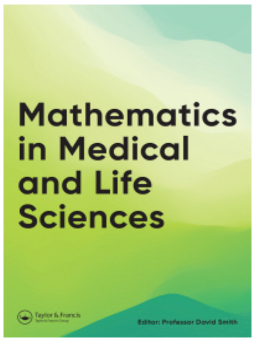

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RESEARCH ARTICLE

Integrating human behaviour and epidemiological modelling: unlocking the remaining challenges

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ABSTRACT
This paper is part of a special issue on Behavioural Epidemiology.
Historically, responses to health-related emergencies (whether public health, veterinary health or plant health related) have exposed the deficiencies of mathematical models to incorporate data-driven and/or theoretical knowledge on outbreak behavioural dynamics. Interdisciplinary collaboration is vital to improve realism in methodological approaches to considering behavioural dynamics in an unfolding situation. We must bring together novel ideas across the behavioural, biological, data and mathematical sciences. The purpose of our article is threefold. We first present our perspective on the vital role of interdisciplinary collaboration to enable the effective integration of the dynamics of human behaviour and epidemiological models – we refer to such integrated models as "epidemiological-behavioural" models. We then summarise issues to be resolved by interdisciplinary teams of experts within four contemporary epidemiological-behavioural modelling challenge areas that we consider to require immediate and sustained research attention: understanding of human behaviour; data; modelling methodologies and parameterisation; how modelling (and communication of its findings) affects behaviour. Lastly, to serve as a resource for research scientists, practitioners and policy makers interested in getting involved in tackling these epidemiological-behavioural modelling challenges, we pose recommendations to make progress in each of the challenge areas and our viewpoint on their potential societal benefits if enacted.

PLAIN LANGUAGE SUMMARY
When faced with health crises like disease outbreaks or pandemics, scientists have struggled to accurately predict how they will spread. One issue is that models of how infections spread in the population do not usually consider how people behave.

We call models that include both how infections spread and behaviour "epidemiological-behavioural" models. To improve these models we need experts from different research areas to work together. These teams include (but are not limited to) scientists who study human behaviour, medical and biological experts, and those who analyse data and who work with mathematical models.

Our article is by organisers and presenters at a workshop on "Mathematical modelling of behaviour to inform policy for societal challenges" hosted at the University of Warwick Mathematics Institute on 10 June 2024. This workshop had participation from behavioural scientists, data scientists, statisticians and mathematical modellers. We state the current challenges we face in creating teams with experts from different research areas and to produce "epidemiological-behavioural" models. We suggest ways to overcome these challenges and outline potential impacts and benefits to society once these challenges are unlocked.

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1. Introduction

Real-world systems are sensitive to human behaviour. The need to quantify the impact of changes in human behaviour on system outcomes is a ubiquitous open problem. Challenges arise due to a lack of readily translatable quantitative behavioural science models that might capture the changing of relevant behaviours, societal norms and policy directives across individuals and/or populations, particularly in novel social contexts. Within epidemiology, the behavioural element in the transmission dynamics of infectious diseases is very influential; as disease affects behaviour and behaviour affects the infection risk of others as well as ourselves, unlike for non-communicable diseases. The COVID-19 pandemic particularly highlighted the deficiencies in availability of both suitable data and of epidemic models to reasonably incorporate data-driven and/or theoretical knowledge regarding the behavioural response to a pandemic, including social contact, mobility, adherence to non-pharmaceutical interventions (NPIs) and the drivers of voluntary behaviour changes [1,2].

Coupled with advice to wield caution when applying behavioural science to policy [3], there has been long standing recognition of challenges to incorporate the dynamics of behaviour amongst the epidemiological modelling community [4]. These challenges are not confined to public health. In veterinary and plant health there are researchers striving to integrate infectious disease and behavioural dynamics in topics such as animal health [5–7], crop disease [8,9] and tree health [10].

To induce the necessary improvements in the behavioural realism of such models, there is a clear need to connect researchers who share this collective interest – including but not limited to biologists, data scientists, mathematical modellers, medical scientists, social scientists – drawing on expertise from academia, industry, lived experience, policy-facing roles and other stakeholders. This ambition motivated a workshop titled "Mathematical modelling of behaviour to inform policy for societal challenges" hosted at the University of Warwick Mathematics Institute on 10 June 2024 [11], with support from the JUNIPER partnership (a collaborative network of researchers from across the UK who work at the interface between mathematical modelling, infectious disease control and public health policy [12]). Authored by workshop organisers and presenters, this commentary article summarises the (yet to be resolved but pressing) challenges faced with bringing together the dynamics of human behaviour and epidemiological models. Throughout this article we refer to such models as "epidemiological-behavioural models" – we remark that as the field at the time of writing is in its relative infancy that there are alternative terms describing this category of model/analytical approach within the literature to also be aware of (for example, "behavioural-epidemiological" [13], "economic-epidemiological" [14, 15] and "socio-epidemiological" [16]).

Our intent with this article is threefold. We begin with the need to embrace interdisciplinary approaches and the provision of support for interdisciplinary collaboration. We contend those developments are imperative to enable interdisciplinary teams to usefully tackle questions within four core present-day epidemiological-behavioural modelling challenge areas: Understanding of human behaviour, data, modelling methodologies and parameterisation, how modelling (and communication of its findings) affects behaviour. Within each challenge area we comment on multiple issues. Note that many of the examples we focus on in this article are public health based, reflecting the current balance in relevant literature across the health areas (which has been exacerbated by the COVID-19 pandemic). Nevertheless, we stress the importance that veterinary and plant sciences are not overlooked; we remark upon a smaller number of examples from those areas, whilst the learnings from the public health settings are also applicable to them. We also consider these issues to be generally relevant for modelling real world systems to support decision-making. We conclude by posing recommendations to make progress in each of the challenge areas, with our view on the potential consequential societal benefits were they implemented. These recommendations can serve as a resource and entry point for research scientists, practitioners and policy makers interested in getting involved in tackling these epidemiological-behavioural modelling challenges.

2. The initial challenge: removing barriers to effective interdisciplinary working

We first highlight what we contend are pertinent general principles to consider in delivering effective interdisciplinary research and to support decision-making: (i) getting the necessary range of expertise amongst the interdisciplinary team; (ii) establishing a "common language" amongst the team members; (iii) standardisation of interdisciplinary methods.

2.1. Team building: getting the necessary blend of expertise

To bring about positive societal changes via addressing problems in behavioural epidemiology, the initial step is the construction of interdisciplinary teams with relevant expertise. A range of participants are needed, integrating

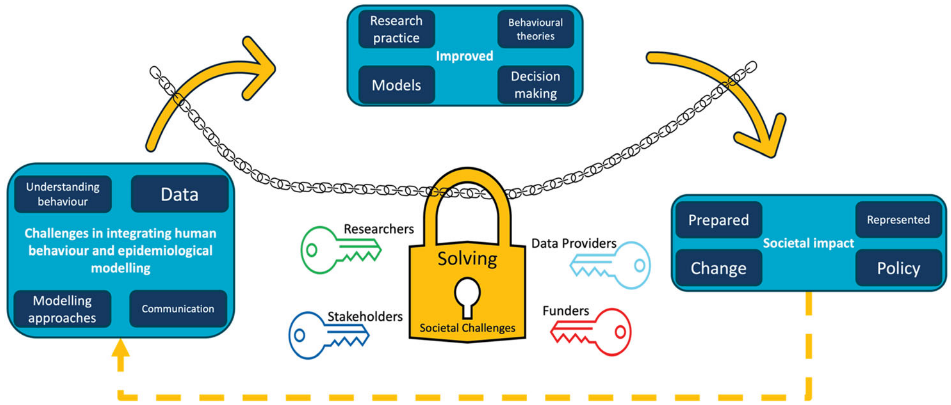

Figure 1. Interdisciplinary approaches to behavioural epidemiology to unlock solutions to societal challenges. We group challenges in integrating human behaviour and epidemiological modelling into four areas: understanding behaviour, data, modelling methodologies and parameterisation, how modelling (and communication of its findings) affects behaviour. By addressing these challenges, we envisage improvements in research practice, behavioural science theory, modelling approaches and decision making (*Improved* box; see *Delivering societal benefits* section). Subsequently, a range of societal impacts can be realised (*Societal impact box*; see *Delivering societal benefits* section). As these societal impacts are realised, we expect new challenges to be discovered, renewing the cycle of improved and impactful modelling (dashed arrow). However, using traditional mono-discipline approaches these improvements are "locked" and unattainable, meaning the societal impacts may not be achieved. To bring about positive societal changes via the construction of interdisciplinary teams with relevant expertise, accessibility of appropriate data and the provision of reliable analyses to stakeholders and the public, collective input is needed from researchers, data providers, stakeholders (including practitioners and decision makers), and funders.

the scientific community, data providers, stakeholders (including practitioners and decision makers), and funders (Figure 1). Within the scientific community, connections must be made between researchers in traditionally siloed disciplines who have this shared collective interest in wanting to address problems in behavioural epidemiology – (including but not limited to) biologists, data scientists, mathematical modellers, medical scientists, social scientists – drawing on expertise from academia, industry and policy-facing roles. Funding paradigms need to acknowledge the requirements of such interdisciplinary work, including the time required to develop and sustain good teams.

This approach, constructing an interdisciplinary team for the purpose of collectively studying problems in behavioural epidemiology, would align with previous successes of incorporating domain expertise to tackle questions that inherently span multiple, traditionally siloed research disciplines. One such example is the Analysis under Uncertainty for Decision-makers Network (AU4DM). AU4DM is a UK-based community of researchers and professionals from policy, academia, and industry, who are seeking to develop a better understanding of decision-making to build capacity and improve the way decisions are made across diverse sectors and domains. AU4DM have created multiple toolkits, including resources seeking to narrow the gap between climate science and climate action (Communicating Climate Risk [17]), and resources to develop a better understanding of how decisions are made across a wide variety of sectors and domains and improve the way they are made (Decision Support Tools for Complex Decisions Under Uncertainty [18]; Visualising Uncertainty: A Short Introduction [19]).

Another useful methodological approach that naturally onboards and considers collectively a range of domain expertise is structured expert judgement. Structured expert judgement refers to a collection of formal methods for obtaining from groups of experts their views on quantities and the uncertainty in those quantities. Structured approaches are designed to avoid groupthink and other biases whilst allowing experts to contribute their honest views. Notable examples of the use and outcomes resulting from structured expert judgement exercises are present in the statistical literature; for eliciting probability distributions where data is poor, biased or non-existent [20,21], the Bayesian ARgumentation via Delphi (BARD) protocol for elicitation of Bayesian networks [22] and a protocol for adapting an existing Bayesian network model [23].

2.2. *Establishing a common language*

For effective working practice interdisciplinary teams need to establish a "common language"; a foundation of definitions, approaches to data collection, and types of models and their use that is understood and agreed by team members.

Agreeing this common language will require resolving tensions between disciplines' terminology and quantification. For example, modellers may prefer participants to specify a precise number of social contacts, but health psychologists will recognise that this will be difficult for participants to estimate accurately – health psychologists may alternatively suggest that study participants specify and/or select from a set list of categorical response options, drawing on expertise to develop surveys that facilitate participation (e.g. surveys that do not feel long or cumbersome) whilst also promoting accuracy [24]. An idea to aid the effective establishment of a common language amongst an interdisciplinary team is to refer to case studies in interdisciplinary pedagogy, the ways in which novices are taught to think, perform and act with integrity in their profession. One area where there has been such collaboration has been in household food insecurity (households that cannot, or are uncertain about whether they can, acquire an adequate quality or sufficient quantity of food in socially acceptable ways). This issue is a complex societal problem that requires a multifaceted approach to evidence-based policy design. For example, the UK is suffering a rise in food insecure households; in 2022/23 there was an estimated 7.2 million people, or 11% of the population, in households experiencing household food insecurity [25]. To that end, a collaboration between the mathematical sciences and public health nutrition has successfully co-produced lecture content on the topic, delivered for students in two universities (one in the UK and one in Australia) with different backgrounds and within different courses where consideration of food security was part of each course [26].

There should be consideration of the possible inaccessibility of mathematical/modelling terminology to people in other research disciplines and vice versa. There could also be differing awareness of or comfort with different types of modelling approaches, which can lead to misunderstandings. For example, those who are comfortable with statistical (non-mechanistic) modelling approaches may be unaccustomed to or less trusting of mechanistic modelling approaches or vice versa. We have also observed the following when working between epidemiology and behavioural economics. In epidemic models, many of the complexities of disease transmission are manifest in the Force of Infection (FOI), which describes the rate at which susceptible individuals in a population acquire an infectious disease in that population, per unit time [27,28]. FOI can account for population heterogeneities and is the source of nonlinearity in epidemic models. In contrast, micro-economic models typically describe dynamic heterogeneities in a population by using utility functions [29], measuring individual received net benefit from a given scenario. Unlike FOI, there is no one consensus on the mathematical formulation of utility, owing to its more abstract nature and to the range of situations in which it can be studied. It is evident that perceived risk/benefit can impact behaviour, which can impact the FOI experienced by an individual and the contribution to FOI from an individual at any time [30]. Crucial observations here are: (i) utility and FOI are dynamic quantities, and FOI is dependent on utility; (ii) perceived risk and true risk are not the same, so utility does not translate directly to FOI; (iii) the impact of external mandates, such as enforced lockdowns, may affect an individual's perception of a scenario, but they also impose a change to FOI that cannot be mitigated by utility alone. To integrate both outlooks when studying systems of disease transmission, clarity in the interpretation and limitations of utility is essential in constructing a link back to FOI.

We lastly comment that trust within an interdisciplinary collaboration may grow when team members perceive that behaviour is appropriately captured in data collection and models, according to their discipline specific pedagogical standards. Co-creation is powerful; people will advocate for models they helped build (one such example is a model co-created with personnel from The National Archives to quantify risk to digital collections [31]).

2.3. Standardising interdisciplinary methods

Investigating questions in behavioural epidemiology involves working with (but not limited to) high-dimensional and incomplete data from diverse sources, studying nonlinear dynamics and likely encountering issues of overfitting models to data, and needing to consider privacy constraints and ethics. There is presently a lack of standardised interdisciplinary methods to cater to problems with such breadth [32]. Nevertheless, the recent emergence of other modern interdisciplinary science disciplines shows how tangible progress on such matters can be made. For example, the interdisciplinary science of uncertainty quantification has bloomed (combining statistics, numerical analysis and computational applied mathematics). The research attention paid to uncertainty quantification has been due to the important real-world need for mathematical and computational modelling methodologies to estimate quantities of interest and make predictions related to real-world processes that can take account of a wide variety of uncertainties [33], especially when these lead to policy. We therefore argue that motivating and driving forward a standardisation of interdisciplinary methods associated with epidemiological-behavioural modelling is a realistic endeavour.

3. Unresolved challenge areas for integrating human behaviour and epidemiological modelling

Unlocking and removing the barriers to effective interdisciplinary working would be useful progress as a standalone item. Nonetheless, giving the current knowledge base a functioning interdisciplinary team alone will not be sufficient to establish informative epidemiological-behavioural models. To target the focus of interdisciplinary teams working in the area, we describe here four challenge areas for integrating human behaviour and epidemiological modelling: understanding of human behaviour; data; modelling methodologies and parameterisation; and how modelling (and communication of its findings) affects behaviour (Figure 1, "Challenges in integrating human behaviour and epidemiological modelling" box). With each challenge area we comment upon multiple issues to address.

3.1. Challenges in our understanding of behaviour

Behavioural science aims to enhance our understanding of human behaviour. This knowledge can provide practical solutions to address societal challenges and improve individual and collective outcomes. That being said, human behaviour is studied across academic disciplines spanning psychology, economics, sociology, statistics, anthropology and beyond. Within these disciplines there are many different concepts of behaviours, models and approaches to understanding behaviour and behaviour change [34]. For epidemiological modelling efforts wanting to reasonably capture behavioural aspects, a constraint faced is readily drawing on existing behavioural science evidence and theory (due to its breadth). There are also inherent challenges in the way behavioural science is conducted that merit attention. Here we outline three issues: (i) existing behavioural science theory and models are generally limited to explaining behaviour only; (ii) generalisability of existing behavioural science evidence; (iii) appropriateness of behavioural science research methodologies for the quantification of human behaviour.

3.1.1. Restrictive, explanatory scope of existing behavioural science theory and models

There is a bank of explanatory models for how a person's attitudes and behaviours are related (e.g. theory of reasoned action [35], theory of planned behaviour [36]), self-efficacy (e.g. protection motivation theory [37], social cognitive theory [38]) and capability (e.g. COM-B model [39]). These explanatory model frameworks can offer us insight into questions posing "why" and "who", but have more limited utility when trying to quantify "when" i.e. to make predictions about behaviour.

The evidence accrued during the COVID-19 pandemic attests to this [40]. For example, in the context of human interaction/social distancing numerous studies identified the factors influencing social distancing (although often limited to "intentions" to be socially distant, rather than actual behaviour). These findings illuminated both the "why" and the "who" and also shaped interventions to change behaviour, but could not be utilised to predict social distancing i.e. provide estimates on how individuals, communities and the population would respond to the imposition or removal of a public health intervention, such as restricting the opening of different hospitality or retail venues, or lifting of a lockdown or travel restrictions. Furthermore, effect sizes of the existing explanatory models appear modest as suggested by comparisons between studies with pre-registered analysis plans and not, suggesting that a prerequisite for obtaining a more reliable picture of population-level behavioural dynamics is having many more pre-registered studies [41]. Lastly on this issue, the scope of studies of behaviour focus on behaviour that is too general to predict the response to a particular intervention [42]. For example, the interaction between social and environmental factors in determining the transmission risk is uncertain; more initiatives are needed in this area akin to the PROTECT COVID-19 National Core Study on transmission and environment – a UK-wide research programme improving our understanding of how SARS-CoV-2 is transmitted from person to person, and how this varies in different settings and environments [43].

3.1.2. Perils of generalising existing behavioural science evidence

It is relevant to scrutinise the generalisability of existing behavioural science evidence due to the known biases and challenges with reproducibility in behavioural science study populations. For example, it is known that historically psychological research drew heavily on participants from academic institutions [44]. However, data suggest that generalising from students to the general public can be problematic when personal and attitudinal variables are used, as students vary mostly randomly from the general public [45]. There is also a reliance on WEIRD (western, educated, industrialised, rich and democratic) populations as participants in behavioural science, but WEIRD populations comprise a minority of the worldwide population [46]. Social groupings, such as class, are often omitted. Furthermore, behavioural science theory has often not been designed to describe variation in individual behaviour when applied to study of intervention effect for policy purposes [47].

Thus, in order to challenge and improve existing behavioural science theories and models, there is a need to both scrutinise existing data assets, maximising the information from them accounting for potential demographic biases in the participants, and create novel behavioural science data sets with more diverse samples. We describe and comment on other data-associated items in the *Data-related challenges* section below.

3.1.3. Advancements in behavioural science research methodologies needed for the quantification of human behaviour

Behavioural research implements many different research methodologies, with presently there being a reliance on qualitative self-report, retrospective and correlational designs. Some of these approaches describe processes (cognitive, social) and their relationship to behaviour only qualitatively, often via path diagrams [47]; these are considered validated in experimental or observational studies if the proposed correlations are observed or are consistent with causal analysis of the data. Furthering our understanding will require collection of quantitative, real-time and objective data on behaviour, synthesising across multiple forms of analysis. Human analytics is a data-driven approach to understanding human behavioural choices, with there being great potential for digitally derived empirical data to inform our understanding of health behaviour [48]. Another analysis construct is sentiment analysis, which may inform behavioural choices by providing information on an individual's ideology and politics [49]. In sum, progression of what are the commonly used behavioural science research methods can enable the collection of real-time and objective data on behaviour.

3.2. Data-related challenges

Establishing an evidence base for conjectured behavioural science theory requires empirical observation across controlled laboratory settings, managed trials and population-based contexts. Acquiring informative behavioural data, which are amenable to use in mathematical models, is just one part of the epidemiological-behavioural model data cycle. Models can be used as an exploratory tool, discerning what model parameters contribute the most to uncertainty in model outputs and/or the model parameters the model outputs are most sensitive to. Findings from these analyses can inform what data attributes would be most useful to collect in the next round of data collection. This cyclic process can both improve the "plug and play" potential of the data into models and reduce uncertainty in model outcomes.

The three data-related issues in epidemiological-behavioural modelling we expand on here are: (i) ability to leverage existing data into existing models; (ii) identifying the relevant data for use in appropriate models; (iii) ethical considerations for the collection, processing and storage of data.

3.2.1. Leveraging existing data into existing models

There is recognition of a lack of context awareness and standardisation amongst existing data on health-related behavioural dynamics. We commented in the previous section about the over-reliance on WEIRD populations for behavioural science study participation (see *Challenges in our understanding of behaviour*). Several existing data are also reliant on self-report approaches for data collection (rather than objective driven data collection); self-report data may suffer from recall bias [50] and responses influenced by social expectations [51]. Collecting data from hidden or vulnerable populations is key to tackle health-related challenges [52].

Another acknowledged data issue is the intention-behaviour gap. The relationship between behavioural intentions and realised behaviour is notoriously complex; predicting behavioural intentions has proved to be easier than predicting behaviour [42]. To reasonably account for the intention-behaviour gap in epidemiological-behavioural models, an open research question is: *can the intention-behaviour gap be reliably quantified* [53]? This is a relevant question for NPIs such as usage of face masks and social distancing. For such NPIs there can be divergence between the intention to adopt/not adopt the behaviour and the actual behaviour carried out. Modelling the uptake of NPIs may also be complicated by variations in the adoption of NPIs across social settings [54]. There is potential to bridge the intention-behaviour gap through increased data sharing and predictive modelling. For example, linking self-reported social distancing (which may suffer from recall bias and conflation with intention in reporting past behaviour) to mobility data [55], or intended face mask usage to observed face mask prevalence in security footage [56,57].

An additional facet to the quantification of the intention-behaviour gap is to include the difference between adequate and inadequate behaviours. For NPIs such as face mask wearing, models also need to quantify the level of intentional or unintentional misuse of face masks (e.g. wearing a mask under your nose). Although many will intend to and actually wear face masks, many will do so inadequately [58]. However, face masks are only effective when worn properly and hygienically [59]. Improving the adequate-inadequate behaviour gap through education is a clear avenue where behavioural science, scientific communication, and health policy can make a tangible impact on society for future infectious disease.

Despite the known biases and limitations of existing data that may be of use for epidemiological-behavioural modelling, by delving into these existing data and model applications there is an opportunity to identify individual – and population-scale drivers of mobility and interactions in response to public health restrictions. This is particularly pertinent in the context of the COVID-19 pandemic, which has seen swathes of data collected, from contact tracing, behavioural surveys, social media, infection and genomic data, travel and retail data. Independent producers of official statistics, such as the Office for National Statistics in the United Kingdom, offer another very useful source of data relevant to epidemiological-behavioural modelling. For example, demographic data from a census (e.g. available for England and Wales from the Office for National Statistics [60]) can inform the overall population structure in an area and can help build epidemiological-behavioural models in localised populations.

There is past precedent for revisiting existing data and models to glean novel insights. One example is Google Flu Trends data. Preis and Moat [61] demonstrated how taking precautions to allow for the fact that human behaviour changes over time could enable public health professionals to use data on the number of Google searches for influenza-related symptoms to improve their estimates of influenza prevalence. Another example is the work by Durham and Casman [62], who demonstrated an application of the Health Belief Model to model the prevalence of facemask use observed over the course of the 2003 Hong Kong SARS epidemic (which is a well-documented example of behaviour change in response to a disease outbreak). These examples show how we have yet to extract from existing data the maximum understanding of behavioural response to a pandemic and public health measures.

3.2.2. Identifying the relevant data for use in appropriate models

Models can help inform the data we need, but the data we have guides the models we can usefully use. Using varied data sources, including first-hand and secondary data, has different impacts on epidemiological-behavioural models. Whereas public or secondary data may lack detailed individual information due to privacy concerns, it is challenging and costly for researchers to collect first-hand data at a large scale, such as the national level, which is often supplied by specific institutes or stakeholders.

Infectious disease models including human behaviour inconsistently use data to parameterise and validate their results. Different data sources can be used depending on the model and purpose. For example, if we want to know vaccine rates we may use epidemiological data to infer these [63], but if we want to know the behavioural and social drivers of vaccine uptake then survey data may be more appropriate [64,65]. Moreover, the lack of robust behavioural and social data limits the efforts of epidemiological-behavioural models to inform policy [32], while the increased psychological complexity in a model does not necessarily lead to a more precise or insightful model [66].

A comprehensive consideration of the data selection as well as model building are two sides of the same coin when modelling epidemiological behaviours. Consequently, what are "relevant" data and "appropriate" models is non-trivial. Questions that must be addressed include: What data do epidemiological-behavioural modellers need to make their models interpretable and usable?; Do we have the infrastructure and investment for robust data collection, storage and access?; Is the idealised data even a feasible ask? Balancing between behavioural detail and model complexity will guide the data necessary to effectively calibrate epidemiological-behavioural models to said data.

3.2.3. Ethical considerations for the collection, processing and storage of data

Many of the proposed approaches for data collection we have mentioned have strong potential to improve real-time modelling and response in the face of new epidemics, such as self-used mobile applications [67]. Nevertheless, there are clear ethical considerations that warrant attention. Transparent policy and communication with individuals from whom the data are collected is vital. From the scientific standpoint, we must strike a balance between the need for comprehensive data and ethically piecing together (and interpreting) large, complex and varied behavioural data [68]. For example, integrating computer vision and machine learning techniques to detect real time prevalence of protective health behaviours is a useful tool in real-time public health planning [56,57]. However, these methods involve processing and storing (at least for a short period) sensitive personal and biometric data, opening the door for privacy risks [56]. Having secure systems in place to account for these privacy risks are essential to ensuring the safety of these data collection methods. It is important to establish public or user confidence in the security measures in place.

3.3. Challenges in modelling methodologies and parameterisation

Human behaviour in relation to epidemics is based on attitudes, belief systems, culture, opinions and awareness of a disease. All of these factors can change over time, both in an individual and in the entire population [69]. Here we review three issues that will naturally arise when attempting to combine and calibrate all these factors into a generalised model of epidemiological and behavioural dynamics: (i) balancing model complexity and interpretability – contained within we have a more expansive view into the role of "simplified models" in the context of epidemiological-behavioural modelling; (ii) ability to select appropriate models, calibrate them and validate them; (iii) useability of developed modelling tools for non-experts.

3.3.1. Balancing model complexity and interpretability

Generalised models can sometimes come to resemble a "black box", with many parameters that intend to capture as many epidemiological-behavioural dynamic processes that may plausibly be part of the system. It can be hard with such models to gain a deep understanding of how many factors contribute together to produce complex outcomes. In some contexts, including in medicine, model users may have to take legal responsibility for their decisions and this can inhibit the use of models they do not fully understand. It is also important to balance the realism of behavioural model components with that of the epidemiological model. There would be less value in analysing a detailed behavioural model and overly simplified epidemiological model and vice versa.

In contrast to generalised models, simplified models are often more interpretable. Many problems in mathematics often employ and expand upon the use of simplified mathematical models of that problem, the idea being to make many controlled assumptions, often rather strong, to gain a deeper understanding of a particular phenomenon. We now discuss the potential contributory role of simplified models in the context of epidemiological-behavioural modelling.

3.3.1.1. Deeper dive into simplified modelling. In epidemiological modelling, simple outbreak dynamics may be obtained using an SIR (susceptible-infected-recovered) type disease status construct, with a number of associated assumptions (e.g. the population is assumed to be homogenous and of a fixed size, transmission is assumed to be proportional to the number of infectives, and the disease is assumed to not have multiple strains, or the ability to reinfect individuals, etc). These simple SIR models are often used to compare with the results of an extended model to gain new insights.

In the epidemiological-behavioural context, the SIR model can be thought of as a "non-behavioural" case. Then as a "behavioural" case, one could modify the transmission term in the SIR model to mimic a population that reduces their contact rate in the presence of a very large number of infectives [70]. It is of benefit to find, propose and explore these highly simplified models with their heavy (and likely unrealistic) assumptions on behaviour. As we then explore the high-dimensional space of models or assumptions about human behaviour, the simplified cases provide reference points and help quantify and locate the uncertainty.

To illustrate the benefit of building from simple behavioural models, consider the process of mechanistically incorporating the rationality of individuals into a mathematical model. Like the SIR model in "pure" epidemiological modelling, we first identify a simplified model with epidemiological-behavioural aspects that can and is being built upon. In this instance, game theory provides useful tools to study simple conflicts of individuals choosing between actions of differing costs and benefits. Some of the basic assumptions that underlie this theory are that individuals pursue well defined objectives (they are rational), and that they take into account the behaviour of other decision makers when deciding on how to behave (they are strategic). It is recognised that this provides a very idealised scenario [71,72], but the focus is not in predicting what decisions people will make, but rather the interest is in the mechanisms of that decision making [73,74]. In epidemiology, the field is mostly used to model vaccine uptake [75,76] in order to better understand the relative costs and decision-making process behind choosing to vaccinate (whether that be yourself or farmers vaccinating livestock). However, recent work has been concerned with modelling contact patterns and social distancing as games [77,78].

Whilst the assumptions made by these model frameworks may not be realistic compared to our current understanding of human rationality (e.g. the whole population is perfectly rational and able to act that way; everyone acts in their own self-interest or in the global good; everyone has the same preferences and costs; individuals have perfect information available to them), we then seek to extend the simplified models (e.g. the population does not act perfectly rational, individuals care about other members of the population and act accordingly, different sub-populations have different costs/preferences (i.e. young and old, unequal opportunity, compassionate and uncompassionate); non-perfect information).

We give examples of three avenues in which researchers have sought to break free of the constraints of simplified models of rationality (Figure 2). Rational social distancing practices used by individuals will vary depending on the response of others and how these responses change the epidemic. A simplified model by Reluga [77] does this by setting up an epidemic as a differential game, where preferences of individuals are given by cost functions that are minimised with respect to control and state variables obeying some system of differential equations (e.g SIR Model). This differential game is played by individuals in a population reacting to population behaviours. This model takes many of the assumptions as given above. Others have since extended this model to consider different aspects of rationality. In the first extended example, Fenichel *et al.* [14] introduced specific contact rates as an individual's measure of social distancing, rather than a simplified willingness to social distance. Ultimately, it is individual contacts between susceptible and infected individuals that lead to disease spread. As a consequence, modelling the utility gained and risk of infection from each of these individual contacts gives insights into the individuals desire to interact with a certain number of other individuals in a given time frame. Second, in many epidemiological-economic models, the population is assumed to be making decisions in the absence of government policy. Schnyder *et al.* [79] relaxed this constraint by introducing rational responses to government incentives to social distance. This interplay was then directly compared to the simplified model to show the specific effect of government policy during an epidemic. Rationality here was not assumed to be complete coherence to government policy, or a social planner, unlike in simplified models. Thus, this approach provides a tool for policymakers to see how a population might react to any given intervention. Third, and finally, whilst much research assumes just one behavioural compartment, recent work has considered the rational behaviours of individuals dependent on infection status. We note work done by Bethune and Korinek [80], which links to measured economic factors in the US economy during the COVID-19 pandemic. They find that rational infected individuals do not see it beneficial to social distance when thinking purely in their own self-interest, raising questions of whether such selfish behaviour is truly rational.

This illustrative example portrays how simplified models of the rationality of human decision making clearly have many steps to take to bring them up to speed with "pure" epidemiological models. However, if this splicing of epidemiological and behavioural models is done early enough, in simple scenarios with many assumptions, such models would provide a useful framework to build on to arrive at integrated, generalised epidemiological-behavioural models. It may not be necessary to capture in detail the differing variability in sub-populations for the insights to be useful.

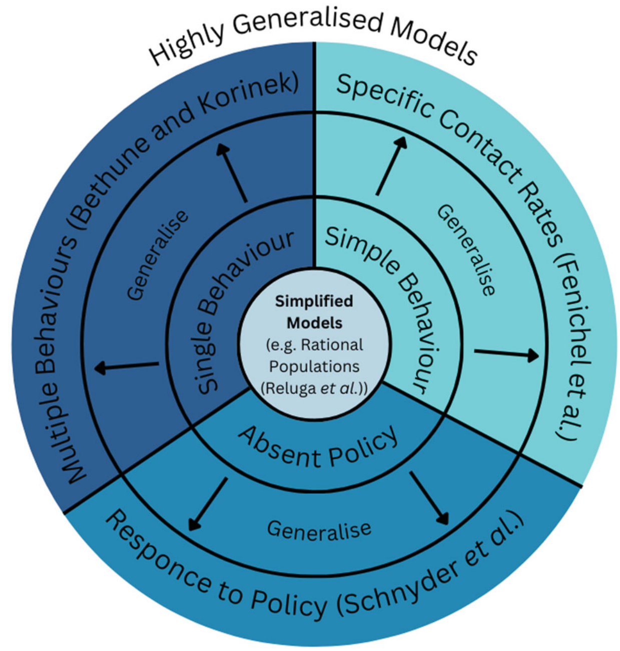

Figure 2. Illustration of assumptions within a simplified behavioural model of rationality and contemporary work on more generalised models that relax those assumptions. We show an example of a simplified behavioural model of epidemics incorporating rational behaviour (centre circle), assumptions of the simplified model (inner ring) and how different groups have sought to extend such simplified models (relaxing a particular assumption to "break-free" of such constraints) as they seek more realistic, generalisable models (outer ring). Fenichel et al. [14] is an earlier paper which generalises to include human to human contact behaviour as being adaptive. Schnyder et al. [79] takes the assumption of no government policy involvement and adds in how populations would respond to government incentives to social distance. Bethune and Korinek [80] take the assumption of a single behavioural class for the whole population and instead consider behavioural classes dependent on infection status.

3.3.2. Ability to select appropriate models, calibrate them and validate them

The most appropriate method for modelling behaviour depends on the problem that is being addressed and the data available. For systems relatively abundant in data it may be possible to derive useful empirical relationships that describe the key drivers of decision making. It is more likely, however, that an underlying theoretical framework is needed to underpin the model structure. Here we can draw on social theory, building on frameworks such as the theory of reasoned action [35], the theory of planned behaviour [36] or the Health Belief Model [81], or work with social theorists to develop bespoke frameworks relevant to the problem.

Once the underlying theory is decided upon or derived then it can be parameterised. With sufficient resources, a survey or questionnaire can be designed to fully parameterise the model. Other more innovative means can also be employed, such as scenario exploration through role play (serious games [82]). All too often, however, this is not feasible and so we must rely on secondary sources of data or expert judgement to parameterise models. As with other types of models, sensitivity analysis can be done to determine the importance of each of the parameters on the modelled outcomes, helping to quantify uncertainties, direct future effort for data collection or caveat research findings.

Many models are theoretical and do not necessarily undergo validation. Validation of proposed model structures is relatively rare [83]. El Fartassi *et al.* [84] proposed the use of structural equation modelling to validate the form of their proposed behaviour model that described farmer behaviour in relation to sustainable water management. This approach is resource intensive as typically questionnaires need to be carefully developed to align with and test the modelled constructs. Sonnenschein *et al.* [85] highlight that behaviour is one of the most challenging aspects to model and validate. They propose a deep learning approach for extracting evidence from scientific articles to validate the structure of simulation and projection models. However, this innovative method relies on a large evidence base. Another more pragmatic approach to this challenge is through "peer review", i.e. validation of model assumptions through consultation with independent epidemiological modellers and social scientists.

In the context of the timely development of epidemiological models to inform outbreak response efforts, Swallow *et al.* [86] expressed an overarching challenge of conducting robust parameter estimation at speed and in the face of considerable uncertainty. Those authors remark how such estimation challenges are contingent on challenges associated with both the model frameworks and the data that feed into estimation approaches. This is particularly pertinent in the early stages of an outbreak, where policy decisions must be made despite scarce data. We therefore reiterate the call that challenges across these areas should not be considered in isolation.

3.3.3. Useability of modelling tools for non-experts

Although the sharing of analytical tools with practitioners can be beneficial, they can sometimes be used or interpreted incorrectly. As part of our role as scientists we should give careful attention to the way we make software available [86]. Comprehensive model documentation, clear code scripts and implementing modular programming can help maximise the accessibility and useability of such analytical tools. User interfaces must be built in collaboration with users to identify their needs and conventions. These factors will ensure that models can be utilised on a technical basis, but it is also important to ensure that non-experts are aware of model limitations and relevant areas of application. Key to conveying such information is ensuring full transparency in terms of the model assumptions and sources of information used to construct and parameterise models, and their uncertainty.

A more systematic approach to help circumvent the accessibility and useability issues of software tools by practitioners is participatory modelling [87]. Participatory modelling has active involvement of stakeholders in the design, development, and use of models. This co-production process can ensure that it is clearly defined to all parties who are the intended users of the developed analytical tools, the user context (what are the outputs, what decisions will they help with) and improve the reliability of model output interpretations (thus aiding decision making). Using a stakeholder workshop approach, Purse et al. [88] demonstrated that co-production of models is particularly important to capture complex interactions in disease systems strongly influenced by human behaviour. Modelling the risk of the tick-borne Kyasanur Forest Disease the authors identified the socio-ecological factors that determine human cases; this required participatory modelling to capture the joint influences of the vector and pathogen dynamics together with the human activities that underpin exposure. Participatory modelling ensured that a wide range of a priori knowledge and data sources were integrated into the model.

Participatory approaches can also be expected to enhance non-expert understanding and confidence in the model outputs. Indeed, participatory modelling has been shown to improve knowledge capture in complex systems and encourage participation and use of models by a diverse range of stakeholders [89]. Co-production can thus facilitate intersectoral collaboration, which is needed to meet the challenges of epidemics that have multiple drivers encompassing environmental, as well as human and behavioural, aspects [90]. Usability and uptake of models can also be enhanced through their integration into live simulation exercises and role-playing [91], which can be used to adapt models and improve their usability. Live simulation exercises and role-playing can also help us better understand the role of modelling as one particular input to contingency planning or outbreak response.

3.4. Challenges in how modelling (and communication of its findings) affects behaviour

Modelling is an important tool that aids our understanding of transmission dynamics, the potential health impacts of a pathogen and can help inform health policy.

Another strand of the language and interpretability discussed earlier is the importance of clear communication.

During the early stages of an interdisciplinary endeavour, it quickly becomes clear that the signature pedagogies of the contributors – recall that these are the ways in which novices are taught to think, perform and act with integrity in their profession – can lead to difficulty in mutual understanding. In language, this can take the form of conveying the same concepts with different language or using common terminology for disparate concepts. In addition, clashing concepts of which approaches are rigorous can hinder forward progress until the relevant negotiations have taken place.

This communication between scientists, policy makers and the public has been previously noted amongst challenges for epidemiological modelling [92,93]. There is a bi-directional relationship between behaviour and modelling. As noted extensively throughout this article, behaviour has to be accurately captured within modelling to produce reliable outputs, but then the publicised outputs of mathematical modelling then often influence behaviour, whether that be through (mandated) policies directly or through public health messaging [94].

The two issues we expand on here are: (i) challenges and opportunities in the communication of epidemiological-behavioural models; (ii) ethical implications of epidemiological-behavioural modelling affecting behaviour.

3.4.1. Challenges and opportunities in the communication of behavioural-epidemiological models

Challenges in the communication of modelling are well-documented [95]. One prominent example is how to balance the very limited space/time the available communication channels, such as the media, have to communicate results (e.g. a news headline), or a scientific advisor to a decision-maker (e.g. a very brief summary in a meeting), with all of the nuance that underpins a modelling result (e.g. the model assumptions and parameterisation, often requiring large paper appendices to detail properly). For example, the literature on the effect of face masks on controlling the transmission of SARS-CoV-2 is varied and dependent on a range of assumptions including, but not limited to, the quality of the mask and how it is worn [96]. This makes the decision on whether or not to advise mask-wearing during a public health emergency difficult to summarise briefly, including in a headline format. Progress is being made in the communication of nuanced messages – guidelines for scientific communicators have been shared by the Winton Centre for Risk and Evidence Communication at the University of Cambridge (with advice based on their experience communicating personal risk from COVID-19) [97].

There are a few ways in which the public consume information about mathematical modelling. Studies have shown that the news media is an important means for this [93,98]. However, a drive in the field for integrated epidemiological-behavioural modelling is not newsworthy by itself until it begins to inform an emergency response. Further consideration of the behavioural impact of communicating modelling is required to strike the careful balance where modelling enhances public health.

For those who are not in the modelling field, it is unlikely that most are actively searching for updates on integrated modelling, which raises questions as to how we can effectively ensure the public are aware of modelling developments such as these ahead of a public, veterinary or plant health emergency? We must draw on the experiences of initiatives tackling other prominent societal challenges in constructing a decision-making value chain incorporating all stakeholders. The Communicating Climate Risk toolkit is one such example; bringing together best practice on the effective communication of climate information from across STEM, social sciences, and arts and humanities, the toolkit provides users with insights, recommendations, resources for all forms of climate-related communication and decision-making, and identifies open problems [17].

Ultimately, citizens are the people who will drive an epidemic. Being able to demonstrate the effect that their everyday actions can have on disease dynamics we conjecture would act as powerful messaging and could increase engagement with models and/or adherence to public health policies and/or messaging.

3.4.2. Ethical implications of epidemiological-behavioural modelling affecting behaviour

Citizens are key stakeholders of modelling being used to inform policy. It is important that the public are well-informed and see their behaviour reflected in these models. For example, under what conditions is the monitoring of human interactions acceptable to the public? Empirical approaches need to be predicated on trust, respect and consent. It is critical to consider different settings and communities, because as we have seen, the response to public, veterinary and plant health emergencies can affect all within our society. This was underlined with the NHS COVID-19 contact tracing app [99,100], with studies showing the decision not to subscribe was driven by privacy concerns [101]. User understanding of the privacy preserving mechanisms is key to confidence. The

NHS COVID-19 contact tracing app was ultimately looking at contact patterns, so as well as helping individual people to inform their decisions, these data were then analysed to answer key public health questions applicable for the whole population [102,103]. Overall, it is imperative we ensure our efforts to understand, develop and evaluate approaches to understand human behaviour are informed by and co-created with the public.

4. Recommendations to deliver societal benefits

The previously mentioned challenges for developing useful epidemiological-behavioural models reveals a potentially overwhelming collection of issues to address. To serve as a resource for all those interested in getting involved in tackling these epidemiological-behavioural modelling challenges (including research scientists, practitioners and policy makers), we outline in Table 1 our recommended action points. Per issue within each challenge area, we provide a recommendation that is "short-term actionable" (i.e. what can plausibly be usefully done now) and a recommendation that is "long-term thinking" (i.e. steps to unlock a long-term vision of how in an idealised setting we envisage studies being conducted). We also link to, but do not comprehensively review, existing evidence of similar actions in other established interdisciplinary fields, drawing from bioinformatics, mathematical biology, neuroscience, climate science, environmental science and health science.

Many of our recommendations for enabling interdisciplinary working echo existing commentary on this topic [4,32,92], but we reiterate them here together with some topic specific suggestions. We emphasise that many of the actionable recommendations require resources from universities and/or funding bodies to execute. The longer-term interdisciplinary success also hinges on the practicality of taking these nascent collaborations further with the continued support of funding, academic institutions and policy makers. Furthermore, for our recommendations related to behavioural science, we stress that we do not wish to dictate the direction of the behavioural science field. Rather, we provide recommendations to aid translation of behavioural science for epidemiological modelling.

5. Envisaged societal benefits

We anticipate the process of embedding behavioural science theory and associated data into epidemiological models can result in these direct improvements for the scientific community (Figure 1, "Improved" box): (i) Research practice: Creation and sustainability of interdisciplinary teams; (ii) Behavioural science theory: Advancements in our understanding of behaviour; (iii) Models: Creation of novel theoretical frameworks that are explainable, transparent and appropriately reported; (iv) Decision making: Enhanced by availability and accessibility of improved data streams & analytic tools.

We believe such scientific progress can bring about a swathe of societal benefits, categorised in four ways: prepared, represented, change and policy (Figure 1, "Societal Impact" box).

<u>Prepared:</u> Not only will there be the personnel capacity and supporting resources to enable the formation and maintenance of interdisciplinary epidemiological-behavioural teams, but the ability to respond to the need for scientific advice in a timely manner. Together, they provide enhanced preparedness against health-related events.

<u>Represented:</u> Improved representation of the community throughout all stages of epidemiological-behavioural modelling analysis (behavioural science theory, data collection, model structure and parameterisation, communication of findings). Crucially, this would not merely be limited to improving the representation of typically thought of demographic characteristics (e.g. age), but also cultural traits.

<u>Change:</u> More informed modelling and interdisciplinary science capabilities, through improved research practice, behavioural science theories and modelling constructs, will change the way behavioural research is conducted in the field of epidemiology. Improved decision making will change how society perceives and trusts the decision makers and the science behind these decisions.

<u>Policy:</u> More robust research studies, whose findings and implications are effectively communicated to both the wider population and decision makers in policy arenas.

On realising these societal benefits, we expect new challenges in behavioural-epidemiological modelling will be unlocked. These new challenges will renew the cycle of improvement and societal benefits achievable through this interdisciplinary approach (Figure 1, dashed arrow).

We once more stress that we consider embracing interdisciplinary working as fundamental in making the aforementioned scientific progress. Mono-discipline approaches would not be capable of delivering these improvements and, therefore, not be able to attain as substantial a level of societal benefits.

6. Conclusion

It is all too apparent that epidemiological events are sensitive to human behaviour. The recent SARS-CoV-2 pandemic has brought to the fore a disconnect between

Table 1. Recommended action points by challenge area and issue within each challenge area. We group the recommendations according to those that are "short-term actionable" (i.e. what can plausibly be usefully done now) and those that are "long-term thinking" (i.e. steps unlock a long-term vision of how in an idealised setting we envisage studies being conducted).

		Recommendation		
Challenge area	Issue	Actionable	Long term thinking	Examples / references
Interdisciplinarity	Constructing a team with required blend of expertise	Apply for small-scale funding to create networking opportunities through joint seminars and workshops, with emphasis on building a common language and goal set.	Funding bodies to support longer term cross disciplinary collaborations. Develop training opportunities to support new researchers in this interdisciplinary field.	Bottom-up models for generation of interdisciplinary science common language [104]. Seed funding from universities can quickly respond to promising interdisciplinary ideas [104,105]. Top-down approaches sometimes successful, e.g. funding for Human Genome Project largely drove the emergence of bioinformatics [106].
	Establishing a common language	Medical practitioners, epidemiologists and the mathematical modelling community to identify and define relevant behaviours for infectious disease modelling (perhaps differentiated by pathogen type), publishing and advertising them to encourage discussion, refinement and use of these definitions.	Promote use of this common language and use it to develop common methodologies that will address agreed aims via long-term collaborations with regular meetings, cross-disciplinary placements, development of dedicated interdisciplinary journals.	Importance of developing a common understanding often recognised, e.g. through analyses of joint field work [107]. Neuroscience "rapidly evolved as a consequence of a series of symposia, conferences, publications, … " (from Sabbatini & Cardoso [108]).
	Standardisation of interdisciplinary methods	Behavioural science and infectious disease modelling communities to collaborate to test existing behavioural science models on existing data sets (e.g. large-scale data sets on behaviour during the COVID-19 pandemic) – establishing the utility of existing theory in the context of infectious disease modelling.	Support cross-sector collaboration – e.g. with policy makers to ensure models inform current policy questions, with the business and technology sectors to support new methods of data collection.	Emulating methodology of successful fields can accelerate progress in interdisciplinary research and can lend emerging interdisciplines *legitimacy* [109]. Potential to expand forecasting hubs for COVID-19 modelling (e.g. Loo et al. [110]) to incorporate behavioural data and behavioural predictions.
Behavioural science	Limitations in existing behavioural science theory and models	Encourage pre-registered studies of objective measures of behaviours to better support reproducibility, quantify drivers and effect sizes.	Invest in interdisciplinary collaborations to design studies that inform key behaviours for (epidemiological-behavioural) models.	Increased prevalence of pre-registered studies has improved the quality of social sciences [111].
	Generalisability of existing behavioural science evidence	Investigate, by co-measurement or meta-analysis of existing data/literature, dependence between relevant behaviours so that adoption of new (disease/pathogen specific) behaviours can be more readily predicted by existing evidence.	Combine qualitative and quantitative data, to develop consensus models that can be tested against (emerging data).	Reviews of mixed methods research in health aim to build on approaches to analyse qualitative and quantitative data within the same study [112].
	Appropriateness of behavioural science research methodologies for the quantification of human behaviour	Review methodology to synthesise evidence across experimental and observational studies, highlighting limitations and fruitful avenues of research.	Development of predictive models (enabled by new ways of collecting data, see *Data* recommendations below).	Other established interdisciplines, e.g. climate science, have grappled with translating information from closed systems (experiments) and open systems (observational studies) [113].
Data	Ability to leverage existing data into existing models	Identify existing data repositories and explore potential for linkage to, e.g. health records and demographic data. Identify limitations of existing data repositories; representation, missing data, other biases.	Support post-hoc analyses of epidemiological events to explore capabilities of existing data and models, enabling cyclic iteration of both data and models to address limitations.	Build on work by organisations such as Health Data Research UK that enable safe sharing of sensitive data [114].

(*continued*)

Table 1. Continued.

		Recommendation		
Challenge area	Issue	Actionable	Long term thinking	Examples / references
	Identifying the relevant data for use in appropriate models	For plausible/emerging models, test inference framework with synthetic data to identify necessary data and granularity (individual vs population average) to accurately parameterise existing models, potentially for different relevant behaviours and pathogens.	Engage with researchers across disciplines (e.g. anthropology, philosophy) to support collation of representative data including hard to reach populations. Build cohort generating data on baseline behaviour, available to test emerging models for behavioural change in epidemic scenarios.	Funding of large representative cohorts to measure health and health behaviours (e.g. ONS COVID-19 Infection Survey [115]; Our Future Health [116]).
	Ethical considerations for the collection, processing and storage of data	Build on existing guidelines for the storage of sensitive data to develop and publicise clear guidelines for the storage of behavioural data.	Co-create design of data assets (e.g. relevant behaviours) with participants. Ensure systems are in place to enable researchers to follow guidelines for generating and using behavioural data.	The UK Data Service provides guidance on social science research outputs [117].
Modelling methodologies and parameterisation	Balancing model complexity and interpretability	Survey successes of incorporating behaviour into models (within infectious disease modelling and in other applied mathematics, e.g. computational social science, cultural anthropology, energy systems modelling) to help elucidate likely relevant behaviours.	Design model structures that make use of emerging (perhaps individual level) data on relevant behaviours and their adaption.	Past successes within epidemic modelling have been broadly surveyed in articles such as Funk et al. [4,69], Bedson et al. [32], and help provide a roadmap for future research.
	Ability to select appropriate models, calibrate them and validate them	Perform identifiability analysis, sensitivity analysis and/or Bayesian inference on epidemic models that include behaviour to identify key data gaps.	Ensure statistical expertise is embedded into co-design of data and modelling to enable robust model estimation. Explore use of AI to discover new models for disease transmission and behaviour change, either standalone or hybrid with mechanistic models.	Identifiability analyses are widely used to inform model and experimental design in e.g. mathematical biology (Browning et al. [118]).
	Useability of developed modelling tools for non-experts	Researchers and journals to champion clear and comprehensive model documentation. Create a checklist that suggests, for a given model type, what data are priority, highly recommended (but could do something still without, but with limitations) and would be nice to have (but not anticipated to vastly increase uncertainty in outcomes if not included).	Liaise with, or co-create where possible, models with policy makers to ensure they capture relevant potential policy responses (i.e. participatory modelling).	Checklist for environmental science modellers to aid translation to policy (e.g. van Voorn et al. [119]).
How modelling (and communication of its findings) affects behaviour	Challenges and opportunities in the communication of epidemiological-behavioural models	Standardise reporting standards to aid reproducibility and facilitate comparisons between models (e.g. meta-analyses). Develop and share guidelines for communicating uncertainty in models, important for building and maintaining public trust. This may be facilitated by working with specialised scientific communicators, such as the Science Media Centre [120].	To build public trust in modelling and behavioural science, have public involvement integrated as a standard component of epidemiological-behavioural modelling research projects. Help develop public communication of the relevance of behavioural feedback in epidemiological systems, drawing on best practice from other applied modelling.	Standardisation of reporting and documentation of integrated assessment modelling has increased the number of climate models informing policy [121].
	Ethical implications of epidemiological-behavioural modelling affecting behaviour.	Understand relationship between scientific communication and influence of epidemic state on behaviour.	Understand relative influence of data sources (friends, family, media, social media) and promote reliable/official communication of epidemic status.	Bioethics has been developed to support bioinformatics (and other biological research) [122]; new fields of ethics may also be required to support applications of behavioural science.

behavioural science knowledge, epidemiological model capabilities and data needs. In this article we have outlined a myriad of challenges that present hurdles to the robust design and validation of epidemiological models that incorporate the dynamics of human behaviour. Nonetheless, reaffirming two conclusions from Funk *et al.* [4], it remains important that we endeavour to identify the limits of predictability of human behaviour and to propagate uncertainty in the dynamics of behaviour onto epidemiological model uncertainty.

Despite these challenges, we view that there is a growing interest in incorporating behavioural realism in mathematical modelling. By bridging interdisciplinary gaps, unlocking the ability to reasonably tackle the core epidemiological-behavioural modelling challenges and actioning measures to address them, we can initiate a new field of mathematical behavioural science to address societal challenges in a truly interdisciplinary fashion. The production of a new generation of epidemiological-behavioural models can be an integral and relevant tool to inform policy decisions, providing evidence-based interventions for the benefit of public, veterinary and plant health.

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