Management of on-farm risk to livestock from bovine tuberculosis in Michigan, USA, white-tailed deer: predictions from a spatially-explicit stochastic model

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Abbreviations
APHIS-VS: Animal and Plant Health Inspection Service-Veterinary Services
bTB: bovine tuberculosis
CLU: Common land unit
DMU 452: Deer Management Unit 452
GIS: Geographic Information Systems
MDARD: Michigan Department of Agriculture and Rural Development
MDNR: Michigan Department of Natural Resources
NRCS: Natural Resources Conservation Service
USDA: United States Department of Agriculture
WTD: white-tailed deer

Abstract

The eradication of bovine tuberculosis (bTB), caused by *Mycobacterium bovis*, from cattle in many locations worldwide is complicated by endemic foci of the disease in free-ranging wildlife. Recent simulation modeling of the bTB outbreak in white-tailed deer (WTD) in Michigan, USA, suggests current management is unlikely to eradicate bTB from the core outbreak area (DMU 452) within the next three decades. However, some level of control short of eradication might sufficiently reduce transmission from deer to cattle to a point at which the negative effects of bTB on the cattle industry could be reduced or eliminated, while minimizing the negative consequences of reducing deer numbers. We extended our existing spatially-explicit, individual-based stochastic simulation model of bTB transmission in WTD to incorporate transmission to cattle, to characterize the effects of vaccination and increased harvest of WTD on cattle herd breakdown rates, to examine the effects of localized culling or vaccination of WTD in the vicinity of cattle farms, to assess the effects of concurrent deer baiting, and to determine the effect of progressive restriction of deer/cattle contact on herd breakdowns. A spatially-explicit "cattle layer" was constructed describing the spatial locations, farm size and cattle density of all farms within and directly adjacent to DMU452. Increased hunter harvest or vaccination of deer, or a combination, would likely decrease the number of cattle herd breakdowns to <1 per year in less than 15 years. Concurrent deer baiting variably increased the time necessary to achieve zero breakdowns. The prevalence of bTB in deer needed to fall below ~0.5% before ≤1 herd breakdown per year could be expected, and below 0.1% before zero breakdowns were likely. Locally applied post-harvest deer culling or vaccination also rapidly reduced herd breakdowns. On farm biosecurity measures needed to reduce deer to cattle contact by >95% in order to

reliably reduce herd breakdowns, and did not achieve zero breakdowns in the absence of other deer controls.

Keywords: Tuberculosis; control strategies; modelling; *Mycobacterium bovis*; *Odocoileus virginianus*; white-tailed deer.

1. Introduction

The eradication of bovine tuberculosis (bTB), caused by *Mycobacterium bovis*, from cattle in many locations worldwide is complicated by endemic foci of the disease in free-ranging wildlife (Gortazar et al., 2011; O'Brien et al., 2011a; Wilson et al., 2011; Gortazar et al., 2015a). Generally, countries with a documented wildlife reservoir have not been successful eradicating *M. bovis* from livestock (Palmer, 2007), although notable exceptions exist (Corner, 2007; Livingstone et al., 2009). Particularly where wildlife maintenance hosts are publicly valued (O'Brien et al., 2011b), bTB control options are often limited by social and economic factors (Carstensen et al., 2011). Implementing biologically sound but publicly controversial management measures, and sustaining them through changing political administrations for sufficient periods to be epidemiologically effective, is often not straightforward (Rudolph et al., 2006; Brown and Middleton, 2012).

Such is the case in Michigan, USA, where free-ranging white-tailed deer (WTD; *Odocoileus virginianus*) are both economically important and publicly esteemed, as well as being the maintenance host of bTB (O'Brien et al., 2006; O'Brien et al., 2011a). Recent simulation modeling has clarified the intensity and duration of control measures likely to be necessary to eradicate bTB from WTD (Cosgrove et al., 2012; Ramsey et al., 2014). Those

results suggest that current Michigan Department of Natural Resources (MDNR) bTB management strategies, which consist principally of liberalized opportunities for hunter harvest combined with restrictions on the feeding and baiting[1] of deer, are unlikely to eradicate bTB from the core outbreak area (Deer Management Unit [DMU] 452) within the next three decades. Moreover, while eradication within thirty years is possible by substantially increasing hunter harvest, eliminating deer baiting, and/or via mass vaccination, the ability of MDNR to coax the cooperation likely to be necessary from hunters is in doubt (Rudolph and Riley, 2014). However, simulations also suggest that even modest increases in harvest are likely to rapidly reduce the prevalence of bTB in WTD (Ramsey et al., 2014, Figs. 3, 4). Although the stated goal of management remains “eradicating bovine tuberculosis in Michigan deer” (Engler, 1998), it is reasonable to question whether, if the public support necessary to reach complete eradication cannot be gained, some level of bTB control short of eradication might sufficiently reduce transmission from deer to cattle to some *de minimis* level. If such a level could be attained, the negative effects of bTB on the cattle industry could be reduced or eliminated, while also allowing decisionmakers to avoid the negative political and economic consequences of reducing WTD numbers more substantially (Rudolph et al., 2006).

Consequently, we extended our existing spatially-explicit, individual-based stochastic simulation model of bTB transmission in WTD to incorporate transmission to cattle. Our objectives were to 1) characterize the effects of vaccination and increased hunter harvest of WTD on infection (breakdown) rates of cattle herds due to bTB; 2) examine the effects of

[1] In the current context, baiting is defined as the intentional placing of food, typically by hunters, to attract deer to a specific location to enhance hunter harvest opportunity (The Wildlife Society, 2007). Baiting, and supplemental feeding of deer in general, have longstanding historical and cultural roots in Michigan (O’Brien et al., 2006). Issues surrounding regulation of deer baiting in Michigan have been discussed elsewhere (Rudolf et al., 2006; Ramsey et al. 2014). An excellent treatment of how human-provided supplemental feed affects pathogen transmission in wildlife is provided by Becker and Hall (2014).

localized culling or vaccination of WTD in the vicinity of cattle farms on breakdown rates; 3) assess the effects of concurrent deer baiting (the use of foodstuffs as an aid to deer harvest) on 1) and 2); and 4) determine the effect of progressive restriction of contact between WTD and cattle on the rate of herd breakdowns. The model was used to simulate the likely effects of increased hunter harvest of deer, vaccination of deer, and culling or vaccination of deer in the vicinity of farms on the number of cattle herd breakdowns in DMU 452, and the probability of having zero breakdowns in a given year.

2. Materials and methods

2.1. Study area

All simulations were conducted over a 48 x 51 km area including DMU 452 (44°40′–45°00′N, 83°30′–84°05′W), located in the northeastern Lower Peninsula of Michigan (Fig. 1). Comprising approximately 149,018 ha (1490 km^2), 93% of which is privately-owned, DMU 452 defines the geographic core area of the bTB outbreak (O'Brien et al., 2002; O'Brien et al., 2006).

2.2. Study data

2.2.1 Deer habitat

To account for resource-related aggregations of deer and the spatial variations in bTB transmission they precipitate, Geographic Information Systems (GIS) layers of habitat potential (deer/ha; (Felix et al., 2007) were used in the model as measures of biological carrying capacity

K_x. These values were mapped on to a raster layer using 100m pixel size to produce the resulting map of habitat potential for DMU452 (Fig. 1).

2.2.2. Cattle

The Michigan Department of Agriculture and Rural Development (MDARD) maintains basic data on all livestock operations in the state. These were accessed to obtain the geographic locations (latitude and longitude) of all cattle producers in Alcona, Alpena, Montmorency and Oscoda Counties, and GIS software (Arc GIS 9, ESRI, Redlands, California) was used to define the subset of producers located within and directly adjacent to DMU 452. All cattle herds in these four counties, which are considered Modified Accredited in the United States Department of Agriculture (USDA)'s Animal and Plant Health Inspection Service-Veterinary Services' (APHIS-VS) split-state bTB accreditation scheme for Michigan, have been subject to annual whole-herd bTB tests since July 2002. All of the accumulated cattle testing data is housed in a USAHERDS (National Agribusiness Technology Center, Arlington, Virginia) database jointly maintained by MDARD and APHIS-VS. Because calves born on the farm are not tested until they reach one year of age, test records encompass cattle 12 months of age and older, plus all purchased additions. The number of cattle on each of the cattle farms in DMU452 as of 29 December 2011 was extracted from USAHERDS.

The estimated area of each premises used as pasture was obtained from the Alpena Conservation District, a local unit of county government dedicated to natural resources conservation and farm programs. Working with Conservation District staff, farms enrolled in the MDARD Wildlife Risk Mitigation Program (MSUE, 2009) developed herd plans which included identification of farm areas used by cattle. Location of pastures were verified during subsequent

site visits, and pasture area was quantified using GIS incorporating 2010 aerial photography. For those cattle farms not enrolled in the program, Conservation District staff contacted the producers for a current description of areas used as pasture, the area of which was then quantified via GIS. For the remaining producers not yet captured, Common Land Unit (CLU) GIS layers (APFO, 2010) were examined to differentiate and quantify areas used as pasture from other crops. Closely related to a farm field by definition, a CLU is an individual farming parcel, the smallest land unit with a permanent, contiguous boundary, common land cover and management, a common owner, and/or a common producer association. Common Land Units enable a quick, automated method for calculating area and for a georeferenced, graphical view of farm records (APFO, 2012). In addition, records maintained by county Equalization Departments and their GIS programs were examined for records of land deeded to the names of producers in the MDARD database. By Michigan law, counties maintain detailed records of land ownership for the purpose of assessing state and local property taxes. This review was carried out to capture any remaining parcels used for cattle pasture that were not found by the Conservation Districts. Area measurements were then derived as described above.

2.3. Computer model

2.3.1. Deer-only model

The model of bTB transmission from WTD to cattle is an extension of a spatially-explicit, individual-based stochastic model of bTB transmission in WTD. The mathematical structure, assumptions, the fit of the model to field data on bTB prevalence, and the sensitivity of model predictions to various parameters are described extensively elsewhere (Cosgrove et al.,

2012; Ramsey et al., 2014). That model was in turn adapted from a model of bTB in brushtail possums (*Trichosurus vulpecula*; Ramsey and Efford, 2010) which is currently being employed in New Zealand to advance bTB eradication efforts there. Forecasts from modeling have been noted as one of the critical factors in the success to date of New Zealand's bTB control program (Livingstone et al., 2009). Of those countries known to have self-sustaining bTB in a wildlife reservoir, New Zealand is currently the only one that appears to be approaching eradication (O'Brien et al., 2011b).

Default parameters for the model were derived from the literature and MDNR field data (see Table 1 in Cosgrove et al. 2012 for parameter-specific references), with the exception of the sex-specific bTB transmission rates. These were estimated by calibrating the model so that steady-state age- and sex- specific bTB prevalence matched long-term field estimates obtained from WTD tested by the Wildlife Disease Laboratory, MDNR, 2003-2007. Details of MDNR bTB surveillance are described elsewhere (O'Brien et al., 2002). The model advanced via two month time steps, corresponding to 6 'seasons' per year. See Ramsey et al. (2014) for additional details.

2.3.2 Cattle layer

To simulate the transmission of bTB between deer and livestock, a spatially-explicit "cattle layer" was constructed describing the spatial locations, farm size and cattle density of all farms within DMU452. The locations (geographic centroids) of all farms within and directly adjacent to DMU452 were mapped on to a raster layer using 100 m pixel size, similar to the map resolution of deer habitat potential. The area of pasture calculated for each farm recorded from the NRCS and tax record data was then used to calculate the number of pixels for each farm

representing farm size (rounded up to 1 ha). The density of cattle for each farm pixel was then calculated as the total herd size divided by the number of pixels for each farm (cattle/ha). The resulting raster map of cattle density per 100 m pixel for DMU452 was then used as the cattle layer in the model (Fig. 2).

2.3.3. Deer-cattle transmission

Transmission of bTB to cattle occurred locally and could only occur when the home range of infected deer overlapped with cattle farms. Transmission to cattle was also dependent on the stocking rate of the farm (increasing contact rate). If on-farm wildlife risk mitigation practices (e.g. fencing, protection of food sources, etc.) occurred this acted to proportionally reduce the contact rate of infected deer with cattle (effective contact rate). The force of infection at a farm located at *x* was thus defined as

$$\lambda(x) = \beta_c \nu(x)\omega(x)\kappa \quad \text{Eqn. 1}$$

Where $\lambda(x)$ is the force of infection at a cattle farm located at *x*, β_c is the deer-cattle transmission rate, $\nu(x)$ is the 'local' infected deer density at *x*, defined as the sum of intensity of home range overlap at *x* by infected deer (see Ramsey and Efford, 2010) for the derivation of $v(x)$), $\omega(x)$ is the stocking rate (density) of cattle at farm *x*, and κ is the proportional reduction in the contact rate due to on-farm wildlife risk mitigation. Estimates of the deer/cattle transmission rate β_c were derived using the results of bTB herd testing occurring 2003-2012. The number of farms within DMU452 that had at least one bTB reactor during whole-herd testing (breakdown) was calculated, as was the mean number of farms with breakdowns per year. The model was then calibrated by conducting a search for the value of β_c that gave the closest match between the

observed and predicted number of breakdowns (Fig. 3). The resulting estimate of β_c was then used in all subsequent simulated bTB control strategies.

2.4. Simulated bTB control strategies

The model was used to simulate the likely effects of a variety of interventions on the number of cattle herd breakdowns among cattle herds in DMU 452, and the probability of having zero breakdowns in a given year. For each simulated control strategy, 5000 replicates were carried out, each running for 80 years, with the first 50 years discarded as a burn-in period. Harvest rates and baiting conditions during each burn-in matched those present during the 2003-2007 period over which the deer-only model was calibrated. Excepting local controls, the model implemented bTB control measures in season six (November and December) of years 51-80. All controls and combinations were modeled both with deer baiting occurring in seasons five and six (September through December) each year, and also without baiting. The default value of κ assumed for all control scenarios was 1 (i.e., unmitigated deer-cattle contact).

2.4.1. DMU-wide control

Simulated WTD control scenarios consisted of increased hunter harvest, vaccination with a hypothetical vaccine, and combinations, and were modeled exactly as described previously (Ramsey et al., 2014). To date, culling has not been given serious consideration as a broad-scale management strategy because of public opposition (Dorn and Mertig, 2005; O'Brien et al., 2011b). Briefly, increases in hunter harvest were modeled as multiples of current harvest rates in DMU 452, estimated by the sex-age kill method (Mattson and Moritz, 2008) to be approximately

40% of antlered (yearling and adult males) and 16% of antlerless (male and female fawns, and yearling and adult females) deer population per year. Four bounding scenarios were modeled: 1.25, 1.5 and two-fold increases in both antlered and antlerless harvest, and a two-fold increase in antlered deer harvest coupled with a three-fold increase in antlerless harvest. Vaccination is also being considered as a bTB management tool (Gortazar et al., 2015a; Palmer et al. 2015). Short duration experimental studies conducted to date using *M. bovis* Bacille Calmette-Guérin (BCG) in WTD suggest it is 66-100% effective, depending on route of exposure and vaccine strain (Palmer et al. 2007, Nol et al. 2008, Palmer et al. 2009). Long term studies of duration and decay of BCG immunity in WTD are underway, but as yet unpublished. However, in cattle, significant immunity persists for at least 1, but not 2, years (Thom et al. 2012). Previous modelling in WTD found that varying vaccine efficacy, duration of guaranteed immunity and the decay of immunity thereafter had only modest effects on the probability of bTB eradication from deer (Ramsey et al. 2014, Table 1). Consequently, the scenarios modelled in this study assumed a 90% efficacious vaccine that provided guaranteed immunity for 1 year, with exponential waning thereafter. Efficacy here was assumed to mean the probability of rendering a susceptible, vaccinated deer immune to infection by *M. bovis*. Because no studies reporting rates of vaccine exposure to WTD in a field setting currently exist, bounding scenarios were modeled in which 50% or 90% of the susceptible population was exposed to the vaccine either annually or triennially.

2.4.2. Local control

Because bTB control measures implemented only in the vicinity of cattle farms seem likely to be less expensive that DMU-wide controls, the model was used to simulate the likely

effects of local control. Using the cattle layer raster map, a buffer area was defined around each farm with the perimeter at a distance of 5 km from the farm boundary. This layer was then converted to raster format, and incorporated into the model as a mask with control measures only implemented within the areas made up of the farms and their surrounding 5 km-wide buffers (Fig. 2). Hence areas outside the 5 km buffer for each farm remained uncontrolled. Simulated control measures carried out within the buffer consisted of 1) annual culling of 20% or 50% of the WTD remaining after hunter harvest; and 2) vaccination of 50% or 90% of the susceptible WTD population annually. To avoid concurrence with hunting seasons, local controls were implemented in season one of years 51-80 (January and February).

2.4.3. Restriction of deer-cattle contact

Other forms of local control involve the use of increased on-farm biosecurity to limit the movement of deer on to farms and the direct or indirect contact of cattle to them. These measures could include improved fencing and/or the exclusion of deer from feed sources (e.g. hay storage). The potential effectiveness of such measures was simulated by reducing the contact rate between cattle and deer achieved by altering the value of κ in the model (between 0 and 1). As there were no data available to estimate the relative effectiveness of biosecurity measures at reducing deer/cattle contact rates, we simulated scenarios under a variety of values of κ from 1.0 (no reduction in the effective contact rate) to 0.05 (95% reduction in the effective contact rate).

2.5. Software

The model was developed in Pascal using Delphi (Borland Software, Austin, TX). Summary graphs of the number of cattle herds infected with bTB and the probability of having zero herd breakdowns over the thirty year period were generated using R (Version 3.0.3, www.r-project.org, accessed 20 March 2014). A probability ≥95% was considered 'high'. Because the prevalence of bTB in DMU 452 deer is a long term metric used by MDNR surveillance to monitor progress of the outbreak over time (Gortazar et al., 2015a), deer prevalence at the time various cattle herd infection thresholds were reached was also calculated with R for scenarios that involved DMU-wide controls.

3. Results

Eighty-six cattle farms were included in the simulations: five, six, ten and sixty-five each from the Oscoda, Alcona, Montmorency and Alpena County portions of DMU452, respectively. The mean (σ) total area and area in pasture for these farms was 116 (57) ha and 58 (22) ha, respectively. The mean number of cattle on premises was 38 (range: 0-496). Ten farms (12%) were classified as dairies by MDARD, with the remainder beef herds, subdivided as follows: general beef 61 (71%); "freezer" beef (herds of ≤6 head being raised for family consumption, with no breeding on site) 7 (8.1%); feedlot 4 (4.7%); beef breeder (i.e. cow-calf operations) 3 (3.5%); "4H" cattle (calves being raised by youths in agricultural clubs for exhibition) 1 (1.2%). Farms in the general beef category included production systems that raised their own calves and sold animals both as breeders and to slaughter. Across all farms, although some variation, particularly seasonal, existed, management practices were typically extensive and pasture-based. Even amongst dairies where cows were kept confined, practices such as green chopping of

forages for immediate feeding were utilized periodically when feed was in short supply. Consequently, even confined cattle were indirectly exposed to *M. bovis* from forage crops (and other feedstuffs stored outside) to which infected deer had access.

3.1. DMU-wide control

Simulations indicated that simply maintaining current harvest levels coupled with perfect compliance with a ban on baiting and feeding would attain a 90% probability of having zero cattle herd breakdowns by the end of thirty years (Fig. 4). Prevalence in wild deer at that juncture was predicted to be 0.06%.

3.1.1. Increased harvest

All four scenarios of increased harvest reduced the rate of herd breakdowns to one per year or less within 12 years, although at least a 50% increase in harvest was necessary to achieve a high probability of zero breakdowns within three decades with baiting occurring (Fig. 5A). Complete compliance with a baiting ban further reduced that time, and achieved a high probability of zero breakdowns by 20 years post burn in (pbi) for all harvest scenarios (Fig. 5B). Depending on the scenario, bTB prevalence was 0.4-0.5% when herd infections reached 1 per year, and 0.07-0.09% when the zero breakdowns threshold was reached.

3.1.2. Vaccination

Annual vaccination of deer also rapidly decreased herd breakdowns to ≤1 per year within 7 years. Ninety percent exposure of susceptible deer led to a high probability of no cattle herd

breakdowns by year 15 pbi, while 50% exposure achieved that threshold in 23 years (Fig. 6A). Eliminating baiting reduced the times to achieve zero breakdowns by 2 and 7 years, respectively (Fig. 6B). Increasing the vaccination interval to once every three years still reduced herd breakdowns to one per year relatively quickly, but was considerably less reliable at bringing about a high probability of zero breakdowns (Fig. 7A), with 26 years required to reach that level even vaccinating 90% of susceptible deer. With baiting eliminated, triennial vaccination attained zero breakdowns by year 17 pbi with 90% exposure and by 23 years pbi with 50% exposure (Fig. 7B). Across all scenarios, prevalence in deer was 0.4-0.6% when cattle herd breakdowns declined to 1 per year, and 0.03-0.09% when breakdowns reached zero.

3.1.2. Vaccination combined with increased harvest

Combining the effects of increased hunter harvest of deer with vaccination further reduced the time necessary to achieve a high probability of zero cattle herd breakdowns, but not greatly. Variations in frequency of vaccination, percent of susceptible deer exposed, or the presence of baiting made little or no difference, depending on the extent of the harvest increase (Table 1). In all scenarios, the number of breakdowns reached one or fewer per year within 7 years, and a high probability of zero breakdowns within 22, but no fewer than 6, years. By the time the threshold of zero breakdowns was reached, bTB prevalence in deer was always less than a tenth of one percent.

3.2. Local control

3.2.1. Post-harvest culling

Annual culling of deer within 5 km of cattle farms following the end of deer hunting seasons also decreased breakdowns to <1 per year within 6 years, but with baiting occurring, 29 years were required to attain a high probability of zero annual breakdowns, even killing half of the deer population remaining after hunter harvest each year (Fig. 8A; Table 2). Here, elimination of baiting was comparatively more influential, attaining the zero breakdowns threshold 21 years earlier with a 50% culling rate, and at least 14 years earlier with a 20% rate (Fig. 8B).

3.2.2. Local vaccination

With baiting continuing concurrently, annually vaccinating even 90% of the susceptible deer within 5 km of DMU 452 cattle farms did not assure a high probability of zero herd breakdowns within three decades (Fig. 9A; Table 2). By eliminating baiting a high probability of eliminating herd breakdowns was attained within 20 years pbi, regardless of whether half or 90% of susceptible deer were vaccinated (Fig. 9B).

3.2.2. Restriction of deer-cattle contact

Restricting contact between deer and cattle with 95% effectiveness reduced the herd breakdown rate to less than 1 per 5 years (Fig. 10). However, this level of contact reduction only achieved a moderately high probability of zero breakdowns of 87% (Figure 10).   Lower rates of restriction of deer/cattle contact (≤50%) had largely negligible effects on the herd breakdown rate with estimates having high variability that were indistinguishable statistically from unmitigated deer/cattle contact.

4. Discussion

It is not an overstatement to say that bTB management in Michigan is currently at a pivotal crossroad. While it is indisputable that significant progress has been made in controlling the outbreak in both livestock (Okafor et al., 2011) and wildlife (O'Brien et al., 2011a; Palmer et al., 2015), progressing further toward overall eradication is in doubt. With the cooperation of cattle producers, both MDARD and USDA APHIS-VS have succeeded in reducing the area of Michigan that is not yet Accredited Free of bTB to just the four counties surrounding DMU 452. These actions have minimized the negative economic and social impacts on >96% of Michigan's cattle farms. However, the remaining 400+ cattle farms in those four counties are eager to be freed of the additional testing and movement controls that accompany their current Modified Accredited status, and continually petition those agriculture agencies to further reduce the area subject to these restrictions. Indeed, that area has now been reduced to the point where bTB continues to be endemic in free-ranging deer in counties which are Accredited Free of bTB for cattle. This dissidence creates confusion among hunters, who often fail to understand how the same county can be both free of bTB (for cattle) and yet infected with bTB (in deer). It also creates justifications for hunters, wildlife managers and legislators tired of MDNR control measures (deer density reductions and baiting and feeding restrictions) who desire to see those measures eased or discontinued. In contrast to agricultural producers and agencies, hunters and wildlife agencies are rarely enthusiastic about pursuing the additional measures likely to be required to bring about the stated policy goal of bTB eradication (Rudolph et al., 2006; Ramsey et al., 2014). In addition, changing hunter demographics (Riley et al., 2003; Winkler and Warnke, 2013) and deer management trends (O'Brien et al., 2012), limits to agency ability to

influence hunter's actions (Rudolph and Riley, 2014; Triezenberg et al., 2016), and concerns about establishment of bTB in feral swine (Gortazar et al., 2015b) which occur in the endemic area may further complicate control efforts.

While there has as yet been little policymaker enthusiasm for pursuing the eradication of bTB from wild deer that previous modelling has suggested is possible (Ramsey et al., 2014), hope remains that quicker, less costly interventions that could reduce or eliminate cattle herd breakdowns may prove to be more attractive. To that end, these results should prove useful for planning purposes. Worthy of note is the rapidity with which modelled scenarios brought about a decline in breakdowns. The majority of measures were predicted to bring breakdowns below the one per year threshold within a decade, a time period which seems more likely to obtain buy in from policymakers than the three decades (or longer) required to eradicate bTB from deer (Ramsey et al., 2014). Similarly, application of local controls would seemingly be a less objectionable policy option owing to the substantial cost and human resource savings garnered from having to apply controls over an area only one third the size of the entire core outbreak area. Despite these advantages, longstanding objections to any agency culling of deer (Dorn and Mertig, 2005; Carstensen et al., 2011; O'Brien et al., 2011b) and challenges to further increasing hunter harvest (Ramsey et al., 2014; Rudolph and Riley, 2014; Triezenberg et al., 2016) make the likelihood of effectively applying such controls over even a limited area far from certain. Even the prospect of vaccination of free-ranging deer, for which the scientific evidence base is both promising and well-advanced (Waters et al., 2012; Buddle et al., 2013), and for which there has, as yet, been minimal public opposition in Michigan, has received little policymaker interest, let alone overt support. Nevertheless, planning optimistically continues (Gortazar et al., 2015a).

Feasibility is an as yet essentially undiscussed policy factor which will be critical to effective implementation of any further bTB eradication strategies. From the outset, management of bTB in Michigan has been, not unexpectedly, divisive (O'Brien et al., 2006), with cattle producers and deer hunters often holding dramatically differing views on how the outbreak should be managed (Dorn and Mertig, 2005). Typically, each group has considered itself to have made the greater sacrifice thus far, and argued that the other should bear any additional burden of control, be it cost or otherwise. The potential interventions considered here are likely to differ greatly in both scope and cost. For example, even as a local control, annual vaccination or agency culling of deer could not be effectively applied piecemeal, thus necessitating government funding, implementation, and sustenance over decades. Additional funding would need to be secured legislatively. It seems unlikely that any of the potential revenue sources (increased deer hunting license fees, a per head levy on cattle marketed, or a tax increase for the general public) would be well received by the affected stakeholders. While increased biosecurity measures for cattle operations would likely cost substantially less overall because they could be implemented as a one-time effort on a fixed number of premises, producers are unlikely to willingly bear those costs without government subsidy. Moreover, farmers may resist biosecurity measures (e.g. high fences) that they consider to be excessively restrictive regardless of their effectiveness, particularly if the cost of those measures is borne by cattle producers. Buyouts of cattle farms in high risk areas, which might be considered the ultimate in heightened biosecurity, have been used effectively in Minnesota's bTB outbreak (Carstensen and DonCarlos, 2011; Carstensen et al. 2011). Reception by producers in Michigan to the idea has thus far been less than enthusiastic. Deer hunters are supportive to indifferent, as

long as they do not have to pay for the buyouts; again, funding from either the state or federal government would likely be necessary.

Previous modelling of bTB in wild deer alone found that, in general, deer baiting slows the rates at which harvest and/or vaccination decrease bTB prevalence, prolongs the time necessary to achieve eradication, and increases the likelihood that once eradicated, bTB will become re-established (Ramsey et al., 2014). Results were similar in the deer to cattle model, although in some scenarios (e.g., DMU-wide vaccination and increased hunter harvest applied simultaneously), the times to zero cattle herd breakdowns were reduced only minimally by elimination of baiting. In general, as controls became more intensive (e.g., higher harvest or culling rates, higher proportions of susceptibles exposed to vaccine more frequently), the magnitude of the effect attributable to baiting was attenuated. That said, complete elimination of baiting alone, without application of any other management, resulted in a reasonably (although not significantly) high probability of achieving zero infected herds within 30 years (Fig. 4) if current deer harvest rates are maintained.

Considerable recent effort has been devoted internationally to quantifying use of farms by wildlife that could result in exposure of livestock to pathogens, particularly bTB (Berentsen et al., 2014; Gooding and Brook, 2014; Kitts-Morgan et al., 2015; O'Mahony, 2015; Payne et al., 2016), and to designing and testing biosecurity measures that could mitigate those risks, including fencing (VerCauteren et al., 2006; Phillips et al., 2012) and livestock protection dogs (Vercauteren et al., 2008; VerCauteren et al., 2012). In our current modelling, when biosecurity measures that restricted contact between deer and cattle were implemented, the herd breakdown rate declined as expected. However, significant reduction in the breakdown rate (<1 breakdown per 5 years) only occurred if at least a 95% reduction in deer/cattle contact occurred. These

results suggest that biosecurity measures must virtually eliminate potential contacts between deer and cattle before herd breakdowns are likely to cease if no additional deer management measures occur. That said, existing studies in both Michigan and the UK have demonstrated that this level of exclusion can be achieved with relatively simple biosecurity measures, if they are properly and consistently applied on farms (Judge et al., 2011; Lavelle et al., 2015).

Because apparent prevalence of bTB in DMU 452 deer has been the primary metric used to monitor Michigan's wildlife reservoir, it possesses both longevity (Gortazar et al., 2015a) and recognition by policymakers and the public. Thus, tying specific milestones of cattle bTB eradication to specific prevalence levels in deer helps all stakeholders quantify the relationship between levels of infection in the two species, and helps identify target thresholds for bTB control in wildlife. In this study, although more intensive deer management scenarios tended to attain the milestones of one or zero annual cattle herd breakdowns at slightly higher bTB prevalence, with the exception of high rates of local post-harvest culling, regardless of the intervention, prevalence had to decline to ≤0.6% before only a single herd breakdown occurred each year, and to ≤0.1% before there was a high probability of zero breakdowns. These are particularly useful and easily communicated targets to convey to policymakers and the public to approximate when they might expect to see herd breakdowns cease, and how far off that might be. These prevalence levels were determined assuming unmitigated contact between deer and cattle, so to the extent that high levels of biosecurity are successful at restricting that contact, deer prevalence at those thresholds could conceivably be higher. Because cattle herd breakdowns have continued to occur, albeit in low numbers, even though bTB prevalence in deer has declined below 2%, it has been speculated that wildlife species other than deer are also likely to be transmitting bTB to cattle (Walter et al., 2012; Walter et al., 2013). Yet these modelling

results suggest otherwise, and predict that herd breakdowns should be expected to continue until bTB prevalence in deer in is maintained below ~0.1%. Currently, genetic lines of evidence also argue against the involvement of wildlife other than deer in transmission of bTB to Michigan cattle (Tsao et al., 2014; Salvador et al., 2015).

Some limitations of this study should be kept in mind. Given extensive cattle production systems in the bTB endemic area, modelling deer-cattle contact via stocking rate is logical. However, to the extent that cattle are held in confinement in other areas, these methods may overestimate contact rates between WTD and susceptible cattle, and so time to zero breakdowns. However, even without direct contact on pasture, exposure of cattle to *M. bovis* is likely to occur via forage crops contaminated by infected deer. In addition, because there were no farm-level data with which to evaluate the effectiveness of biosecurity measures at reducing deer to cattle contacts, the model assumed that κ was the same for all farms so that β_c and κ were separately estimable. Given the similarity of management practices across farms in the modelled area, this is not unreasonable. Yet it is also possible that unmeasured differences in the effective deer to cattle contact rate do exist from farm to farm, the magnitude of which are unknown. Work to better define such variation would be a fitting priority for future research.

5. Conclusions

Our individual-based stochastic simulation model of bTB shows that increased hunter harvest or vaccination of free-ranging deer, or a combination, would likely decrease the number of cattle herd breakdowns to < 1 per year in less than 15 years. Concurrent deer baiting increased the time necessary to achieve zero herd breakdowns to a variable extent. The

prevalence of bTB in deer needed to fall below approximately 0.5% before less than one cattle herd breakdown per year could be expected, and below 0.1% before a high probability of zero breakdowns was likely. Post-harvest deer culling or vaccination applied only within close proximity of cattle farms also rapidly reduced herd breakdowns. On farm biosecurity measures need to reduce deer to cattle contact rates by 95% in order to reliably reduce herd breakdowns, and even then did not achieve a high probability of zero breakdowns in the absence of other deer controls.

Acknowledgements

The authors gratefully acknowledge the assistance of R. Mellberg, K. Parsons, and E. Sewell of USDA-NRCS and J. Averill, S. Maniacci, D. Minier and M. VanderKlok of MDARD for assistance in collecting the cattle farm data. Thoughtful comments from two anonymous reviewers significantly improved the manuscript, and are greatly appreciated.

This work was supported in part by the U.S. Federal Aid in Wildlife Restoration Act under Michigan Pittman-Robertson Project W-147-R.

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Figure Captions

Fig. 1. Study area in northeastern lower Michigan, USA, used in the modeled simulations (2,448 km^2) encompassing Deer Management Unit (DMU) 452 (black polygon). Darker colors represent higher deer habitat potential ($K_{x;}$ Felix et al., 2007), corresponding to biological carrying capacity.

Fig. 2. The locations and areas of cattle farms (squares) in or directly adjacent to Deer Management Unit (DMU) 452 (black polygon), including 5 km buffer areas around each farm boundary (white squares), used to simulate ‘local’ deer control measures. Shading of cattle farms (scale) depicts cattle density (head/ha). Summed over all farms, the farms and their buffer areas comprised 32% (~477 km2) of the total area of DMU 452, and 19% of the entire modelled landscape.

Fig. 3. The mean number of cattle farms that had at least one bTB reactor (breakdown) per year in DMU452 (Obs) versus the number of breakdowns predicted by the deer/cattle spatial model (Predicted). Vertical lines depict 95% binomial confidence limits.

Fig. 4. Model predicted number of cattle herd breakdowns (left) and probability of zero breakdowns (right) in farms within and directly adjacent to Deer Management Unit (DMU) 452, Michigan, USA, under current hunter harvest levels but with deer baiting eliminated. Current harvest was assumed to be 40% of the antlered deer and 16% of antlerless deer population per year.

Fig. 5. Model predicted number of cattle herd breakdowns (left) and probability of zero breakdowns (right) under four scenarios of increased hunter harvest, with deer baiting occurring (A) and with baiting eliminated (B). Line types correspond to rates of harvest: solid, 25% increase above current harvest; dashed, 50% increase; dotted, doubling of harvest; dot-dashed, doubling of antlered harvest coupled with tripling of antlerless harvest.

Fig. 6. Model predicted number of cattle herd breakdowns (left) and probability of zero breakdowns (right) under two scenarios of annual vaccination, with deer baiting occurring (A) and with baiting eliminated (B). Line types depict exposure rates to the vaccine: solid, 50% of susceptible deer in the population vaccinated; dashed, 90% of susceptibles vaccinated.

Fig. 7. Model predicted number of cattle herd breakdowns (left) and probability of zero breakdowns (right) under two scenarios of triennial vaccination, with deer baiting occurring (A) and with baiting eliminated (B). Line types depict exposure rates to the vaccine: solid, 50% of susceptible deer in the population vaccinated; dashed, 90% of susceptibles vaccinated.

Fig. 8. Model predicted number of cattle herd breakdowns (left) and probability of zero breakdowns (right) under two scenarios of annual local post-harvest culling, with deer baiting occurring (A) and with baiting eliminated (B). Line types depict culling intensities applied only on the farms themselves and to a 5 km buffer area surrounding the farms: solid, 20% of the deer remaining in the population after hunting seasons culled; dashed, 50% of remaining deer culled.

Fig. 9. Model predicted number of cattle herd breakdowns (left) and probability of zero breakdowns (right) under two scenarios of annual local vaccination, with deer baiting occurring (A) and with baiting eliminated (B). Line types depict exposure rates to the vaccine applied only on the farms themselves and to a 5 km buffer area surrounding the farms: solid, 50% of susceptible deer in the area vaccinated; dashed, 90% of susceptibles vaccinated.

Fig. 10. Model predicted number of cattle herd breakdowns (left) and probability of zero breakdowns (right) with increasing proportional reduction in deer-cattle contact rate.

Table 1. Model predicted years post burn-in to attain a 95% probability of having zero cattle herd breakdowns due to bovine tuberculosis (bTB) in Deer Management Unit (DMU) 452, Michigan, USA, and prevalence of bTB in free-ranging deer in DMU 452 in that year. Results based on the means of 5000 simulations over 80 years excluding a 50 year burn in period.

			Vaccination interval			
			Annual		Triennial	
Vaccine exposure rate	Baiting?	Increase in deer harvest rate	Years to zero breakdowns	bTB prevalence in deer (%)	Years to zero breakdowns	bTB prevalence in deer (%)
50%	Yes	1.25x	16	0.025	22	0.033
		1.5x	12	0.033	15	0.031
		2x	9	0.038	10	0.036
		2x antlered/ 3x antlerless	6	0.077	7	0.054
	No	1.25x	13	0.027	16	0.026
		1.5x	11	0.030	14	0.017
		2x	8	0.047	9	0.040
		2x antlered/	6	0.069	6	0.078

		3x antlerless				
90%	Yes	1.25x	13	0.020	17	0.065
		1.5x	11	0.024	13	0.051
		2x	9	0.027	10	0.036
		2x antlered/	6	0.064	6	0.089
		3x antlerless				
	No	1.25x	12	0.020	14	0.048
		1.5x	10	0.027	11	0.048
		2x	8	0.037	9	0.040
		2x antlered/	6	0.058	6	0.074
		3x antlerless				

Table 2. Model predicted years post burn-in to attain a 95% probability of having zero cattle herd breakdowns due to bovine tuberculosis (bTB) in Deer Management Unit (DMU) 452, Michigan, USA, and prevalence of bTB in free-ranging deer in DMU 452 in that year under scenarios of local (within 5 km of each cattle farm) control. Results based on the means of 5000 simulations over 80 years excluding a 50 year burn in period.

Control	Rate of vaccine exposure or culling	Baiting?	Years to zero breakdowns	bTB prevalence in deer (%), DMU 452
Annual vaccination	50%	Yes	>30	—
		No	19	0.062
	90%	Yes	>30	—
		No	17	0.071
Post-harvest culling	20%	Yes	>30	—
		No	16	0.094
	50%	Yes	29	0.32
		No	8	0.27

Figure 1.

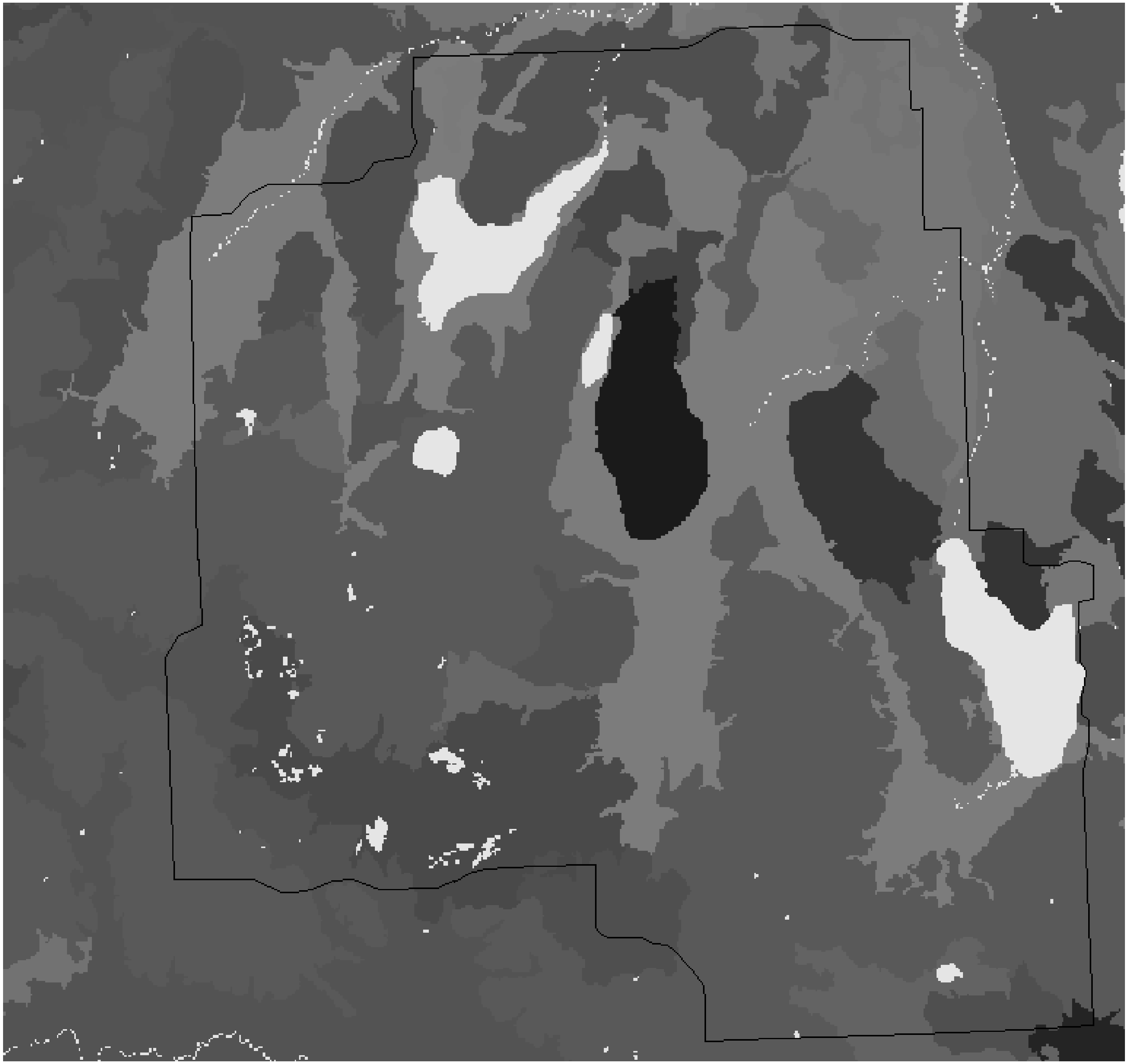


Figure 2.

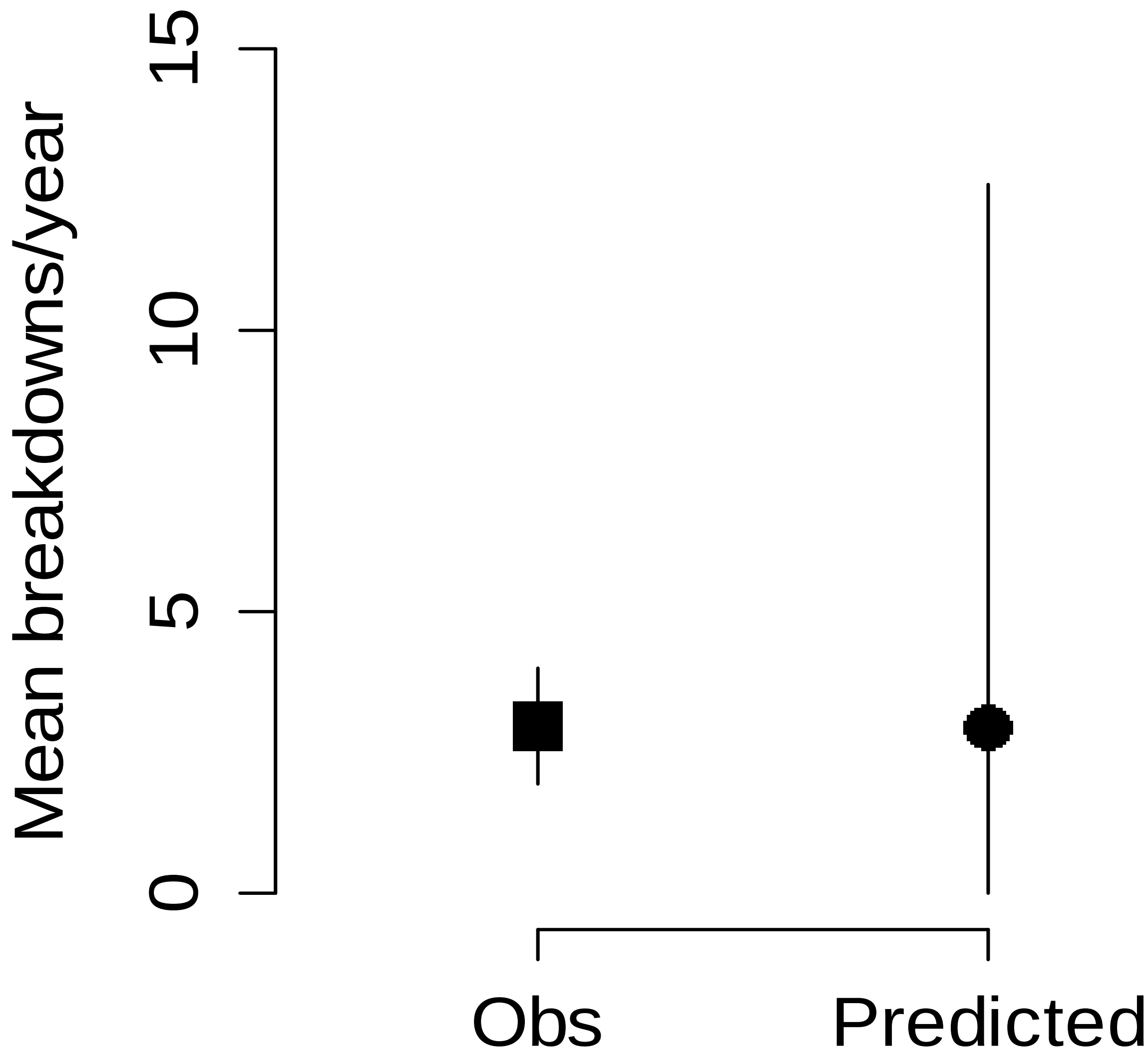


Figure 3.

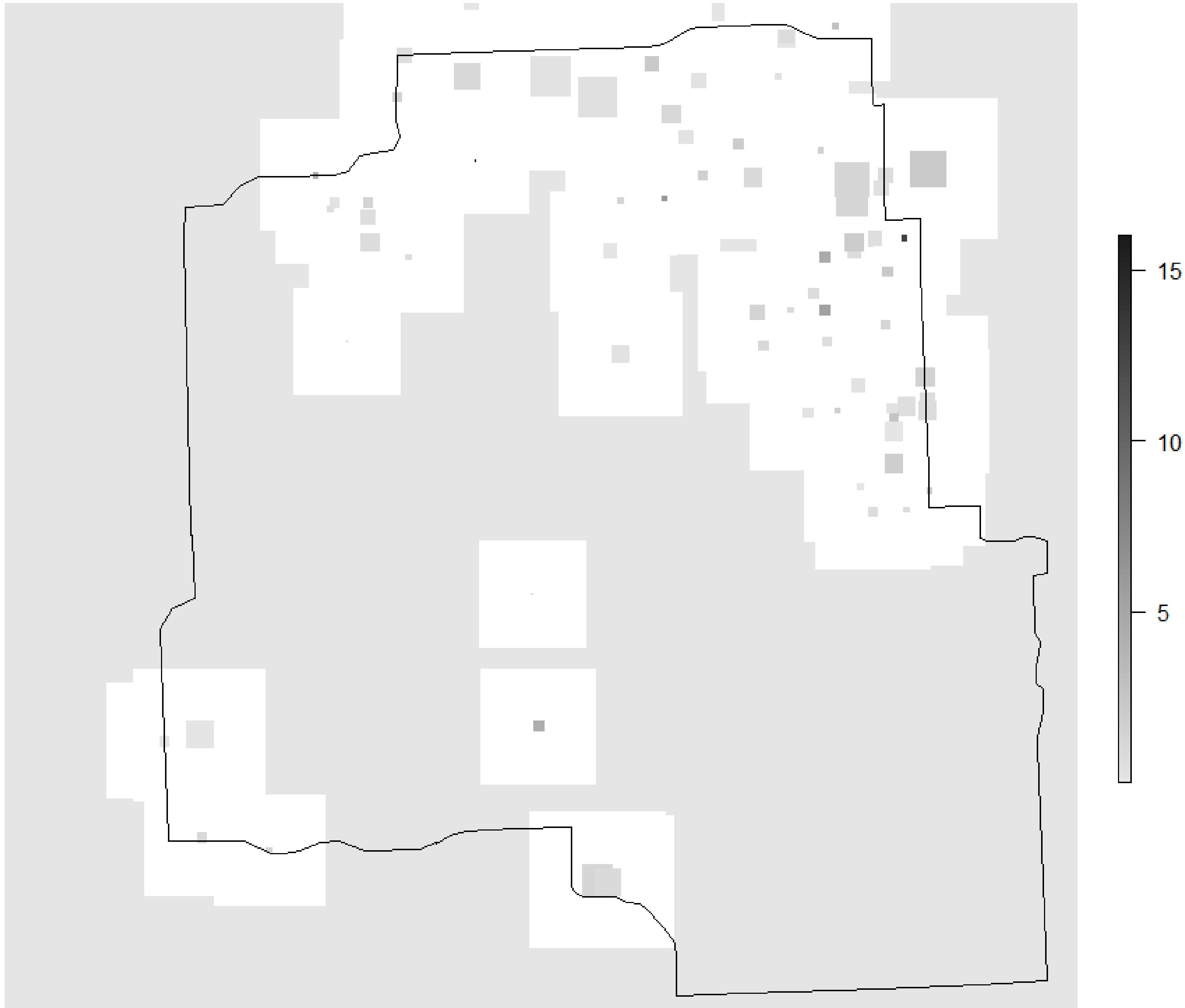
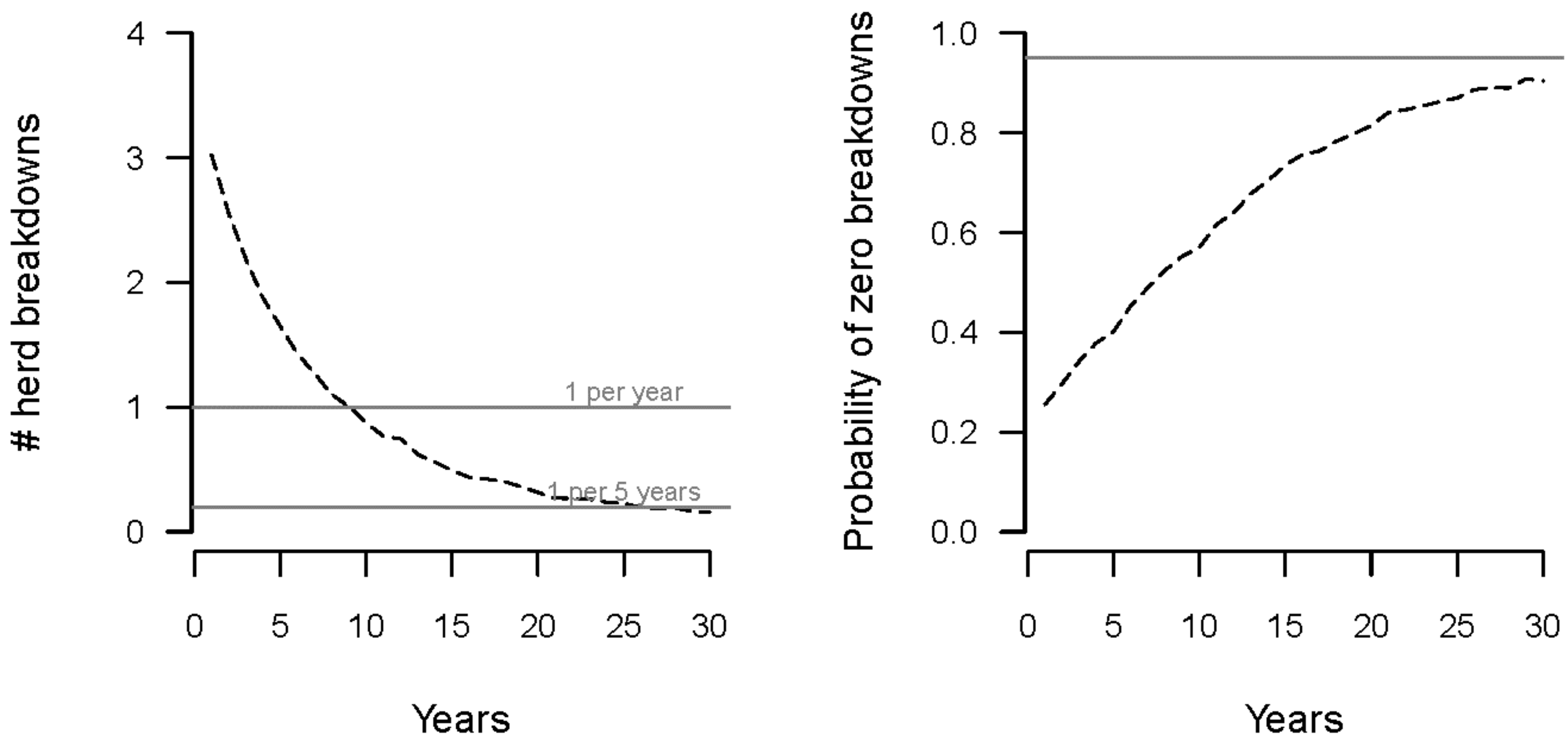


Figure 4.



herd breakdowns
4
3
2
1
0
1 per year
1 per 5 years
0
5
10
15
20
25
30
Years
Probability of zero breakdowns
1.0
0.8
0.6
0.4
0.2
0.0
0
5
10
15
20
25
30
Years

Figure 5.

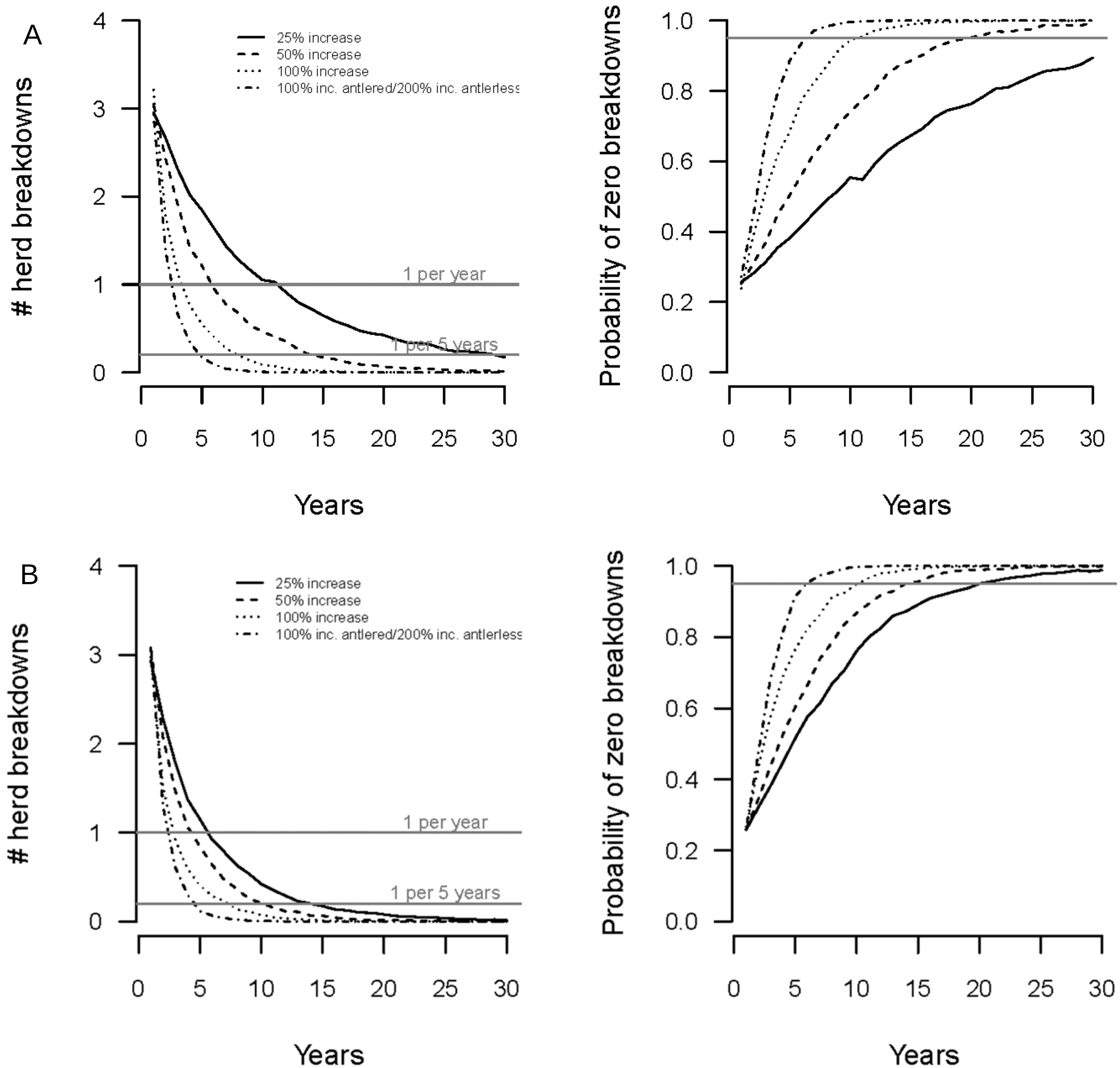
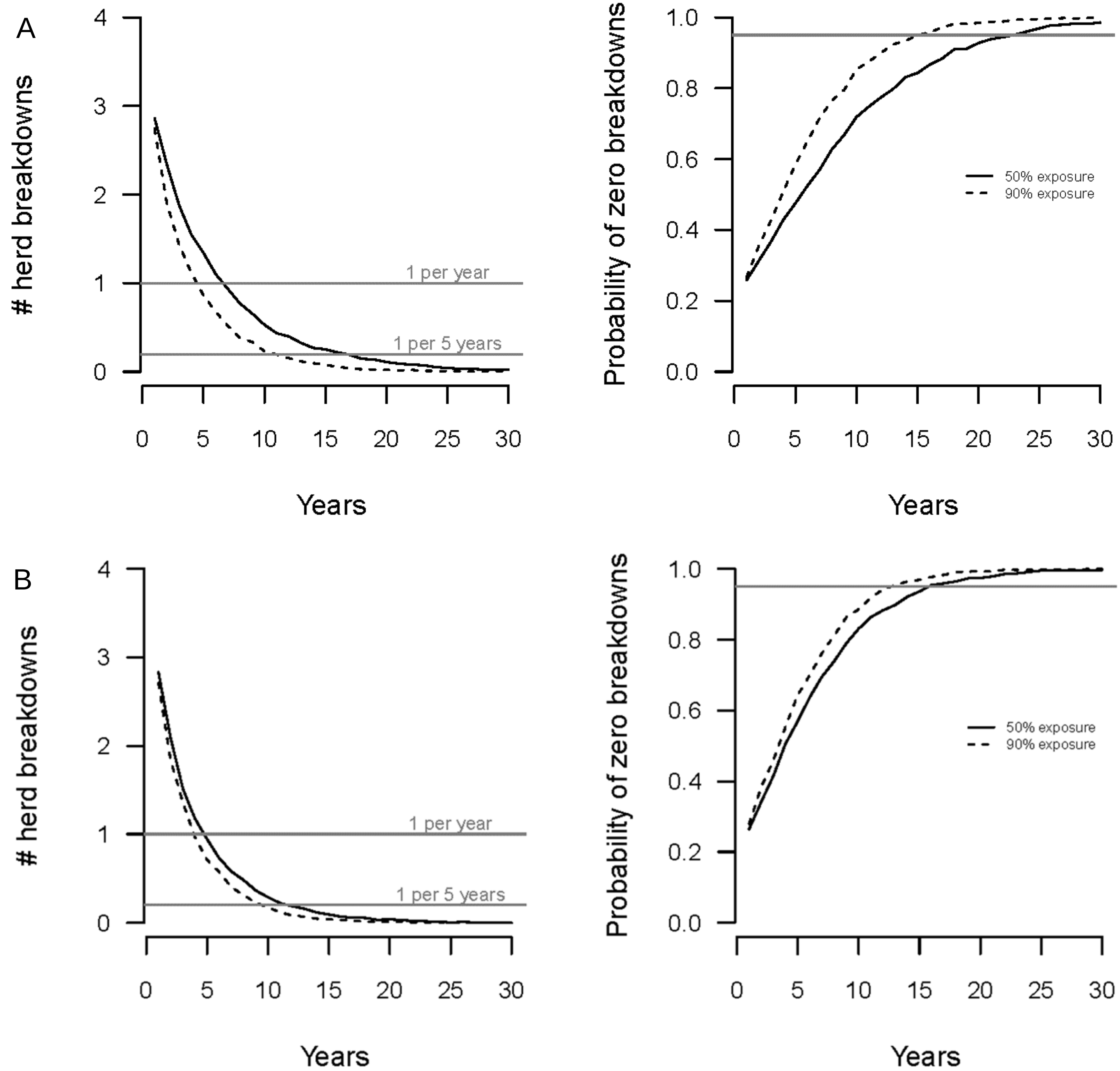
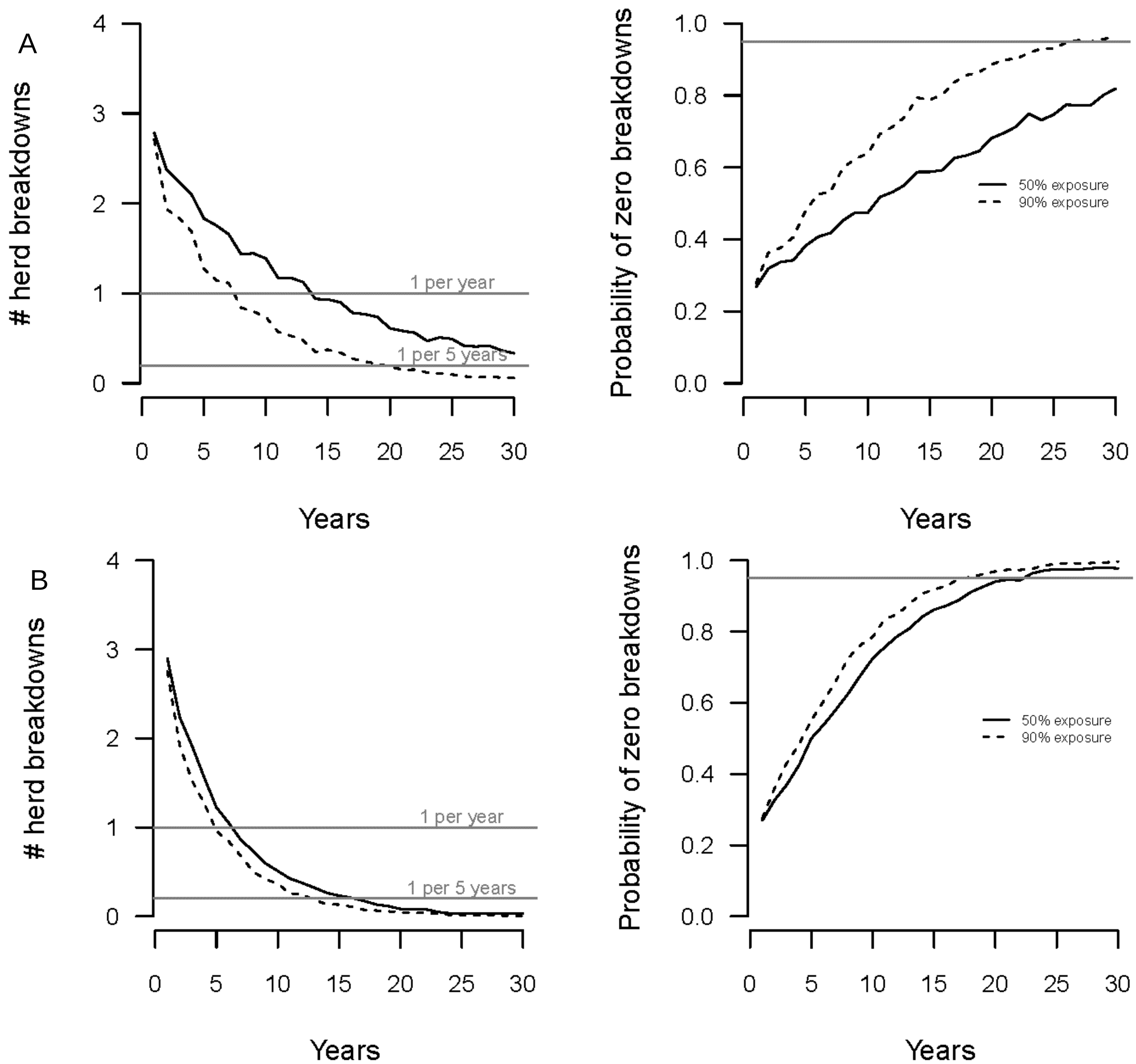

A
B
25% increase
50% increase
100% increase
100% inc. antlered/200% inc. antlerless
herd breakdowns
Probability of zero breakdowns
1 per year
1 per 5 years
Years

Figure 6.



A
herd breakdowns
1 per year
1 per 5 years
Years
Probability of zero breakdowns
50% exposure
90% exposure
Years
B
herd breakdowns
1 per year
1 per 5 years
Years
Probability of zero breakdowns
50% exposure
90% exposure
Years

Figure 7.



A
herd breakdowns
4
3
2
1
0
1 per year
1 per 5 years
0
5
10
15
20
25
30
Years
Probability of zero breakdowns
1.0
0.8
0.6
0.4
0.2
0.0
50% exposure
90% exposure
Years
B
herd breakdowns
1 per year
1 per 5 years
Years
Probability of zero breakdowns
50% exposure
90% exposure
Years

Figure 8.

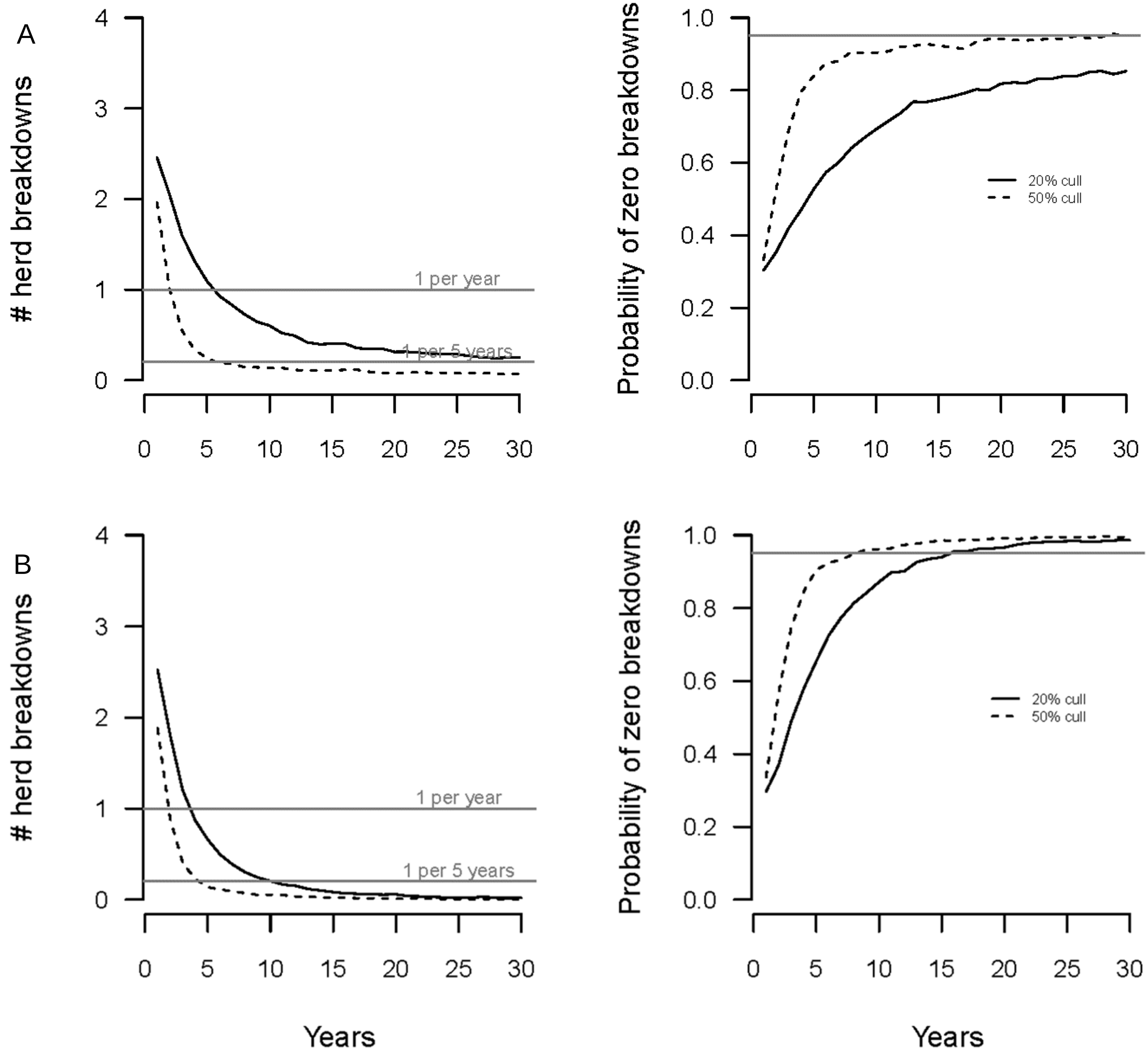

A
B
herd breakdowns
1 per year
1 per 5 years
Probability of zero breakdowns
20% cull
50% cull
Years
0
1
2
3
4
5
10
15
20
25
30
0.0
0.2
0.4
0.6
0.8
1.0

Figure 9.

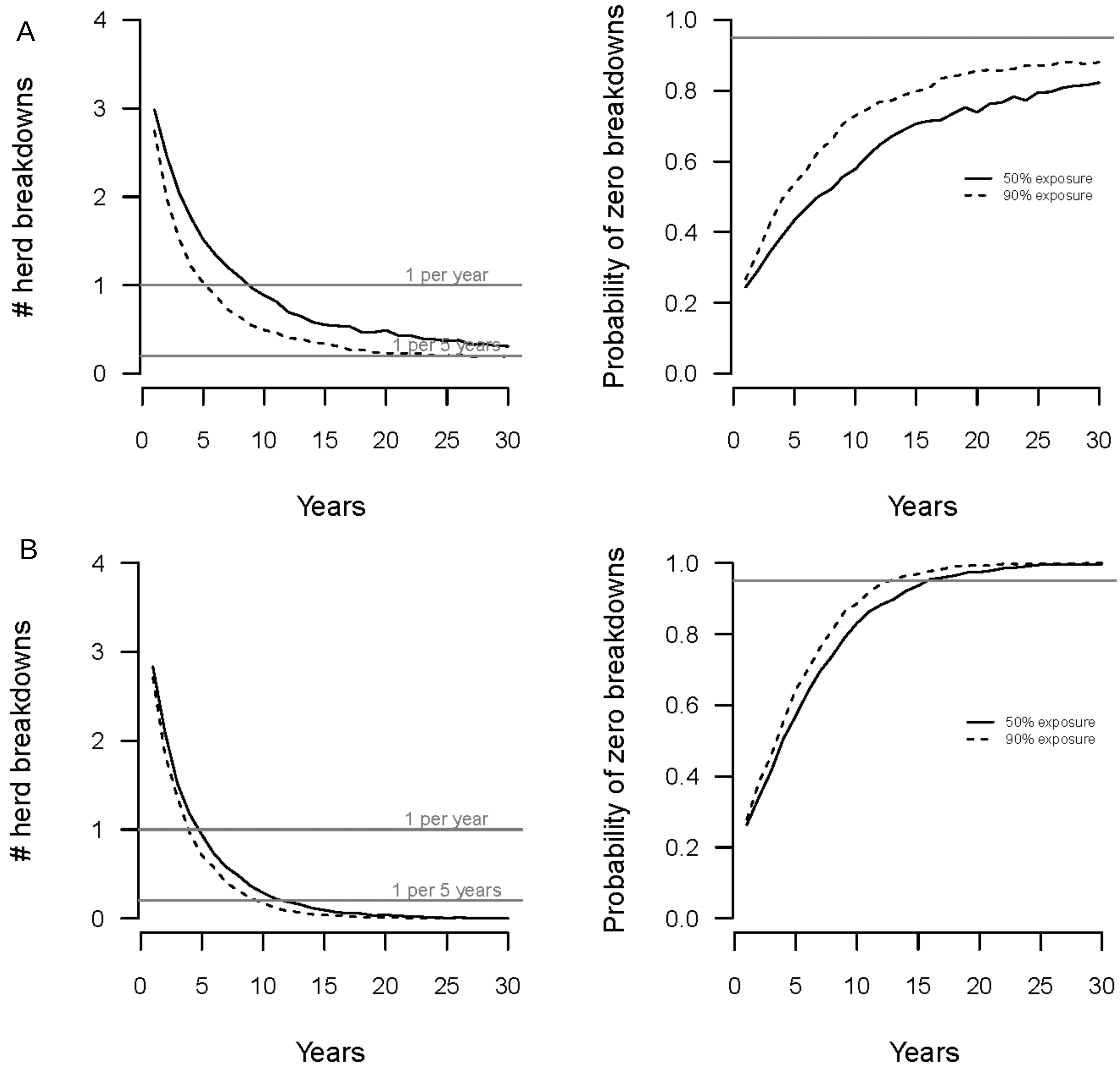
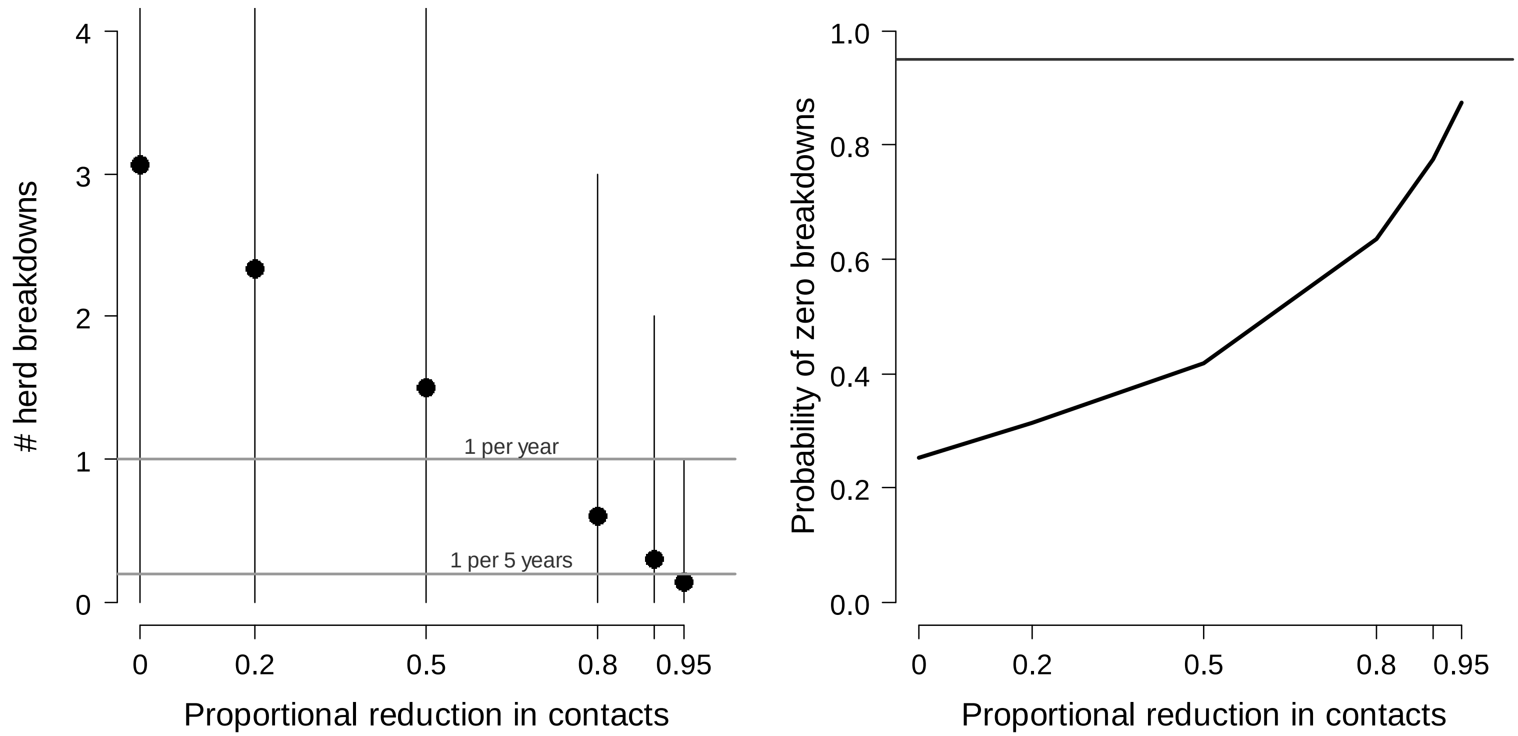

A
B
herd breakdowns
Probability of zero breakdowns
Years
1 per year
1 per 5 years
50% exposure
90% exposure
0
1
2
3
4
0.0
0.2
0.4
0.6
0.8
1.0
0
5
10
15
20
25
30

Figure 10.



4
3
2
1
0
herd breakdowns
1 per year
1 per 5 years
0
0.2
0.5
0.8
0.95
Proportional reduction in contacts
1.0
0.8
0.6
0.4
0.2
0.0
Probability of zero breakdowns
0
0.2
0.5
0.8
0.95
Proportional reduction in contacts