Zealand

THE EFFECT OF FERTILITY CONTROL ON THE POPULATION DYNAMICS AND BEHAVIOR OF BRUSHTAIL POSSUMS (*TRICHOSURUS VULPECULA*) IN NEW ZEALAND

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ABSTRACT: A large-scale field experiment began in late 1995 to determine the effectiveness of fertility control for managing brushtail possum populations in New Zealand. Six study populations received one of three sterility treatments, either 0%, 50%, or 80% of female possums sterilized by tubal ligation, with the level of sterility in each treatment maintained each year. Mark-recapture methods and analysis are being used to investigate the effect of the sterility treatments on demographic parameters such as population growth rate, survival, and recruitment. Recruitment of locally born young was successfully suppressed by sterility treatments, with lower yearling recruitment occurring on 80% and 50% sterility sites than on control sites. Negative population growth rate has been observed on one replicate set of 50% and 80% sterility sites, but growth rates have remained stable on the other replicate set of treatment sites. Examination of the contribution of immigrant animals to population growth rate has suggested that the settlement pattern of immigrants was compensating for reduced *in situ* recruitment. Analysis of survival rates revealed that sterile female possums had significantly higher survival rates than intact females, indicating a survival cost for reproduction. The effects of fertility control on the transmission rate of *Leptospira interrogans* serovar *balcanica* using a failure rate model revealed that the rate at which possums encounter *leptospira* infection in the treatment sites (80% females sterile) was greater than the rate in control sites. As *leptospira* infection is believed to be spread by direct contact, increased transmission in the 80% sterility sites suggests that contact rates between possums (mating contacts) are higher in areas subject to fertility control. Increased transmission is hypothesised to be driven by the increased frequency of oestrus resulting from the method of sterilization (tubal ligation) that was used to model the potential effects of immunocontraception. This result has direct relevance to both the epidemiology of disease as well as the potential spread of any biocontrol vector that relies on direct contact for transmission.

KEY WORDS: brushtail possum, fertility control, immunocontraception, mark-recapture, population dynamics, epidemiology, leptospirosis

INTRODUCTION

Introduced brushtail possums (*Trichosurus vulpecula*) are New Zealand's number one vertebrate pest and the main wildlife vector for Bovine Tuberculosis (Tb), which they transmit to livestock (Caley et al. 1999). Current methods of controlling possums in the wild usually involve the use of poison bait, spread over large areas. While this method is effective, it is often costly, and needs continual maintenance to give long-lasting results. There are increasing concerns about possible effects on non-target populations and public health, as well as ethical considerations. For these reasons, research is currently aimed at developing fertility control using contraceptive vaccines for possums to provide a long-term, cost-effective solution. Research into fertility control is mainly directed at developing an immunocontraceptive vaccine to block fertilization or lactation (Cowan 1996) or manipulating hormonal regulation and gonadal development (Eckery et al. 1998). Delivery of fertility or lactation-inhibiting vaccines to wild populations will involve the use of baits or ultimately, dissemination using a recombinant organism (Jolly 1993; Cowan and Tyndale-Biscoe 1997).

Fertility control aims to reduce recruitment of animals into the population. However, the technique will generally be less effective than culling for reducing populations, and may only slow or stabilize population growth (Bomford 1990; Garrott 1995). For example, population responses such as compensatory increases in juvenile production and survival may render fertility control ineffective (Sinclair 1997). There is a pressing need, therefore, to determine the effectiveness of fertility control in reducing wild possum populations before it can be considered a viable control technique.

Immunocontraceptive methods of fertility control that block fertilization may leave the individual hormonally intact and should not significantly interfere with the established social structure of possums. However, in captivity, oestrous cycles continue in tubally ligated possums until the end of the breeding season, and males penned with these females continue to have elevated testosterone levels during that time (Rekha 1997). Increased mating interactions among animals and other changes in behavior could result in an increased prevalence of diseases or vectors, especially if they are sexually transmitted. Any investigation into the effect of fertility control on wild populations, therefore, should also consider the potential effects on possum behavior. To investigate the effects of fertility control on both the population dynamics and behavior of wild populations, we are conducting a field experiment to determine the population responses of wild possums to various levels of fertility control (sterilized females). Additional data are also being collected to determine if induced sterility changes leads to changes in possum behavior and hence, disease prevalence.

METHODS
Population Dynamics

The effect of fertility control on the population dynamics of possums is being investigated on six 14 ha study sites established in late 1995 in native podocarp/hardwood forest. Sites were situated in two localities in the lower North Island of New Zealand: three in the Orongorongo Valley, east of Wellington, and three in the Turitea catchment, east of Palmerston North. At each site, 150 cage traps were placed on a marked grid at 30 m spacing. Each population is trapped at least three times a year in sessions consisting of four or five consecutive nights of trapping. Monitoring started on all sites during October/November 1995. Newly caught possums were anaesthetized with ether, given a unique tattoo and ear tag, and measured and weighed before the animal was released at point of capture. Recaptured animals were identified and weighed before being released. An estimate of breeding success was made in late September by examining the pouch for young and all pouch young were given a unique tag. Recaptures of tagged pouch young as independent animals were used to estimate the rate of *in situ* recruitment. Animals not first caught with their mother were assigned a minimum age using a combination of tooth wear and a logistic regression algorithm discriminating on body-size measurements. Independent possums were classified as either "yearlings" (8 to 20 months old) or "adults" (>20 months old) (Efford 1998).

Sterilization Treatments

Fertility control was imposed by surgically sterilizing females by ligating the oviducts. This method ensured that ovarian function remained intact, and mimicked the action of candidate fertility control vaccines. Three levels of sterilization treatment were applied with 0%, 50%, or 80% of adult females at a particular site sterilized. One complete replicate set of treatments was applied to sites in the Orongorongo Valley, with the other applied to sites in the Turitea catchment. As the effect of surgery on survival of animals was unknown, sham operations (no sterilization) were undertaken to balance the level of surgical manipulation across treatments. Treatments were applied during January to April 1996, with adjustments to maintain sterility levels made annually on recruits.

Disease Transmission

The effect of fertility control on disease transmission was investigated by estimating the transmission rate of *Leptospira interrogans* serovar *balcanica* between possums in both control and 80% sterility sites. *L. balcanica* is a commonly occurring, benign disease in possums that is thought to be spread by direct contact (Day et al. 1997). Five ml of blood was collected from 60 to 100 animals in each of the four sites in June of each year from 1996 to 1999. The serological micro-agglutination test (MAT) was used to detect the presence of leptospiral antigens.

Statistical Analyses

Population abundance at each site was estimated for each capture session using the jackknife closed population estimate (Burnham and Overton 1978). The effect of sterility treatments on the population growth rate (ë) and survival rates were compared by fitting Cormack-Jolly-Seber (CJS) models in a generalized linear model framework using program MARK (White and Burnham 1999). Treatment effects were assessed by comparing model fit using the Akaike Information Criterion (AIC). Recruitment rates for each sterility treatment were separated into the relative contributions from *in situ* births and immigration using the age structured Jolly/Seber model of Pollock (1981) and Efford (1998). The time to seroconversion for *L. balcanica* was compared between control and treatment sites using the Mantel-Haenszel log-rank test (Mantel and Haenszel 1959). Right censoring was used on incomplete observation times. All statistical tests were performed in S-plus (Statistical Sciences 1995).

RESULTS
Population Dynamics

Unusually low breeding success was recorded during 1996, which resulted in similar birth rates between control and sterility treatment sites during that year. However, during subsequent years, birth rates were successfully suppressed by sterility treatments, with the number of young produced per adult female in the population equivalent to the rate of sterility (Figure 1).
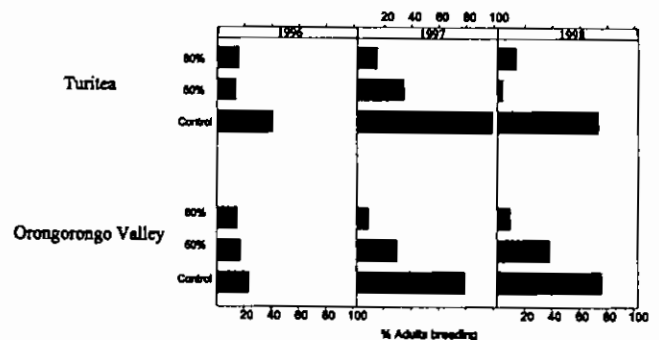

Figure 1. The percentage of adult females with pouch young in September/October for each sterility treatment in the Orongorongo Valley and Turitea.

Population abundance in October of each year fluctuated according to the net effects of annual recruitment and apparent mortality. Mortality was pronounced during 1996, which resulted in the decline of populations at most sites (Figure 2). However, sterility treatments did not inhibit partial recoveries in these populations in the following year. Analysis of the relative contributions of *in situ* recruitment and immigration revealed that immigration made the major contribution to relative population growth during 1996/97 (Figure 3). At sites in the Orongorongo Valley, immigration was also the dominant component of recruitment during 1997/98, and compensated almost perfectly for the reduction in local recruitment due to sterility. However, immigration was less important at Turitea during 1997/98 with both low *in situ* recruitment and immigration occurring on 50% and 80% sterility sites. Although mortality rates for 1998/99 are not yet estimable, preliminary analysis suggests that the pattern of recruitment is similar to that
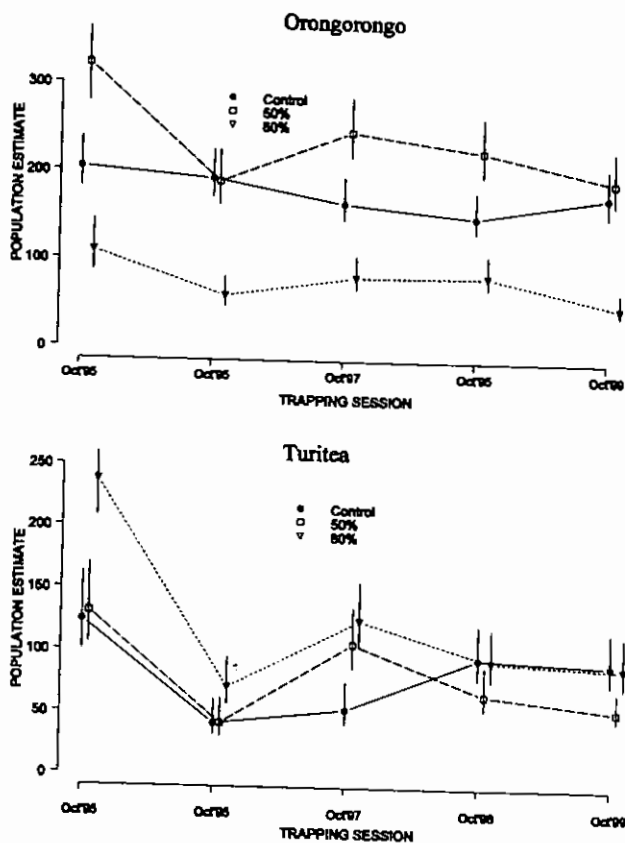
Figure 2. Jackknife estimates of population abundance (±95% c.i.) in October of each year for control and sterility treatment sites in the Orongorongo Valley and Turitea.

Figure 3. Relative contributions of local (*in situ*) recruitment and immigration of female yearlings to the relative annual populationg rowth rate (i.e., the proportional change between N_t and N_{t+1}. Local recruitment and immigration are estimated from an age-structured Jolly/Seber model.

observed in 1997/98. Consequently, the underlying annual trends in the population growth rate over the study period revealed different trends for each sterility treatment between geographic locality. Sites in the Orongorongo Valley had similar population growth rates, with no upward or downward trend over the study period. This compares with sites at Turitea, where 50% and 80% sterility treatments were declining, on average, compared with the control site (Figure 4).
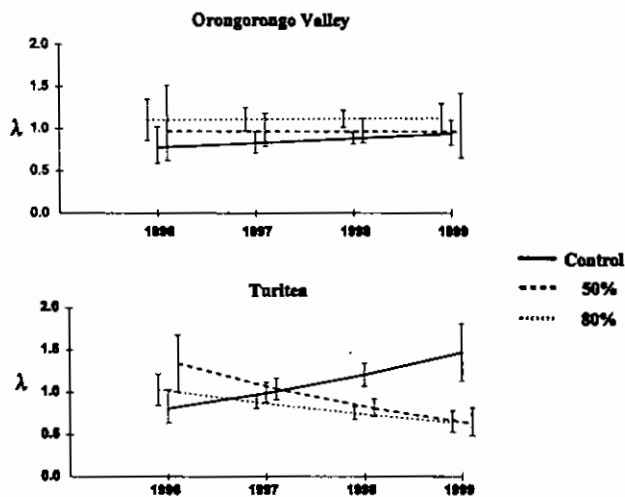

Figure 4. The trend population growth rate (λ) for each sterility treatment site in the Orongorongo Valley and Turitea. Trend lines were estimated in program MARK using the Pradel parameterization of the Cormack-Jolly-Seber model.
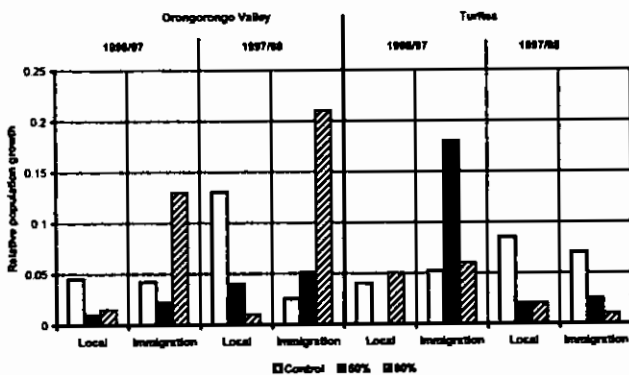
Comparison of intact and sterile female survival from each locality revealed survival of sterile females was significantly higher than that of intact females for possums in the Orongorongo Valley, as determined by the difference in AIC values for models fitted with and without treatment effects (Figure 5). Although sterile females also had higher survival rates than intact females for possums in Turitea, the difference was not significant (Figure 5).

Disease Transmission
Analysis of the effects of sterility on the seroconversion rate of *L. balcanica* revealed that the seroconversion rate was higher on the 80% sterility sites than on control sites, which was marginally significant (p=0.06) (Figure 6). Calculation of the instantaneous incidence (ë) estimated that from every 100 possums at-risk, 7.2 would seroconvert per four month period in the 80% sterility sites compared with 5.5 per four month period in the control sites.
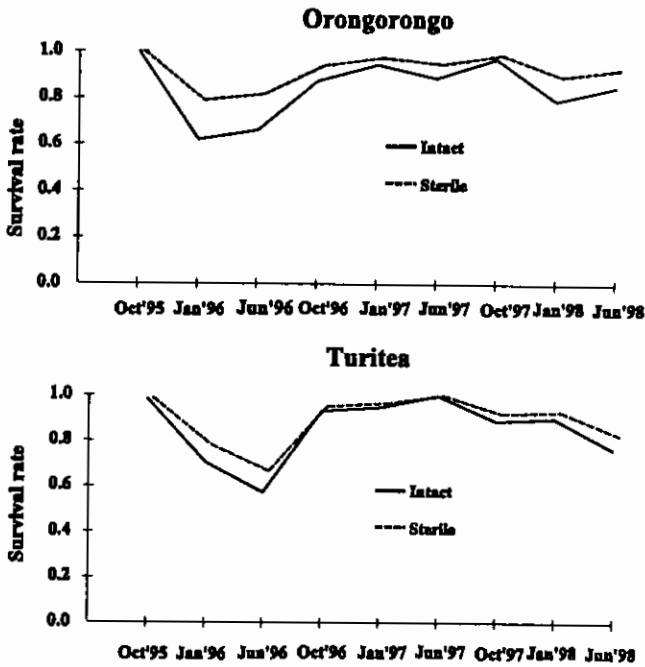
Orongorongo

Turitea

Figure 5. Per capita survival probabilities estimated from an additive model fitted in program MARK (phi(g+t)p(g*t)) for sterile and intact female possums in the Orongorongo Valley and Turitea.
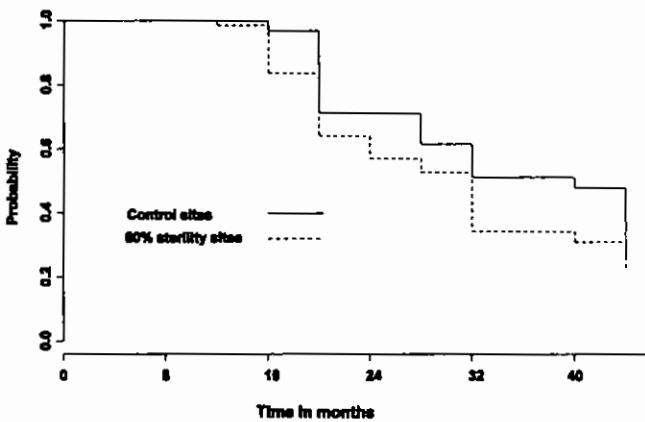

Figure 6. Kaplan-Meier survival curves representing the probability of remaining seronegative for *L. balcanica* for possums on control and 80% sterility treatment sites.

DISCUSSION
Population Dynamics

The marked differences in the patterns of recruitment at each site were major influences on population trajectories. Low juvenile (yearling) recruitment of locally born young occurred during 1997 as a result of the general poor breeding success in 1996. Immigration of yearlings during this year made the predominant contribution to recruitment. However, during 1997/98 a different pattern of recruitment occurred on sites in each locality. While sterility treatments successfully suppressed the recruitment of locally born young in the Orongorongo Valley, immigration levels were higher on sterility treatment sites, which compensated for the reduction in local recruitment. However, immigration did not compensate for the suppression of yearling recruitment due to sterility treatments at Turitea. The net effect of recruitment patterns in each locality has resulted in declining populations on 50% and 80% sterility sites in Turitea, but not on sterility sites in the Orongorongo Valley. One explanation for the disparity in immigration between localities is that widespread possum control operations have occurred in areas surrounding the study sites at Turitea, which may have reduced numbers of dispersing possums.

Overall, the balance of evidence suggests that high levels of sterility (80% of females sterile) are required to suppress the local recruitment of young sufficiently to produce negative population growth as has occurred for the Turitea 80% site. However, immigration has the potential to compensate for reduced local recruitment and, consequently, to arrest population decline, at least in small areas. A study of dispersal patterns in a local population of brushtail possums by Efford (1998) indicated that net immigration by yearlings and young adults was the primary mechanism maintaining stability in the population, compensating for disappearance of locally born young. If density is low or declining, the relative compensatory effects of immigration increase due to the increasing per capita rate of immigration. This was the case for the Orongorongo 80% site, which saw no upward or downward trend in abundance despite suppression of local yearling recruitment.

Sterile females had higher average survival rates than reproductively active females, indicating a survival cost of reproduction in brushtail possums. The enhanced survival of sterile females observed would also contribute to a slower rate of population decline. However, the reduced turnover of the sterile fraction of the population should serve to maintain the level of sterility in the population. With the exception of the enhanced survival of sterile females, no processes have been observed in the local population that would be likely to compensate for the reduced fecundity of the population. One caveat to this conclusion is that, with the exception of the Turitea 80% site, immigration has more or less maintained population densities, thus preventing any density dependent mechanisms from becoming apparent.

Disease Transmission

Fertility control in wild populations can be achieved either by immunocontraceptive methods or by inhibiting sex-steroid function. To be successful, any method must ensure that reproductive and/or social behavior remain largely unchanged, or that any changes do not have undesirable effects. For example, compromising sex-steroid secretion may disrupt social hierarchies and could lead to improved survival of subordinate individuals through access to mates and food resources that would otherwise be denied them. This could reduce the effectiveness of the control method (Jolly et al. 1996).

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A potential behavioral effect of animals sterilized by immunocontraceptive methods is multiple oestrus cycles that may result in prolonged breeding behavior (McShea et al. 1997; Heilmann et al. 1998). This could result in an increase in the rate of mating contacts, leading to a higher transmission rate of potential vectors or diseases, as suggested by Barlow (1994). Transmission of *L. balcanica* was elevated in the 80% sterility sites. Since *L. balcanica* is thought to be spread by direct contact (Day et al. 1997), we take this as evidence that contact rates between individuals were higher at sites with sterile females. Thus, the hypothesis that immunocontraceptive methods of fertility lead to increased mating interactions driven by an increased frequency of oestrus, seems to be supported. Hence, immunocontraception could lead, indirectly, to higher transmission rates of potential biocontrol vectors or diseases. However, this may not hold for vectors or diseases that are not predominantly transmitted by direct contact, as has been found for myxomatosis in populations of the European rabbit subject to imposed sterility (Kerr et al. 1998).

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