Fertility control is much less effective than lethal baiting for controlling foxes

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ABSTRACT

In some environments, red foxes (*Vulpes vulpes*) are major pests of agricultural systems. The main methods of controlling foxes rely on poison baiting, den fumigation and den destruction. There are concerns that ongoing use of poisons and fumigants may become unacceptable on the grounds of humaneness. Additional control options that are humane and effective need to be investigated. In this study we developed models to examine the efficacy of using contraceptive agents as an alternative method of control for fox populations. The models simulated the dynamics of structured (by age and sex) fox populations. The models were then used to identify the level of infertility required to achieve target levels of control, the need for ongoing maintenance, and the benefits of an integrated pest management strategy that included lethal control. The models indicated that an annual control campaign using baits that sterilised female foxes would reduce mean red fox population density by about 30%. An annual campaign of poisoning (using the same effort as the sterilisation campaign) would reduce mean fox density by about 80%. Payoff, in terms of reduced fox density, indicated that for any given bait density the payoff for poison baits was generally three to four times greater than for contraceptive baits. Additionally, integrated control—culling and fertility control—offered no advantage over culling only. For foxes, contraception delivered via bait is unlikely to provide a useful alternative to poisoning.

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1. Introduction

Red foxes (*Vulpes vulpes*) can have a large impact on agricultural production and the environment (Saunders et al., 1995). They are a highly adaptable invasive species as demonstrated by their worldwide distribution (Forsyth et al., 2004). In Australia, foxes are a pest in agricultural production systems and areas of biodiversity and conservation importance (Saunders et al., 1995; McLeod, 2004). A number of experimental studies have concluded that predation by foxes is a major source of mortality that could compromise the viability of some native fauna populations (Banks et al., 2000, 1998; Kinnear et al., 2002, 1998, 1988; Priddel and Wheeler, 1996; Short et al., 2002). There is less quantitative evidence that fox predation causes significant production losses in agricultural systems (Rowley, 1970), although there is anecdotal and circumstantial support (Lugton, 1993; Moberly et al., 2003).

In Australia, the principal method for managing predator impacts is poison baiting. However, the use of poisons in pest control programs is continually under review. Viable alternative control options, which are acceptable to industry and the broader community, need to be investigated for vertebrate pests. Contraception is one method that has attracted interest as a humane and effective control method (Barfield et al., 2006; Barlow, 2000; Delves et al., 2002; Tyndale-Biscoe, 1994). Ideally the contraceptive response would be long lasting and would not require repetitive treatments, with initial treatments remaining effective for several years (Miller et al., 1995; Tuyttens and Macdonald, 1998).

In this study we developed models to compare the efficacy of contraception with poisoning for managing foxes. The models simulated the dynamics of fox populations, based on Australian demographic studies, under alternative management scenarios that included poisoning and contraception. However, the general principles, results and conclusions are applicable to fox populations elsewhere in the world. Examining the efficacy of contraception for managing foxes will assist in the development of management options for these important pests. The models helped identify the frequency of poison or contraceptive baiting needed for ongoing maintenance, the efficacy of bait delivered contraceptives for controlling foxes, and the benefits of an integrated pest management strategy that combines contraception with lethal control.

The feasibility of using contraception for broad scale management of vertebrate pests is not presently understood (Hardy et al., 2006; Strive et al., 2008). The outcomes of this study will help to identify the feasibility of using contraception to reduce the impact of one of Australia's worst vertebrate pests. For foxes, the optimal

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combinations of contraceptive and lethal control have not been previously defined. Models will help identify the best combinations of these control measures to maximise benefits and effectiveness whilst minimising costs.

2. Model overview and description

We used an 'escalator boxcar train' algorithm (De Roos, 1997; Goudriaan and van Roermund, 1989) to simulate the dynamics of an age and sex structured fox population subjected to a range of management methods and scenarios (Fig. 1). The model does not include spatial structure. The population was divided into seven age cohorts. Foxes are birth pulse breeders (Lloyd, 1980), and in

the model we assumed that all births take place in one month (September), which corresponds with the median month of birth for foxes in south-eastern Australia (McIlroy et al., 2001). The maximum age of foxes in the model was 6 years and 11 months, and all foxes died just prior to their seventh birthday since the probability of surviving beyond this age in the wild is very low. The time-step of the model was one month. The contraceptive agent was delivered by bait. During preliminary stages of the project we examined if the longevity of sterility was important. We compared the mean density of a population of foxes that consumed bait that caused sterility to last twelve months with bait that caused permanent sterility and found that there was a negligible difference between the mean densities. Therefore, induced infertility was assumed to
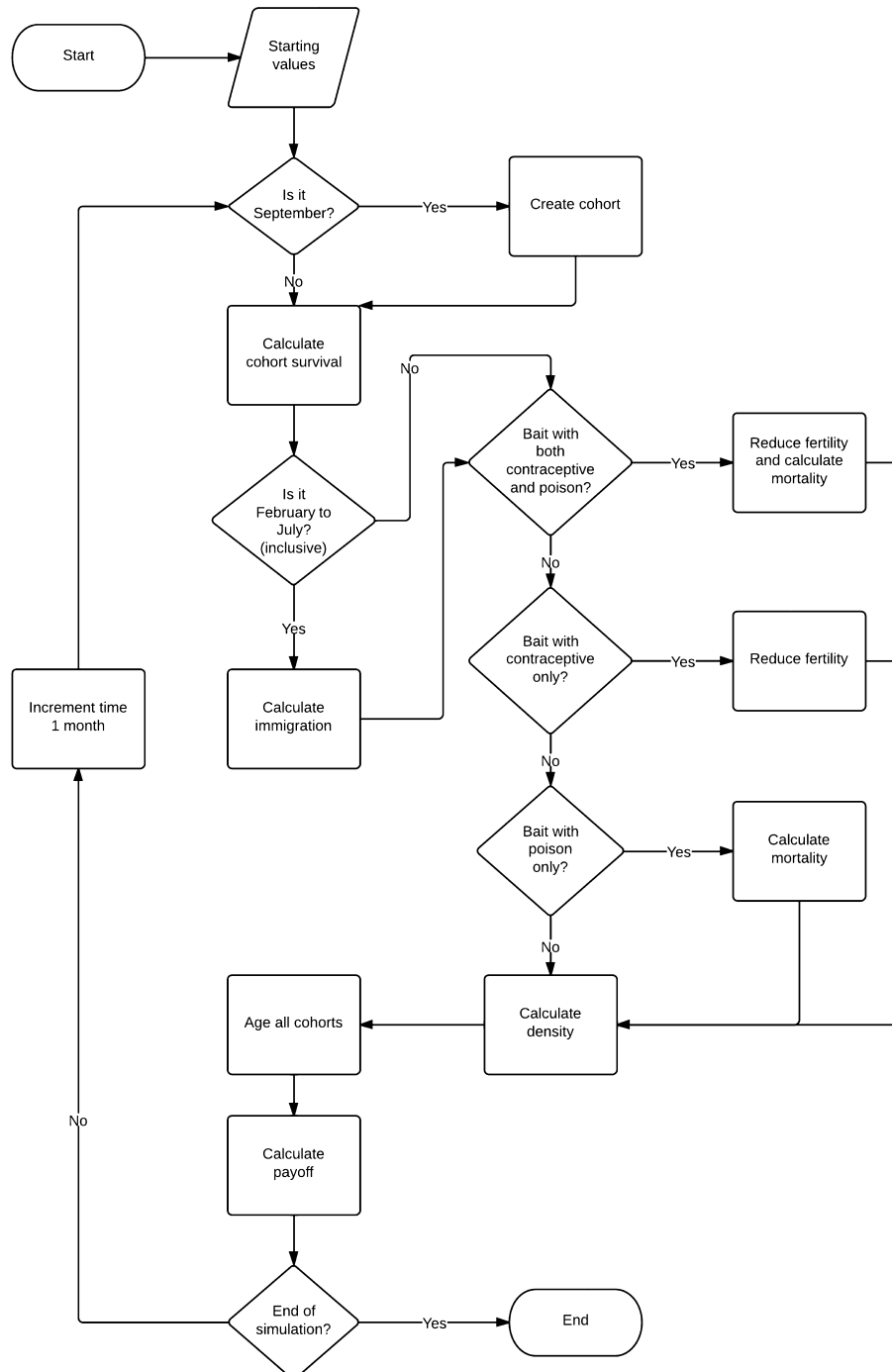

Fig. 1. Flowchart of model execution.

last for twelve months, after which a female would revert to fertile status which is the more likely situation of the two (McLeod et al., 2007). Permanent sterility would reduce the ongoing costs of maintenance baiting but in terms of effectiveness at reducing fox density, and thereby reducing their impact, there is little difference between sterility that lasts for twelve months and permanent sterility. It is also important to note that, at present, there are no contraceptives that can be delivered in baits to foxes that can cause permanent sterility.

2.1. The model of fox population dynamics

Mathematically, the dynamics of the fox population are

$$\frac{\partial n_f(a, t)}{\partial t} + \frac{\partial n_f(a, t)}{\partial a} = -[\mu(a, N) + {}_P\alpha(t)] n_f(a, t)$$
$$+ \nu_s n_s(a, t) + \tau_f(a^\zeta, t, N)$$

$$\frac{\partial n_s(a, t)}{\partial t} + \frac{\partial n_s(a, t)}{\partial a} = -[\mu(a, N) + \nu_s(t)]n_s(a, t)$$

$$\frac{\partial n_m(a, t)}{\partial t} + \frac{\partial n_m(a, t)}{\partial a} = -[\mu(a, N) + {}_P\alpha(t)]n_m(a, t) + \tau_m(a^\zeta, t, N)$$

$$n_f(0, t) = \int_0^\infty m(a, N)n_f(a, t)da$$

$$n_m(0, t) = s \cdot n_f(0, t)$$

$$n_f(a, 0) = n_{f,0}(a)$$

$$n_s(a, 0) = 0$$

$$n_m(a, 0) = n_{m,0}(a)$$

(1)

where $\mu(a, N)$ was the natural mortality rate, ${}_P\alpha(t)$ was mortality rate due to poisoning at time t, $\nu_s(t)$ was the recovery rate for sterilised females that had eaten a bait containing the contraceptive agent, $n_f(a, t)$, $n_s(a, t)$ and $n_m(a, t)$ were the densities of fertile females, sterile females and males at age a and time t respectively, $\tau_f(a^\zeta, t, N)$ and $\tau_m(a^\zeta, t, N)$ were the immigration rates of females and males respectively of foxes aged a^ζ, $n_f(0, t)$ and $n_m(0, t)$ were the densities of female and male births respectively, $m(a, N)$ was the maternity function (female births per female, and s was the sex ratio of newborns (males/females). The initial densities of females and males were given by the vectors $n_f(a, 0)$ and $n_m(a, 0)$.

2.1.1. Reproduction
The age specific number of births was

$$B_{s,x} = F_x M_x E_x r_s$$

(2)

where $B_{s,x}$ was the number of births of sex s from females aged x, F_x was the density of female foxes aged x years, M_x was age specific frequency of pregnancy, E_x was age specific embryonic litter size and, r_s was the proportion of embryos that are of sex s. This derivation of age specific number of births differs from Pech et al. (1997), since we have not included in utero mortality, and we assumed that all embryos were born. In our model the mortality of this cohort was accounted for during the first month of life.

The age specific number of embryos per female and frequency of pregnancy were derived from the data of Saunders et al. (2002a,b). A linear regression was fitted using least-squares methods to the mean number of embryos per female for ages 1 to 5. The resulting regression, $E_x = 2.97 + 0.57x$ ($r^2 = 0.95$, $F = 54.45$, $P_{0.05} = 0.005$), explained much of the variance in E_x for these age classes. Age class 6 was not included in the regression because it appeared to be an outlier and did not fit the linear function fitted to ages 1–5. Age class 6 took a value of 3.95. A least-squares linear regression was also fitted to the frequency of pregnancy as a function of age.
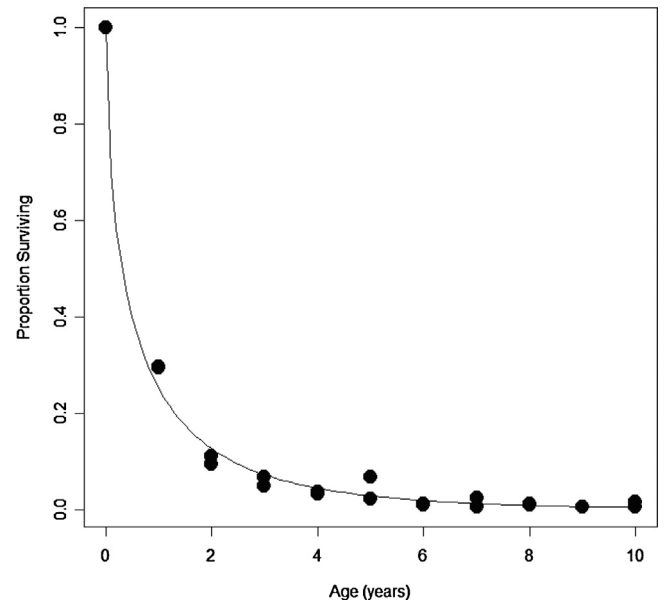

Fig. 2. Age specific survival (l_x) of foxes from the Central Tablelands region of NSW (data from Saunders et al., 2002b). Points are observed data and the line is the fitted survival function.

The resulting regression, $M_x = 0.758 + 0.0391x$ ($r^2 = 0.89$, $F = 32.6$, $P_{0.05} = 0.005$), provided a good fit to the data. Sex ratio was assumed to be at parity.

2.1.2. Cohort survival
A Weibull function was used to describe age specific survival using the data of Saunders et al. (2002a,b). The function was fitted using maximum likelihood and assuming that observation errors followed a multinomial distribution (Edwards, 1992). The function provided a good fit to the data (Fig. 2). Although Saunders et al. (2002a,b) found that a small proportion (3.2%) of their sampled foxes were older than 7 years of age, in the model all foxes die just prior to their seventh birthday. There were no differences in age specific survival between the sexes (Saunders et al., 2002b). Age specific survival was

$$l_x = e^{-(\lambda x)^\gamma}$$

(3)

where l_x was the proportion of individuals surviving from birth to age x, λ is the shape parameter and γ is the scale parameter of the Weibull distribution. The instantaneous mortality rate was calculated from the survivorship function.

2.1.3. Density dependence
Two forms of density-dependence were included in the model, which affected respectively, the number of embryos produced per female and age-specific survival. When population density was approaching carrying capacity, fecundity and survival were reduced. The reduction was determined by a scaling-factor (y in Eq. (4)) that was in the range 0–1. If the population was close to carrying capacity y approached 0. As the population density moved further from carrying capacity the closer the scaling-factor approached 1. The scaling-factor was

$$y = 1 - \frac{e^{(\omega + \beta x)}}{[1 + e^{(\omega + \beta x)}]}$$

(4)

where y was either fecundity or survival, x was total population density, and ω and β are shape parameters of the logistic function and have no meaningful biological interpretation.

A logistic function was chosen because it has desirable features such as having little impact on fecundity or survival when density is

low but then having a stronger influence as density increases. Also, being a simple 2 parameter function, the values of its parameters could easily be modified to suit the dynamics of the studied population, in this case a population living in the temperate climate of eastern Australia.

The values of the parameters ω and β, −5.0 and 1.5 respectively, were chosen by adjusting their values so that the dynamics of the modelled population were similar to that of foxes in temperate, eastern Australia—that is, a stable population size with a long term annual rate of increase close to zero and mean density close to 3–5 foxes km^{-2} (Coman et al., 1991; Saunders et al., 2002b, 1995; Thompson and Fleming, 1994). For the modelled population, not subject to management, the mean annual rate of increase was 0.0, and the mean density was 3.3 foxes km^{-2}, with a range of 2.7–5.9.

2.2. Bait-intake sub-model

Contraceptive baits could be eaten by either fertile females (the target group) or by males and sterile females (competitors for the baits). Although baits that are laid for foxes may be eaten by other species (Saunders et al., 1995), for simplicity this source of bait loss was not included in the model. Bait intake by a group was proportional to its relative abundance and was a function of the number of baits per square kilometre, the number of foxes per square kilometre (targets and competitors), the efficiency of predation (efficiency that foxes find baits), and the time elapsed since the baits were laid. The bait-intake function was proposed by Selhorst et al. (2001) for modelling the vaccination of foxes against rabies infection. Bait consumption rate was described by

$$\frac{dB}{dt} = -Bg\left(1 - \frac{t}{t_c}\right)N \tag{5}$$

where B was bait density (baits km^{-2}), N was consumer density (targets and competitors), g was the efficiency that foxes find baits, t was time since the baits were laid and t_c was the 'perishability' of the baits. Perishability is a determinant of bait consumption, such that after t_c the baits are no longer eaten.

For combinations of contraceptive and lethal baiting, the rate of change in the number of susceptible male ($S_m(a, t)$), poisoned male ($Y_m(a, t)$), susceptible and fertile female ($S_f(a, t)$), poisoned female ($Y_{f,p}(a, t)$) and sterile female ($Y_{f,s}(a, t)$) foxes was based on Hone's (1992a,b) modelled framework for poisoning a pest population. Hone (1992a, 1994) argued that poisoning was analogous to epidemiological infection of a host population from the environment. While Hone concentrated on modelling poison baits, his model can be extended to include contraceptive baits. The derived model (Eq. (6)) was

$$\frac{\partial S_m(a, t)}{\partial t} + \frac{\partial S_m(a, t)}{\partial a} = -c_P p_P w_P S_m(a, t) + \nu_P Y_m(a, t)$$

$$\frac{\partial Y_m(a, t)}{\partial t} + \frac{\partial Y_m(a, t)}{\partial a} = c_P p_P w_P S_m(a, t) - (\alpha + \nu_P) Y_m(a, t)$$

$$\frac{\partial S_f(a, t)}{\partial t} + \frac{\partial S_f(a, t)}{\partial a} = -(c_P p_P w_P + c_S p_S w_S) S_f(a, t)$$
$$+ \nu_S Y_{f,S}(a, t) + \nu_P Y_{f,P}(a, t) \tag{6}$$

$$\frac{\partial Y_{f,P}(a, t)}{\partial t} + \frac{\partial Y_{f,P}(a, t)}{\partial a} = c_P p_P w_P (S_f(a, t) + Y_{f,S}(a, t)) - (\nu_P + \alpha) Y_{f,P}(a, t)$$

$$\frac{\partial Y_{f,S}(a, t)}{\partial t} + \frac{\partial Y_{f,S}(a, t)}{\partial a} = c_S p_S w_S S_f(a, t) - (c_P p_P w_P + \nu_S) Y_{f,S}(a, t)$$

where c_P was the rate at which poison baits are eaten ($(c_i = (B_t - B_{t+1})/t)$), p_P was the probability that an eaten bait was poisonous. (This will be 1 if only one type of bait was being used but will
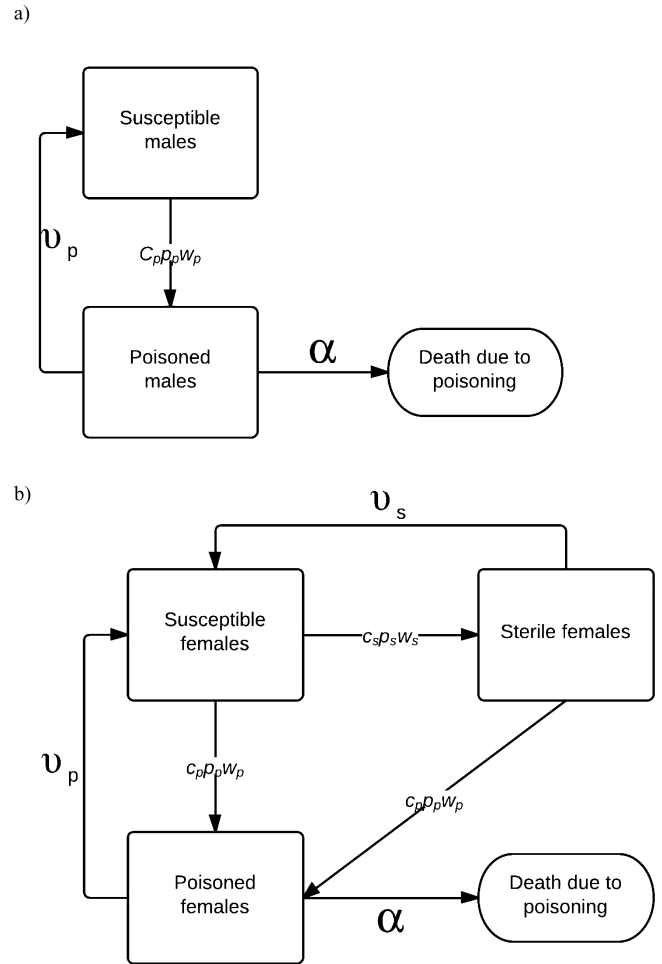
Fig. 3. (a) Flowchart of male foxes when they consume poison bait (consuming bait containing a contraceptive agent has no affect on male foxes). (b) Flowchart of female foxes when they consume poison bait or bait that contains a contraceptive agent.

be a proportion corresponding to a bait type's relative abundance if both lethal and contraceptive baits are used.) The parameter w_P was the proportion of foxes that were tolerant to poisoning (i.e. consumed a bait but did not die). For the purposes of this study tolerance to poisoning was assumed to be zero. The subscript S refers to baits that contain a contraceptive agent. The parameter w_S was the proportion of female foxes that are non-responders (sensu Cooper and Herbert, 2001) to the contraceptive agent. The transition terms $c_P p_P w_P$ and $s_S p_S w_S$ were based on Begon's et al. (2002) derivation of the rate at which susceptible individuals become infected in epidemiological models. The parameters ν_P and ν_S are the rates at which foxes that consume poisoned baits recover if they are tolerant to poisoning and sterile female foxes recover fertility, respectively. The parameter α was the death rate due to consumption of poison bait.

If sterility is permanent, after a fertile female eats bait containing a contraceptive agent, she will move permanently to the sterile female class and becomes a bait competitor. However, if sterility is not permanent ($\nu_S > 0$) then a sterile female eating bait containing the contraceptive agent will remain in the sterile class until the recovery period ($1/\nu_S$) has elapsed (Fig. 3). In the model we assumed that the poison in poison baits and the anti-fertility agent in contraceptive baits remained active until the bait itself became unpalatable to foxes (after about 40 days) (Selhorst et al., 2001).

2.2.1. Immigration

In Australia, immigration by foxes occurs from the end of summer (February) to the commencement of reproductive activity (July) (Saunders et al., 1995). In the model, immigrants were assumed to be sub-adults that had been born the previous year, since it is this age class that most commonly disperses in the months February to July (Saunders et al., 1995; Smith and Harris, 1991). The rate of immigration was not constant but peaked in April. The modelled immigration rates are based on the results of Smith and Harris (1991). We averaged the probability of male and female sub-adult foxes dispersing, using the data given in Table 4 of Smith and Harris (1991). We then normalised the result to calculate the proportion of immigrants per month from the total immigration rate. Unfortunately there are no comparable data on immigration rates of foxes in Australia. We assumed that the pattern of immigration from foxes in England was similar in Australia, once seasonal differences were taken into account (i.e. in Australia sub-adult dispersal starts in February (Saunders et al., 1995), in England sub-adult dispersal starts in October (Smith and Harris, 1991)).

Immigration rate was derived from the product of: (i) the complement of the ratio of population density and carrying capacity; (ii) the percent per month immigrating; and (iii) the maximum immigration rate for each sex (density year^{-1}). If population density (N_{Feb}) in February was close to carrying capacity (K) then the immigration rate approached zero. However, if $N_{Feb} \ll K$ then immigration rate approached its maximum value.

$$I_S = \frac{p_{month}}{100} \left(1 - \frac{N_{Feb}}{K} \right) I_S^{max} \tag{7}$$

where I_S was immigration per month for each sex, p_{month} was the percent per month of the maximum rate of immigration per year, and I_S^{max} was the maximum rate of immigration for each sex per year.

The parameter values and descriptions of the parameters of the models are listed in Table 1.

2.2.2. Payoff

Hood et al. (2000) coined the term 'payoff' to refer to the degree of host suppression by a sterilising virus. Their derivation was based on the earlier work of Beddington et al. (1978) who were interested in measuring the impact that a parasitoid has on its host. Both of these studies were interested in equilibrium population sizes in the presence and absence of a putative limiting factor, a sterilising virus and parasitoid respectively. We have modified the payoff function described by Hood et al. (2000) so that it is applicable to non-equilibrium populations (Eq. (8)). The payoff determines the degree of suppression of host population density by the introduction of a contraceptive agent. Payoff was

$$O_N = \frac{1}{T} \sum_{t=1}^{T} \left(1 - \frac{N_t^m}{N_t^{nm}} \right) \tag{8}$$

where O_N was the payoff in terms of reduced mean population size, N_t^{nm} was the population size at time t when the population was unmanaged, N_t^m was the population size at time t when the population was managed (which includes sterilisation and poisoning) and T was the total time over which the projection was made.

2.3. Model evaluation and validation

We validated the model by comparing the model's outputs with empirical data on fox populations typical of temperate, eastern Australia. We found that the model's predicted mean density was similar to observed densities recorded in empirical studies of wild fox populations (Coman et al., 1991; Saunders et al., 2002b, 1995; Thompson and Fleming, 1994). Furthermore, the simulated range in density (2.7–5.9 foxes km^{-2}) was also similar to the empirical data from these studies.

Furthermore, we examined the robustness of the model to a small (10%) increase or decrease in the value of each parameter listed in Table 1—while holding other parameters at their default values. We found that the model behaved in a predictable manner—for example, a reduction in E_x (the slope of the function of age specific number of embryonic females per female) resulted in a reduction in mean fecundity and average population size, which was expected. We conclude that the conclusions of the model are qualitatively not sensitive to small changes in the values of the modelled parameters.

3. Simulation results

The results of the models are presented in two stages. First, the effects of imposing fertility control, poisoning or both on population size are examined. Second, calculated pay-offs are used to determine the best combinations of fertility and lethal control.

3.1. Fertility control and poisoning

A projection of red fox population size in the absence of control (Fig. 4a) indicated that the modelled population showed a clear annual cycle. Female red foxes are monoestrous and exhibit a birth pulse in August–September in Australia. This, and the observation that fox populations tend to be stable in size with an observed rate of increase close to zero (Saunders et al., 2002a,b), lead to dynamics characterised by annual peaks in density (that coincide with births) with no trend in long-term mean density.

The same projected red fox population subjected to an annual campaign of sterilisation in July of each year (Fig. 4b) indicated that sterilisation will reduce the magnitude of the annual fluctuation in density and reduce mean population density. However, the reduction in density was modest, with density averaging 2.3 foxes km^{-2}, for a population subjected to an annual contraceptive bait campaign compared with 3.3 foxes km^{-2} in an untreated population. This equates to a reduction of about 30%.

Whereas annual baiting campaigns using baits that induce sterility caused a modest reduction in mean density, baiting with poison baits had a much greater affect on density (Fig. 4c). Under a similar baiting regime (annual baiting in September, baits distributed at 10 baits km^{-2}) to that modelled for sterilising baits resulted in a reduction in density to an average of 0.64 foxes km^{-2}; a reduction of about 80%.

A combined strategy of using contraceptive bait in July and poison bait in September resulted in a reduction in density to an average of 0.62 foxes km^{-2} (Fig. 4d). The difference in average density resulting from using poison bait alone and a combined strategy was very small and indicates that contraceptive baiting adds very little to effectiveness.

Poisoning had a greater effect on density than sterilisation (Fig. 5). Under a strategy of frequent poison baiting (defined as every 6 months or more frequently), sterilising baits contributed little to the efficacy of control, regardless of the frequency of using sterilising baits. Furthermore, high frequency poison baiting strategies maintained mean fox density at less than 0.5 foxes km^{-2}. The effectiveness of poison baiting for reducing fox density sharply declined as the frequency of poison baiting decreased (from once every year to once every three years). For poison baiting campaigns conducted every 3–10 years there was little difference in effectiveness, and were regarded as ineffective at reducing mean density (and the reason why infrequent baiting campaigns are not used to control foxes).

Table 1
Parameters and variables used in the model of fox population dynamics and the bait-intake sub-model. (1) Saunders et al. (2002b), (2) Saunders et al. (2002a), (3) McIlroy et al. (2001), (4) Selhorst et al. (2001) (5). Smith and Harris (1991).

Parameter	Description	Value	Source
Survival			
λ	Shape parameter of the Weibull distribution	1.73	Saunders et al. (2002a)
γ	Scale parameter of the Weibull distribution	0.584	Saunders et al. (2002a)
l_x	Proportion surviving from birth to age x	(Variable)	
Density dependence			
ω	Shape parameter of the logistic equation	−5.0 (for both survival and fecundity)	This study
β	Shape parameter of the logistic equation	1.5 (for both survival and fecundity)	This study
Reproduction			
s	Sex ratio	1:1	Saunders et al. (2002a) and McIlroy et al. (2001)
M_x (slope)	Slope of the function of age-specific frequency of pregnancy	0.0391	Saunders et al. (2002a) and McIlroy et al. (2001)
M_x (intercept)	Intercept of the function of age-specific frequency of pregnancy	0.758	Saunders et al. (2002a) and McIlroy et al. (2001)
E_x (slope: ≤5 years)	Slope of the function of age specific number of embryonic females per female	0.57	Saunders et al. (2002a) and McIlroy et al. (2001)
E_x (intercept: ≤5 years)	Intercept of the function of age specific number of embryonic females per female	2.97	Saunders et al. (2002a) and McIlroy et al. (2001)
E_x (≥5 years)	Age specific number of embryonic females per female	3.95	Saunders et al. (2002a) and McIlroy et al. (2001)
Bait intake			
g	Efficiency of predation	0.0232	Selhorst et al. (2001)
t_c	Perishability of baits (days)	40.4	Selhorst et al. (2001)
Immigration			
p_{month}	Proportion of total immigrants per month	February: 0.10 March: 0.13 April: 0.32 May: 0.21 June: 0.15 July: 0.09	Smith and Harris (1991)
N_{Feb}	Density of resident foxes at the end of February	(Variable)	
K	Carrying capacity (foxes km^{-2})	5.0	Saunders et al. (2002a,b)
I_s^{max}	Maximum rate of immigration per sex per year (foxes km^{-2})	0.5	This study
Poisoning and sterilisation			
c_P	Consumption rate of poison baits (baits eaten per day)	Variable depending on the number of baits, the number of foxes and time since baits were laid	
p_P	Proportion of baits distributed that are poisonous	1 if only poison baits used, otherwise a variable[a]	
w_P	Proportion of foxes that are vulnerable to poisoning	1	
c_S	Consumption rate of poison baits (baits eaten per day)	Variable depending on the number of baits, the number of foxes and time since baits were laid	
p_S	Proportion of baits distributed that are sterilising	1 if only immunocontraceptive baits used, otherwise a variable[b]	
w_S	Proportion of foxes vulnerable to the immunocontraceptive agent	Range: 0–1	This study
v_p	Recovery rate from poisoning	0.0	This study
v_s	Recovery rate of fertility	0.00548	This study
α	Death rate due to poisoning	2.0	This study
S_m	Density of susceptible males (foxes km^{-2})	(Variable)	
Y_m	Density of poisoned males (foxes km^{-2})	(Variable)	
S_f	Density of susceptible and fertile females (foxes km^{-2})	(Variable)	
$Y_{f,p}$	Density of poisoned females (foxes km^{-2})	(Variable)	
$Y_{f,s}$	Density of sterile females (foxes km^{-2})	(Variable)	

[a] Equal to the (density of poison baits)/(density of poison baits + density of immunocontraceptive baits).

[b] Equal to the (density of immunocontraceptive baits)/(density of poison baits + density of immunocontraceptive baits).

Baits containing a sterilising agent were far less effective at reducing mean fox density than poison baits, irrespective of the frequency of use of sterilising baits.

Fox control for conservation usually aims to maintain low fox density throughout the year (Kinnear et al., 1988, 2002). Baiting strategies that include frequent poison baiting campaigns will achieve low fox density, and our results suggested that there was a steady increase in effectiveness as frequency increased. If frequency of baiting were reduced to an annual basis (or less frequent) then the effectiveness of poison baiting to maintain low fox density was greatly reduced.

In an agricultural setting, fox baiting is more likely to be annual (Saunders et al., 1995), and timed to coincide with an event such as lambing. An annual poison baiting campaign will be less effective at reducing mean fox density than a strategy of frequent poison baiting; however, the aim of managing foxes for agricultural production is usually to reduce fox density just prior to lambing, so mean fox density is not a good measure of baiting success for agricultural production. Although there is evidence that at a regional level predation on lambs is correlated with fox density (Moberly et al., 2003), there is an absence of reliable fox density-damage relationship data in agricultural systems,
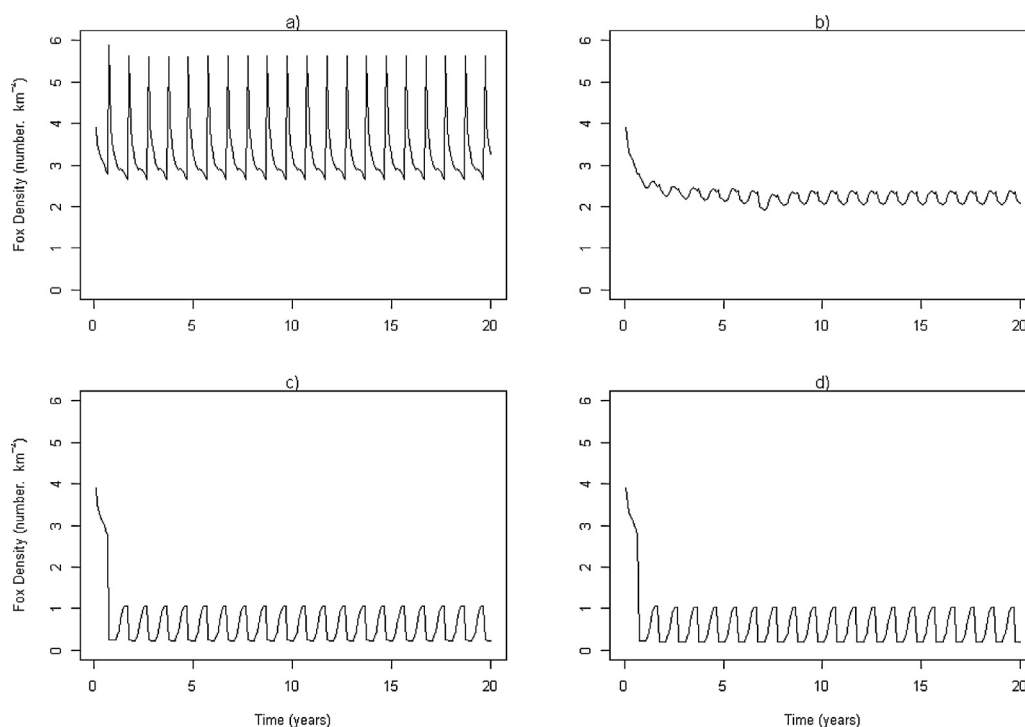
Fig. 4. (a) Projection of an uncontrolled fox population for 20 years. (b) Projection of a fox population subject to an annual campaign of contraceptive baiting in July of each year. Bait density was set at 10 baits km^{-2}. (c) Projection of a fox population subject to an annual campaign of poison baiting in September of each year. Bait density was set at 10 baits km^{-2}. (d) Projection of a fox population subject to an annual campaign of contraceptive baiting in July and poison baiting in September of each year. Bait density was set at 10 baits km^{-2} for each bait type.

and a more appropriate measure of baiting strategy success is not available.

3.2. Payoff

If baiting was done once per year, payoff as a function of bait density (Fig. 6) indicated that for any given bait density the pay-off for poison baits was generally three to four times greater than for contraceptive baits. Furthermore, poison baits distributed at

a low density of 2 baits km^{-2} were more effective at reducing density than contraceptive baits laid at much higher densities of up to 20 baits km^{-2}. If a once per year baiting campaign is planned, then the efficacy of the campaign will be much higher if poison baits are used rather than contraceptive baits.

The pattern of payoff as a function of bait density was similar for both poison and contraceptive baits. The payoff asymptotes so that increasing bait density above about 10 baits km^{-2} provided little benefit. There were also only minimal gains with bait densities between 5 and 10 baits km^{-2} (Fig. 6).
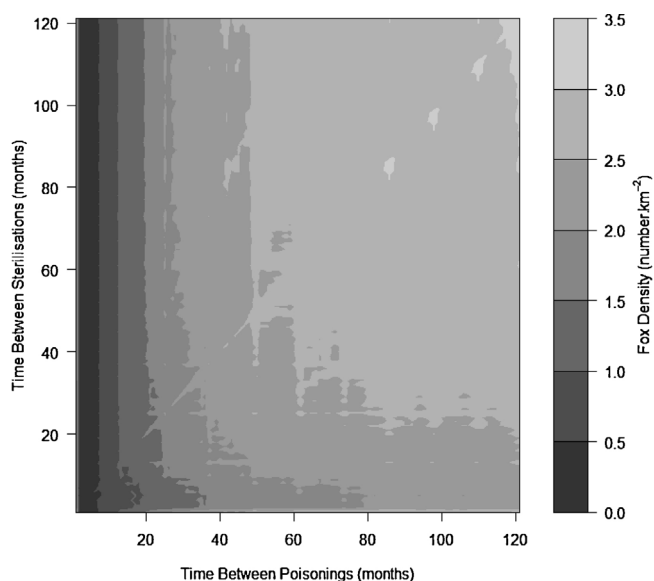

Fig. 5. The simulated mean density of foxes (number km^{-2}) resulting from combinations of sterilisation and poisoning for managing foxes across a range of baiting frequencies.
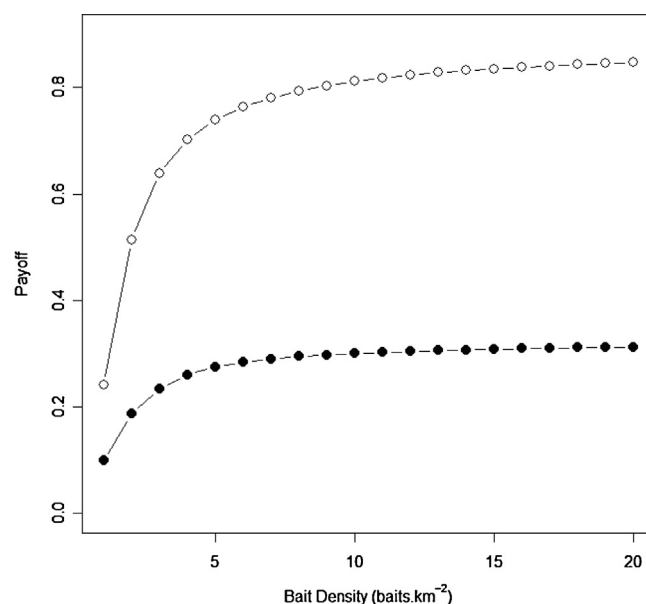

Fig. 6. The payoff resulting from a reduction in density from baiting with contraceptive baits (●) and with poison baits (○) for a range of bait densities.
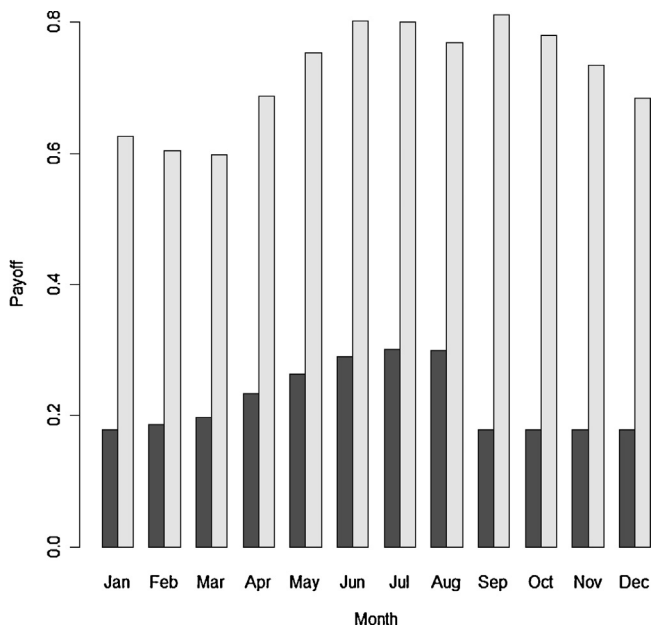
Fig. 7. The payoff resulting from either an annual contraceptive baiting (dark bars) or an annual poison baiting (light bars) campaign, comparing the month the campaign was undertaken.

For baiting strategies that only include a once-per-year baiting campaign, the efficacy of both poisoning or sterilisation were highest in the months spanning late autumn to early spring (May–September). However, there were large differences between the efficacies of the two methods: poisoning clearly provides a better payoff than sterilisation (Fig. 7). The payoff for poisoning ranged from a minimum in February to a maximum in May. For bait delivered sterilisation, the minimum payoff occurred in February and the maximum in July. These results suggest that poisoning or sterilisation would be best avoided in late February, but if baiting in this month is unavoidable the efficacy of either technique will not be greatly impaired.

4. Discussion

This study used simulation models to assess the efficacy of using contraception to control wild populations of foxes. The models simulated the dynamics of structured fox populations. The models helped define the level of infertility required to achieve a range of pest densities, the need for ongoing maintenance, the benefits of bait delivered contraceptives, and the benefits of an integrated pest management strategy that included both lethal control and contraception.

The primary aims of fox management programs are to protect native fauna and increase agricultural production. In agricultural systems, baiting for foxes often coincides with specific events, such as lambing. It is generally thought that lambs are mainly vulnerable to predation for a short time, usually the first few days after birth, so most fox management in agricultural areas has the objective of reducing the number of foxes just prior to lambing. The results of the models presented here indicate that contraceptive baits will not be suitable for reducing the density of foxes at these key events. Poison baiting would remain the most effective method for rapidly reducing fox density. In areas of conservation importance, fox control is not usually associated with a key event but more likely to be maintained at a high level (e.g. Kinnear et al., 1988; Saunders et al., 1995), with the objective of suppressing long-term fox density. For the protection of conservation values fox management is on-going and frequently intensive (NSW National Parks and Wildlife Service,

2001). The results of the present study indicate that fertility control is unlikely to satisfy the requirements of protecting native fauna. Population control using contraceptive baits is less effective than poison baiting, and control strategies using combinations of poison and contraceptive bait are no more effective at reducing long term fox density than poison baiting alone. Furthermore, sterilised foxes will still be consuming prey, be they native or domesticated species.

A re-evaluation of the importance of predation to agricultural production is warranted. The main focus of fox control for agricultural production has been the reduction of predation on lambs (Saunders et al., 1995). A number of studies have now documented low levels of fox predation on lambs; 2.9% (McFarlane, 1964), <2% (Mann, 1968), 2.7% (Dennis, 1969), 4.7% (Jordan and Le Feuvre, 1989) and 0.8–5.3% (Greentree et al., 2000). It appears that the importance of predation may have been over-estimated (Moberly et al., 2003). It may be more profitable to invest in addressing other causes of lamb mortality, such as improved husbandry practices or ewe nutrition, rather than invest in fox control. This issue will not be resolved before a quantitative benefit–cost analysis of fox control in agricultural systems is completed. The long-term costs and benefits of reducing fox control effort would also need to be factored into these analyses.

Hone (1992b, 2004) reported that the best strategic timing of fertility control was after the pest's population density had been first reduced by lethal control. Thus fertility control could be used in conjunction with other control methods to prevent rapid recovery of the controlled populations (Bomford, 1990). Naturally disseminated fertility control agents have also been suggested to target bait-shy and genetically resistant animals which survive poisoning campaigns (Garrott, 1995). However, given that the bait likely to be used for delivering a contraceptive agent will be similar to bait used for poisoning, it is unlikely that fertility control for foxes will target bait-shy individuals. This could partially be overcome by using a bait matrix that is dissimilar to the matrix used in poison baits. Furthermore, the results of our modelling suggest that fertility control may slow the recovery of pest populations, but populations open to even small rates of immigration of fertile foxes will recover quickly leaving contraception as an ineffective tool. This issue is particularly relevant to foxes given their capacity to disperse and rapidly recolonise areas temporarily freed of foxes (Saunders et al., 1995).

Sensitivity analysis of life table vital rates is a useful method of identifying age classes that have the greatest influence on rate of increase (Caswell, 2001). McLeod and Saunders (2001) used this approach to suggest ways of improving fox management strategies. Their results suggested that under some circumstances, fertility control has the potential to have as great an effect on population growth rate as conventional methods of control that target survivorship, such as poisoning. This conclusion is not supported by the results of our study. Our modelling indicated that, for any equal level of effort, poison baiting was always more effective than fertility control baiting.

An effective delivery system for an anti-fertility agent must be cost-effective to manufacture and administer and also be environmentally safe (Bradley et al., 1997). The development of an effective anti-fertility agent and associated delivery system for foxes may one day become a reality, but there are still many hurdles to overcome before the technique will become available for broadscale use (McLeod et al., 2007). Concerns regarding biosafety and animal welfare issues will be particularly important to overcome. Acceptance of contraception and its use of genetically modified organisms by the public, and national and international regulators will be difficult. Research from the United Kingdom suggests that humaneness of the method of control is an important concern of the general public with fertility control viewed as more humane than alternative methods of control such as poisoning, shooting or trapping

(Barr et al., 2002). This result suggests that issues of humaneness and efficacy are important decision variables and public education that provides information on the need, risks, humaneness and efficacy may address many of the concerns the general public may have regarding the use of contraception for the control of pest animals. Concern is also being expressed about the likelihood that fertility control using contraceptives will produce strong artificial selection and the rapid evolution of resistance to the contraceptive (Cooper and Herbert, 2001). Development of resistance can also occur with lethal control agents such as Compound 1080 (Twigg et al., 2002) suggesting that it may be better to use a range of management options, rather than relying on a single control method. Given the ineffectiveness of fertility control found in the present study, we suggest that the options for management will most likely be alternative lethal methods, although exclusion methods (such as fencing) should not be ruled out in some situations.

The use of bait to distribute the contraceptive agent for foxes overcomes the potential humaneness issues encountered by using a virus to disseminate an immunocontraceptive, such as the use of myxoma virus as the vector for rabbits (Oogjes, 1997). However, the reduced efficacy of contraceptive baits relative to poison baits must be taken into account. The results of the models presented here suggest that poison baits are at least twice as effective at reducing fox density than baits containing a contraceptive. At the moment it is not clear if a combination of poison baiting and contraceptive baiting will produce a better welfare outcome by reducing the density of foxes in the long-term, thereby reducing the number of foxes that are killed by poisoning. Based on our analysis, we suspect that such an approach may not be effective.

The advantage of poison baits over contraceptive baits is that all foxes are vulnerable to poisoning, whereas only a fraction of foxes are vulnerable to contraception. For any method of control that uses baits, bait competitors (both target and non-target species) may consume baits intended for the target species (Selhorst and Müller, 1999; Selhorst, 2000; Selhorst et al., 2001). When poison baits are used, target species that consume bait may die and are therefore removed as competitors for bait, but when contraceptive baits are used all bait competitors remain. A consequence is that the cost-effectiveness of fertility control using baits, compared with poison baiting, is reduced. And as stated earlier, foxes continue to consume prey after they have been sterilised.

Our modelling results indicate that contraception can reduce the long term density of foxes. Even though fertility control is viewed as a more humane control method than lethal alternatives, such as poisoning, fumigation or shooting, the efficacy of fertility control must also be considered in any comparison with existing lethal methods of control. The results of our study indicate that for managing pest populations of foxes, the efficacy of contraception, relative to poisoning, is too low for fertility control to be considered as a viable alternative to poison baiting.

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References

Banks, P.B., Dickman, C.R., Newsome, A.E., 1998. Ecological costs of feral predator control: foxes and rabbits. Journal of Wildlife Management 62, 766–772.

Banks, P.B., Newsome, A.E., Dickman, C.R., 2000. Predation by red foxes limits recruitment in populations of eastern grey kangaroos. Austral Ecology 25, 283–291.

Barfield, J.P., Nieschlag, E., Cooper, T.G., 2006. Fertility control in wildlife: humans as a model. Contraception 73, 6–22.

Barlow, N.D., 2000. The ecological challenge of immunocontraception: editor's introduction. Journal of Applied Ecology 37, 897–902.

Barr, J.J.F., Lurz, P.W.W., Shirley, M.D.F., Rushton, S.P., 2002. Evaluation of immunocontraception as a publicly acceptable form of vertebrate pest species control: the introduced grey squirrel in Britain as an example. Environmental Management 30, 342–351.

Beddington, J.R., Free, C.A., Lawton, J.H., 1978. Characteristics of successful natural enemies in models of biological control of insect pests. Nature 273, 513–519.

Begon, M., Bennett, M., Bowers, R.G., French, N.P., Hazel, S.M., Turner, J., 2002. A clarification of transmission terms in host-parasite models: numbers, densities and areas. Epidemiology and Infection 129, 147–153.

Bomford, M., 1990. A Role for Fertility Control in Wildlife Management? Bureau of Rural Resources Bulletin No. 7. Australian Government Publishing Service, Canberra.

Bradley, M.P., Hinds, L.A., Bird, P.H., 1997. A bait-delivered immunocontraceptive vaccine for the European red fox (Vulpes vulpes) by the year 2002? Reproduction Fertility and Development 9, 111–116.

Caswell, H., 2001. Matrix Population Models: Construction, Analysis, and Interpretation. Sinauer Associates, Sunderland, Massachusetts.

Coman, B., Robinson, J., Beaumont, C., 1991. Home range, dispersal and density of red foxes (Vulpes Vulpes L.) in Central Victoria. Wildlife Research 18, 215–223.

Cooper, D.W., Herbert, C.A., 2001. Genetics, biotechnology and population management of over-abundant mammalian wildlife in Australasia. Reproduction Fertility and Development 13, 451–458.

De Roos, A.M., 1997. A gentle introduction to physiologically structured population models. In: Tuljapurkar, S., Caswell, H. (Eds.), Structured-population Models in Marine, Terrestrial, and Freshwater Systems. Chapman and Hall, New York, pp. 119–204.

Delves, P.J., Lund, T., Roitt, I.M., 2002. Future prospects for vaccines to control fertility. Trends in Immunology 23, 220–221.

Dennis, S.M., 1969. Predators and perinatal mortality of lambs in Western Australia. Australian Veterinary Journal 45, 6–9.

Edwards, A.W.F., 1992. Likelihood. John Hopkins University Press, Baltimore, Maryland.

Forsyth, D.M., Duncan, R.P., Bomford, M., Moore, G., 2004. Climatic suitability, life-history traits, introduction effort, and the establishment and spread of introduced mammals in Australia. Conservation Biology 18, 1–13.

Garrott, R.A., 1995. Effective management of free-ranging ungulate populations using contraception. Wildlife Society Bulletin 23, 445–452.

Goudriaan, J., van Roermund, H.J.W., 1989. Model of ageing, development delays and dispersion. In: Rabbinge, R., Ward, S.A., van Laar, H.H. (Eds.), Simulation and Systems Management in Crop Protection. Pudoc, Wageningen, pp. 47–80.

Greentree, C., Saunders, G., McLeod, L., Hone, J., 2000. Lamb predation and fox control in south-eastern Australia. Journal of Applied Ecology 37, 935–943.

Hardy, C.M., Hinds, L.A., Kerr, P.J., Lloyd, M.L., Redwood, A.J., Shellam, G.R., Strive, T., 2006. Biological control of vertebrate pests using virally vectored immunocontraception. Journal of Reproductive Immunology 71, 102–111.

Hone, J., 1992a. Modelling of poisoning for vertebrate pest control, with emphasis on poisoning feral pigs. Ecological Modelling 62, 311–327.

Hone, J., 1992b. Rate of increase and fertility control. Journal of Applied Ecology 29, 695–698.

Hone, J., 1994. Analysis of Vertebrate Pest Control. Cambridge University Press, Cambridge.

Hone, J., 2004. Yield, compensation and fertility control: a model for vertebrate pests. Wildlife Research 31, 357–368.

Hood, G.M., Chesson, P., Pech, R.P., 2000. Biological control using sterilizing viruses: host suppression and competition between viruses in non-spatial models. Journal of Applied Ecology 37, 914–925.

Jordan, D.J., Le Feuvre, A.S., 1989. The extent and cause of perinatal lamb mortality in three flocks of Merino sheep. Australian Veterinary Journal 66, 198–201.

Kinnear, J.E., Onus, M.L., Bromilow, R.N., 1988. Fox control and rock-wallaby population dynamics. Australian Wildlife Research 15, 435–450.

Kinnear, J.E., Onus, M.L., Sumner, N.R., 1998. Fox control and rock-wallaby population dynamics – II. An update. Australian Wildlife Research 25, 81–88.

Kinnear, J.E., Sumner, N.R., Onus, M.L., 2002. The red fox in Australia – an exotic predator turned biocontrol agent. Biological Conservation 108, 335–359.

Lloyd, H.G., 1980. The Red Fox. B.T. Batsford, London.

Lugton, I.W., 1993. Diet of red foxes (Vulpes vulpes) in south-west New South Wales, with relevance to lamb predation. Rangelands Journal 15, 39–47.

Mann, T.L.J., 1968. A comparison of lamb survival in fox proof and unprotected enclosures. Proceedings of the Australian Society of Animal Production 7, 250–254.

McFarlane, D., 1964. The effects of predators on perinatal lamb losses in the Monaro, Oberon and Canberra districts. Wool Technology and Sheep Breeding 11, 11–14.

McIlroy, J., Saunders, G., Hinds, L.A., 2001. The reproductive performance of female red foxes, Vulpes vulpes, in central-western New South Wales during and after a drought. Canadian Journal of Zoology 79, 545–553.

McLeod, R., 2004. Counting the Cost: Impact of Invasive Animals in Australia 2004. Cooperative Research Centre for Pest Animal Control, Canberra.

McLeod, S.R., Saunders, G., Twigg, L.E., Arthur, A.D., Ramsey, D., Hinds, L.A., 2007. Prospects for the future: is there a role for virally vectored immunocontraception in vertebrate pest management? Wildlife Research 34, 555–566.

McLeod, S.R., Saunders, G.R., 2001. Improving management strategies for the red fox by using projection matrix analysis. Wildlife Research 28, 333–340.

Miller, L.A., Johns, B.E., Elias, D.J., 1995. Immunocontraception as a wildlife management tool: some perspectives. Wildlife Society Bulletin 26, 237–243.

Moberly, R.L., White, P.C.L., Webbon, C.C., Baker, P.J., Harris, S., 2003. Factors associated with fox (*Vulpes vulpes*) predation of lambs in Britain. Wildlife Research 30, 219–227.

National Parks, N.S.W, Wildlife Service, 2001. Threat Abatement Plan for Predation by the Red Fox (*Vulpes vulpes*). NSW National Parks and Wildlife Service, Hurstville.

Oogjes, G., 1997. Ethical aspects and dilemmas of fertility control of unwanted wildlife: an animal welfarist's perspective. Reproduction Fertility and Development 9, 163–167.

Pech, R., Hood, G.M., McIlroy, J., Saunders, G., 1997. Can foxes be controlled by reducing their fertility? Reproduction, Fertility and Development 9, 41–50.

Priddel, D., Wheeler, R., 1996. Effect of age at release on the susceptibility of captive-reared malleefowl *Leipoa ocellata* to predation by the introduced fox *Vulpes vulpes*. Emu 96, 32–41.

Rowley, I., 1970. Lamb predation in Australia: incidence, pre-disposing conditions and the identification of wounds. CSIRO Wildlife Research 15, 79–123.

Saunders, G., Coman, B., Kinnear, J., Braysher, M., 1995. Managing Vertebrate Pests: Foxes. Australian Government Publishing Service, Canberra.

Saunders, G., McIlroy, J., Berghout, M., Kay, B., Gifford, E., Perry, R., van de Ven, R., 2002a. The effects of induced sterility on the territorial behaviour and survival of foxes. Journal of Applied Ecology 39, 56–66.

Saunders, G., McIlroy, J., Kay, B., Gifford, E., Berghout, M., van de Ven, R., 2002b. Demography of foxes in central-western New South Wales, Australia. Mammalia 66, 247–257.

Selhorst, T., 2000. Improving the oral immunization of foxes (*Vulpes vulpes*) against rabies with the help of an evolutionary algorithm. Ecological Modelling 129, 297–305.

Selhorst, T., Müller, T., 1999. An evaluation of the efficiency of rabies control strategies in fox (*Vulpes vulpes*) populations using a computer simulation program. Ecological Modelling 124, 221–232.

Selhorst, T., Thulke, H., Müller, T., 2001. Cost-efficient vaccination of foxes (*Vulpes vulpes*) against rabies and the need for a new baiting strategy. Preventive Veterinary Medicine 51, 95–109.

Short, J., Kinnear, J.E., Robley, A., 2002. Surplus killing by introduced predators in Australia – evidence for ineffective anti-predator adaptations in native prey species? Biological Conservation 103, 283–301.

Smith, G.C., Harris, S., 1991. Rabies in urban foxes (*Vulpes vulpes*) in Britain: the use of a spatial stochastic simulation model to examine the pattern of spread and evaluate the efficacy of different control régimes. Philosophical Transactions of the Royal Society London B 334, 459–479.

Strive, T., Hardy, C.M., Reubel, G.H., 2008. Prospects for immunocontraception in the European red fox (*Vulpes vulpes*). Wildlife Research 34, 523–529.

Thompson, J., Fleming, P., 1994. Evaluation of the efficacy of 1080 poisoning of red foxes using visitation to non-toxic baits as an index of fox abundance. Wildlife Research 21, 27–39.

Tuyttens, F.A.M., Macdonald, D.W., 1998. Fertility control: an option for nonlethal control of wild carnivores? Animal Welfare 7, 339–364.

Twigg, L.E., Martin, G.R., Lowe, T.J., 2002. Evidence of pesticide resistance in medium-sized mammalian pests: a case study with 1080 poison and Australian rabbits. Journal of Applied Ecology 39, 549–560.

Tyndale-Biscoe, C.H., 1994. Virus-vectored immunocontraception of feral mammals. Reproduction Fertility and Development 6, 281–287.