



Dynamics of bed bug infestations and control under disclosure policies

Sherrie Xie^a, Alison L. Hill^b, Chris R. Rehmann^c, and Michael Z. Levy^{a,1}

^aDepartment of Biostatistics, Epidemiology and Informatics, University of Pennsylvania, Philadelphia, PA 19104-6021; ^bProgram for Evolutionary Dynamics, Harvard University, Cambridge, MA 02138; and ^cDepartment of Civil, Construction, and Environmental Engineering, Iowa State University, Ames, IA 50011-1066

Edited by Alan Hastings, University of California, Davis, CA, and approved January 23, 2019 (received for review September 10, 2018)

Bed bugs have reemerged in the United States and worldwide over recent decades, presenting a major challenge to both public health practitioners and housing authorities. A number of municipalities have proposed or initiated policies to stem the bed bug epidemic, but little guidance is available to evaluate them. One contentious policy is disclosure, whereby landlords are obligated to notify potential tenants of current or prior bed bug infestations. Aimed to protect tenants from leasing an infested rental unit, disclosure also creates a kind of quarantine, partially and temporarily removing infested units from the market. Here, we develop a mathematical model for the spread of bed bugs in a generalized rental market, calibrate it to parameters of bed bug dispersion and housing turnover, and use it to evaluate the costs and benefits of disclosure policies to landlords. We find disclosure to be an effective control policy to curb infestation prevalence. Over the short term (within 5 years), disclosure policies result in modest increases in cost to landlords, while over the long term, reductions of infestation prevalence lead, on average, to savings. These results are insensitive to different assumptions regarding the prevalence of infestation, rate of introduction of bed bugs from other municipalities, and the strength of the quarantine effect created by disclosure. Beyond its application to bed bugs, our model offers a framework to evaluate policies to curtail the spread of household pests and is appropriate for systems in which spillover effects result in highly nonlinear cost–benefit relationships.

bed bugs | disclosure | mathematical model

Bed bugs (*Cimex lectularius*) have reemerged in the United States and worldwide since the early 2000s (1–4). The prevalence of infestations in major US cities is high, although only poorly described. In 2014, the New York City Community Health Survey estimated the annual prevalence of bed bug infestations to be 5.1% city-wide and as high as 12% in some neighborhoods (5). Similarly, a door-to-door survey of bed bug infestations conducted in a Philadelphia census tract in 2013 found that 11.1% of respondents had recent bed bug infestations (6).

The health consequences of the current bed bug pandemic are inarguably enormous. Bed bugs inflict physical and psychological distress to those they bite and whose dwellings they infest, causing itching, rashes, allergies, sleep loss, anxiety, and other symptoms (7–9). In addition to these direct effects, bed bug infestations prevent homebound patients—especially senior citizens and disabled individuals—from receiving care, as many home-care providers are reluctant to enter infested houses (10, 11). Poisoning by insecticides inappropriately applied to combat bed bugs has caused at least one fatality and left scores acutely ill and countless more exposed, often unknowingly (12). Bed bugs are competent vectors of *Trypanosoma cruzi* (13, 14) and *Bartonella quintana* (15), the etiological agents of Chagas disease and trench fever, respectively. Whether or not bed bugs currently are, or will become, epidemiologically relevant in the transmission of infectious agents remains unknown.

The optimal political response to the bed bug epidemic has yet to be determined. Policies must balance the rights of tenants, landlords, and the public at large. Treatment of infestations with insecticide or heat-based interventions is generally paid for by individuals, not municipalities, and so policies strive to incentivize rapid and effective treatment while minimizing stigma, cost, and lost housing opportunities. An increasing number of US states and municipalities are responding to the rise in bed bug prevalence with disclosure policies, which require landlords to notify potential tenants of bed bug infestation histories. For example, in New York City, landlords are required to disclose the bed bug infestation and treatment histories of their units for the previous year to all tenants entering a lease agreement (16). Similar, though less stringent, versions of this policy have been passed in San Francisco (17); Mason City, Iowa (18); Connecticut (19); and Maine (20).

The primary aim of disclosure policies is to protect individuals from unknowingly leasing an infested rental unit. Nonetheless, these policies may have community-wide effects: Disclosure can decrease the desirability of infested units, thereby imposing a kind of partial quarantine that could decrease the prevalence of infestations on a city or even regional scale. The potential benefits of disclosure seemingly come at a cost,

Significance

Bed bugs are household pests that bite humans and cause myriad medical, psychological, social, and economic problems. Infestation levels have resurged across the United States in recent decades, and cities and states are debating strategies to deal with them. Here, we introduce a mathematical model to study the spread of bed bugs and predict the costs and benefits of policies aimed at controlling them. In particular, we evaluate disclosure, a policy that requires landlords to notify potential tenants of recent infestations in a unit. While disclosure aims to protect individual tenants, our results suggest that these policies also reduce infestation prevalence market-wide. Disclosure results in some initial cost to landlords but leads to significant savings in the long term.

Author contributions: S.X., A.L.H., C.R.R., and M.Z.L. designed research, performed research, and wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

This open access article is distributed under [Creative Commons Attribution License 4.0 \(CC BY\)](https://creativecommons.org/licenses/by/4.0/).

Data deposition: All analyses and figures presented in *Results* and *S1 Appendix* can be reproduced using code available at <https://github.com/sherriexie/bedbugdisclosure>. An R Shiny web application allowing users to simulate the authors' model and additional animation are available at <https://bedbugdisclosure.shinyapps.io/shinyapp/>.

¹To whom correspondence should be addressed. Email: mzlevy@penmedicine.upenn.edu.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1814647116/-DCSupplemental.

Parameters	Description	Best estimate	Range	Ref(s).
p (%)	Baseline prevalence	5	0.1–10	—
β	Infectivity	Fit	Fit	—
s	Renter selectivity	0.5	0.01–1	—
$1/\gamma$ (mo)	Average duration of infestation	6	2–12	—
k	Probability of relocation transmission	0.3	0–1	—
b	Vacancy multiplier	1.3	1–5	—
m (y^{-1})	Move-out rate	0.5	—	(24)
n (y^{-1})	Move-in rate	6	—	(24, 25)
D (y)	Length of disclosure	1	—	(16)
Cost				
Treatment (c_{trt} , \$)	Average cost of successfully exterminating a bed bug infestation	1,225	—	(1)
Vacancy (c_{vac} , \$)	Average cost of a rental unit lacking tenants for 1 mo	1,000	—	(26)
Turnover (c_{tov} , \$)	Average cost of turning over a rental unit to new tenants	1,000	—	(27)

two rental units have an equal probability of “interacting” with each other, via in-person visits, exchange of objects, or turnover of tenants. We discuss the implications of relaxing these assumptions in the final section of *Results*.

The Model in the Presence of Disclosure. We expand the model to account for the effects of disclosure policies (Fig. 1). Under this model, units in the I_v class are immediately disclosed and, upon treatment, move to a new susceptible-vacant-disclosed (S'_v) class. The expanded model is as follows:

$$\begin{aligned} \frac{dS_r}{dt} &= -\beta S_r I_r / N + \gamma I_r + n(1 - kf(t))S_v + (1 - s)n(1 - kf(t))S'_v - mS_r \\ \frac{dI_r}{dt} &= \beta S_r I_r / N + nkf(t)S_v + (1 - s)nkf(t)S'_v + (1 - s)nI_v - (\gamma + bm)I_r \\ \frac{dS_v}{dt} &= mS_r + (1/D)S'_v - nS_v \\ \frac{dI_v}{dt} &= bml_r - (\gamma + (1 - s)n)I_v \\ \frac{dS'_v}{dt} &= \gamma I_v - ((1 - s)n + 1/D)S'_v \\ N &= S_r + I_r + S_v + I_v + S'_v \\ f(t) &= \frac{bl_r}{S_r + bl_r}. \end{aligned} \quad [2]$$

We assume all disclosed units are less desirable to potential tenants proportional to a renter-selectivity parameter (s). Units in the I_v and S'_v class might be thought to be in a “leaky quarantine,” the strength of which is determined by s . When $s = 1$, no currently (I_v) or recently (S'_v) infested units are rented out, meaning that disclosure results in a full quarantine. At the other extreme, when tenants do not change their renting behavior based on a unit’s disclosure status ($s = 0$), the model reduces to the model in the absence of disclosure. We assume landlords comply fully with disclosure and units in class S'_v return to class S_v at rate $1/D$, where D represents the mandated disclosure period. Although in reality disclosure is of a fixed length, we have modeled it as a continuous transition for simplicity. In [SI Appendix](#), we show that relaxing this assumption does not impact our conclusions.

Estimating Disclosure Costs. Our primary outcome of interest is the change in expected cost due to disclosure, which we define as the difference in cost to landlords in the presence of disclosure compared to the absence of disclosure. In the context of a rental market with bed bugs endemic, cost can take the following forms: bed bug treatment costs, rental turnover costs, and opportunity costs due to vacancy. Bed bug treatment costs are the expenses associated with the extermination or attempted extermination of bed bugs and include fees to pest-control companies and contractors. Turnover costs include the expenses involved in repairing, advertising, and showing units to prospective tenants. Opportunity costs due to vacancy are incurred anytime a rental unit lacks tenants and are equal to the rental price for that unit. Hereafter, we will use the term “cost” to refer to total additional cost to landlords that result from disclosure. Similarly, we will use the terms “treatment cost,” “turnover cost,” and “vacancy cost” to refer to these component costs with respect to disclosure (i.e., the difference of each component in the presence and absence of disclosure).

The average per-unit number of bed bug treatments occurring in a given year is equal to the number of transitions from infested to susceptible classes for that year divided by the number of rental units in the system N , and the average number of turnover events is equal to the number of transitions from vacant to occupied classes divided by N . Similarly, the average time that each unit is vacant is equal to the total unit-time spent in vacant classes divided by N . Then, if c_{trt} , c_{tov} , and c_{vac} are constants equal to the average ancillary cost of bed bug treatment, average cost of moving, and average cost of untreated infestation, respectively, the component costs of disclosure from the perspective of renters can be expressed for a given year Y by the following:

$$\begin{aligned}\text{Treatment cost} &= \frac{C_{\text{trt}}}{N} \left(\int_Y^{(Y+1)} (\gamma l_r + \gamma l_v) dt \Big|_{s=s} - \int_Y^{(Y+1)} (\gamma l_r + \gamma l_v) dt \Big|_{s=0} \right) \\ \text{Turnover cost} &= \frac{C_{\text{tov}}}{N} \left(\int_Y^{(Y+1)} (nS_v + n(1-s)S'_v + n(1-d)l_v) dt \Big|_{s=s} \right. \\ &\quad \left. - \int_Y^{(Y+1)} (nS_v + n(1-s)S'_v + n(1-d)l_v) dt \Big|_{s=0} \right) \\ \text{Vacancy cost} &= 12 \frac{C_{\text{vac}}}{N} \left(\int_Y^{(Y+1)} (S_v + S'_v + l_v) dt \Big|_{s=s} \right. \\ &\quad \left. - \int_Y^{(Y+1)} (S_v + S'_v + l_v) dt \Big|_{s=0} \right).\end{aligned}$$

Above, each component cost is calculated as the difference in the average quantity of treatment, turnover, and vacancy in the presence vs. in the absence of disclosure multiplied by the cost constant. Cost can then be calculated as the sum of the treatment, turnover, and vacancy costs.

Model Implementation and Parameter Estimates. We ran the model with a total (N) of 1,000 units (although our results are insensitive to population size). The average cost of bed bug treatment was set to equal \$1,225, the median cost of bed bug treatment for single-family homes reported by a national survey of pest-management professionals in 2015 (1). The average cost of turnover was set equal to \$1,000, a figure that has been cited on property-management blogs (24). The average monthly rent (and monthly opportunity cost due to vacancy) was set to equal \$1,000, roughly the national median reported by the American Community Survey for 2017 (25).

Initial conditions for the start of each simulation were the equilibrium values for the same system in the absence of disclosure, assuming that the overall baseline prevalence of infestation, $(I_r + I_v)/N$, was p :

$$\begin{aligned} S_r^* &= \frac{N}{m+n} \left((1-p)n - p m \frac{b\gamma}{bm + \gamma + n} \right) \\ I_r^* &= N p \frac{\gamma + n}{bm + \gamma + n} \\ S_v^* &= N \frac{m}{m+n} \left((1-p) + p \frac{b\gamma}{bm + \gamma + n} \right) \\ I_v^* &= N p \frac{bm}{bm + \gamma + n}. \end{aligned} \quad [4]$$

Estimated values or ranges for parameters are reported in Table 1. Move-in and -out rates were estimated according to data from the US Census Bureau Housing Vacancy Survey for 2017 and the 2017 National Apartment Association Survey of Operating Income and Expenses in Rental Apartment Communities (26, 27). The move-out rate, m , was estimated based on the average frequency of moves (once every 2 y). To estimate the move-in rate (n), we calculated the percent of units that would be vacant in our model at baseline [percent vacant = $(S_v + I_v)/N$ in Eq. 4, $\approx m/(n + m)$ when prevalence is low] and chose a move-in rate so this matched the national average of 7% rental vacancy. The length of disclosure D was set to equal 1 y, which is equivalent to the length mandated by New York City (16). The infectivity β cannot be observed directly; we calculated it by solving for the value that would yield a given baseline prevalence p , which is more easily observed and interpreted:

$$\beta = \frac{N}{S_r^* I_r^*} \left((\gamma + bm) I_r^* - \frac{k b I_r^*}{S_r^* + b I_r^*} n S_v^* - n I_v^* \right), \quad [5]$$

where S_r^* , I_r^* , S_v^* , and I_v^* are given in Eq. 4.

Some parameters, including the average duration of infestation ($1/\gamma$), probability of relocation transmission (k), and vacancy multiplier (b), could not be estimated from available data; they were thus assigned realistic point values and assessed over ranges of values in subsequent sensitivity analyses. No data exist on the duration of bed bug infestations, although there are several factors impeding timely treatment. Recent genetic analyses suggest that infestations are founded by small populations consisting of few individuals or even a single mated female (28, 29), and reactions to bites are nonspecific and often misdiagnosed (30, 31), both of which retard detection by tenants and landlords. Even detection by pest-management professionals, which occurs by visual inspection and is sometimes aided by trained canines, has imperfect sensitivity and specificity (31). Moreover, treatment failure is common, even after multiple visits (32–34). Due to the challenges involved in bed bug detection and treatment, the average duration of infestation was estimated to equal 6 mo; sensitivity analysis evaluated how results changed if $1/\gamma$ were as brief as 2 mo or as long as 1 y.

There are anecdotal reports of tenants moving out of apartments prematurely due to bed bug infestations (35, 36), but data that can be used to estimate the factor by which infestation increases move-out rate are lacking. We chose a relatively conservative estimate for b (1.3, where move-out is assumed to be 30% greater in infested units relative to noninfested units) and found in subsequent sensitivity analyses that higher values of b led to even greater prevalence reduction and cost savings over the long term (SI Appendix, Fig. S9). Because bed bugs find harborage in furniture and clothing and much of their long-range dispersal is believed to be human-mediated (29), we reasoned that relocation transmission (whereby individuals moving out of an infested unit inadvertently bring bed bugs that seed a new infestation in their next unit) occurs, although at an unknown rate. Given the lack of data with which to estimate the probability of relocation transmission k , we set it to an intermediate value (0.3). Sensitivity analyses determined results to be robust to changes in k across its full range of possible values (SI Appendix, Figs. S6 and S7).

The model was coded and run in R using a differential equation solver in the *deSolve* library (37), and results were reported after each 1-y interval. An R Shiny web application allowing users to simulate our model themselves under alternate parameter values and visualize the output is available at <https://bedbugdisclosure.shinyapps.io/shinyappl/>. All analyses and figures presented in *Results* and SI Appendix can be reproduced by using code we have made available at <https://github.com/sherriexie/bedbugdisclosure>.

Results

Effects of Disclosure on Cost and Prevalence. Using our model and our best estimated parameter values (Table 1), we evaluated the impact of a newly implemented disclosure policy on the prevalence of bed bugs and the cost to landlords (Fig. 2). The cost of disclosure is high initially—reaching \$25 per unit on the market after 2 y—but it decreases steadily, so that by year 5, landlords experience savings. The trends in total cost can be understood by examining the cost components. While turnover cost remains relatively constant and minimal, vacancy and treatment costs vary over time. Vacancy cost escalates directly after the implementation of disclosure, as disclosure makes infested and recently infested units less appealing to potential tenants. Meanwhile, this pseudo-“quarantine” of infested and recently infested units

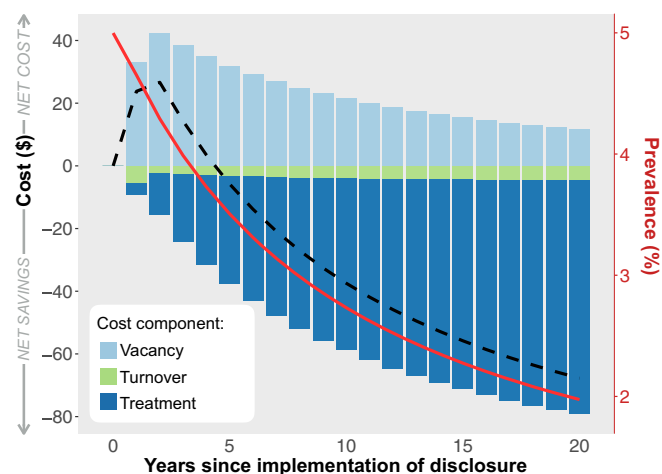


Fig. 2. Impact of disclosure on bed bug prevalence and cost over time. Cost to landlords, defined as the difference in average, per-unit cost in the presence of disclosure compared with no disclosure, is shown by the dashed black line. The components of cost are shown as bars representing averages over 1-y periods and are broken down into cost due to unrented vacant units (“vacancy”), cost due to treating infested units (“treatment”), and cost from moving tenants into vacant units (“turnover”). The overall prevalence of infestation in the population is shown by the solid, red line. The model was run by assuming that before the implementation of disclosure, the baseline prevalence of infestations was at a steady-state value of 5%. We assumed that disclosure discouraged but did not prevent rental of disclosed units ($s = 0.5$). Other parameter values are shown in Table 1, and results for additional parameter values are shown in SI Appendix.

causes a steady decrease in prevalence (Fig. 2). Accordingly, the cost of treatment starts slightly negative—reflecting a cost savings, and these savings increase over time as prevalence continues to decline. Because bed bug infestations increase vacancy due to the larger move-out rate ($b > 1$), the decline in prevalence also mitigates the effect of disclosure on vacancy; vacancy cost—although high initially—decreases over time. The net effect is that cost is high when disclosure is first introduced but quickly converts to savings that subsequently increase with time.

We examined in more detail how the predicted impact of disclosure policies depends on two parameter values that may vary between municipalities and are difficult to estimate: the baseline prevalence and the renter selectivity s (Figs. 3 and 4 and SI Appendix, Figs. S1 and S2). In all cases, year 5 marks the approximate turning point where vacancy costs are offset by savings from decreased treatment and total cost begins to dip below zero (Fig. 3E). In the initial years of disclosure, costs are greater if baseline prevalence is higher, and they are greatest when both the baseline prevalence and renter selectivity are high (Fig. 3A–D). The initial effect of disclosure policies under parameter regimes where both baseline prevalence and renter selectivity are high is to increase vacant units and the associated vacancy costs. In later years, the trend between cost and baseline prevalence actually reverses, and higher baseline prevalence results in increased savings. The same combination of high baseline prevalence and high renter selectivity that resulted in the greatest cost during the initial years of disclosure results in the greatest savings in later years. If we discount costs and savings that occur in later years (using methods detailed in SI Appendix), the results are similar, although the eventual savings decrease by an amount that is commensurate with the discount rate (SI Appendix, Fig. S3).

The greater cost savings accrued in later years are mediated by the effect of disclosure on the overall bed bug infestation prevalence (Fig. 4). Reductions in prevalence are seen as long as tenants show any selectivity in favor of units with no disclosed

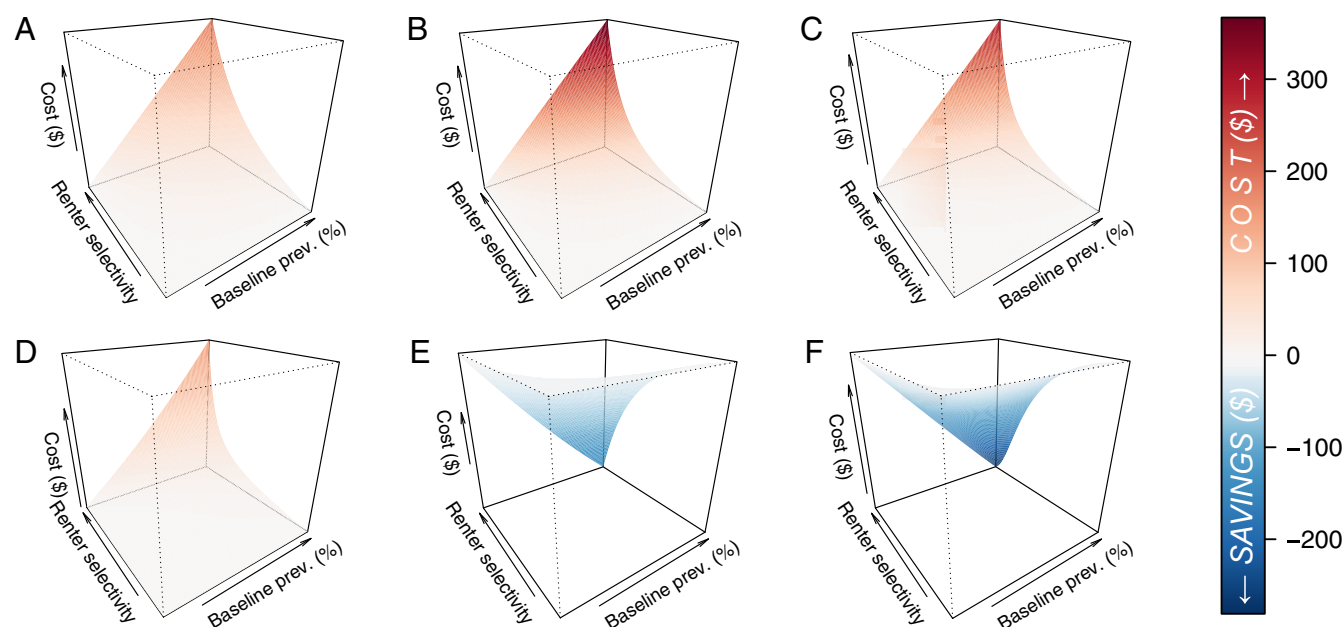


Fig. 3. Total per-unit cost due to disclosure over time, as a function of the baseline prevalence (prev.) and renter selectivity. Results are presented for years 1 (A), 2 (B), 3 (C), 4 (D), 5 (E), and 20 (F) after the implementation of a disclosure policy. Cost is calculated as the sum of the total cost in the population due to vacancy, treatment, and tenant turnover, for the given 1-y interval, averaged over the total rental units. Red indicates situations where the cost to landlords is higher due to disclosure, whereas blue indicates situations where costs have decreased from baseline (savings). Baseline prevalence (p) ranges from 0.1 to 10%, and renter selectivity (s) ranges from 0.01 to 1. To see the dependence of the cost components on these parameters, refer to *SI Appendix, Fig. S1*. An animation showing the dependence of cost on p and s over the initial 20 y of disclosure is available at <https://bedbugdisclosure.shinyapps.io/shinyapp/>.

bed bug history compared with units with a disclosed bed bug history ($s > 0$) but are more extreme for greater renter selectivity ($s \rightarrow 1$). This result holds at all times, and in some cases, we predict that prevalence can be driven to zero (bed bugs eliminated from the population). Overall, this analysis suggests that situations with unfavorable initial costs may be the same situations which lead to greater savings and prevalence reduction in the long run.

In addition to estimating disclosure costs for landlords, we also assessed the economic impact of disclosure on renters via methods outlined in *SI Appendix*. Disclosure policies are aimed at protecting tenants, and, as expected, we found this group to benefit financially from disclosure. Unlike landlords, who do not experience a net savings until later years, renters immediately benefit, with savings that grow over time as bed bug prevalence falls (*SI Appendix, Fig. S4*). In simulations with higher initial bed bug prevalence or higher renter selectivity (s), the savings in any given year are higher (*SI Appendix, Fig. S5*).

Analytic Results and Threshold Behavior. Similar to classic SIS infection models, our model of bed bug spread and control has two possible long-term outcomes: persistence of infection at an endemic equilibrium or decline of infestation levels toward zero. For any particular parameter set, one and only one of these outcomes represents a stable steady state of the dynamical system. We used the next-generation matrix method (38, 39) to calculate the basic reproductive ratio R_0 for our model as

$$R_0 = \left(\frac{n}{n+m} \beta + kbm \right) \left[\gamma + bm \frac{\gamma}{n(1-s) + \gamma} \right]^{-1}. \quad [6]$$

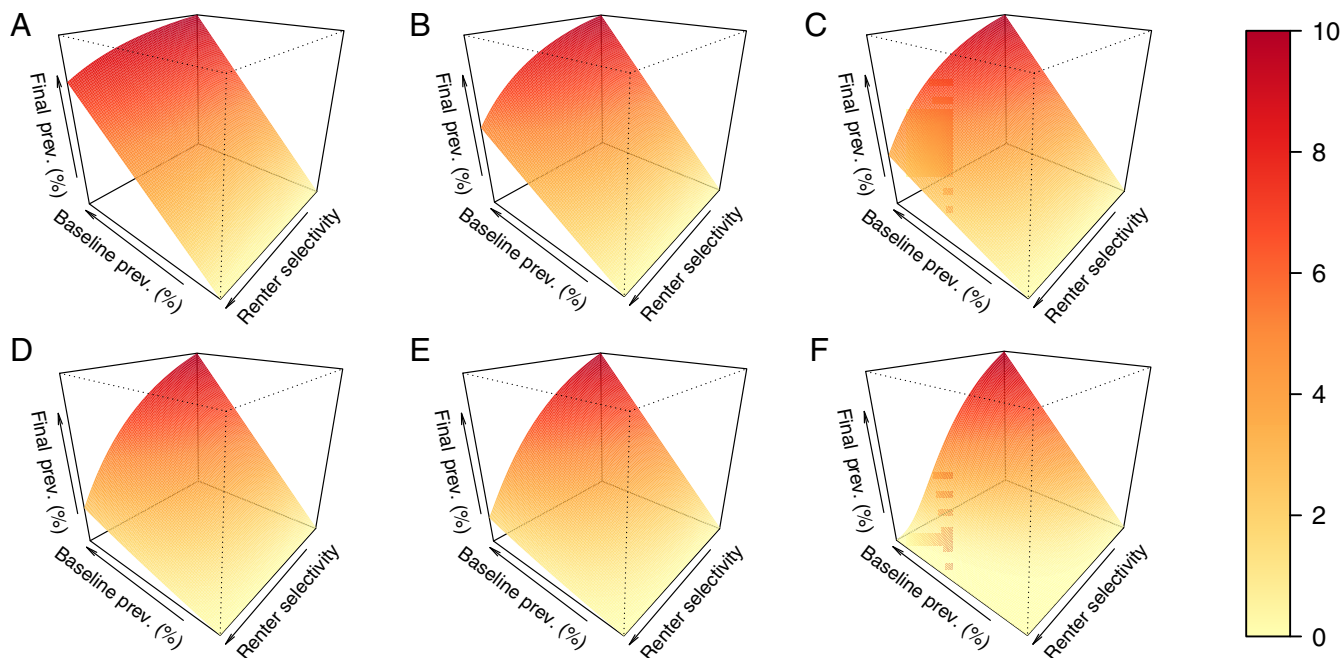
R_0 describes the average number of secondary infestations caused by the introduction of a single infested unit into a market of otherwise susceptible units. In addition, it determines the stability of the two possible equilibria for this model: Infestation persists as long as $R_0 > 1$ and declines to zero for $R_0 < 1$. In the

absence of infestation (Eq. 4 with $p = 0$), a fraction $S_r^*(0)/N = n/(n+m)$ of units are rented, and $S_v^*(0)/N = m/(n+m)$ are vacant. The first part of R_0 (within the parentheses) describes the initial spread of infestations by two independent routes: infectious transmission of already rented units [$\beta S_r^*(0)$] and relocation transmission of previously vacant units [$nkf(0)S_v^*(0) = kbm$]. The second part is the average time that an infested unit stays infested before being treated (either while still occupied or after being vacated). Disclosure reduces this infestation time by discouraging renters from moving into infested vacant apartments, preventing these units from contributing to interhousehold transmission.

For our baseline parameter values (Table 1 and β calibrated to give $p = 5\%$ steady-state prevalence), R_0 is near 1: In the absence of disclosure ($s = 0$), $R_0 = 1.05$, and it decreases to 0.88 as the renter selectivity increases to 1. R_0 is dominated by infectious transmission, while relocation transmission plays a more minor role (contributing $\sim 8\%$). Note that the length of the disclosure period does not directly influence the value of R_0 , and hence will not affect the persistence of infestation. Disclosure policies will have more impact on the value of R_0 when there is more apartment turnover (higher m and n) and when tenants are effectively turned off from disclosed rental units ($s \rightarrow 1$).

The functional form of R_0 also suggests that other additional policies could have a greater impact on reducing prevalence than disclosure alone. Policies that incentivize the rapid identification and treatment of bed bug infestations (increasing γ) are likely to have the greatest effect in terms of stemming the epidemic. Disclosure policies, if enacted well, may be among these, as landlords would likely wish to retain tenants in infested units, and treat these effectively, to avoid the requirement of disclosing infestations to future tenants.

Sensitivity of Results to Parameter Estimates. We analyzed the sensitivity of results to uncertainty in the estimates for the probability of relocation transmission (k), average duration of



Impact of Intermarket Migration. To determine how a rental market with legislated disclosure policies might be impacted by surrounding markets that do not adopt such policies, we considered a model that relaxes the assumption of a closed population and includes immigration of new tenants from external markets with a stable bed bug endemic. This model, outlined in [SI Appendix](#), assumes that a fraction, i , of new tenants moving into vacant units come from external markets that have a net bed bug prevalence e . First, we assumed that the prevalence of bed bug infestation in the external market (e) was 5% and examined the effect of disclosure on cost and bed bug prevalence ranging the external tenant fraction (i , the proportion of new rentals that are taken by external vs. internal tenants) from 0 to 40%. Second, we assumed that 20% of new rentals were by tenants from an external market ($i = 0.2$) and then evaluated cost and prevalence for a range of possible levels of infestation prevalence in these immigrant tenants (e from 5 to 20%). As expected, we found that migration into the system decreased the eventual savings caused by disclosure policies but that these savings were still apparent after approximately 5 y and significant after 10 y in all cases ([SI Appendix, Fig. S10 A and C](#)). Similarly, migration from regions with stable infestation levels dampened the decline in prevalence under disclosure policies, particularly when bed bug prevalence in the external market was much greater than the baseline prevalence of the system. For instance, prevalence declined to only 3.7% after 10 y when 20% of new tenants were immigrants from an external market with 20% prevalence, compared with 2.7% in the reference case with no immigration ([SI Appendix, Fig. S10D](#)). When the external prevalence is comparable to the baseline prevalence of the system ($e = 5\%$), intermarket migration had less impact on prevalence decline, even with a large fraction of immigrant tenants ($i = 40\%$; [SI Appendix, Fig. S10B](#)).

Due to the relative dearth of data on bed bug infestations, our model was formulated under a few simplifying assumptions, and our results should be interpreted in the context of these limitations. Our model does not incorporate elasticities that are likely to exist in the rental-housing market. Landlords might prefer to lower the rent of disclosed units rather than let them sit vacant, and not allowing prices to respond to disclosure may lead us to overestimate vacancy costs and, potentially, the decrease in prevalence due to the quarantine effect. Our model is most relevant to a single segment of a rental market in which units, landlords, and tenants are expected to be relatively similar. Results from our metapopulation models, which considered two hypothetical subpopulations that exist in isolation, suggest that disparities in the populations of interest that are not accounted for in our mass-action model could lead us to overestimate the benefits of disclosure; however, some benefits are likely to be recovered with more realistic levels of intermediate mixing between groups. We did not consider more complex metapopulation or network structures beyond our two-population models, and it is unclear before parametrizing such models how their results might diverge from those obtained from our mass-action model (49).

While our model included a single value for the treatment rate (γ), it was able to at least partially account for variability in treatment time that could result from some infestations being intrinsically more difficult to detect or treat; this property follows from the formulation of our model as a system of ordinary differential equations, which makes the implicit assumption that treatment times are exponentially distributed (and thus have a long tail). However, our model does not include temporal dynamics and feedback effects on γ . Disclosure policies require the disclosure of treatment along with infestation histories and would likely put pressure on landlords to treat vacant units before showing them to potential tenants. Not capturing these

changes in γ as landlords respond to disclosure may lead us to underestimate the benefits of disclosure. On the other hand, our model does not and cannot anticipate the evolution of additional insecticide resistance in bed bug populations, which could have enormous effects on γ and the future of the epidemic as a whole. Additional model limitations, along with possible extensions, are presented in *SI Appendix*.

Despite recent advances in pest-management strategies (34, 50) and improvements to urban housing, bed bugs have reemerged as a household pest and public health concern. Our model provides a first step toward evidence-based prospective analysis of policies to control the spread of bed bugs. Our results show that bed bug control is a classic collective action problem: Individual landlords bear the initial costs of disclosure policies, but after a few years, both landlords and tenants will benefit from the reduction in prevalence of infestations. Additionally, we show that while bed bugs are extremely difficult to eliminate from homes, they are likely to be less difficult to control in cities. We predict that, on average, a single infested residence infests little more than one additional residence ($R_0 \gtrsim 1$), whether by infectious or relocation transmission. Consequently, rational and enforced policies have great potential to stem the bed bug epidemic.

ACKNOWLEDGMENTS. We thank the other participants in the workshop "Socio-Spatial Ecology of the Bed Bug and its Control"—Claudia Arevalo, Dawn Biehler, Stephen Billings, Warren Booth, Ludovica Gaze, Andrew Greenlee, Kate Hacker, Loren Henderson, Sara McLafferty, Daniel Schneider, Shannon Sked, and Chris Sutherland—for discussions that helped shape this paper. This work was supported by the National Socio-Environmental Synthesis Center under funding received from National Science Foundation Grant DBI-1639145. A.L.H. was supported by Bill and Melinda Gates Foundation Grant OPP1148627 and National Institutes of Health Grant DP5OD019851. M.Z.L. was supported by NIH National Institute of Allergy and Infectious Disease Grant 5R01 AI101229, and S.X. was supported by NIH National Heart Lung and Blood Institute Grant F31 HL142153.

- Potter MF, Haynes KF, Fredericks J (2015) *Bed Bugs Across America: The 2015 Bed Bugs Without Borders Survey* (National Pest Management Association, Fairfax, VA), pp 4–14.
- Doggett SL, Geary MJ, Russell RC (2004) The resurgence of bed bugs in Australia: With notes on their ecology and control. *Environ Health* 4:30–38.
- Kilpinen O, Jensen KMV, Kristensen M (2008) Bed bug problems in Denmark, with a European perspective. *Proceedings of the Sixth International Conference on Urban Pests 1316* (OOK Press, Veszprém, Hungary), pp 395–399.
- Faúndez EI, Carvajal MA (2014) Bed bugs are back and also arriving is the southernmost record of *Cimex lectularius* (Heteroptera: Cimicidae) in South America. *J Med Entomol* 51:1073–1076.
- New York City Department of Health and Mental Hygiene (2014) Community health survey. Available at www1.nyc.gov/site/doh/data/data-sets/community-health-survey.page. Accessed June 3, 2017.
- Wu Y, Tracy DM, Barbarin AM, Barbu CM, Levy MZ (2014) A door-to-door survey of bed bug (*Cimex lectularius*) infestations in row homes in Philadelphia, Pennsylvania. *Am J Trop Med Hyg* 91:206–210.
- Goddard J, et al. (2009) Bed bugs (*Cimex lectularius*) and clinical consequences of their bites. *J Am Med Assoc* 301:1358–1366.
- Ashcroft R, et al. (2015) The mental health impact of bed bug infestations: A scoping review. *Int J Public Health* 60:827–837.
- Susser SR, et al. (2012) Mental health effects from urban bed bug infestation (*Cimex lectularius* L.): A cross-sectional study. *BMJ Open* 2:e000838. 1–5.
- Laliberté M, Hunt M, Williams-Jones B, Feldman DE (2013) Health care professionals and bedbugs: An ethical analysis of a resurgent scourge. *HEC Forum* 25:245–255.
- Miller DM, Kells S (2014) Bed bug action plan for home health care and social workers (Virginia Cooperative Extension, Blacksburg, VA). Available at <https://vtechworks.lib.vt.edu/handle/10919/55941>. Accessed August 19, 2018.
- Centers for Disease Control and Prevention (CDC) (2011) Acute illnesses associated with insecticides used to control bed bugs—seven states, 2003–2010. *MMWR Morb Mortal Wkly Rep* 60:1269–1274.
- Salazar R, et al. (2015) Bed bugs (*Cimex lectularius*) as vectors of *Trypanosoma cruzi*. *Am J Trop Med Hyg* 92:331–335.
- Brumpt E (1912) Le *Trypanosoma cruzi*, evolue chez *Conorhinus megistus*, *Cimex lectularius*, *Cimer boueti* et *Ornithodoros moubata*, Cycle évolutif de ce parasite. *Bull Soc Pathol Exot* 5:360–367.
- Leulmi H, et al. (2015) Competence of *Cimex lectularius* bed bugs for the transmission of *Bartonella quintana*, the agent of trench fever. *PLoS Negl Trop Dis* 9:e0003789.
- Notice of bedbug infestation history, New York City Administrative Code, Sect. 27-2018.1 (2010).
- Bedbug infestation prevention, treatment, disclosure, and reporting, San Francisco Health Code, Art. 11A, Sect. 620-623 (2012).
- Amendments to Code; Chapter 3, Mason City, IA, City Code 10-2f-5 (2018).
- An act concerning the rights and responsibilities of landlords and tenants regarding the treatment of bed bug infestations, Connecticut General Assembly, Public Act No. 16-51 (2016).
- Treatment of bedbug infestation, 14 - Maine Revised Statutes, Sect. 6021-A (2009).
- Gartland M (April 24, 2017) Landlords furious over possible bedbug disclosure law. *New York Post*. Available at <https://nypost.com/2017/04/24/landlords-furious-over-possible-bedbug-disclosure-law/>. Accessed August 5, 2018.
- Buckley C (June 25, 2010) Legislature passes bedbug-notification law. *The New York Times*. Available at <https://www.nytimes.com/2010/06/25/nyregion/25bedbugs.html>. Accessed August 5, 2018.
- Keeling MJ, Rohani P (2008) *Modeling Infectious Diseases in Humans and Animals* (Princeton Univ Press, Princeton).
- Collins G (April 13, 2018) The high cost of tenant turnover. *ManageCasa*. Available at <https://blog.managecasa.com/true-costs-tenant-turnover/>. Accessed August 6, 2018.
- U.S. Census Bureau (2018) American Community Survey 2017 American Community Survey 1-year estimates, table B25064: Median gross rent. Available at factfinder.census.gov. Accessed December 12, 2018.
- U.S. Census Bureau Housing vacancies and homeownership (CPS/HVS) (2018) Available at <https://www.census.gov/housing/hvs/index.html>. Accessed March 26, 2018.
- Munger P (2017) 2017 NAA survey of operating income & expenses in rental apartment communities. *National Apartment Association*. Available at https://www.naahq.org/sites/default/files/naa-documents/about-membership/ies_executive_summary_2017.pdf. Accessed March 26, 2018.
- Saenz VL, Booth W, Schal C, Vargo EL (2012) Genetic analysis of bed bug populations reveals small propagule size within individual infestations but high genetic diversity across infestations from the eastern United States. *J Med Entomol* 49:865–875.
- Fountain T, Duvaux L, Horsburgh G, Reinhardt K, Butlin RK (2014) Human-facilitated metapopulation dynamics in an emerging pest species, *Cimex lectularius*. *Mol Ecol* 23:1071–1084.
- Doggett SL, Dwyer DE, Peñas PF, Russell RC (2012) Bed bugs: Clinical relevance and control options. *Clin Microbiol Rev* 25:164–192.
- Vaidyanathan R, Feldlaufer MF (2013) Bed bug detection: Current technologies and future directions. *Am J Trop Med Hyg* 88:619–625.
- Cooper RA, Wang C, Singh N (2016) Evaluation of a model community-wide bed bug management program in affordable housing. *Pest Manage Sci* 72:45–56.

33. Wang C, Saltzmann K, Bennett G, Gibb T (2012) Comparison of three bed bug management strategies in a low-income apartment building. *Insects* 3:402–409.
34. Wang C, Gibb T, Bennett GW (2009) Evaluation of two least toxic integrated pest management programs for managing bed bugs (heteroptera: Cimicidae) with discussion of a bed bug intercepting device. *J Med Entomol* 46:566–571.
35. Gilbert SR (2011) Don't let them bite: Defining the responsibilities of landlords and tenants in the event of a bedbug infestation. *George Wash L Rev* 80:243–273.
36. Bryks S (2011) Analysis of 44 cases before the landlord and tenant board involving bed bug infestations in Ontario, Canada: Focus on adjudicator decisions based on entomological/pest management evidence and accountability under the residential tenancy act and other applicable legislation. *Insects* 2:343–353.
37. Soetaert K, Petzoldt T, Setzer RW (2010) Solving differential equations in R: Package desolve. *J Stat Softw* 33:1–25.
38. van den Driessche P, Watmough J (2002) Reproduction numbers and sub-threshold endemic equilibria for compartmental models of disease transmission. *Math Biosci* 180:29–48.
39. Heffernan JM, Smith RJ, Wahl LM (2005) Perspectives on the basic reproductive ratio. *J R Soc Interf* 2:281–293.
40. U.S. Census Bureau (2018) American Community Survey 2017 American community survey 1-year estimates, table B25063: Gross rent. Available at factfinder.census.gov. Accessed March 26, 2018.
41. Gharouni A, Wang L (2016) Modeling the spread of bed bug infestation and optimal resource allocation for disinfection. *Math Biosci Eng* 13:969–980.
42. Barker K (May 20, 2018) Behind New York's housing crisis: Weakened laws and fragmented regulation. *The New York Times*. Available at <https://www.nytimes.com/interactive/2018/05/20/nyregion/affordable-housing-nyc.html>. Accessed August 5, 2018.
43. Richter W (July 17, 2018) Here's how San Francisco's housing market took a turn toward crisis. *Business Insider*. Available at <https://www.businessinsider.com/san-francisco-housing-market-is-now-commonly-seen-as-being-in-crisis-2018-7>. Accessed August 13, 2018.
44. Phillips K (December 10, 2017) A woman tries to kill bed bugs with alcohol—and set a fire that left 10 without a home. *Washington Post*. Available at <https://www.washingtonpost.com/news/post-nation/wp/2017/12/10/a-woman-tried-to-kill-bed-bugs-with-alcohol-and-set-a-fire-that-left-10-without-a-home>. Accessed August 21, 2018.
45. Schwartz AF (2014) *Housing Policy in the United States* (Routledge, New York).
46. Biehler DD (2013) *Pests in the City: Flies, Bedbugs, Cockroaches, and Rats* (University of Washington Press, Seattle).
47. Johnson M, Hill A (1948) Partial resistance of a strain of bed bugs to DDT residual. *Med News Lett* 12:26–28.
48. Sentana-Lledo D, et al. (2016) Seasons, searches, and intentions: What the internet can tell us about the bed bug (Hemiptera: Cimicidae) epidemic. *J Med Entomol* 53:116–121.
49. Keeling M (2005) The implications of network structure for epidemic dynamics. *Theor Popul Biol* 67:1–8.
50. Barbarin AM, Jenkins NE, Rajotte EG, Thomas MB (2012) A preliminary evaluation of the potential of *Beauveria bassiana* for bed bug control. *J Invertebr Pathol* 111:82–85.