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Game theory of vaccination and depopulation for managing livestock diseases and zoonoses on small-scale farms

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A B S T R A C T

Livestock producers adapt their farm management to epidemiological risks in different ways, through veterinary interventions but also by modulating their farm size and the removal rate of animals. The objective of this theoretical study was to elucidate how these behavioral adaptations may affect the epidemiology of highly-pathogenic avian influenza in domestic poultry and the outcome of the implemented control policies. We studied a symmetric population game where the players are broiler poultry farmers at risk of infection and where the between-farms disease transmission is both environmental and mediated by poultry trade. Three types of farmer behaviors were modelled: vaccination, depopulation, and cessation of poultry farming. We found that the transmission level of the disease through trade networks has strong qualitative effects on the system's epidemiological-economic equilibria. In the case of low trade-based transmission, when the monetary cost of infection is high, depopulation behavior can maintain a stable disease-free equilibrium. In addition, vaccination behavior can lead to eradication by private incentives alone – an outcome not seen for human diseases. In a scenario of high trade-based transmission, depopulation behavior has perverse epidemiological effects as it accelerates the spread of disease via poultry trade. In this situation, state interventions should focus on making vaccination technologies available at a low price rather than penalizing infected farms.

1. Introduction

Behavioral epidemiology – the study of human behavioral responses to infectious disease circulation – has been receiving an increasing amount of research attention over the last two decades (Funk et al., 2010). The behavioral responses of humans to disease can generate externalities resulting in both positive and negative feedback in the infection process, justifying the application of different economic theories in the decentralized control of infectious disease. Theoretical advances in this field have mostly focused on the adoption of voluntary vaccination programs. The broad consensus is that, because of the effect of herd immunity, a free market for vaccines is not able to maintain a disease-free state in any population as long as vaccination has a positive cost (i.e. either a production cost or a perceived health risk like during times of vaccine scares) (Geoffard and Philipson, 1997; Bauch and Earn, 2004). Logically the same result holds in livestock systems where farmers usually incur a positive cost for vaccinating their animals (Rat-Aspert and Fourichon, 2010). However, private interventions are not limited to vaccination, and the game-theoretical literature has demonstrated a variety of possible strategic interactions among actors depending on the considered behavioral variables and epidemiological contexts (Hennessy, 2007). For example, players' interventions aimed at preventing their own infection or the infection of their animals (through biosecurity, vaccination, prophylactic treatments, or social distancing) are strategic substitutes (i.e. a player's incentive decreases when other players increasingly adopt the same behavior) and, therefore, their adoption by players is self-defeating (Reluga, 2010; Sykes and Rychtár, 2015). On the other hand, actions aimed at preventing the entry of a pathogen into a disease-free region (through biocontainment, testing of newly introduced animals, or trade restrictions) or at eradicating a disease at regional or international level may be strategic complements (a player's incentive increases when other players increasingly adopt the same behavior) and, therefore, their adoption is self-reinforcing (Hennessy, 2008; Murray, 2014). In this case farmers can reach a Pareto optimal strategy through coordination. These strategic properties have important implications for policymakers in choosing the appropriate state intervention to enhance livestock owners' welfare and protecting public health (Barrett, 2004).

Aside from applying veterinary interventions, farmers may modulate their herd demographic and production structure in response to

Abbreviations: FOI, force of infection; HPAI, highly pathogenic avian influenza

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health risks. These adaptations are especially significant in small- and medium-scale livestock systems of developing countries where farmers have limited access to veterinary technologies and are less likely to make long term biosecurity investments due to a limited access to capital (Hennessy, 2007). A small number of studies have addressed this question. Focusing on a smallholder farm system with a single decision maker, Boni et al. (2013) described how farmers may expend or contract their poultry population size to manage an endemic disease. Horan et al. demonstrated that, in a system of two populations of farmers facing different incentives for breeding and feeding cattle, the spread of livestock diseases may, counterintuitively, incentivize a higher trade activity (Horan et al., 2015), and Tago et al. pointed out the risk of increased cattle sales in anticipation of cattle movement restrictions implemented in response to a disease outbreak (Tago et al., 2016). However, none of these studies considered the possibility that farmers may apply different sell rates to healthy and sick animals (or batches of animals). Meanwhile, a growing number of empirical surveys, conducted in developing countries, report that poultry farmers sell or slaughter their sick birds at a higher rate than their healthy birds, and that epidemics of severe poultry diseases cause higher-than-normal levels of poultry sales (Zhang and Pan, 2008; Padmawati and Nichter, 2008; Phan et al., 2009; Sultana et al., 2012; Paul et al., 2013; Delabouglise et al., 2016).

Highly pathogenic avian influenza (HPAI) is one example of a zoonotic poultry disease motivating substantial governmental intervention. HPAI outbreaks have occurred regularly in eastern and southern Asia, Egypt, and West Africa since 2003 (Gilbert et al., 2008; FAO, 2010, 2014). HPAI has also been reported in Europe and North America (FAO, 2014). Some avian influenza virus strains of the H5, H7, and H9 subtypes have the ability to cause severe and fatal disease in humans. Therefore, poultry originating from farms contaminated with HPAI are potentially harmful to farmers, consumers, and other persons handling poultry. While human infections with these subtypes are rare, their case fatality rates are generally higher than 25% (WHO, 2014). In addition, the risk that such viruses acquire a phenotype of human-to-human transmission constitutes a major global health threat and justifies national-level interventions to reduce the exposure of humans to infected poultry (Imai et al., 2012). The epidemiology of the disease in endemic countries is complex, mediated both by direct infectious contact between poultry farms and by the trade of birds carrying the virus (Desvaux et al., 2011). Since the emergence and global spread of the H5N1 subtype of HPAI in 2003, interventions have mainly focused on strengthening avian disease surveillance, preventive culling of domestic birds in outbreak areas, and restrictions on poultry trade; in addition, Vietnam and China implemented mandatory poultry vaccination programs against H5N1 (Sims, 2007; FAO, 2011; Peyre et al., 2009).

In a theoretical model investigating individual responses of poultry farmers to different policies, the main finding for density-dependent transmission was that preventive culling of and compensation for poultry can have perverse effects as it may incentivize an increase in farm size (higher average poultry price incentivizes more production), while investments in surveillance, diagnostics, and penalties targeted at infected farms were found to lower overall health risk (for both frequency- and density-dependent transmission) (Boni et al., 2013). These findings are in agreement with other economic models describing issues associated with the indemnification of farms affected by diseases (Hennessy, 2007; Gramig and Horan, 2011). According to another economic model, compensation accompanying preventive culling policies should be indexed to the prevention effort invested by farmers against HPAI (Beach et al., 2007). However, no clear comparisons between outcomes of targeted penalties and vaccination subsidies were ever made.

The present study has two purposes. First it aims to describe the strategic interactions between poultry farmers adapting their farm management (sales, restocking, turnover, vaccination) to the infection status of their farm and the population as a whole. The second purpose is to identify how these strategic interactions affect the outcome of different HPAI control policies (e.g. penalizing infected farms, subsidizing vaccination). For this purpose we introduce a symmetric population game, with broiler poultry farmers as players, and we link this to a compartmental model of between-flock disease transmission. Although we use the current knowledge of the economy of small scale poultry farming systems of southeast Asia and the epidemiology of HPAI to build our model, our objective here is not to formulate specific policy recommendations tailored to each country where HPAI is endemic. Rather, we aim at demonstrating how farmers' behavioral adaptations may affect the outcome of HPAI control policies and how, as a result, the policy recommendations could be best adapted to different epidemiological and economic contexts of poultry farming.

2. Model

2.1. Description of the system

Our system consists of an large and homogeneous population of poultry farmers who practice broiler production for earning an income. We specifically use the small-scale broiler farming systems of Vietnam as an example, although the results are generalizable to similar systems found in other countries where HPAI is endemic. Small-scale poultry farms are considered to play a significant role in perpetuating HPAI circulation while being the most severely impacted by the disease (ACI, 2006). Farm sizes vary from 50 to 2000 birds. The main bird species raised in these systems are chickens and ducks. The chicken breeds are usually a mix of exotic and local breeds with relatively long growing periods (2.5–4.5 months) and a strong appeal to Vietnamese consumers, while the duck breeds are mainly exotic ones (Desvaux et al., 2008). Broiler farmers purchase groups of chicks of equal age (hereafter referred to as "flocks") and sell them as finished birds, primarily to itinerant poultry traders, after keeping them during a given production period. Poultry traders sell the purchased poultry, mainly on live bird markets, to consumers, retailers, or secondary traders and the birds are slaughtered either by consumers at home or by intermediary actors. Chicks are mainly supplied by large breeding farms, state-owned farms, livestock companies, or hatcheries. The revenue from broiler production is derived from the sale of finished broilers whose price is determined by their weight at sale (a minor revenue can be obtained from the sale of manure and feathers but it is neglected here). The cost of poultry farming is mainly composed of poultry feed production and purchase ($>70\%$ of the production cost) while expenses for animal health are usually very low ($<4\%$ of the production cost) (Phan, 2013).

We assume that flocks are kept in individual coops on farms. Each coop can contain one flock and is owned by a single farmer. Broiler flocks occupying coops are initially disease-free and can be infected in the course of the growing period if the virus is introduced in the flock. The disease transmission between coops is modeled but the disease transmission within coops is not; flocks are simply assumed to be infected or uninfected. Coops lose their infected status at the time of depopulation, when infected flocks are sold to the traders and replaced by susceptible flocks. Poultry flocks are always sold but the revenue generated by a flock depends on both its growing period (which determines poultry weight) and its infection status. If traders notice the infection in poultry flocks at the time of sale, they apply a penalty on the sale price. This penalty results from the anticipated reluctance of consumers to buy infected poultry and from the risk of birds being seized during sanitary inspections. Note that governmental actions such as disease surveillance increase the price penalty (i.e. lower the sale price of infected flocks), as surveillance for HPAI can be used by traders as an argument for further decreasing the sale price. This penalty can also be viewed as the cost incurred if a fraction of the birds die from the disease, whether these dead birds are sold at a very low price or simply disposed of. Government-initiated flock depopulation (i.e. culling via burying or burning) is not considered as an option here. It is assumed poultry can be sold at any age, sparing the farmer the cost of culling and disposing of birds. Birds which are either dead, too young or too sick to be used for human consumption can still be sold as food for pythons, crocodiles, or fish. However the commercial value of birds strongly depends on their body weight, and the value of the very young ones is considered to be close to zero. Farmers can vaccinate their poultry flocks at an additional cost per coop in order to prevent infection. Coops with vaccinated flocks are considered to be fully protected. In a disease-free environment, farmers apply a constant optimal growing period $\sigma_\varnothing^{-1}$, and $\sigma_\varnothing$ is the rate of poultry removal (sale) from farms (see Supplementary Information 1).

2.2. Farm economic model

Farmers are assumed to make rational decisions, to be aware of the infection status of their poultry flocks and have rational expectations on their income. Every farmer adapt a set of three farm variables p, v, and d, all comprised between 0 and 1, to maximize his income. A farmer will keep a coop populated with poultry with probability p. For a populated coop, a farmer will vaccinate his flock with probability v. For an unvaccinated flock, a farmer will depopulate the flock with probability d in the event that the flock becomes infected. For a depopulation event, we say that the sell rate is σ_D with $\sigma_D > \sigma_\varnothing$. The rate σ_D is chosen by the farmer to be as high as possible since farmers either sell infected flocks immediately or at a standard sell rate $\sigma_\varnothing$; any intermediate sell rate is suboptimal (see Supplementary Information 1). Later we will consider two cases: $\frac{\sigma_\varnothing}{\sigma_D} = 0$ (infinitely high sell rate), which allows mathematical tractability, and $\frac{\sigma_\varnothing}{\sigma_D} = \frac{1}{20}$, for which numeric solutions will be derived for comparison. Arguably, we could have used the rate of introduction of new flocks in the farm as a behavioral variable. However, as we assume that farms are at a steady state equilibrium, this rate of introduction is fully dependent on p and d.

The income of a given farmer per time period $\sigma_\varnothing^{-1}$ is defined as:

$$U(p, v, d) = p(vU_V + (1-v)(dU_D + (1-d)U_\varnothing) - c(\bar{p})) + (1-p)U_E \tag{1}$$

$U_\varnothing$, U_D and U_V are the revenue per populated coop over a time period $\sigma_\varnothing^{-1}$ where, respectively, status quo ($\varnothing$), vaccination (V) and fast depopulation of infected flocks (D) are applied. U_E is the income earned from an alternative activity (an income-generating activity farmers can practice instead of poultry farming), which is considered constant. $c(\bar{p})$ is the production cost incurred by the farmer per coop populated with poultry per time period $\sigma_\varnothing^{-1}$, which is an increasing function of $\bar{p}$, the average of p in the population of farmers. Costs mainly include poultry feed whose price tend to increase with the total size of the poultry population as an increasing amount of the agricultural resources are consumed by farms. For the sake of simplicity, we assume a strict proportionality between $c(\bar{p})$ and $\bar{p}$:

$$c(\bar{p}) = \epsilon\bar{p} \tag{2}$$

with $\epsilon > 0$ a given constant. Using λ as the per-production cycle force of infection (FOI), the revenues $U_\varnothing$, U_D and U_V associated with status quo ($\varnothing$), vaccination (V) and fast depopulation of infected flocks (D) are:

$$\begin{aligned} U_\varnothing &= \frac{1}{\lambda+1}(1-\gamma)c_P + \frac{\lambda}{\lambda+1}(1-\theta-\gamma)c_P \\ U_D &= \frac{\sigma_D/\sigma_\varnothing}{(\sigma_D/\sigma_\varnothing)+\lambda}(1-\gamma)c_P + \frac{\lambda}{(\sigma_D/\sigma_\varnothing)+\lambda}\frac{\sigma_D}{\sigma_\varnothing}\left(f\left(\frac{\sigma_D}{\sigma_\varnothing}\right)(1-\theta)-\gamma\right)c_P \\ U_V &= (1-\gamma-c_V)c_P \end{aligned} \tag{3}$$

The parameter $c_P > 0$ is the price of a fully-grown flock which is considered constant (we normalize so that $c_P = 1$); $c_V > 0$ is the cost of vaccination, and $\gamma > 0$ is the cost of introducing a new flock in a coop. $\lambda \geq 0$ is the FOI in the population of coops, i.e. the rate of introductions of the virus in the coop per production period $\sigma_\varnothing^{-1}$. The function f links the sell rate to the expected weight at sale. A bird sold after a full production period $\sigma_\varnothing^{-1}$ has weight one, and as the sell rate approaches infinity (immediate sale) we consider the bird to have weight zero as it is too small to be sold for any revenue. The function is detailed in Supplementary Information 1. The parameter $\theta \geq 0$ is the price penalty, the proportion decrease in the sale price of infected flocks.

Letting $c_P = 1$, and assuming that infected flocks are sold without delay ($(\sigma_\varnothing/\sigma_D) = 0$), the expressions (3) simplify to

$$\begin{aligned} U_\varnothing &= 1-\gamma-\theta\left(\frac{\lambda(\bar{p},\bar{v},\bar{d})}{1+\lambda(\bar{p},\bar{v},\bar{d})}\right) \\ U_D &= 1-\gamma(1+\lambda(\bar{p},\bar{v},\bar{d})) \\ U_V &= 1-\gamma-c_V \end{aligned} \tag{4}$$

We have made explicit in the above equations that the FOI λ depends on the population averages of the behavioral variables $(\bar{p}, \bar{v}, \bar{d})$. See Fig. 1 for a diagram of the farmer's decision tree and payoffs. Additionally we assume that $1-\gamma \geq \epsilon > 0$ and $U_E = 1-\gamma-\epsilon$ so that the total opportunity cost of poultry production is:

$$U_E + c(\bar{p}) = (1-\gamma-\epsilon) + \epsilon\bar{p} \tag{5}$$

2.3. Disease transmission in the population of coops

The dynamics of infection among coops are characterized by the following seven differential equations describing interactions among susceptible (X) and infectious (Y) coops. X_T and Y_T can be thought of as the number of susceptible and infected flocks, respectively, currently in the possession of a poultry trader. The equations below are scaled so that one unit of time equals $\sigma_\varnothing^{-1}$

$$\begin{aligned} \dot{X}_\phi &= Y_\phi - \beta^E X_\phi\left(Y_\phi + Y_D\right) - \beta^T\frac{\sigma_T}{\sigma_\phi}\frac{X_\phi}{\bar{p}}Y_T \\ \dot{Y}_\phi &= \beta^E X_\phi\left(Y_\phi + Y_D\right) + \beta^T\frac{\sigma_T}{\sigma_\phi}\frac{X_\phi}{\bar{p}}Y_T - Y_\phi \\ \dot{X}_D &= \frac{\sigma_D}{\sigma_\phi}Y_D - \beta^E X_D\left(Y_\phi + Y_D\right) - \beta^T\frac{\sigma_T}{\sigma_\phi}\frac{X_D}{\bar{p}}Y_T \\ \dot{Y}_D &= \beta^E X_D\left(Y_\phi + Y_D\right) + \beta^T\frac{\sigma_T}{\sigma_\phi}\frac{X_D}{\bar{p}}Y_T - \frac{\sigma_D}{\sigma_\phi}Y_D \\ \dot{X}_V &= 0 \\ \dot{X}_T &= X_D + X_\phi + X_V - \frac{\sigma_T}{\sigma_\phi}X_T \\ \dot{Y}_T &= \frac{\sigma_D}{\sigma_\phi}Y_D + Y_\phi - \frac{\sigma_T}{\sigma_\phi}Y_T \end{aligned} \tag{6}$$

where

$$\bar{p}\bar{v} = X_V, \quad \bar{p}(1-\bar{v})\bar{d} = X_D + Y_D, \quad \text{and} \quad \bar{p}(1-\bar{v})(1-\bar{d}) = X_\varnothing + Y_\varnothing$$

are the fractions of farmers exhibiting vaccination behavior, depopulation behavior, and null behavior, respectively. There is no change in the X_V class as we assume that the vaccine has high enough efficacy to prevent a coop-level infection.

Two types of disease transmission are considered (Fig. 2). Environmental transmission, or direct transmission from one coop to another, is proximity-based while trade-based transmission occurs through contacts between farms and trade networks in which infected poultry are transported, sold and/or slaughtered (Desvaux et al., 2011; Biswas et al., 2008, 2009; Kung et al., 2007; Fournie et al., 2011). Infected flocks are sold to traders at a rate $\sigma_\varnothing$ (from compartment $Y_\varnothing$) or σ_D (from compartment Y_D) and are kept for a time period σ_T^{-1} in a "trade compartment" before being slaughtered. This trade compartment refers either to the trader's storage place, a wholesale or retail marketplace

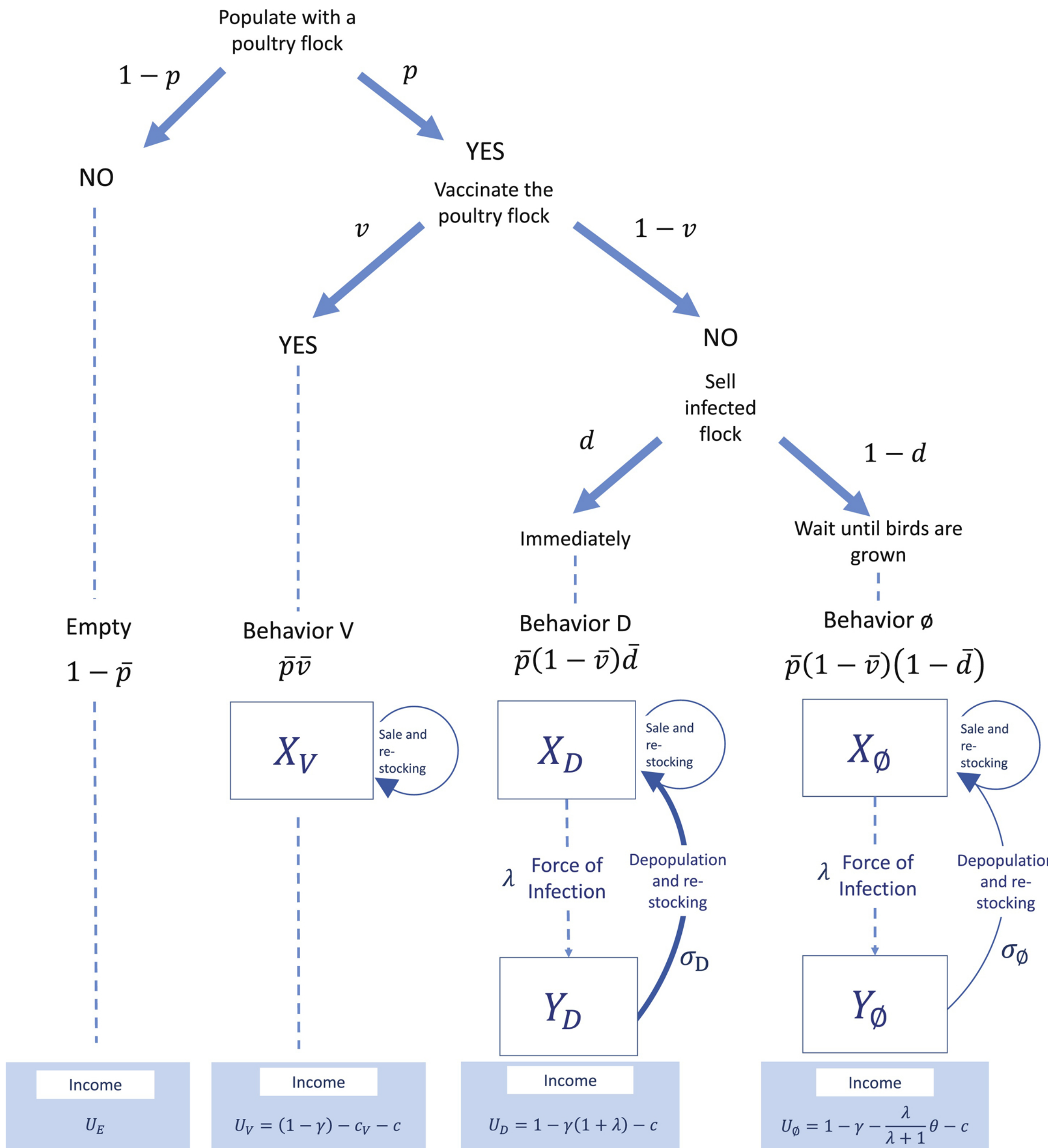

Fig. 1. Schematic representation of the farmer's decision process and associated incomes for the four management behaviors.

with live birds, or a slaughterhouse. Meanwhile, traders carrying the virus (on their vehicles, cages, clothes, or boots) may visit other farms and introduce the virus into susceptible coops. Alternatively poultry farmers may visit retail marketplaces and subsequently carry the virus to their farm. Note that we do not consider any disease transmission inside the trade compartment. The parameter β^E is the transmission coefficient for proximity-based infectious contacts between coops (scaled to the standard growing period $\sigma_\emptyset^{-1}$), while β^T is the transmission coefficient of contacts between infected flocks in the trade compartment and susceptible coops (scaled to the period σ_T^{-1} flocks are kept in the trade compartment).

Trade-based transmission is frequency-dependent as the number of contacts between populated coops and the trade compartment does not dependent on the number of populated coops: traders visit a fixed number of populated coops and farmers visit a fixed number of marketplaces per time unit irrespective of the poultry population size. As the number of populated coops increase or decrease, the number of traders varies accordingly as one trader can only carry a limited number of poultry per time unit. In this regard, the trade-based transmission can be compared to a vector-borne disease transmission process where traders are assimilated to biological vectors carrying the pathogen (Anderson and May, 1991; Keeling and Rohani, 2008).

On the other hand, environmental transmission is likely to be proximity-based: the disease is propagated to the neighboring coops through virus dissemination in flooded areas or scavenging areas shared by birds of different farms or, alternatively, when farmers visit their neighbors and carry the virus on their boots or clothes. Therefore, an infected coop has a higher probability of transmitting the disease if the number of populated coops in its neighborhood is increased. In the remainder of the manuscript this transmission pathway is therefore assumed to be density-dependent. In order to test the robustness of the results to this hypothesis, a separate analysis assuming frequency-dependent environmental transmission was conducted and its results are displayed in the Supplementary Information.

Note one unusual feature of the construction of these equations. A very high rate σ_D (fast exit from the Y_D class) translates to a large value of Y_T and rapid re-entry into the Y_D class. In other words, σ_D does not behave like a true recovery term; rather, it represents a transfer of the

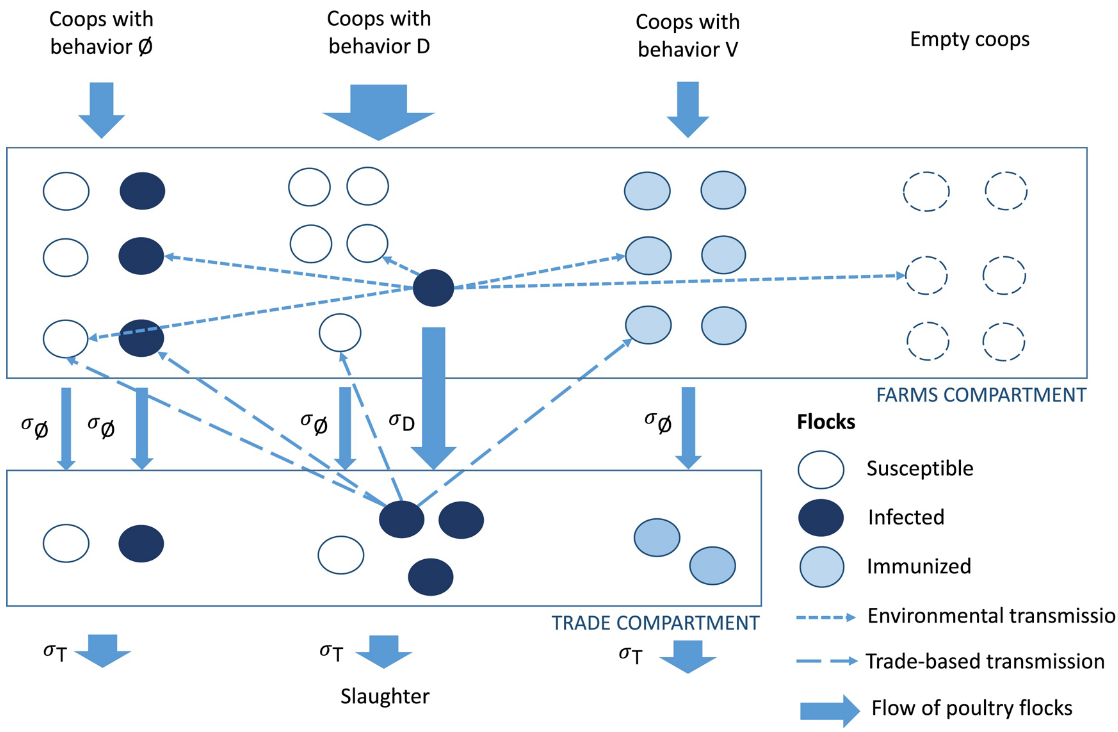

Fig. 2. Schematic representation of the flow of flocks and the between-coop disease transmission process. Coops managed with behavior *D* displace their infected flocks to the trade compartment at a higher rate than coops managed with behavior ∅ and, as a result, introduce new flocks at a higher rate.

Table 1
System variables.

Notation	Meaning
$\bar{p}$	Proportion of coops populated with poultry
$\bar{v}$	Proportion of populated coops where vaccination is applied (behavior *V*)
$\bar{d}$	Proportion of populated unvaccinated coops where depopulation is applied in case of infection (behavior *D*)
$U_\varnothing$	Income earned from a populated coop with behavior ∅
U_V	Income earned from a populated vaccinated coop (behavior *V*)
U_D	Income earned from a populated unvaccinated coop where depopulation is applied in case of infection (behavior *D*)
$\hat{\lambda}$	Equilibrium force of infection
$\bar{s}(\bar{p}, \bar{v}, \bar{d})$	Population-average strategy (or system state) composed of $\bar{p}$, $\bar{v}$ and $\bar{d}$

infection from the farmer's coop to the trader.

The dimensionality of the system can be reduced as susceptible plus infected coops will always add up to the number of farmers practicing a particular behavior. Note that the basic reproduction ratio of the disease, when $\bar{p} = 1$, $\bar{v} = 0$ and $\bar{d} = 0$, is $R_0 = \beta_E + \beta_T$. In general it is assumed to be higher than unity ($\beta_E + \beta_T > 1$).

The assumption $(\sigma_\varnothing/\sigma_D) = 0$ allows us to derive a simplified expression for the FOI at endemic equilibrium, denoted $\hat{\lambda}$, for any particular population behavioral profile described by $\bar{p}$, $\bar{v}$, and $\bar{d}$. If $(1-\bar{v})(\beta^E\bar{p}(1-\bar{d}) + \beta^T) < 1$, the basic reproduction rate in the system is less than one and $\hat{\lambda} = 0$. If $(1-\bar{v})(\beta^E\bar{p}(1-\bar{d}) + \beta^T) > 1$ and $\beta^T(1-\bar{v})\bar{d} < 1$, then we have

$$\hat{\lambda} = \frac{(1-\bar{v})(\beta^E\bar{p}(1-\bar{d}) + \beta^T - 1)}{1 - \beta^T(1-\bar{v})\bar{d}}$$

which is the equilibrium FOI when the combined reproduction number from trade and environmental transmission is larger than one. When both $(1-\bar{v})(\beta^E\bar{p}(1-\bar{d}) + \beta^T) > 1$ and $\beta^T(1-\bar{v})\bar{d} > 1$, the reproduction number approaches infinity and all coops are infected (see details in Supplementary Information 2). If the between-coop environmental disease transmission is assumed to be frequency-dependent rather than density-dependent then the FOI is not affected by $\bar{p}$ but the dynamics of the FOI with respect to the two other behavioral variables ($\bar{v}$ and $\bar{d}$) remains unchanged (see details in Supplementary Information 3).

2.4. Game theory equilibria

Players (farmers) are assumed to optimize a strategy $s = (p, v, d)$ comprising three behavioral variables, whose utilities are dependent on the population variable $\hat{\lambda}(\bar{p}, \bar{v}, \bar{d})$ which, in turn, is determined by the population-average strategy $\bar{s} = (\bar{p}, \bar{v}, \bar{d})$ (Table 1). Players are assumed to change their strategy at defined time steps separated by a sufficiently long period to allow an epidemiological equilibrium to be reached and maintained (i.e. we ignore the effects of transient epidemiological dynamics on farmers' choices). Farmers adapt their strategy by comparing the income earned from behaviors ∅, *V* and *D*, which can be done by observation of other farms and information exchange among farmers; this does not necessarily require a precise knowledge of the FOI. Since farmers' income expectations are assumed to be rational, the general principles for Nash equilibria in symmetric population games are applicable to our system. More specifically, we refer to Thomas's criteria (Thomas, 1984) to identify evolutionary stable population strategies: a given set of behavioral variables $s^* = (p^*, v^*, d^*)$ is a local evolutionary stable strategy if and only if for every small neighborhood $N(s^*)$ of s^*, we have

$$\forall\, r \in N(s^*),\quad U(r|\bar{s} = s^*) \leq \quad U(s^*|\bar{s} = s^*) \tag{7}$$

$$\forall\, r \in N(s^*),\quad U(r|\bar{s} = r) < \quad U(s^*|\bar{s} = r) \tag{8}$$

Condition (7) is the definition of a Nash equilibrium while (8) is the condition of stability, wherein an evolutionary stable strategy cannot be invaded by a different strategy applied by a sufficiently small minority of players.

The endemic equilibrium $\hat{\lambda}$ is associated with different payoffs for each of the four options of keeping an empty coop, vaccinating, depopulating, and null behavior (i.e. keeping unvaccinated flocks and raising them to full growth irrespective of infection status) (Table 1). As the four options can be described by three degrees of freedom, we will use the notation (p, v, d). We denote the Nash-equilibrium FOI as $\hat{\lambda}^*$. In general, the asterisk will be used to refer to a stable Nash equilibrium.

According to the principles of dynamic game theory, the stability of a mixed strategy s^* is dependent on the linear stability of the following system of differential equations:

$$\dot{\bar{p}}(\bar{s}) = \bar{p}(1 - \bar{p})(\bar{v}U_V + (1 - \bar{v})(\bar{d}U_D(\bar{s}) + (1 - \bar{d})U_\varnothing(\bar{s})) - c(\bar{p}) - U_E) \quad (9)$$

$$\dot{\bar{v}}(\bar{s}) = \bar{v}(1 - \bar{v})(U_V - (\bar{d}U_D(\bar{s}) + (1 - \bar{d})U_\varnothing(\bar{s}))) \quad (10)$$

$$\dot{\bar{d}}(\bar{s}) = \bar{d}(1 - \bar{d})(U_D(\bar{s}) - U_\varnothing(\bar{s})) \quad (11)$$

Eqs. (9)–(11) are the replicator equations of the game for poultry farming, vaccination and depopulation behavior respectively (Taylor and Jonker, 1978; Cressman and Tao, 2014). They show that poultry farming (i.e. keeping coops populated with poultry), behaviors V (vaccination) and D (depopulation) are increasingly adopted (i.e. implemented with a higher probability) as long as they are expected to return a higher income than their competing choice.

Note that in a disease-free environment and without vaccination the revenue per populated coop is equal to $1 - \gamma$ and the farmers are expected to keep $\bar{p}$ at one (all coops are populated with poultry). Indeed when $\bar{p} = 1$ then $1 - \gamma - c(1) = U_E$ (the income from poultry farming equals the income from its alternative) while if $\bar{p} < 1$ then $1 - \gamma - c > U_E$ which incentivizes the population of additional coops with poultry. Conversely, if the revenue per populated coop drops to zero, $\bar{p}$ is expected to drop to zero (all farmers invest in the alternative activity and keep their coops empty). It is assumed here that ϵ is close enough to $1 - \gamma$ so that some coops are kept populated even when the average revenue per populated coop is very low.

2.5. Parameters used in the analysis

Parameters used for the analysis are displayed in Table 2. They are mostly derived from the literature on small-scale poultry production in Vietnam (ACI, 2006; Burgos et al., 2008; Desvaux et al., 2008; Phan et al., 2009, 2013a; Fournie et al., 2012; Delabouglise et al., 2016, 2019).

Some critical parameters cannot be easily quantified. The penalty parameter θ may vary considerably. It will depend on the level of disease transmission and disease severity in the flock, which in turn depends on the viral strain, poultry species, and concomitant infections with other pathogens. The size of the penalty also depends on decisions by traders on the reduction of the price paid for infected flocks, which may vary from 17% to 67% of the flock value (Delabouglise et al., 2016). The disease is considered to be most severe in chickens, especially in densely populated coops (with some reported mortality rates higher than 50%) and may be comparatively mild in ducks and other waterfowl species, in which some HPAI strains are low pathogenic (Hulse-Post et al., 2005; OIE, 2009). The cost of vaccination is also variable. While a vaccine dose itself has low cost (0.05–0.1 USD/dose), the technical training, labor, and storage facility required to implement vaccination against avian influenza may represent a high investment for small-scale farmers. Additionally, vaccination used in isolation provides little protection because the circulating avian influenza strains are genetically diverse and high exposure of poultry to other pathogens undermines their immune response to the vaccine. It is usually believed that effective vaccine protection can be obtained only if combined with the implementation of a good farm hygiene, regular disinfection, and biosecurity practices (Peyre et al., 2009; McLeod et al., 2007). In regard to this constraint, we considered a broad range of values for the vaccination cost c_V (0–25% of the flock commercial value).

To the best of our knowledge the transmission parameters β_E and β_T were never quantified. We considered arbitrarily that the basic disease reproduction ratio (with $\bar{p} = 1$, $\bar{v} = 0$ and $\bar{d} = 0$), is $R_0 = \beta_E + \beta_T = 2.5$, i.e. an infected coop in a population of fully

Table 2
Parameters used in the model.

Notation	Meaning	Values	Explanation	Reference
c_P	Commercial value of a healthy fully grown flock	2-4 USD/kg	The farm-gate sale price of a fully grown chicken (per kg live weight) on the Vietnamese market. It mainly depends on the breed (local or mixed local-exotic)	Phan (2013)
γ	Cost of introducing a new flock in a coop	10% of c_P	Purchase cost of new chicks from breeding farms or hatcheries	Phan (2013)
ϵ	Slope of the marginal cost function of farming a poultry flock over a production period $\sigma_\varnothing^{-1}$	70% of c_P	It is equal to the cost of farming a poultry flock when $\bar{p} = 1$. It is essentially composed of feed ($> 70\%$)	Phan (2013)
U_E	Highest income earned from an alternative activity over a production period $\sigma_\varnothing^{-1}$ if the coop is not populated with poultry	20% of c_P	It is equal to the difference between the revenue and the cost of a poultry flock when $\bar{p} = 1$ and the disease is absent $U_E = 1 - \gamma - \epsilon$	Phan (2013)
c_V	Cost of keeping a flock fully protected against the disease infection over a production period $\sigma_\varnothing^{-1}$	0–25% of c_P	Full protection can be obtained through combining vaccination, regular disinfection and enhanced farm biosecurity	Peyre et al. (2009), McLeod et al. (2007) and Phan et al. (2009)
θ	Penalty on the commercial value of infected flocks	0–100% of c_P	Highly variable. Depends on the transmission and severity of the disease in the flock and the enforced policies which may further reduce the commercial value of the infected flock (surveillance, sanitary controls)	ACI (2006), Otte (2008) and Delabouglise et al. (2016)2222
$\sigma_\varnothing$	Standard rate of removal of poultry flocks from farms. Applied to all susceptible and vaccinated flocks and infected flocks with behavior $\varnothing$	1/100 day^{-1}	Production period of broiler chickens of small-scale farms range from 2.5 to 4.5 months depending on the breed	Desvaux et al. (2008), Phan (2013) and Delabouglise et al. (2019)
σ_D	Accelerated rate of removal of infected flocks from farms with behavior D	1/5-1 day^{-1}	Time taken to arrange the early sale or slaughter of an infected flock can be as long as 5 days	Delabouglise et al. (2016)
σ_T	Rate of removal of poultry from the trade compartment	1/5-1 day^{-1}	Time between the sale of the poultry by farmers and their slaughter and consumption is variable but relatively short	Fournie et al. (2012)
β_E	Proximity-based infectious contact rates between infected flocks kept in farms and other coops	Unknown	This parameter is highly dependent on the context:presence of flooded areas, type of housing of poultry, frequency of entrance of visitors inside the farms	
β_T	Trade-based infectious contact rates between infected flocks kept by traders and populated coops	Unknown	This parameter is highly dependent on the context: frequency of contacts between farmers and traders, condition of transport, and storage of sold birds	

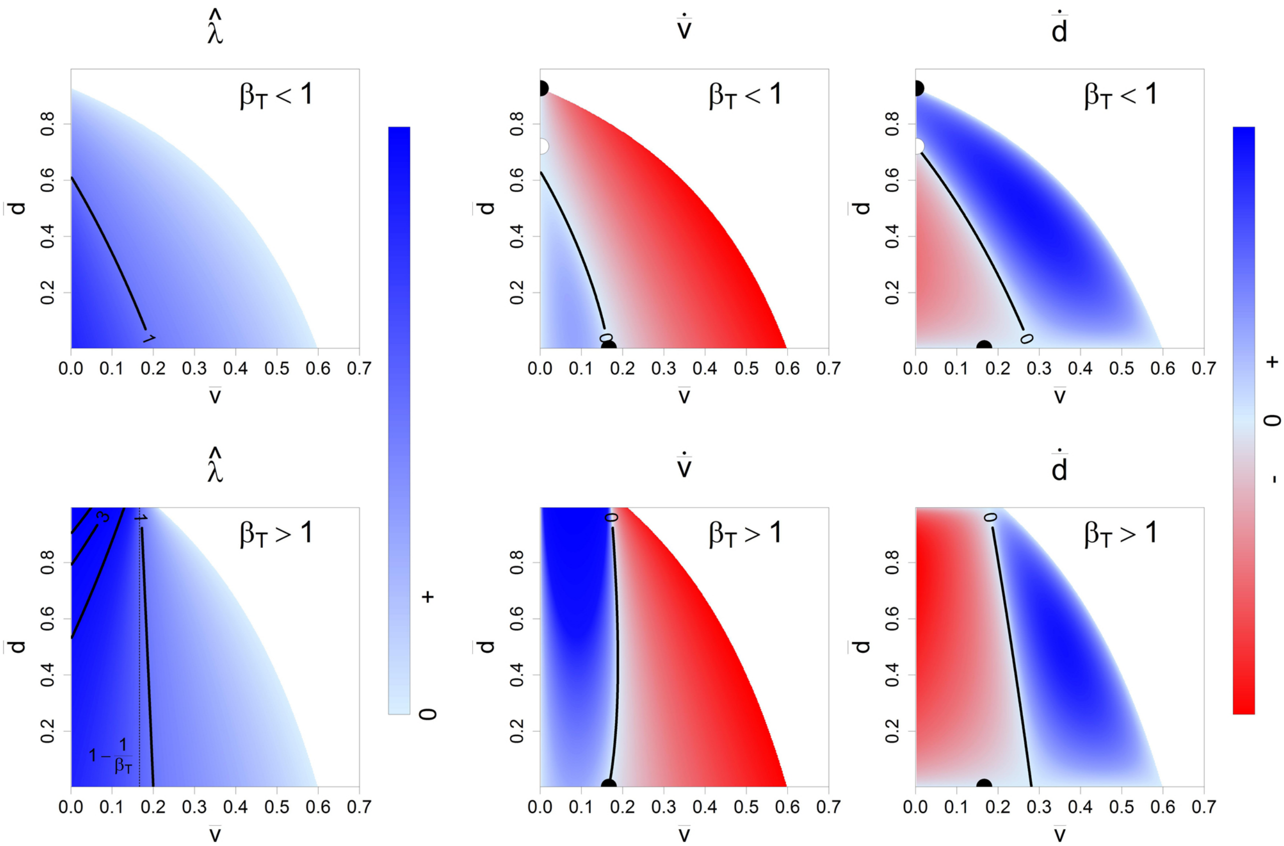

Fig. 3. Effect of farmers' behavior on the force of infection and feedback effect on the behavioral dynamics. Color bars correspond to the quantity shown above each panel. Left, middle and right panels show changes in the FOI, $\dot{\bar{v}}$, and $\dot{\bar{d}}$ in the two-dimensional space ($\bar{v}$, $\bar{d}$). White areas indicate a disease-free state. Top: $\beta^T = 0.8$. Bottom: $\beta^T = 1.2$. Other parameters are: $\beta^E = 2.5 - \beta^T$, $\frac{\sigma_\varnothing}{\sigma_D} = \frac{1}{20}$, $\theta = 0.25$, $\gamma = 0.1$, $c_V = 0.13$, $\bar{p} = 1$. The effects of varying the $\bar{p}$ variable are displayed in Supplementary Information 4. In the left panels, contours correspond to values 1, 2, 3 and 4 of the FOI. In the middle and right panels, contours correspond to $\dot{\bar{v}} = 0$ and $\dot{\bar{d}} = 0$ respectively. Black circles and white circles are, respectively, stable and unstable Nash equilibria (assuming $\bar{p}$ is constant). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

susceptible non vaccinated coops may infect 2.5 other coops. The main purpose of the analysis is to analyse the effect of the respective contribution of environmental and trade-based transmission (β_E and β_T) on the game theoretical equilibrium.

3. Results

3.1. Strategic interactions

Farmers' individual poultry management choices have clear effects on the system's epidemiology. In general, because of density dependence built into the model, an increase in vaccination uptake ($\bar{v}$) or a decrease in the number of populated coops (i.e. poultry population size) ($\bar{p}$) leads to a lower FOI. The effects of wider adoption of depopulation behavior ($\bar{d}$) are not as easily predicted, as they depend on β^T and $\bar{v}$. The reason is that populated coops managed with behavior D are not likely to contaminate other coops through environmental transmission because their infectious period is short; however, these coops relay all of their incoming infections into the trader network, and therefore sell a higher absolute number of infected flocks than coops managed with behavior $\varnothing$. As a result, as $\bar{d}$ increases, susceptible coops are less likely to be contaminated through environmental transmission from neighboring farms and are more likely to be contaminated through contacts with poultry traders. The effect of $\bar{d}$ on $\hat{\lambda}$ can be positive or negative depending on the values of β^T and $\bar{v}$, as illustrated in Fig. 3. If $\beta^T > 1/(1 - \bar{v})$, the FOI $\hat{\lambda}$ is positively associated with $\bar{d}$, as the level of trade-based transmission in this scenario is high enough that we observe more depopulation leading to more infection in the trading network and thus a higher force of infection. In other words, in systems where pathogen circulation can be maintained through trade, adoption of behaviour D generates negative externalities as the FOI increases via the trade of infected birds. If $\beta^T < 1/(1 - \bar{v})$, the FOI $\hat{\lambda}$ is negatively associated with $\bar{d}$ as the intrinsic level of trade-based transmission is not high enough to maintain an endemic level of infection in the current vaccination environment; in this case, adopting depopulation behavior has a larger effect on lowering environmental transmission and a smaller effect on increasing trade-based transmission (see Supplementary Information 4).

The effect of the epidemiological environment on farmer choice can be described similarly. As a general rule, a high FOI tends to favor vaccination and emptying coops, while a low FOI favors depopulation. At high FOI, depopulation behavior is very costly as farmers would have to repeatedly depopulate and reintroduce healthy flocks to maintain their farm size; in other words, it is worth foregoing the revenue of infected flocks and replacing them early with susceptible flocks only if subsequent new flocks have a sufficiently low risk of being infected. Vaccination and emptying coops are both effective ways of limiting income losses due to the disease when the FOI is high. Indeed, vaccination substantially increases the flock value by avoiding a likely infection while keeping a coop empty limits farm costs and allows investing the saved expenses in a more profitable activity. When the FOI is low (and the penalty on infected flocks is sufficiently high) depopulation is a profitable strategy as a re-stocked healthy coop is unlikely to become reinfected. However, vaccination is an expensive ways of ensuring that an unlikely infection event will not occur and keeping the coop empty may be a suboptimal choice when poultry farming returns a

Table 3
Nash equilibria.

Notation	Behaviors present	Force of infection	Transmission settings	Description
$(p^*, 0, 0)$	$\varnothing$	See Eq. (14)	All	Pure strategy of null behavior, where no vaccination or depopulation is practiced; stabilizes when price penalty is low enough and/or vaccination cost is high enough
$(p^*, v^*, 0)$	V, $\varnothing$	$\hat{\lambda}^* = \frac{c_V}{\theta - c_V}$	All	Mixed strategy of vaccinating and null behaviors; may stabilize if vaccination cost is low enough
$(p^*, v^*, 1)$	V, D	$\hat{\lambda}^* = \frac{c_V}{\gamma}$	$\beta^T > 1$	Mixed strategy of vaccinating and depopulation; stabilizes when price penalty is high enough and vaccination cost is low enough
$(p^*, 0, d^*)$	D, $\varnothing$	$\hat{\lambda}^* = \frac{\theta}{\gamma} - 1$	$\beta^T > 1$	Mixed strategy of depopulation and null behaviors; stabilizes when price penalty is high enough
$(1, 0, d^*)$	D, $\varnothing$	$\hat{\lambda}^* = 0$	$\beta^T < 1$	Mixed strategy where the presence of depopulation behavior keeps the basic reproduction number below one

high revenue.

3.2. Stable Nash equilibria

The system allows five types of stable Nash equilibria, summarized in Table 3, that are present at different transmission levels, different vaccination costs, and different values of the price penalty (θ) on infected flocks (see derivation in Supplementary Information 5). There is a substantial qualitative difference between poultry producer communities where poultry trade alone cannot sustain viral circulation ($\beta^T < 1$) (Fig. 4) and those where it can ($\beta^T > 1$) (Fig. 5). We refer to the systems with $\beta^T > 1$ as systems with "trade-maintained endemicity". This result is robust to the nature of the between-coop environmental transmission (frequency-dependent or density-dependent) as shown in Supplementary Information 6. The Nash equilibrium mixed strategy $(p^*, 0, d^*)$ allowing endemicity is always unstable in the absence of trade-maintained endemicity and can be stable in case of trade-maintained endemicity, given a high enough penalty (see demonstration in Supplementary Information 5). When trade-maintained endemicity is absent ($\beta^T < 1$), the expansion of the depopulation behavior establishes a stable disease-free equilibrium at $(1, 0, d^*)$. These differences are linked to the natures of the externalities of behavior D under different epidemiological settings. If $\beta_T > 1$ and the vaccination coverage is low, increasing $\bar{d}$ always increases the FOI, making behavior D self-defeating. In the absence of trade-maintained endemicity, depopulation behavior in the population is self-reinforcing: as $\bar{d}$ increases, the FOI drops, and the payoff to the depopulation strategy increases as it becomes less likely that a farmer's subsequent flock will experience infection. This explains the bistability and hysteresis observed in the system with respect to changes in the penalty (Fig. 4).

Since vaccination behavior is self-defeating (vaccines cause lower $\hat{\lambda}$ which increases the payoff of other behaviors $U_\varnothing$ and U_D as compared with U_V), a mixed strategy $(p^*, v^*, 0)$ may stabilize when the vaccination cost c_V is sufficiently low (see demonstration in Supplementary Information 5). As demonstrated in previous theoretical analyses of private incentives for vaccination (Geoffard and Philipson, 1997; Bauch and Earn, 2004), vaccination alone cannot maintain a disease-free state ($(p^*, v^*, 0)$ is never a disease-free equilibrium unless $c_V = 0$). However, in the farm management model considered here, the decrease of FOI due to vaccination of a fraction of the coops incentivizes the depopulation of unvaccinated infected coops, provided the penalty is sufficiently high and the vaccination cost sufficiently low. In the absence of trade-maintained endemicity, this synergistic effect between vaccination and depopulation leads to and maintains a disease-free state as the presence and incentivization of the depopulation behavior among non-vaccinators breaks the transmission chain (Fig. 4C). Thus, vaccination leads to disease eradication by private incentives alone. In case of trade-maintained endemicity a mixed strategy $(p^*, v^*, 1)$ may stabilize (Fig. 5) as both V and D are self-defeating (see demonstration in Supplementary Information 5). This mixed strategy where every farmer adopts some disease intervention method does not lead to disease eradication as the depopulators maintain the infection in the population by propagating the disease solely through the poultry trade network while benefiting from the lower FOI due to a proportion v^* of farms practicing vaccination.

3.3. Effect of targeted penalties on Nash equilibria

The price penalty on infected flocks only affects the revenue of farmers with the null behavior $\varnothing$ (see the set of Eqs. (4) and Fig. 1). This implies that the utility of the null behavior $U_\varnothing$ decreases relative to the utility of the two other behaviors U_D and U_V when the targeted penalty increases, resulting in different types of stable Nash equilibria.

The equilibrium outcome of the game can be neatly characterized by three natural threshold values of the price penalty θ (see Figs. 4A and 5 A). When θ is below both

$$\theta_V = c_V \frac{\epsilon(\beta^E + \beta^T) - c_V \beta^E}{\epsilon(\beta^E + \beta^T - 1) - c_V \beta^E} \tag{12}$$

and

$$\theta_D = \gamma \frac{\epsilon(\beta^E + \beta^T) + \gamma\beta^E}{\epsilon + \gamma\beta^E} \tag{13}$$

in the strategic environment $(p, 0, 0)$ the null behavior has a higher payoff than vaccination and depopulation ($U_\varnothing > U_V$ and $U_\varnothing > U_D$), making this strategy a stable Nash equilibrium. Since $U_\varnothing$ depends on θ, increasing the penalty θ under the Nash equilibrium $s^* = (p^*, 0, 0)$ disincentivizes the populating of coops with poultry (i.e. decreases p^*) and, in turn, moderately decreases the FOI (Figs. 4 and 5). $\hat{\lambda}^*$ is the unique positive solutions of:

$$\hat{\lambda}^2 + \left(\frac{\theta\beta^E}{\epsilon} + 2 - \beta^T - \beta^E\right)\hat{\lambda} - (\beta^T + \beta^E - 1) = 0 \tag{14}$$

When $\theta > \theta_V$, this is the exact condition when vaccination returns a higher payoff than the null behavior in the $(p, 0, 0)$-environment, and the $(p^*, 0, 0)$ strategy becomes unstable; the mixed strategy $(p^*, v^*, 0)$ stabilizes as V behavior is self-defeating (Fig. 4B and C). When $\theta > \theta_D$, this is the exact condition when the strategy $(p, 0, 0)$ is able to be invaded by the depopulation behavior ($U_D > U_\varnothing$ in the strategic environment $(p, 0, 0)$). The resulting stable Nash equilibrium depends on β_T. In case of trade-maintained endemicity, D is self-defeating and $(p^*, 0, d^*)$ stabilizes (Fig. 5D and E) while in the absence of trade-maintained endemicity D is self-reinforcing, the strategy $(1, 0, d^*)$ stabilizes and maintains a disease-free equilibrium (Fig. 4D and E). This disease-free $(1, 0, d^*)$ strategy is stable for any value of price penalty $\theta > \gamma$.

The targeted penalty may be raised above a third threshold

$$\theta_{\mathrm{VD}} = c_V + \gamma \tag{15}$$

above which the null behavior achieves the lowest utility among the three behaviors at the currently stable Nash equilibrium. In a $(p, v, 0)$ strategic environment depopulation behavior D is able to invade ($U_D > U_V = U_\varnothing$). In the presence of trade-maintained endemicity and a $(p, 0, d)$ strategic environment, vaccination behavior V invades ($U_V > U_D = U_\varnothing$). Again, the resulting stable Nash equilibrium depends

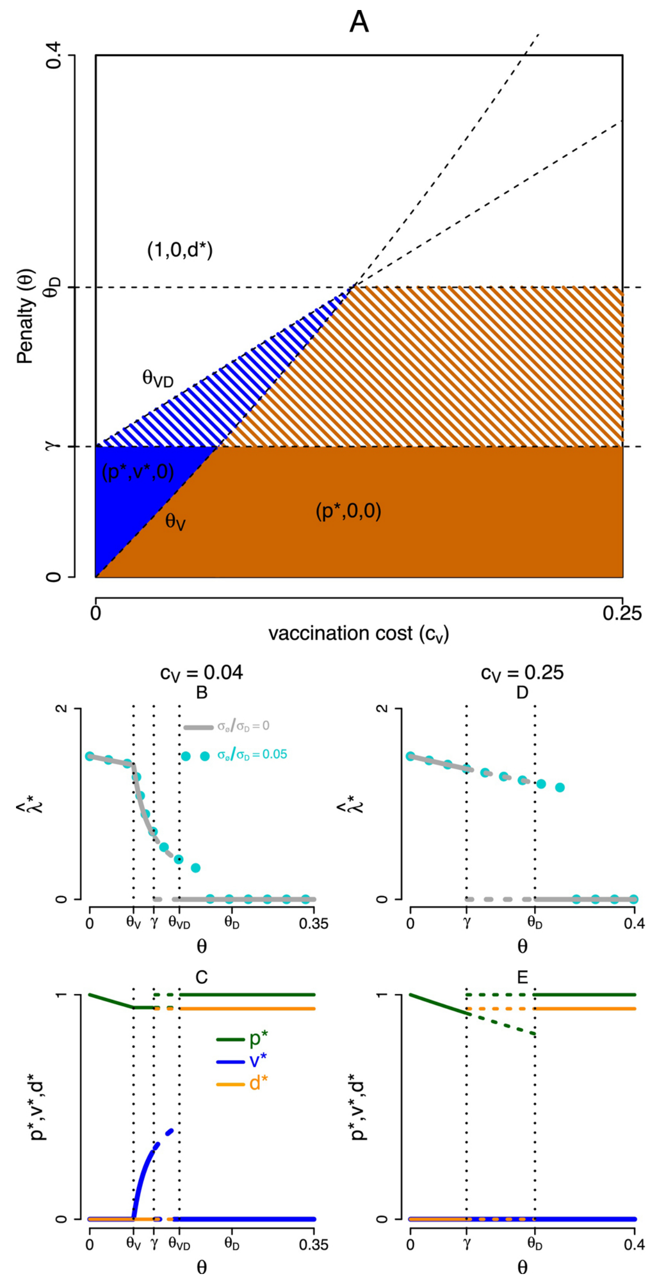

Fig. 4. Stable farmer strategies and resulting force of infection when $\beta^T < 1$. (A) Predicted stable equilibrium strategies in response to given sets of policy-dependent parameters (vaccination cost, penalty) (shaded areas are bistable Nash equilibria). Middle (B and D): evolution of the equilibrium force of infection ($\hat{\lambda}^*$) in response to varying the penalty when vaccination cost is low ($c_V = 0.04$) (panel B) and high ($c_V = 0.25$) (panel D), with $(\sigma_\emptyset/\sigma_D) = 0$ and $(\sigma_\emptyset/\sigma_D) = 0.05$ (computed numerically). Bottom (C and E): evolution of the equilibrium behavioral variables in response to varying penalty when vaccination cost is low ($c_V = 0.04$) (panel C) and high ($c_V = 0.25$) (panel E), with $(\sigma_\emptyset/\sigma_D) = 0$. Parameter values are: $\beta^T + \beta^E = 2.5$, $\beta^T = 0.9$, $\gamma = 0.1$ and $\epsilon = 0.7$. When vaccination is too expensive, increasing the penalty makes the system transit through, successively, an endemic state with pure $\emptyset$ behavior strategy, a bistable equilibrium with either pure $\emptyset$ or disease-free (with a high proportion of depopulators), and a unique disease-free state. When vaccination cost is low intermediate values of the penalty result in a mixed strategy of null behavior and vaccination $(V, \emptyset)$. A sufficiently low vaccination cost can establish a disease-free equilibrium.

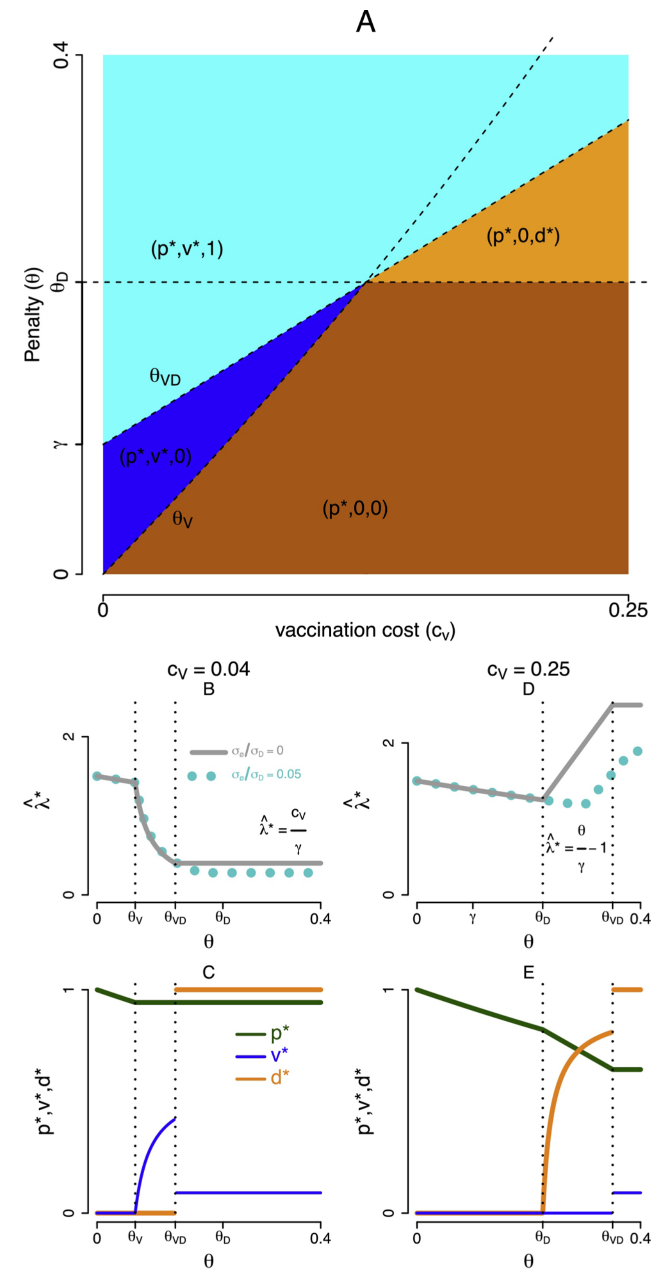

Fig. 5. Stable farmer strategies and resulting force of infection when $\beta^T > 1$. (A) Predicted stable equilibrium strategies in response to given sets of policy-dependent parameters (vaccination cost, penalty). Middle (B and D): evolution of the equilibrium force of infection ($\hat{\lambda}^*$) in response to varying penalty when vaccination cost is low ($c_V = 0.04$) (panel B) and high ($c_V = 0.25$) (panel D), with $(\sigma_\emptyset/\sigma_D) = 0$ and $(\sigma_\emptyset/\sigma_D) = 0.05$ (computed numerically). Bottom (C and E): evolution of the equilibrium behavioral variables in response to varying the penalty when vaccination cost is low ($c_V = 0.04$) (panel C) and high ($c_V = 0.25$) (panel E), with $(\sigma_\emptyset/\sigma_D) = 0$. Parameter values are: $\beta^T + \beta^E = 2.5$, $\beta^T = 1.1$, $\gamma = 0.1$ and $\epsilon = 0.7$. Increasing the penalty when vaccination is too expensive makes the system transit from an endemic stable equilibrium where farmers implement the null behavior as a pure strategy to another endemic stable equilibrium where farmers implement a mixed strategy of $(D, \emptyset)$; at this new equilibrium the force of infection increases when the penalty increases. If the penalty crosses the threshold $c_V + \gamma$, farmers settle into a (D, V) mixed strategy and the disease remains endemic.

on β_T. In the absence of trade-maintained endemicity D is self-reinforcing while V is disincentivized by the lowering of FOI due to the expansion of behavior D in the farmers' population and $(1, 0, d^*)$ stabilizes and maintains a disease-free equilibrium. In case of trade-maintained endemicity, D and V are both self-defeating and a mixed strategy $(p^*, v^*, 1)$ stabilizes. Under this stable Nash equilibrium $(p^*, v^*, 1)$ the high penalty and low vaccination cost guarantee that

Table 4
Policy recommendations.

Policy aspects	$\beta^T < 1$	$\beta^T > 1$
Establishment of a disease-free equilibrium through private incentives	Possible, by enforcing targeted penalties, decreasing vaccine costs or both	Impossible unless vaccination has no cost
Effect of targeted penalties	Generate beneficial public health effects, reduce disease incidence, establish a disease-free equilibrium	High penalties can increase the force of infection through trade. They must be associated with low cost vaccination to avoid this adverse effect.
Effect of low vaccine costs	Generate beneficial public health effects, reduce disease incidence, help establish a disease-free equilibrium	Always have beneficial effects, reduce disease incidence but do not maintain a disease-free equilibrium

$U_D = U_V > U_\varnothing$. All farmers being either vaccinators or depopulators, their revenue is not affected by the price penalty and the system is irresponsive to further changes in θ (Fig. 5B and C).

3.4. Policy implications

Our results reveal a substantial qualitative difference between poultry producer communities where poultry trade alone cannot sustain viral circulation (Fig. 4) and those where it can (Fig. 5). Resulting policy considerations are summarized in Table 4. When trade-maintained endemicity is absent, the incentives created by a sufficiently high penalty on infected poultry allow the depopulation strategy to establish and maintain a disease-free equilibrium. Regions with bistability, indicated in Fig. 4, can be seen as cases of coordination games where players are either applying a suboptimal strategy (either $s^* = (p^*, 0, 0)$ or $s^* = (p^*, v^*, 0)$) or an optimal strategy $s^* = (1, 0, d^*)$.

In practice, every system needs to be analyzed in its own economic detail to determine which behaviors are likely to stabilize. In Figs. 4 and 5, θ_D is close to 0.23, i.e. 23% of the flock value. For some types of farms, the penalty on a flock's commercial value can be above θ_D if, for example, the mortality induced by HPAI is higher than 50%, even if we take into account the possibility of selling dead birds. This would be true for large flocks of chickens in densely-populated coops where HPAI spreads easily (we refer to this type of farm as “severely affected”). Farms of this type face strong incentives for early depopulation (D) regardless of the implemented policy. In other production types, the disease and morbidity impact of HPAI may be milder, especially in duck flocks ($\theta < 0.1$), and we refer to this type of flock as “mildly affected”. Farms of this latter type would be unlikely to adopt depopulation or vaccination in the absence of specific government policy aimed at increasing the penalty θ and/or decreasing the vaccination cost c_V.

In the absence of trade-maintained endemicity, severely affected farms are unlikely to perpetuate the infection as they depopulate their infected coops early, cutting short the environmental transmission chain of the virus. In this case, to improve social welfare, policymakers may aim at establishing the depopulation behavior D in the population of mildly affected farms. They may do so by temporarily enforcing very high targeted penalties ($\theta > \theta_D$) (with enhanced surveillance or sanitary control on sold birds) or by temporarily combining an increase in the targeted penalty with financial subsidies on vaccination ($\theta > \theta_{VD}$). These subsidies on vaccination do not need to be maintained on the long term as the disease-free equilibrium $s^* = (1, 0, d^*)$ can be sustained provided the penalty on infected flocks is maintained above γ (10% of the flock value here).

In the presence of trade-maintained endemicity, however, depopulators generate perverse epidemiological effects in the presence of low vaccination coverage (low $\bar{v}$) and severely affected farms may amplify the virus circulation by depopulating their infected coops. In this scenario, increasing the penalty may have a perverse effect, as under the equilibrium $s^* = (p^*, 0, d^*)$, $\hat{\lambda}^*$ is positively correlated with θ ($\hat{\lambda}^* = (\theta/\gamma) - 1$). By concentrating all public efforts on targeted penalty enforcement, policymakers run the risk of increasing the FOI and reducing poultry production (Fig. 5D and E). Decreasing the cost of vaccination is the only policy approach that is guaranteed to have beneficial public health effects and maintain a high level of poultry production (see Fig. 5B and C): for a sufficiently low vaccination cost, one of the mixed strategies $s^* = (p^*, v^*, 0)$ or $s^* = (p^*, v^*, 1)$ stabilizes and the equilibrium FOI $\hat{\lambda}^*$ and the penalty θ are negatively correlated or independent respectively; in both cases, $\hat{\lambda}^*$ is positively correlated with the vaccination cost (Table 3), confirming the beneficial effect of a subsidy on vaccines. However, under trade-maintained endemicity, none of the three stable (mixed) strategies $s^* = (p^*, v^*, 0)$, $s^* = (p^*, 0, d^*)$ or $s^* = (p^*, v^*, 1)$ is associated with a disease-free equilibrium.

4. Discussion

To the best of our knowledge, our study is the first one to investigate the effect of varying the timing of harvest of infected livestock and disease transmission through animal trade networks from a theoretical epidemiological-economic perspective. It represents are a significant theoretical departure from the previous applications of game-theory to epidemiological systems which have mainly focused on private disease management interventions which are strategic substitutes with positive externalities (vaccination, social distancing, farm biosecurity) (Geoffard and Philipson, 1997; Bauch and Earn, 2004; Reluga, 2010; Hennessy, 2007). Such interventions are unlikely to maintain a disease-free equilibrium. Here, we demonstrate that with low levels of trade-based disease transmission, it is possible, by incentivizing either depopulation alone or a combination of depopulation and vaccination, to establish a disease-free equilibrium which can be sustained in the long run. However, with high levels of trade-based disease transmission, the disease cannot be eradicated as growing adoption of depopulation behavior increases the FOI. Vaccination does reduce transmission in this scenario, but the lower overall FOI caused by increased vaccination leads to depopulators free-riding on this lower FOI, resulting in an increase of the FOI in the network of traders specifically. As a result, the depopulation behavior cannot be avoided because it has high utility when the FOI is low enough (but not zero), which prevents disease eradication when $\beta^T > 1$.

The relevance of the game-theoretical stability to epidemiological-economic systems relies on the assumption of perfect mobility of players: it is assumed that in the long run, actors initially implementing a suboptimal strategy either switch to the optimal one (through adaptation or imitation) or quit the poultry farming industry. This assumption might hold in the context of poultry farming in Vietnam and most developing countries, as they are characterized by limited institutional regulation and few barriers to entrance and exit of the sector (ACI, 2006; Hong Hanh et al., 2007; Burgos et al., 2008). Note that, as the system is subject to the economic and ecological changes affecting disease dynamics (fluctuation in market prices and climatic variables) (Delabouglise et al., 2017), stable equilibria remain theoretical and should be interpreted as states towards which the system tends to converge.

Avian influenza is ultimately not eradicable at the global level because it has an enzootic reservoir in wild birds which cannot be managed by actors of the poultry industry (Gilbert et al., 2006). However, provided the rate of virus re-introduction from the wild-bird reservoir into the considered farming community is sufficiently low, the identified disease-free epidemio-economic equilibrium remains stable since the depopulation behavior of a sufficiently high proportion of farmers keeps the pathogen reproduction ratio below one. Any virus introduction is thereby unable to generate an epidemic in the population of domestic birds. Therefore, the eradication results in our analysis are applicable to areas where poultry farming is common, but not to general avian influenza circulation in wild bird populations.

These results highlight the importance of trade-based disease transmission and modulation of the timing of sale – two real-life features of smallholder livestock systems – on the epidemiological-economic equilibria of avian influenza circulating in a network of profit-maximizing farmers. The economic context of poultry farming in some endemic countries is favorable to depopulation in response to disease infection: chicks and finished poultry are traded with limited equipment (motorcycle for transportation, storage of poultry at home or in enclosures of live bird markets) (Van Kerkhove et al., 2009; Fournie et al., 2012; Phan, 2013) which limits transaction costs associated with the sale and introduction of flocks. Moreover, the limited sanitary controls and the flexibility of the trade networks allow the sale of sick and/or young birds and their use for human consumers or by other livestock farms (python, crocodile, fish) (Sultana et al., 2012; Paul et al., 2013; Phan et al., 2013a; Delabouglise et al., 2016; Nguyen et al., 2017). The depopulation behavior could partly explain why avian influenza viruses of the H5 subtype are more likely isolated from poultry sampled in live bird markets (Phan et al., 2013b; Nguyen et al., 2014; Turner et al., 2017) than in poultry farms (Henning et al., 2011; Desvaux et al., 2013; Thanh et al., 2017). Several epidemiological investigations suggested contacts with poultry traders or live bird markets increase the risk of farm infections with H5N1 HPAI (Desvaux et al., 2011; Biswas et al., 2008, 2009; Kung et al., 2007). A time series analysis showed the contribution of time variation of trade activity to the seasonality of HPAI H5N1 (Delabouglise et al., 2017). Spatial analyses conducted in Indonesia and China also showed that proximity to trade networks is a risk factor of H5N1 HPAI reporting (Fang et al., 2008; Loth et al., 2011). Among factors contributing to infection from trade-based transmission are the high frequency of trader visits to poultry farms and the lack of cleaning and disinfection of traders' vehicles and equipment.

In order to effectively design disease control policies, it is crucial to elucidate the respective contributions of trade-based and environmental transmission in the circulation of endemic poultry diseases. In the absence of trade-maintained endemicity, the hysteretic property of the system (Fig. 4) implies that there is an opportunity for social planners (i.e. the state, a livestock farming organization, or an integrating private actor) to significantly improve disease control and, in turn, poultry farmers' welfare. Indeed, temporarily implementing a subsidized or mandatory vaccination program or increasing the targeted penalties on infected farms (through sanitary inspections and disease surveillance) may incentivize fast depopulation of infected coops and establish a disease-free equilibrium which is sustained in the long term, provided a minimal targeted penalty is maintained. We did not consider the option of mass culling accompanied with financial indemnities here as such a policy can have the perverse effect of increasing the value of infected flocks and, in turn, disincentivizing depopulation of infected farms and increasing the number of coops with poultry (Boni et al., 2013). Eradication is not possible when endemicity is maintained through trade. In this case, increasing the penalty, in the absence of affordable vaccine technology, risks simultaneously increasing the FOI and lowering farmer income, leading to higher costs for both the public health and the poultry industry. Here, two options seem reasonable. One is enhancing sanitary inspections and/or biosecurity practices in the network of traders (Moslonka-Lefebvre et al., 2016). A second is providing farmers with an affordable vaccine technology in order to maintain immunity in poultry populations and decrease the overall FOI. Policymakers may encourage the creation of trustworthy and sustainable certification schemes ensuring that vaccinated birds are sold at higher prices on the open market (Ifft et al., 2012).

Two assumptions on the epidemiology of HPAI were made in this study. First, the possibility that a virus shed by an infected flock in the farm compartment persists and infects a susceptible flock subsequently introduced in the same coop was ignored (Paek et al., 2010). Second, between-flock disease transmission in the trade compartment was not taken into account, while it may occur in practice when poultry flocks from different farms are mixed together in live bird markets (Fournie et al., 2011). While these transmission pathways are possible, their actual significance for the epidemiology of HPAI has not been clearly documented in countries where HPAI is endemic. Further work would be needed to assess the sensitivity of our results to these assumptions.

It was assumed here that farmers aim at maximizing an income flow function in coops populated with poultry. A recent field study suggested that poultry farmers' decision making may be affected by altruistic considerations and be influenced by other actors in the poultry value chain (Delabouglise et al., 2016). Farmers are concerned with the welfare of neighboring poultry farmers with whom they have social/family connections. For this reason, they may be more inclined to depopulation than our model predicts, as depopulation would be perceived as reducing local disease transmission. It was shown in Vietnam that poultry farmers cooperate mostly with local feed and chick suppliers to manage poultry diseases, partly because these actors sell feed on credit to farmers, conferring them economic influence over their customers (Delabouglise et al., 2015). Those chick suppliers might perceive the depopulation behavior as advantageous for them as it increases the demand for chicks and limits the local spread of the disease, therefore preserving poultry production in their sale area.

The control of avian influenza – on smallholder farms, in markets, and in trading networks – will remain on the global health agenda as long as certain avian influenza subtypes continue exhibiting high mortality in humans. Identifying the origin of these infections and outbreaks is a critical component of their control. Understanding the relationship between the microeconomics of poultry production and microepidemiology of avian influenza transmission will allow us to develop better tools for the control of avian influenza outbreaks in smallholder poultry contexts.

Conflict of interest

The authors declare they have no competing interests.

Authors' contribution

AD conducted the analysis and wrote the manuscript. MFB provided ideas and technical support, reviewed and edited the manuscript.

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Appendix A. Supplementary data

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Supplementary information

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Contents

1 Epi-economic model

Poultry farmers purchase day-old chicks from breeding farms or hatcheries and sell them as finished birds after a given growing period. Farmers divide their poultry into groups of birds of similar age (flocks) which are purchased and sold together. Poultry flocks are sold to actors referred to as poultry traders who purchase, transport, and sell live poultry to other traders, slaughterers, retailers, and consumers. Any income derived from the sale of eggs, chicks, manure, feather, male cocks used in cockfighting, and other by-products of farming is ignored. The price paid by traders to farmers is primarily based on the carcass weight of sold poultry, which depends on the duration of their growing period. We propose a function f linking the sale rate σ applied by the farmer to the carcass weight of his sold poultry. f can be modeled as a hill function in conformity to the classic models of poultry growth (Darmani Kuhi et al. (2010)) :

$$f(\sigma) \;=\; \frac{n}{n + (1-\gamma)\left((\sigma/\sigma_\emptyset)^n - 1\right)}$$

With $n \geq 2$ an integer controlling the shape of the poultry growth curve. For high values of σ (high sale rate, short waiting time to sale) the function is convex in the waiting time $1/\sigma$, while for low values of σ (low sale rate, long waiting time to sale) the function is concave in $1/\sigma$ (**Figure 1**). There is an inflexion point σ_i delimiting the convex and concave portions of the curve, which corresponds to the age of maximal growth rate of poultry. This inflexion point is:

$$\sigma_i = \sigma_\emptyset \sqrt[n]{\frac{n+1}{1-\gamma}\frac{n+\gamma-1}{n-1}}$$

When σ^{-1} reaches 0, $f(\sigma)$ takes the value 0: when coops are depopulated too early, farmers earn no revenue from the sale. Farmers choose σ so as to maximize their income per bird per unit of time. In a disease-free environment, this optimal period is only based the physical growth of poultry. This optimal sale rate is noted $\sigma_\emptyset$ (and $\sigma_\emptyset^{-1}$ is the standard age of depopulation) and satisfies:

$$\frac{df}{d\sigma}(\sigma = \sigma_\emptyset) = \frac{\gamma - f(\sigma)}{\sigma}$$

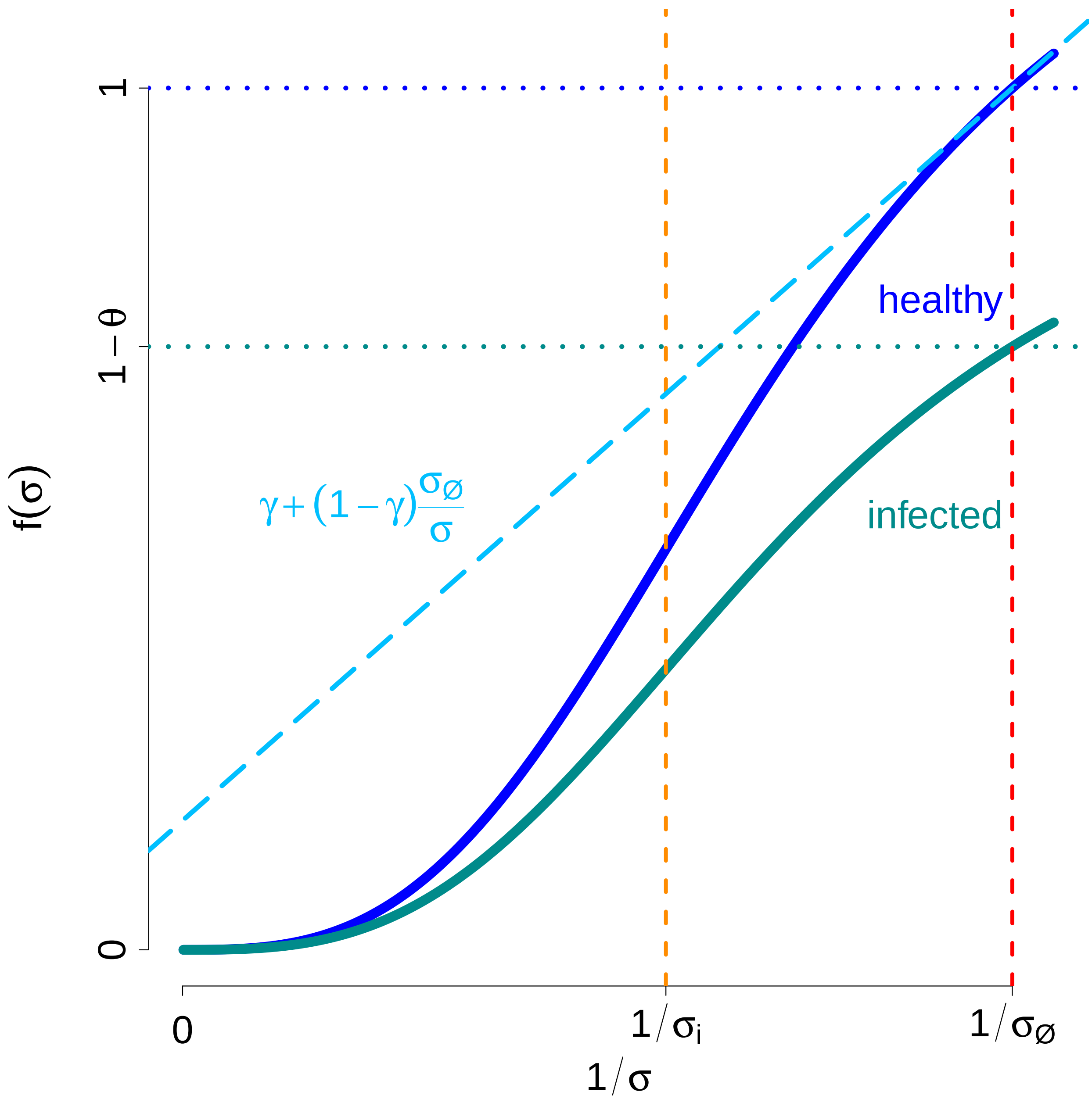

Figure 1: Relationship between the growing period of birds (inverse sale rate) and the expected revenue derived from their sale. The relationship is shown for both healthy and infected bird flocks. The orange dashed line indicates the inflexion age $1/\sigma_i$ separating the convex and concave sections of the function. The red dashed line indicates the optimal age at sale of healthy flocks, where the revenue curve crosses the dashed light blue tangent.

The income U per standard duration of poultry production cycle $\left(\sigma_{\emptyset}^{-1}\right)$ generated by a populated coop is:

$$U\left(p, v, x_H, x_I\right) = \left(v(x_H\left(f(x_H)-\gamma\right)-c_V) + (1-v)\left(\frac{x_I}{x_I+\lambda}x_H\left(f(x_H)-\gamma\right) + \frac{\lambda}{x_I+\lambda}x_I i\left(f(x_I)(1-\theta)-\gamma\right)\right)\right)c_P - c(\bar{p})$$

Where v is the probability of vaccination, $x_H = \frac{\sigma_H}{\sigma_\emptyset}$ and $x_I = \frac{\sigma_I}{\sigma_\emptyset}$. σ_H, and σ_I are the sale rates of healthy and infected poultry flocks respectively. Here the FOI λ is scaled to $\left(\sigma_\emptyset^{-1}\right)$ as well.

Any optimum sale rate x^* must satisfy $\frac{dU}{dx}(x = x^*) = 0$ and $\frac{d^2U}{dx^2}(x = x^*) < 0$.

It is notable that whatever the values of other variables the optimum value of x_H is $x_H = 1$. The optimal production cycle duration of susceptible and vaccinated flocks is constant and equal to $\left(\sigma_\emptyset^{-1}\right)$. In the remainder of the text it will be considered that $x_H = 1$ and we will refer to σ_I as σ and to x_I as x.

The derivative of U with respect to x is:

$$\begin{aligned}\frac{dU}{dx} =& c_P(1-v)\frac{\lambda}{\left(\mathbf{x}+\lambda\right)^2\left(n+(1-\gamma)(\mathbf{x}^n-1)\right)^2}\\ &\times\left((1-\gamma)^2\left(1-\gamma(1+\lambda)\right)\mathbf{x}^{2n}\right.\\ &- n^2(1-\gamma)(1-\theta)\mathbf{x}^{n+1}\\ &+ (1-\gamma)\left(2\left(n-(1-\gamma)\right)\left(1-\gamma(1+\lambda)\right) - \lambda n(n-1)(1-\theta)\right)\mathbf{x}^n\\ &\left.+ \left(n-(1-\gamma)\right)\left(\left(1-\gamma(1+\lambda)\right)\left(n-(1-\gamma)\right) + \lambda n(1-\theta)\right)\right)\end{aligned}$$

Four situations can be distinguished (**Figure 2**). (i) if $\lambda > (1-\gamma)/\gamma$ only one local optimum x^* exists. $x^* < 1$ if $\theta > 0$ and $x^* = 1$ if $\theta = 0$. The infection pressure is so high that farmers are better off fattening their infected flocks during a longer period to limit the replacement costs; (ii) there are two local optimums x^* and one global optimum x^* corresponding a to limited increase in the sale rate of infected flocks ($x^* > 1$); (iii) there are two local optimums x^* and one global optimum x^* corresponding to an immediate sale of infected flocks (x^* tends towards $+\infty$); (iv) there is only one local optimum corresponding to an immediate sale of infected flocks (x^* tends towards $+\infty$). As the situation (i) is quite unrealistic, in the remainder of the manuscript we will only focus on situations where $\lambda < (1-\gamma)/\gamma$. An exhaustive exploration of the values of the global optimum x^* differing from infinity was conducted across ranges of values of $\lambda([0,4]), \gamma([0,0.2]), \theta([0,0.6])$ and $n(\{2,3,4,5\})$. The maximum value taken by x^*, when it does not tends towards $+\infty$ was below 1.21. The optimum sale rate of infectious flocks x^* either slightly departs from 1 or tends towards infinity (which corresponds to an immediate sale). Consequently, for the sake of mathematical tractability of the game theoretical equilibriums, we can assume that the farmers' best response to disease infection is either a sale of the infected flock at standard sale rate $x^* = 1$ (an option noted $\emptyset$ in the manuscript) or an immediate depopulation, i.e. sale rate as high as possible, tending to infinity $x^* = +\infty$ (an option noted D in the manuscript).

References

H. Darmani Kuhi, T. Porter, S. LÓPez, E. Kebreab, A. B. Strathe, A. Dumas, J. Dijkstra, and J. France. A review of mathematical functions for the analysis of growth in poultry. *World's Poultry Science Journal*, 66(02):227–240, 2010.

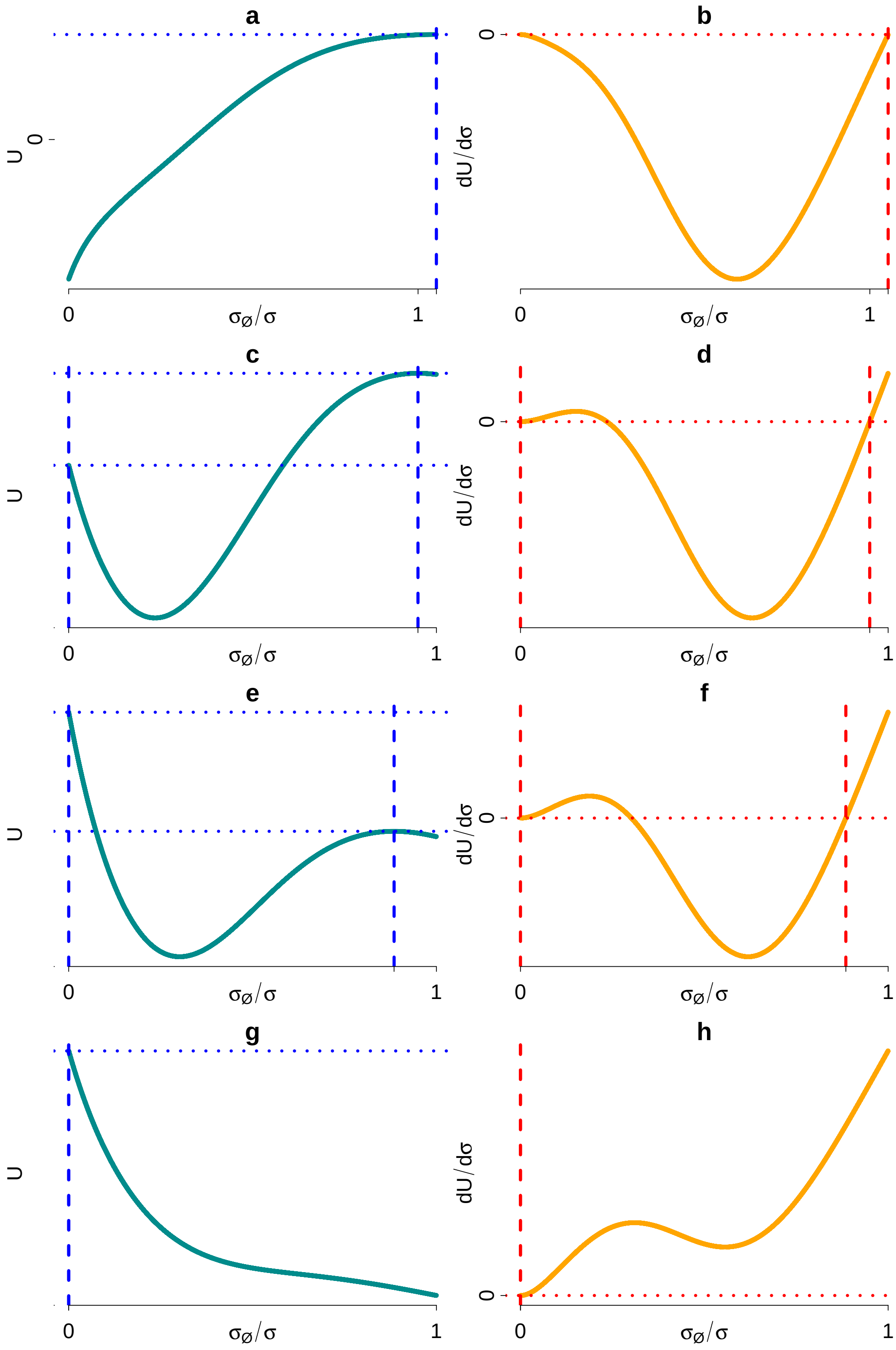

Figure 2: Relationship between the income flow per bird generated by coops populated with poultry and not vaccinated and the sale rate of infected flocks. Left panels: income flow (U). Right panels: derivative of income flow on sale rate of infected flocks ($x = \frac{\sigma_\emptyset}{\sigma}$). Four situations are illustrated. **a, b**: Only one optimum exists $x^* < 1$. **c-f**: In both cases, two local optimums exist but the global optimums correspond either to a moderate increase in the sale rate $x^* > 1$ (c, d) or an immediate sale of infected flocks ($x^* = +\infty$) (e, f). **g, h**: Only one optimum exists, corresponding to an immediate sale ($x^* = +\infty$).

2 Epidemiological equilibrium with density-dependent environmental transmission

At epidemiological equilibrium we have:

$$\begin{aligned}
\beta^E X_\emptyset (Y_\emptyset + Y_D) \; + \; \beta^T \frac{\sigma_T}{\sigma_\emptyset} \frac{X_\emptyset}{\bar{p}} Y_T \; - \; Y_\emptyset &= 0 \\
\beta^E X_D (Y_\emptyset + Y_D) \; + \; \beta^T \frac{\sigma_T}{\sigma_\emptyset} \frac{X_D}{\bar{p}} Y_T \; - \; \frac{\sigma_D}{\sigma_\emptyset} Y_D &= 0 \\
\frac{\sigma_D}{\sigma_\emptyset} Y_D + Y_\emptyset \; - \frac{\sigma_T}{\sigma_\emptyset} Y_T &= 0
\end{aligned} \tag{1}$$

The FOI scaled to the basic sell rate ($\sigma_\emptyset$) is:

$$\lambda = \beta^E (Y_D + Y_\emptyset) + \frac{\beta^T}{\bar{p}} \left(\frac{\sigma_D}{\sigma_\emptyset} Y_D + Y_\emptyset \right)$$

Remember that the optimum $\frac{\sigma_D}{\sigma_\emptyset}$ is infinite. We show in this section that solutions using large values of $\frac{\sigma_D}{\sigma_\emptyset}$ are close to the analytical solutions obtained by assuming that $\frac{\sigma_D}{\sigma_\emptyset}$ is infinite.

Combining the equilibrium equations above, we find the following third-order equation in $X_\emptyset$:

$$\begin{aligned}
\bar{p}(1-\bar{v})(1-\bar{d}) - X_\emptyset &= 0 \\
&\mathit{or} \\
\left(\frac{\sigma_D}{\sigma_\emptyset} - 1 \right) \left(\left(\beta^E + \frac{\beta^T}{\bar{p}} \right) X_\emptyset \right)^2 & \\
+ \left(1 - \frac{\sigma_D}{\sigma_\emptyset} + \bar{p}(1-\bar{v}) \left(\beta^E + \frac{\beta^T}{\bar{p}} \left(\bar{d} \frac{\sigma_D}{\sigma_\emptyset} + 1 - \bar{d} \right) \right) \right) \left(\left(\beta^E + \frac{\beta^T}{\bar{p}} \right) X_\emptyset \right) & \\
- \bar{p}(1-\bar{v})(1-\bar{d}) \left(\beta^E + \frac{\beta^T}{\bar{p}} \right) &= 0
\end{aligned}$$

The disease-free equilibrium solution is:

$$\begin{aligned} X_\emptyset &= \bar{p}(1-\bar{v})(1-\bar{d}) \\ Y_\emptyset &= 0 \\ X_D &= \bar{p}(1-\bar{v})\bar{d} \\ Y_D &= 0 \end{aligned} \tag{2}$$

It is noteworthy that if $\bar{d} = 0$ the endemic equilibrium solution to equation (1) is simply $X_\emptyset = \frac{1}{\beta^E + \frac{\beta^T}{\bar{p}}}$ and $Y_\emptyset = \bar{p}\,(1-\bar{v}) - \frac{1}{\beta^E + \frac{\beta^T}{\bar{p}}}$

If we assume that $\frac{\sigma_D}{\sigma_\emptyset}$ tends towards infinity (which corresponds to the optimum sell rate for a farmer practicing the depopulation behavior) the equation (1) can be simplified to:

$$X_\emptyset \left(\bar{p}(1-\bar{v})(1-\bar{d}) - X_\emptyset\right) \left(\left(\beta^E + \frac{\beta^T}{\bar{p}}\right) X_\emptyset - \left(1 - \beta^T(1-\bar{v})\bar{d}\right)\right) = 0$$

Which has two endemic solutions:

$$\begin{aligned} X_\emptyset &= \frac{1 - \beta^T(1-\bar{v})\bar{d}}{\beta^E + \frac{\beta^T}{\bar{p}}} \\ Y_\emptyset &= \bar{p}(1-\bar{v})(1-\bar{d}) - \frac{1 - \beta^T(1-\bar{v})\bar{d}}{\beta^E + \frac{\beta^T}{\bar{p}}} \end{aligned} \tag{3}$$

where $0 \leq Y_\emptyset \leq \bar{p}(1-\bar{v})(1-\bar{d})$ will ensure that the solution is positive, and

$$\begin{aligned} X_\emptyset &= 0 \\ Y_\emptyset &= \bar{p}(1-\bar{v})(1-\bar{d}) \end{aligned} \tag{4}$$

Solution (3) implies:

$$\begin{aligned} X_D &= \bar{p}(1-\bar{v})\bar{d} \\ Y_D &= 0 \end{aligned}$$

and the equilibrium FOI is:

$$\hat{\lambda} = \frac{(1-\bar{v})\left(\beta^E \bar{p}(1-\bar{d}) + \beta^T\right) - 1}{1 - \beta^T(1-\bar{v})\bar{d}}$$

$$\begin{array}{lll}
\text{if } (1-\bar{v})\left(\beta^E \bar{p}(1-\bar{d}) + \beta^T\right) \leq 1 & & \text{only solution (2) is stable} \\
\text{if } (1-\bar{v})\left(\beta^E \bar{p}(1-\bar{d}) + \beta^T\right) > 1 & \text{and} \quad \beta^T(1-\bar{v})\bar{d} \leq 1 & \text{solution (3) is stable} \\
\text{if } (1-\bar{v})\left(\beta^E \bar{p}(1-\bar{d}) + \beta^T\right) > 1 & \text{and} \quad \beta^T(1-\bar{v})\bar{d} > 1 & \text{solution (4) is stable}
\end{array}$$

In solution (4) Y_D is the solution of

$$\left(\bar{p}\bar{d}(1-\bar{v}) - Y_D\right)\left(\left(\beta^E + \frac{\sigma_D}{\sigma_\emptyset}\frac{\beta^T}{\bar{p}}\right)Y_D + \left(\beta^E + \frac{\beta^T}{\bar{p}}\right)\bar{p}(1-\bar{v})(1-\bar{d})\right) - \frac{\sigma_D}{\sigma_\emptyset}Y_D = 0$$

Again, assuming $\frac{\sigma_D}{\sigma_\emptyset}$ tends towards infinity we show that solution (4) implies:

$$\begin{aligned}
Y_D &= \bar{p}\left((1-\bar{v})\bar{d} - \frac{1}{\beta^T}\right) \\
X_D &= \bar{p}\frac{1}{\beta^T}
\end{aligned}$$

The equilibrium conditions are summarized in **Table1**.

Table 1: Epidemiological equilibrium as a function of set of values $(\bar{p}, \bar{v}, \bar{d})$ under the assumption $\frac{\sigma_\emptyset}{\sigma_D} = 0$

Condition	$X_\emptyset$	X_D	$\hat{\lambda}$
$(1-\bar{v})\left(\beta^E \bar{p}(1-\bar{d}) + \beta^T\right) \leq 1$	$\bar{p}(1-\bar{v})(1-\bar{d})$	$\bar{p}(1-\bar{v})\bar{d}$	0
$(1-\bar{v})\left(\beta^E \bar{p}(1-\bar{d}) + \beta^T\right) > 1$ and $\beta^T(1-\bar{v})\bar{d} \leq 1$	$\frac{1-\beta^T(1-\bar{v})\bar{d}}{\beta^E + \frac{\beta^T}{\bar{p}}}$	$\bar{p}(1-\bar{v})\bar{d}$	$\frac{(1-\bar{v})\left(\beta^E \bar{p}(1-\bar{d}) + \beta^T\right) - 1}{1-\beta^T(1-\bar{v})\bar{d}}$
$(1-\bar{v})\left(\beta^E \bar{p}(1-\bar{d}) + \beta^T\right) > 1$ and $\beta^T(1-\bar{v})\bar{d} > 1$	0	$\bar{p}\frac{1}{\beta^T}$	$+\infty$

Under the assumption that $\frac{\sigma_D}{\sigma_\emptyset}$ tends towards infinity $\left(\frac{\sigma_\emptyset}{\sigma_D} = 0\right)$, when $(1-\bar{v})\left(\beta^E \bar{p}(1-\bar{d}) + \beta^T\right) > 1$ and $\beta^T(1-\bar{v})\bar{d} \leq 1$ the sign of $\frac{d\hat{\lambda}}{d\bar{d}}$ only depends on the value of β^T and $\bar{v}$.

$$\begin{array}{llll} \text{If } \beta^T > 1 & \text{and} & \bar{v} < 1 - \frac{1}{\beta^T} & \text{then} \quad \frac{d\hat{\lambda}}{d\bar{d}} > 0 \\ \text{If } \beta^T < 1 & \text{or} & \bar{v} > 1 - \frac{1}{\beta^T} & \text{then} \quad \frac{d\hat{\lambda}}{d\bar{d}} < 0 \end{array}$$

In practice $\frac{\sigma_D}{\sigma_\emptyset}$ is finite since it always takes some time to any farmer to arrange the sale of the poultry (although this time can be assumed to be very short in comparison to the standard duration of a poultry production cycle). **Figure 3** displays the evolution of λ, the proportion of infected coops in category $\emptyset$ and D and the revenue of coops of category $\emptyset$ and D for varying values of $\bar{d}$ and with different assumptions on $\frac{\sigma_D}{\sigma_\emptyset}$.

Logically, reducing the value of $\frac{\sigma_D}{\sigma_\emptyset}$ blunts the effect of $\bar{d}$ on the FOI, disease prevalence, and income flows. If $\beta^T > 1$ and $\bar{d}$ is high (close to or higher than $\frac{1}{\beta^T(1-\bar{v})}$) the FOI is substantially affected by the value of $\frac{\sigma_D}{\sigma_\emptyset}$. In practice, however, since the very high FOI makes depopulation highly unprofitable farmers would not maintain such a high value of $\bar{d}$ while keeping $\bar{p}$ and $\bar{v}$ constant. It also is noticeable that, regardless of the value of $\frac{\sigma_D}{\sigma_\emptyset}$, the direction of the variation of the FOI in response to an increase in $\bar{d}$ depends on the sign of $\beta^T - 1$. The same observation holds for the evolution of the revenue of coops of category $\emptyset$ and D in response to an increase in $\bar{d}$. Proportion of infected coops and revenue in each of the two categories when $\frac{\sigma_D}{\sigma_\emptyset} = 20$ and when $\frac{\sigma_D}{\sigma_\emptyset} = +\infty$ are close. Therefore, if we assume that $\frac{\sigma_D}{\sigma_\emptyset}$ is close and/or higher than 20, the assumption $\frac{\sigma_D}{\sigma_\emptyset} = +\infty$ enables us to adequately model the evolution of the system variables of interest in response to farmers' choices while allowing mathematical tractability.

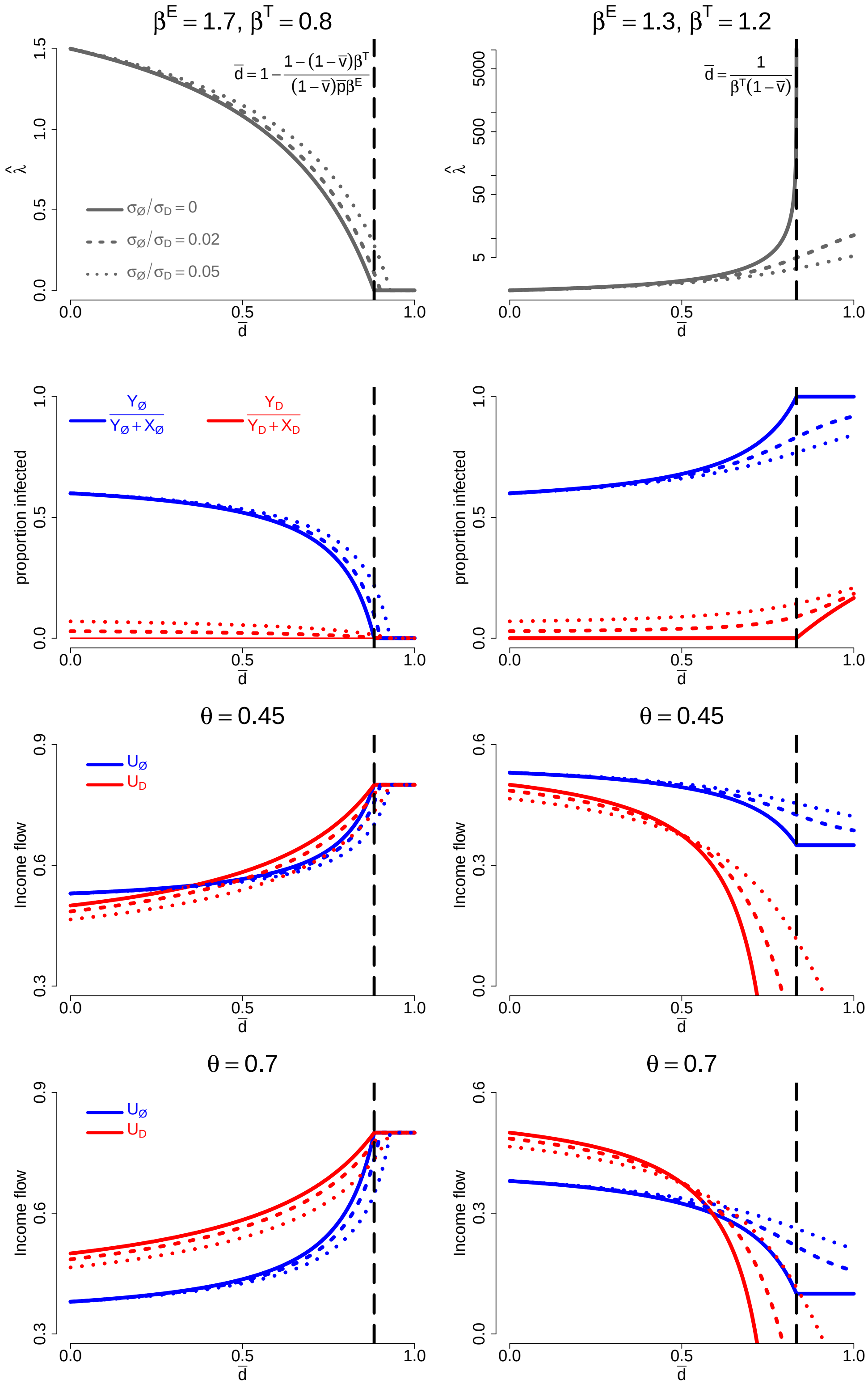

Figure 3: Evolution of system variables according to $\bar{d}$ (i.e. the proportion of populated unvaccinated coops applying the depopulation behavior). Force of infection (FOI) $\hat{\lambda}$. Second row: proportion of coops D and $\emptyset$ infected. Bottom rows: revenue generated by populated coops managed with behavior D and $\emptyset$ (respectively U_D and $U_\emptyset$) with low price penalty (third row) and high price penalty (fourth row). Other farming variables are kept constant here: $\bar{p} = 1$ and $\bar{v} = 0$.

3 Epidemiological equilibrium with frequency-dependent environmental transmission

With frequency-dependent environmental transmission the dynamics of infection are different. They are characterized by the following seven differential equations describing interactions among susceptible (X) and infectious (Y) coops. The equations are scaled so that one unit of time equals $\sigma_\emptyset^{-1}$

$$
\begin{aligned}
\dot{X}_\emptyset &= Y_\emptyset \;-\; \beta^E \frac{X_\emptyset}{\bar{p}}(Y_\emptyset + Y_D) \;-\; \beta^T \frac{\sigma_T}{\sigma_\emptyset}\frac{X_\emptyset}{\bar{p}} Y_T \\
\dot{Y}_\emptyset &= \beta^E \frac{X_\emptyset}{\bar{p}}(Y_\emptyset + Y_D) \;+\; \beta^T \frac{\sigma_T}{\sigma_\emptyset}\frac{X_\emptyset}{\bar{p}} Y_T \;-\; Y_\emptyset \\
\dot{X}_D &= \frac{\sigma_D}{\sigma_\emptyset} Y_D \;-\; \beta^E \frac{X_D}{\bar{p}}(Y_\emptyset + Y_D) \;-\; \beta^T \frac{\sigma_T}{\sigma_\emptyset}\frac{X_D}{\bar{p}} Y_T \\
\dot{Y}_D &= \beta^E \frac{X_D}{\bar{p}}(Y_\emptyset + Y_D) \;+\; \beta^T \frac{\sigma_T}{\sigma_\emptyset}\frac{X_D}{\bar{p}} Y_T \;-\; \frac{\sigma_D}{\sigma_\emptyset} Y_D \\
\dot{X}_V &= 0 \\
\dot{X}_T &= X_D \;+\; X_\emptyset \;+\; X_V \;-\; \frac{\sigma_T}{\sigma_\emptyset} X_T \\
\dot{Y}_T &= \frac{\sigma_D}{\sigma_\emptyset} Y_D + Y_\emptyset \;-\; \frac{\sigma_T}{\sigma_\emptyset} Y_T
\end{aligned}
\tag{5}
$$

The dimensionality of this equation can be reduced. At epidemiological equilibrium we have:

$$
\begin{aligned}
\beta^E \frac{X_\emptyset}{\bar{p}}(Y_\emptyset + Y_D) \;+\; \beta^T \frac{\sigma_T}{\sigma_\emptyset}\frac{X_\emptyset}{\bar{p}} Y_T \;-\; Y_\emptyset &= 0 \\
\beta^E \frac{X_D}{\bar{p}}(Y_\emptyset + Y_D) \;+\; \beta^T \frac{\sigma_T}{\sigma_\emptyset}\frac{X_D}{\bar{p}} Y_T \;-\; \frac{\sigma_D}{\sigma_\emptyset} Y_D &= 0 \\
\frac{\sigma_D}{\sigma_\emptyset} Y_D + Y_\emptyset \;-\; \frac{\sigma_T}{\sigma_\emptyset} Y_T &= 0
\end{aligned}
\tag{6}
$$

The FOI scaled to the basic sell rate ($\sigma_\emptyset$) is:

$$\lambda = \frac{\beta^E}{\bar{p}}(Y_D + Y_\emptyset) + \frac{\beta^T}{\bar{p}}\left(\frac{\sigma_D}{\sigma_\emptyset}Y_D + Y_\emptyset\right)$$

Remember that the optimum $\frac{\sigma_D}{\sigma_\emptyset}$ is infinite. We show in this section that solutions using large values of $\frac{\sigma_D}{\sigma_\emptyset}$ are close to the analytical solutions obtained by assuming that $\frac{\sigma_D}{\sigma_\emptyset}$ is infinite.

Combining the equilibrium equations above, we find the following third-order equation in $X_\emptyset$:

$$\begin{aligned}
\bar{p}(1-\bar{v})(1-\bar{d}) - X_\emptyset &= 0 \\
&\textit{or} \\
\left(\frac{\sigma_D}{\sigma_\emptyset} - 1\right)\left(\frac{1}{\bar{p}}\left(\beta^E + \beta^T\right)X_\emptyset\right)^2 & \\
+\left(1 - \frac{\sigma_D}{\sigma_\emptyset} + (1-\bar{v})\left(\beta^E + \beta^T\left(\bar{d}\frac{\sigma_D}{\sigma_\emptyset} + 1 - \bar{d}\right)\right)\right)\left(\frac{1}{\bar{p}}\left(\beta^E + \beta^T\right)X_\emptyset\right) & \\
-(1-\bar{v})(1-\bar{d})\left(\beta^E + \beta^T\right) &= 0
\end{aligned}$$

The disease-free equilibrium solution is:

$$\begin{aligned}
X_\emptyset &= \bar{p}(1-\bar{v})(1-\bar{d}) \\
Y_\emptyset &= 0 \\
X_D &= \bar{p}(1-\bar{v})\bar{d} \\
Y_D &= 0
\end{aligned} \tag{7}$$

It is noteworthy that if $\bar{d} = 0$ the endemic equilibrium solution to equation (6) is simply $X_\emptyset = \bar{p}\frac{1}{\beta^E+\beta^T}$ and $Y_\emptyset = \bar{p}\left(1 - \bar{v} - \frac{1}{\beta^E+\beta^T}\right)$

If we assume that $\frac{\sigma_D}{\sigma_\emptyset}$ tends towards infinity (which corresponds to the optimum sell rate for a farmer practicing the depopulation behavior) the equation (6) can be simplified to:

$$X_\emptyset\left(\bar{p}(1-\bar{v})(1-\bar{d}) - X_\emptyset\right)\left(\frac{1}{\bar{p}}\left(\beta^E + \beta^T\right)X_\emptyset - \left(1 - \beta^T(1-\bar{v})\bar{d}\right)\right) = 0$$

Which has two endemic solutions:

$$
\begin{aligned}
X_{\emptyset} &= \bar{p}\frac{1-\beta^T(1-\bar{v})\bar{d}}{\beta^E+\beta^T} \\
Y_{\emptyset} &= \bar{p}\left((1-\bar{v})(1-\bar{d}) - \frac{1-\beta^T(1-\bar{v})\bar{d}}{\beta^E+\beta^T}\right)
\end{aligned}
\tag{8}
$$

where $0 \leq Y_{\emptyset} \leq \bar{p}(1-\bar{v})(1-\bar{d})$ will ensure that the solution is positive, and

$$
\begin{aligned}
X_{\emptyset} &= 0 \\
Y_{\emptyset} &= \bar{p}(1-\bar{v})(1-\bar{d})
\end{aligned}
\tag{9}
$$

Solution (8) implies:

$$
\begin{aligned}
X_D &= \bar{p}(1-\bar{v})\bar{d} \\
Y_D &= 0
\end{aligned}
$$

and the equilibrium FOI is:

$$
\hat{\lambda} = \frac{(1-\bar{v})\left(\beta^E(1-\bar{d})+\beta^T\right)-1}{1-\beta^T(1-\bar{v})\bar{d}}
$$

if $(1-\bar{v})\left(\beta^E(1-\bar{d})+\beta^T\right) \leq 1$			only solution (7) is stable
if $(1-\bar{v})\left(\beta^E(1-\bar{d})+\beta^T\right) > 1$	and	$\beta^T(1-\bar{v})\bar{d} \leq 1$	solution (8) is stable
if $(1-\bar{v})\left(\beta^E(1-\bar{d})+\beta^T\right) > 1$	and	$\beta^T(1-\bar{v})\bar{d} > 1$	solution (9) is stable

In solution (9) Y_D is the solution of

$$
\left(\bar{p}\bar{d}(1-\bar{v})-Y_D\right)\left(\left(\beta^E+\frac{\sigma_D}{\sigma_{\emptyset}}\beta^T\right)\frac{Y_D}{\bar{p}}+\left(\beta^E+\beta^T\right)(1-\bar{v})(1-\bar{d})\right)-\frac{\sigma_D}{\sigma_{\emptyset}}Y_D = 0
$$

Again, assuming $\frac{\sigma_D}{\sigma_\emptyset}$ tends towards infinity we show that solution (9) implies:

$$
\begin{aligned}
Y_D &= \bar{p}\left((1-\bar{v})\bar{d} - \frac{1}{\beta^T}\right) \\
X_D &= \bar{p}\frac{1}{\beta^T}
\end{aligned}
$$

The equilibrium conditions are summarized in **Table2**.

Table 2: Epidemiological equilibrium as a function of set of values $(\bar{p}, \bar{v}, \bar{d})$ under the assumption $\frac{\sigma_\emptyset}{\sigma_D} = 0$

Condition	$X_\emptyset$	X_D	$\hat{\lambda}$
$(1-\bar{v})\left(\beta^E(1-\bar{d})+\beta^T\right) \leq 1$	$\bar{p}(1-\bar{v})(1-\bar{d})$	$\bar{p}(1-\bar{v})\bar{d}$	0
$(1-\bar{v})\left(\beta^E(1-\bar{d})+\beta^T\right) > 1$ and $\beta^T(1-\bar{v})\bar{d} \leq 1$	$\bar{p}\frac{1-\beta^T(1-\bar{v})\bar{d}}{\beta^E+\beta^T}$	$\bar{p}(1-\bar{v})\bar{d}$	$\frac{(1-\bar{v})\left(\beta^E(1-\bar{d})+\beta^T\right)-1}{1-\beta^T(1-\bar{v})\bar{d}}$
$(1-\bar{v})\left(\beta^E(1-\bar{d})+\beta^T\right) > 1$ and $\beta^T(1-\bar{v})\bar{d} > 1$	0	$\bar{p}\frac{1}{\beta^T}$	$+\infty$

It is noteworthy that the endemic equilibriums under density-dependent and frequency-dependent environmental transmission have very similar properties. The only major difference is that under frequency dependent environmental and trade-based transmission the FOI is, logically, not affected by $\bar{p}$ (i.e. the proportion of coops populated with poultry).

4 Strategic interactions with density-dependent environmental transmission

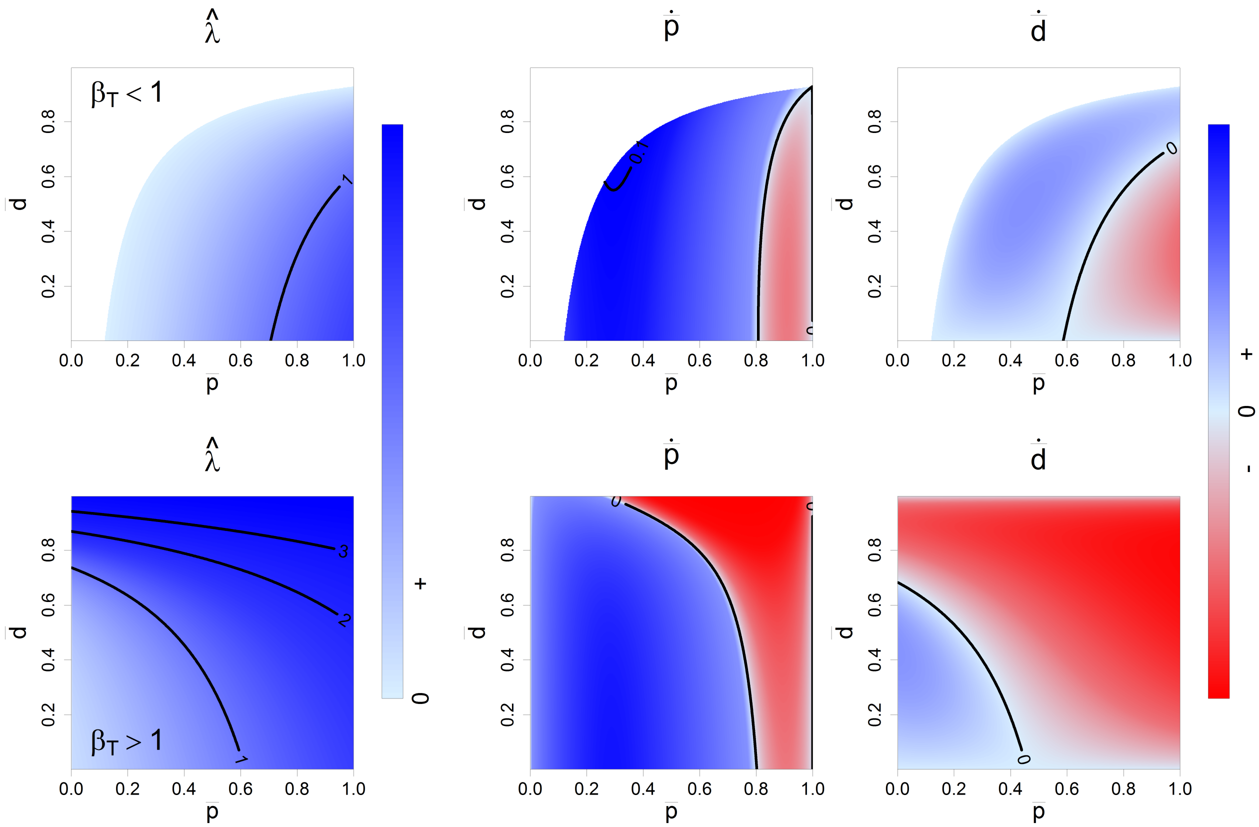

Figure 4: Effect of farmer's behavior on the force of infection and feedback effect on the behavioral dynamics. Left, middle and right panels display the evolution of incidence, $\dot{\bar{p}}$ and $\dot{\bar{d}}$ in the two-dimensional space $(\bar{p}, \bar{d})$. White area indicate a disease-free state. Top: $\beta^T = 0.8$. Bottom: $\beta^T = 1.2$. Other parameters are : $\beta^E = 2.5 - \beta^T$, $\frac{\sigma_\emptyset}{\sigma_D} = \frac{1}{20}, \theta = 0.25, \gamma = 0.1, c_V = 0.13, \epsilon = 0.7, \bar{v} = 0$.

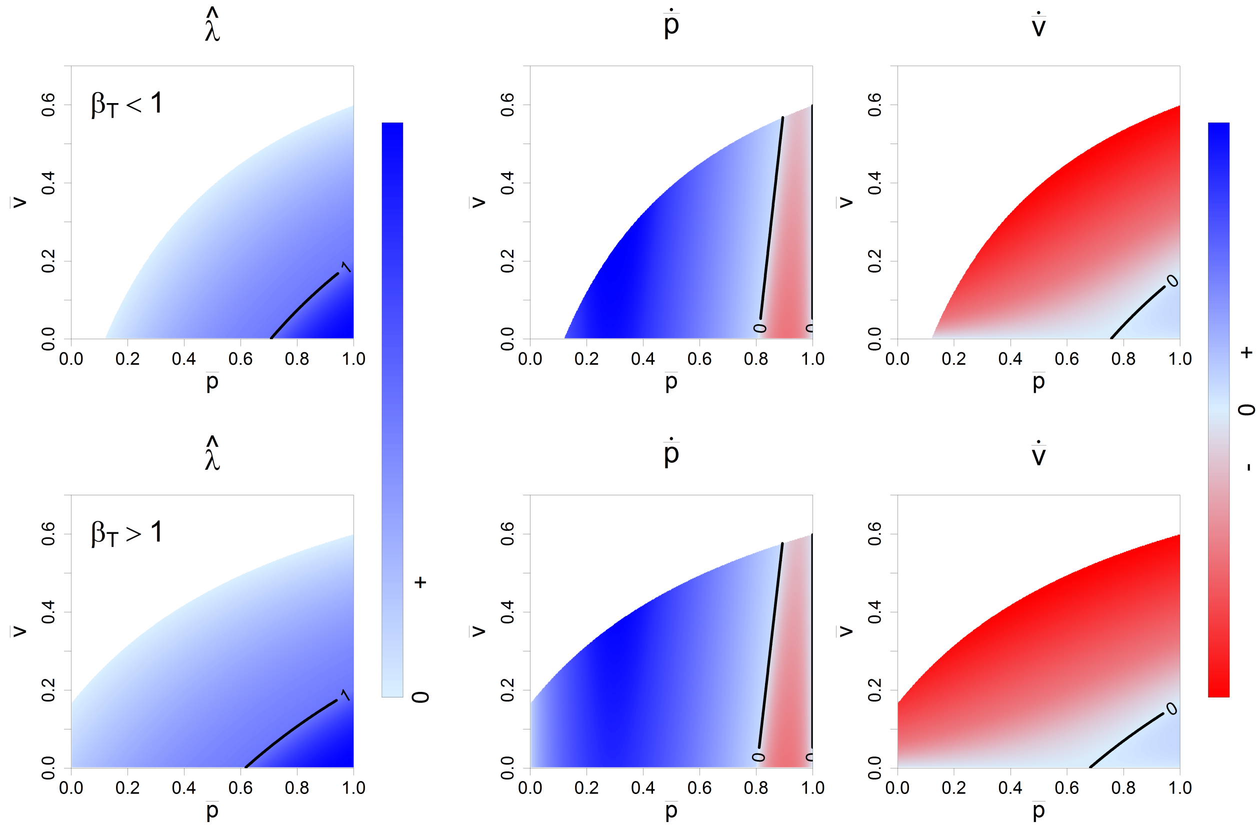

Figure 5: Effect of farmer's behavior on the force of infection and feedback effect on the behavioral dynamics. Left, middle and right panels display the evolution of incidence, $\dot{\bar{p}}$ and $\dot{\bar{v}}$ in the two-dimensional space $(\bar{p}, \bar{v})$. White area indicate a disease-free state. Top: $\beta^T = 0.8$. Bottom: $\beta^T = 1.2$. Other parameters are : $\beta^E = 2.5 - \beta^T$, $\frac{\sigma_\emptyset}{\sigma_D} = \frac{1}{20}, \theta = 0.25, \gamma = 0.1, c_V = 0.13, \epsilon = 0.7, \bar{d} = 0$.

5 Game theoretical equilibria with density-dependent environmental transmission

The strategy dynamics are determined by the set of differential equations:

$$\begin{aligned}
\dot{\bar{p}}(\bar{s}) &= \bar{p}\,(1-\bar{p})\left(\bar{v}U_V + (1-\bar{v})\left(\bar{d}U_D(\bar{s}) + \left(1-\bar{d}\right)U_\emptyset(\bar{s})\right) - ((1-\gamma-\epsilon)+\epsilon\bar{p})\right) \\
\dot{\bar{v}}(\bar{s}) &= \bar{v}(1-\bar{v})\left(U_V - \left(\bar{d}U_D(\bar{s}) + \left(1-\bar{d}\right)U_\emptyset(\bar{s})\right)\right) \\
\dot{\bar{d}}(\bar{s}) &= \bar{d}\left(1-\bar{d}\right)(U_D(\bar{s}) - U_\emptyset(\bar{s}))
\end{aligned}$$

Any equilibrium population strategy $s^* = (p^*, v^*, d^*)$ must satisfy:

$$\dot{\bar{p}}(s^*) \;=\; \dot{\bar{v}}(s^*) \;=\; \dot{\bar{d}}(s^*) \;=\; 0$$

And any equilibrium population strategy s^* is considered stable if the real parts of the eigenvalues of the Jacobian matrix J are negative under s^*, with:

$$J = \begin{bmatrix} \frac{\partial\dot{\bar{p}}}{\partial\bar{p}} & \frac{\partial\dot{\bar{p}}}{\partial\bar{v}} & \frac{\partial\dot{\bar{p}}}{\partial\bar{d}} \\ \frac{\partial\dot{\bar{v}}}{\partial\bar{p}} & \frac{\partial\dot{\bar{v}}}{\partial\bar{v}} & \frac{d\dot{\bar{v}}}{d\bar{d}} \\ \frac{\partial\dot{\bar{d}}}{\partial\bar{p}} & \frac{\partial\dot{\bar{d}}}{\partial\bar{v}} & \frac{\partial\dot{\bar{d}}}{\partial\bar{d}} \end{bmatrix}$$

As a reminder we consider that under behavior D infected flocks are sold without delay $\left(\frac{\sigma_\emptyset}{\sigma_D} = 0\right)$, therefore the utilities associated with each behavior $\emptyset$, V and D are written:

$$\begin{aligned}
U_\emptyset(\bar{s}) &= 1-\gamma-\theta\left(\frac{\hat{\lambda}(\bar{s})}{1+\hat{\lambda}(\bar{s})}\right) \\
U_D(\bar{s}) &= 1-\gamma\,(\,1+\hat{\lambda}(\bar{s})\,) \\
U_V &= 1-\gamma-c_V
\end{aligned}$$

We can rule out two types of strategies: first, $\bar{v} = 1$ cannot be an equilibrium strategy since it is disease-free ($\hat{\lambda} = 0$), in which case behaviors $\emptyset$ and D return a higher income than V. Second, any equilibrium strategy with $0 < \bar{v} < 1$ and $0 < \bar{d} < 1$ is conditional on $U_\emptyset = U_D = U_V$, which is equivalent to the very specific situation $\theta = c_V + \gamma$.

5.1 pure "null" strategy $(p^*, 0, 0)$ with $v^* = 0,\ d^* = 0$

The Jacobian matrix can be rewritten:

$$J = \begin{bmatrix} \frac{\partial \dot{\bar{p}}}{\partial \bar{p}} & \frac{\partial \dot{\bar{p}}}{\partial \bar{v}} & \frac{\partial \dot{\bar{p}}}{\partial \bar{d}} \\ 0 & U_V - U_\emptyset & 0 \\ 0 & 0 & U_D - U_\emptyset \end{bmatrix}$$

One necessary and sufficient condition for this strategy to be an equilibrium is that there exists a set of values $s = (\bar{p}, 0, 0)$ with $\dot{\bar{p}}(s) = 0$, $U_\emptyset(s) > U_D(s)$ and $U_\emptyset(s) > U_V$.

These conditions are met if and only if:

$$\theta \ < \ \gamma \frac{\epsilon\left(\beta^E + \beta^T\right) + \gamma\beta^E}{\epsilon + \gamma\beta^E}$$

and

$$\theta \ < \ c_V \frac{\epsilon\left(\beta^E + \beta^T\right) - c_V\beta^E}{\epsilon\left(\beta^E + \beta^T - 1\right) - c_V\beta^E}$$

The equilibrium value of p, noted p^*, is the unique positive root of the quadratic equation :

$$\epsilon\beta^E\mathbf{p}^2 \ + \ \left(\epsilon\left(\beta^T - \beta^E\right) \ + \ \theta\beta^E\right)\mathbf{p} \ - \epsilon\beta^T - \theta\left(1 - \beta^T\right) \ = \ 0$$

While the stable equilibrium value of the FOI $\hat{\lambda}$, noted $\hat{\lambda}^*$ is the unique positive solution of the quadratic equation :

$$\hat{\lambda}^2 \ + \ \left(\frac{\theta\beta^E}{\epsilon} + 2 - \beta^T - \beta^E\right)\hat{\lambda} \ - \ \left(\beta^T + \beta^E - 1\right) \ = \ 0$$

Note that if $\epsilon < \theta\frac{\beta^T - 1}{\beta^T}$, then the unique equilibrium solution is $p^* = 0$, farmers keep all their coops empty as the cost of the disease is too high anyway.

Since this equilibrium satisfies $\epsilon - \theta - \epsilon\bar{p} + \frac{\theta}{\beta_E\bar{p} + \beta_T} \ = \ 0$, the derivative of $\dot{\bar{p}}$ on $\bar{p}$ is:

$$\frac{\partial \dot{\bar{p}}}{\partial \bar{p}}(s^*) = p^*(1 - p^*)\left(-\epsilon - \frac{\theta\beta_E}{(\beta_E\bar{p} + \beta_T)^2}\right)$$

It is obvious that $\frac{\partial \dot{\bar{p}}}{\partial \bar{p}} < 0$ and, therefore, that $s^* = (p^*, 0, 0)$ is a stable Nash equilibrium.

5.2 mixed strategy $(p^*, 0, d^*)$ with $v^* = 0,\ 0 < d^* < 1$

The Jacobian matrix can be rewritten:

$$J = \begin{bmatrix} \frac{\partial \dot{\bar{p}}}{\partial \bar{p}} & \frac{\partial \dot{\bar{p}}}{\partial \bar{v}} & \frac{\partial \dot{\bar{p}}}{\partial \bar{d}} \\ 0 & U_V - \big((1-\bar{d})U_\emptyset + \bar{d}U_D\big) & 0 \\ \frac{\partial \dot{\bar{d}}}{\partial \bar{p}} & \frac{\partial \dot{\bar{d}}}{\partial \bar{v}} & \frac{\partial \dot{\bar{d}}}{\partial \bar{d}} \end{bmatrix}$$

One necessary and sufficient condition for this strategy to be an equilibrium is that there exists a set of values $s = (\bar{p}, 0, \bar{d})$ with $\dot{\bar{p}}(s) = 0$, and $U_D(s) = U_\emptyset(s) > U_V$.

This condition can be satisfied for two values of the FOI $\hat{\lambda}$, namely:

$$\hat{\lambda} = 0 \quad (10)$$

$$\hat{\lambda} = \frac{\theta}{\gamma} - 1 \quad (11)$$

- **Solution (10)** : If $\beta^T < 1$ the equilibrium set of values s^* satisfying solution (10) is:

  $$s^* = \left(p^* = 1, v^* = 0, d^* \geq 1 - \frac{1-\beta^T}{\beta^E}\right)$$

  If $\beta^T > 1$ however, no disease free equilibrium can be reached as long as $\bar{v} = 0$. The eigenvalues of the Jacobian at strategic equilibrium s^* are the solutions $\mathbf{y}$ of the equation:

  $$\left(\frac{\partial \dot{\bar{d}}}{\partial \bar{d}} - \mathbf{y}\right)\big(U_V - \big((1-\bar{d})U_\emptyset + \bar{d}U_D\big) - \mathbf{y}\big)\big(1 - \gamma - \epsilon - \big((1-\bar{d})U_\emptyset + \bar{d}U_D - \epsilon\bar{p}\big) - \mathbf{y}\big) = 0$$

  Which can be rewritten

  $$\left(-d^*(\theta - \gamma)\frac{1-\beta^T}{1-\beta^T d^*} - \mathbf{y}\right)(-c_V - \mathbf{y})\,\mathbf{y} = 0 \quad (12)$$

  Since $\beta^T < 1$ two situations are distinguished:

  - If $\theta < \gamma$ (12) has one strictly positive real solution. The strategy is unstable.
  - If $\theta > \gamma$ (12) has no strictly positive real solution. The strategy can be considered a stable equilibrium.

- **Solution (11)** : the equilibrium set of values s^* satisfying solution (11) is:

$$s^* = \left(p^* = 1 - \frac{\theta - \gamma}{\epsilon}, v^* = 0, d^* = 1 - \epsilon \frac{\theta}{\gamma} \frac{1 - \beta^T}{\epsilon\beta^E - (\gamma\beta^E + \epsilon\beta^T)(\frac{\theta}{\gamma} - 1)} \right)$$

This strategy s^* is conditional on:

 - If $\beta^T < 1$: $\gamma < \theta < \gamma \frac{\epsilon(\beta^E + \beta^T) + \gamma\beta^E}{\epsilon + \gamma\beta^E}$, $\theta < c_V + \gamma$ and $\epsilon > \theta - \gamma$
 - If $\beta^T > 1$: $\theta > \gamma \frac{\epsilon(\beta^E + \beta^T) + \gamma\beta^E}{\epsilon + \gamma\beta^E}$, $\theta < c_V + \gamma$ and $\epsilon > \theta - \gamma$

Note that if $\epsilon < \theta - \gamma$, then $p^* = 0$, farmers keep all their coops empty since the cost of the disease is too high. The eigenvalues of the Jacobian at strategic equilibrium s^* are the solutions $\mathbf{y}$ of the equation:

$$\left(\left(\frac{\partial \dot{\bar{d}}}{\partial \bar{d}} - \mathbf{y} \right) \left(\frac{\partial \dot{\bar{p}}}{\partial \bar{p}} - \mathbf{y} \right) - \frac{\partial \dot{\bar{d}}}{\partial \bar{p}} \frac{\partial \dot{\bar{p}}}{\partial \bar{d}} \right) \left(U_V - \left((1 - \bar{d}) U_\emptyset + \bar{d} U_D \right) - \mathbf{y} \right) \ = \ 0$$

Which can be rewritten

$$\left(\mathbf{y}^2 + \left(d^* \left(\theta - \gamma \right) \frac{\beta^T - 1}{1 - \beta^T d^*} + p^* (1 - p^*) \left(\epsilon + \left(\theta d^* + \gamma (1 - d^*) \right) \frac{\beta^E}{\beta^E p^* + \beta^T} \right) \right) \mathbf{y} + \epsilon p^* (1 - p^*) d^* \left(\theta - \gamma \right) \frac{\beta^T - 1}{1 - \beta^T d^*} \right) \times \left(\theta - (\gamma + c_V) - \mathbf{y} \right) \ = \ 0 \quad (13)$$

Since $\gamma < \theta < c_V + \gamma$ two situations are distinguished:

 - If $\beta^T < 1$ (13) has one positive and two negative real solutions. The strategy is unstable.
 - If $\beta^T > 1$ (13) has three negative real solutions. The strategy is a stable equilibrium.

5.3 mixed strategy $(p^*, v^*, 0)$ or $(p^*, v^*, 1)$ with $0 < v^* < 1$ and $d^* \in \{0, 1\}$

We posit the behavior r which corresponds to the sale rate of infected flocks in the considered population strategy and the variable $x_r = \frac{\sigma_r}{\sigma_\emptyset}$. Therefore $r = \emptyset$ and $x_r = 1$ if $\bar{d} = 0$ and $r = D$ and $x_r = \frac{\sigma_D}{\sigma_\emptyset}$ if $\bar{d} = 1$. We also consider the following function ω of x_r:

$$\omega(x_r) = 1 - \gamma + x_r \left(\gamma - f(x_r)(1 - \theta) \right)$$

Note that $\omega(1) = \theta$ and ω is a strictly increasing function of x_r on the interval $[1, +\infty)$. Therefore for any value of x_r in this interval, $\omega(x_r) \geq \theta$.

We also define the variable Δ_U with $\Delta_U = U_D - U_\emptyset$ if $\bar{d} = 0$ and $\Delta_U = U_\emptyset - U_D$ if $\bar{d} = 1$.

The Jacobian matrix can be rewritten:

$$J = \begin{bmatrix} \frac{\partial \dot{\bar{p}}}{\partial \bar{p}} & \frac{\partial \dot{\bar{p}}}{\partial \bar{v}} & \frac{\partial \dot{\bar{p}}}{\partial \bar{d}} \\ \\ \frac{\partial \dot{\bar{p}}}{\partial \bar{p}} & \frac{\partial \dot{\bar{p}}}{\partial \bar{v}} & \frac{\partial \dot{\bar{p}}}{\partial \bar{d}} \\ \\ 0 & 0 & \Delta_U \end{bmatrix}$$

One necessary and sufficient condition for this strategy to be an equilibrium is that there exists a set of values $s = (\bar{p}, \bar{v}, 0)$ with $U_V(s) = U_\emptyset(s) > U_D(s)$ and $\dot{\bar{p}}(s) = 0$ (for $\bar{d} = 0$) or $s = (\bar{p}, \bar{v}, 1)$ with $U_V = U_D(s) > U_\emptyset(s)$ and $\dot{\bar{p}}(s) = 0$ (for $\bar{d} = 1$).

The values of the FOI $\hat{\lambda}$ satisfying these conditions are:

- general solution: $\hat{\lambda} = \frac{x_r c_V}{\omega(x_r) - c_V}$ which is satisfied by the strategy set:

$$s^* = \left(p^* = 1 - \frac{c_V}{\epsilon}, v^* = 1 - \frac{x_r \omega(x_r)}{(\omega(x_r) - c_V)(\beta^E \left(1 - \frac{c_V}{\epsilon}\right) + x_r \beta^T)}, d^* \in \{0, 1\} \right)$$

- $d^* = 0$ ($r = \emptyset$ and $x_\emptyset = 1$) : $\hat{\lambda} = \frac{c_V}{\theta - c_V}$ which is satisfied by the strategy set :

$$s^* = \left(p^* = 1 - \frac{c_V}{\epsilon}, v^* = 1 - \frac{\theta}{(\theta - c_V)\left(\beta^E \left(1 - \frac{c_V}{\epsilon}\right) + \beta^T\right)}, d^* = 0 \right)$$

  Conditional on: $\theta > c_V \frac{\epsilon\left(\beta^E + \beta^T\right) - c_V \beta^E}{\epsilon(\beta^E + \beta^T - 1) - c_V \beta^E}$, $\theta < \gamma + c_V$ and $\epsilon > c_V$

- $d^* = 1$ ($r = D$ and $x_D = +\infty$): $\hat{\lambda} = \frac{c_V}{\gamma}$ which is satisfied by the strategy set:

$$s^* = \left(p^* = 1 - \frac{c_V}{\epsilon}, v^* = 1 - \frac{1}{\beta^T}, d^* = 1 \right)$$

  Conditional on: $\beta^T > 1$, $\theta > \gamma + c_V$ and $\epsilon > c_V$. Note that if $\beta^T < 1$, $\bar{d} = 1$ leads to disease eradication.

The eigenvalues of the Jacobian at strategic equilibrium s^* are the solutions $\mathbf{y}$ of the equation:

$$\left(\left(\frac{\partial \dot{\bar{v}}}{\partial \bar{v}} - \mathbf{y} \right) \left(\frac{\partial \dot{\bar{p}}}{\partial \bar{p}} - \mathbf{y} \right) - \frac{\partial \dot{\bar{v}}}{\partial \bar{p}} \frac{\partial \dot{\bar{p}}}{\partial \bar{v}} \right) (\Delta_U - \mathbf{y}) = 0$$

Which can be rewritten

$$\left(\mathbf{y}^2 + \left(v^*\left(\omega(x_r) - c_V\right) + p^*(1-p^*)\left(\epsilon + \frac{\beta^E \omega(x_r)}{x_r\left(\frac{\beta^E p^*}{x_r} + \beta^T\right)^2}\right)\right)\mathbf{y} + \epsilon p^*(1-p^*)v^*\left(\omega(x_r) - c_V\right)\right)(\Delta_U - \mathbf{y}) \; = \; 0 \tag{14}$$

Since $\Delta_U < 0$ and $\omega(x_r) \geq \theta \geq c_V$ the equation (14) has three real negative solutions. The strategy s^* is a stable equilibrium.

6 Game theoretical equilibria with frequency-dependent environmental transmission

The game theoretical equilibria under the assumption of frequency-dependent environmental transmission are illustrated in **figure 6** and **figure 7**.

6.1 pure “null” strategy $(p^*, 0, 0)$ with $v^* = 0,\ d^* = 0$

The Jacobian matrix can be rewritten:

$$J = \begin{bmatrix} \frac{\partial \dot{\bar{p}}}{\partial \bar{p}} & \frac{\partial \dot{\bar{p}}}{\partial \bar{v}} & \frac{\partial \dot{\bar{p}}}{\partial \bar{d}} \\ 0 & U_V - U_\emptyset & 0 \\ 0 & 0 & U_D - U_\emptyset \end{bmatrix}$$

One necessary and sufficient condition for this strategy to be an equilibrium is that there exists a set of values $s = (\bar{p}, 0, 0)$ with $\dot{\bar{p}}(s) = 0$, $U_\emptyset(s) > U_D(s)$ and $U_\emptyset(s) > U_V$.

These conditions are met if and only if:

$$\theta \ < \ \gamma \left(\beta^E + \beta^T\right)$$

and

$$\theta \ < \ c_V \frac{\beta^E + \beta^T}{\beta^E + \beta^T - 1}$$

The equilibrium value of p, noted p^*, is :

$$p^* \ = \ 1 - \frac{\theta}{\epsilon} \left(1 - \frac{1}{\beta^E + \beta^T}\right)$$

While the stable equilibrium value of the FOI $\hat{\lambda}$, noted $\hat{\lambda}^*$ is independent on $\bar{p}$:

$$\hat{\lambda}^* \ = \ \beta^E + \beta^T - 1$$

Note that if $\epsilon < \theta \left(1 - \frac{1}{\beta^T + \beta^E}\right)$, then the unique equilibrium solution is $p^* = 0$, farmers keep all their coops empty as the cost of the disease is too high anyway.

At equilibrium the derivative of $\dot{\bar{p}}$ on $\bar{p}$ is:

$$\frac{\partial \dot{\bar{p}}}{\partial \bar{p}}(s^*) = -\epsilon p^*(1 - p^*)$$

It is obvious that $\frac{\partial \dot{\bar{p}}}{\partial \bar{p}} < 0$ and, therefore, that $s^* = (p^*, 0, 0)$ is a stable Nash equilibrium.

6.2 mixed strategy $(p^*, 0, d^*)$ with $v^* = 0,\ 0 < d^* < 1$

The Jacobian matrix can be rewritten:

$$J = \begin{bmatrix} \frac{\partial \dot{\bar{p}}}{\partial \bar{p}} & \frac{\partial \dot{\bar{p}}}{\partial \bar{v}} & \frac{\partial \dot{\bar{p}}}{\partial \bar{d}} \\ 0 & U_V - \left((1-\bar{d})U_\emptyset + \bar{d}U_D\right) & 0 \\ \frac{\partial \dot{\bar{d}}}{\partial \bar{p}} & \frac{\partial \dot{\bar{d}}}{\partial \bar{v}} & \frac{\partial \dot{\bar{d}}}{\partial \bar{d}} \end{bmatrix}$$

One necessary and sufficient condition for this strategy to be an equilibrium is that there exists a set of values $s = (\bar{p}, 0, \bar{d})$ with $\dot{\bar{p}}(s) = 0$, and $U_D(s) = U_\emptyset(s) > U_V$.

This condition can be satisfied for two values of the FOI $\hat{\lambda}$, namely:

$$\hat{\lambda} = 0 \quad (15)$$

$$\hat{\lambda} = \frac{\theta}{\gamma} - 1 \quad (16)$$

- **Solution (15)** : If $\beta^T < 1$ the equilibrium set of values s^* satisfying solution (15) is:

  $$s^* = \left(p^* = 1, v^* = 0, d^* \geq 1 - \frac{1-\beta^T}{\beta^E}\right)$$

  If $\beta^T > 1$ however, no disease free equilibrium can be reached as long as $\bar{v} = 0$. The eigenvalues of the Jacobian at strategic equilibrium s^* are the solutions $\mathbf{y}$ of the equation:

  $$\left(\frac{\partial \dot{\bar{d}}}{\partial \bar{d}} - \mathbf{y}\right)\left(U_V - \left((1-\bar{d})U_\emptyset + \bar{d}U_D\right) - \mathbf{y}\right)\left(1 - \gamma - \epsilon - \left((1-\bar{d})U_\emptyset + \bar{d}U_D - \epsilon\bar{p}\right) - \mathbf{y}\right) = 0$$

  Which can be rewritten

  $$\left(-d^*(\theta - \gamma)\frac{1-\beta^T}{1-\beta^T d^*} - \mathbf{y}\right)(-c_V - \mathbf{y})\,\mathbf{y} = 0 \quad (17)$$

  Since $\beta^T < 1$ two situations are distinguished:

  - If $\theta < \gamma$ (17) has one strictly positive real solution. The strategy is unstable.
  - If $\theta > \gamma$ (17) has no strictly positive real solution. The strategy can be considered a stable equilibrium.

- **Solution (16)** : the equilibrium set of values s^* satisfying solution (16) is:

$$s^* = \left(p^* = 1 - \frac{\theta - \gamma}{\epsilon}, v^* = 0, d^* = 1 - \frac{\theta}{\gamma} \frac{1 - \beta^T}{\beta^E - \beta^T \left(\frac{\theta}{\gamma} - 1\right)}\right)$$

  This strategy s^* is conditional on:

  - If $\beta^T < 1$: $\gamma < \theta < \gamma\left(\beta^E + \beta^T\right)$, $\theta < c_V + \gamma$ and $\epsilon > \theta - \gamma$
  - If $\beta^T > 1$: $\theta > \gamma\left(\beta^E + \beta^T\right)$, $\theta < c_V + \gamma$ and $\epsilon > \theta - \gamma$

  Note that if $\epsilon < \theta - \gamma$, then $p^* = 0$, farmers keep all their coops empty since the cost of the disease is too high. The eigenvalues of the Jacobian at strategic equilibrium s^* are the solutions $\mathbf{y}$ of the equation:

$$\left(\left(\frac{\partial\dot{\bar{d}}}{\partial\bar{d}} - \mathbf{y}\right)\left(\frac{\partial\dot{\bar{p}}}{\partial\bar{p}} - \mathbf{y}\right) - \frac{\partial\dot{\bar{d}}}{\partial\bar{p}}\frac{\partial\dot{\bar{p}}}{\partial\bar{d}}\right)\left(U_V - \left((1-\bar{d})U_\emptyset + \bar{d}U_D\right) - \mathbf{y}\right) \;=\; 0$$

  Which can be rewritten

$$\left(\mathbf{y}^2 + \left(d^*\left(\theta - \gamma\right)\frac{\beta^T - 1}{1 - \beta^T d^*} + p^*(1-p^*)\epsilon\right)\mathbf{y} + \epsilon p^*(1-p^*)d^*\left(\theta - \gamma\right)\frac{\beta^T - 1}{1 - \beta^T d^*}\right) \times \left(\theta - (\gamma + c_V) - \mathbf{y}\right) \;=\; 0 \quad (18)$$

  Since $\gamma < \theta < c_V + \gamma$ two situations are distinguished:

  - If $\beta^T < 1$ (18) has one positive and two negative real solutions. The strategy is unstable.
  - If $\beta^T > 1$ (18) has three negative real solutions. The strategy is a stable equilibrium.

6.3 mixed strategy $(p^*, v^*, 0)$ or $(p^*, v^*, 1)$ with $0 < v^* < 1$ and $d^* \in \{0, 1\}$

We posit the behavior r which corresponds to the sale rate of infected flocks in the considered population strategy and the variable $x_r = \frac{\sigma_r}{\sigma_\emptyset}$. Therefore $r = \emptyset$ and $x_r = 1$ if $\bar{d} = 0$ and $r = D$ and $x_r = \frac{\sigma_D}{\sigma_\emptyset}$ if $\bar{d} = 1$. We also consider the following function ω of x_r:

$$\omega(x_r) = 1 - \gamma + x_r\left(\gamma - f(x_r)(1-\theta)\right)$$

Note that $\omega(1) = \theta$ and ω is a strictly increasing function of x_r on the interval $[1, +\infty)$. Therefore for any value of x_r in this interval, $\omega(x_r) \geq \theta$.

We also define the variable Δ_U with $\Delta_U = U_D - U_\emptyset$ if $\bar{d} = 0$ and $\Delta_U = U_\emptyset - U_D$ if $\bar{d} = 1$.

The Jacobian matrix can be rewritten:

$$J = \begin{bmatrix} \frac{\partial \dot{\bar{p}}}{\partial \bar{p}} & \frac{\partial \dot{\bar{p}}}{\partial \bar{v}} & \frac{\partial \dot{\bar{p}}}{\partial \bar{d}} \\ \\ \frac{\partial \dot{\bar{p}}}{\partial \bar{p}} & \frac{\partial \dot{\bar{p}}}{\partial \bar{v}} & \frac{\partial \dot{\bar{p}}}{\partial \bar{d}} \\ \\ 0 & 0 & \Delta_U \end{bmatrix}$$

One necessary and sufficient condition for this strategy to be an equilibrium is that there exists a set of values $s = (\bar{p}, \bar{v}, 0)$ with $U_V(s) = U_\emptyset(s) > U_D(s)$ and $\dot{\bar{p}}(s) = 0$ (for $\bar{d} = 0$) or $s = (\bar{p}, \bar{v}, 1)$ with $U_V = U_D(s) > U_\emptyset(s)$ and $\dot{\bar{p}}(s) = 0$ (for $\bar{d} = 1$).

The values of the FOI $\hat{\lambda}$ satisfying these conditions are:

- general solution: $\hat{\lambda} = \frac{x_r c_V}{\omega(x_r) - c_V}$ which is satisfied by the strategy set:

$$s^* = \left(p^* = 1 - \frac{c_V}{\epsilon}, v^* = 1 - \frac{x_r \omega(x_r)}{(\omega(x_r) - c_V)(\beta^E + x_r \beta^T)}, d^* \in \{0, 1\} \right)$$

- $d^* = 0$ ($r = \emptyset$ and $x_\emptyset = 1$) : $\hat{\lambda} = \frac{c_V}{\theta - c_V}$ which is satisfied by the strategy set :

$$s^* = \left(p^* = 1 - \frac{c_V}{\epsilon}, v^* = 1 - \frac{\theta}{(\theta - c_V)(\beta^E + \beta^T)}, d^* = 0 \right)$$

  Conditional on: $\theta > c_V \frac{\beta^E + \beta^T}{\beta^E + \beta^T - 1}$, $\theta < \gamma + c_V$ and $\epsilon > c_V$

- $d^* = 1$ ($r = D$ and $x_D = +\infty$): $\hat{\lambda} = \frac{c_V}{\gamma}$ which is satisfied by the strategy set:

$$s^* = \left(p^* = 1 - \frac{c_V}{\epsilon}, v^* = 1 - \frac{1}{\beta^T}, d^* = 1 \right)$$

  Conditional on: $\beta^T > 1$, $\theta > \gamma + c_V$ and $\epsilon > c_V$. Note that if $\beta^T < 1$, $\bar{d} = 1$ leads to disease eradication.

The eigenvalues of the Jacobian at strategic equilibrium s^* are the solutions $\mathbf{y}$ of the equation:

$$\left(\left(\frac{\partial \dot{\bar{v}}}{\partial \bar{v}} - \mathbf{y} \right) \left(\frac{\partial \dot{\bar{p}}}{\partial \bar{p}} - \mathbf{y} \right) - \frac{\partial \dot{\bar{v}}}{\partial \bar{p}} \frac{\partial \dot{\bar{p}}}{\partial \bar{v}} \right) (\Delta_U - \mathbf{y}) = 0$$

Which can be rewritten

$$\left(\mathbf{y}^2 + \left(v^* \left(\omega(x_r) - c_V\right) + p^*(1-p^*)\epsilon\right)\mathbf{y} + \epsilon p^*(1-p^*)v^* \left(\omega(x_r) - c_V\right)\right)\left(\Delta_U - \mathbf{y}\right) \quad = \quad 0 \quad (19)$$

Since $\Delta_U < 0$ and $\omega(x_r) \geq \theta \geq c_V$ the equation (19) has three real negative solutions. The strategy s^* is a stable equilibrium.

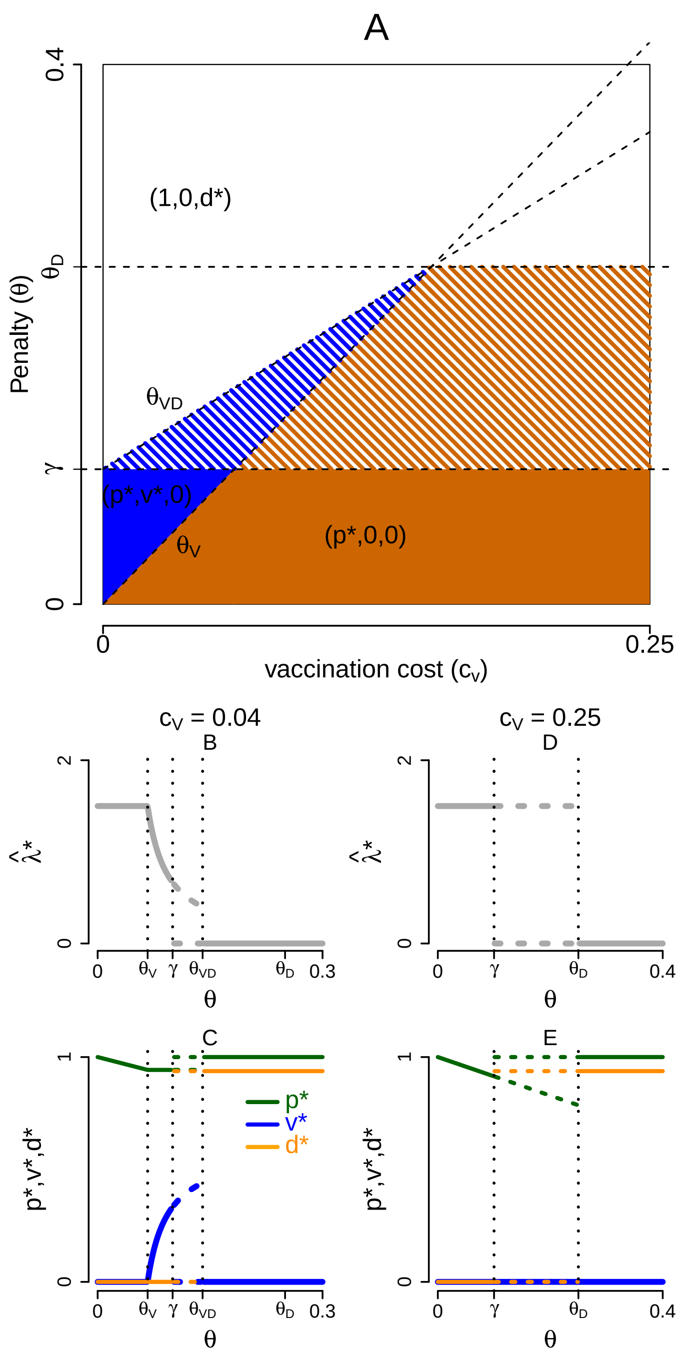

Figure 6: Stable farmer strategies and resulting force of infection with frequency-dependent environmental transmission when $\beta^T < 1$. (A) predicted stable equilibrium strategies in response to given sets of policy-dependent parameters (vaccination cost, penalty) (shaded areas are bistable Nash equilibria). middle (B and D): evolution of the equilibrium force of infection ($\hat{\lambda}^*$) in response to varying penalty when vaccination cost is low ($c_V = 0.04$) (panel B) and high ($c_V = 0.25$) (panel D). bottom (C and E): evolution of the equilibrium behavioral variables in response to varying penalty when vaccination cost is low ($c_V = 0.04$) (panel C) and high ($c_V = 0.25$) (panel E). Parameter values are: $\beta^T + \beta^E = 2.5$, $\beta^T = 0.9$, $\gamma = 0.1$ and $\epsilon = 0.7$.

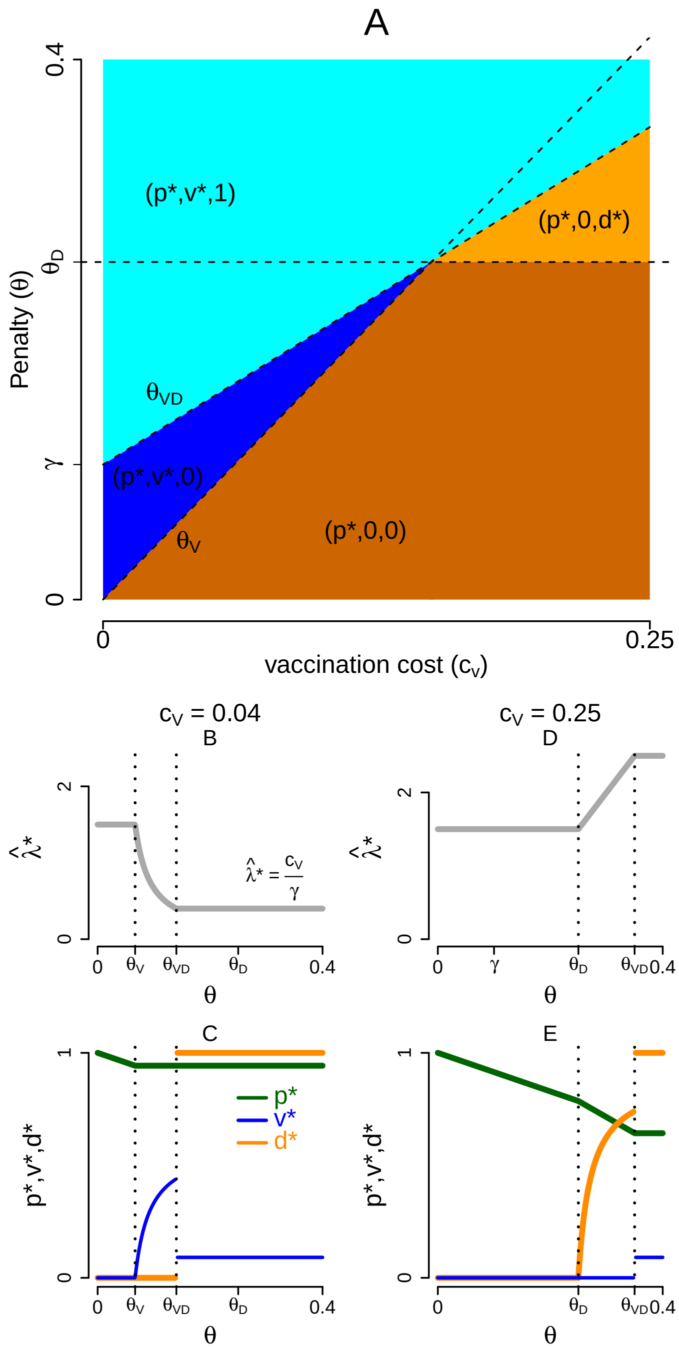

Figure 7: Stable farmer strategies and resulting force of infection with frequency-dependent environmental transmission when $\beta^T > 1$. (A) predicted stable equilibrium strategies in response to given sets of policy-dependent parameters (vaccination cost, penalty). middle (B and D): evolution of the equilibrium force of infection ($\hat{\lambda}^*$) in response to varying penalty when vaccination cost is low ($c_V = 0.04$) (panel B) and high ($c_V = 0.25$) (panel D). bottom (C and E): evolution of the equilibrium behavioral variables in response to varying penalty when vaccination cost is low ($c_V = 0.04$) (panel C) and high ($c_V = 0.25$) (panel E). Parameter values are: $\beta^T + \beta^E = 2.5$, $\beta^T = 1.1$, $\gamma = 0.1$ and $\epsilon = 0.7$.