

Use of host population reduction to control wildlife disease in a pest species: rabbits and paratuberculosis

Ross S. Davidson¹, Glenn Marion², Piran C.L. White³ & Michael R. Hutchings^{1*}

¹SAC, West Mains Road, Edinburgh EH9 3JG, Scotland, UK

²Biomathematics and Statistics Scotland, Edinburgh EH9 3JZ, Scotland, UK

³Environment Department, University of York, Heslington, York, YO10 5DD, UK

*Correspondence: Dr Michael Hutchings, Animal Health, SAC, Bush Estate, Penicuik EH26 0PH, UK. Email: mike.hutchings@sac.ac.uk Tel: 0131 535 3231 Fax: 0131 535 3121

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Abstract

Paratuberculosis (*Map*) is a widespread and difficult disease to control in livestock populations and also has possible links to Crohn's disease in humans. Rabbits have recently been identified as the key wildlife species in terms of paratuberculosis transmission to the wider host community and infection will persist in rabbit populations for extended periods of time in the absence of external sources of infection (e.g. from cattle). As such it is recommended that disease control strategies include rabbits. Here we use a spatially-explicit stochastic simulation model of *Map* dynamics in rabbit populations to quantify the effects of rabbit population control on disease persistence. The model was parameterised based on empirical studies on rabbit population dynamics and on rabbit to rabbit routes of *Map* transmission. Three rabbit control strategies were compared, single one-off population reductions based on removal of entire social groups, single one-off population reductions based on removing individual animals and repeated annual population reductions based on removing individual animals. Unrealistically high rabbit culls (>95% population reduction) are needed if infection is to be eradicated from local rabbit populations with a single one-off population reduction event. Repeated annual control events are more effective at reducing the prevalence of infection in rabbit populations and eradicating infection. However, annual population reductions of greater than 50% are required over extended periods of time (many years). Following a reduction in rabbit numbers the population recovers before the disease prevalence suggesting the theoretical possibility of an optimal culling strategy that removes infection from a rabbit population whilst the population itself is maintained. The results are discussed in relation to practical disease control measures.

Introduction

Host population reduction is a common strategy used to control disease prevalence in wildlife and livestock. Randomly reducing the host population can have a number of effects on disease stability, for example it can produce a more fractured contact structure, which reduces mixing and leaves the disease more vulnerable to localised chance extinctions, as well as potentially reducing the overall rate of contacts. Trapping or shooting of individuals is likely to have a different impact to measures which remove entire groups (e.g. gassing of badger setts), as is varying the intensity and timing of control events. The aim of this study is to investigate these sources of variation using a model of paratuberculosis in rabbit populations as a worked example in order to quantify the effects of population reduction on infection and host population dynamics.

Paratuberculosis (also known as Johne's disease) is a chronic, usually fatal, enteritis of wild and domestic ruminants, with purported links to Crohn's disease in humans (Naser *et al.* 2004), caused by *Mycobacterium avium* subsp. *Paratuberculosis* Bergey (*Map*). It causes not only great economic losses but also welfare issues for the agricultural industry worldwide (Chiodini, van Kruiningen & Merkal 1984; Sweeney 1996). The disease is notoriously difficult to control in ruminant livestock populations, a difficulty that may be partially accounted for by the recent extension of the known host range to include a number of non-ruminant wildlife species (Daniels *et al.* 2003). Among these, rabbits are likely to have a particularly important role, following recent evidence for persistence of infection in rabbit populations over large timescales (Judge *et al.* 2007). This persistence suggests that control of the infection in rabbit populations should be included in any strategies directed at reducing human and livestock exposure to the organism.

Here we use an existing simulation model of paratuberculosis dynamics in rabbit populations to quantify the relative efficacies of removing hosts either at the individual or social group level, as one-off measures or as long-term repeated strategies.

Materials and Methods

The model

An existing model of *M. a. paratuberculosis* dynamics in rabbit populations was used to address the aims of the study (Judge et al. 2007). In this model each individual belongs to one of three age classes (infant, adolescent or mature), and one of N of social groups, which for the runs carried out here was chosen to be 100. Each age class is separated into male and female. The carrying capacity for the social groups was set to 90, although actual populations are likely to remain somewhat below this level due to logistic decay of birth rate. Population and infection dynamics in the system are simulated by generating random inter-event times for different event types, such as birth, death and individuals moving between different age classes, disease states and social groups. These inter-event times are each drawn from a one parameter continuous distribution, the parameter for each event type being equivalent to an average rate of occurrence. This results in a stochastic process in continuous time with exponentially distributed waiting times. The rate parameters for each event depend on the state of the system, the configuration space being defined by the age class, sex, disease status and location (social group) of each animal, so that the rate parameters and hence the probabilities of occurrence in a given time interval change after each event. An exception to this is that the weaning period (the time animals spend in the infant age class) is fixed rather than random, but all other events are generated as described above.

In order to generate inter-event times from a continuous distribution a variable time step must be used which prior to evolving the system is set such that the probability of two events occurring in a single step is negligible (see e.g. Renshaw, 1991). The unit interval is then divided into segments in the ratio of the rates and the choice of event occurs by picking a random number between zero and one which triggers the corresponding event. In this type of stochastic process, for any given model run (realisation of the stochastic process) the actual number of occurrences of a particular event need not coincide exactly with the specified rate for that event type, but nonetheless the average

number over many realisations will converge to the event rate. For this reason many realisations must be generated in order to present meaningful results (e.g. means, variances or distributions) from a stochastic model. For a full description of the model see Judge et al. (2007).

Model parameterisation

The rabbit population dynamics and disease parameter values were taken from Judge et al. (2007) and are given in Table 1. All rates are expressed as a mean number of events per month and therefore one unit of model time corresponds to one month real-time. The parameters defining rabbit demography were obtained from the literature sources noted in the table. The estimations of the disease transmission parameters are taken from data collected in a previous study from a low to moderate density wild Scottish population of rabbits naturally infected with *Map*, in which a maximum likelihood fitting procedure was used to derive probabilities of vertical and horizontal transmission from the field data (Judge *et al.* 2006). The probability of transmission via vertical routes, p_v , is 0.326. The horizontal transmission coefficient per month (β) based on the monthly per capita rate of infection from the empirical study was estimated to be in the range between 0.013 and 0.046 (Judge *et al.* 2006). When simulating rabbit control a β value of 0.019 was used (see below for discussion on this β value).

Model runs performed

The state used to initiate the rabbit population and disease has no impact on the system after a relatively short time, except when a very low initial population or prevalence is used. In this case there would be a significant extra probability of extinction beyond the inherent extinction probability of large fluctuations around the equilibrium state. For each run of the model the rabbit-paratuberculosis system was initiated in a standardized manner which avoided the possibility of such extinctions. Initially individual rabbits are allowed to migrate into the system from outside at a fixed rate. After this initial period in which the host population is created the immigration from

outside is stopped and the individual populations allowed to reach equilibrium, at a level which is independent of the size and duration of the initial immigration period. After the population has equilibrated the disease is introduced into the population by inoculating a number of randomly selected individuals. Again, this is allowed to evolve to its equilibrium level, which is independent of the number of inoculations initially carried out as long as this is above a low threshold value. Once both population and disease have reached their equilibrium values, the control measure is implemented by removing a fixed number of randomly selected individuals or social groups.

Three techniques of rabbit control were simulated

(1) One-off culls of random rabbits (similar to shooting): One-off rabbit culls were simulated by instantaneous removal of a specified fraction of randomly selected individual rabbits from the host population.

(2) One-off culls of complete social groups (similar to warren removal techniques): In this control measure a fixed number of groups were completely emptied, leaving their nest sites free for expansion of the remaining groups.

(3) Repeated culls of random rabbits (similar to repeated shooting events). The slow recovery rate of the disease after a single cull event suggests that repeated culling may have a more significant impact upon prevalence. Repeated culls were simulated by repeating control option (1) above on an annual basis.

To quantify the probability of disease extinction in the wake of a control event the number of realisations of the stochastic process (individual model runs) in which the disease became extinct was recorded. From the distribution of the total number of infected rabbits remaining after the population control event(s) across realisations, the proportion of the distribution crossing the y axis was taken as the probability of the disease becoming extinct.

Results

Removal of individuals

Single population reduction events targeting individual animals of up to 96% do not result in any noticeable chance of disease extinction (Figure 1), while culls at the unrealistically high levels of 98% and 99% of the population yield disease extinction probabilities of 0.08 and 0.34 respectively. For larger culls the disease takes slightly longer to recover to its full equilibrium level, but in all cases the slow transmission rate of *Map* means that this takes around 180 months. These results can also be seen in Figures 2 and 3, where the distribution of the population size and number of infected animals among model runs immediately after a population reduction event is shown. Although no model runs were disease free straight away, even in the 98% and 99% culls, many were left with a very low prevalence which resulted in chance eradication in the subsequent recovery period.

Removal of groups

Removing complete social groups of rabbits at the same overall proportional reduction produces a similar result to that seen in the case of removal of individuals (Figure 4). A slight broadening in the distributions of the population size and number of infected animals among model runs is apparent when targeting social groups for removal from the population compared to targeting individuals (Figure 5). In the 99% cull some model runs become extinct as a direct consequence of the cull, with an eradication probability immediately post-cull of 0.02, as visible in the non-zero value of the post-cull distribution at this cull size (see figure 5). After allowing the system to recover to equilibrium the final eradication probabilities were 0.01 and 0.16 for cull levels of 98% and 99% respectively. These values are considerably poorer than removal of individuals, despite a better performance immediately post-cull, a consequence of the faster recovery time of the disease in this case due to the higher level of clustering of individuals.

The use of repeated cull strategies

Repeated annual population reductions were carried out once the population and disease reached a steady state, which in all cases was achieved within 120 months of the inoculation, which in turn occurred 120 months after the simulations were begun. Repeated culling was then carried out until the disease level reached a stable value, for which 840 months was sufficient in all cases. The results show that such repeated strategies are more effective than single one-off reductions with annual reductions of 45% or more resulting in disease eradication (Figure 7). This threshold in the cull size will be reduced if more frequent culls are performed. In Figure 6 the population and the disease prevalence gradually reduce over the culling period, until they reach a level at which the number removed is equal to the number of individuals or disease cases that can reestablish in the inter-cull period. At culling rates equal to 45% or more this condition is never met for the disease, as shown in figures 7 and 8, and it becomes extinct. At 45% the population level, with its faster recovery rate, does eventually balance the removals, while at 50% the population becomes extinct in the majority of realizations resulting in a post-cull mean population significantly below its pre-cull value. It should be noted that in those realizations where the population does not become extinct it will recover to its original value, so that the lowering of the average in the 50% cull is a result of a proportion of realizations going extinct rather than a change in the equilibrium value.

Runs in which the disease is eradicated will remain disease free since the system as a whole is isolated with no external sources of infection. The disease eradication probability as a function of time is shown in Figure 9 for each repeated-cull size (e.g. 40%, 45%, and 50%).

Discussion

By use of a numerical stochastic model likely outcomes have been demonstrated for three different control strategies for *Map*; random removal of individuals, random removal of social groups and repeated random removal of individuals on an annual basis. Extremely high rabbit population reduction levels (Greater than 96%) are necessary if either of the one-off rabbit cull strategies are to have even a small probability of eradicating the disease. The main contribution to this small eradication probability emerges not from the contribution of the probability of removing all infected individuals at the cull (which is small), but from subsequent fluctuations while the disease is at a low prevalence i.e. the disease fails to spread through the recovering population. This effect can only be captured with a stochastic model.

It has been shown that targeting entire social groups for removal results in a higher probability of eradicating the disease during the cull event itself than random removal of individuals at an equivalent level, reflected in a higher degree of variability post-cull in the number of individuals infected between runs. It is likely that this broadening of the post-cull distribution of infection is due to correlations in the infective status of individuals in the same group. This is also the likely cause of the increased rate of recovery of the disease, so that although a better result is obtained in the immediate aftermath of the cull, the prevalence remains low for a much smaller amount of time, leaving less opportunity for fluctuations to take the system to zero prevalence, and a worse long-term performance.

The ineffectiveness of single cull strategies, together with the difference in population and disease recovery rates, points to the use of repeated cull strategies. For these the random removal of individuals is superior to group removal due to the faster disease recovery rate in the latter. The differential response of the population and disease gives rise to a lag between the respective times to recovery to equilibrium. Thus a point in time will be reached when the population has almost fully

recovered but the disease has not. At this point, a further cull would bring the expected prevalence to a lower level than a cull of the same size would upon an equilibrated population. Repetition of this procedure should result in a much depleted disease level, distinctly increasing the probability of eradicating the disease but without causing the population to go extinct. This hypothesis was investigated by exploring different cull sizes while keeping the cull frequency fixed, in this case at one cull per year. The findings indicate that the disease can feasibly be eradicated from rabbit populations using repeated culls, however this is likely to take a number of years to achieve. In the case of an annual cull removing 45% of the population this may be as long as 33 years, although this period is for the eradication probability to approach 1, so that in most cases eradication would be achieved before this time. Eradicating *Map* whilst maintaining the rabbit population is only possible due to the fact that rabbits reproduce faster than *Map* transmits between rabbits.

Although *Map* has been used as a case study, these results apply in principle to other diseases with low transmission rates and hence low rates of recovery of the infection. With any disease at high prevalence a single cull is highly unlikely to eradicate disease, although will produce short-term reductions in prevalence. Moderate repeated culls will eradicate the disease and the level of culling necessary will be a function of the frequency with which it is carried out. Cull sizes beyond the threshold level for a given inter-cull period will lead to faster eradication of the disease, but with a greater impact on the population. Beyond a second threshold the population will also be driven to extinction.

Eradication of both the population and the disease may, in the case of rabbits and *Map*, be seen as advantageous as the rabbit is a pest species, however the possibility of removing the disease without the population may have advantages from a disease control point of view, as competition effects could act to reduce the rates of immigration from outside areas post cull and consequently slow reinfection. The study of such effects would require an extended model with external sources of

infection. Another potential advantage occurs where the host population is a conserved species (e.g. badgers and TB), in which case eradication without population removal is an ideal scenario. The results presented here suggest that this effect is a theoretical possibility for any disease for which disease transmission occurs at a lower rate than reproduction, as with rabbits and *Map*.

The horizontal transmission rate used here is taken from a range of estimates given in Judge et. al. (2006). There the real value was considered to be at the higher end of the range, however a value towards the lower end of the range has been considered here, giving a lower bound on times to reach a given eradication probability. Higher values of β will give rise to larger values for these eradication times. However, the simulations used here with the lower β value suggest that *Map* is extremely persistent and difficult to eradicate, with repeated culling strategies taking many years before achieving success. As such it is likely that sustained effort over extended periods is required to control *Map* in rabbit populations and this effort is likely to be greater than that predicted here. Increases in the value of β result in a faster recovery of the infection in rabbit populations after a population reduction event. At β values of greater than 0.034 the infection recovers faster than the population and the effect described above where optimal culling rates result in infection eradication but population survival are lost. The parameters used represent a typical set estimated from field data, but uncertainty in these values leads to inevitable uncertainty in estimates of the extinction times. The lack of data on *Map* makes a more precise statistical inference of eradication probabilities, optimal cull frequency and size, and consequently the time to eradication unfeasible; indeed if the true β value is higher than about 0.034 repeated culling may be completely ineffective. In this case it may be necessary to seek other control strategies. These are likely to give rise to a decreased effective β value, re-establishing the possibility of repeated cull disease eradication procedures.

In conclusion, paratuberculosis control strategies based on single rabbit population reduction events require unrealistically high proportions of the rabbit population to achieve infection eradication. Control strategies based on repeated population reduction events have greater chances of success at eradicating infection from the rabbit population. That rabbits reproduce faster than the rabbit to rabbit rate of *Map* transmission suggests the potential for optimal control strategies that lead to paratuberculosis eradication with rabbit survival. The notorious persistence of *Map* in livestock systems despite control seems to be mirrored in infected rabbit populations with significant effort over an extended period (i.e. many years) being required to eradicate *Map* from rabbit populations. The difficulties in controlling *Map* in rabbit populations demonstrated here further highlight the risk rabbits pose to livestock, especially given the high levels of exposure of cattle to rabbit faeces and the likely persistence of infection in rabbit populations in the absence of control.

Currently *Map* infected rabbit populations may be considered relatively rare, however, given the ubiquitous distribution of the rabbit in the UK and the likely persistence of infection in rabbit populations, the use of repeated control strategies may be advisable, and where possible these should be extended to local areas via landowner cooperation.

Acknowledgements

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Figure legends

Table **1**. Model parameters and values used.

Figure **1**. The evolution of the population and number of rabbits infected, up to and after a control event at $t = 350$.

Figure **2**. The distribution among runs of the population of rabbits for three sizes of individual based cull.

Figure **3**. The distribution among runs of the number of rabbits infected for three sizes of individual based cull.

Figure 4. The distribution among runs of the population of rabbits for three sizes of cull for cull strategies which remove entire groups.

Figure 5. The distribution among runs of the number of rabbits infected for three sizes of cull for cull strategies which remove entire groups.

Figure 6. The mean population size and disease prevalence among several realisations of the model with an annual cull of 40% of the population.

Figure 7. The mean population size and disease prevalence among several realisations of the model with an annual cull of 45% of the population.

Figure 8. The mean population size and disease prevalence among several realisations of the model with an annual cull of 50% of the population.

Figure 9. The probability of eradicating the disease as a function of time.

Table 1. Model parameters and values used.

Symbol	Definition	Value	Reference for, or estimate of, value
	Max number of adult males per social group	4	Myers & Poole (1959; 1961), von Holst <i>et al.</i> (2002)
	Max number of adult females per social group	6	Myers & Poole (1959; 1961), von Holst <i>et al.</i> (2002)
	Max number of juveniles per social group	80	Calculated from maximum number of offspring per group and maximum number of adolescents potentially alive at any one time
r_{mm} (r_{af})	Adult dispersal rate	0.0043	5% disperse (Daly 1981; Bell 1983; Gibb, White & Ward 1985)
r_{am} (r_{af})	Adolescent dispersal and/or maturation rate	0.167	Calculated so maturation/dispersal occurs after an average of 6 months in adolescent class
P_l	Probability of local dispersal	0.8	Estimated from dispersal distances (Cowan 1991a; Twigg <i>et al.</i> 1998; Richardson <i>et al.</i> 2002)
π_m	Probability of staying in natal group - male	0.26	Average of 74% disperse (Dunsmore 1974; Parer 1982)
π_f	Probability of staying in natal group - female	0.92	Average of 80% remain on in the natal group (Dunsmore 1974; Daly 1981; Parer 1982; Cowan 1991a)
	Length of infancy (months)	1.0	Approximate age at weaning (Cowan 1991b)
μ_{mm} (μ_{mf})	Adult death rate	0.0909	Estimated to give an average time in the adult group of 11 months to give an average life span of 18 months (Tyndale-Biscoe & Williams 1955; Lockley 1961)
μ_{am}	Adolescent male death rate	0.667	80% mortality (Southern 1940; Myers & Schneider 1964; Parer 1977; Wood 1980; Richardson & Wood 1982; Cowan & Roman 1985; Cowan 1991b; von Holst <i>et al.</i> 2002) over 6 months
μ_{af}	Adolescent female death rate	0.25	60% mortality (Southern 1940; Myers & Schneider 1964; Parer 1977; Wood 1980; Richardson & Wood 1982; Cowan & Roman 1985; Cowan 1991b; von Holst <i>et al.</i> 2002) over 6 months
μ_i	Infant death rate	0.66	Estimated to have an average of 50% of kits born surviving to weaning (Gilbert <i>et al.</i> 1987; Robson 1993; von Holst <i>et al.</i> 2002)
R_b	Adult female birth rate	1.67	Estimated from average number of young produced per doe per year (Wood 1980; Thompson 1994; Trout & Smith 1995)
	Sex ratio at birth	1:1	Lockley (1961); Myers & Poole (1962); Daly (1981); Boyd (1985); Bell & Webb (1991); von Holst <i>et al.</i> (2002)

p_v	Probability of vertical & pseudo-vertical transmission	0.326	Judge <i>et al.</i> (2006)
β	Horizontal transmission coefficient	0.013 – 0.046	Judge <i>et al.</i> (2006)

Figure 2. The distribution among runs of the population of rabbits for three sizes of individual based cull.

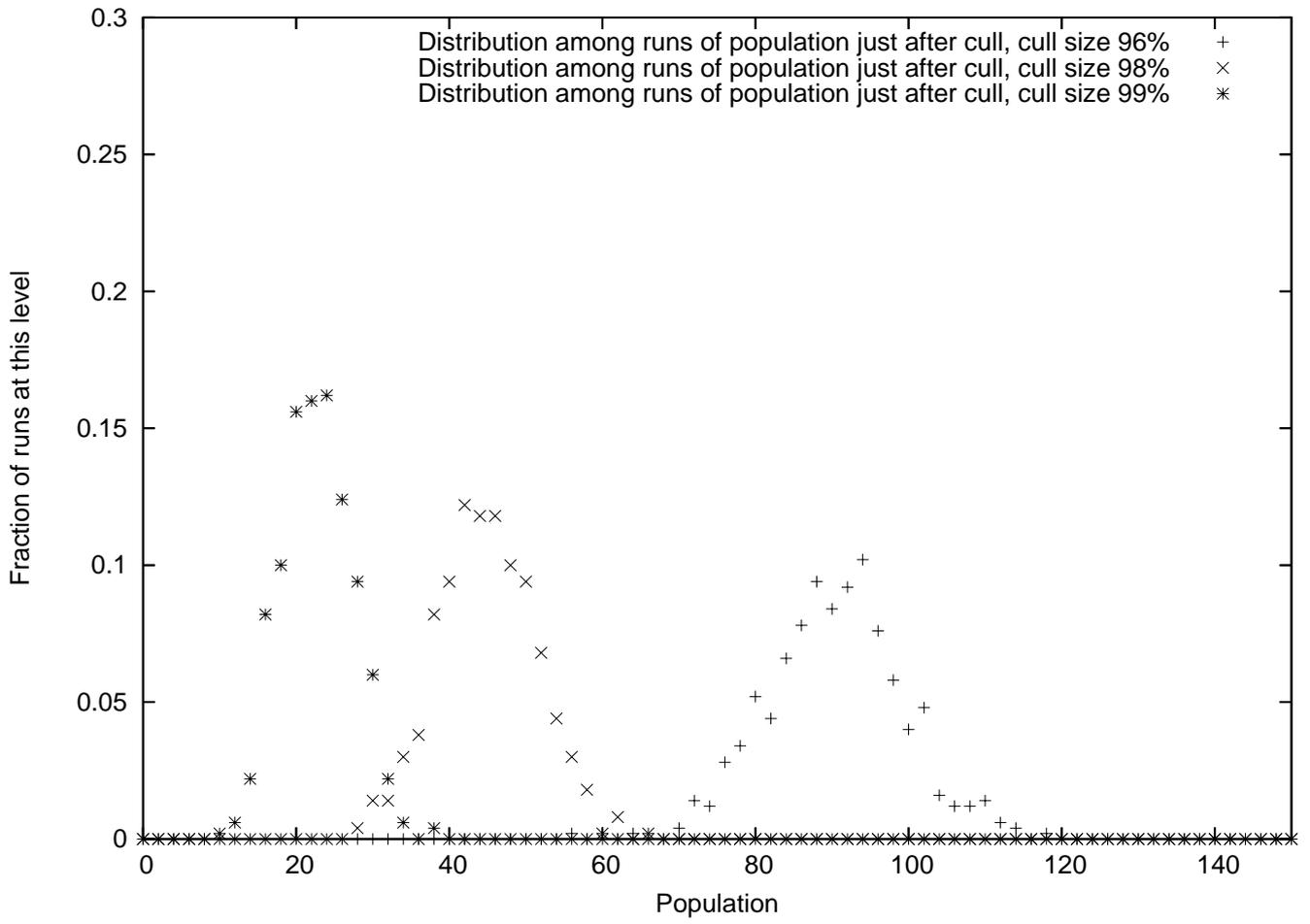


Figure 3. The distribution among runs of the number of rabbits infected for three sizes of individual based cull.

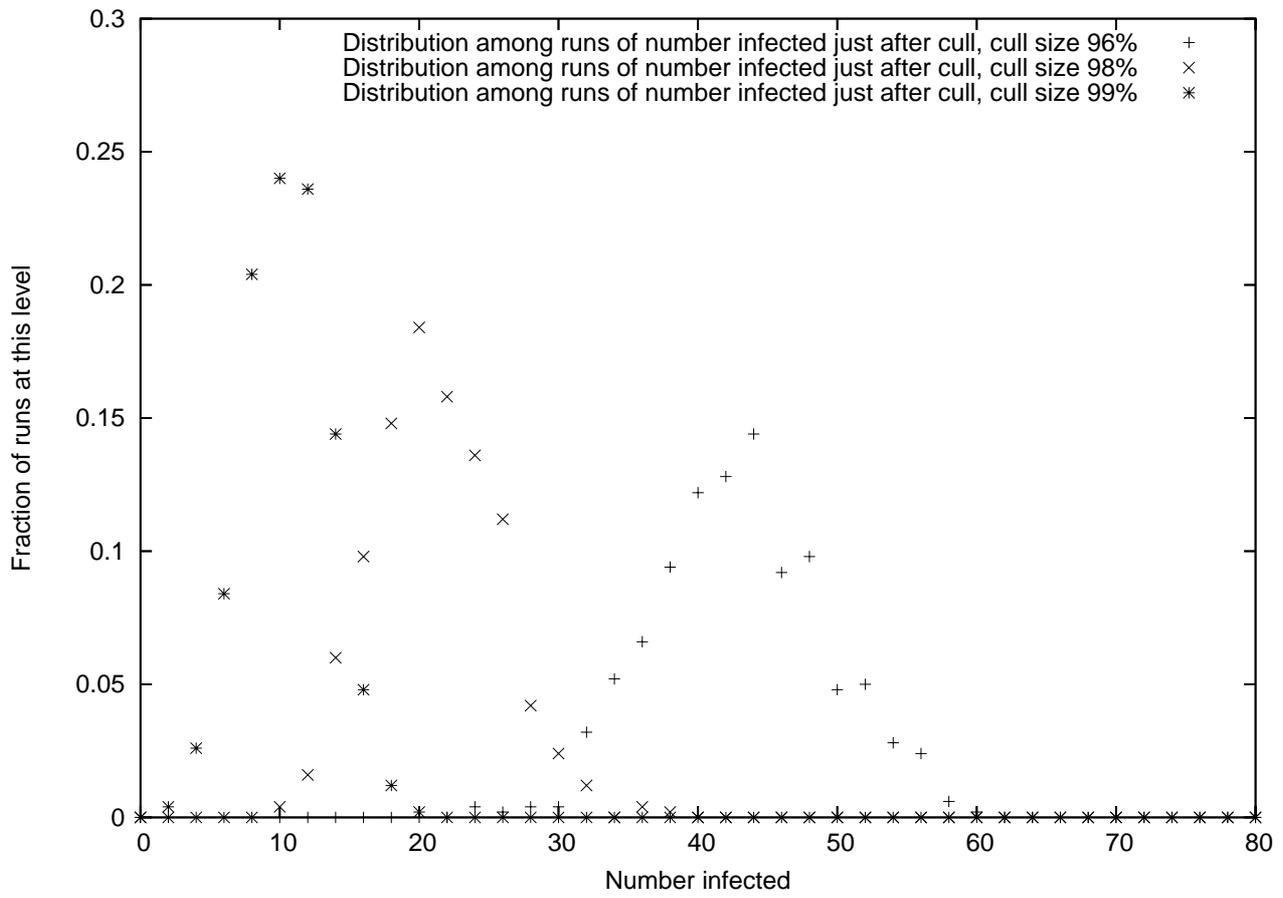


Figure 4. The distribution among runs of the population of rabbits for three sizes of cull for cull strategies which remove entire groups.

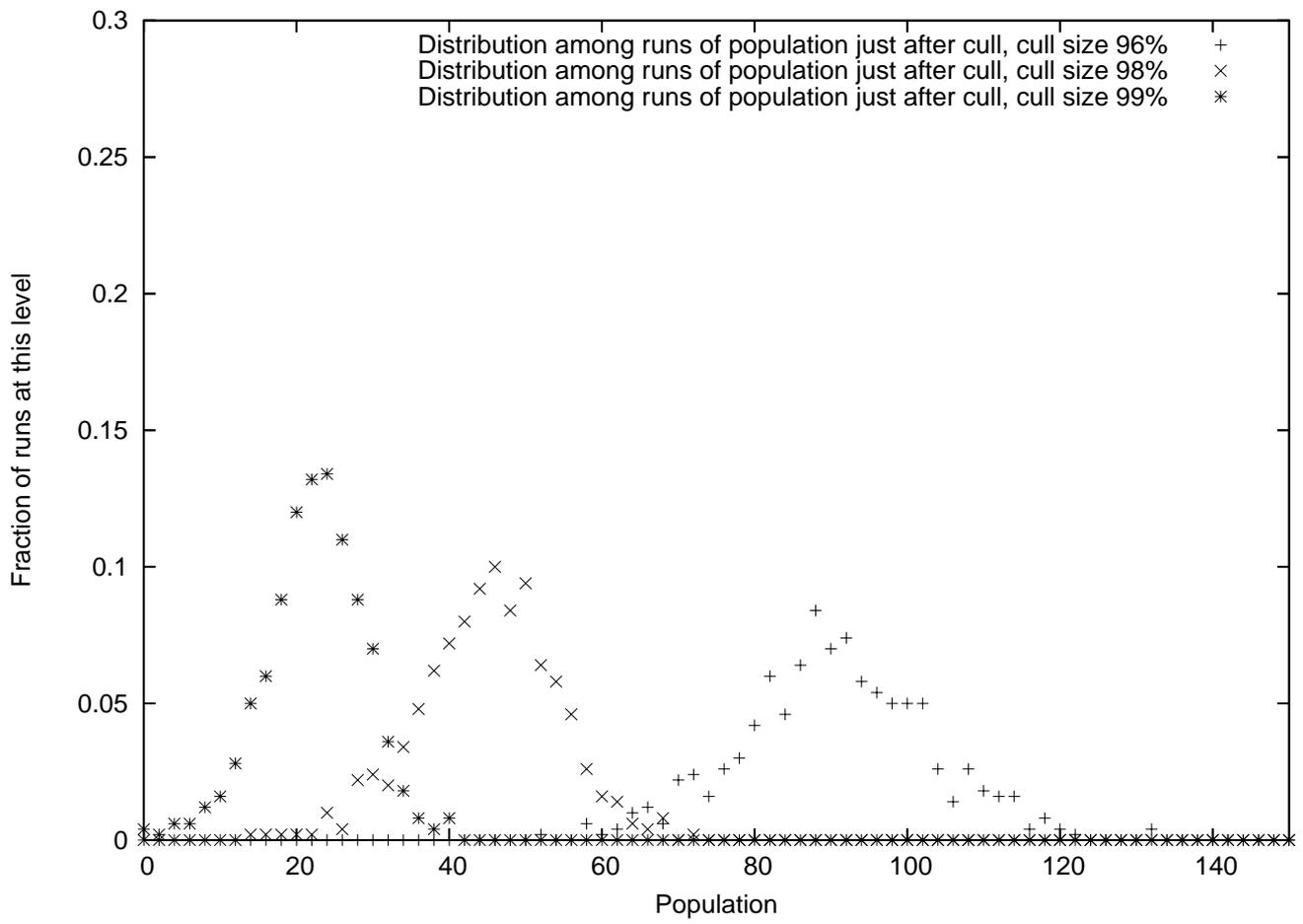


Figure 5. The distribution among runs of the number of rabbits infected for three sizes of cull for cull strategies which remove entire groups.

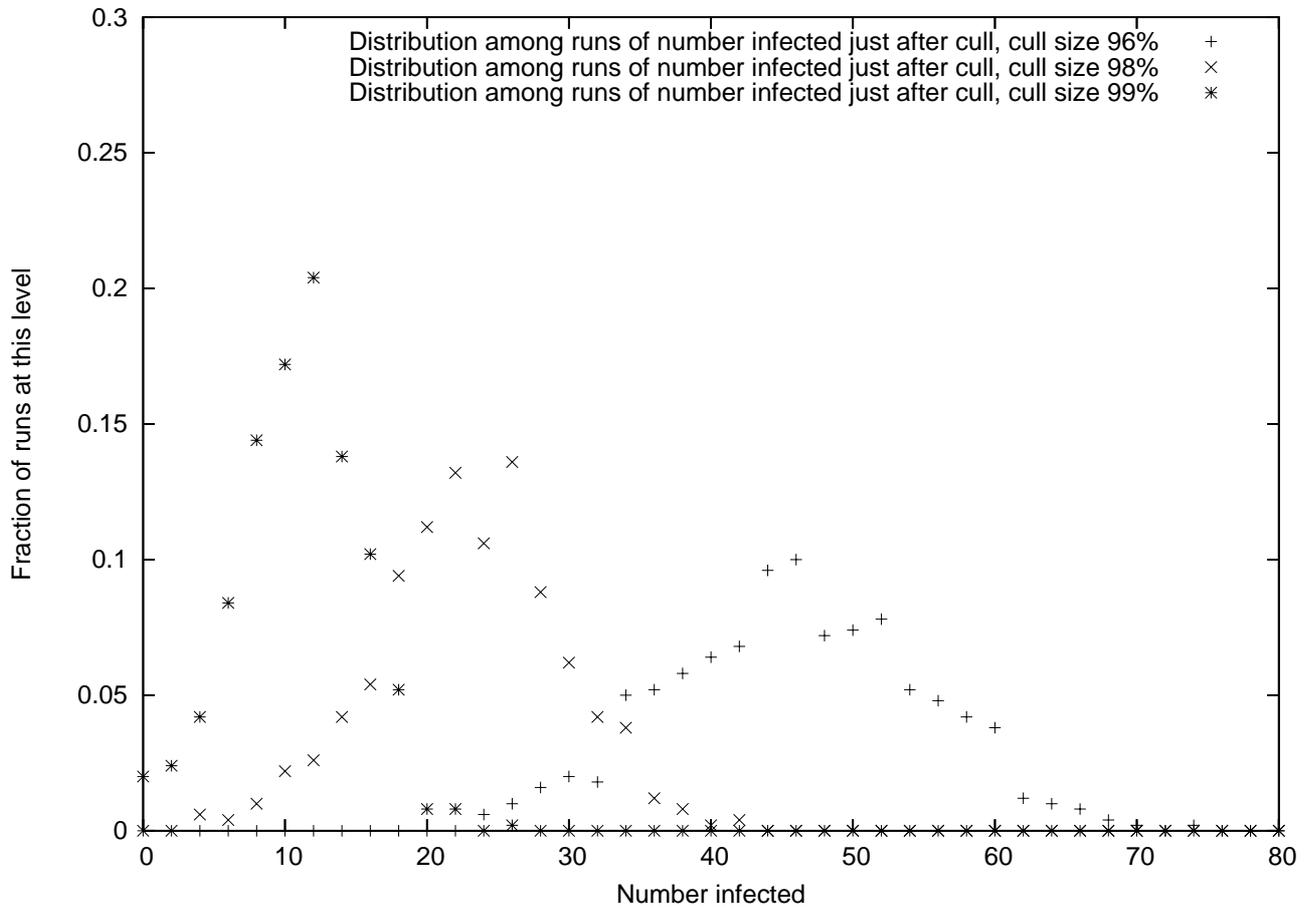


Figure 6. The mean population size and disease prevalence among 200 realizations of the model with an annual cull of 40% of the population. Culling commences once population and disease are at equilibrium, here at 240 months, and continues annually for a further 840 months. During this

period numbers oscillate, reaching a maximum (for that year) just before the cull and a minimum directly afterwards. These maxima and minima are represented by the lines surrounding the two curves displaying the means.

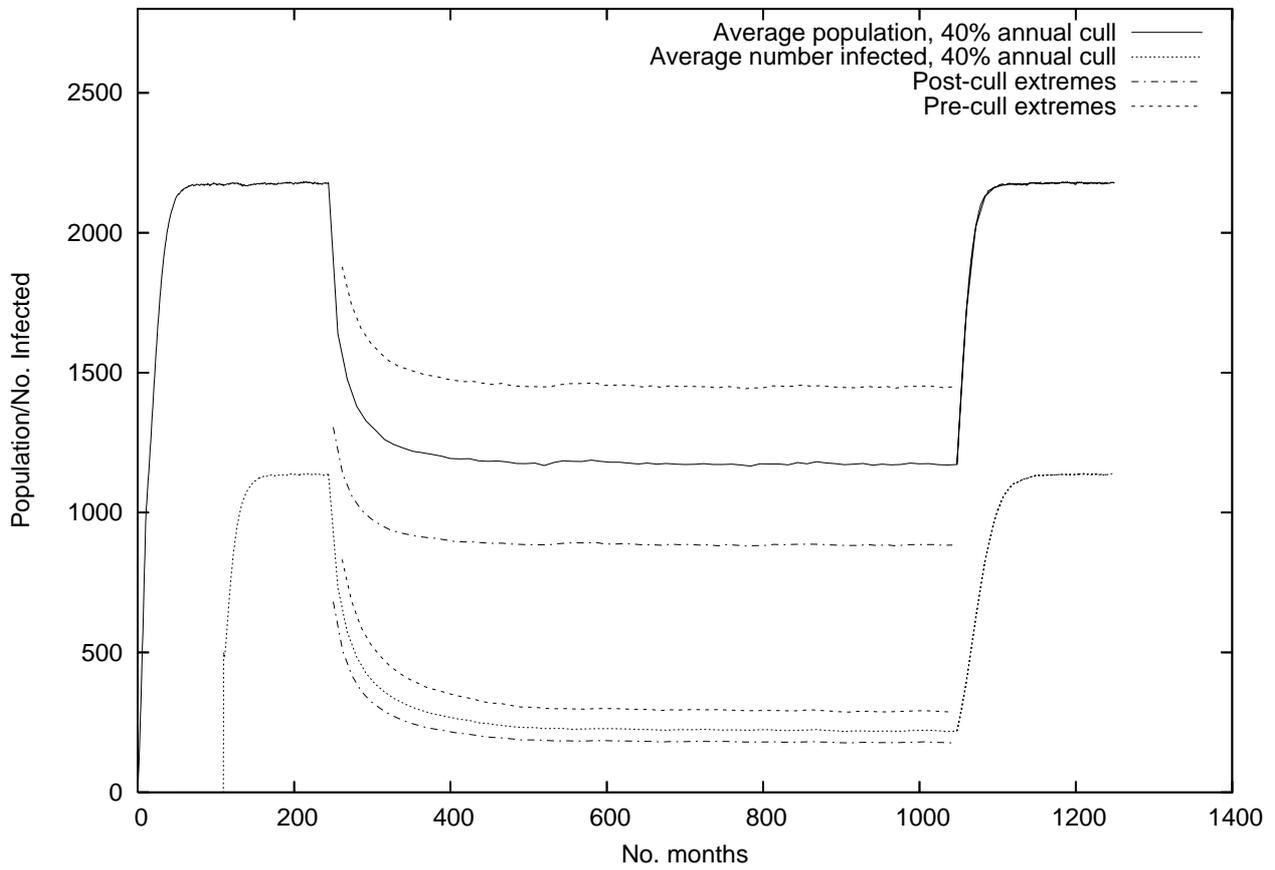


Figure 7. The mean population size and disease prevalence among several realisations of the model with an annual cull of 45% of the population.

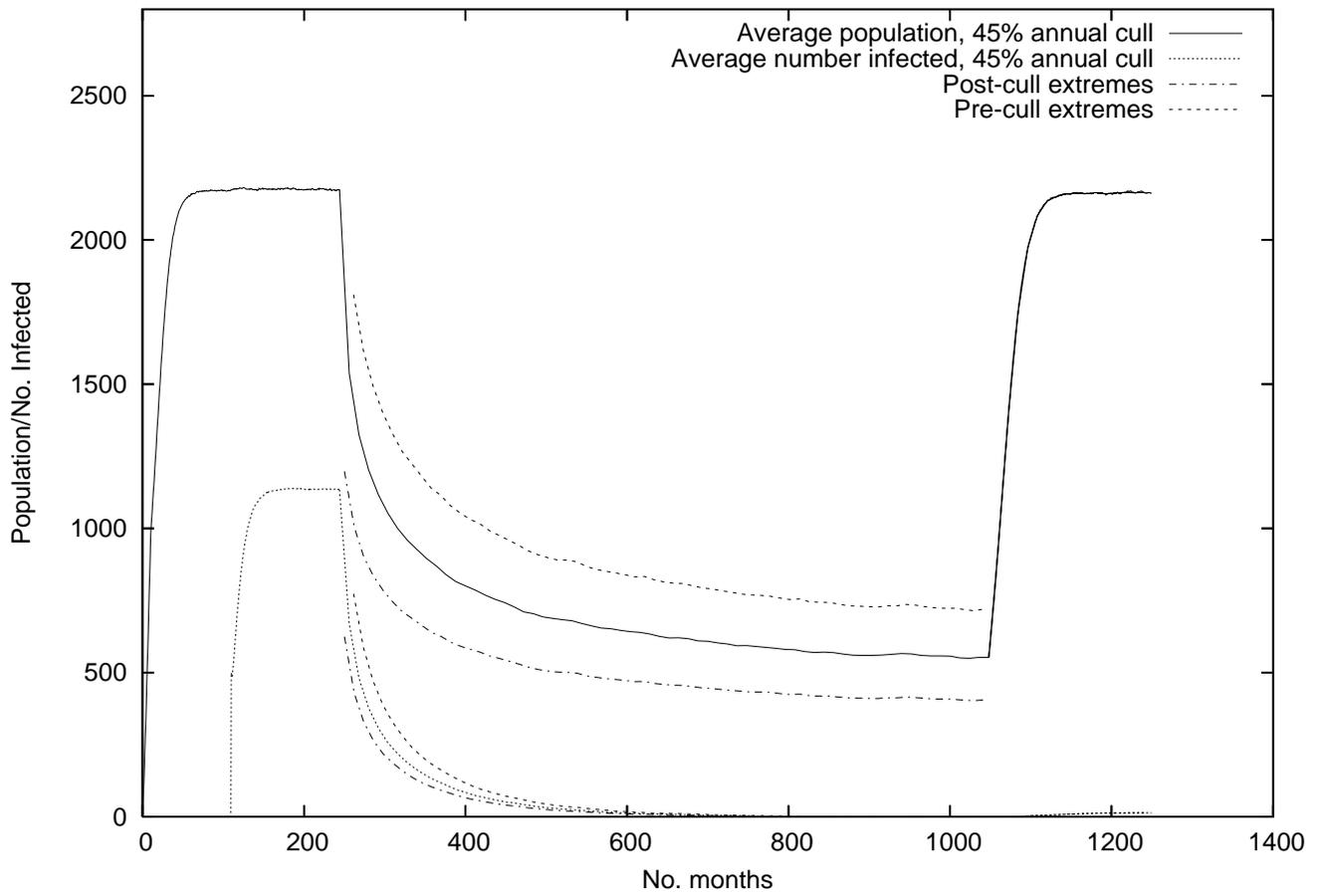


Figure 8. The mean population size and disease prevalence among several realisations of the model with an annual cull of 50% of the population.

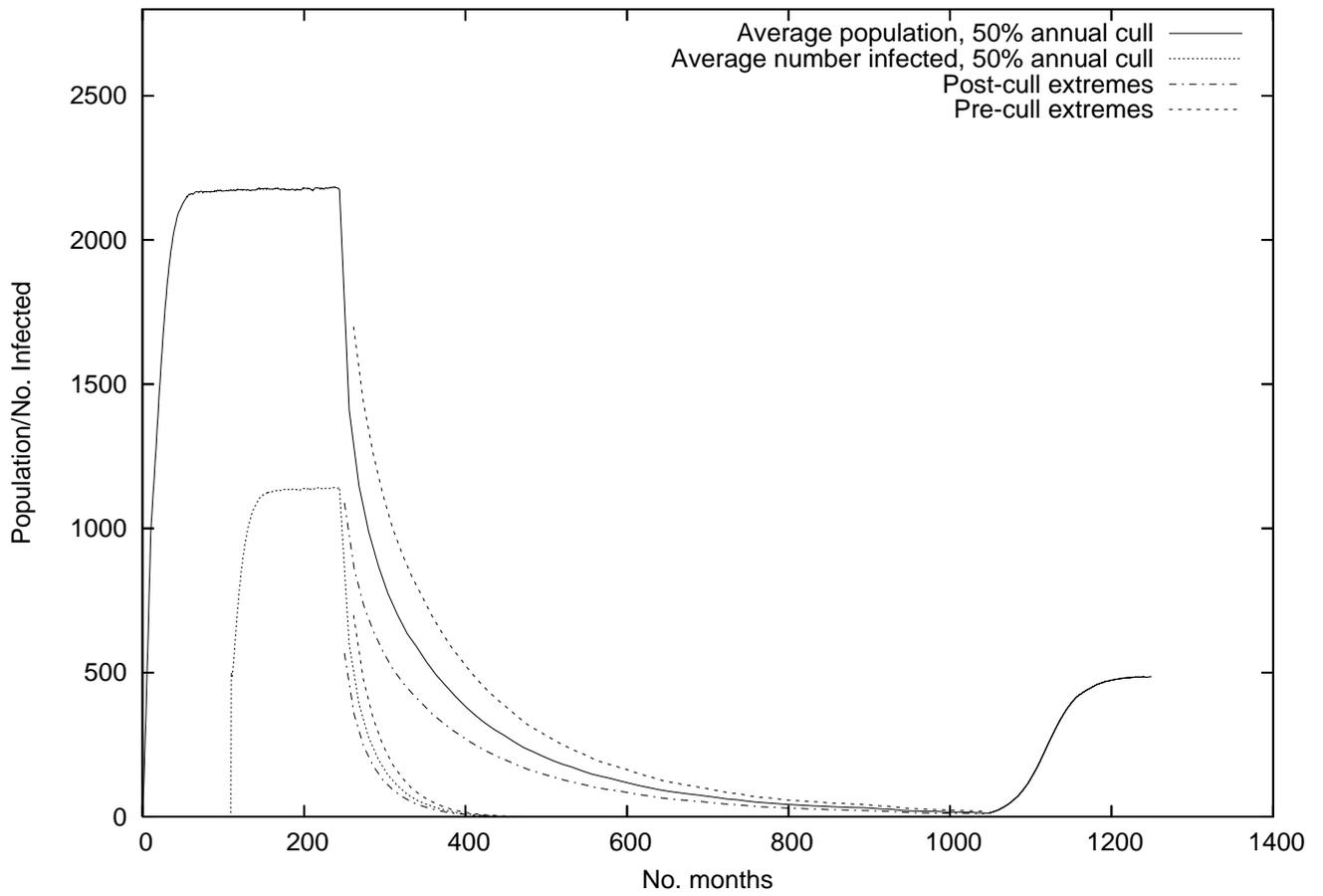


Figure 9. The probability of eradicating the disease as a function of time.

