

Incorporating heterogeneity in farmer disease control behaviour into a livestock disease transmission model

Edward Hill

`edward.hill@warwick.ac.uk`

University of Warwick <https://orcid.org/0000-0002-2992-2004>

Naomi Prosser

University of Nottingham <https://orcid.org/0000-0001-8391-7153>

Paul Brown

University of Warwick <https://orcid.org/0000-0002-8764-4583>

Eamonn Ferguson

Nottingham <https://orcid.org/0000-0002-7678-1451>

Martin Green

University of Nottingham

Jasmeet Kaler

University of Nottingham

Matt Keeling

University of Warwick <https://orcid.org/0000-0003-4639-4765>

Michael Tildesley

Warwick

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Abstract

Human behaviour is critical to effective responses to livestock disease outbreaks, especially with respect to vaccination uptake. Traditionally, mathematical models used to inform this behaviour have not taken heterogeneity in farmer behaviour into account. We address this by exploring how heterogeneity in farmers vaccination behaviour can be incorporated to inform mathematical models. We developed and used a graphical user interface to elicit farmers (n = 60) vaccination decisions to an unfolding epidemic and linked this to their psychosocial and behavioural profiles. We identified, via cluster analysis, robust patterns of heterogeneity in vaccination behaviour. By incorporating these groupings into a mathematical livestock disease model, we explored how heterogeneity in behaviour impacts epidemiological outcomes. When assuming homogeneity in farmer behaviour versus configurations informed by the psychosocial profile cluster estimates, the modelled scenarios revealed a disconnect in projected distributions and threshold statistics across outbreak size, outbreak duration and health economic measures.

Introduction

Human society is characterised by a higher degree of cooperation than would be expected from the perspective of evolutionary theory^{1,2}. Thus, there must be benefits to be derived from cooperation at both an individual and societal level that afford a selection advantage, and, indeed, many have been identified at the individual (e.g., warm-glow, reputation building) and group levels²⁻⁷. However, human cooperation presents the individual with the dilemma of deciding between what is good for them versus what is good for others. If everyone else has a flu vaccination, then I do not have to. However, what others do or are likely to do is unknown^{1,4}. Indeed, successful responses to wider societal threats (e.g., COVID-19) or sustained healthcare (e.g., blood/organ donation, vaccination) are social dilemmas requiring wider cooperation⁸⁻¹⁰.

Given these are all social dilemmas, how can wider-scale cooperation be encouraged and maintained? Two approaches have been taken. The first is to use mathematical modelling to explore and support the role of large-scale social policies (e.g., closing schools, social distancing, culling livestock, mandated or voluntary vaccination) that are then implemented by Governments¹¹. The second is to develop interventions that target individual behavioural change with respect to such practices as vaccinations, and social distancing, with the assumption that if enough people change their behaviour the desired outcome will be achieved⁸. Indeed, it has been argued that behavioural science has a key role to play in helping manage responses to pandemics⁸, encourage vaccination behaviour¹² and health based philanthropy^{9,10}. However, the focus on heterogeneity in behaviour that is central to a behavioural science approach needs to be incorporated within large-scale policy-based approaches that rest on modelling population-based outcomes to disease outbreaks. Indeed, Chater and Loewenstein¹³ refer to policy-based population approaches as s-framed strategies and individual behavioural change approaches as i-framed strategies, arguing that the former is much more effective than the latter. S-frames strategies, however, tend to be generic (e.g., opt-out organ donation defaults) and ignore individual variation in attitudes and

behaviour. Therefore, this raises the question whether s-framed strategies can be made more effective by incorporating individual heterogeneity in attitudes and behaviour. Thus, in this paper we explore how mathematical models that examine the role of vaccination behaviour can be developed to include individual heterogeneity in behaviour. We do this in the context of vaccination decisions in farmers with respect to an unfolding epidemic in livestock, but argue that the principles have applications to modelling and understanding wider behavioural change associated with social dilemmas.

The actions of farmers are fundamental to disease control in their livestock, with the disease management behaviours they enact in their own herds contributing to the success of wide-scale disease control. Yet, this presents a social dilemma. For example, (i) engaging with bovine viral diarrhoea testing is voluntary in England and Wales, however, it is necessary for UK-wide farmer engagement with these practices for the goal of bovine viral diarrhoea eradication by 2031 to be achievable^{14,15}, (ii) risky cattle purchasing behaviour by individual farmers is associated with new bovine tuberculosis herd breakdowns, with implications for both regional and national bovine tuberculosis control¹⁶, and (iii) willingness of farmers to report the presence of disease on their farm is important for the control of many epidemics¹⁷. Farmer heterogeneity towards disease management, therefore, warrants consideration when establishing veterinary health policies. That being said, analytical approaches that can contribute useful insights to the formulation of livestock disease control plans, such as mathematical modelling, traditionally treat farmers as passive bystanders and omit the observed variation in disease management behaviours. Multiple methodological developments are consequently required to overcome these deficiencies.

People are well known to show different behaviours with respect to disease control; for example people can be mutually cooperative (acting for the benefit of both the self and other people), or show parasitism (gain benefit from other people taking action)¹⁸. This is seen for human infections where there is considerable variability in the uptake of vaccine or the decision to vaccinate children^{19,20}, and this concept translates to farmers with the decision to protect their livestock. The heterogeneity in farmer behaviour for disease control is in part due to psychosocial and behaviour factors. Trust is a key component underlying cooperation²¹ and trust in other farmers improves willingness to join disease control schemes^{22,23}. However, trust in other farmers is also associated with farmers not controlling specific diseases such as bovine viral diarrhoea²⁴ - increased trust means that farmers are more likely to believe that purchased animals will be disease-free. Trust also has implications for sources of advice, with farmers preferring to trust veterinary rather than Government advice²⁵⁻²⁷. Related to trust is psychological proximity (closeness) to others. Psychological proximity includes close feelings and behaviours, and connection, interdependence and similarities with the other person²⁸. Psychological proximity has implications for human health behaviour²⁹⁻³¹ but to date has received little investigation in farmer behaviour for controlling livestock disease. Farmers with high psychological proximity to their veterinarian are more likely to control bovine viral diarrhoea in their herd²⁴. Behaviour is also influenced by capability, opportunity and motivation which are theorised in the COM-B behaviour change framework³². Capability is the physical ability (physical capability) and the knowledge and understanding

(psychological capability) required to perform a behaviour. Opportunity is the time and money (physical opportunity) and the support from others (social opportunity) that enable a behaviour. Finally, motivation is decision-making and goals (reflective motivation) and habits and emotions (automatic motivation). Factors that make up this framework are often investigated in isolation in the context of disease control and use of the entire COM-B framework in livestock disease is rare. One study that used the COM-B framework found that farmers with high automatic and reflective motivation, high psychological capability and high physical opportunity were more likely to control disease in their herds²⁴.

There has been a growing interest in the incorporation of psychosocial factors and behavioural heterogeneity into disease transmission models³³, which will allow improved model predictions for successful disease control. A fundamental component of delivering these methodological advances is having appropriate, well-informed behavioural data available to parameterise models and enhance the robustness of model outputs. One previous example of such data collection activities includes Merrill *et al.*³⁴, who conducted an experimental simulation game to quantitatively explore the effect of interventions that would increase information sharing among stakeholders. Nevertheless, a known challenge of fusing livestock infectious disease models and dynamic human behavioural change is a dearth of quantitative behavioural data that can capture interpersonal and contextual factors³⁵.

Through an interdisciplinary approach, we strive to form a methodological pipeline that can generate novel quantitative data on farmer beliefs and hone epidemiological-behavioural models so the gathered data is amenable for direct usage (and equally, a pipeline where model outputs can inform what attributes may require particular focus in future data collection). To make initial advancements in this emerging research space - establishing a proof-of-concept - requires a well-defined scenario to make elicitation feasible. In this study, we investigated farmer behaviour in a fast, spatially spreading disease outbreak scenario using a novel graphical user interface (GUI) to dynamically show the progress of the epidemic and elicit when farmers would use a vaccine that was available to them. This is an important scenario to consider as a pathogen spreading rapidly between farms has the potential to cause substantial negative impacts, albeit a rare occurrence in Great Britain, and would likely need a concerted effort by farmers to control. We chose vaccination as an intervention response because the types of heterogeneity observed in vaccination behaviour and attitudes has been well documented³⁶⁻³⁸.

Using multiple validated measures, we studied how trust, psychological proximity and COM-B factors were associated with farmer vaccination behaviour in the face of the disease outbreak. We then used the attained behavioural groups within an infectious disease model to explore, through computational simulation, the impact on anticipated epidemiological outcomes (outbreak size, outbreak duration, intervention unit cost whilst remaining cost-effective) when making specific assumptions regarding heterogeneity in behaviour towards disease management. It is revealed how omitting heterogeneity in farmers' disease management of livestock infections can result in ill-judged assessments of the likely projected distributions and threshold statistics associated with outbreak size, outbreak duration and health economic measures.

Results

Our approach consisted of three methodological stages: (i) design of a GUI to act as a core, interactive component of the interview exercise; (ii) development and usage of an interview script to elicit farmer disease vaccination behaviours; (iii) incorporation of these vaccination behaviours into an epidemiological model for a fast-spreading livestock infection.

Further details on how each stage was conducted are provided in the Methods

GUI design and usage

The bespoke GUI created for this investigation can be found at <https://feed.warwick.ac.uk/map.html> and an example screenshot is shown in Supplementary Fig. 1. The GUI illustrated the spread of the hypothetical cattle disease epidemic outbreak to the farmers and created a common outbreak experience in terms of distance to the nearest infected herd for all farmers. The GUI also contained a panel summarising the distance from the farmer's herd to the nearest infected herd, and the total number of infected herds and the number of localised outbreaks of infection in GB.

Elicitation findings

Sixty farmers (39 beef and 21 dairy) completed the elicitation interview. Forty-four (73%) were from England, nine (15%) from Scotland and seven (12%) from Wales. The median number of cows in the herd was 155 cows for dairy herds (range = 30–330, one herd only reared heifers) and 35 for beef herds (range = 5–200, one herd only fattened cattle). The herd sizes were slightly larger than the national averages and English farmers were slightly over-represented³⁹.

The farmers differed in when they used preventive vaccination, with 58 (96.7%) using vaccination at some point during the scenario: eight (13.3%) vaccinated at the first opportunity (a localised outbreak restricted to southern France), 16 (26.7%) vaccinated when cases were first detected in GB and 34 (56.7%) vaccinated at a later stage of the GB epidemic. The vaccination behaviour of the farmers can be labelled as mutually cooperative (vaccinates during epidemic stages 1–2), weak parasitism (vaccinates during epidemic stages 3–5), strong parasitism (vaccinates during epidemic stages 6–8) or free-riding (never vaccinates)¹⁸ (Table 1).

Table 1

The number of infected herds, the distance of the nearest infected herd from the interviewee's herd and the number of farmers that vaccinated for each week during the disease epidemic scenario.

Stage of epidemic	Time since previous stage (weeks)	Number of infected herds (in GB)	Distance to nearest infected herd (km)	Number of farmers vaccinating (/60)
1	2	0	> 500*	8
2	2	2	322	16
3	1	10	322	5
4	1	40	161	14
5	1	100	161	1
6	1	150	48	10
7	1	450	16	3
8	1	600	5	1
*Epidemic confined to southern-central France				

We fit multinomial logistic regression models testing for associations between the psychosocial and behaviour change factors and when farmers vaccinated to bootstrap repeats of the dataset. The covariates selected by a higher proportion of the models were more likely to be truly associated with when farmers vaccinated. We calculated stability thresholds for different levels of confidence of the selected covariates being false positives (see "Analysis of elicitation data" in the Methods). Two covariates were above a stability threshold when there was only a 10% probability of not being associated with when farmers vaccinated (0.24). These covariates were: trust in governmental judgements about how to control infectious diseases in cattle; and physical opportunity (Table 2). Three additional covariates were selected when the stability threshold was relaxed to a 15% probability of not being associated with when farmers vaccinated (0.20), which were: trust in the quality of advice from the veterinary profession; trust in other farmers nationally to control infectious diseases; and herd size at time of disease outbreak. There was no evidence of poor model fit in a Hosmer-Lemeshow goodness-of-fit test ($p = 0.814$), by visual inspection of a decile plot of the observed and expected vaccination classes (Supplementary Fig. 2), or when comparing the proportion of farmers for which the model predicted the correct vaccination class between the full model (0.62) and the 10 x 10-fold cross-validated models (mean = 0.58).

Using k-means clustering⁴⁰, we clustered farmers by their scores for the psychosocial and behaviour change covariates that were selected by the above regression models. A model consisting of four groups of farmers gave the best fit when using the two most stable covariates. Three groups gave the best fit using the five most stable covariates (Supplementary Fig. 3). In brief, for the clustering on the two most stable covariates, the four clusters were: (1) high trust in Governmental judgements for disease control and high physical opportunity; (2) low trust in Governmental judgements for disease control and high

physical opportunity; (3) high trust in Governmental judgements for disease control and low physical opportunity; (4) low trust in Governmental judgements for disease control and low physical opportunity (Fig. 1). For the clustering on the five most stable covariates, the three clusters were: (1) high general trust, high physical opportunity and small herd size; (2) low trust in Governmental judgements for disease control and in other farmers to control disease; (3) high trust in Governmental judgements for disease control and in other farmers to control disease, low physical opportunity and a large herd (Fig. 2).

Table 2

The stability and mean odds ratio (OR) of the covariates associated with when farmers vaccinated their cattle in a hypothetical disease epidemic, above the stability threshold for a 15% probability of a covariate reaching the threshold without being truly associated with when farmers vaccinated their cattle (0.20).

Covariate	Stability	Mean OR	
		Epidemic stage 3–5	Epidemic stage 6 – never
Trust in governmental judgements for infectious disease control	0.28	0.29	0.66
Physical opportunity	0.26	0.85	0.19
Trust in quality of advice from the veterinary profession	0.22	1.82	0.14
Trust in other farmers nationally to control infectious diseases	0.20	6.18	1.25
Herd size at time of disease outbreak	0.20	1.01	1.01

Impact of heterogeneity assumptions for farmer vaccination behaviour on livestock disease modelling assessments

In the final component of our analyses, we constructed a disease transmission model for a fast-spreading pathogen amongst cattle, first emerging in a spatially localised area of Great Britain from a low case level. With this model, we evaluated the ramifications on disease modelling assessments of differing assumptions on the amount of heterogeneity in vaccination behaviour amongst farmers (for a vaccine that had similar properties as that described to the interviewed farmers), including examples that incorporated the empirical findings from the elicitation exercise.

Intervention behaviour configurations

We tested eight different behavioural group population compositions, hereafter referred to as configurations, each governing the proportion of the population that would implement interventions at a given time with respect to the outbreak situation. Note that in all configurations we applied controls at holdings with confirmed infection (i.e., removal of cattle).

In four behavioural configurations we imposed a homogeneous assumption to farmer vaccination behaviour, assuming all farmers had the same disease management behaviour: all *uncooperative* - no holdings would use vaccination ; all *strong parasitism* - apply vaccination to herd upon infection being confirmed within 50km (approx. 30 miles) of their holding; all *weak parasitism* - apply vaccination to herd upon infection being confirmed within 320km (approx. 200 miles) of their holding; all *mutual cooperation* - all holdings pre-emptively vaccinated, no outbreak occurred.

In two behavioural configurations we sought to represent a situation where there was an absence of behavioural response data, but there was a desire to include heterogeneity in farmer intervention response through subjectively chosen distributions. To enable us to examine the implications of including or omitting *uncooperative* farmers in such an assumption, we explored two parsimonious, uniform stratifications of the population across intervention stance groups. The first included *uncooperative* farmers, named *Cooperation-Parasitism-Free riders (Coop-Parasitism-FR)*, whilst the second omitted *uncooperative* farmers, named *Cooperation-Parasitism (Coop-Parasitism)*.

In our final two configurations we used the elicitation findings to parameterise: (i) the split of holdings between behavioural groups; (ii) within each behavioural group, the partitioning of the holdings between the different intervention timings (see Figs. 1–2 and Supplementary Tables 1–2). We parameterised the *Trust-Expectancy* configuration using the empirical estimates for psychosocial profile clusters from the model comprising the two most stable variables (Fig. 1). For the *Herd size dependent* configuration, we used the empirical estimates for psychosocial profile clusters from the model comprising the five most stable variables, which included herd size (Fig. 2).

To assess the implications of differing psychosocial and geographical attributes on epidemiological outcomes, we tracked the percentage of holdings infected and outbreak duration. To evaluate the economic implications of behavioural attributes on intervention usage, relative to the baseline control strategy, we computed threshold intervention unit costs (the maximum cost per intervention unit where the total intervention cost equaled the costs saved from averted infections).

See the Methods subsection “Mathematical transmission model of infectious livestock disease” for an overview of the data sources used to inform cattle demography, the epidemiological model framework, our implementation of vaccination in the model, expanded details about the intervention behaviour configurations and the simulation protocol.

Homogeneous behavioural configuration outcomes

We begin by inspecting outbreak size, outbreak duration and threshold cost per intervention unit outcomes for the four homogeneous configurations: where all farmers had uniform disease management behaviour (i.e., all *uncooperative*, all *strong parasitism*, all *weak parasitism*, or all *mutual cooperation*).

By its construction, for the *uncooperative* behavioural configuration (where interventions were only used on holdings with confirmed infection) in all simulation replicates most holdings were infected, returning a median outbreak size of 99.5% of all holdings (Fig. 3(a)). We therefore observed very few instances of

small-scale outbreaks. The percentage of simulations that had greater than 1%, 10% and 20% of all holdings infected was 98.4% for all three threshold values (Fig. 3(b)). This contrasted with everyone having *strong parasitism* (the next slowest to vaccinate). Although the majority of these simulations did still result in large outbreaks, with 96.3% of simulations having more than 20% of holdings infected, there was a greater prospect that outbreak size could be curtailed without the majority of holdings applying interventions. Explicitly, whilst for everyone being *uncooperative meant* less than 1% of holdings became infected in 1.6% of simulations, under the *strong parasitism* configuration the chance of fewer than 1% of holdings being infected more than doubled (3.7% of simulations). Having all farmers being more precautionary, resembling our *weak parasitism* configuration, many outbreaks were small-scale. The median outbreak size was just 1.6% of holdings infected and no simulations resulted in more than 10% of holdings being infected. The *mutual cooperation* set up resulted in no outbreaks, as intended by its construction.

Analysing outbreak duration (which may be a major consideration for some outbreaks), our reference *uncooperative* behavioural configuration gave outbreaks with a duration typically in the region of 200–300 days, with a median of 251 days (Fig. 3(c)). The majority of simulated outbreaks (93.1%) lasted more than 180 days (Fig. 3(d)). For *strong parasitism*, the outbreak duration was reduced compared with the *uncooperative* scenario (median of 153 days), although it remained likely that outbreaks would last in excess of 100 days (96.3% of simulations). Under *weak parasitism* there was little variation in outbreak duration, with no realisations exceeding an outbreak duration of 30 days.

Pivoting to economic considerations and the threshold cost per intervention unit (Figs. 3(e,f)), for our *strong parasitism* realisations there were examples where outbreaks resulted in few onward infections beyond the initial three infected holdings (seeded with infection at the beginning of the simulation). In such instances, one would be willing to spend a higher amount per intervention unit whilst keeping the strategy cost-effective compared with the baseline strategy (reflected by 2.2% of simulations returning a threshold unit intervention cost above 2). Meanwhile, the threshold unit intervention cost exhibited more variability for *weak parasitism* than in most other scenarios, spanning 0 to 11.5. It was very likely to be in the range of 0.5 to 1, with a small chance of it being larger than 2 (achieved in 10.1% of simulations). Finally, though outbreaks were prevented under *mutual cooperation*, for the pre-emptive use of vaccination by all to be cost effective, the intervention unit cost would have to be less than the cost of infection of a single cow.

Non-data informed, heterogenous behavioural configuration outcomes

We next examine our epidemiological metrics for our simple implementations of heterogeneity in behaviour amongst the population, with a uniform split of specified behavioural groups across holdings (*Coop-Parasitism-FR* and *Coop-Parasitism*). We found similar lower bounds across the configurations. As anticipated, the *Coop-Parasitism-FR* configuration - having a quarter of the population in the non-vaccination group - resulted in a greater median and upper uncertainty bounds for holdings infected and

outbreak duration. There was a striking difference in the number of simulations that resulted in more than 20% of holdings infected, 96.2% vs 0.0% (Fig. 3(b)), and in an outbreak duration of more than 180 days, 60.6% vs 13.9% (Fig. 3(d)). We found quantitatively similar intervention unit threshold costs (Figs. 3(e,f)), with a median relative cost versus infection of 0.74 (for *Coop-Parasitism-FR*) and 0.77 (for *Coop-Parasitism*).

Data informed, heterogenous behavioural configuration outcomes

We conclude our modelling analysis by viewing the configurations informed by the interview data (*Trust-Expectancy* and *Herd size dependent*). Comparing these two behavioural configurations, we observed both quantitatively similar distributions and threshold summary statistics. That being said, a marked result was the distributions and threshold outcomes being distinct from the other assessed behavioural configurations (Fig. 3). Epidemiological outcomes most closely resembled the *Coop-Parasitism* configuration, with a reduced risk of large outbreaks but an increase in the likelihood of outbreaks being elongated. On the health economics measures, rather than asserting homogeneity in behaviour or simple uniform splits between groups, when we grounded the behavioural configurations with empirical data the intervention unit threshold cost was raised (medians of 0.85 for *Trust-Expectancy* and 0.79 for *Herd size dependent*). Additionally, the threshold unit intervention cost was very likely to be in the range of 0.5 to 1, mimicking outcomes under the *Coop-Parasitism* scenario.

Role of seed infection region

We have primarily focused on the aggregated results from all seed infection realisations, but our spatial simulations allow for inspection of epidemiological and health economic metrics dependent upon the region containing the seed infected premises. We provide further details in Supplementary Text 1 and Supplementary Figs. 4–9.

Discussion

By understanding the factors associated with heterogeneity in farmer behaviour towards disease management and intervention response, and their incorporation into mechanistic disease transmission models, we can enhance the likelihood of national disease prevention schemes delivering their desired impact. To that end, we have successfully designed and applied a novel GUI for eliciting farmer behaviour in a livestock disease outbreak scenario. The farmers showed diverse behaviour when presented with the disease outbreak and this behaviour was associated with psychosocial factors. Prompt uptake of vaccination was associated with specific psychosocial factors. We layered these behavioural components into a mathematical transmission model of a fast-spreading pathogen amongst cattle, demonstrating how different modelling assumptions with respect to farmer disease control behaviour can result in vastly disparate simulated epidemiological outcomes. This knowledge could be of substantial value in planning and administering national disease control strategies. Specifically, the effectiveness of policy-level interventions (s-frame), which are generally more successful than targeting

interventions on individual behavioural factors (i-frame)¹³, can be enhanced by incorporating individual heterogeneity in behaviour into the s-frame. Thus, the power of s-frames can be consolidated to maximise policy effectiveness. The methods and approach demonstrated here show how this can be easily and effectively implemented.

The GUI was effective in eliciting farmer behaviour and successfully separated farmers out behaviourally. Scenarios and games are occasionally used to elicit farmer behaviour⁴¹⁻⁴³, however their use has focused on routine decision-making and the control of endemic diseases. Sok *et al.*⁴⁴ used a choice experiment to investigate farmer preferences between possible government strategies for controlling a bluetongue epidemic in the Netherlands, and in a similar way described a hypothetical disease outbreak, however they did not investigate how farmers would behave voluntarily during an epidemic as was done in this study.

The behavioural heterogeneity shown by farmers was associated with psychosocial and behaviour change factors. Farmers with high trust in Governmental judgements for disease control, high physical opportunity and fewer cattle to vaccinate were most likely to vaccinate early, which is consistent behaviour with being mutually cooperative¹⁸. This association indicates that increasing the trust that farmers have in Government would improve the efficacy of disease control strategies. Also, farmers are more likely to look to and trust Government advice in uncertain situations⁴¹, therefore it is likely that their behaviour would have changed if there was Government advice given during this disease scenario. Physical opportunity and herd size were related in this intervention, with vaccination being more costly and time consuming for farmers with greater numbers of cattle than those with smaller herds. Vaccination was particularly costly in this disease scenario and high vaccination costs have been shown to decrease the likelihood of farmers vaccinating in a bluetongue outbreak⁴⁴. Subsidising an intervention measure is another tool that could change farmer behaviour for earlier intervention use⁴⁵, because farmers are more likely to use disease control measures if they are affordable^{46,47}. However, subsidisation is unlikely to change farmer behaviour if it is impractical⁴⁸, and a large level of subsidisation was required to increase the preference for bluetongue vaccination in the Netherlands⁴⁹.

Farmers with high trust in advice from the veterinary profession and high trust in other farmers to control disease were most likely to vaccinate mid-epidemic. This behaviour is consistent with the behavioural label of parasitism¹⁸, waiting to see what happens to others first and expecting to be protected by other farmers vaccinating their herds, only vaccinating if it becomes necessary. Other research has identified that high trust in farmers to control disease can reduce the disease prevention behaviours farmers use in their own herd because they perceive their risk of disease from other farms to be low^{24,50}, therefore this can be a barrier in disease control. Veterinary advice is generally trusted by farmers^{25,27} and this could be a route to promoting interventions to achieve prompt uptake and better epidemic control.

Our infectious disease model assessment, considering how different modelling assumptions with respect to farmer disease control behaviour impacted epidemiological outcomes for a fast-spreading disease

outbreak scenario, revealed a disconnect in outcomes between the configurations that assumed homogeneity in farmer behaviour (*Strong parasitism, Weak parasitism, Mutual cooperation*) and those that used the empirical estimates for psychosocial profile clusters from the interview data (*Trust-Expectancy* and *Herd size dependent*). In contrast, our simplistic assumption for a heterogeneous behavioural profile composition amongst the farmer population (*Coop-Parasitism*) resulted in a closer correspondence across outbreak size, outbreak duration and threshold intervention cost metrics to results obtained for our *Trust-Expectancy* and *Herd size dependent* scenarios. An implication is that in the absence of behavioural response data, having even a simplified implementation of heterogeneity in farmer intervention response (such as our *Coop-Parasitism* configuration) may deliver modelling results comparable to those that would have been obtained had the behavioural profile of the population of farmers been known.

We lastly remark that the inclusion of herd size in assigning farmers to a particular behaviour group in the livestock disease model did not lead to any appreciable difference in modelled outcomes (compared to the *Trust-Expectancy* configuration). Given these two empirically informed configurations gave the most robust fit to the interview data, getting similar outcomes when aggregating across all seed infection regions is not unsurprising. Nevertheless, there was also little difference when inspecting how the results depended upon the seed infection region, despite the spatial variation in the cattle population in Great Britain.

In this paper, we have explored farmer behaviour as a model population to explore how through behavioural elicitation, heterogeneity in behavioural approach influences vaccination decisions to an approaching epidemic, and how this can be modelled using a mathematical model of livestock disease outbreak. Although explored within a farming population, the principles and findings have immediate applicability to wider disease prevention behaviour. It has been argued that behavioural science has a key role to play in helping manage responses to pandemics⁸, encouraging vaccination behaviour¹² and health based philanthropy^{9,10}. However, the focus on heterogeneity in behaviour that is central to a behavioural science approach needs to be incorporated within large-scale policy-based approaches. In this study, we have shown how this can be achieved in the context of farmer vaccination decisions to an approaching infectious livestock disease. The same principles can be applied to any disease outbreak or behaviour that rests on human cooperative and shared action. One such example would be uptake of childhood vaccination. The view of parents, guardians, and carers of children, from different cultural and demographic backgrounds could be elicited under different disease progression and outcome scenarios. Modelling at the population level would not only say which population strategies may be more effective but how they could be tailored. The same could be done for any approach to a novel disease or infection.

The relatively small number of interviews conducted as part of the elicitation exercise is a limitation which precluded the investigation of behavioural cluster compositions at the national or regional level. The consequences of regional correlations between farmer disease management behavioural traits and measurable demographic attributes (such as herd size) on livestock disease outbreak dynamics merits further study. Such advancements would go towards the call for encapsulating social behaviour,

demography and disease dynamics within models, meaning the formulation of disease-management strategies fully exploit both behavioural and demographic information⁵¹.

There was also no individual covariate that had a stability over a more stringent threshold, where there would only be a 5% probability of the covariate not being associated with when farmers vaccinated (0.30). However, the threshold we used is expected to lead to the selection of fewer false positive covariates than by a model built on the full dataset without bootstrapping⁵², giving more confidence that the covariates identified are associated with the vaccination behaviour. Also, although the scenario was carefully controlled to investigate vaccination, there are other practices that farmers would have used to lower their risk, which could have different associations with psychosocial factors, and further research will be needed to investigate such combinations of interventions. Furthermore, the farmers differed in the time it took them to make a decision about vaccination at each time point and we could have investigated their certainty in their decision by recording the time taken to make a decision^{53,54}, which would have enhanced our confidence in the behavioural differences shown by the farmers.

As with any model, the disease transmission model we devised here is not capable of perfectly replicating the biological real-world system and multiple simplifying assumptions have been made. Relaxing these constraints presents opportunities for further investigation, though was beyond the scope of this study. A primary example is that in the model we focused on a limited set of interventions. Expansions in the intervention space can be conceived, such as considering a vaccine with imperfect efficacy and/or requiring multiple doses, evaluating other intervention methods such as pre-emptive culling or enhanced biosecurity, and making assessments for scenarios where a package of multiple interventions may be used collectively. Furthermore, for optimising the cost of the intervention we took one perspective. In prior work we have shown how there can be a divergence in the optimal scale of reactive voluntary vaccination response to a fast-spreading livestock pathogen between a 'population' perspective - seeking an outcome that brings the greatest total benefit across all farmers (stakeholder responsible for supporting the livestock industry) - versus an 'individual' perspective that maximises the benefit from the viewpoint of sole livestock owners⁵⁵. We also recognise that we have considered only one particular set of epidemiological parameters, representing a highly contagious, fast-spreading pathogen amongst cattle. For epidemics with less transmission potential, both the qualitative and quantitative implications on the epidemiological outcomes (relative to this different reference scenario) of different behavioural assumptions requires further study.

Our study contributes to the need for more quantitative studies into veterinary health associated behaviours that can capture individual, interpersonal and contextual factors. However, the current study design only grants a snapshot assessment of behavioural traits at one point in time. To inform how farmers' attitude, perceptions, beliefs and behaviours on disease management change over time, support is needed to establish longitudinal elicitation studies³⁵.

Other questions remain open for investigation. Our epidemiological context here was a fast-spreading pathogen, an epizootic scenario. For pathogens that are regularly affecting livestock, an enzootic disease,

the appropriate disease management may require bespoke approaches that require elongated usage to tackle a consistent risk of infection flare ups. Two such pathogens of note in Great Britain are bovine tuberculosis⁵⁶ and bovine viral diarrhoea⁵⁷. Tailored elicitation exercises (akin to this study) are needed to instruct behavioural group attributes amongst farmers towards control of enzootic diseases, producing data in a format directly usable in mathematical models. In these cases it would also not necessarily be the case that controls are implemented at the herd level, meaning within-herd transmission dynamics should be considered in such circumstances.

In conclusion, our novel GUI successfully allowed us to identify heterogeneity in farmer behaviour in a realistic disease epidemic scenario. We have been able to identify new psychosocial and demographic factors that are associated with the timing of farmers vaccinating their herd in response to an outbreak of a fast-spreading livestock pathogen. With these data, we have subsequently demonstrated how ignoring behavioural differences in disease management of livestock infections can increase the prospect of misinformed judgments being drawn from models of infectious disease dynamics. We therefore contend that the integration of behavioural heterogeneity into veterinary health decision making merits continued study.

Methods

GUI

We created a novel graphical user interface (GUI) to dynamically illustrate the spread of an epidemic disease of cattle and used the GUI to investigate farmer behaviour during a simulated disease epidemic. The GUI showed a series of maps, with infected herds plotted, week by week. The outbreak started in southern-central France (epidemic stage 1), was introduced to the UK (epidemic stage 2), then spread throughout the UK (epidemic stages 3–8). The GUI presented a common outbreak experience at each stage of the epidemic, in terms of distance to the nearest infected farm, for each participating farmer regardless of the location of their farm. Table 1 describes the scenarios presented to the farmers for each week of the scenario. An example screenshot from the GUI can be seen in Supplementary Fig. 1 and the GUI can be accessed online (<https://feed.warwick.ac.uk/map.html>).

Elicitation exercise (farmer interviews)

We conducted interactive online interviews with GB cattle farmers, which consisted of three parts: (i) demographic questions, (ii) hypothetical disease scenario using the GUI and (iii) online questionnaire of validated psychosocial and behaviour change measures. The interview script (i and ii) and the online survey (iii) are in Supplementary Text 2 and Supplementary Text 3, respectively. For the disease scenario, we gave farmers a detailed description of the hypothetical disease and a vaccine that was available to them. The vaccine cost £50 per animal, had to be given to all cattle on the same day and was 100% protective after five days.

The farmers then proceeded with the scenario using the GUI and were asked at weekly intervals whether they would vaccinate or do any other preventative measures. Farmers answered the questions in the online questionnaire directly after the disease scenario, which used validated measures to investigate trust in others, psychological proximity to others and the COM-B behaviour change framework. Trust in others was measured using Likert-scale statements^{24,58}, psychological proximity to others was measured using the Inclusion of Other in the Self (IOS) scale^{28,59} and the COM-B factors were investigated using Likert-scale statements based on the framework guide⁶⁰. The survey web page generated an individual code for each respondent, which was used to anonymously link the responses with the interview responses once all interviews were completed.

We pilot tested the GUI, interview and online questionnaire on three dairy farmers from three counties and two countries in GB. For the research interviews, we then recruited GB cattle farmers from two sources: (i) farmers who took part in previous research²⁴ and confirmed interest in participating in further research, and (ii) via advertisement through multiple cattle interest organisations. The interviews lasted up to one hour, were online (Microsoft Teams) and farmers received a £40 voucher for their time.

Analysis of elicitation data

We analysed the interview results using R statistical software v4.2.1⁶¹. To investigate associations between a farmer being an Early (epidemic stages 1–2), Mid (epidemic stages 3–5) or Late (epidemic stages 6–8 or never) vaccinator (Table 1) and their psychosocial and COM-B factor scores, we used a multinomial logistic regression model. We fit the regression model to 500 bootstrapped datasets in the following way. Starting at the null model, each covariate was tested in the model and the covariate with the lowest p-value retained. At each iteration, any covariates in the model with a p-value greater than 0.05 were removed before all remaining covariates were retested in the model and the process was stopped when no remaining covariate had a p-value less than 0.05 when added to the model. We calculated the stability of each covariate (the proportion of multinomial logistic regression models fit to the 500 bootstrapped datasets that selected the covariate) to mitigate overfitting in this wide dataset⁵². We calculated stability thresholds for different probabilities of a variable being a true positive using the methods by Green et al.⁶². Selected covariates had a stability higher than a threshold where covariates had a 15% probability of not being associated with when farmers vaccinated. We calculated odds ratios of the stable covariates by refitting the model to the bootstrapped datasets with the candidate covariates limited to those above the stability threshold and taking the mean of the coefficients. Finally, model fit was assessed by fitting the multinomial logistic regression model to the full dataset and comparing the observed and expected data using a Hosmer-Lemeshow goodness-of-fit test and decile plots⁶³, and by comparing predicted vaccination class from the full and 10 x 10-fold cross validated models.

Using k-means clustering⁴⁰, we grouped farmers based on their scores for the covariates selected by stability thresholds for a 10% and 15% probability of not being associated with when farmers vaccinated respectively. We used visual inspection of a plot of total within-cluster sum of squares against number of

clusters to determine the number of clusters that gave the best fit (Supplementary Fig. 2). These psychosocial groupings were incorporated into the mathematical livestock disease transmission model.

Mathematical transmission model of infectious livestock disease

We simulated an epidemic process in Great Britain amongst holdings with cattle to ascertain the impact of differing population compositions with regards to behavioural stances on intervention usage on an emergent outbreak of a fast-spreading pathogen. Within this subsection we overview: (i) the data sources used to inform cattle demography, (ii) the epidemiological model framework that was conceptually based on a swift, locally spreading pathogen with no long-range movement of animals, (iii) our implementation of vaccination, (iv) expanded details on the eight behavioural configurations and (v) the simulation protocol used to assess the scenarios of interest.

Livestock data description

We used the Cattle Tracing System database to procure average holding cattle herd sizes throughout 2020. The Cattle Tracing System contains virtually complete records of the births, deaths, and movements of individual cattle in Great Britain since 2001⁶⁴.

These data contained 59,774 holdings. Cattle herd sizes ranged from 1 to 7634, with a median of 58, interquartile range of 16–155, and 97.5th percentile of 622. There was regional variation in the number of holdings and cattle. Most populous regions included the south-west of England (particularly Devon), south-west Wales, north-west England (most notably Cumbria) and Dumfries and Galloway in south-west Scotland (Fig. 4).

Epidemiological model

We formulated the infectious disease dynamics as a stochastic, spatially explicit, holding level Susceptible-Exposed-Infectious-Removed (SEIR) model. With the epidemiological unit being a holding (rather than at the individual animal level), we inherently assumed that once infection had entered the cattle herd on the holding the within-premises disease spread occurred rapidly, leaving the whole cattle herd infected.

Time was discretised into daily time steps. The daily probability of a susceptible holding j becoming infected by an infectious holding i obeyed:

$$p_{ij} = 1 - \exp(-\lambda_{ij})$$

where, $\lambda_{ij} = \xi N_i^\psi N_j^\varphi K(d_{ij})$

In detail, the force of infection between two herds, λ_{ij} , was a nonlinear function of the transmissibility of cattle (ξ), the number of cattle on the infectious holding (term N_i^ψ) and the number of cattle on the susceptible holding (term N_j^φ). For the herd size exponents, ψ and φ , we used cattle epidemiological parameter estimates inferred from the 2001 UK FMD epidemic for Cumbria⁶⁵.

The fourth contributor to the force of infection was the transmission kernel K , which was a function of the Euclidean distance between holdings i and j (d_{ij} , measured in metres). We applied a power-law transmission kernel, with a maximum range of 50km:

$$K(d_{ij}) = \frac{k_1}{1 + (\frac{d}{k_2})^{k_3}}, \text{ for } 0 \leq d_{ij} \leq 50000; \text{ Otherwise, } K(d_{ij}) = 0.$$

We recognise that our parameterisation of the force of infection is an amalgamation of values that were inferred for an FMD-like pathogen in different contexts. Yet, for demonstrating the utility of the model framework, in particular how one may use behavioural-associated data gathered from an elicitation study, our chosen parameterisation suited the investigative purposes of our study. Notably, in the absence of additional controls beyond infected holdings, the simulated outbreaks were extensive irrespective of the seed infection location.

Upon a holding becoming infected, we assumed a latent period of five days (based on epidemiological and veterinary records from the 2001 UK FMD outbreak⁶⁶). Thereafter, the entire livestock population at that holding was considered infectious for a period of eight days (days 6–13 after infection). We assumed all infected holdings provided notification of infection nine days after the initial infection event, meaning there was no under-reporting of infection, but there was a four-day delay between the holding becoming infectious and subsequent notification of infection. At the end of the infectious period (13 days after infection) the cattle herd and holding were considered removed from the population.

See Table 3 for an overview of the epidemiological model values.

Table 3
Summary of the livestock disease model epidemiological and intervention parameter notation, descriptions and values.

Notation	Description	Value
Epidemiological parameters		
λ_{ij}	Infectious pressure on susceptible holding j from infectious holding i .	Variable
N_i	Number of cattle on premises i	Variable
ξ	Transmissibility of cattle.	10^6
ψ	Exponent on the cattle population on an infectious holding, for calculating the infectious pressure.	0.42
φ	Exponent on the cattle population on a susceptible holding, for calculating the infectious pressure.	0.41
k_1	Transmission kernel normalisation constant (to 2 s.f.)	1.2×10^{-8}
k_2	Transmission kernel distance length scaling	2000
k_3	Transmission kernel exponential parameter on the distance component	2
t_{incub}	Time elapsed until end of incubation period (relative to the day of infection)	5 days
t_{notif}	Time elapsed until notification (relative to the day of infection)	9 days
t_{removal}	Time elapsed until removal (relative to the day of infection)	13 days
Intervention parameters		
v_{eff}	Vaccine efficacy	100%
v_{delay}	Delay in vaccine effectiveness	5 days

Implementation of vaccination

To correspond with the intervention descriptions in the interview study, we modelled the administration of vaccine to livestock (relevant parameter values are contained in Supplementary Table 3).

We present the idealised situation of having a vaccine available with 100% effectiveness in blocking infection. As per the description of the vaccine product in the interview script, we included a lag for the

vaccine inducing an immune response (fixed at 5 days, based on measures of FMD virus titres in milk from inoculated cows in the days post-inoculation⁶⁷). As the vaccine could be administered to an infected population during its latent phase (thus prior to onset of symptoms and subsequent notification of infection), in these circumstances it was feasible for a cattle herd at a holding to be vaccinated but to still become infected.

Intervention behaviour configurations

We tested eight different behavioural group population compositions, referred to as configurations, each governing the proportion of the population that would implement interventions at a given time (with respect to the outbreak situation). Note that in all configurations controls are applied at holdings with confirmed infection. As the basis for naming the different groupings, we used the conceptual framework to categorise cooperation suggested by Bshary and Bergmüller¹⁸.

Uncooperative

Controls only applied at holdings with confirmed infection (cattle removed). No holdings applied vaccination, irrespective of the epidemiological situation.

Strong parasitism

All holdings administered vaccines in their herds upon infection being confirmed within 50km (approx. 30 miles) of their holding. This configuration resembles a situation where all individuals wait to see what is happening, how the infection spreads and as such they are exploiting others or benefit from what happens to others.

Weak parasitism

All holdings administered vaccines in their herd upon infection being confirmed within 320km (approx. 200 miles) of their holding. Similar to the strong parasitism scenario, where all individuals observe the epidemiological situation and as such they are exploiting others or benefit off what happens to others, although in this instance all individuals are more precautionary.

Mutual cooperation

All holdings vaccinated their herds prior to pathogen emergence (no outbreak occurs). Represents a scenario where all individuals cooperate to produce the maximum epidemiological benefit to all.

Cooperation-Parasitism-Free riders (Coop-Parasitism-FR)

Uniform partitioning of the population across four intervention stance groups. A quarter of holdings never vaccinated, irrespective of the epidemiological situation (free-riders); a quarter of holdings vaccinated their herd upon infection being confirmed within 50km of their holding (strong parasitism); a quarter of

holdings vaccinated their herd upon infection being confirmed within 320km of their holding (weak parasitism); a quarter of holdings vaccinated their herds prior to pathogen emergence (cooperators).

Cooperation-Parasitism (Coop-Parasitism)

Uniform partitioning of the population across the three intervention timing groups. A third of holdings vaccinated their herd upon infection being confirmed within 50km (strong parasitism) of their holding; a third of holdings vaccinated their herd upon infection being confirmed within 320km (weak parasitism) of their holding; a third of holdings vaccinated their herds prior to pathogen emergence (cooperators).

Trust-Expectancy

Partitioning of holdings into four behavioural groups, using the empirical estimates for psychosocial profile clusters from the model comprising the two most stable variables (Fig. 1). The four groups covered combinations of two trust groups (high, low) and two “expectancy” groups, their ability to physically intervene (high, low).

Herd size dependent

Partitioning of holdings into three behavioural groups, using the empirical estimates for psychosocial profile clusters from the model comprising the five most stable variables (Fig. 2). Specific to the *Herd size dependent* configuration, herd size determined the probability of the holding being assigned to each of the three behavioural groups (Fig. 5).

For the *Trust-Expectancy* and *Herd size dependent* configurations, we used the interview results to parameterise: (i) the split of holdings between behavioural groups; (ii) in each behavioural group the partitioning of the holdings between the different intervention timings (see Figs. 1–2 and Supplementary Tables 1–2).

Simulation outline

We considered the fast-spreading pathogen first emerging in a spatially localised area of Great Britain from a low case level. Therefore, in each simulation replicate we seeded infection in a randomly selected cluster of three premises (we selected one premises at random and found the two premises that were closest in terms of Euclidean distance). A replicate terminated upon there being no premises in an infected state.

For each behaviour configuration, to explore the sensitivity of epidemiological and economic outcomes to the geographical location of initial infected premises we assessed 89 different seed region scenarios. We ran 500 replicates for each scenario, comprising a behaviour configuration and seed infection region.

To assess the implications of differing psychosocial and geographical attributes on epidemiological outcomes, we tracked the percentage of holdings infected and outbreak duration. To evaluate the

economic implications of behavioural attributes on intervention usage, relative to the baseline control strategy, we computed threshold intervention unit costs (the maximum cost per intervention unit where the total intervention cost equalled the costs saved from averted infections).

Given our use of a large-scale spatially explicit model, for our simulation procedure we employed an optimised gridding approach (the conditional subsample algorithm) as described in Sellman *et al.*⁶⁸. We performed all model simulations and produced plots in Julia v1.8. The code repository for the study is available at https://github.com/EdMHill/FEED_farmer_disease_management_heterogeneity.

Declarations

Author contributions

Edward M. Hill: Conceptualisation, Data curation, Formal analysis, Methodology, Software, Validation, Visualisation, Writing - Original Draft, Writing - Review & Editing.

Naomi S. Prosser: Conceptualisation, Data curation, Formal analysis, Methodology, Software, Validation, Visualisation, Writing - Original Draft, Writing - Review & Editing.

Paul E. Brown: Software, Writing - Review & Editing

Eamonn Ferguson: Conceptualisation, Funding acquisition, Methodology, Supervision, Visualisation, Writing - Review & Editing.

Martin J. Green: Conceptualisation, Funding acquisition, Methodology, Supervision, Visualisation, Writing - Review & Editing.

Jasmeet Kaler: Conceptualisation, Funding acquisition, Methodology, Supervision, Visualisation, Writing - Review & Editing.

Matt J. Keeling: Conceptualisation, Funding acquisition, Methodology, Supervision, Visualisation, Writing - Review & Editing.

Michael J. Tildesley: Conceptualisation, Funding acquisition, Methodology, Supervision, Visualisation, Writing - Review & Editing.

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Ethical considerations

Ethical approval was granted by the University of Warwick Biomedical and Scientific Research Ethics Committee (BSREC 100/19-20) prior to commencement of the study.

Data availability

We were supplied holding-level records from the Cattle Tracing System by the Rapid Analysis and Detection of Animal-related Risks (RADAR) team at the Animal and Plant Health Agency (APHA). These data contain confidential information, with public data deposition non-permissible for socioeconomic reasons. For data access, the RADAR team at APHA can be contacted on RADAR@apha.gov.uk.

Spatial maps display digital vector boundaries for countries, counties and unitary authorities in Great Britain that are owned and made available by ONSGeography_data. Source: Office for National Statistics licensed under the Open Government Licence v.3.0. Contains OS data © Crown copyright and database right 2022. Terms and conditions of supply for the digital boundaries and reference maps are provided at <https://www.ons.gov.uk/methodology/geography/licences>.

All other data utilised in this study are publicly available, with relevant references and data repositories stated within the main manuscript.

Code availability

The code repository for the study is available at https://github.com/EdMHill/FEED_farmer_disease_management_heterogeneity.

Competing interests

All authors declare that they have no competing interests.

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Figures

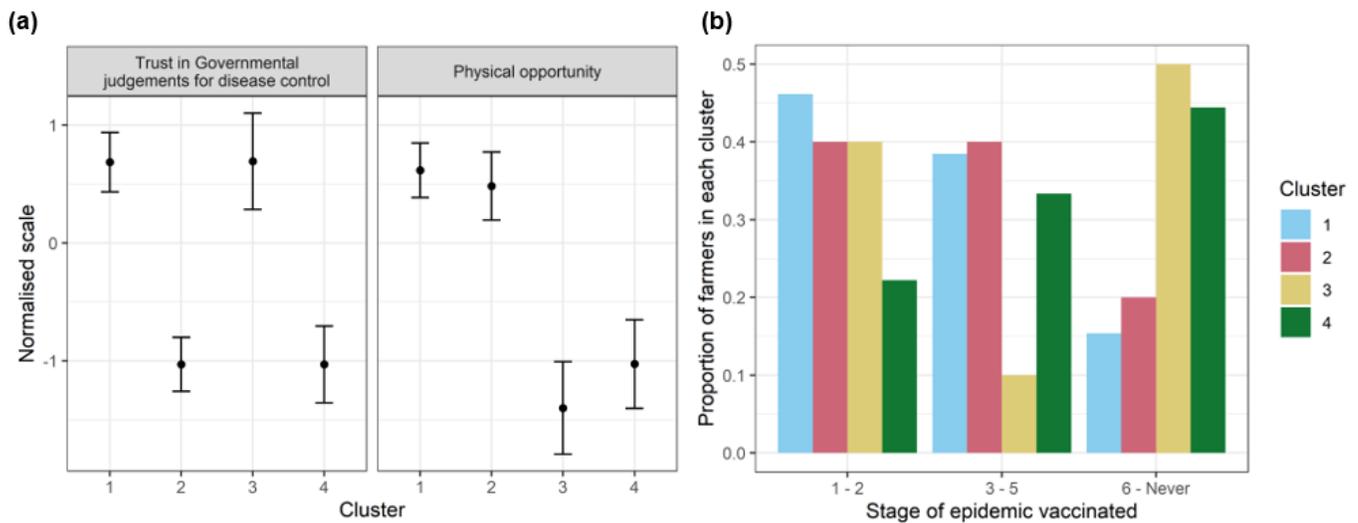


Figure 1

The farmer groups from k-means clustering conducted on the two most stable covariates (Trust in Governmental judgements about disease control and Physical opportunity). **(a)** The mean (point) and 95% confidence interval (error bars) scores of the covariates for each group. **(b)** The proportion of farmers in each group that vaccinated at different stages of the epidemic (Epidemic stages 1 - 2, Epidemic stages 3 - 5 and Epidemic stage 6 - 8 or never uses vaccination). Associated values are given in Supplementary Table 1 and Supplementary Table 2.

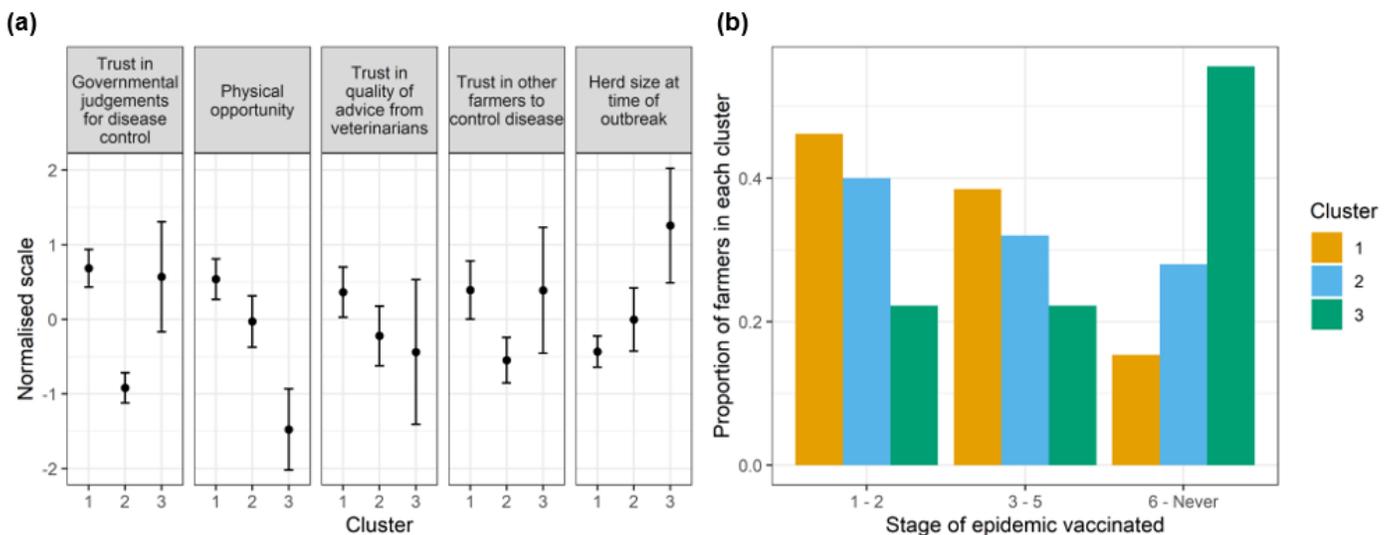


Figure 2

The farmer groups from k-means clustering conducted on the five most stable covariates (Trust in Governmental judgements about disease control, Physical opportunity, Trust in quality of advice from the

veterinary profession, Trust in other farmers nationally to control infectious diseases and Herd size at time of outbreak). **(a)** The mean (point) and 95% confidence interval (error bars) scores of the covariates for each group. **(b)** The proportion of farmers in each group that vaccinated at different stages of the epidemic (Epidemic stages 1 - 2, Epidemic stages 3 - 5 and Epidemic stage 6 - 8 or never uses vaccination). Associated values are given in Supplementary Table 1 and Supplementary Table 2.

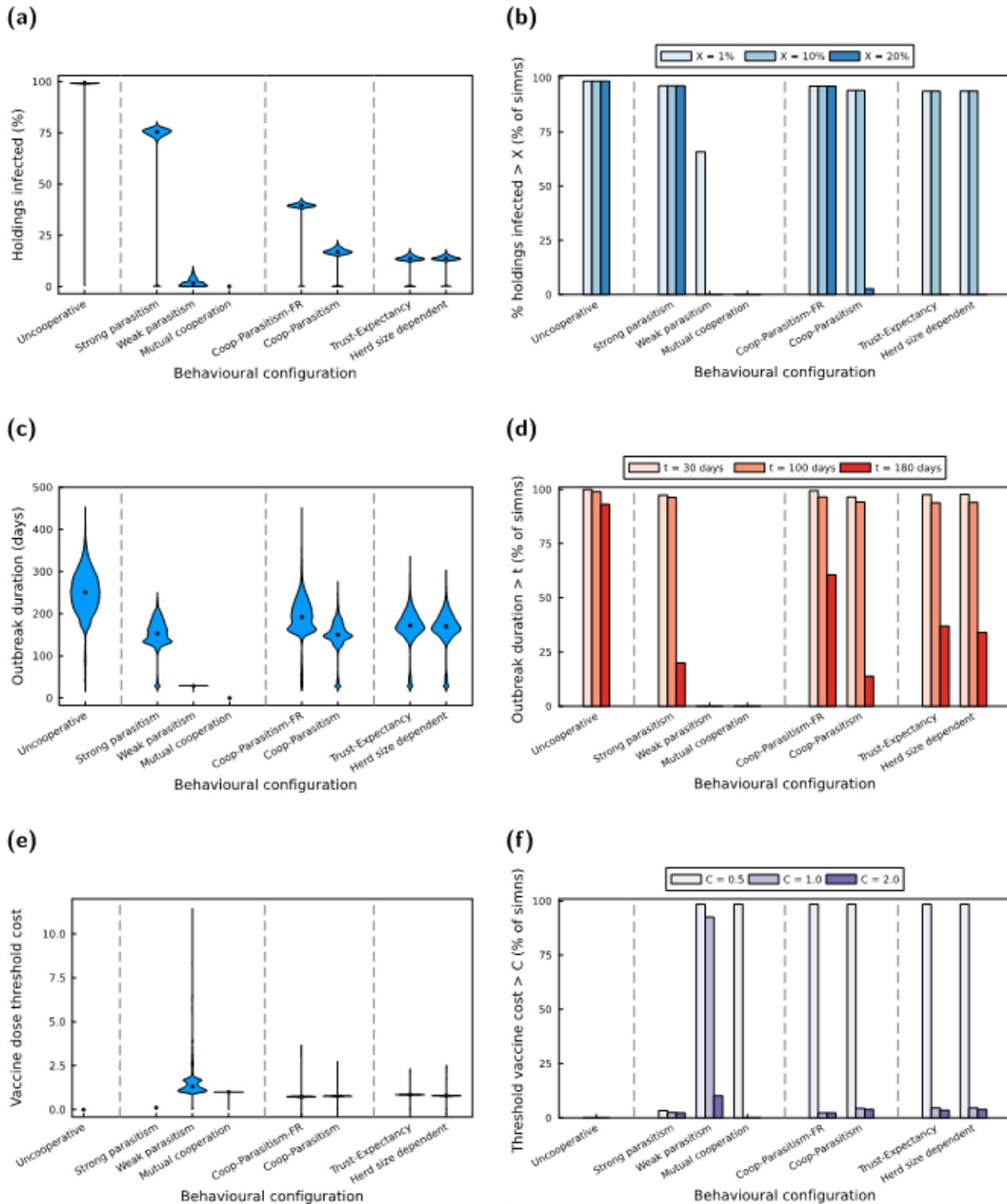


Figure 3

Epidemiological summary statistics for Great Britain when aggregating outbreaks over all 89 infection seed regions. We computed the summary statistics for each behavioural configuration using 44,500 replicates (500 replicates for each of the 89 seed region locations). In **(a,c,e)**, the filled red markers represent the medians and the violin plots depict an estimate of the probability density. In **(b,d,f)**, the bars represent the percentage of simulations where the stated epidemiological outcome was exceeded. Darker shaded bars correspond to a higher valued threshold, with threshold values stated in the figure legends. The summary statistics presented are: **(a,b)** percentage of holdings infected during the entire outbreak; **(c,d)** outbreak duration (in days); **(e,f)** threshold cost per intervention unit. Associated values are given in Supplementary Table 3.

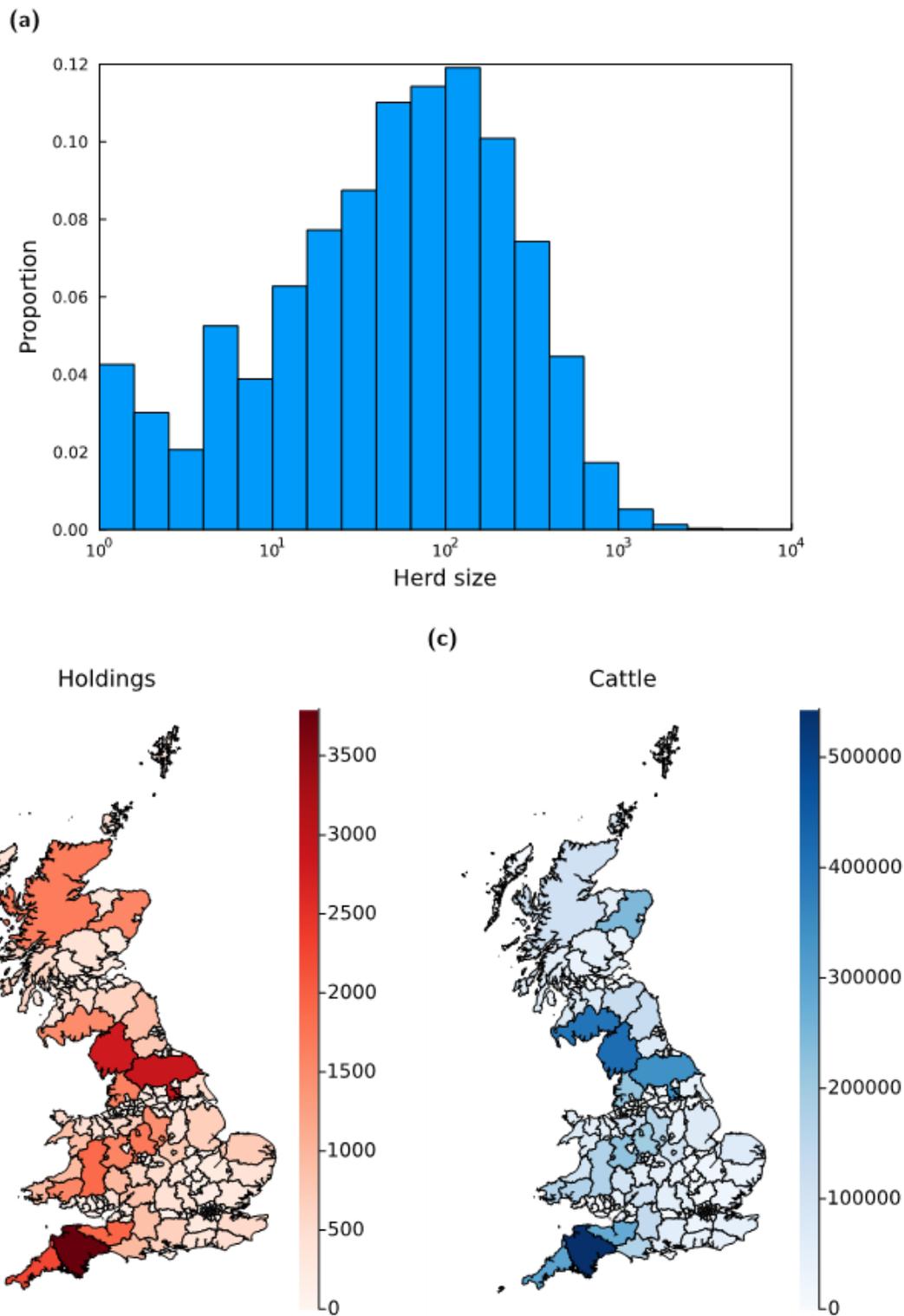


Figure 4

Size and spatial distribution of cattle herds in Great Britain. We used the Cattle Tracing System database with data from 2020 to estimate an average cattle herd size for each holding. These data contained 59,774 holdings. **(a)** Distribution of cattle herd sizes. Note the x-axis is presented on a log scale. Cattle herd sizes ranged from 1 to 7634, with a median of 58, interquartile range of 16 - 155, and 97.5th percentile of 622. **(b)** Number of holdings with cattle present per region. Darker shading corresponds to

higher counts. (c) Number of cattle present per region. Darker shading corresponds to higher counts. There was regional variation in the number of holdings and total number of cattle. Most populous regions included Devon in the south-west of England, Cumbria in north-west England, and Dumfries and Galloway in south-west Scotland.

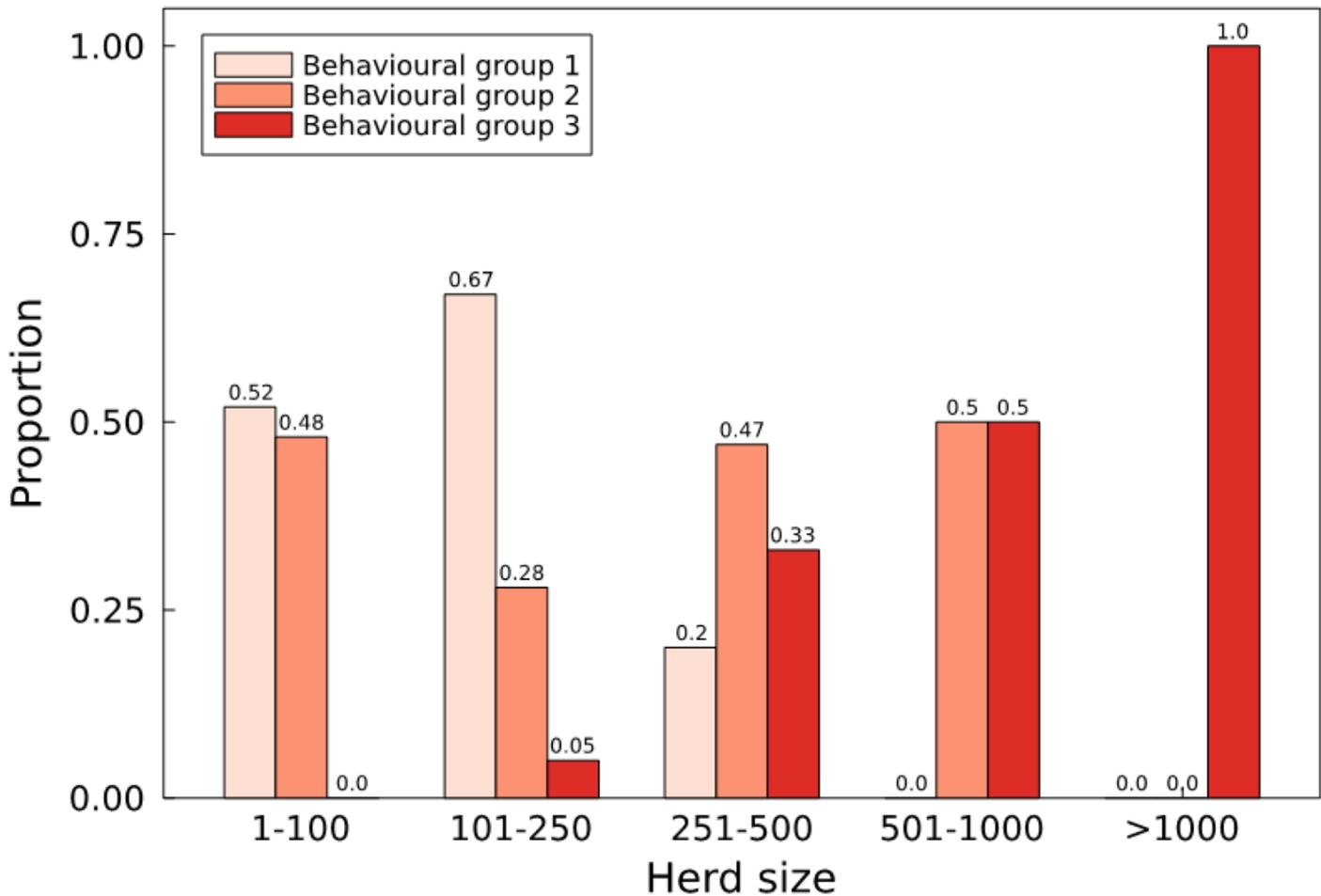


Figure 5

The probability of a holding being assigned to each of the behavioural groups with respect to the herd size, under the “Herd size dependent” behavioural configuration. The bars depict the probability of a holding being assigned to each of the behavioural groups with respect to the stated herd size stratification. Above each bar, we state the associated probability to a precision of at most 2 decimal places.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

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