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ESTIMATING THE RISK OF CATTLE EXPOSURE TO TUBERCULOSIS POSED BY WILD DEER RELATIVE TO BADGERS IN ENGLAND AND WALES

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ABSTRACT: Wild deer populations in Great Britain are expanding in range and probably in numbers, and relatively high prevalence of bovine tuberculosis (bTB, caused by infection with *Mycobacterium bovis*) in deer occurs locally in parts of southwest England. To evaluate the *M. bovis* exposure risk posed to cattle by wild deer relative to badgers in England and Wales, we constructed and parameterized a quantitative risk model with the use of information from the literature (on deer densities, activity patterns, bTB epidemiology, and pathology) and contemporary data on deer, cattle, and badger (*Meles meles*) distribution and abundance. The median relative risk score for each of the four deer species studied—red (*Cervus elaphus*), fallow (*Dama dama*), and roe (*Capreolus capreolus*) deer, and muntjac (*Muntiacus reevesi*)—was lower than unity (the relative risk set for badgers, the putative main wildlife reservoir of *M. bovis* in England and Wales). However, the 95th percentiles associated with risk estimates were large, and the upper limits for all four deer species exceeded unity. Although *M. bovis* exposure risks to cattle from deer at pasture are likely to be lower than those from badgers across most areas of England and Wales where cattle are affected by bTB because these areas coincide with high-density badger populations but not high-density deer populations, we predict the presence of localized areas where relative risks posed by deer may be considerable. Moreover, wherever deer are infected, risks to cattle may be additive to those posed by badgers. There are considerable knowledge gaps associated with bTB in deer, badgers, and cattle, and data available for model parameterization were generally of low quality and high variability, and consequently model output were subject to some uncertainty. Improved estimates of the proportion of time that deer of each species spend at pasture, the likelihood and magnitude of *M. bovis* excretion, and local badger and deer densities appear most important for improving estimates of relative risk in this system.

Key words: Bovine tuberculosis, Eurasian badger, fallow deer, *Mycobacterium bovis*, quantitative risk assessment, red deer, Reeves' muntjac, risk model, roe deer.

INTRODUCTION

The identification of significant reservoirs of infection is a fundamental prerequisite to the management of diseases transmitted between wildlife and domestic livestock (Fröhlich et al., 2002). For bovine tuberculosis (bTB caused by *Mycobacterium bovis*) in cattle, wildlife reservoirs considered to be important include the Eurasian badger (*Meles meles*) in the UK, the white-tailed deer (*Odocoileus virginianus*) in northern USA, the Cape buffalo (*Syncerus caffer*) in South Africa, and the introduced brushtail possum (*Trichosurus vulpecula*) in New Zealand. However, there are many other potential mammalian hosts (Delahay et al., 2002; de Lisle et al., 2002), some of which may be capable of transmission to other species, including cattle.

In southern and midland England and southern Wales, where bTB in cattle has been a considerable and increasing problem in recent decades, badgers are locally abundant (Wilson et al., 1997). Badgers can maintain infection independently within their populations and are known to excrete *M. bovis* in sputum, urine, feces and pus from wounds (Clifton-Hadley et al., 1993). Results of a major field experiment (the Randomized Badger Culling Trial [RBCT]) have strongly implicated the badger in transmitting *M. bovis* to cattle (Donnelly et al., 2003, 2006), although transmission routes and dynamics remain unclear. However, little is known about the potential role of other wild mammals in maintaining bTB in cattle in these areas.

In recent years, the national distribution of wild deer has expanded in Great Britain (Ward, 2005) and populations also probably are growing in number. Infection with *M. bovis* has been detected in five of the six deer species present in Britain (Delahay et al., 2002), and epidemiologic reports have implicated wild deer in localized cattle herd breakdowns (Gunning, 1985). However, the potential role of wild deer in perpetuating bTB in cattle has yet to be adequately evaluated.

Delahay et al. (2007) carried out surveys of *M. bovis* infection in wild mammal carcasses collected from cattle bTB hot spots in southwest England. They used bTB prevalence estimates, published information on deer biology, and expert opinion on bTB epidemiology and the behavior and ecology of each species to assess the potential risks of transmission to cattle. The results suggested that, in particular, red deer (*Cervus elaphus*) and fallow deer (*Dama dama*) could potentially be implicated. Although this was a useful first step in understanding the potential role of other wildlife species in perpetuating bTB in cattle, considerable uncertainty was associated with their risk estimates for deer because of the limited availability of high-quality, deer-specific information required to parameterize their models. Moreover, their outputs were only semiquantitative because some knowledge gaps were addressed by incorporating expert opinion.

The process followed by Delahay et al. (2007) was a form of risk assessment. In essence, risk assessment requires identification of hazards (in this context, the potential for *M. bovis* excreted by wildlife to infect cattle) and an understanding of exposure to the target system (the likelihood that this potential will be realized; Calow, 1998). Typically, this understanding is captured by the construction of a conceptual model. Difficulties arise in identifying all factors contributing to risk, and all uncertainty can rarely be quantified (Calow, 1998). Consequently, uncertainty may be taken into account by simulation, or by some other assessment of potential consequences. The absence of rigorous scientific evidence for every parameter does not preclude completing a risk assessment (Suter, 1998). For example, quantifying the relationship between dose and response is an important part of the risk assessment process, so that acceptable and unacceptable levels of exposure can be defined (Calow, 1998). However, in the context of bTB risk, the relationship between the dose (the amount *M. bovis* excreted by populations of wild animals) and the response (the number of cattle becoming infected) is far from clear because even routes of *M. bovis* transmission have yet to be conclusively demonstrated. In such circumstances, exposure risks may be estimated without progressing to estimation of the effects (transmission risks; King, 1998). In this context, exposure is the amount of *M. bovis* that is available for encounter by cattle.

The governments of many countries are increasingly adopting the risk assessment process, and the UK and USA have used this as a proactive tool for risk management and priority setting for many years (King, 1998). A study by the Veterinary Laboratories Agency (VLA) (2004) provides an example of risk assessment applied to the importation of some livestock diseases to the UK. The VLA (2004) identified illegally imported contaminated meat as posing a potential disease hazard to British livestock. The study characterized risks associated with the importation, exposure, and subsequent infection of domestic livestock within a modeling framework, using data drawn from the literature and from government databases. Key data gaps (of which there were several) were addressed with the use of

[1]A cattle herd bTB breakdown is defined as "… when one or more reactors are revealed by tuberculin skin test or when disease is suspected in either live cattle showing clinical disease or in carcases with lesions at post-mortem examination." (Krebs et al., 1997).

expert opinion to construct probability distributions for parameters. The implications for risk estimates of these and other assumptions were thoroughly discussed. By estimating the frequency of infection for each disease likely to be caused by illegal meat imports, and by defining the main pathways through which risks were incurred, the VLA (2004) was able to advise on the relative priority of each of the diseases and which routes ought to be addressed to reduce risks.

The aim of the present study was to evaluate *M. bovis* exposure risks posed by wild deer to cattle in England and Wales in order to progress toward identifying the likely relative importance of each species for perpetuating this disease in cattle. We did not attempt to model the epidemiology of bTB in a system containing deer, badgers, and cattle; nor did we aim to model interspecific *M. bovis* transmission, because requisite information on transmission pathways and dose–response relationships were not available. Our objectives were to estimate the likely "loads" of *M. bovis* excreted at pasture (*M. bovis* pressure) by each of four species of British deer, and to express this as relative exposure risk to cattle, with the badger used as a reference point. Another important objective of our risk assessment process was to identify knowledge gaps that enhanced uncertainty associated with risk model outputs.

MATERIALS AND METHODS

Risk model construction

A risk model to quantify relative *M. bovis* pressure and cattle exposure at pasture arising from each deer species and from badgers (Fig. 1) was constructed in Crystal Ball (Decisioneering Inc, Denver, Colorado), a Monte Carlo add-on to Microsoft Excel® (Microsoft Corporation, Redmond, Washington). Estimating *M. bovis* pressure at pasture required multiplying the likely amount of *M. bovis* excreted by an infected individual, bTB prevalence, animal density, and the proportion of time spent at pasture, for each species. We assumed that excretion at pasture included all possible routes (e.g., feces, urine, sputum, and any other infectious secretions). Information on TB prevalence, animal density and the proportion of time spent at pasture were taken from the literature (Table 1). We assumed that the proportion of time spent at pasture approximated the risk of exposure (direct and indirect) of cattle to an individual of the species in question and its potentially infectious products.

Estimating absolute exposure risk was hampered by a lack of data on the relative importance of different potential transmission routes. Consequently, because the badger is considered to be the main wildlife reservoir for *M. bovis* in British cattle, and thus poses the greatest potential exposure risk to them, we made all estimates of the risk posed by deer relative to the risk posed by the badger. That is, during all analyses, risk attributed to badger exposure was fixed at a relative value of one.

Excretion of *M. bovis*

The amount of *M. bovis* excreted by an infected individual was assumed to be a function of body weight, and the likelihood of excretion (that is, whether an animal is likely to void *M. bovis* into the environment) and relative magnitude of excretion per unit of infected tissue. Johnson et al. (2008) provided quantitative data on the histopathologic characteristics of tuberculous lesions in tissue samples from fallow, red, and roe (*Capreolus capreolus*) deer and Reeves' muntjac (*Muntiacus reevesi*). We used the scoring system developed by Johnson et al. (2008) to estimate the likelihood of *M. bovis* excretion among species. For each species, we calculated the proportion of samples with each lesion encapsulation score (complete capsule=0, incomplete=1, absence of capsule=2), which also had each erosion score (not eroded into tissue lumen=0, eroded=1). Where the product of the encapsulation and erosion score was zero, we assumed that this proportion of samples were from deer that were unlikely to have been excreting. Where the product of the scores was greater than zero, we assumed that this proportion of samples were from deer that were likely to have been excreting.

Confidence intervals were calculated around the proportions of each species likely to be excreting by the normal approximation of a one-sampled binomial test. We used the acid-fast bacilli (AFB) score (Johnson et al., 2008) to describe the relative load of bacilli that would probably be excreted should excretion occur (Table 2). Our estimates of excretion likelihood were likely to be biased

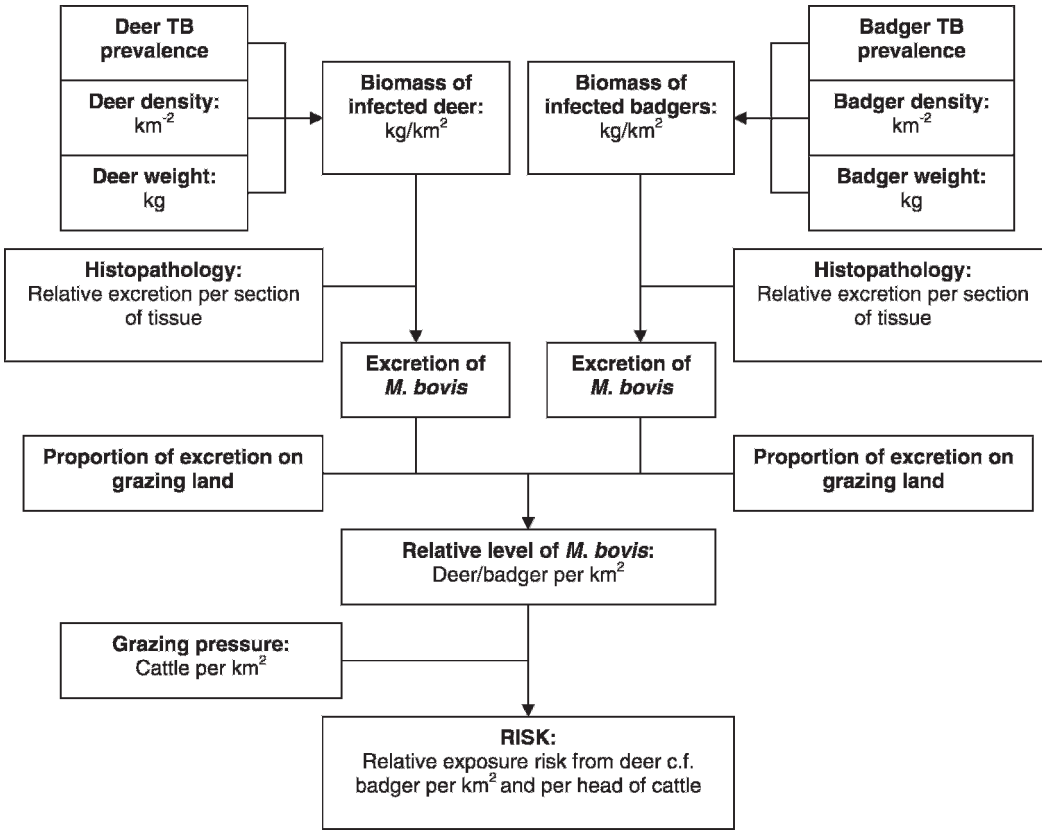

FIGURE 1. A flow diagram for estimating the relative risk of *Mycobacterium bovis* excretion from four deer species and badgers to cattle. The four cervid species considered in the risk assessment model were fallow (*Dama dama*), red (*Cervus elaphus*), and roe (*Capreolus capreolus*) deer and muntjac (*Muntiacus reevesi*).

TABLE 1. Parameters used in the risk model and their source.

Parameter	Data source
Tuberculosis prevalence (deer)	Delahay et al. (2007)
Tuberculosis prevalence (badgers)	Independent Scientific Group on Cattle TB (2007)
Density (deer)	Harris and Yalden (2008)
Density (badgers)	Independent Scientific Group on Cattle TB (2007)
Body weight (deer and badgers)	Harris and Yalden (2008)
Excretion probability (badgers)	Veterinary Laboratories Agency (2006)
Amount of bacilli excreted (badgers)	Johnson et al. (2008)
Proportion of excretions on grazing land	
Fallow deer	Lazarus (1993), Thirgood (1995)
Roe deer	Lazarus (1993), Putman (1986)
Red deer	Langbein (1997)
Muntjac	Wyllie et al. (1998)
Badger	Hounsome et al. (2005)
Grazing pressure	VetNet database (extracted 2007)

TABLE 2. Adjustment of scores for acid-fast bacilli (AFB) by the Veterinary Laboratories Agency (2006) for badgers to allow comparison with estimates for deer by Johnson et al. (2008).

Johnson et al. (2008)		Veterinary Laboratory Agency (2006)		
Score	No. AFB	Original score	Adjusted score	No. AFB
0	0	0	0	0
1	1–10	1	1	1
2	11–50	+	2	<20
3	>50	++	2	20–50
		+++	3	>50

low, because Johnson et al. (2008) presented information from only a single plane of section for each sample, observations were made in isolation of information on gross pathology, and the number of samples was small. Quantified estimates of gross lesions and histopathology were not available from the literature for any British deer species, nor for white-tailed deer or elk (*Cervus elaphus*) in the USA. Similarly, among reports on the distribution of gross tuberculous lesions in deer that we consulted, observations were purely descriptive and did not quantify the number or proportion of samples exhibiting lesions in different locations or at different stages of gross pathology. Consequently, we were not able to improve our estimates of excretion among deer. More information on *M. bovis* excretion was available for badgers, but to provide comparability and avoid potential bias we used an excretion assessment for badgers similar to that used for deer.

A similar scoring system to that used by Johnson et al. (2008) for deer also has been used to quantify bTB pathology in badgers (VLA, 2006), with the exception that no score was given for granuloma erosion into the lumen of source tissues. For this score, we assumed 50% erosion into tissue lumena for infected badgers, broadly consistent with the findings of Gavier-Widen et al. (2001). We adjusted the AFB score for infected badgers presented by VLA (2006) to bring it in line with the system for deer (Johnson et al., 2008), by combining two of their score categories into a single category (Table 2). VLA (2006) observed collagen and fibrin (the constituent components of fibrotic capsules) associated with granulomas in badgers, but did not observe complete fibrotic capsules around any lesions. However, three of 17 tissues from four animals showed signs of incomplete fibrotic capsules. We parameterized the proportion of infected badgers with complete fibrotic capsules (score 0) as 0.000, partial capsule (score 1) as $3/17=0.176$, and no capsule (score 2) as $1-0.176=0.824$.

Relative risk calculation

To estimate *M. bovis* pressure risks from deer in areas of Britain where cattle have been persistently affected by bTB, initial analyses were undertaken with the use of average parameter values for southwest England and Wales. For each parameter for which multiple estimates were available we constructed probability distributions (Table 3). For each deer species, 2,000 model simulations were performed with parameter values drawn at random from each probability distribution. This produced an average estimate of relative *M. bovis* pressure (risk) and an error term interpreted as a measure of uncertainty. A sensitivity analysis was carried out within the Crystal Ball software to quantify the relative contribution of each variable to the total variance around each risk score. This process calculated the correlation between input values and output risk estimates, for each parameter simultaneously, with the use of all values selected during the Monte Carlo procedure. The normalized correlation for each parameter was then expressed as a percentage of all correlations.

In order to illustrate the geographic pattern of risks, the model was applied to each cell of a 5×5-km square grid (5-km cell hereafter) overlaid across England and Wales, with average deer, badger, and cattle density estimates replaced with total abundance estimates specific to each cell. For illustrative purposes, average estimates for the remaining parameters were used without error.

Distribution and abundance of deer, badgers, and cattle

Distribution data were available for all species, but abundance estimates for wild species required extrapolation from local density estimates. All mapping and spatial

TABLE 3. Parameter values and their distributions used in the risk model.

Host species	Variable	Value and distribution
Badger	bTB[a] prevalence	Triangular: 0.016, 0.113, 0.372
	Density (km^{-2})	Triangular: 0.01, 10.00, 25.00
	Mean weight (kg)	Triangular: 6.6, 10.9, 16.7
	Excretion probability	Triangular: 0.093, 0.500, 0.907
	Excretion magnitude	Fixed: 1.82
	Proportion on grazing land	Normal: mean 0.485 SD[b] 0.171
Roe deer	bTB prevalence	Triangular: 0.0047, 0.0102, 0.0192
	Density (km^{-2})	Triangular: 0.05, 34.00, 75.00
	Mean weight (kg)	Triangular: 18.0, 23.1, 28.2
	Excretion probability	Triangular: 0.000, 0.170, 0.501
	Excretion magnitude	Uniform: 0.00, 2.31
	Proportion on grazing land	Lognormal: mean 0.476, SD 0.194
Red deer	bTB prevalence	Triangular: 0.0012, 0.0102, 0.0364
	Density (km^{-2})	Triangular: 3.00, 8.50, 14.00
	Mean weight (kg)	Triangular: 80.0, 116.5, 225.0
	Excretion probability	Triangular: 0.099, 0.300, 0.501
	Excretion magnitude	Fixed: 2.31
	Proportion on grazing land	Lognormal: mean 0.126, SD 0.092
Fallow deer	bTB prevalence	Triangular: 0.0276, 0.0437, 0.0653
	Density (km^{-2})	Triangular: 5.00, 35.00, 75.00
	Mean weight (kg)	Triangular: 36.0, 47.6, 105.0
	Excretion probability	Triangular: 0.000, 0.040, 0.112
	Excretion magnitude	Fixed: 2.31
	Proportion on grazing land	Lognormal: mean 0.263, SD 0.274
Muntjac	bTB prevalence	Triangular: 0.0108, 0.0517, 0.1438
	Density (km^{-2})	Triangular: 0.01, 15.00, 30.00
	Mean weight (kg)	Triangular: 10.0, 13.5, 17.0
	Excretion probability	Triangular: 0.000, 0.170, 0.501
	Excretion magnitude	Uniform: 0.00, 2.31
	Proportion on grazing land	Triangular: 0.000, 0.100, 0.210

[a] bTB=bovine tuberculosis.

[b] SD=standard deviation.

analyses were undertaken in ArcGIS 9.1 (ESRI, Redlands, California, USA).

Cattle: Data on cattle abundance and herd bTB status on each farm holding in England and Wales during 2007 were obtained from the VetNet database (a cattle bTB testing database managed by the UK Department for Environment, Food, and Rural Affairs [Defra]). These data were used to calculate the total number of cattle, and of bTB herd breakdowns per 5-km cell throughout England and Wales.

Deer: Presence data for fallow, red, and roe deer and muntjac collected from 1973 to 2002 on a 10-km grid across Britain (Ward, 2005) were supplemented with more recent distribution data gathered from the membership of the British Deer Society during their national deer survey. Deer presence was rescaled to 5-km cells. We did not include Japanese sika (*Cervus nippon*) or Chinese water deer (*Hydropotes inermis*) within our study, because bTB prevalence estimates were not available for either species.

The total number of individuals of a deer species within a 5-km cell was estimated by multiplying a local woodland density estimate by the total area of woodland within the cell. This was repeated for each species and every cell in England and Wales. Woodland area was extracted from Land Cover Map 2000 (Centre for Ecology and Hydrology, UK). Deer density estimates collected between 2000 and 2007 were received from nine individuals, three estates, and government bodies including Forest Research and the 15 English and Welsh Forestry Commission districts (Table 4). We applied density estimates from the same geographic region or the nearest region for which an estimate was available to

TABLE 4. Deer density estimates used to map abundance in 5-km cells. The number of estimates used to derive the average value are presented in parentheses.

Region	Deer density (km^{-2})			
	Red deer	Roe deer	Fallow deer	Muntjac
East	7.4 (9)	16.7 (8)	53.9 (27)	34.6 (38)
Central	1.1 (3)	8.1 (11)	35.3 (33)	13.0[b] (40)
Northeast	1.1 (1)	10.6 (3)	11.7[a] (4)	13.0[b] (40)
Northwest	9.4 (4)	32.5 (38)	11.7[a] (4)	13.0[b] (40)
Southeast	5.3 (1)	11.8 (9)	11.7 (4)	13.0 (40)
Southwest	7.9 (13)	5.2 (2)	11.6 (5)	13.0[b] (3)
Wales	5.3[c] (13)	4.5 (2)	36.8 (3)	13.0[b] (3)

[a] Estimates of fallow deer density were not available for these regions, so estimates from southeast England were used.

[b] Estimates of muntjac density were not available for these regions, so estimates from southeast England were used.

[c] Estimates of red deer density were not available for Wales, so estimates from southwest England were used.

each cell within that region. Where discrete populations of certain species were well known (e.g., red deer on Exmoor and the Quantock hills, and fallow deer in central Wales; see Fig. 2), these were simply added to the relevant cell.

Badgers: Data on badger density were not available, so their local abundance was estimated with the use of a spatial model of main sett density based on data from the RBCT (Etherington et al., 2009). Main sett abundance estimates were converted into badger abundance estimates assuming one social group with 5.9 badgers per main sett (Cresswell et al., 1990).

RESULTS

Distribution and abundance

Density estimates for each deer species and areas of woodland within 5-km cells varied considerably within and between regions in England and Wales. This resulted in a highly varied pattern of predicted abundance (Fig. 3A–D). Deer were estimated to be particularly abundant in parts of East Anglia (all four species), central England (fallow deer and muntjac), Cumbria and southern England (red deer), and the northwest and southeast of England (roe deer; Fig. 3A–D). The estimated distribution of badger abundance (Fig. 3E) broadly followed the same pattern as that for cattle abundance (Fig. 3F), being focused in west and southwest England and southwest Wales. The distribution of new cattle herd bTB breakdowns during the same year (2007) also followed this pattern (Fig. 4).

M. bovis pressure calculations

Because of the limited number of bTB positive roe deer and muntjac samples, variation in their respective estimated excretion probabilities was very large, and was therefore not significantly different from those for red or fallow deer. Therefore a combined distribution was used for roe deer and muntjac. For the magnitude of bacterial excretion, red and

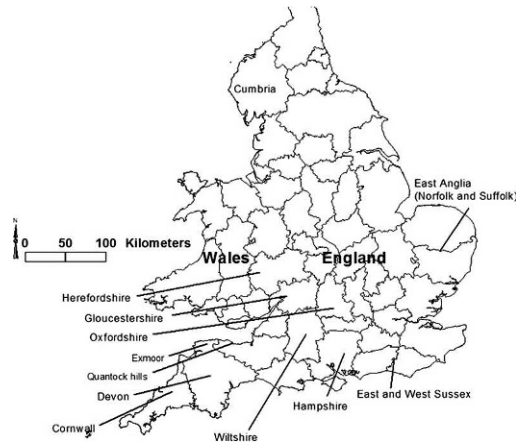

FIGURE 2. Counties and localities in which study sites were established, or important observations made.

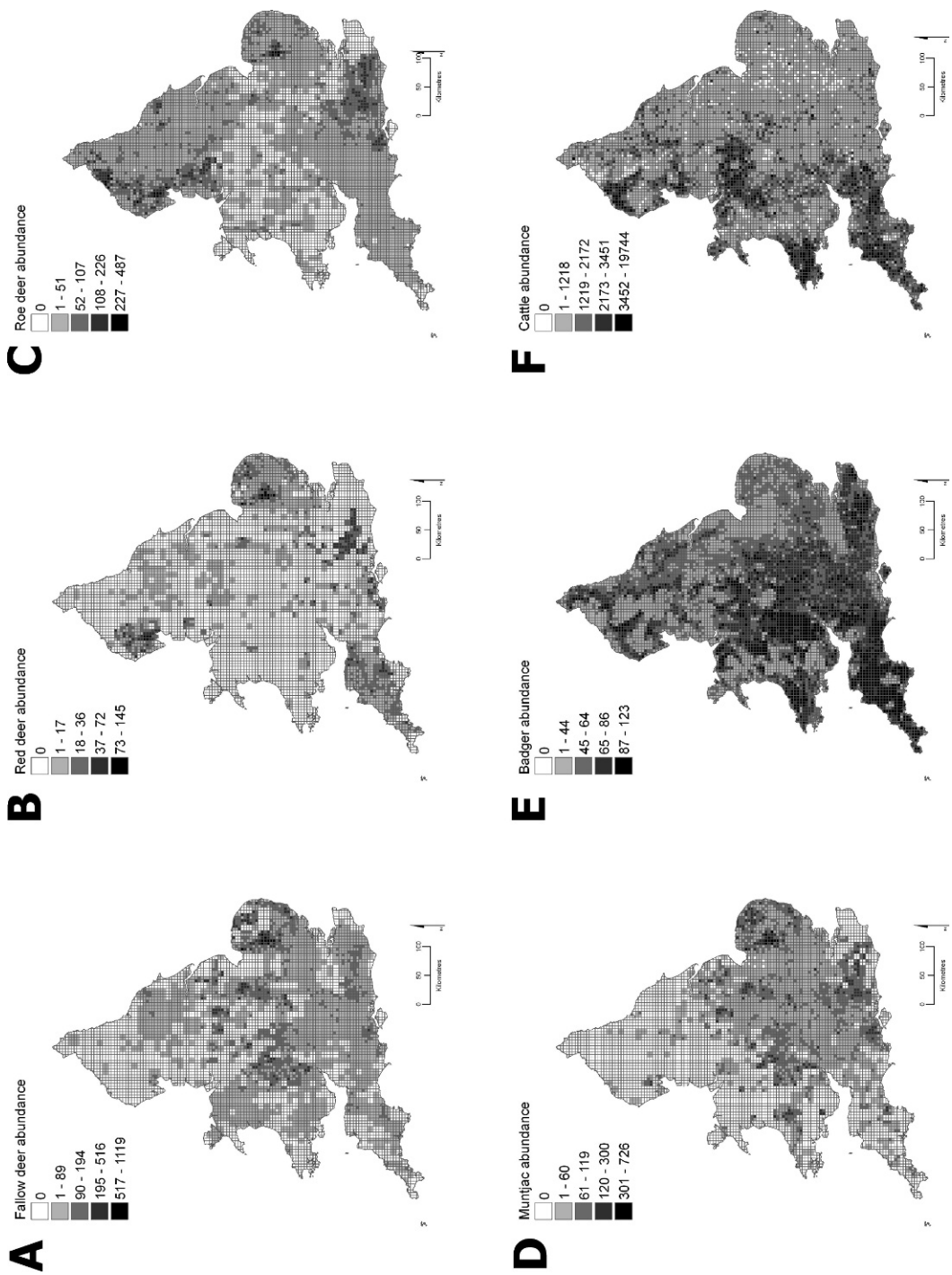

FIGURE 3. Predicted abundance maps for (A) fallow deer (*Dama dama*), (B) red deer (*Cervus elaphus*), (C) roe deer (*Capreolus capreolus*), (D) muntjac (*Muntiacus reevesi*), (E) badgers (*Meles meles*), and (F) cattle during 2007. "Abundance" refers to the number of individuals of each species predicted to be present in each 5-km cell.

fallow deer had identical distributions. Both roe deer and muntjac were assumed to have a uniform distribution of between zero and 2.31, as none were categorized as excretors (Table 3).

Because the relative *M. bovis* pressure risk from each deer species in comparison to the badger was highly skewed (to the left), we chose to report the median risk and the 95th percentile (Table 5). In southwest England and Wales, median risk scores were below one and the upper 95th percentiles were above one for all four deer species. Fallow deer were estimated to pose the highest median risk among deer species studied with a relative score of 0.27, but also had the greatest level of associated uncertainty.

Sensitivity analyses showed that risk score variances were most dependent on the proportion of time deer spent on grazing land, badger density, badger bTB prevalence, the probability of excretion by deer, and deer density (Table 6). Reduced variability in these parameters would improve the precision of risk estimates.

The geographic pattern of *M. bovis* pressure on pasture caused by the four species of wild deer in comparison with the badger suggested that in most areas where deer and badgers are infected the latter are likely to contribute most to cattle risk (Fig. 5). However, in some cattle bTB areas, notably parts of Cornwall, Devon, Somerset, Gloucestershire, Midlands, and mid- and south Wales, the four deer species combined may pose a risk comparable or higher than risk associated with badgers. Nevertheless, combining estimates from deer and badgers and multiplying by cattle density illustrated that areas where deer potentially could pose the greatest exposure risk did not correspond to those areas where cattle were estimated to be most at risk (Fig. 6). Although the estimated local abundance of each deer species (except for fallow deer) was significantly correlated with the total local risk to cattle, all correlation coefficients were very small, and most were negative (Table 7). In contrast, local badger abundance was strongly and significantly correlated with the total local exposure risk to cattle (Table 7), suggesting that, among the species studied, the distribution and abundance of badgers and their coincidence with abundant cattle herds was likely to be the most important component of the overall *M. bovis* exposure risk arising from wildlife.

DISCUSSION

In the model presented here no deer species had a median *M. bovis* pressure risk value higher than unity and values were strongly skewed to the left. These results suggest that, based on available information, deer likely pose a generally lower *M. bovis* pressure risk for cattle at pasture than that posed by badgers in southwest England and Wales. However, the 95th percentiles of the risk scores for all deer species were very wide and exceeded one, limiting confidence that any deer species poses less of a risk to cattle than badgers where those deer are present and infected. Fallow deer were estimated to pose the greatest potential risk of any deer species, but also had the greatest level of associated uncertainty. The vast majority of this uncertainty (30.9%) was caused by variation in estimates of *M. bovis* excretion at pasture, which is a product of likely excretion magnitude and the proportion of time spent at pasture. Across all species, greater risk estimate variance also was associated with badger and deer density and bTB prevalence, and deer excretion probability. In order to increase the precision of our risk estimates and decrease uncertainty, these parameters require better quantification.

Muntjac were estimated to pose the lowest risk of the species studied, with the upper 95th percentile only slightly higher than unity. We conclude that under current conditions this species is unlikely to pose a significant risk to cattle, relative

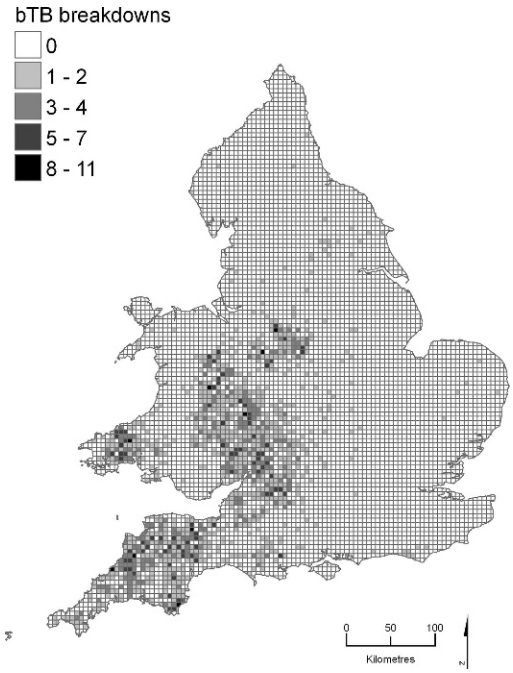

FIGURE 4. Observed number of cattle herd bTB "breakdowns" in 5-km cells during 2007.

to that from badgers and other deer species. However, in recent years muntjac have spread across England and Wales more rapidly than any other deer species (Ward, 2005) and can reach exceptionally high local densities (Cooke and Farrell, 1998). Hence, it would seem prudent to monitor muntjac distribution and abundance, particularly in cattle farming areas in the west of the country, so that potential risks to cattle can be reassessed if muntjac densities increase substantially.

TABLE 5. The median relative risk to cattle from four deer species relative to the badger, and the 95th percentile of the distribution, estimated from 2,000 simulations.

	Relative risk		
Species	Median	Lower 95th percentile	Upper 95th percentile
Roe deer	0.25	0.02	3.32
Red deer	0.16	0.01	2.58
Fallow deer	0.27	0.02	4.79
Muntjac	0.08	0.00	1.14

Our median *M. bovis* pressure risk estimates were lower than those presented by Delahay et al. (2007) for all deer, but associated uncertainty was considerably higher. This may, at least in part, have been due to Delahay et al. (2007) presenting median and interquartile ranges of risk estimates, in contrast to median and 95th percentiles in the present study. Moreover, whereas Delahay et al. (2007) used expert opinion to fill knowledge gaps on bacterial excretion and deer contact with cattle, we used empirical data. However, estimates of *M. bovis* excretion likelihood and magnitude remained uncertain owing to the absence of data on the relationship between histopathologic observations and the excretion of *M. bovis* bacilli. Nevertheless, fallow deer had the highest risk score in both studies, which is consistent with the contention (Delahay et al., 2007) that where they are present and infected with *M. bovis* they are likely to pose the greatest potential risk to cattle amongst the four deer species investigated.

In the present study, potential interspecific contact was modeled as the proportion of time spent by individuals of each species at pasture, which we assumed represented the rates of direct and indirect contact and exposure to *M. bovis* excreted through any possible route. The most important routes of *M. bovis* transmission among wildlife and cattle in Britain remain uncertain. Indirect intra- and interspecific transmission has been demonstrated for white-tailed deer via contamination of feed with infected saliva (Palmer et al., 2004a,b). Although British deer species potentially may spread their excretory products diffusely over pasture, it is not known whether they are likely to contaminate cattle feed. Badgers have been observed to visit farm buildings in cattle bTB hot spots in southwest England (Garnett et al., 2002; Ward et al., 2008), but such behavior has not been reported in deer (Hill, 2005; Central Science Laboratory, 2005). Most cattle in Britain are housed from late autumn to early

TABLE 6. Sensitivity analysis on the relative risk score for four deer species compared to the risk from badgers. Figures are the percentage contribution to the total variance in the risk estimate from each parameter.

Parameters	Roe deer	Red deer	Fallow deer	Muntjac
Excretion at grazing land (deer)	8.3	23.7	30.9	10.9
Density (badger)	16.6	13.7	12.6	18.8
bTB[a] prevalence (badger)	15.6	16.6	12.9	10.8
Excretion probability (deer)	15.9	3.5	13.9	17.6
Density (deer)	16.8	5.4	9.5	14.5
bTB prevalence (deer)	4.3	15.8	2.3	10.8
Excretion at grazing land (badger)	9.7	8.8	6.4	6.8
Excretion probability (badger)	9.0	7.8	8.1	8.0
Mean weight (badger)	2.4	1.9	1.9	1.5
Mean weight (deer)	1.5	2.7	1.6	0.4

[a] bTB=bovine tuberculosis.

spring, so although they may potentially be exposed to badgers all year round, exposure to deer may be limited to the period when both have access to pasture (late spring to early autumn). Consequently, the figures presented here are likely to overestimate the total relative *M. bovis* exposure risk posed by deer to cattle.

Use of cattle pasture by deer is clearly an important behavioral factor affecting the risk of *M. bovis* transmission to cattle.

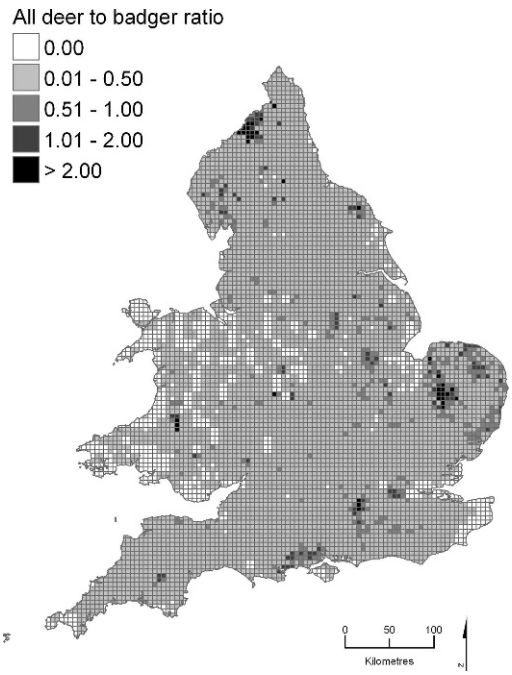

FIGURE 5. Combined relative *Mycobacterium bovis* pressure exerted at pasture by four species of wild deer relative to the badger (*Meles meles*); the four cervid species evaluated in the risk assessment model were fallow (*Dama dama*), red (*Cervus elaphus*), and roe (*Capreolus capreolus*) deer and muntjac (*Muntiacus reevesi*).

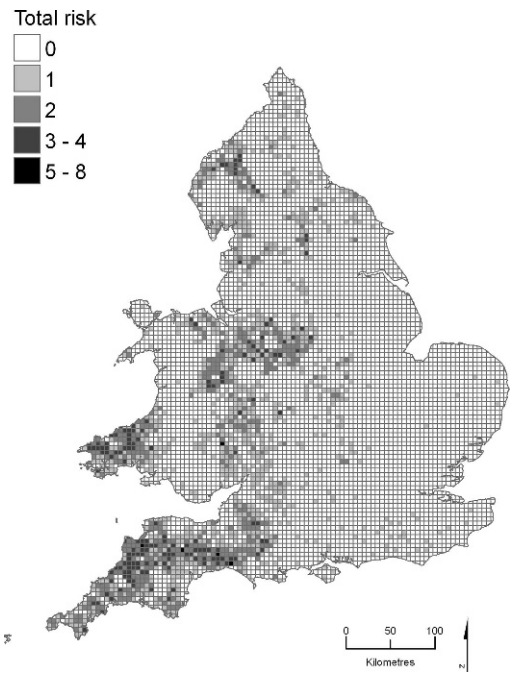

FIGURE 6. Combined risk of *Mycobacterium bovis* exposure posed by four deer species and badgers (*Meles meles*) to cattle; the four cervid species evaluated in the risk assessment model were fallow (*Dama dama*), red (*Cervus elaphus*), and roe (*Capreolus capreolus*) deer and muntjac (*Muntiacus reevesi*).

TABLE 7. Pearson correlations between the estimated abundance of four species of deer and badgers, and the total estimated risk posed to cattle.

	Species				
	Badger	Muntjac	Fallow deer	Roe deer	Red deer
R	0.656	−0.065	−0.024	−0.049	0.067
P	<0.001	<0.001	0.052	<0.001	<0.001

The longer infected deer spend on pasture, the greater the probability of contamination of the environment with *M. bovis* bacilli and of contact with cattle. Information on deer activity on pasture was extremely limited, but this contributed to the most important factor responsible for risk estimate variance for red and fallow deer. No studies have specifically investigated deer movement patterns in pastoral landscapes in southwest England or Wales. Instead, most studies have focused on movement in woodlands and arable fields and again, generally not in southwest England (but see Langbein, 1997). This represents a priority area for future research, as deer also may carry other diseases of importance to cattle. Nevertheless, the limited information available suggested that fallow deer and red deer spend more time at cattle pasture than roe deer and muntjac. Red deer and fallow deer have been observed to lie among cattle at pasture in some localities (A.I.W., pers. obs.), but this behavior has not been recorded for the other deer species in Britain. During observations of deer at pasture, muntjac, roe and fallow deer all typically avoided fields occupied by cattle, and fled in response to their approach (CSL, 2006). Behavioral differences between deer species, not all of which could be accounted for within our models, suggest that the potential for both direct and indirect contact and hence disease transmission to cattle from red and fallow deer are probably greater than for roe deer and muntjac. Badgers also have been recorded to flee in response to approaching cattle at pasture (Benham and Broom, 1989), although they may lose this tendency when in very advanced stages of bTB progression (Cheeseman and Mallinson, 1981). The same may be true for moribund deer, but this has yet to be reported.

Cattle may investigate or consume grass contaminated with wildlife feces, urine, pus, or sputum (Muirhead et al., 1974). Cattle may not avoid grass contaminated with badger urine (Hutchings and Harris, 1997), and since urine tends to be distributed randomly across pasture and can contain exceptionally high concentrations of *M. bovis* (Ministry of Agriculture, Fisheries, and Food, 1979) this may pose a serious exposure risk to cattle. The same may be true for deer urine, although concentrations of *M. bovis* have yet to be reported in infected wild deer urine. In contrast, cattle may consume grass contaminated with deer feces more than that contaminated by badger feces (Smith et al., 2008). Moreover, badgers typically accumulate feces at latrines, which cattle tend to avoid grazing (Benham and Broom, 1989), whereas deer do not use latrines but distribute feces more randomly. Smith et al. (2008) observed that cattle consumed grass contaminated with feces distributed in a diffuse pattern more than they did when distributed in clumped aggregations. Variation in response of cattle to potentially infectious products left at pasture by wild animals will influence exposure and transmission risks. Assuming equality in loads and survival of *M. bovis* in feces and urine between badgers and deer, and assuming transmission to cattle can occur via the fecal–oral route, the component of our exposure risk estimates contributed by deer feces may be underestimated.

The geographic pattern of *M. bovis* pressure posed at pasture by deer relative to badgers (Fig. 5) illustrates the generally lower estimated risk from deer throughout most of England and Wales. Because data used to generate estimates within 5-km cells were coarse, it is inappropriate to conclude that the output for any single cell

is a true approximation of risks posed within that cell. Instead, Figures 5 and 6 should be taken as broadly representing the general pattern of possible risks across the landscape. However, the categories in which estimates were plotted were wide, reflecting the imprecision associated with our risk estimates. It would seem prudent to monitor for bTB in deer in potentially high-risk areas, especially where these are close to current cattle bTB hot spots or if the pattern of cattle farming shifts into these areas. Detection of bTB in deer in such areas may justify investigation of potential contacts between deer and cattle to examine evidence of potential for *M. bovis* transmission, to re-estimate risks to cattle, and to develop strategies for breaking potential transmission pathways.

Within cattle bTB areas during 2007, the combined exposure risks posed to cattle by deer and badgers appeared to be highest in Devon, Cornwall, Gloucestershire, Midlands, and southwest Wales. The distribution of levels of predicted absolute exposure risk was remarkably similar to the pattern of cattle herd bTB breakdowns during 2007 (Fig. 4). However, this does not imply that the distribution of herd breakdowns in southwest England and Wales is caused by the distribution of deer and badgers. Indeed, the distribution and abundance of cattle (Fig. 3) forms a fundamental component of this risk map. Causation and the potential direction of transmission cannot be inferred from these data. Indeed, *M. bovis* transmission may be multidirectional within the deer–badger–cattle system. However, it was interesting to note that local badger abundance was strongly correlated with total exposure risks to cattle, whereas local abundance of deer were only weakly correlated. This pattern is consistent with wild deer playing a less significant role in the epidemiology of bTB in cattle than badgers.

Within each 5-km cell in Britain, the spatial distribution of risks is likely to vary due to deer behavior and movement patterns. Risks posed to cattle by gregarious red and fallow deer are probably highly clumped and concentrated on those cattle pastures habitually used by deer herds. However, these species may also range widely (Langbein, 1997), perhaps leading to a widespread but clumped distribution of risks within a given cell. In contrast, roe deer and muntjac make more use of thick woodland cover and less of pasture, usually remaining close to woodland edges (Chapman et al., 1994; Tufto et al., 1996). Risks posed to cattle by roe deer and muntjac may be more evenly distributed in a homogeneous environment, but in heterogeneous environments are likely to be concentrated at pasture-woodland edges or within woodland to which cattle have access.

Histopathologic findings have been used to make inferences regarding *M. bovis* excretion in infected badgers (Gavier-Widen et al., 2001) and deer (Johnson et al., 2008). However, these studies did not attempt to confirm excretion by collecting appropriate samples from carcasses prior to the removal of tissues for sectioning. Moreover, Johnson et al. (2008) were not able to relate histopathology to gross pathology because the samples they examined were from incomplete carcasses. Consequently, our estimates of *M. bovis* excretion by deer were based on the assumption that material examined by Johnson et al. (2008) was representative of all tuberculous lesions in lymph nodes and lungs, and hence that excretion was just as likely through any potential route. Clearly this is unrealistic, but was unavoidable given the absence of other data from which the likelihood and magnitude of excretion could be quantified. In the absence of information on the relationship between pathologic findings and excretion of *M. bovis* bacilli, we made speculative assumptions in order to assess the likelihood and quantity of *M. bovis* excretion by each deer species and badgers, potentially resulting in unquantifiable biases. However, because we took a consistent approach

to excretion estimation for deer and badgers, it seems likely that potential biases also were consistent, so that our relative risk estimates may have been reliable relatively. Nevertheless, knowledge on *M. bovis* excretion by wild deer is an important limitation in our assessment of risk, and we consider it a priority to describe the relationships between pathology and excretion or to conduct alternative studies in order to identify the relative importance of routes through which deer may excrete *M. bovis* in order to improve the reliability of our predictions.

Mycobacterium bovis has been cultured from feces, nasal, tracheal, and oropharyngeal samples of naturally infected red deer (Lugton et al., 1998), and from nasal secretions, saliva, feces, the tonsils, and urine of experimentally infected white-tailed deer (Palmer et al., 1999, 2001, 2002). Lugton (1997) cultured *M. bovis* orally and from feces of culled New Zealand red deer, although the proportion of deer culturing positive via these routes was low (7% and 2%, respectively, of 162 samples, of which 58 were confirmed culture positive). Lugton's failure to culture *M. bovis* from deer urine does not imply that red deer do not excrete bacilli in urine, because a small sample size precluded robust conclusions. The low sensitivity of mycobacterial culture as a diagnostic technique and the likely intermittency of excretion also mean that the proportions of red deer that cultured positive for each route reported by Lugton (1997) are likely to underestimate the prevalence of excretion via these routes within the population.

Among badgers, sputum most commonly cultured positive for *M. bovis* (54% of all positive cultures from 11,000 badger capture events, representing 2,600 badgers sampled at Woodchester Park, UK between 1982 and 2000), but 39% of fecal samples and 35% of urine samples also cultured positive (Delahay et al., 2005). Clearly, the culture results for badgers and red deer are incomparable because they represented different temporal sampling regimes, used different methods, and arose from different sample sizes, so it is not possible to infer their relative effect on our exposure risk estimates. However, because sputum and feces have cultured positive for badgers and deer, it seems reasonable to conclude that direct and indirect routes of exposure pose transmission risks to cattle.

Among infected wild deer (Lugton et al., 1998; O'Brien et al., 2001; Delahay et al., 2007), badgers (Muirhead et al., 1974), and cattle (Pollock and Neill, 2002) tuberculous lesions are commonly found in the lungs and associated lymph nodes. The accepted inference is that infection is acquired aerogenously, although common involvement of the tonsils in cattle and deer suggests that transmission may in fact be more complex (Pollock and Neill, 2002; Nugent, 2005). Among red deer in New Zealand, common tonsil involvement and lesions in head lymph nodes caused Nugent (2005) to conclude that wild red deer may typically acquire infection orally, but not during consumption of food. Ingestion and investigation of contaminated material are thought to be of secondary importance for intraspecific transmission among cattle (Menzies and Neill, 2000) but it is clear that the exact processes through which cattle usually become infected have yet to be fully understood or described (Pollock and Neill, 2002). Consequently, we do not believe that it is possible to progress beyond an assessment of the likely exposure risks posed by wild animals to cattle because neither the relative nor absolute importance of potential transmission routes are yet clear.

Irrespective of the low relative risk values calculated here for wild deer, these hosts may potentially enhance levels of *M. bovis* contamination in the environment. Furthermore, infected deer carcasses could expose scavengers such as foxes (*Vulpes vulpes*) and badgers given the

high loads of bacilli observed in tissues (Johnson et al., 2008) and the potential for wide dissemination of lesions (Delahay et al., 2007). Nugent (2005) suggested that red deer in New Zealand pose a risk to scavenging possums for many years after the disease has been controlled in possum populations. Furthermore, messy feeding on infected carcasses by scavengers might render infected material more available for investigation by nonscavengers, including other deer and cattle (Nugent, 2005).

There currently is insufficient evidence that deer play an important role in perpetuating bTB in cattle to warrant management intervention for disease control in cattle. Nevertheless, in high-risk areas for bTB in cattle the collection and appropriate disposal of deer carcasses may provide opportunities to reduce key foci of infection. Similarly, preventing deer from gaining access to cattle feed at pasture may reduce potential opportunities for transmission. In Michigan, USA, reducing local deer density by limiting artificial feeding forms an important component of efforts to eradicate bTB from wild white-tailed deer populations (Miller et al., 2003). Culling has been widely employed to manage deer populations in Great Britain, usually in relation to damage to agriculture and forestry. However, it is not clear whether this would be a suitable approach for the control of bTB in British deer, as culling wildlife populations can lead to unexpected ecological consequences that may be counterproductive to disease control (McDonald et al., 2008) or other human interests.

In summary, our calculations suggest that wild deer in England and Wales are likely to pose a lower risk of *M. bovis* exposure to cattle than do badgers. However, these risks may vary spatially and between species, with fallow deer probably posing the greatest risk among the four deer species studied. Many knowledge gaps and considerable uncertainty remain regarding some of the assumptions underlying our calculations, particularly regarding excretion of *M. bovis* by infected deer. Significant variability in estimates of several parameters, including pasture occupancy by deer, resulted in the low precision of our risk estimates. Further information on the epidemiology of bTB in British wild deer is needed to improve our understanding of their potential role in perpetuating bTB in cattle.

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