

Spread of Nontyphoidal *Salmonella* in the Beef Supply Chain in Northern Tanzania: Sensitivity in a Probabilistic Model Integrating Microbiological Data and Data from Stakeholder Interviews

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East Africa is a hotspot for foodborne diseases, including infection by nontyphoidal *Salmonella* (NTS), a zoonotic pathogen that may originate from livestock. Urbanization and increased demand for animal protein drive intensification of livestock production and food processing, creating risks and opportunities for food safety. We built a probabilistic mathematical model, informed by prior beliefs and dedicated stakeholder interviews and microbiological research, to describe sources and prevalence of NTS along the beef supply chain in Moshi, Tanzania. The supply chain was conceptualized using a bow tie model, with terminal livestock markets as pinch point, and a forked pathway postmarket to compare traditional and emerging supply chains. NTS was detected in 36 (7.7%) of 467 samples throughout the supply chain. After combining prior belief and observational data, marginal estimates of true NTS prevalence were 4% in feces of cattle entering the beef supply and 20% in raw meat at butcheries. Based on our model and sensitivity analyses, true NTS prevalence was not significantly different between supply chains. Environmental contamination, associated with butchers and vendors, was estimated to be the most likely source of NTS in meat for human consumption. The model provides a framework for assessing the origin and propagation of NTS along meat supply chains. It can be used to inform decision making when economic factors cause changes in beef production and consumption, such as where to target interventions to reduce risks to consumers. Through sensitivity and value of information analyses, the model also helps to prioritize investment in additional research.

KEY WORDS: Bayesian hierarchical model; food safety; *Salmonella*; sensitivity analysis; value of information

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1. INTRODUCTION

Agricultural intensification and environmental change are linked to the emergence of zoonotic and foodborne disease (Jones et al., 2013). Nontyphoidal *Salmonella* (NTS) is zoonotic (transmissible between humans and animals) as well as foodborne (obtained from food, with potential origins in humans, animals, crops, water, or the environment), and has emerged as a major pathogen in Africa (Crump et al., 2020). World Health Organization estimates indicate that NTS caused 896 cases of diarrhea per 100,000 people across Africa in 2010—approximately six times the rate in the European Union (Havelaar et al., 2015). In addition, diarrheal disease agents, especially NTS, were responsible for most of the deaths attributed to foodborne disease, with over 58% of the worldwide estimated deaths due to NTS occurring in Africa (Havelaar et al., 2015).

In the United Republic of Tanzania, the incidence of invasive NTS disease is high (Biggs et al., 2014; Grace et al., 2012) and salmonellosis is among its 10 priority zoonoses (Anonymous, 2017). The situation in the country exemplifies several opportunities and challenges associated with population growth and agricultural intensification. Since 2001, Tanzania's annual gross domestic product growth has been 6–7%, which has been accompanied by steady population growth (World Bank Group, 2019). This has triggered rapid changes in agricultural production, food supplies, and consumption. Such changes seem to be driven and shaped primarily by small scale economic dynamics, although the Tanzanian

Livestock Modernization Initiative, a national policy, expresses support for development of commercial beef farming operations (Ministry of Livestock and Fisheries Development, 2015). The red meat value chain in Tanzania has several shortcomings, including food hygiene concerns, which were highlighted in an FAO report in 2015 and are shared by consumers and regulators (Mugarula, 2016; Wilson, 2015). Considering that beef is a potential source of NTS (Thomas et al., 2020), there is a need to gain insight into the contribution of the beef supply chain to human NTS exposure in the country, for both traditional and emerging supply chains. This requires consideration of information from a wide range of actors and sources, beyond simple measures of observed prevalence, and should encompass stakeholder values, resource limitations and uncertain human behaviors as well as targeted data collection. Existing models of NTS amplification through the food supply chain, including for pork, poultry, or dairy cattle, have generally been based on the situation in high income countries and do not represent the situation in Tanzania. In addition, their focus tends to be biomedical, without consideration of socioeconomic or cultural drivers and constraints on food safety (Pin et al., 2011; van der Fels-Klerx et al., 2008; Xiao et al., 2005).

In this article we report an interdisciplinary effort to examine a specific foodborne pathogen in a clearly identified emerging livestock system: NTS associated with the beef supply chain for Moshi Municipal Council in northern Tanzania, which has a resource-constrained but rapidly expanding economy. Data obtained through collaboration across multiple disciplines, including epidemiology, microbiology, anthropology, and human geography, were combined in a Bayesian hierarchical model, a form of probabilistic graphical model that allows for integration of information from disparate sources and includes a consistent representation of uncertainties. Specifically, we explored the collection and management of information relating to the identification and spread of NTS in the beef supply chain and, crucially, we have considered how decisions that concern food safety can be influenced by the information supply. This enabled us to compare the estimated prevalence of NTS in traditional and emerging beef supply chains, to identify hitherto underappreciated sources of contamination, and to prioritize areas for further research based on value of information and other sensitivity analyses.

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2. METHODS

2.1. Data Collection

2.1.1. Ethics

The work was approved by the Tanzanian National Institute of Medical Research (NIMR/HQ/R.8a/Vol. IX/2028, NIMR/HQIR.8cNoI. 11/1069), Kilimanjaro Christian Medical Centre Research Ethics Committee (Certificate No. 832), Ethics Committee of the College of Medical, Veterinary and Life Sciences, University of Glasgow (200140183, 200140152) and Human Research Ethics Committee, University of Otago (H15/069). Interviewees gave recorded, verbal consent to participate in interviews, as approved by ethics committees.

2.1.2. Interviews

Semistructured interviews were conducted from 2016 through 2018 with actors across the beef value chain in Moshi Municipal Council (MMC), including butchers, fresh meat vendors, livestock extension officers, meat inspectors, and health officers. Actors at regional or district level were selected based on their key role, whereas others were recruited from five randomly selected wards each in Moshi Rural District and Moshi Municipality in consultation with local authorities, as detailed previously (Hrynicky et al., 2019; Prinsen et al., 2020; Waldman et al., 2020). Interviews were conducted in Swahili, audio-recorded, translated and transcribed into English by a Tanzanian interviewer with knowledge of local dialect, policy, regulation, and commerce, which were covered in the interviews, together with perceptions of food safety (Hrynicky et al., 2019; Prinsen et al., 2020; Waldman et al., 2020). Information from interviews contributed to model structure and assumptions, for example, information about dispersed origins and destinations of cattle and meat, respectively, informed the choice of a bow tie model to depict the supply chain (Fig. 1). Statements about trade and lairage informed on the prior distribution of time between market and slaughter. Observations during site visits helped to identify contact and noncontact surfaces in the slaughter and butchery environment, which are incorporated in the model, and additional risks, for example, related to dogs, birds, or onward transmission of NTS through run-off (Fig. 2).

2.1.3. Microbiology

Slaughter locations for ruminants and data on throughput were identified with the MMC District

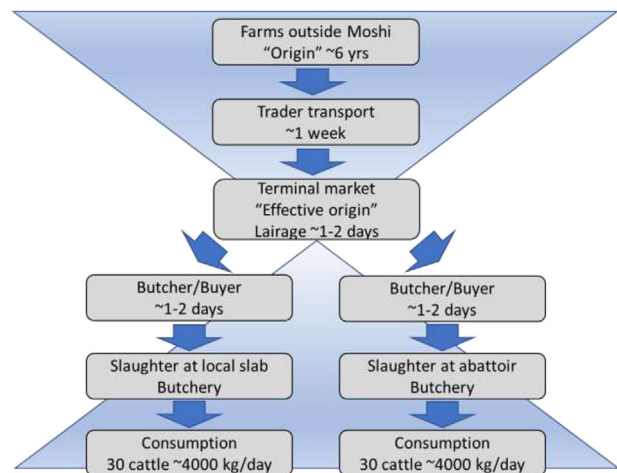


Fig 1. Schematic representation of the beef supply chain in Moshi Municipal Council, northern Tanzania. The beef supply chain is shown using a bow tie model of dispersed origins, pinch point at markets, and dispersed consumers, with forked postmarket pathway representing traditional (slaughter slab) and emerging (abattoir) beef supply chains.

Veterinary Officer and Livestock Field Officers responsible for meat inspection. Locations included slaughter slabs and a local abattoir or slaughterhouse. Slaughter slabs generally have concrete floors, with the carcass placed on the floor, the skin, or atop a wooden pallet. The number of workers in slaughter slabs is limited, and tools are simple, for example, knives, cleavers, and ropes. By contrast, abattoirs are roofed, enclosed buildings with tiled walls, running water, and drainage systems, with formal operating procedures, multiple workers, and (mechanized) equipment such as rails, hooks, and scales. Slaughterhouses are similar to abattoirs in structure but less sophisticated operationally. In our study, the term slaughterhouse may be more appropriate, as some aspects of processing were similar to those at slaughter slabs, for example, dressing of the carcass on a splayed skin on the floor and use of knives and cleavers. For ease of differentiation between slaughter slabs and the more mechanized facility, however, we use the word abattoir throughout the text. Slaughter facilities ($n = 14$) were sampled repeatedly between December 2015 and August 2017 (inclusive), as were shops ($n = 14$) whose meat was supplied by the slaughter facilities sampled (Table 1). Fecal samples were collected at five primary markets (Mgagao, Endulen, Oldonyosambu, Terrat, and Emboret) across northern Tanzania and Weru Weru Secondary livestock market located on the periphery of Moshi Municipal Council. Market cattle were



Fig 2. Beef supply chain in Moshi Municipal Council, northern Tanzania. Top left: cow in lairage at slaughter slab; top right: slaughter slab; center left: abattoir; center right: run-off used to fertilize crops; bottom left: warm meat at butcher shop; bottom right: contact surfaces including butcher's block and panga. Photos by N. French (top left, center left and right), and G. Prinsen (top right, bottom left, and right).

sampled to represent the effective origin of the beef as primary markets supply cattle that move through the market system toward secondary markets, including Weru Weru, which is the main source of animals supplying the Moshi beef chain (Chaters et al., 2019). Samples collected at slaughter included cattle feces (rectal sample), carcass swabs (rump and shoulder, collected using dry cotton-tipped swabs and cotton-tipped swabs moistened with Maximum Recovery Diluent (Oxoid) and sterile metal 100 cm² templates) and environmental samples (using boot socks or environmental sponge swabs). At butcheries, samples were collected from retail meat (ca. 0.5 kg from lowest hanging section of beef) and the environment, as detailed previously (Crump et al., 2020). Samples were transported to the Kilimanjaro Clinical Research Institute Zoonoses Laboratory in a cool box with three or more freezer packs on the day of sampling. Isolation and identification of *Salmonella* followed a protocol from the U.S. Food

and Drug Administration—Bacteriological Analytical Manual, with modifications. Briefly, homogenized fecal (1 g) or meat (25 g) samples, carcass swabs or sponges were added to buffered peptone water, vortexed or massaged for a short period, and incubated over night at 37°C, followed by selective enrichment, culture on selective indicator media (xylose lysine deoxycholate agar with 5 µg/ml novobiocin), and phenotypic and genotypic confirmation of prospective *Salmonella* colonies as detailed elsewhere (Crump et al., 2020; Sindiyo et al., 2018).

2.2. Network Representation

Hide contamination was attributed to contamination with NTS from feces, whilst carcass contamination was attributed to NTS from feces, hides, or the environment. The gastrointestinal (GI) tract and hide are removed to produce the carcass, so

Table 1. Detection of Nontyphoidal *Salmonella* (NTS) from Samples Obtained from the Beef Supply Chain in Moshi Municipal Council, Northern Tanzania, 2015–2017. Fecal Samples Represent the Effective Origin of all Cattle Processed Via Slaughter Slabs and Abattoirs, Whereas Remaining Data Represent Traditional (Slaughter Slab) and Emerging (Abattoir) Beef Supply Chains. The Contact Environment Includes Knives, Butchers’ Blocks, and Other Items in Direct Contact with Carcasses or Meat. The Noncontact Environment Includes Run-Off, Walls, Floors, and Other Physical Structures that Are Not in Direct Contact with Carcasses or Meat

| Sample type | Number of samples | Number (%) of NTS positives | |
|--------------------------|-----------------------|-----------------------------|----------|
| Feces at market | 113 | 3 (2.7) | |
| Feces at slaughter | 93 | 2 (2.2) | |
| | Slaughter Slab | Abattoir | |
| Carcass | 36 | 0 (0) | 0 (0) |
| Meat | 116 | 19 (16.4) | 2 (8.3) |
| Environmental—contact | 44 | 2 (4.5) | 0 (0) |
| Environmental—noncontact | 13 | 6 (46.1) | 2 (22.2) |

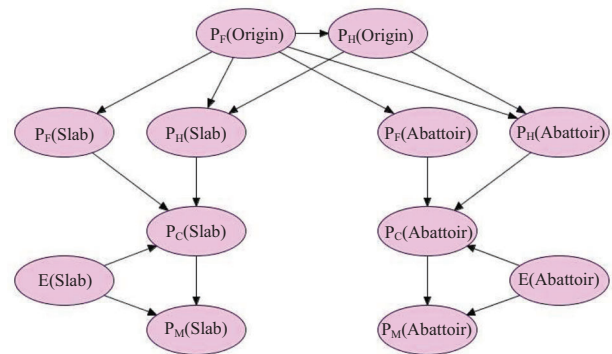


Fig 3. Network representing dependencies between steady state prevalence of nontyphoidal *Salmonella* within the beef supply in Moshi Municipal Council, northern Tanzania. P_F , P_H , P_C , and P_M are the prevalence of nontyphoidal *Salmonella* in feces, on hides, on carcasses and in meat and E represents the effective strength of the environmental source (a weighted combination of contact and noncontact sources). “Slab” and “Abattoir” represent the traditional and emerging branches of the beef supply, respectively, and “Origin” represents the effective origin at terminal markets that supply most of the beef cattle slaughtered for consumption in Moshi.

meat contamination is attributed to carcass or environmental contamination only. Thus, microbiological sampling, network representation and network quantification focus on three effective sources: NTS from cattle (feces and hide) contaminating a carcass, environmental NTS contaminating a carcass and environmental NTS contaminating meat. Prevalence relationships are summarized conceptually in Fig. 3 and computationally in Table 2, which introduces a minimal number of uncertain parameters as described below. The full model is available in Appendix A.

Assuming a steady state, the prevalence, P , of NTS in feces (indicated by subscript F) at the effective origin, $P_F(\text{Origin})$, is related to the prevalence of NTS on hides (indicated by subscript H) at the effective origin, $P_H(\text{Origin})$ (Fig. 3). The form of this relationship can be obtained from steady state solutions of compartmental models (Arthur et al., 2009; Narvaez-Bravo et al., 2013). The relationship is monotonic and can be represented as:

$$P_H(\text{Origin}) = \frac{\alpha P_F(\text{Origin})}{1 + \alpha P_F(\text{Origin})}, \quad (1)$$

where α is a single uncertain shape parameter. Considering the short time between market (effective origin) and slaughter, we assumed that fecal prevalence of NTS at slaughter is the same as $P_F(\text{origin})$. In contrast, hide contamination is assumed to increase from

Table 2. Elements of the Network of Prevalence for Nontyphoidal *Salmonella* (NTS) in the Beef Supply for the Moshi Municipal Council, northern Tanzania. Parameters have Prior Distributions $\alpha \sim \text{Normal}(20,10)$, $\Delta T \sim \text{Uniform}[1,10]$ days, α_{CS} , α_{ES} , α_{CA} , α_{EA} , β_S , β_A , $\rho_M \sim \text{Uniform}[0,1]$

| Prevalence | Variable | Relationship | Parameters | Data |
|------------------------|--|--|--|--|
| $P_F(\text{Origin})$ | Steady state prevalence of NTS in feces for cattle at effective origin (market) | Not applicable | Not applicable | Fecal samples from cattle at terminal market |
| $P_H(\text{Origin})$ | Steady state prevalence of NTS contaminated cattle hides at effective origin (market) | $P_H(\text{Origin}) = \frac{\alpha P_F(\text{Origin})}{1 + \alpha P_F(\text{Origin})}$ | α : shape parameter for the monotonic relationship between prevalence of NTS on hides and in feces for cattle at effective origin | Not collected |
| $P_F(\text{Slab})$ | Steady state prevalence of NTS in feces of cattle slaughtered at a slaughter slab | $P_F(\text{Slab}) = P_F(\text{Origin})$ | Not applicable | Fecal samples from cattle at slaughter slabs |
| $P_H(\text{Slab})$ | Steady state prevalence of NTS contaminated hides for cattle slaughtered at a slaughter slab | $P_H(\text{Slab}) = 1 - (1 - P_H(\text{Origin}))e^{-\frac{t_S}{\Delta T}}$ | ΔT : time constant for the decay of the fraction of uncontaminated hides for cattle in the transition from origin to slaughter at a slab in the Moshi municipal district | Not collected |
| $P_F(\text{Abattoir})$ | Steady state prevalence of NTS in feces for cattle slaughtered at the abattoir | $P_F(\text{Abattoir}) = P_F(\text{Origin})$ | Not applicable | Fecal samples from cattle at the abattoir |
| $P_H(\text{Abattoir})$ | Steady state prevalence of NTS contaminated hides for cattle slaughtered at the abattoir | $P_H(\text{Abattoir}) = 1 - (1 - P_H(\text{Origin}))e^{-\frac{t_A}{\Delta T}}$ | ΔT : time constant for the decay of the fraction of uncontaminated hides for cattle in the transition from origin to slaughter at the abattoir in the Moshi municipal district | Not collected |
| $P_C(\text{Slab})$ | Steady state prevalence of NTS contaminated carcasses for cattle slaughtered at a slaughter slab | $P_C(\text{Slab}) = 1 - (1 - \alpha_{CS}(P_H(\text{Slab}) + P_F(\text{Slab}) - P_H(\text{Slab})) - \alpha_{ES}E(\text{Slab}))$ | α_{CS} : effective probability for transfer of NTS contamination from an animal to its own carcass during slaughter at a slab α_{ES} : effective probability for transfer of NTS contamination from the environment to a carcass during slaughter at a slab | Postevisceration carcass swabs at slaughter slabs |
| $P_C(\text{Abattoir})$ | Steady state prevalence of NTS contaminated carcasses for cattle slaughtered at the abattoir | $P_C(\text{Abattoir}) = 1 - (1 - \alpha_{CA}(P_H(\text{Abattoir}) + P_F(\text{Abattoir}) - P_H(\text{Abattoir})) - \alpha_{EA}E(\text{Abattoir}))$ | α_{CA} : effective probability for transfer of NTS contamination from an animal to its own carcass during slaughter at a slab α_{EA} : effective probability for transfer of NTS contamination from the environment to a carcass during slaughter at the abattoir | Postevisceration carcass swabs at the abattoir |
| $P_M(\text{Slab})$ | Steady state prevalence of NTS from meat for cattle slaughtered at a slaughter slab | $P_M(\text{Slab}) = (\rho_M + \beta_S E(\text{Slab})(1 - \rho_M)) P_C(\text{Slab}) + \beta_S E(\text{Slab})(1 - P_C(\text{Slab}))$ | ρ_M : the fraction of retail units that are NTS contaminated following the partition of a single contaminated carcass by a butcher β_S : effective probability for transfer of NTS contamination from the environment to a unit of retail meat during butchery of a carcass obtained from a slaughter slab | Fresh meat samples purchased from butchers that obtain meat from slaughter slabs |

(Continued)

Table 2. (Continued)

| Prevalence | Variable | Relationship | Parameters | Data |
|------------------------|---|--|---|---|
| $P_M(\text{Abattoir})$ | Steady state prevalence of NTS from meat for cattle slaughtered at the abattoir | $P_M(\text{Abattoir}) = (\rho_M + \beta_A E(\text{Abattoir}) (1 - \rho_M)) P_C(\text{Abattoir}) + \beta_A E(\text{Abattoir}) (1 - P_C(\text{Abattoir}))$ | ρ_M : as above β_A : effective probability for transfer of NTS contamination from the environment to a unit of retail meat during butchery of a carcass obtained from the abattoir | Fresh meat samples purchased from butchers that obtain meat from the abattoir |
| $E(\text{Slab})$ | The fraction of all the contacts between carcasses or meat and the environment (summed over all cattle slaughtered at a slaughter slab) for which the environmental element making contact is contaminated with NTS | None | Not applicable | Surface swabs, run-off, knives, butchers' blocks, and so on at slaughter slabs or in butcheries that obtained meat from slaughter slabs |
| $E(\text{Abattoir})$ | The fraction of all the contacts between carcasses or meat and the environment (summed over all cattle slaughtered at the abattoir) for which the environmental element making contact is contaminated with NTS | None | Not applicable | Surface swabs, run-off, knives, butchers' blocks, and so on at the abattoir or in butcheries that obtained meat from the abattoir |

market to slaughter due to comingling and stress associated with transportation:

$$P_H(\text{Slab}) = 1 - (1 - P_H(\text{Origin})) e^{-\frac{t_S}{\Delta T}}, \quad (2)$$

where t_S indicates time in days and the fraction of uncontaminated hides decays with a single uncertain time constant ΔT . Low ΔT indicates rapid decay, implying rapid increase of hide contamination with time. A similar expression connects the prevalence of NTS on animal hides with the fecal prevalence at origin in the abattoir branch.

After slaughter, animals are exsanguinated and dressed (removal of head, hide, GI tract, and other organs), leaving a carcass. The carcass may become contaminated by the animal's hide or GI-content, or indirectly from contamination of the slaughter environment, for example following aerosolization of bacteria (Rahkio & Korkeala, 1997), or through contact with floors, walls, knives, people, dogs, chickens, rodents, and so on. (Fig. 2). If the prevalence for feces and hides have a complex joint distribution it is convenient to express the complex probability of carcass contamination from the feces, or the hide, as a logical OR operator based on their marginal values, using a correction for the joint probability known as exception independence (i.e., it does not matter

where or how many times contamination occurred). The conditional probability for carcass contamination, given a vector of sources, can be expressed in an efficient noisy-OR table, using probabilistic transfer (Woudenberg & van der Gaag, 2011). This approximation introduces two uncertain parameters, representing effective transfer probabilities from the animal or the environment onto the carcass for the slaughter slab pathway (α_{CS} , α_{ES}) and the abattoir pathway (α_{CA} , α_{EA}). Carcass prevalence of NTS can be related to fecal, hide, and environmental contamination, and effective transfer probabilities according to:

$$P_C(\text{Slab}) = 1 - (1 - \alpha_{CS} (P_H(\text{Slab}) + P_F(\text{Slab}) - P_H(\text{Slab}) P_F(\text{Slab}))) (1 - \alpha_{ES} E(\text{Slab})), \quad (3)$$

or the abattoir specific equivalent. Both animal and environmental carcass contamination pathways are active based on NTS data from South Africa (Madoroba et al., 2016) and Tanzania (Crump et al., 2020).

Finally, butchers partition carcasses into meat for retail. Based on our interviews, a typical retail volume is 250–500 g so a single carcass corresponds with several hundred retail units. The change in

operating volume introduces an uncertain rate, ρ_M , which is the fraction of retail units that are contaminated following the partition of a contaminated carcass (Table 2). The process also introduces opportunities for additional contamination from the environment. We assumed that the effective strength of environmental contamination is invariant along branches (slaughter slab, abattoir), that is, at slaughter, butcher, or vendor stages of the supply chain. The final expression for NTS prevalence in retail meat introduces one additional uncertain parameter in each branch, effective transfer coefficients β_S and β_A , respectively (Table 2) and for the slaughter slab branch is:

$$P_M(\text{Slab}) = (\rho_M + \beta_S E(\text{Slab})(1 - \rho_M)) P_C(\text{Slab}) + \beta_S E(\text{Slab})(1 - P_C(\text{Slab})). \quad (4)$$

In equations (3) and (4), $E(\text{Slab})$ or $E(\text{Abattoir})$ are effective strengths of contamination from the environment. Environmental contamination arises from a series of discrete stochastic events that can each transfer bacteria, but the dynamics are unpredictable and complex, as illustrated using computational videography (Julian & Pickering, 2015). With appropriate approximations (e.g., mean field) the essential behavior can be captured with an effective strength, $E(\text{Slab})$ or $E(\text{Abattoir})$, that can be considered as an additional prevalence or the fraction of all contacts for which the environment is contaminated with NTS. The effective strength for environmental contamination can be estimated from swab samples taken from floors, walls, knives, and so on (Table 1).

2.3. Network Quantification

2.3.1. Prior and Posterior Probabilities

The Bayesian approach is based on the updating of prior probabilities with data to generate posterior probabilities. There are no data to quantify the value of α , the shape parameter for the relationship between fecal prevalence, and hide contamination, for NTS in the MMC beef supply (Equation (1)). Reported values for different pathogens and different cattle populations (Arthur et al., 2009; Jacob et al., 2010) are centered on $\alpha = 20$, which can be included in a probabilistic model as the center of a broad, weakly informative, prior belief. Similarly, the time constant ΔT for decay in noncontamination of hides (Equation (2)) is unknown. The constant was assumed to be uniformly distributed in the interval

1–10 days. The time interval between market and slaughter is also uncertain but prior belief can be represented by a truncated normal distribution with a mean and standard deviation of one day and a maximum of seven days, based on information from stakeholder interviews.

Our microbiological data can be included into the network representation of the domain model to build a quantitative picture for the steady state prevalence of NTS. Assuming that results from laboratory samples can be considered as independent Bernoulli trials (Vose, 2000), the number of positive test results from animals, the environment, carcasses, and meat has a binomial probability determined by the scaled prevalence (the prevalence multiplied by the sensitivity of tests for NTS in feces, on carcasses, in the environment, and in meat, Se_F , Se_C , Se_E , and Se_M respectively). Then the application of Bayes' theorem gives the reverse probability for the prevalence of NTS in feces, on the carcass, in the environment, or in meat given a number of positive observations. These probabilities quantify the model domain. Based on the dependence relationships in Table 2 this quantification has a “knock on” effect on other prevalence values in the network, for example, $P_H(\text{Origin})$ or $P_F(\text{Abattoir})$. The consistent updating of probabilities within the network can be implemented efficiently as a Bayesian network structure (Kjærulff & Madsen, 2008). The effective sources of NTS can be represented as $S_1(\text{Slab})$, $S_2(\text{Slab})$, $S_3(\text{Slab})$, $S_1(\text{Abattoir})$, and so on where Slab and Abattoir represent traditional and emerging supply chains, and subscripts 1, 2 and 3 refer to transfer from animal to carcass, environment to carcass, and environment to meat, respectively.

The prevalence representing the environment, for each branch of the supply, is constructed from a weighted combination of the prevalence associated with contact and noncontact sources. This evidence, combined with the prevalence dependency relationships included in the network model and with the uncertainty distributions assigned as prior belief for parameter values, contribute to a “quantitative picture” of the unobserved true prevalence of NTS in the beef supply for Moshi Municipal Council. The quantitative picture (a full joint probability) represents the whole domain as a single coherent mathematical object and, because of the consistency that is maintained by the links in the network, each piece of evidence affects all the unknown quantities to some extent. However, it is always possible to look at each unknown quantity individually by averaging

over all the others (called marginalization). The effective strengths for the three sources in the slaughter slab branch of the beef supply are $\rho_{MA_{CS}}P_F(\text{Origin})$, $\rho_{MA_{ES}}E(\text{Slab})$, and $\beta_S E(\text{Slab})$ with corresponding expressions for the abattoir branch. For example, the strength for transfer of contamination from animal sources to meat, $\rho_{MA_{CS}}P_F(\text{Origin})$, is constructed as the product of three probabilities that represent the prevalence of contamination in feces, the probability of transfer of fecal contamination to a carcass and the probability that meat is contaminated when it is obtained from a contaminated carcass.

The sensitivity of detection of NTS in cattle feces is uncertain but there is some evidence for pig feces. For naturally positive porcine samples, the observed prevalence decreases with sample volume so that inhomogeneous distribution of bacteria is considered a dominant factor for sensitivity of detection. The accumulated data for pigs (Funk et al., 2000), using 25 g fecal samples, indicate that 255 naturally positive samples provide 160 positive tests, that is, a sensitivity $\sim 63\%$. Assuming initial ignorance, an appropriate prior uncertainty distribution for the sensitivity would be $Se_F = \beta(161,96)$. We processed ~ 25 g samples and assume that sensitivity of pathogen detection does not differ between host species. For carcass swabs, informal elicitation of expert opinion (Experts from AgResearch, New Zealand, 2017) indicated that the most likely sensitivity is $\sim 40\%$ and that 95% confidence can be assigned to a sensitivity which exceeds 20%. This uncertainty can be represented by a beta distribution, $Se_C = \beta(5.03,7.04)$, consistent with some independent evidence that relates swabbing with an excision method for recovery of *Enterobacteriaceae* (Gallina et al., 2015). For meat, too, the detection sensitivity for NTS is uncertain and it reflects complex factors associated with the particular cut, and so on. A substantial quantity of classical microbiology, for example Holbrook et al. (1989), indicates typical sensitivity in the range 60–70% and a beta distribution, $Se_M = \beta(31,16)$, has been used to represent an appropriate uncertainty.

To estimate the strength of environmental contamination in the food chain, weighted sampling from a variety of locations is a practical scheme. Sites of environmental contamination can be partitioned as contact (knives, work surfaces, etc.) or non-contact (drains, boots, etc.) sources for carcasses or meat. An effective environmental prevalence can be constructed as a weighted combination of two corresponding uncertainty distributions for the prevalence in contact and noncontact environmental sites,

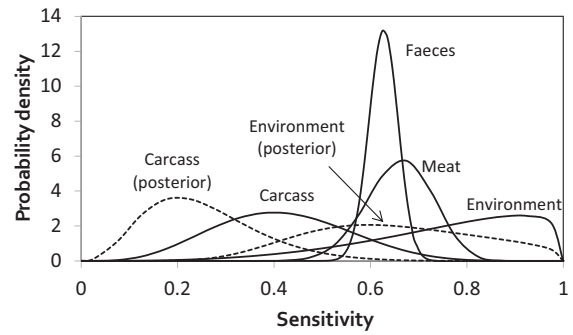


Fig 4. Distributions for the sensitivity of detection of nontyphoidal *Salmonella* from samples obtained from locations in the beef supply for Moshi Municipal Council, northern Tanzania. From left to right full lines (peaks) correspond with the prior distributions for sensitivity of detection in carcass samples, fecal samples, meat samples, and environmental samples. Broken lines are posterior distributions for sensitivity of detection of nontyphoidal *Salmonella* in carcass samples and environmental samples. For feces and meat, posterior probabilities are similar to prior probabilities and not shown separately.

respectively, whereby contamination from contact sources is given more weight than contamination from noncontact sources. Assuming the weight associated with noncontact sources has a modal value ~ 0.2 , and that there is a 90% chance that this weight does not exceed 0.4, an appropriate uncertainty distribution for the weight of noncontact environmental sources is $f_{EnonC} = \beta(3.3,10.1)$. For each branch of the model, we estimated the strength of the environmental source for contamination, $E(\text{Slab})$ and $E(\text{Abattoir})$, as the sum of two beta distributions weighted by f_{EnonC} and $1 - f_{EnonC}$. The two component beta distributions are obtained from the corresponding environmental sampling results (Table 1). It is impossible to quantify the sensitivity of environmental sampling at unstructured sampling sites. Although the efficiency of microbiological testing is relatively insensitive to the sample type, other underlying causes of detection sensitivity vary significantly. For example, knife blades can be swabbed in full whereas water from drains can only be subsampled. For that reason, a broad (relatively) uninformative prior distribution for the sensitivity of environmental sampling, $Se_E = \beta(4,1.3)$, was used. This distribution is consistent with uncertain sensitivity that has a modal value of 90% and 90% chance of exceeding 50%. Four prior distributions representing the uncertain sensitivity of tests used to quantify the domain model for the prevalence of NTS in the beef supply chain are illustrated in Fig. 4.

2.3.2. Parameter Sensitivity and Evidence Sensitivity

Analysis of complex probabilistic structures has many forms but can be achieved efficiently using network methods. Sensitivity analysis includes measuring the change in output values with respect to input parameters (parameter sensitivity), measuring the change in output values with respect to the particular details of the observations (evidence sensitivity), checking for consistency within the observed data (conflict analysis), and measuring the ability of new data to reduce uncertainties in outputs (value of information). These concepts, and their implementations are discussed in detail in chapters 9–11 of Kjærulff and Madsen (2008). Uncertainties relating to the science underpinning the model (sometimes referred to as deeper uncertainty) are additional to statistical uncertainties and can be considered by comparison with results from alternative model structures.

Analysis of sensitivity with respect to parameter values was determined using the sensitivity function, which links changes in the individual elements from any two conditional probability tables (Kjærulff & Madsen, 2008). For practical applications, the individual sensitivity elements can be combined to give sensitivities, $S(p_O, X)$, that express the rate of change of an output probability, p_O , with respect to variation of the location of a discretized uncertain model parameter X (Barker & Gomez-Tome, 2013). These sensitivity values are evaluated by including an additional Boolean variable in the network model to represent the output measure, for example, $P_M > 0.25$, and using standard network operations.

To determine evidence sensitivity of the model output, cost-of-omission analysis was used. Cost-of-omission for an output Y with respect to the j th item of evidence, e_j , is evaluated as

$$c(Y, e_j) = \sum_i p(y_i | \{e\}) \ln \left(\frac{p(y_i | \{e\})}{p(y_i | \{e\} \setminus e_j)} \right), \quad (5)$$

where the sum is over states, y_i , of the output distribution and $\{e\} \setminus e_j$ is the full set of evidence $\{e\}$ with item e_j omitted. Cost-of-omission is a special case of the Kullback-Liebler divergence (Kjærulff & Madsen, 2008). It is used to measure the difference between two probability distributions and has very small values when the impact of evidence is small but increases when output distributions with and without an item of evidence diverge.

2.3.3. Value of Information

Sampling processes can be extended in many ways, but this invariably incurs additional costs. Within a structured model it is practical to evaluate the potential impact of additional diagnostic findings using a value-of-information approach and, hence, direct the use of additional resources. For a variable Y , with probability $p(Y)$, in the probabilistic model of the beef supply it is practical to identify an information entropy as the expectation of $-\log(p(Y))$. Information entropy is widely used to quantify uncertainty in probabilistic scenarios. It represents the disorder associated with the distribution and quantifies the information deficit that exists in the presence of the current evidence. A decrease in entropy associated with the addition of new data quantifies the added value which would result from a corresponding data gathering process. This decrease can be evaluated systematically as a mutual entropy (Kjærulff & Madsen, 2008).

3. RESULTS

3.1. Visualization of the Beef Supply Chain

Collectively, the slaughter slabs processed about 30 animals per day (often as singletons, for many sites intermittently, and potentially by multiple users) and the abattoir processed another 30 animals. Most cattle for slaughter arrive via a small number of secondary (terminal) markets such as the livestock market at Weru Weru, in rural Moshi District, or Duka Bovu market 20 kilometer south of Arusha. Cattle belong predominantly to indigenous Zebu breeds and have traveled from northern Tanzania, sometimes over long distances. For example, the Manara Region is a dominant source of cattle, with distances to Moshi of several hundreds of kilometers (Allan, 2016). Survey data and interviews (Allan, 2016; Hrynick et al., 2019; Prinsen et al., 2020) indicated beef cattle slaughtered in MMC are on average six years old. The traders collect small numbers of animals, mostly adult males, from livestock keepers or primary markets and deliver them to a terminal market that was considered the “effective origin” for cattle entering the MMC beef supply. Group size is constrained by transport options and is typically 20–60 cattle. Given the widely dispersed origins, a single dominant breed and a relatively low stocking density (pastoral herds are grazed, and no feedlots or other confinement systems are used for the

majority of cattle in Tanzania (Wilson, 2015), it was practical to assume a single (homogeneous, steady state) population for cattle at terminal markets. Were Weru market took place twice a week, and slaughter occurred almost every day, so a proportion of cattle were held in lairage for several days, although buyer and butcher could be the same person so that time from purchase to retail was often less than 24 hours. Cooling of meat prior to retail was generally impractical, so butchers bought and held live animals to satisfy immediate demand and sold “warm meat” (Fig. 2). Meat from an individual slaughter event could be associated with multiple butchers or retailers and vendors who supplied customers directly. The dispersed nature of true origins and the large number of consumers, which is similar to the structure of the red meat supply chain in the Southern Highlands of Tanzania (Wilson, 2015), meant that a classic bow tie model (Wein & Liu, 2005) could be used to describe the structure of the beef supply chain, with the pinch point located at the terminal markets. For comparison of traditional and emerging supply systems, a forked path emanating from the market-based pinch point was deemed most suitable (Fig. 1).

3.2. Posterior Probability of Nontyphoidal Salmonella Prevalence

Nontyphoidal *Salmonella* was isolated from 36 of 467 or 7.7% of samples from the beef supply chain (Table 1). Based on the short time lag between market and slaughter, and the observed prevalence of NTS in feces at market and slaughter, fecal prevalence data were pooled. The model domain, which uses observational data to update prior beliefs, indicates a narrow posterior probability distribution for the estimated prevalence of NTS in cattle feces at the effective origin $P_F(\text{Origin}) = 0.04 \pm 0.02$. The corresponding posterior probability distribution is illustrated for the slaughter slab branch of the supply chain (Fig. 5). This figure also shows the posterior probabilities for the prevalence of NTS on cattle hides at slaughter, on post evisceration intact carcasses, for meat at retail in the slaughter slab branch of the beef supply chain, and for the effective strength of contamination in the process environment, which can be represented as a prevalence. The distributions representing the prevalence of NTS downstream from the effective origin of the beef chain are relatively wide, reflecting increased uncertainty. The prevalence of NTS on hides was used in model development but not augmented by data

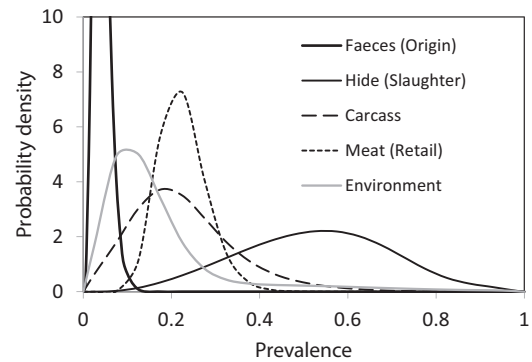


Fig 5. Posterior probability distributions for the prevalence of nontyphoidal *Salmonella* in the traditional or slaughter slab branch of the beef supply for Moshi Municipal Council. Depicted are distributions of prevalence in feces at effective origin (bold line, truncated for ease of visualization), hides at slaughter (full line), carcasses (broken line), meat for retail (dotted line), and processing environment (grey line). Distributions for the abattoir branch as shifted slight to the left, but not significantly different.

(hides were not sampled) and, therefore, includes substantial uncertainty. Distributions that represent the prevalence of NTS in the abattoir branch of the beef supply are shifted slightly to lower prevalence values but there is not a strong belief that one prevalence is larger than the other. For example, the posterior probability shows that a hypothesis expressed as “The prevalence of NTS in meat is higher for the slaughter slab branch of the supply” is false with probability ~ 0.25 .

The estimated true prevalence of NTS in fresh meat, weighted by volume in the two branches of the supply chain, is $P_M = 0.20 \pm 0.08$. The risk ratio for the two branches has a very broad distribution with expectation $\langle P_M(\text{Slab})/P_M(\text{Abattoir}) \rangle \sim 1.8$ and a 95% credible interval 0.3 to 4 (Appendix B, Fig. A1), where $P_M(\text{Slab})$ and $P_M(\text{Abattoir})$ are the estimated prevalence for NTS in meat in the two branches of the supply, respectively. Based on posterior probabilities there is not a strong belief that the risk ratio is bigger than unity. Counterintuitively, for both branches, the strength of the environmental contamination arising from noncontact sources is greater than that for contact sources. For contact sources the estimated “effective” prevalence, that is, the fraction of all contacts between carcasses or meat and the environment for which the environmental element making contact is contaminated with NTS (see Table 2, Fig. 3) are $E(\text{Slab}) \sim 0.13 \pm 0.07$ and $E(\text{Abattoir}) \sim 0.15 \pm 0.14$ while for noncontact

sources $E(\text{Slab}) \sim 0.67 \pm 0.19$ and $E(\text{Abattoir}) \sim 0.42 \pm 0.22$.

Assuming the effective sources of NTS introduction behave randomly and independently, the posterior probability for transfer of NTS from each source, given transfer from at least one source within that branch of the supply chain, can be considered as a quantitative food chain hazard assessment in which the origin of contamination of carcasses and meat can be evaluated. The transfer probabilities are $p(S_i(\text{Slab})/S(\text{Slab})) = 0.47, 0.16,$ and 0.43 for sources $i = 1, 3,$ and $p(S_j(\text{Abattoir})/S(\text{Abattoir})) = 0.51, 0.19$ and 0.36 for sources $j = 1, 3$ where $S(\text{Slab})$ and $S(\text{Abattoir})$ represent the presence of at least one source in a branch of the beef supply. In many situations a likelihood ratio is preferred to posterior probability for source level inference (Taroni et al., 2006). Likelihood ratios are ratios of conditional probabilities, which are used to assess the impact of evidence and quantify the probability of an outcome given a piece of evidence divided by the probability of the outcome without the evidence. In this case, the likelihood ratios for sources 1 through 3 in the slaughter slab branch of the beef supply are 7.5, 5.1, and 7, respectively, and those for the abattoir branch of the supply are 10.8, 7.0, and 8.5, respectively. Thus, source level inference points to animals entering the food chain and to the postslaughter environment for meat processing as the strongest sources for NTS in meat in both branches of the supply.

In addition to the marginal distributions for the true prevalence of NTS, the updated network model provides posterior probabilities for the values of uncertain model parameters. For example, in the updated model, the posterior distributions for the sensitivity for detecting NTS in feces and on meat, Se_F and Se_M , are very similar to the priors, but the posterior distributions for the sensitivity of detecting NTS on carcasses and in the environment, Se_C and Se_E , are both shifted to the left of their priors (Fig. 4). Evidence included in the network therefore indicates the detection methods are less sensitive than expected by prior belief.

3.3. Parameter Sensitivity

Sensitivity analysis was performed to assess the impact of uncertainty of model parameters on model outputs, such as the probability of a high prevalence (25% or higher) of NTS in meat. Fig. 6 (top) shows the model sensitivities, $S(p(P_M > 0.25 = \text{True}), X)$, with respect to several parameters, X , that quantify

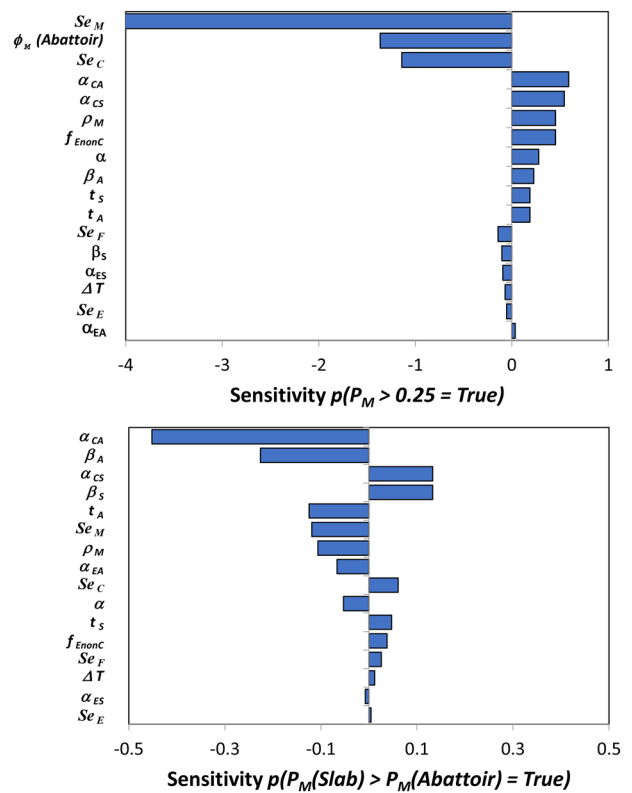


Fig 6. Sensitivity of selected model output measures with respect to parameter values. Results are shown for the probability that the prevalence of nontyphoidal *Salmonella* in meat is greater than 25%, or $p(P_M > 0.25 = \text{True})$, and for the probability that this prevalence is higher in the traditional slab-based system than in the modernized abattoir-based system, that is, $p(P_M(\text{Slab}) > P_M(\text{Abattoir}) = \text{True})$, with respect to parameter values in a network model of the beef supply in the Moshi Municipal Council of Tanzania. For detail on model parameters (α, β, ρ), see Table 2, $\phi_M(\text{abattoir})$ is the fraction of meat in the abattoir branch of the process chain.

the network model of the MMC beef supply chain. The posterior probability of a high NTS prevalence in meat is most sensitive to changes in the detection sensitivity for NTS in meat samples (Se_M). For a fixed number of positive observations, in this case meat samples testing positive for NTS, an increase in detection sensitivity corresponds with a decrease in the probability of a large prevalence in meat, hence the model sensitivity with respect to detection sensitivity is negative. The posterior probability for high NTS prevalence is also sensitive to the relative quantities (ϕ_M) of meat entering the supply from the two branches of the slaughter pathway, to the sensitivity of detection of NTS from carcass swabs (Se_C), and to coefficients that quantify transfer of

contamination from the animal to the carcass at slaughter (α_{CA} , α_{CS}).

Similar parameter sensitivity analysis for the probability that NTS prevalence is higher for meat processed via slaughter slabs than for meat coming through the abattoir, indicated by the output probability $p(P_M(\text{Slab}) > P_M(\text{Abattoir}) = \text{True})$, shows that variations of transfer coefficients, notably those that quantify the contamination of a carcass by the animal feces or hides (α_{CA} , α_{CS}) and the contamination of meat from the process environment (β_A , β_S), have most impact on differences in prevalence between the two slaughter pathways (Fig. 6, bottom). In this case, the output probability represents a difference, which makes the efficiencies of the microbiological detection relatively unimportant because they affect both branches of the supply equally. Fig. 6 also shows that both output measures are relatively insensitive to the parameter (α) that describes changes in prevalence of NTS on hides during the transition from the effective origin to slaughter and to the sensitivity of detection of NTS in feces or the environment (Se_F , Se_E).

3.4. Evidence Sensitivity

The data collection process, which uses many distinct observations collected under different conditions and at different times is fundamentally stochastic and there could be many alternative but equally valid data sets that quantify the model. The probability for observing the complete data set in Table 1 is approximately 8.4×10^{-12} , which is larger than the product of the probabilities for observing each piece of evidence separately. This comparison indicates that each piece of the observed data makes the probability of observing the supporting data more likely. Thus, there is an absence of conflict in the data that has been used to quantify the model of NTS in the beef supply. In addition, it is possible to conclude that statistical fluctuations within the data do not disrupt the coherent picture of the model quantification.

The impact of a particular piece of evidence can be estimated by omission (comparing outputs constructed with and without the evidence). For both output measures, $P_M > 0.25$ and $P_M(\text{Slab}) > P_M(\text{Abattoir})$, the cost-of-omission for 10 pieces of evidence is shown in Fig. 7. Positive test results for NTS in meat samples, particularly following slaughter at a slab (19 of 116 samples positive), have a dominant impact on the posterior probability of the two output variables. The inset in Fig. 7 shows the

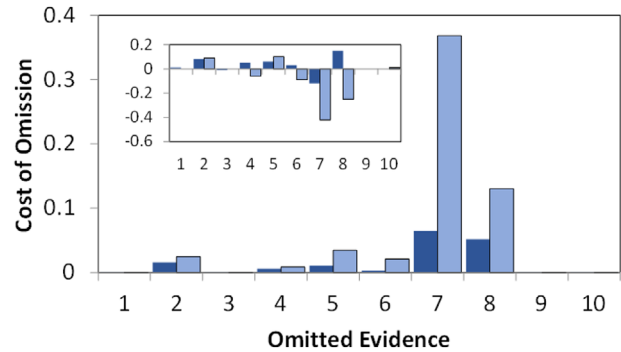


Fig 7. Cost of omission for two output measures in a network model of the beef supply for Moshi Municipal Council, Tanzania. Results are shown for high prevalence of nontyphoidal *Salmonella* in meat ($P_M > 0.25$) (dark bars) and the probability that NTS is more common in traditional than emerging supply chains ($P_M(\text{Slab}) > P_M(\text{Abattoir})$) (light bars), for ten items of evidence (1 = Noncontact environment samples at slaughter slabs, 2 = Contact environment samples at slaughter slabs, 3 = Noncontact environment samples at the abattoir, 4 = Contact environment samples at the abattoir, 5 = Carcass swab samples at slaughter slabs, 6 = Carcass swab samples at the abattoir, 7 = Meat samples following slab slaughter, 8 = Meat samples following abattoir slaughter, 9 = Fecal samples at slaughter, 10 = Fecal samples at origin). The inset shows the corresponding increment in posterior probability for the “True” state of each output variable after omission of evidence.

change of the posterior probabilities following omission of evidence and indicates that $p(P_M(\text{Slab}) > P_M(\text{Abattoir}) = \text{True})$ decreases by 0.41 (from 0.75 to 0.34) if evidence from meat, following slaughter at slab sites, is omitted. It also shows that omission of evidence from meat samples, following slaughter at the abattoir (2 of 24 samples positive), increases the probability $p(P_M > 0.25 = \text{True})$ by 0.15 (from 0.22 to 0.37). Evidence from fecal samples or the non-contact environment at slab and abattoir sites has very little impact on the selected posterior probabilities of the two chosen output variables. Dependencies in the model (illustrated in Fig. 3) ensure that the omission of this evidence leads to increased probabilities for high prevalence of NTS on carcasses and in the environment for the abattoir branch of the beef supply chain and hence (counterintuitively) to an increased probability for higher prevalence in meat (even though the omission includes some positive results from meat samples). Thus, the connected network of prevalence extends the interpretation of the evidence beyond consideration of isolated observations.

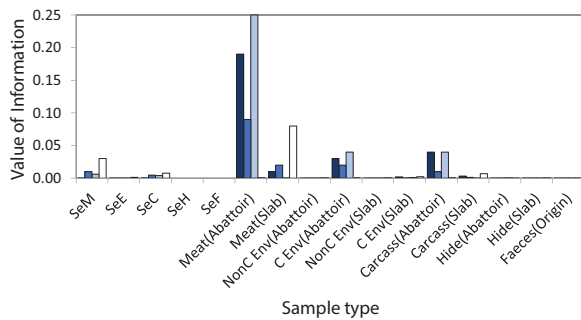


Fig 8. Value of Information (mutual entropy) of additional evidence in a model of the beef supply chain in Moshi Municipal Council, northern Tanzania. Results are shown for estimation of the risk ratio $P_M(\text{Slab})/P_M(\text{Abattoir})$ (dark blue) and the prevalence of nontyphoidal *Salmonella* in all meat (blue), in meat from the abattoir (light blue) and in meat from slaughter slabs (white). In each case evidence corresponds to (uncertain) results for detection of nontyphoidal *Salmonella* in 25 independent samples. The value of information is calculated for five detection sensitivities (Se; for meat (M), the environment (E), carcasses (C), hides (H), and feces (F)), and 11 sampling sites, that is meat, contact (C Env) and noncontact environments (NonC Env), carcasses and hides in the slab and abattoir branches of the beef supply, and feces at the effective origin.

3.5. Value of Information

The value of information or reduction in entropy associated with 16 possible additional information sources is illustrated for the distributions of four model variables in Fig. 8. Five of the sources of additional information correspond with laboratory exercises to measure detection sensitivities, five sources correspond with sample types in the traditional supply chain, five sources correspond with the same sample types in the emerging supply chain, and the final source represents feces from animals at effective origin. In this analysis, the potential examination of animal hides assumes that the sensitivity for detection of NTS is similar to that for carcasses. The value of information is calculated using four model variables as examples: the risk ratio $P_M(\text{Slab})/P_M(\text{Abattoir})$ and the prevalence of NTS in meat for each branch of the beef supply, and for the total supply. Each potential source of additional information corresponds with a hypothetical set of 25 new samples, although any practical number would be suitable. Additional testing of meat from the abattoir branch adds most value for reduced uncertainty in $P_M(\text{Slab})/P_M(\text{Abattoir})$, and the prevalence of NTS in the abattoir branch or overall beef supply, but not for the prevalence of NTS in the slaughter slab branch. The entropy reduction, arising from 25 additional meat samples, is $\sim 10\text{--}20\%$

of the information entropy for those output variables. For the abattoir branch, additional tests from carcass samples and from the contact environment provide added value but tests on feces, hides and investigations of detection sensitivities are unlikely to have a significant impact on the amount of disorder within the model. By contrast, for the slaughter slab branch, only additional meat samples add value to the current modeling.

3.6. Model Uncertainty

To highlight the importance of the assumptions and possible biases included in the causal model explored here, four alternative models were considered. The features of alternative models are (1) no transmission of NTS from animal hides; (2) aggregation of environmental sources of NTS; (3) no distinction between slaughter slabs and the abattoir with respect to transmission of NTS (a single branch); and (4) no sequential steps in the transmission of NTS in the beef supply (a simple linear superposition of measured prevalence for feces, carcasses, and environments). Although the altered models involve different parameterizations, and some pooling of the data, none indicate data conflict and all result in posterior distributions for the prevalence of NTS in meat, with $0.17 \leq \langle P_M \rangle \leq 0.22$, very similar to the distribution for the proposed causal model. Altered models other than that with a single branch indicate that the slaughter slab branch makes the dominant contribution to the prevalence of NTS in meat with $1.8 \leq \langle P_M(\text{Slab})/P_M(\text{Abattoir}) \rangle \leq 2.9$. Two altered models, one that excludes animal hides as source, and one that aggregates contact and noncontact environmental sources, lead to results for source level inference that deviate from those for the causal model; both extend the posterior probability for the two sources that correspond with transfer of NTS from the environment to carcasses or to meat at the expense of the probability of contamination originating with animals that enter the food supply ($p(S_i(\text{Slab})|S(\text{Slab})) = 0.07, 0.24, \text{ and } 0.74$ for sources $i = 1, 3$, and $p(S_j(\text{Abattoir})|S(\text{Abattoir})) = 0.10, 0.31, \text{ and } 0.63$ for sources $j = 1, 3$ for an altered model that omits transfer of NTS via animal hides). The model that does not include a distinction between slaughter slabs and the abattoir indicates source level inferences that are very similar to those for the slaughter slab branch of the original model. Although we cannot be completely confident about the possibility of unspecified or surprising events, the altered models

provide strong indications that the properties of our mathematical model representing the prevalence of NTS in the beef supply for Moshi Municipal Council is dominated by the data supply, and that assumptions and biases associated with the modeling process itself do not constrain the application of the model results.

4. DISCUSSION

This project was part of a program on Zoonoses and Emerging Livestock Systems (ZELS), which was premised on the expectation that emergence of new, generally more intensive, livestock systems might contribute to increased risk of zoonoses and foodborne diseases. In our modeling of the beef supply chain in northern Tanzania, which covered cattle markets, slaughter, and meat retail, no such evidence was found for NTS when using slaughter slabs to represent the traditional beef supply and the local abattoir as exemplar for the emerging beef supply. In other production systems, intensification is not necessarily associated with increased risk either, as heightened biosecurity and hygiene measures may mitigate the risk of contamination with foodborne pathogens (O'Brien, 2013; Pollari et al., 2017; Sears et al., 2011).

A key finding from our model was that the environment is an important but hitherto underappreciated source of NTS. The relationship between the prevalence of NTS in cattle feces and noncontact or contact-environments is complex, as all elements are interconnected, but analysis of model uncertainty showed that aggregation of environmental sources of NTS did not result in data conflict or major changes in estimated prevalence of NTS in meat. Both noncontact and contact environments can be considered proximate sources of NTS, whereby the ultimate sources may include cattle feces as well as feces from other host species, including wild rodents, domestic and wild birds, dogs, and humans (Chlebicz & Slizewska, 2018; Crump et al., 2020). Persistence of foodborne pathogens, including NTS, in processing environments may be facilitated by the formation of biofilm, a process that is encouraged by presence of meat juice (Lamas et al., 2018). In addition, fresh meat itself provides a good environment for growth of NTS due to its high nutrient and water content (Chlebicz & Slizewska, 2018). During our site visits, we often observed fragments of meat on environmental contact surfaces such as wooden chopping blocks, which may allow for amplification of NTS in the processing environment.

The distinction between parameter sensitivity, evidence sensitivity, and model uncertainty described in our study allows for explicit exploration of the impact of uncertain parameter estimates, significance of available data, and model assumptions on model output. For example, although the median sensitivity of detection of NTS on carcasses and in the environment was lower than previously thought (Fig. 5), and posterior probability distributions for prevalence on carcasses and in the environment were wide (Fig. 4), the cost of omission of carcass data or environmental data was low compared to the cost of omission of data from meat samples (Fig. 7). Value of information analysis identified additional sampling of the abattoir branch of the beef supply, particularly retail meat, as a strategic focus for resources to confirm a real difference between traditional and emerging supply chains and showed that investments in improved test sensitivity for meat samples would be better value than similar efforts for carcass swabs (Fig. 8), even though the sensitivity of detection in meat is already much higher than for carcasses. The ability to quantify the value of information and hence to prioritize future investment in research is a major benefit of our modeling approach, especially for countries where resources are limited.

The model also provides a framework for informing food chain interventions to reduce the risk to consumers, and for assessing effectiveness of interventions. Considering the low fecal prevalence of NTS in cattle, commensurate with the best values observed elsewhere in Africa (Thomas et al., 2020), preharvest interventions are unlikely to improve food safety significantly. By contrast, postharvest prevalence of NTS is relatively high, certainly in comparison with retail beef products outside Africa (Khen et al., 2014; Thung et al., 2017), so a precautionary approach suggests that strategies for maintaining consumer awareness of the importance of cooking and the risk of cross contamination are appropriate. While awareness of foodborne disease appears high among cooked meat vendors in the study area (Prinsen et al., 2020), we did not address consumer knowledge or household practices. In addition, sensitivity analysis highlighted that transfer coefficients have a strong influence on the model results. Transfer is affected by clean water supply, hygiene protocols, and food safety awareness and could be used to frame productive dialogue and underpin policy development. Current food safety policy implementation in Tanzania is primarily concerned with pathogens that cause visible lesions in

animal organs or tissue, and actors in the beef supply have limited awareness of the presence, transmission routes, or control of foodborne pathogens like NTS that may be carried asymptotically by livestock (Waldman et al., 2020).

Another important feature of the probabilistic graphical model used here is that it enabled us to integrate quantitative and qualitative information generated by the natural and social sciences arms of our project (Crump et al., 2020; Hrynich et al., 2019; Prinsen et al., 2020; Waldman et al., 2020) in a single coherent framework. Limitations to our study include the focus on a single animal species without consideration of other important sources of red meat such as sheep or goats, or other likely sources of NTS such as poultry, and the focus on a relatively small geographic area and a single abattoir, which is partly inherent in the in-depth nature of the stakeholder interviews and microbiological analysis. Videography could be used to gain deeper understanding of routes and risks of transmission of NTS during and after slaughter (Julian & Pickering, 2015), while genomic data from spatially matched animal, food, and human isolates could provide insight into sources of NTS in the environment, and the contribution of NTS from the beef supply to public health problems in Tanzania (Crump et al., 2020). The high prevalence of NTS in noncontact environment samples raises concern about the destination of effluent from slaughter slabs and abattoirs. Wastewater in Tanzania is a known source of NTS and can cause contamination of food handlers, farmed fish, and irrigated crops (Mhongo et al., 2017). From conversations and observations during the study, it was clear that such nutrient rich effluent is often harvested and used to fertilize crops, creating the risk of onward transmission via produce, which may absorb NTS through their root system (Esteban-Cuesta et al., 2018; Jechalke et al., 2019).

In conclusion, NTS is a major cause of blood stream infection and diarrheal disease in East Africa, and there was concern that intensification of the beef supply chain in Tanzania might increase human exposure to NTS from food. Using a probabilistic model to integrate prior beliefs, interview data, and microbiological evidence, we found no indication that intensification of the beef supply in northern Tanzania, as explored through comparison of traditional small-scale slaughter slabs and a more modern, larger-scale facility, would contribute to emergence of NTS as a foodborne pathogen. The model shows that the environment, and the likelihood of transfer from the environment to the animals' carcass or meat, play an

important role in the estimated NTS prevalence in meat, regardless of the processing pathway, and implies that closer attention needs to be paid to environmental hygiene throughout the beef supply chain. Moreover, it illustrates the value of this approach as a tool to integrate data across data types and provides an interdisciplinary framework for prioritization of investment in disease control, food hygiene and further research.

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REFERENCES

- Allan, K. J. (2016). Leptospirosis in northern Tanzania: exploring the role of rodents and ruminant livestock in a neglected public health problem. (PhD dissertation). University of Glasgow, Glasgow, UK. <http://theses.gla.ac.uk/id/eprint/7565>
- Anonymous. (2017). *Workshop summary One Health zoonotic disease prioritization for multisectoral engagement in Tanzania*. Dar es Salaam, Tanzania: Center for Disease Control and Prevention. <https://fundacionio.com/wp-content/uploads/2019/04/tanzania-report-508.pdf>
- Arthur, T. M., Keen, J. E., Bosilevac, J. M., Brichta-Harhay, D. M., Kalchayanand, N., Shackelford, S. D. ... Koohmaraie, M. (2009). Longitudinal study of *Escherichia coli* O157:H7 in a beef cattle feedlot and role of high-level shedders in hide contamination. *Applied and Environmental Microbiology*, 75(20), 6515–6523. <https://doi.org/10.1128/AEM.00081-09>
- Barker, G. C., & Gomez-Tome, N. (2013). A risk assessment model for enterotoxigenic *Staphylococcus aureus* in pasteurized milk: a potential route to source-level inference. *Risk Analysis*, 33(2), 249–269. <https://doi.org/10.1111/j.1539-6924.2011.01667.x>
- Biggs, H. M., Lester, R., Nadjm, B., Mtove, G., Todd, J. E., Kinabo, G. D. ... Crump, J. A. (2014). Invasive *Salmonella* infections in areas of high and low malaria transmission intensity in Tanzania. *Clinical Infectious Diseases*, 58(5), 638–647. <https://doi.org/10.1093/cid/cit798>
- Chaters, G. L., Johnson, P. C. D., Cleaveland, S., Crispell, J., de Glanville, W. A., Doherty, T. ... Kao, R. R. (2019). Analysing livestock network data for infectious disease control: an argument for routine data collection in emerging economies. *Philosophical Transactions of the Royal Society B*, 374(1776), 20180264. <https://doi.org/10.1098/rstb.2018.0264>

- Chlebicz, A., & Slizewska, K. (2018). Campylobacteriosis, salmonellosis, yersiniosis, and listeriosis as zoonotic foodborne diseases: A review. *International Journal of Environmental Research and Public Health*, 15(5). <https://doi.org/10.3390/ijerph15050863>
- Crump, J. A., Thomas, K. M., Benschop, J., Knox, M. A., Wilkinson, D. A., Midwinter, A. C. ... Zadoks, R. N. (2020). Investigating the meat pathway as a source of human nontyphoidal *Salmonella* bloodstream infections and diarrhea in East Africa. *Clinical Infectious Diseases* <https://doi.org/10.1093/cid/ciaa1153>
- Esteban-Cuesta, I., Drees, N., Ulrich, S., Stauch, P., Sperner, B., Schwaiger, K. ... Gottschalk, C. (2018). Endogenous microbial contamination of melons (*Cucumis melo*) from international trade: an underestimated risk for the consumer? *Journal of the Science of Food and Agriculture*, 98(13), 5074–5081. <https://doi.org/10.1002/jsfa.9045>
- Funk, J. A., Davies, P. R., & Nichols, M. A. (2000). The effect of fecal sample weight on detection of *Salmonella enterica* in swine feces. *Journal of Veterinary Diagnostic Investigation*, 12(5), 412–418. <https://doi.org/10.1177/104063870001200504>
- Gallina, S., Bianchi, D. M., Ru, G., Maurella, C., Barzanti, P., Baioni, E. ... Decastelli, L. (2015). Microbiological recovery from bovine, swine, equine, and ovine carcasses: Comparison of excision, sponge and swab sampling methods. *Food Control*, 50, 919–924. <https://doi.org/10.1016/j.foodcont.2014.10.052>
- Grace, D., Mutua, F., Ochungo, P., Kruska, R., Jones, K., Brierley, L. ... Ogutu, F. (2012). *Mapping of poverty and likely zoonoses hotspots. Zoonoses Project 4*. Report to Department for International Development, UK.
- Havelaar, A. H., Kirk, M. D., Torgerson, P. R., Gibb, H. J., Hald, T., Lake, R. J. ... Devleeschauwer, B. (2015). World Health Organization global estimates and regional comparisons of the burden of foodborne disease in 2010. *PLoS Medicine*, 12(12), e1001923. <https://doi.org/10.1371/journal.pmed.1001923>
- Holbrook, R., Anderson, J. M., Baird-Parker, A. C., Dodds, L. M., Sawhney, D., Stuchbury, S. H., & Swaine, D. (1989). Rapid detection of *Salmonella* in foods—A convenient two-day procedure. *Letters in Applied Microbiology*, 8(4), 139–142. <https://doi.org/10.1111/j.1472-765X.1989.tb00259.x>
- Hrynicky, T. A., Barasa, V., Benschop, J., Cleaveland, S., Crump, J. A., Davis, M. ... Waldman, L. (2019). Street-level diplomacy and local enforcement for meat safety in northern Tanzania: knowledge, pragmatism and trust. *BMC Public Health*, 19(1), 863. <https://doi.org/10.1186/s12889-019-7067-8>
- Jacob, M. E., Renter, D. G., & Nagaraja, T. G. (2010). Animal- and truckload-level associations between *Escherichia coli* O157:H7 in feces and on hides at harvest and contamination of preeviceration beef carcasses. *Journal of Food Protection*, 73(6), 1030–1037. <https://doi.org/10.4315/0362-028x-73.6.1030>
- Jechalke, S., Schierstaedt, J., Becker, M., Flemer, B., Grosch, R., Smalla, K., & Schikora, A. (2019). *Salmonella* establishment in agricultural soil and colonization of crop plants depend on soil type and plant species. *Frontiers in Microbiology*, 10, 967. <https://doi.org/10.3389/fmicb.2019.00967>
- Jones, B. A., Grace, D., Kock, R., Alonso, S., Rushton, J., Said, M. Y. ... Pfeiffer, D. U. (2013). Zoonosis emergence linked to agricultural intensification and environmental change. *Proceedings of the National Academy of Sciences of the United States of America*, 110(21), 8399–8404. <https://doi.org/10.1073/pnas.1208059110>
- Julian, T. R., & Pickering, A. J. (2015). A pilot study on integrating videography and environmental microbial sampling to model fecal bacterial exposures in peri-urban Tanzania. *PLoS One*, 10(8), e0136158. <https://doi.org/10.1371/journal.pone.0136158>
- Khen, B. K., Lynch, O. A., Carroll, J., McDowell, D. A., & Duffy, G. (2014). Prevalence and characteristics of *Salmonella* in the beef chain in the Republic of Ireland. *Zoonoses and Public Health*, 61(8), 534–536. <https://doi.org/10.1111/zph.12099>
- Kjærulff, U. B., & Madsen, A. L. (2008). *Bayesian networks and influence diagrams: A guide to construction and analysis* (1 ed.). New York: Springer-Verlag.
- Lamas, A., Regal, P., Vazquez, B., Miranda, J. M., Cepeda, A., & Franco, C. M. (2018). *Salmonella* and *Campylobacter* biofilm formation: A comparative assessment from farm to fork. *Journal of the Science of Food and Agriculture*, 98(11), 4014–4032. <https://doi.org/10.1002/jsfa.8945>
- Madoroba, E., Kapeta, D., & Gelaw, A. K. (2016). *Salmonella* contamination, serovars and antimicrobial resistance profiles of cattle slaughtered in South Africa. *The Onderstepoort Journal of Veterinary Research*, 83(1), a1109. <https://doi.org/10.4102/ojvr.v83i1.1109>
- Mhongole, O. J., Mdegela, R. H., Kusiluka, L. J., Forslund, A., & Dalsgaard, A. (2017). Characterization of *Salmonella* spp. from wastewater used for food production in Morogoro, Tanzania. *World Journal of Microbiology and Biotechnology*, 33(3), 42. <https://doi.org/10.1007/s11274-017-2209-6>
- Ministry of Livestock and Fisheries Development. (2015). *Tanzania livestock modernization initiative*. Dar es Salaam, Tanzania: Ministry of Livestock and Fisheries. <https://hdl.handle.net/10568/67749>
- Mugarula, F. (2016, April 27). Many abattoirs are dirty, says CAG. *The Citizen*. <https://www.thecitizen.co.tz/tanzania/news/many-abattoirs-are-dirty-says-cag-2553870>
- Narvaez-Bravo, C., Rodas-Gonzalez, A., Fuenmayor, Y., Flores-Rondon, C., Carruyo, G., Moreno, M. ... Hoet, A. E. (2013). *Salmonella* on feces, hides and carcasses in beef slaughter facilities in Venezuela. *International Journal of Food Microbiology*, 166(2), 226–230. <https://doi.org/10.1016/j.ijfoodmicro.2013.07.009>
- O'Brien, S. J. (2013). The “decline and fall” of nontyphoidal *Salmonella* in the United Kingdom. *Clinical Infectious Diseases*, 56(5), 705–710. <https://doi.org/10.1093/cid/cis967>
- Pin, C., Avendano-Perez, G., Cosciani-Cunico, E., Gomez, N., Gounadac, A., Nychas, G. J. ... Barker, G. (2011). Modelling *Salmonella* concentration throughout the pork supply chain by considering growth and survival in fluctuating conditions of temperature, pH and a(w). *International Journal for Food Microbiology*, 145(Suppl 1), S96–102. <https://doi.org/10.1016/j.ijfoodmicro.2010.09.025>
- Pollari, F., Christidis, T., Pintar, K. D. M., Nesbitt, A., Farber, J., Lavoie, M. C. ... Johnson, R. P. (2017). Evidence for the benefits of food chain interventions on *E. coli* O157:H7/NM prevalence in retail ground beef and human disease incidence: A success story. *Canadian Journal of Public Health*, 108(1), e71–e78. <https://doi.org/10.17269/CJPH.108.5655>
- Prinsen, G., Benschop, J., Cleaveland, S., Crump, J. A., French, N. P., Hrynicky, T. A. ... Waldman, L. (2020). Meat safety in Tanzania's value chain: Experiences, explanations and expectations in butcheries and eateries. *International Journal of Environmental Research and Public Health*, 17(8). <https://doi.org/10.3390/ijerph17082833>
- Rahkio, T. M., & Korkeala, H. J. (1997). Airborne bacteria and carcass contamination in slaughterhouses. *Journal of Food Protection*, 60(1), 38–42. <https://doi.org/10.4315/0362-028x-60.1.38>
- Sears, A., Baker, M. G., Wilson, N., Marshall, J., Muellner, P., Campbell, D. M. ... French, N. P. (2011). Marked campylobacteriosis decline after interventions aimed at poultry, New Zealand. *Emerging Infectious Diseases*, 17(6), 1007–1015. <https://doi.org/10.3201/eid1706.101272>
- Sindiyo, E., Maganga, R., Thomas, K. M., Benschop, J., Swai, E. S., Shirima, G., & Zadoks, R. (2018). Food safety, health management, and biosecurity characteristics of poultry farms in Arusha City, northern Tanzania, along a gradient of intensification. *East African Health Research Journal*, 2(2), 168–180.
- Taroni, F., Aitkin, C., Garbolino, P., Biedermann, A. (2006). *Bayesian networks and probabilistic inference in forensic science*. Chichester, UK: Wiley.

- Thomas, K. M., de Glanville, W. A., Barker, G. C., Benschop, J., Buza, J. J., Cleaveland, S. ... Crump, J. A. (2020). Prevalence of *Campylobacter* and *Salmonella* in African food animals and meat: A systematic review and meta-analysis. *International Journal of Food Microbiology*, 315, 108382. <https://doi.org/10.1016/j.ijfoodmicro.2019.108382>
- Thung, T. Y., Radu, S., Mahyudin, N. A., Rukayadi, Y., Zakaria, Z., Mazlan, N. ... Wan Mohamed Radzi, C. W. J. (2017). Prevalence, virulence genes and antimicrobial resistance profiles of *Salmonella* serovars from retail beef in Selangor, Malaysia. *Frontiers in Microbiology*, 8, 2697. <https://doi.org/10.3389/fmicb.2017.02697>
- van der Fels-Klerx, H. J., Tromp, S., Rijgersberg, H., & van Asselt, E. D. (2008). Application of a transmission model to estimate performance objectives for *Salmonella* in the broiler supply chain. *International Journal of Food Microbiology*, 128(1), 22–27. <https://doi.org/10.1016/j.ijfoodmicro.2008.06.034>
- Vose, D. (2000). *Risk analysis; A quantitative guide*. Chichester, England: John Wiley & Sons.
- Waldman, L., Hrynick, T. A., Benschop, J., Cleaveland, S., Crump, J. A., Davis, M. A. ... Zadoks, R. N. (2020). Meat safety in northern Tanzania: Inspectors' and slaughter workers' risk perceptions and management. *Frontiers in Veterinary Science*, 7, 309. <https://doi.org/10.3389/fvets.2020.00309>
- Wein, L. M., & Liu, Y. (2005). Analyzing a bioterror attack on the food supply: the case of botulinum toxin in milk. *Proceedings of the National Academy of Sciences of the United States of America*, 102(28), 9984–9989. <https://doi.org/10.1073/pnas.0408526102>
- Wilson, R. T. (2015). *The red meat value chain in Tanzania; A report from the Southern Highlands Food Systems Programme*. www.fao.org/fileadmin/user_upload/ivc/PDF/SFVC/Tanzania_Red_Meat.pdf
- World Bank Group. (2019). *Tanzania overview*. <https://www.worldbank.org/en/country/tanzania/overview>
- Woudenberg, S. P. D., & van der Gaag, L. C. (2011). Using the noisy-OR model can be harmful ... but it often is not. In *Proceedings of the 11th European Conference on Symbolic and Quantitative Approaches to Reasoning with Uncertainty*, Belfast, UK (pp. 122–133).
- Xiao, Y., Bowers, R. G., Clancy, D., & French, N. P. (2005). Understanding the dynamics of *Salmonella* infections in dairy herds: A modelling approach. *Journal of Theoretical Biology*, 233(2), 159–175. <https://doi.org/10.1016/j.jtbi.2004.09.015>

APPENDIX A

Portable Bayesian network file

HAZEL_MU_Net_Supp.net is a flat file (ascii), in portable network file format, that describes the dependency and conditional probability tables for a discrete Bayesian Network of sources and prevalence of nontyphoidal *Salmonella* along the beef supply chain in Moshi Municipal Council, Tanzania. The encoded network has 60 nodes, 77 edges and total table size 803051. Reconstruction of the Bayesian Network from this net file was verified, by gcb, using HUGIN Researcher v8.4 (other application tools may also generate the operational Bayesian Network).

APPENDIX B

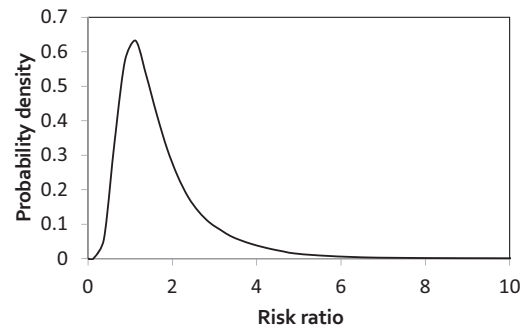


Fig A1. Posterior probability density distribution for the risk ratio of the prevalence of nontyphoidal *Salmonella* in meat processed through slaughter slabs relative to meat processed through the abattoir in the beef supply chain of Moshi Municipal Council, northern Tanzania. The 95% credible interval for the risk ratio is 0.3–4.