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Abstract

Locust swarms hit subsistence-staple-crop-growing households at random and are not privately controllable. A regional aerial-spraying scheme that supports these households' livelihood at the least cost is proposed. The properties of this scheme are analysed and two steady states are identified. The saddle one is socio-economically superior to the stable spiral. Simulations reveal that the respective stationary probability of a household's crop being devoured by the swarm diminishes with the number of households, yield per household, staple crop's replacement price and spraying efficacy, but rises with the spraying cost coefficient, locusts' multiplication rate and public planner's discount rate.

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1. Introduction

From time immemorial the growing of essential crops in large parts of North and West Africa and other less developed areas inhibited by indigenous people pursuing a traditional way of life has been impeded by swarms of locusts.[1] Due to the large size and high mobility of the locust swarms and the random nature of the timing and target of their raids, on the one hand, and due to insufficient private capital, skill, coordination, cooperation and willingness to share common-control costs, on the other hand, the locust plague has not been effectively dealt with by small, traditional, staple-crop-growing households. A locust swarm's survival and regeneration depend on cultivation size and type. A drastic change in the scale and types of farming activities and technology, such as in California during the Gold-Rush period, can reduce the number and size of locust swarms. However, a drastic change in the farming activities, practices and scale can also adversely affect the well being of the indigenous farming households which; for ethnic, cultural and human capital reasons; are not willing to give up their traditional way of life and relocate. As is the case in North and West Africa, the mean for supporting crop production and the traditional way of life of the indigenous population in regions raided by locust swarms is a regionally and internationally coordinated and financed aerial spraying of organophosphate pesticides with relatively short environmental persistence.[2] [3]

The locusts' lifecycle is six weeks, during which they are transformed from albino crawlers to green walkers and hopers, to pink flyers and, finally, to yellow

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[1] An early reference to this problem appears in *Exodus*, chapter 10, where it is respectfully ordered as the seventh plague—the fourth one from the last and most painful plague inflicted on Egypt.

[2] See Cowan and Gunby (1996) for an explanation to why chemical control of agricultural pests remains the dominant technology.

[3] The severe outburst of this plague in North and West Africa in the second half of the 1980s is due, in part, to the public complacency over a period of thirty years following the initial high control obtained with the application highly toxic, but environmentally persistent, dieldrin in the 1950s.

mating insects. They dwell in equal life-phase groups clearly identifiable by their colours. The principal crop-devastating one is that of the flying pink locusts—the swarm. Unlike many other groups of much smaller and better-camouflaged agricultural pests the pink-locust swarms are highly visible and their impact is immediately noticeable.

The locust swarm-control model constructed in the second and third sections and calibrated and simulated in the fourth section of this paper is socioeconomic. It considers a locust alley, such as those in North and West Africa, dominated by a perpetuated swarm and housing a large, stable number of similar, infinitely lived, traditional, farming households endowed with small fields for self-sustaining staple-crop production. The proposed model differs from the existing agricultural and environmental economic pest-control models for technologically advanced cash-crop farms[4] by its design to stabilise the production and supply of staple crops in less developed areas, and thereby support the native inhabitants' traditional way of life, at the least cost for the public planner. The model takes into account that, due to the high level of mobility of the pink locusts and variations in air temperature and currents, the swarm moves quickly and erratically and hence hits clusters of staple-crop-growing households at random. It also takes into account that, due to an immediately and highly noticeable presence and adverse impact, the swarm's location and density are accurately assessed and reported by the affected farming households. In view of the standard practice of scheduling the aerial spraying to the time when the swarm's is most vulnerable—the dawn that follows a reporting of the swarm's location and density by the affected households—the efficacy of the aerial spraying is also taken to

[4] See Shoemaker (1973) for an early agricultural pest-control modelling and Saphores (2000) for a brief survey of agricultural and environmental pest control models and a recent modification.

be certain.[5] However, the large size of the swarm and the convexity of the spraying costs prevent the eradication of the swarm. As is commonly the case, it is further taken that the crop of the raided households is completely devoured. Hence, previously sprayed fields are not revisited by the locust swarm during a growing season and, in turn, the number and timing of pesticide applications (cf. Hall and Norgaard, 1973; Saphores, 2000) and reentry (cf. Lichtenberg, Spear and Zilberman, 1993) are not relevant issues.

2. Locust-control model

Consider a topographically and climatically homogeneous locust alley with:

$N(t)$ indicating the size of the swarm (i.e., number of pink locusts) at t;

$F(N(t))$ the swarm natural multiplication at t, $F_N > 0, F_{NN} \leq 0$;

L the time-invariant number of farming households;

$\varphi(t)$ the probability of a household's field being raided by the swarm at t;

$y(t)$ the yield (in physical units) of a household field at t;

$s(t)$ the quantity of pesticide aerially sprayed against the swarm at t;

$R(s(t), N(t))$ the number of members of the swarm exterminated by aerial spraying at t, $R_s > 0,\quad R_{ss} \leq 0,$ $R_N > 0, R_{NN} \leq 0,$ and $R_{sN} > 0$;

$C(s(t))$ the cost (including the environmental damage) of aerial spraying at t, $C_s > 0, C_{ss} > 0$; and

$$\dot{N}(t) = F(N(t)) - R(s(t), N(t)) \qquad (1)$$

the instantaneous change in the swarm size.

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[5] See Feder (1979) for an analysis of pest management with a random pesticide effect.

Due to the long-range mobility of the pink locusts and variations in air temperature and currents, fields are hit by the swarm at random and independently of their particular location. Carlson and Wetzstein (1993) have argued that the likelihood of a crop getting eaten by pests is a function of cultivation size and is given by the entropy distribution. In the present case of small, numerous, identical and sharing similar climate and topography staple-crop-growing households, each household field has, *ex ante*, an equal probability of being hit by the swarm. It is assumed that this probability diminishingly increases with the ratio of the swarm size to the number of household fields in the locust alley: $\varphi(N(t)/L)$, $\varphi' > 0$, $\varphi'' < 0$, $\lim_{\frac{N}{L}\to 0} \varphi = 0$ and $\lim_{\frac{N}{L}\to\infty} \varphi = 1$. It is further assumed that in the event of being hit the household's crop is completely devoured by the swarm. The yield of a household field spared by the swarm is a positive, time-invariant (due to traditional cultivation methods) scalar y. Under these assumptions the yield of a household field in the locust alley at t is binomially distributed:

$$y(t) = \begin{cases} 0 & \varphi(N(t)/L) \\ y & 1-\varphi(N(t)/L) \end{cases}. \qquad (2)$$

In turn, the expected aggregate loss of yield in the locust alley at t is $\varphi(N(t)/L)yL$.

The proposed swarm-control model is based on the following premises. There is a trade-off between the instantaneous cost of aerial spraying and the instantaneous yield salvaged. The livelihood of households hit by the swarm depends on a free-of-charge public aid. The public aid fully compensates affected households for the loss of yield with purchased and delivered quantities of the staple crop. The public planner is risk neutral and farsighted and selects the aerial spraying trajectory, subject to the swarm-density motion equation, which minimizes the sum of the discounted instantaneous expected cost caused by the swarm—the instantaneous expected cost of compensating for the aggregate loss of yield plus the instantaneous cost of spraying.

The public planner's problem is formally expressed as

$$\min_{\{S\}} \int_0^{\infty} e^{-\rho t}[p(t)\varphi(N(t)/L)yL + C(s(t))]dt \qquad (3)$$

subject to the state-equation 1, where p denotes the crop-replacement price (i.e., the full price of delivering the staple crop grown in the locust alley to the affected households) and $0<\rho<1$ the public planner's instantaneous, fixed discount rate. The solution to this problem implies that the optimal instantaneous change in the intensity of aerial spraying is given by

$$\dot{s} = \frac{[\rho - F_N + R_N + \frac{R_{sN}}{R_s}(F-R)]C_s - p\varphi' y R_s}{[C_{ss} - C_s R_{ss}/R_s]}. \qquad (4)$$

(See Appendix A for details.)

Since $C_s, C_{ss}, R_s > 0$ and $R_{ss} \leq 0,$ the denominator in the above expression is positive. Consequently, a rise in the intensity of aerial spraying from one instance to another is supported by the planner's discount rate, by the positive swarm-density effect on the locust-extermination capacity (R_N) and by the swarm's instantaneous net growth ($F-R$). Likewise, a decline in the intensity of aerial spraying from one instance to another is supported by the marginal regeneration of locusts, by a marginal rise in the probability of a household field being raided, by the replacement cost for the planer of a devoured household yield (py) and by the efficacy of spraying (R_s). In any case, the change in the intensity of aerial spraying from one instance to another is moderated by the level of convexity of the aerial-spraying costs, but the effect of the marginal cost of aerial spraying on the instantaneous change in the spraying intensity is not clear.

3. Phase-plane portrait of a special case

In steady state (*SS*),

$$F(N_{SS}) = R(s_{SS}, N_{SS}) \tag{5}$$

and

$$[\rho - F_N(N_{SS}) + R_N(s_{SS}, N_{SS})]C_s(s_{SS}) = p\varphi'(N_{SS}/L)yR_s(s_{SS}, N_{SS})\,. \tag{6}$$

The computation of the steady-state swarm size and aerial-spraying intensity and the analysis of their asymptotic stability properties consider a case with the following computationally convenient specifications:

$$C = cs^2 \tag{7}$$

$$\varphi = 1 - \frac{1}{1 + \mu N / L} \tag{8}$$

$$F = \alpha N \tag{9}$$

and

$$R = \beta s N \tag{10}$$

where c, μ, α and β are positive scalars indicating the spraying cost coefficient, the hit-probability coefficient, the locusts' multiplication rate and the aerial spraying efficacy coefficient, respectively.

On the one hand, this case takes into account the worst-case scenario of exponentially multiplying locusts ($F_{NN} = 0$). On the other hand, it considers a linearly increasing marginal extermination power of spraying in the swarm size ($R_{NN} = 0$). These specifications are plausible when the locust alley is vast; which is typically the case due to the high and long-range mobility of locusts; and inhibited by numerous farming households. The carrying capacity of such an alley is very large relatively to the swarm size. Hence, locust congestion is insignificant and the decline in the swarm's marginal growth (F_{NN}) is negligible. With regard to $R_{NN} = 0$ we may argue that the larger the swarm the better the monitoring of its whereabouts in a vast alley. The increase in the accuracy of aerial spraying compensates for the diminishing stock effect on the spraying extermination power.

By substituting specifications 7-10 into equation 4 we obtain

$$\dot{s} = \rho s - \frac{p\mu\beta y N}{2c[1+\mu N/L]^2}\,. \tag{11}$$

In turn, $\frac{d(\dot{s}/s)}{dN} = -\frac{p\mu\beta y\{[L-\mu N]/(L+\mu N)\}}{2cs[1+\mu N/L]^2} \overset{<}{\underset{>}{=}} 0$ as $N \overset{<}{\underset{>}{=}} L/\mu$. As long as the swarm size is lower (greater) than the ratio of the number of farming households to the coefficient of the probability of being raided, a slight increase in the swarm size decelerates (accelerates) pesticide spraying.

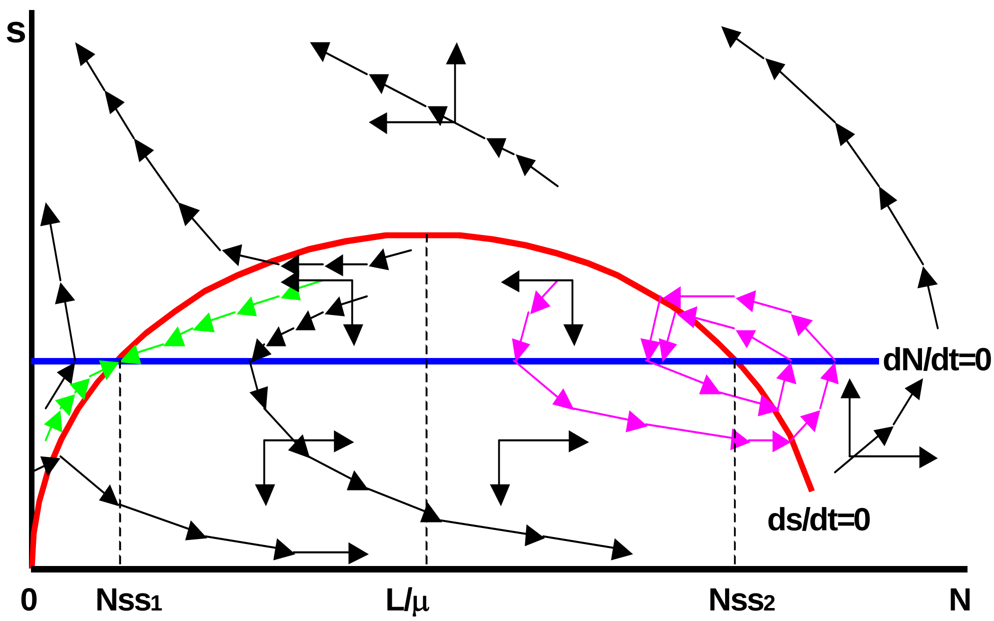

Figure 1. Phase-plane diagram of the swarm size and aerial spraying

As displayed by the phase-plane diagram there are two steady states: a saddle point and an asymptotically stable spiral. (See Appendix B for details.) The stationary aerial-spraying intensity is, however, unique and equal to the ratio of the locusts' multiplication rate to the aerial-spraying efficacy coefficient:

$$s_{SS} = \alpha / \beta . \quad (12)$$

This result is due to $F_{NN} = 0 = R_{NN}$. If F_{NN} is rather negative, the steady-state aerial spraying is less intensive. For instance, when locusts multiply in the alley in accordance with the logistic function $F = \alpha N(1 - N / N^{\max})$, the stationary spraying intensity is moderated by the ratio of the stationary number of locusts to the alley's carrying capacity ($N^{\max}$). Namely, $s_{SS} = (1 - \frac{N_{SS}}{N^{\max}})\frac{\alpha}{\beta}$.[6] Conversely, if R_{NN} is rather negative, the steady-state aerial spraying is more intensive. For example, when $R = \beta s N^{\gamma}$ with $0 < \gamma < 1$, the stationary aerial spraying is given by $s^{ss} = \frac{\alpha}{\beta}(N_{SS})^{1-\gamma}$.

In the combined case, where $F = \alpha N(1 - N / N^{\max})$ and $R = \beta s N^{\gamma}$, the stationary aerial spraying is given by $s_{SS} = (1 - \frac{N^{ss}}{N^{\max}})(N_{SS})^{1-\gamma}\frac{\alpha}{\beta}$ and it is not clear whether it is greater than, equal to, or larger than α / β. Hence, the computationally convenient case of $F_{NN} = 0 = R_{NN}$ is not a bad compromise.

The stationary swarm sizes are

$$N_{SS1} = \frac{1}{2(\mu / L)^2}\left\{\left(\frac{p\mu\beta^2 y}{2c\rho\alpha} - 2(\mu / L)\right) - \left[\left(\frac{p\mu\beta^2 y}{2c\rho\alpha} - 2(\mu / L)\right)^2 - 4(\mu / L)^2\right]^{0.5}\right\} \quad (13)$$

$$N_{SS2} = \frac{1}{2(\mu / L)^2}\left\{\left(\frac{p\mu\beta^2 y}{2c\rho\alpha} - 2(\mu / L)\right) + \left[\left(\frac{p\mu\beta^2 y}{2c\rho\alpha} - 2(\mu / L)\right)^2 - 4(\mu / L)^2\right]^{0.5}\right\}. \quad (14)$$

[6] The alley's carrying capacity might be proportional to the aggregate potential yield (i.e., $N^{\max} \propto Ly$).

The steady state with N_{SS1} can be approached along two trajectories: the north-eastern arm displays a gradual reduction in spraying as the swarm size decreases whereas the south-western arm displays intensifying spraying as the swarm size increases. The steady state with N_{SS2} is approachable along a spital trajectory.

From the perspectives of the farming households and the public planner, the probability of an individual household's crop being devoured is a meaningful indicator of the prevalence of the locust plague. By virtue of equation 8 and the stability of the number of farming households, a positive association between the stationary swarm size and the stationary probability of an individual household's crop being devoured exists. Hence, (s_{SS}, N_{SS1}) is preferred to (s_{SS}, N_{SS2}) by the farming households. As the stationary pesticide spraying level (and hence the stationary cost of spraying) is unique, (s_{SS}, N_{SS1}) is also preferred to (s_{SS}, N_{SS2}) by public planner. The following numerical simulations of the model parameter effects are therefore focused on N_{SS1} and employ equation 13. Equation 8 is subsequently used for computing the respective stationary probability of an individual household's crop being devoured by the swarm.

4. Effects of the model parameters

4.1 Parameters' benchmark values

The benchmark computations of the model parameter effects on the stationary swarm size and probability of an individual household's crop being devoured are conducted for a large locust alley with 10,000,000 traditional farming households, each potentially producing 1,000 kilograms of the traditional staple crop, whose replacement price is one dollar per kilogram, in a growing season. Due to harsh climate and soil conditions (e.g., on the edges of the Sahara, but not along the lower Nile) a single growing season a year is assumed.

The setting of the benchmark value of the natural growth rate α takes into account that a mating female locust lays, on the average, 35 eggs protected by cells made in the soil. Assuming gender balance in the group of the mating (yellow) locusts, these 35 eggs represent a 1750 percent of preliminary reproduction (i.e., a 17.5 initial reproduction rate). However, the four phases of locust life and the natural attrition rates during these phases moderate the (pink) swarm natural growth rate. The crop-growing season in the locust alley (in North Africa) is roughly three months. Since locusts dwell in life-phase groups and their life cycle is six weeks there are two full cycles of locust life and two waves of (flying, pink locust) swarms during a crop-growing season. The following chart displays the evolution of locusts during a crop-growing season in the locust alley from an initial cohort of N_0 crawling (albino) locusts and for the case where the rate of natural attrition of locusts is assumed, for simplicity and lack of information, to remain the same over the four life-phases, $0 < \delta < 1$.

Table 1. The locust population growth in a crop-growing season

Crawling $\rightarrow$	Walking $\rightarrow$	Flying $\rightarrow$	Mating $\rightarrow$
N_0	$(1-\delta)N_0$	$(1-\delta)^2 N_0$	$(1-\delta)^3 N_0$
Crawling $\rightarrow$	Walking $\rightarrow$	Flying $\rightarrow$	Mating $\rightarrow$
$17.5(1-\delta)^4 N_0$	$17.5(1-\delta)^5 N_0$	$17.5(1-\delta)^6 N_0$	$17.5(1-\delta)^7 N_0$

The natural rate of growth of the swarm during the crop-growing season can be computed by considering the sizes of the two consecutive groups of flying locusts:

$$\alpha = \frac{10(1-\delta)^6 N_0}{(1-\delta)^2 N_0} - 1 = 10(1-\delta)^4 - 1. \tag{15}$$

Assuming that the natural rate of attrition in each phase is 0.5, $\alpha \cong 0.1$.

The setting of the benchmark value of the aerial-spraying efficacy coefficient β is consistent with a stationary volume of pesticide sprayed during a growing season of 1,000 cubic meters and with $\alpha = 0.1$. Recalling equation 12,

$$\beta = 0.1/1000 = 0.0001. \qquad (16)$$

The benchmark value of the cost coefficient *c* is set by assuming that the price (including an implicit tax for environmental damage) of a cubic metre of pesticides is $ 4,000 and hence the costs of the aforementioned 1,000 cubic meters of pesticides used in a crop-growing season is $ 4,000,000 and by assuming that the costs of monitoring the swarm managing, and operating the fleet of aerial sprayers in the locust alley is taken to be $ 6,000,000. Recalling equation 7,

$$c = C/s^2 = (4{,}000{,}000 + 6{,}000{,}000)/1{,}000^2 = 10. \qquad (17)$$

The benchmark value of the probability coefficient μ was set by assuming that prior to implementing an aerial spraying campaign *N/L*=1,000 and the probability of an individual household field being raided by the swarm during the crop-growing season is 0.25. By substituting these figures into equation 8

$$0.25 = 1 - [1/(1 + 1000\mu)] \qquad (18)$$

and subsequently $\mu = 0.000333$.

Assuming that there is only one crop-growing season a year and that farming is the main economic activity, the benchmark figure for the discount rate is taken to be five percent ($\rho = 0.05$) for the growing season of the regional staple crop—roughly the current interest rate in the financial global market.

4.2 Simulation results

Table 2 summarizes the simulation results of the model parameter effects on N_{SS1} and φ_{SS1} obtained by using equations 13 and 8. The benchmark model parameters and the associated computational results are reported in the central column. The off-central column cells in each row report the simulation results obtained by gradually changing the value of one parameter from a very much below its benchmark value to a very much above its benchmark value while holding the rest at their benchmark levels.

The simulation results suggest that the probability of an individual household's crop being devoured by the swarm diminishes with the number of farming households, with the yield of a farming household, with the replacement price of the staple crop and with the aerial-spraying efficacy, but rises with the spraying cost coefficient, with the locusts' multiplication rate and with the public planner's discount rate.

Table 2. Parameters' effects on N_{SS1} and φ_{SS1}

Parameter level→	Very much below benchmark	Below benchmark	Benchmark	Above benchmark	Very much above benchmark
L	1,000,000	5,000,000	10,000,000	15,000,000	20,000,000
N_{SS1}	*30,646,079*	*30,150,754*	*30,090,241*	*30,070,137*	*30,060,098*
φ_{SS1}	*0.010102*	*0.002004*	*0.001001*	*0.000667*	*0.000500*
y (kg/season)	500	750	1,000	1,250	1,500
N_{SS1}	*60,301,508*	*40,147,171*	*30,090,241*	*24,062,540*	*20,046,758*
φ_{SS1}	*0.002004*	*0.001335*	*0.001001*	*0.000801*	*0.000667*
μ	0.000111	0.000222	0.000333	0.000444	0.000555
N_{SS1}	*90,270,722*	*45,135,361*	*30,090,241*	*22,567,680*	*18,054,144*
φ_{SS1}	*0.001001*	*0.001001*	*0.001001*	*0.001001*	*0.001001*
α (per season)	0.0333	0.0666	0.1000	0.1333	0.1666
N_{SS1}	*10,006,666*	*20,026,684*	*30,090,241*	*40,137,107*	*50,197,428*
φ_{SS1}	*0.000333*	*0.000666*	*0.001001*	*0.001335*	*0.001669*
β	0.0000333	0,0000666	0.0001	0.0001333	0.0001666
N_{SS1}	*276,000,000*	*68,009,911*	*30,090,241*	*16,919,390*	*10,827,268*
φ_{SS1}	*0.009101*	*0.00226*	*0.001001*	*0.000563*	*0.000360*
c ($)	5	7.5	10	12.5	15
N_{SS1}	*15,030,049*	*22,556,370*	*30,090,241*	*37,631,676*	*45,180,689*
φ_{SS1}	*0.0005*	*0.000751*	*0.001001*	*0.001252*	*0.001502*
p ($ per kg)	0.5	0.75	1	1.25	1.5
N_{SS1}	*60,301,508*	*40,147,171*	*30,090,241*	*24,062,540*	*20,046,758*
φ_{SS1}	*0.002004*	*0.001335*	*0.001001*	*0.000801*	*0.000667*
ρ (per season)	0.01	0.03	0.05	0.07	0.09
N_{SS1}	*6,008,410*	*18,039,672*	*30,090,241*	*42,160,173*	*54,249,529*
φ_{SS1}	*0.0002*	*0.0006*	*0.001001*	*0.001402*	*0.001803*

5. Conclusions

The paper deals with an agricultural plague affecting many small-scale farming households in less developed areas: locust swarms hit clusters of subsistence-staple-crop-growing households in their passage at random, inflict a complete, immediate damage and cannot be controlled by the uncoordinated households. An optimal control model is designed in this paper to stabilise the supply of staple crops in such areas and to support their inhabitants' traditional way of life at the least cost for the public planner. The solution of the public planner's optimal control problem reveals that a change in the intensity of aerial spraying from one instance to another is moderated by the level of convexity of the aerial-spraying costs. It also indicates that a rise in the intensity of aerial spraying from one instance to another is supported by the planner's discount rate, the swarm-density effect on the locust-extermination capacity and the swarm's instantaneous net growth; whereas a decline in the intensity of aerial spraying from one instance to another is supported by the marginal regeneration of locusts, a marginal rise in the probability of a household field being raided, the replacement cost for the planer of a devoured household yield and the efficacy of spraying.

The solution of the public planner's optimal control problem for the special case indicates further the existence of two steady states where the socioeconomically superior one is a saddle point. This saddle point may optimally be approached from an initial position characterised by a relatively large swarm and high pesticide use along a unique trajectory displaying a decline in the swarm density and accompanied by a decreasing aerial-spraying intensity. It may also be optimally approached from an initial position of low swarm density and low spraying level along a trajectory displaying increasing swarm density and aerial spraying of pesticides.

Numerical computations indicate the direction of the effects of the number of farming households, the yield of a farming household, the replacement price of the staple crop, the aerial-spraying efficacy, the spraying cost coefficient, the locusts' multiplication rate and the public planner's discount rate on the stationary probability of an individual household's crop being devoured by the swarm.

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Appendix

A. Solution of the optimal control problem

The Hamiltonian associated with this problem is:

$$H(t) = e^{-\rho t}[p(t)\varphi(N(t)/L)Ly + C(s(t))] + \lambda(t)[F(N(t)) - R(s(t), N(t))] \quad \text{(A1)}$$

where the co-state variable $\lambda(t)$ can be interpreted as the shadow cost of the locust swarm. In addition to the state equation (2), the necessary conditions for minimum require that the change in the shadow cost is

$$\dot{\lambda}(t) = -e^{-\rho t} p(t)\varphi'(N(t)/L)y - \lambda(t)[F_N(N(t)) - R_N(s(t), N(t))] \quad \text{(A2)}$$

and that the intensity of aerial spraying at any instance satisfies the following equality

$$e^{-\rho t}C_s(s(t)) - \lambda(t)R_s(s(t), N(t)) = 0\,. \quad \text{(A3)}$$

Consequently, the singular-control equation is compactly rendered as

$$-\rho e^{-\rho t}C_s + e^{-\rho t}C_{ss}\dot{s} - \dot{\lambda}R_s - \lambda(R_{ss}\dot{s} + R_{sN}\dot{N}) = 0\,. \quad \text{(A4)}$$

Recalling equations (1), (A2) and (A3)

$$-\rho C_s + C_{ss}\dot{s} + p\varphi' y R_s + C_s(F_N - R_N) - \frac{C_s}{R_s}[R_{ss}\dot{s}(t) + R_{sN}(F - R)] = 0 \quad \text{(A5)}$$

and by rearranging terms the optimal instantaneous change in the intensity of spraying is

$$\dot{s} = \frac{[\rho - F_N + R_N + \frac{R_{sN}}{R_s}(F - R)]C_s - p\varphi' y R_s}{[C_{ss} - C_s R_{ss}/R_s]}\,. \quad \text{(A6)}$$

B. Phase-plane diagram

From equation 1, the isocline $\dot{N} = 0$ is given by $s = \alpha/\beta$. Since $\frac{d\dot{N}}{ds} = -\beta N < 0$, $\dot{N} < 0$ in the region above this isocline and $\dot{N} > 0$ in the region below it (as displayed by the horizontal arrows in Figure 1).

Recalling equation 11, the isocline $\dot{s} = 0$ is given by

$$s = \frac{p\mu\beta yN}{2c\rho[1+\mu N/L]^2} \tag{B1}$$

and its slope

$$\frac{ds}{dN}_{|\dot{s}=0} = \frac{p\mu\beta y 2c\rho[1+\mu N/L]^2 - p\mu\beta y 4c\rho[1+\mu N/L]\mu(N/L)}{\{2c\rho[1+\mu N/L]^2\}^2}$$

$$= \frac{p\mu\beta y\{1-2\mu N/L[1+\mu N/L]\}}{2c\rho[1+\mu N/L]^2} = \frac{p\mu\beta y\{[L-\mu N]/(L+\mu N)\}}{2c\rho[1+\mu N/L]^2} \overset{>}{\underset{<}{=}} 0 \quad .\text{(B2)}$$

Hence,

$\frac{ds}{dN}_{|\dot{s}=0} \overset{>}{\underset{<}{=}} 0$ as $N \overset{<}{\underset{>}{=}} L/\mu$. Namely, the isocline $\dot{s}=0$ is an inverted parabola.

By differentiating equation 11,

$\frac{d\dot{s}}{dN} = -\frac{p\mu\beta y\{[L-\mu N]/(L+\mu N)\}}{2c[1+\mu N/L]^2} \overset{<}{\underset{>}{=}} 0$ as $N \overset{<}{\underset{>}{=}} L/\mu$ (displayed by the vertical arrows in Figure 1).

The stationary levels of N are obtained as follows. By substituting $\dot{s}=0$ and $s_{SS} = \alpha/\beta$ into equation 11,

$$2c\rho\alpha/\beta = \frac{p\mu\beta yN_{ss}}{[1+\mu N_{ss}/L]^2}\ . \tag{B3}$$

By rearranging terms,

$$2c\rho(\alpha/\beta)(\mu/L)^2 N_{SS}{}^2 - [p\mu\beta y - 4c\rho(\alpha/\beta)(\mu/L)]N_{SS} + 2c\rho(\alpha/\beta) = 0 \tag{B4}$$

and, in turn,

$$(\mu/L)^2 N_{SS}{}^2 - [(p\mu\beta^2 y/2c\rho\alpha) - 2(\mu/L)]N_{SS} + 1 = 0\ . \tag{B5}$$

N_{SS1} and N_{SS2} are the roots of this second-order polynomial. The real part of the eigenvalues of the state-transition matrix (A) of the linearized system of the differential equations 1 and 11 at the vicinity of any of the steady states is equal to

$$trA = (\alpha - \beta s_{SS}) + \rho = (\alpha - \beta(\alpha / \beta)) + \rho = \rho \in (0,1) \quad \text{(B6)}$$

and the directions of the arrows at the vicinity of (s_{SS}, N_{SS2}) imply

$$trA^2 - 4\det A < 0\,. \quad \text{(B7)}$$

Since the eigenvalues of the state-transition matrix constitute a conjugate complex pair whose real part is within the unit interval, (s_{SS}, N_{SS2}) is an asymptotically stable spiral.