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Wildlife Reservoirs of Livestock Disease: Planning Responses to Suspected Outbreaks of Classical Swine Fever in Feral Swine

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ABSTRACT: Food security and international trade require healthy livestock. A wildlife reservoir can compromise control of livestock disease. When disease is suspected in wildlife, initial questions include whether their behaviour, ecology and proximity to livestock pose a significant risk. Then, what options are there for mitigating risk? If we respond, how should we measure success? Following action, lessons must be learned so that we are more effective during the next disease outbreak. At least 4 discrete populations of feral swine currently exist in England at relatively low densities. In the event of a suspected classical swine fever (CSF) outbreak, investigation zones and control strategies may need to be initiated, and so new models need to be created to fit these English populations. Here, we present an approach to using data collected during scientific research projects and wildlife management exercises to aid decisions on how to resource a program of disease detection and control if CSF was suspected to have broken out in feral swine populations in England. Culling efficiency was estimated through trapping and shooting records. Results were used to create predictive models which determined resources and costs required to carry out an efficient cull within various possible scenarios. Trapping over 26 months at one 427-ha site resulted in the capture of 130 swine at an average of 0.21 swine per trap-night and US\$477 per animal. Shooting by two government hunters over 12 months at another site resulted in the culling of 56 swine, equating to 1 swine shot for every 18 hrs 40 mins; total effort was 41 hrs 44 mins with total cost around US\$75,628 (US\$1,350) per animal. Using simulation models, we estimated the costs of delivering a cull via a combined approach of trapping and shooting to detect CSF at 1% and 5% seroprevelance. Costs ranged widely, depending on scenario, with minimum costs of US\$51,404 and \$69,029, and maximum costs of US\$231,545 and \$203,109, respectively. Results suggest that at present it is feasible to deliver a sampling strategy that could detect and potentially resolve the occurrence of CSF in feral swine in England.

KEY WORDS: classical swine fever, culling, disease control, effort, England, modelling, shooting, trapping, resource planning, *Sus scrofa*, swine, wild pigs

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INTRODUCTION

Food security and international trade require healthy livestock. However, a wildlife reservoir can compromise control of livestock disease. When disease that is communicable to humans or livestock is suspected in wildlife, initial questions focus on whether their behaviour, ecology, and proximity to livestock pose a significant risk. Then, what options are there for mitigating risk? If action is taken, how should we measure success? Following action, lessons must be learned so that we are more effective during the next disease outbreak.

Classical swine fever (CSF, also known as hog cholera) is a highly contagious viral disease of domestic swine, wild boar (both *Sus scrofa*), and collared peccaries (*Pecari tajacu*). It is endemic to much of Europe, Asia, Africa, and South America, but has been eradicated from North America and the United Kingdom. The disease poses a serious threat to the domestic pig industry, which is worth approximately US\$2 billion annually in England alone (Lewis and Grayshon 2012) in comparison with \$14 billion for the U.S. industry. Measures to remain CSF-free include border controls to prevent import of infected porcines or porcine products. These have been effective in the UK since 2000 (the year of the last outbreak) but cannot reduce the risk of incursion to zero.

Following the extinction of wild boar from the UK approximately 500 years ago, feral swine became established via escapes from farms stocking hybrids between European wild boar and domestic pigs (Wilson

2003). Feral swine are currently known to be present in 4 discrete populations in England: the Forest of Dean, the Sussex/Kent border, Dorset, and Dartmoor (Wilson 2003). Populations are believed to be quite small, generally numbering fewer than 200 in each population (Hartley 2010), and limited distance sampling surveys have corroborated presence at low densities in comparison with other parts of Europe (Gill and Brandt 2010). Such densities and their isolated nature mean that incursion of CSF into any of these populations would be a localised problem; it would nevertheless require eradication to protect nearby domestic pig farms.

On suspicion of CSF in any UK feral swine population, a Feral Pig Investigation Zone (FPIZ) will be declared by the government's Secretary of State and if disease is confirmed a Feral Pig Infected Area (FPIA) would be established (DEFRA 2010). The size of the control zone is determined on a case-by-case basis and will include information such as estimates of the feral swine population size and distribution in the area. Once disease is suspected or confirmed, a culling and testing programme would commence that would utilise standard trapping and shooting methods at a rate required for disease eradication. Therefore, it is necessary to ensure that sufficient resources are committed at an early stage of such an outbreak to meet the requirements set by the disease control strategy.

Current European Commission guidelines on CSF surveillance in wild boar states that "The minimum number of animals to be sampled within a defined

sampling area must allow detection of 5% seroprevalence with 95% confidence. To achieve this, at least 59 animals must be sampled in each area identified. In [European] Member States with a small population of wild boar, due to the difficulties of surveillance as set out above, the Member State should adapt based on epidemiological advice their proposed surveillance plan in wild boar to the local conditions." (European Commission 2010). However, to demonstrate disease freedom, the European Food Safety Authority recommends a sample size sufficient to detect 1% seroprevalence with 95% confidence (EFSA 2008). The EC-proposed sample of 59 animals is based on far larger populations than any of the feral swine populations in England. Therefore, new models need to be created to better fit these populations.

Here, we present an approach for the estimation of the rate of culling necessary to detect CSF at 1% and 5% seroprevalence in English feral swine populations, and we illustrate how information available *a priori* can be used to plan surveillance and, if necessary, control.

MATERIAL AND METHODS

The basis of our approach was to use currently-available information on feral swine populations and methods of removing feral swine from the wild to model the effort likely to be required to obtain a sufficient sample to detect CSF at 1% and 5% seroprevalence within given English populations. We built predictive models using information on the relationships between resources needed to cull at a required rate with varying swine population density and size, so that predictions could be made under a range of scenarios for each population.

Data on the efficacy of live trapping was collected during a series of research projects led by us in Penyard and Chase Woods, using single-capture steel mesh box traps baited with maize. We recorded information on trapping effort (in trap-nights), numbers caught, age class, and sex of feral swine between January 2008 and April 2010.

Feral swine are routinely shot to control their impacts by government hunters currently in one area of England only (Forest of Dean). These hunters provided us with information on shooting effort (in hours), numbers shot, age class, and sex of feral swine shot during a single year (2009).

Mean estimates of the pre-breeding density and abundance of feral swine in the District were received from R. Gill. These values were calculated by direct observation and line transect distance sampling during January 2009 (Forest of Dean) and January 2010 (Penyard and Chase Woods) (Gill and Brandt 2010).

Culling rates were calculated separately for shooting and trapping. We divided the number removed per unit of effort (measured in man-hours for shooting and trapnights for trapping) by estimated population size to calculate the likely proportion of the population removed per unit of effort.

The rate of change was also estimated separately for trapping and shooting. It was assumed that trapping effort was fixed over time, and that shooting removed a constant proportion of the population throughout the campaign. Thus, the rate of change (λ) was modelled using the following equation:

$$\lambda = \frac{\ln \frac{N_{t+1}}{N_t}}{E}$$

where:

 N_{t+1} = Number of swine remaining at the end of the culling campaign

 N_t = Number of swine at the start of the culling campaign E = Effort (trap-nights for trapping and man-hours for shooting).

Costs were initially estimated in GB£ and then converted to US\$ using the current exchange rate (US\$1 = GB£0.607). Cost per feral swine culled and the total cost of a campaign was estimated by multiplying the effort expended shooting and trapping by the cost per hour (in terms of labour) and adding the setup costs (including equipment purchase and installation) and transport costs. For all calculations, a daily labour cost of US\$400 was assumed, which equates to approximately \$50 per hour for an 8-hour working day. Note that this is a daily labour cost that includes institutional overheads, and it does not represent a daily wage.

Shooting and trapping returns were modelled, using a Monte Carlo procedure, across the range of input population sizes observed in England throughout the year, and effort required in order to simulate variation in these quantities. We assumed that the proportion culled for a given effort was the same between populations of feral swine. However, the culling rate for shooting was modelled with a uniform distribution, with the lower and upper limits described by the two hunters' culling rates. Scenarios were run for each population using each of 3 different abundances as starting values (Table 1) to approximate the likely differences in feral swine abundance during winter (lowest abundance), spring/summer (highest abundance), and fall (median abundance).

Starting abundance was multiplied by the culling rate (the proportion of the total population culled per manhour) and effort (man-hours), ranging from 0 to 4,250 in 250 man-hour increments. Simulations were run 2,000 times each in Crystal Ball software (Decisioneering Inc. Denver, CO). Outputs were the median, 2.5th, and 97.5th percentiles of the cumulative number of feral swine culled for each increment of effort. These were plotted as curves to illustrate the relationship between effort and numbers of swine culled.

A similar analysis was undertaken using the trapping data and swine abundance estimates for Penyard and Chase Woods in 2009. Trapping rate data were modelled with a triangular distribution since they could be broken down into seasonal rates and summarised across the year (Figure 1), giving 3 rates with which to work (highest, lowest, and most likely). Effort (trap-nights) was varied from 0 to 200 in 10 trap-night increments.

The number of feral swine required to be tested for disease (Table 1) was then applied to these curves to derive an estimate of the effort required to demonstrate disease presence for each scenario. The number of samples required was estimated from the sample size calculations in Cannon and Roe (1982) in order to detect, with 95% certainty, disease at 1% and 5% seroprevalence within the population. Then, we plotted the starting number of feral swine against the effort required to yield the requisite number of carcasses. Effort (in man-hours) was multiplied by the cost per unit effort to estimate the total costs associated with the level of trapping or shooting required.

To investigate the changes that could lead to disease detection not becoming feasible, simulations were run with varying culling efficiency. The underlying assumption was that absolute culling efficiency (whether by trapping or shooting) declines with density, so that varying culling efficiency would indicate the effects of changes in local abundance and/or distribution, thereby implying changes in effort required should feral swine disperse in response to a culling campaign. We ran simulations, for both trapping and shooting independently, for culling efficiencies of 10% and 50% of the values measured in the field.

RESULTS Population Size

It was estimated that from March to April 2009, feral

swine were present in Sussex/Kent at a density of 3.6/km², in the Forest of Dean at 1.1/km² and in Penyard and Chase Woods during February 2010 at 5.0/km². These densities equate to approximate mean breeding populations of 17, 62, and 21 feral swine at each location, respectively. Estimates of feral swine density were highly uncertain. During 2009 the coefficient of variation (CV) for the Sussex/Kent estimate was 50.5%, rising to 60.1% in 2010 (Gill and Brandt 2010), and 60.1% declining to 52.3% in 2010 for the Forest of Dean. For Penyard and Chase Woods, the CV in 2010 was 42.6%.

To estimate the likely mean population size post breeding, it was assumed there was a 1:1 sex ratio at birth and in the adult population (Moretti 1995, Focardi et al. 1996) and a mean annual reproductive output of 1.0 to 2.0 female piglets per adult female (Holland et al. 2009), which equates to 2.0 to 4.0 piglets per female per year. Extrapolating from the mean pre-breeding abundances above, this means the likely post-breeding population size for each area was 34-51, 124-186, and 42-63, respectively.

Wilson (2003) estimated that minimum feral swine abundance in Dorset varied from five to 30 between 1995 and 2002. From these data, Wilson constructed a retrospective census, predicting a minimum population of 15 adult swine and a maximum of 70.

Table 1. Input abundance values for 4 feral swine scenarios. Numbers in parentheses are the number of feral swine that would need to be sampled in order to detect, with 95% certainty, disease present at 1% and 5% seroprevalence, respectively, within the population.

Site	Area (ha)	Abundance				
Site	Area (ha)	Winter	Spring/Summer	Autumn		
Sussex/Kent	480	17 (17,17)	51 (51,35)	34 (34,28)		
Penyard and Chase Woods	427	21 (21,20)	63 (63,38)	42 (42,32)		
Forest of Dean	5787	62 (62,38)	186 (149,50)	124 (113,47)		
Dorset	1100	15 (15,15)	70 (69,40)	30 (30,26)		

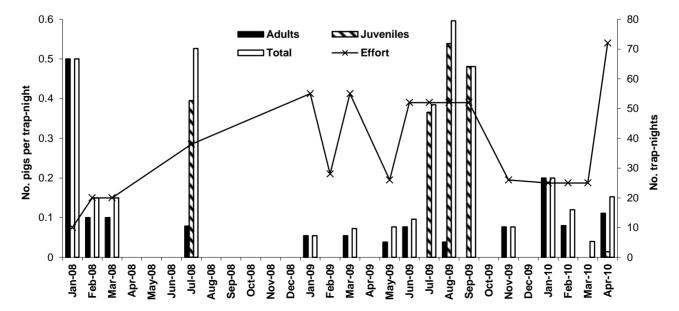


Figure 1. Feral pig trapping results. The line represents trapping effort, and the bars number of pigs caught per trap night. The Total column combines all captures, including re-captures of females.

Culling Rates

From January 2008 to March 2010, a total of 26 adult females, 16 adult males, and 88 juvenile feral swine were trapped in Penyard and Chase Woods over 633 trapnights involving 10 to 14 traps per night (Figure 1). This resulted in an average of 0.21 feral swine per trapnight. In total, 13 adult females were re-trapped; however, it was not possible to distinguish whether the trapped adult males and juveniles were re-captures since they were not marked before release.

Trapping effort varied over time (Figure 1). Neither the number of adults nor juveniles captured correlated with effort (Pearson's correlation, P>0.01), but the total number of captures did (r=0.502, n=17, P=0.04). Total number of captures was significantly higher during the summer months (Poisson count regression, with 'effort' and 'season' as explanatory variables $\chi^2=135.8$, d.f. = 6, P<0.001), but the number of adults trapped per trap-night was fairly constant.

Two government hunters (A and B) undertook the vast majority of the feral swine culling work in the Forest of Dean, while one further hunter (C) opportunistically shot feral swine during deer culling duties. 1January to 31 December 2009, Hunter A spent 616 hours targeting feral swine, approximately establishing bait points (0.5 hours per day for 8 days), and shooting from a high seat (3 hours at dawn and at dusk per day for 14 days). This was repeated every month for 7 months. In total, 13 males and 20 females were culled, equating to 1 swine shot for every 18 hrs 40 mins of effort. In addition, 2 males killed by collisions with road traffic were retrieved. Hunter B spent approximately 960 hours targeting feral swine throughout the 12-month period; 8.5 hours per week pre-baiting and shooting from high seats, and 12 hours per week of hunting on foot. This yielded 13 males and 10 females and equates to 1 swine shot for every 41 hrs 44 mins of effort. In addition, 3 males and 2 females killed in collisions with road traffic were retrieved. Hunter C opportunistically shot 2 female feral swine, 3 males, and retrieved a male road casualty. As these swine were not deliberately targeted by this hunter, it was not possible to estimate the effort expended culling them.

Culling rates were not constant throughout the year. More swine were shot during the summer than at any other time of year, although Hunter B shot slightly more swine in fall.

Costs

Our feral swine box traps cost US\$832 to manufacture and took 8 man-days (at US\$399 per day) to place 13 of them. The traps also required pre-baiting with maize, which cost \$17 per day for 7 days and took 3 hrs per day (including \$8 in local travel costs). Thus, the cost of establishing each trap came to US\$1,161.

Trap setting took 40 mins per trap per night and 10 mins per trap the following morning to check each trap. This cost US\$42 per trap in labour and <\$1 in local travel costs. Staff engaged in trapping also needed local accommodation and expenses, estimated at US\$126 per person per day for 2 people. Trapping resulted in the capture of 9 males, 6 females, and 72 piglets, at a cost of

US\$477 per animal, from a breeding population of approximately 21 adults. The culling of trapped feral swine should be fairly quick, if despatched by gunshot. However, carcasses will need to be extracted, probably by quad-cycle and sled moving, to a 4-wheel-drive vehicle equipped with an internal winch to lift the carcass into the vehicle. These additional costs were not included in the analysis.

Rifles and peripheral equipment suitable for shooting feral swine can be purchased for approximately US\$1,663. Each hunter may require approximately 100 rounds of ammunition per year to allow for culling, zeroing, and practice, costing approximately US\$166. Government hunters spent 1,576 hrs culling feral swine during 2009, at a labour cost of US\$50 per hr. Local travel is also likely to have cost approximately \$8 per day. Assuming that new rifles were purchased specifically for culling feral swine, the government may have spent US\$3,660 on rifles and ammunition, US\$1,638 on local travel, and US\$70,330 on labour to cull 56 swine. The total cost then may have been approximately US\$75,628.

Simulation Models

As described above, shooting rates varied from 1 feral swine every 18 hrs 40 mins to 1 every 41 hrs 44 mins of effort. This equates to 0.0129% to 0.0288% of the population culled per hour of effort with a simple average of 0.0191%. Applying these values to the estimates of feral swine abundance yielded sigmoidal curves of effort versus cull numbers (Figure 2).

Trapping rates varied from 0.183% of the population removed per trap-night during the fall to 0.427% during the summer, with a simple average across the year of 0.251%. Applying these values to the estimates of feral swine abundance yielded sigmoidal curves of effort versus cull numbers (Figure 2).

The effort required to cull sufficient swine varied widely between scenarios. For shooting, and to detect disease at 1% seroprevalence, maximum effort (3,750 man-hours) was estimated at the 2.5th percentile for populations between 40 and 65 feral swine, and minimum effort (1,500 man-hours) at the 97.5th percentile for populations of 186 individuals (Table 2). For trapping, maximum effort (200 trap-nights) was estimated at the 2.5th percentile for populations between 50 and 70 feral swine, and minimum effort (75 trap-nights) at the 97.5th percentile for populations of 186 (Table 2). Under the less stringent test of 5% seroprevalence, the greatest shooting effort (3,250 man-hours for shooting and 170 trap-nights for trapping) was at the 2.5th percentile for populations of fewer than 20 animals. Effort was curvilinearly related to population size due to a reduction in the proportion of animals needing to be sampled for populations of more than 70 (Figure 3).

Estimated Costs of Control

The required sample size for each scenario could be achieved by varying the number of traps and the number of nights of trapping or by varying the number of hunters and number of hours spent shooting. Assuming the cost structures detailed above, but including accommodation

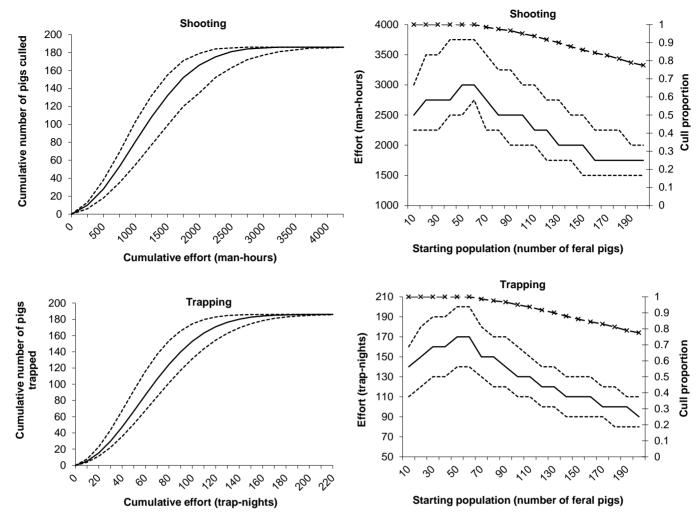


Figure 2. Predicted change in the total number of feral pigs culled with increasing effort in (shooting and trapping) with a starting population of 186 feral pigs. The solid curves represent the median values over 2,000 Monte Carlo simulations, and the dashed lines are the 2.5th and 97.5th percentiles.

Figure 3. Median effort (solid lines) required to shoot and trap a sufficient number of feral pigs to detect disease at 1% seroprevalence with 95% certainty given varying starting population sizes. The dotted lines are the 2.5th and 97.5th percentiles of estimated effort. The dashed lines with "x" markings illustrates the change in the proportion of the population needing to be sampled with increasing population size.

Table 2. Effort required to cull a sufficient number of feral pigs, using shooting (measured in man-hours) and trapping (measured in trap-nights), to detect disease at 1% seroprevalence with 95% certainty for representative scenarios likely to be experienced in England.

Population Sample			Shooting		Trapping			
Size	ze Required Median L		Lower 95 th Percentile			Lower 95 th Percentile	Upper 95 th Percentile	
15	15	2500	3250	2250	140	170	120	
30	30	2750	3500	2250	160	190	130	
51	51	3000	3750	2500	170	200	140	
63	63	3000	3750	2500	170	200	140	
124	113	2000	2750	1750	120	140	100	
186	149	1750	2250	1500	100	115	75	

and expenses for shooting as well as trapping, for comparative purposes, these relationships can be described by surface plots (Figure 4). Trapping could be more cost-effective using fewer traps over more nights than more traps over fewer nights, largely due to the enhanced establishment costs associated with purchasing large numbers of traps. The reverse may be true for shooting, which could be marginally more cost-effective using more hunters over shorter periods of time than fewer hunters over longer periods (Figure 4).

Using the cost matrices constructed to derive these curves, the optimal costs (cheapest combination) required to achieve target culls was estimated for each scenario. Results presented in Table 3 are based on the 2.5th percentile estimate of effort (the greatest estimate of effort required) for detection of CSF at 1% seroprevalence, since budgeting is recommended on the worst-case scenario. Budgeting according to the median or 97.5th

percentiles poses a greater risk of providing inadequate resources to achieve the required cull.

Predictably, as culling efficiency (modelled as the shooting and trapping rate) reduced, the effort required to sample sufficient feral swine to detect disease increased (Table 4). Under most scenarios, and regardless of whether disease was to be detected at 1% or 5% seroprevalence, both trapping and shooting required approximately 3 times the effort when culling efficiency was 10% of that measured in the field. However, the required shooting effort increased dramatically for larger populations when disease was to be detected at 1% seroprevalence. The same pattern was true when culling efficiency was varied to 50% of that measured in the field. Effort required was approximately 1.5 times higher except for larger populations, when the effort required rose to 2.8 times higher.

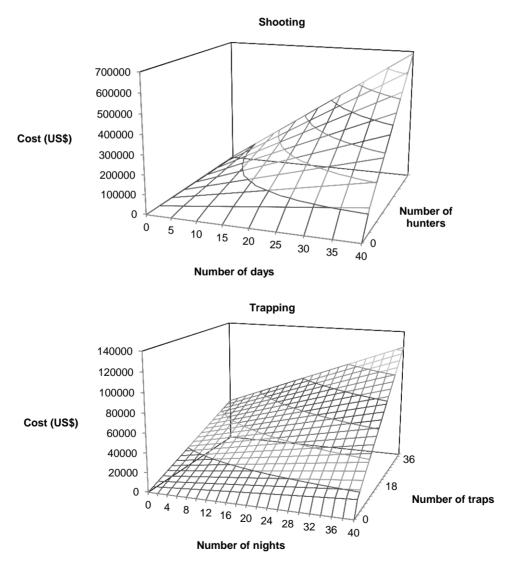


Figure 4. The costs of shooting and trapping with variation in 2 sets of effort parameters.

Table 3. Estimated costs (US\$) of delivering a cull, by shooting or trapping, sufficient to detect disease at 1% seroprevalence with 95% certainty in feral pigs in selected scenarios likely to be experienced in England.

Population Sample Required		Shooting			Trapping			Total Cost	
		Number of Hunters	Number of Nights	Cost	Number of Nights	Number of Traps	Cost	(combined approach)	
15	15	11	37	178897	28	6	20838	199734	
30	30	13	33	194548	32	6	22834	216384	
51	51	14	33	203439	20	10	24754	228193	
63	63	14	33	203439	20	10	24754	228193	
124	113	10	34	150630	24	6	18841	169470	
186	149	7	40	124328	18	6	15848	140175	

Table 4. Maximum effort required to cull a sufficient number of feral pigs, using shooting and trapping, to detect disease at 1% and 5% seroprevalence with 95% certainty, and for culling rates (eff.) at 10% and 50% of that measured in the field, for selected scenarios likely to be experienced in England.

Population	Shooting				Trapping			
Population size	10% eff. 1% prev.	10% eff. 5% prev.	50% eff. 1% prev.	50% eff. 5% prev.	10% eff. 1% prev.	10% eff. 5% prev.	50% eff. 1% prev.	50% eff. 5% prev.
15	11000	11000	4750	4750	560	560	250	250
30	11500	8250	5250	3500	620	420	270	190
51	12750	6500	5500	2750	650	330	280	140
63	13000	5750	5500	2500	670	290	290	130
124	13750	4250	6000	1750	470	210	210	90
186	14250	3250	6250	1500	390	170	170	80

Although not explicitly included in analyses, results for the fairly new population of feral swine on Dartmoor, which is estimated to number approximately 30 animals (Wilson pers. comm. in Hartley 2010) can be deduced, since the population size falls within the range of other populations modelled here.

DISCUSSION

As with most free-living animals, reliable estimation of feral swine densities can be very challenging, particularly when densities are low (Engeman et al. 2013). Although it was possible to estimate the abundance of feral swine at each site, abundance data were extremely limited, covering one population completely (Forest of Dean and Penyard and Chase woods) and one partially (Sussex/Kent). The density estimates that we used were consistent with those experienced during some other feral swine control campaigns [e.g., 10.3/km² (Saunders and Bryant 1988), 0.8/km² (Sweitzer et al. 2000)] but much lower than others [e.g., 27.2/km² (Parkes et al. 2010)]. Effort estimation would be more reliable with precise estimates of abundance collected for each season and for each discrete feral swine population in England.

Trapping rates varied over time with particularly low results during 2008. These poor trapping results may be explained by a high degree of trap-interference. Relationships between field staff and members of the public using the study site were actively improved during late 2008, and the frequency of trap interference was subsequently reduced. In addition, concomitant tracking of feral swine using GPS tags has allowed more effective targeting towards areas more heavily used by feral swine. It is also worth noting that whilst estimating trapping rates in this study, it was assumed that all male and piglet captures represented first-time captures, which may have over-estimated some of the higher trapping rates. Other

variables that may have affected trapping rates include topography, time of year, type of trap, number and density of traps deployed, number of nights each trap is used, trap location, type of bait, duration of pre-feeding before the traps are set, and availability of natural food (Hone 1980, Saunders et al. 1993, Choquenot et al. 1996, Massei et al. 2011).

Field staff have continually improved their trapping techniques and this is an ongoing process. The results reported here are for the use of single-capture box traps, which have been successful. However, recently trialled multi-capture corral traps, which may be more expensive to purchase and install, can capture several animals (including entire maternal groups) at a time, leading to potential efficiency savings. As costs and efficiencies become apparent for this type of trap, it may be helpful to quantify the contribution that they could make during a suspected outbreak of CSF in feral swine.

Seasonal variation was noted in the shooting data as well as the trapping data. Fewest swine were shot by government hunters during the winter. This is likely to be largely due to population density being lowest during the winter and highest during the spring and summer. In addition, less effort tends to be devoted to deer culling during the summer months due to legal restrictions and vegetation cover, leaving more time for feral swine Variables other than effort and feral swine abundance that are likely to explain the number of swine that can be culled include animal adaptability. Indeed, swine are highly adaptable and have been shown to change their behaviour in response to hunting (Saunders and Bryant 1988, Massei et al. 2011), so measures of human disturbance might explain an additional portion of this variation (Dexter 1996). Indeed, the likely response of feral swine and wild boar to intensive shooting prompted EFSA (2014) to discount this method to control African Swine Fever in their widespread, contiguous, and dense populations across continental Europe.

The low variation in estimated shooting effort required, and hence costs, were largely due to having only 2 estimates of hunter effort with which to build a data distribution. This was undoubtedly suitable for application to the Forest of Dean situation, from where the data were derived, but may be unrealistic for other areas. Consequently, empirical estimates of effort and numbers of feral swine culled are required to better describe variation in this crucial measure. Juvenile feral swine have not appeared in government cull records to date. Consequently, estimates of effort derived from shooting data are likely to over-estimate the effort required to shoot sufficient numbers of feral swine to detect disease, since juveniles will need to be included (and probably specifically targeted) during disease surveillance.

Trapping was predicted to offer lower cost than shooting, so it may seem sensible to rely solely on trapping to deliver the necessary cull. However, the comparison of shooting with trapping may not have been entirely valid in this sense, since shot animals were killed, whereas trapped animals were released alive. The potential for bias in favour of trapping was partially controlled by only using data from the first time of capture for adult females. Unfortunately, it was not possible to identify and therefore control for re-trapped males and piglets, since these were not marked during the field study. This could have resulted in our estimates of trapping efficiency being biased high if the recapture rate was higher than the rate of trap avoidance. While both trap avoidance and attraction have been inferred for individuals of other species [e.g., in Eurasian badgers (*Meles meles*) (Tuyttens et al. 1999)] as well as feral swine (Reeser and Harry 2005), we were not able to quantify the rates of these for feral swine in England. Moreover, during several feral swine eradication campaigns, success was deemed to have been the consequence of a combined approach, using a variety of culling methods and adapting to changing circumstances (Barrett et al. 1988, Saunders et al. 1993, Lombardo and Faulkner 2000, McCann and Garcelon 2008, Parkes et al. 2010).

This study has provided an example of how current information can be used to plan allocation of resources to drive the efficiency of a culling campaign using shooting and/or trapping, and information to facilitate the efficient timing of trapping programmes. Overall, the results suggest that efficient feral swine culling should employ several shooters for short-duration, intensive shooting campaigns and approximately 4 to 16 traps over several nights of trapping. These preliminary data suggest that campaigns conducted during the summer are more likely to be successful for less investment than those run at other times of year, although more data are required to confirm whether this is correct. It was not possible to provide novel information on how best to conduct a feral swine cull by shooting on the ground. Other authors have described some factors associated with greater trapping success [e.g., trap placement, baiting strategy (Saunders et al. 1993, Massei et al. 2011, Higginbotham 2012)] and shooting strategies for closed populations, but the potential for feral swine to disperse in response to intensive shooting (Saunders and Bryant 1988, but see Keuling et al. 2008) should be considered when defining a Feral Pig Investigation Zone and devising a shooting strategy.

Changes in population density and total abundance have implications for disease epidemiology as well as disease surveillance and detection. Consequently, it would be helpful to be able to access contemporary density and abundance estimates at the time of a suspected outbreak of CSF in feral swine, in order to evaluate risks to domestic pigs as well as to accurately assess the resources needed to collect an adequate sample. The true abundance of feral swine populations in England could have been substantially different to the mean estimates presented here, and even intensive pre-cull surveys might not produce sufficiently precise population estimates to reliably estimate the effort needed to sample them adequately (Engeman et al. 2013). Inclusion of such estimates into a more flexible approach could turn this uncertainty from a problem into an anticipated feature of an adaptive management program. A preliminary population estimate could be used to plan likely resource requirements, followed by derivation of increasingly reliable population estimates and hence estimates of effort required, as the cull progresses, perhaps using a catchper-unit-effort approach (Kaji et al. 2010) until decisionmakers are sufficiently confident that an adequate sample has been collected or the population eradicated.

The key implication of our simulation modelling is that under either test (1% or 5% seroprevalence) it was likely to be feasible to deliver culling at a sufficient rate to collect the requisite sample during 2010, and in most cases this may have resolved the potential occurrence of CSF disease in feral swine in England due to eradication of the population in question. By way of cost comparison, eradication of 144 feral swine from an area of 22 km² cost US\$75,000 during the 1980s (Barrett et al. 1988), and eradication of 200 from a fenced area of 194 km² between 2003 and 2006 cost US\$623,202 (McCann and Garcelon 2008). Our predictions are of the same orders of magnitude. However, it seems unlikely that the English populations have remained static, and evidence is starting to accumulate to suggest that they are growing and spreading (Gill 2014). Consequently, our calculations will need to be re-run when new abundance estimates are available, if reliable estimates of required effort are desired.

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