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Do niches help in controlling disease spread in ecoepidemic models?

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Abstract

We present three models for refuges in interacting population systems of predator-prey type, with the prey hosting a transmissible disease. The safety niche is assumed to lessen the disease spread, but not to protect prey from predators. This represents a novelty with respect to standard ecosystems where the refuge prevents predators' attacks. The niche is assumed either to protect the healthy individuals, or to hinder the infected ones to get in contact with the susceptibles, or finally to reduce altogether contacts that might lead to new cases of the infection. Some counterintuitive results are obtained. The effectiveness of the three different strategies are compared. The best situation in terms of disease containment appears to be the environment which provides a place where the healthy individuals cannot come in contact with disease carriers.

Key words: refuge, niches, disease transmission, ecoepidemics
MSC 2000: AMS codes 92D30, 92D25, 92D40

1 Introduction

In population models predator-prey and competition systems play a dominant role, since the blossoming of this discipline about a century ago. In more recent times, more refined models try to better describe reality. Since prey try to seek protection against attacks of their predators in the features of the environment, scientists have tried to incorporate this behavior into the interaction models. The introduction of refuges has lead to the observation that the Lotka-Volterra models gets stabilized [3] even to show global asymptotic stability, [1, 2]. This shows the relevant role that spatial refuges exert in shaping the dynamics of

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predator-prey interplay. The refuge is expressed in the equations by reducing the amount of prey population available for hunting by the predators.

In this classical setting, if Y denotes the prey population that can take cover, by Y_n we denote the number of individuals who find protection in the niches that are available for their safety. Thus there are only $Y - Y_n$ individuals that can interact with the predators. There could be several functional forms that can be chosen for Y_n. The simplest one is a constant value, $Y_n = Y_0$, with $Y_0 \in \mathbf{R}_+$, or alternatively one could take a linear function of the prey population, $Y_n = Y_0 Y$, [3] or also a linear function of the predators X, $Y_n = Y_0 X$ [6]. More recently, a model has been proposed in which the form is taken as a bilinear function of both populations, $Y_n = Y_0 XY$, [4].

Ecoepidemiology investigates the influence of diseases in ecosystems, see Chapter 7 of [5]. It appears therefore that the refuges for some of the populations involved can be introduced also in this context. However, instead of using the environmental niches as protection against the predators, i.e. as an ecological tool as described above, we employ them in order to investigate whether they can influence the disease spread, i.e. we give them an epidemiological meaning. Therefore, it is not against predators that prey are protected, but we rather consider the case in which the healthy prey for some reason due to the conformation of the environment can avoid to come in contact with disease-carriers of their own population and therefore be somewhat protected from the epidemics. This is achieved by reduced contact rates that they have with infected individuals. Of all the various possible types of niche, to keep things simple, we just take the constant case, $Y_n = Y_0$.

In the next Sections, we present three models, based on the ecoepidemic system presented in [7], differing in the way the refuge is modeled. In Section 2, some of the susceptibles are prevented from interaction with infected individuals. In Section 3, it is part of the infected that are unable to become in contact with healthy individuals. In Section 4, we look at a reduced contact rate. A final discussion compares the results.

2 The model with a refuge for the healthy prey

Consider at first the system in which the susceptibles are more able to wander about than the infected ones, because the latter indeed are in general weakened by the disease. In this way, it is possible that the susceptibles reach places unattainable by the diseased individuals. Thus the latter cannot come in contact with the healthy remote individuals, and therefore these sound individuals cannot be infected. We assume that s denotes the fixed number of susceptibles that escape from the spread of the epidemics using the refuge.

The model is formulated as follows. The healthy prey R reproduce with net reproduction rate a, are subject to intraspecific competition only with other sound individuals at rate b and are hunted by predators at rate c. Those that can be infected by the diseased prey individuals U, as discussed above, leave their class at rate λ, to enter into the class of sick

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invividuals. The latter do not reproduce, are hunted at a rate $k \neq c$ by the predators. Here $k > c$ means that they are weaker than sound ones, and therefore more easy to capture, while $k < c$ instead takes into account the fact that they might be less palatable than the healthy ones. Finally, they can recover the disease at rate ω and therefore reenter into the S population. As mentioned above, infected are assumed not to contribute to intraspecific pressure, either of sound prey or among themselves; this again is grounded in the fact that their disease-related weakness prevents them to compete with the other individuals in the population. The predators are assumed to have also other food sources, for which they reproduce at rate d, but clearly get a benefit from the interactions with the healthy prey expressed by the parameter $e < c$. This constraint expresses the fact that the amount of food they get from the captured prey cannot exceed its mass. So far all the system parameters are nonnegative. For the predators hunting the infected prey, instead, we could model two different situations. For $h > 0$, the infected cause a damage to the predators, killing them. In this paper we concentrate only on this case. In the opposite case we could have the normal situation in which predators get a reward from capturing the diseased prey, so that in this situation we would have $0 < -h < k$. In summary, the ecoepidemic model with inclusion of a disease-safety niche for the susceptibles reads

$$\begin{aligned}\frac{dR}{dt} &= R[a - bR - cF] - \lambda(R - s)U + \omega U \\ \frac{dU}{dt} &= \lambda(R - s)U - U[kF + \omega] \\ \frac{dF}{dt} &= F[d + eR - fF - hU]\end{aligned} \tag{1}$$

Note that the above system needs some further qualifications. In fact when $R < s$ the next to last term in the first equation and the first one in the second equation would become positive and negative respectively, which makes no sense biologically. Therefore in such situations they should be understood to be identically zero. But in such case the infected prey in the system are easily seen to vanish, since in the second equation the term on the right hand side is always negative. The system then would settle to one of the equilibria of the classical disease-free predator-prey model, with logistic correction for the prey alternative food supply for the predators, see [7] for its brief analysis. For the benefit of the reader a short summary of its findings is presented also here at the top of Section 5.

The equilibria of (1) are $P_1 = (0, 0, 0)$ and

$$P_2 = \left(0, 0, \frac{d}{f}\right), \quad P_3 = \left(\frac{a}{b}, 0, 0\right), \quad P_4 = \left(\frac{af - cd}{bf + ce}, 0, \frac{ae + bd}{bf + ce}\right).$$

The first three points are always feasible, P_4 is feasible for

$$af > cd. \tag{2}$$

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Then there is coexistence $P_5 = (R_5, U_5, F_5)$. Its population values are obtained solving for F and U respectively the second and third equations in (1), thus giving

$$F_5 = \frac{1}{k}\left[\lambda(R_5 - s) - \omega\right], \quad U_5 = \frac{1}{h}\left[d + eR_5 - fF_5\right].$$

Substituting into the first one, we obtain the quadratic equation $W(R) \equiv \sum_{k=0}^{2} a_k R^k = 0$ whose roots give the values of R_5. Its coefficients have the following values

$$\begin{aligned} a_2 &= \frac{\lambda}{h}\left(\frac{f}{k}\lambda - e\right) - b - \frac{c}{k}\lambda, \quad a_0 = \frac{1}{hk}\left(dk + fs\lambda + f\omega\right)(s\lambda + \omega), \\ a_1 &= a + \frac{c}{k}(s\lambda + \omega) + \frac{1}{hk}[(s\lambda + \omega)(ek - f\lambda) - \lambda(dk + fs\lambda + f\omega)]. \end{aligned}$$

Now, since $a_0 > 0$, if the parabola $W(R)$ is concave one positive root will exist. Thus a sufficient condition for the existence of P_5 is $a_2 < 0$, i.e., explicitly,

$$f\lambda^2 < h[(b + e)k + c\lambda]. \tag{3}$$

For feasibility, we need also the other population values at a nonnegative level, a fact which is attained for U_5 if $ek > f\lambda$, else we must impose it, giving

$$R_5 < \frac{dk + f\lambda + f\omega}{f\lambda - ek}, \tag{4}$$

as we do for F_5 to obtain

$$R_5 > s + \frac{\omega}{\lambda}. \tag{5}$$

The Jacobian of (1) is

$$J = \begin{bmatrix} a - 2bR - \lambda U - cF & -\lambda(R - s) + \omega & -cR \\ \lambda U & \lambda(R - s) - kF - \omega & -kU \\ eF & -hF & d + eR - hU - 2fF \end{bmatrix}$$

The eigenvalues for P_1 are $-\lambda s - \omega$, d, a, entailing its instability. Those for P_2 are $-(dk + f\lambda s + f\omega)f^{-1}$, $-d$, $(af - cd)f^{-1}$ giving the stability condition

$$af < cd. \tag{6}$$

Comparing this condition with (2), we observe that there is a transcritical bifurcation, for which P_4 emanates from P_2 when the latter becomes unstable. In other words, introducing the healthy prey invasion number

$$R^{(i)} \equiv \frac{af}{cd}. \tag{7}$$

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we have that for $R^{(i)} > 1$ the healthy prey establish themselves in the environment.

For P_3 the eigenvalues are $(bd + ae)b^{-1}$, $(\lambda a - \lambda sb - b\omega)b_1$, $-a$, giving instability.

At P_4 one eigenvalue is easily factored out,

$$\frac{\lambda(af - cd) - k(bd + ae)}{ce + bf} - \lambda s - \omega,$$

while the remaining ones are roots of the quadratic equation

$$T(\delta) = \delta^2 + b_1\delta + b_2 = 0, \tag{8}$$

where letting $D = ce + bf$,

$$\begin{aligned} b_1 &= \frac{t_1}{D}, \quad b_2 = \frac{t_3}{D}, \quad t_1 = af(b + e) + bd(f - c), \\ t_3 &= (bd + ae)(af - cd), \quad t_2 = t_1^2 - 4t_3(bf + ce). \end{aligned}$$

Explicitly,

$$T_{1,2} = \frac{-b_1 \pm \sqrt{b_1^2 - 4b_2}}{2} = \frac{-t_1 \pm \sqrt{t_2}}{2(ec + bf)}. \tag{9}$$

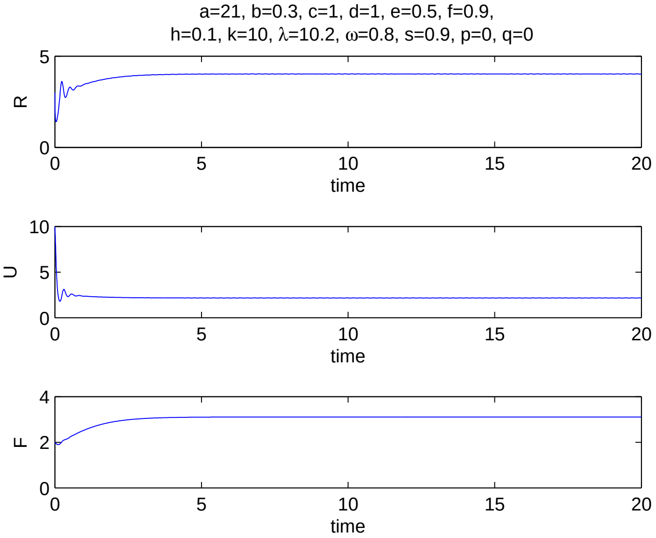

Figure 1: The coexistence equilibrium is attained for the following choice of parameters: $a = 21$, $b = 0.3$, $c = 1$, $d = 1$, $e = 0.5$, $f = 0.9$, $h = 0.1$, $k = 10$, $\lambda = 10.2$, $\omega = 0.8$, $s = 0.9$.

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By the feasibility condition (2), $t_3 > 0$ so that $t_2 < t_1^2$. Hence both roots of (9) have negative real part. Stability hinges then just on the first eigenvalue, i.e. $\lambda R_4 < kF_4 + \lambda s + \omega$ or explicitly the following condition

$$\lambda \frac{af - cd}{bf + ce} < k \frac{ae + bd}{bf + ce} + \lambda s + \omega. \tag{10}$$

For the coexistence equilibrium P_5, we have run some simulations to show that it can be attained at a stable level. Figure 1 shows one such instance, for the parameter values $s = 0.9$ and

$$\begin{gathered} a = 21, \quad b = 0.3, \quad c = 1, \quad d = 1, \quad e = 0.5, \quad f = 0.9, \\ h = 0.1, \quad k = 10, \quad \lambda = 10.2, \quad \omega = 0.8. \end{gathered} \tag{11}$$

Here the R_5 equilibrium value is much higher than the number of individuals s that can take cover in the safety niche. Observe also that the same inequality holds also for all the healthy prey population values before attaining the equilibrium level.

3 The case of a cover for the infected

Assume now that part of the infected are somehow confined in an environment in which healthy prey cannot enter. In this way the contagion risk is reduced. Let p denote the fixed number of infected that inhabit the unreacheable territory. With the remaining notation similar to model (1), the system in our present case reads

$$\begin{aligned} \frac{dR}{dt} &= R[a - bR - cF - \lambda(U - p)] + \omega U \\ \frac{dU}{dt} &= \lambda(U - p)R - U[kF + \omega] \\ \frac{dF}{dt} &= F[d + eR - fF - hU] \end{aligned} \tag{12}$$

Again, here we have to remark that for $U < p$ the contributions to the infected class is to be understood to drop to zero. In such case, once again, the infected prey in the system vanish, and the system settles to any equilibrium of the classical disease-free predator-prey model $\widetilde{P}_4 \equiv P_4$, [7].

For (12) the equilibria are again the origin $\widetilde{P}_1 \equiv P_1 = (0, 0, 0)$ and the point $\widetilde{P}_2 \equiv P_2$ but here we find a new predator-free point, while coexistence of healthy prey and predators is forbidden. We thus have

$$\widetilde{P}_0 = \left(\frac{a}{b}, \frac{a\lambda p}{a\lambda - b\omega}, 0 \right).$$

The latter is feasible for $a\lambda > b\omega$, i.e. introducing the disease basic reproduction number R_0, if

$$R_0 \equiv \frac{a\lambda}{b\omega} > 1. \tag{13}$$

The presence of the coexistence equilibrium $\widetilde{P}_5 = (\widetilde{R}_5, \widetilde{U}_5, \widetilde{F}_5)$ can be discussed as follows. From the last equation of (12) we solve for F

$$\widetilde{F}_5 = \frac{1}{f}(d + eR - hU)$$

and substitute into the remaining equations to obtain two conic sections

$$\Phi(R,U) \equiv \frac{k}{f}hU^2 - e\frac{k}{f}RU + U\left(\lambda - \frac{k}{f}d - \omega\right) - p\lambda = 0,$$
$$\Psi(R,U) \equiv -\left(b + \frac{c}{f}e\right)R^2 + \left(\frac{c}{f}h - \lambda\right)RU + \left(p\lambda - \frac{c}{f}d + a\right)R + \omega U = 0,$$

of which we seek an intersection $(\widetilde{R}_5, \widetilde{U}_5)$ in the first quadrant. We study the each one of them separately.

The implicit function $\Phi = 0$ can be solved as a function $R = \rho(U)$,

$$\rho(U) \equiv \frac{1}{fU}\left[khU^2 + (f\lambda - dk - f\omega)U - fp\lambda\right].$$

The numerator is a convex quadratic, which has two real roots with opposite signs, $\widetilde{U}_\pm$. In fact Descartes rule shows that independently of the sign of $f\lambda - dk - f\omega$ there is always one variation and one permanence of signs in its coefficients. For $U > 0$ it is therefore a continuous function crossing the U axis at $\widetilde{U}_+ > 0$, that has a vertical asymptote coinciding with the R axis and for $U > 0$ it raises up to infinity, asymptotically approaching the straight line $R = hkf^{-1}U$. Its inverse, $U = \rho^{-1}(R)$, has the R axis as horizontal asymptote for $R \to -\infty$ and goes to infinity for large positive R, crossing the U axis at U_+. This curve corresponds to the level 0 of the surface $\Phi(R,U)$. This implicit function is clearly negative at the origin, since $\Phi(0,0) = -p\lambda < 0$, and by continuity retains this sign everywhere below the curve $U = \rho^{-1}(R)$, while it is positive above it.

The function $\Psi(R,U)$ instead vanishes at the origin. Studying it on the R axis, we find that it must cross it also at the point

$$\widetilde{R}^{(1)} = \frac{fp\lambda - c + af}{bf + ce},$$

which can have either sign. If $\widetilde{R}^{(1)} < 0$, then $\Psi(R,U) > 0$ in the whole first quadrant. Therefore in this case Φ and Ψ do not meet in the first quadrant and the coexistence equilibrium $\widetilde{P}_5$ does not exist.

Conversely, if

$$f p\lambda + af > c \tag{14}$$

since Ψ is a conic section, it must raise up from the origin and then go down to meet the R axis at $\widetilde{R}_1$, thus it defines an arc of a concave function $U \equiv A(R)$ in the first quadrant. We must investigate when this arc $U = A(R)$ and the function $U = \rho^{-1}(R)$ meet. We do so by comparing their respective slopes at $R = 0$. Evidently, since $A(0) = 0$ and $\rho^{-1}(0) = \widetilde{U}_+ > 0$, if $A'(0) < (\rho^{-1})'(0)$, no intersection can exist, recalling the concavity of A and the fact that ρ^{-1} is monotonically increasing, as we can easily verify that $[\rho^{-1}(R)]' = [\rho'(U)]^{-1} > 0$ for $U > 0$. One can also explicitly find the expression of $A(U)$ as

$$A(U) = R\frac{(bf + ce)R + cd - fp\lambda - af}{(ch - f\lambda)R + f\omega}.$$

We must impose the converse condition $A'(0) > (\rho^{-1})'(0)$. Implicit differentiation of Φ and Ψ and evaluation at $R = 0$ yields

$$(\rho^{-1})'(0) = \frac{ekU_+}{2hkU_+ f\lambda - dk - f\omega}, \quad A'(0) = \frac{1}{\omega}(cd - fp\lambda - af).$$

For $U = 0$ we then need to have the slope of A larger than the one of ρ^{-1}, but this does not automatically imply an intersection of the two curves. In fact two intersections exist if we additionally require for instance that at the maximum of the arc A, or in general for any suitable value of the abscissa $\bar{R}$ in $[0, R_1]$, the values of A and ρ^{-1} "interlace", i.e. the following conditions are met

$$A'(0) > (\rho^{-1})'(0), \quad A\left(\bar{R}\right) \geq \rho^{-1}\left(\bar{R}\right). \tag{15}$$

The above conditions are then sufficient for the existence of $\widetilde{P}_5$. In particular we could here easily locate the reference point as $\bar{R} \equiv \frac{1}{2}\widetilde{R}_1$,

The Jacobian of (12) is

$$\widetilde{J} = \begin{bmatrix} a - 2bR - cF - \lambda(U - p) & -\lambda R + \omega & -cR \\ \lambda(U - p) & \lambda R - kF - \omega & -kU \\ eF & -hF & d + eR - hU - 2fF \end{bmatrix}.$$

$\widetilde{P}_1$ is always unstable, since the eigenvalues are d and

$$-\frac{1}{2}\,\omega + \frac{1}{2}\,a + \frac{1}{2}\,\lambda\,p \pm \frac{1}{2}\,\sqrt{\omega^2 + 2\,a\,\omega - 2\,\lambda\,p\,\omega + a^2 + 2\,a\,\lambda\,p + p^2\,\lambda^2}.$$

For $\widetilde{P}_2$ we find the eigenvalue $A_0 = -d$ and

$$\begin{aligned} A_\pm &= \frac{1}{2f}\left[af - kd - \omega f - cd + fp\lambda \pm \sqrt{Y}\right], \\ Y &= 2\,kd\omega\,f + \omega^2 f^2 - 2\,kd^2 c + 2\,\omega\,f^2 a + 2\,kdaf - 2\,\omega\,fcd + 2\,kd\lambda\,pf \\ &\quad -2\,\lambda\,p\omega\,f^2 - k^2 d^2 + 2\,cd\lambda\,pf + 2\,afcd - 2\,af^2\lambda\,p - a^2 f^2 - c^2 d^2 - p^2\lambda^2 f^2. \end{aligned}$$

Stability is then ensured if

$$f(a+p\lambda) < kd + \omega f + cd. \tag{16}$$

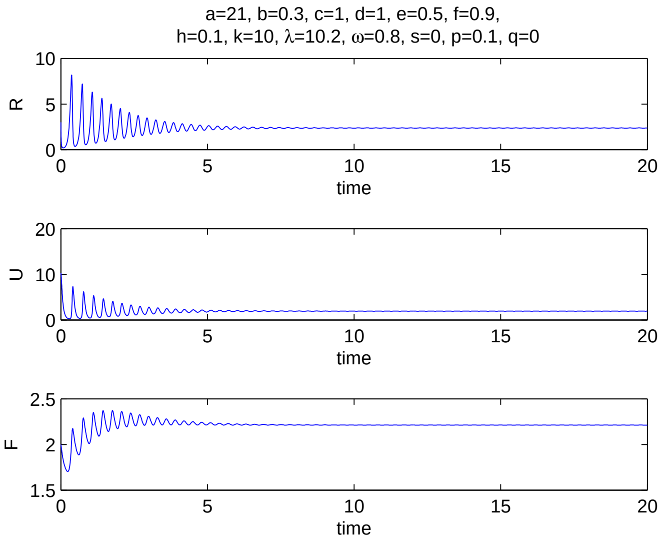

Figure 2: The coexistence equilibrium $\widetilde{P}_5$ is achieved when $p = 0.1$ and the remaining parameters are given by (11) as in Figure 1.

For the point $\widetilde{P}_0$ we have the following eigenvalues

$$B_1 = \frac{dba\lambda - db^2\omega + ea^2\lambda - eab\omega - ha\lambda pb}{b\,(a\lambda - b\omega)}$$

and the pair

$$\begin{aligned}
B_{\pm} &= \frac{1}{2b(a\lambda - b\omega)}\left[a^2\lambda^2 - a\lambda\, b\omega - b\omega\, a\lambda + b^2\omega^2 - ba^2\lambda + ab^2\omega - \lambda\, pb^2\omega \pm \sqrt{X}\right],\\
X &= b^2\omega^2a^2\lambda^2 - 2\,b^3a^3\lambda\,\omega + \lambda^2p^2b^4\omega^2 + a^2b^4\omega^2 + b^2a^4\lambda^2 + b^4\omega^2\omega^2 + 2\,a^4b\lambda^3\\
&\quad + a^2\lambda^2b^2\omega^2 - 2\,a^3\lambda^3b\omega - 2\,a^3\lambda^3b\omega - 2\,ab^4\omega\,\omega^2 - 2\,a^3b^2\omega\,\lambda^2 + 2\,a^2b^3\lambda\,\omega^2 + a^4\lambda^4\\
&\quad + 4\,a^2\lambda^2b^2\omega\,\omega - 2\,a\lambda\,b^3\omega^2\omega - 2\,b^3\omega^2a\lambda\,\omega - 2\,ab^4\omega^2\lambda\,p - 4\,a^3b^2\lambda^2\omega + 4\,a^2b^3\omega\,\lambda\,\omega\\
&\quad - 2\,a^2\lambda^3pb^2\omega + 2\,a\lambda^2b^3\omega^2p - 2\,b^4\omega\,\omega^2\lambda\,p + 2\,\lambda^2pb^3a^2\omega + 2\,b^3\omega\,a\lambda^2p\omega.
\end{aligned}$$

Using feasibility (13), stability in this case is ensured by the following set of conditions

$$a\lambda(db + ea - bhp) > db^2\omega + eab\omega, \quad a\lambda[a\lambda - 2b\omega - ab] < b\omega[bp\lambda - b\omega - ab]. \tag{17}$$

With the help of some simulations we can show that the coexistence equilibrium can be stably achieved, Figure 2. The refuge parameter used is $p = 0.1$ while all the remaining ones are those (11) as in Figure 1. Note that in this case raising the niche level to $p = 0.4$ causes the infected population at some point to fall below this threshold, so that they are wiped out, Figure 3. So while we stated that the disease-free point is not an equilibrium of (12) per se, in suitable situations it would certainly occur. In fact when the infected population U becomes smaller than the level p, and this occurs pretty early in the simulation as observed in Figure 3, the sound prey first and then also the predator populations suddenly surge to finally settle to the coexistence equilibrium of the underlying demographic model.

4 The case of reduced contacts

We consider now another situation, in which we assume that it is the rate of contacts between infected and susceptibles that gets somewhat reduced, due to the effect of a protective niche. In this case then we introduce the fraction $0 \leq q \leq 1$ of avoided contacts. The model, using

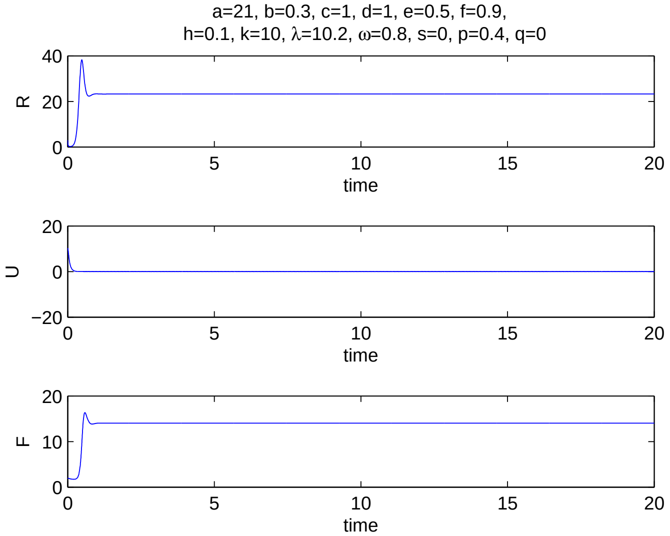

Figure 3: The disease-free equilibrium is attained for $p = 0.4$ with the remaining parameters given by (11) as in Figure 1. Note that the diseased population U falls below the level p very soon, and consequently both the healthy prey first and subsequently the predators pick up, and finally settle to the coexistence equilibrium of the underlying demographic model.

again the very same previous notation, now becomes

$$\begin{aligned} \frac{dR}{dt} &= R[a - bR - cF - (1-q)\lambda U] + \omega U \\ \frac{dU}{dt} &= U[(1-q)\lambda R - kF - \omega] \\ \frac{dF}{dt} &= F[d + eR - fF - hU] \end{aligned} \tag{18}$$

Clearly, by redefining $\beta = (1-q)\lambda$ for $\omega = 0$ we get the same model studied in [7]. For the convenience of the reader we summarize the basic results on the equilibria in which at least one of the population vanishes and then extend the study for the coexistence, to encompass here the situation $\omega \neq 0$ not considered in [7] for this specific equilibrium. The equilibria are again all the equilibria of the system (1), namely the origin $\widehat{P}_1 \equiv P_1 \equiv \widetilde{P}_1$, and $\widehat{P}_2 \equiv P_2 \equiv \widetilde{P}_2$, $\widehat{P}_3 \equiv P_3$, $\widehat{P}_4 \equiv P_4$. For feasibility of $\widehat{P}_4$ clearly we need again (2).

Coexistence $\widehat{P}_5 = (\widehat{R}_5, \widehat{U}_5, \widehat{F}_5)$ is obtained by solving the second equation in (18) at equilibrium and substituting into the third equation of (18) to get

$$\widehat{F}_5 = \frac{(1-q)\lambda \widehat{R}_5 - \omega}{k}, \quad \widehat{U}_5 = \left(\frac{e}{h} - \frac{f}{hk}(1-q)\lambda\right)\widehat{R}_5 + \frac{d}{h} + \frac{f}{hk}\omega,$$

and finally from the first equation in (18) we get the quadratic $\sum_{k=0}^{2} c_k R^k$, whose roots determine the value of $\widehat{R}_5$, with $c_0 = (dk\omega + f\omega^2)(hk)^{-1} > 0$ and

$$c_2 = \left(\frac{c}{k} - \frac{e}{h}\right)(1-q)\lambda + \frac{f}{hk}(1-q)^2\lambda^2 - b, \quad c_1 = a + \frac{c}{k}\omega + \frac{e}{h}\omega - (1-q)\lambda\left(\frac{d}{h} + 2\frac{f}{hk}\omega\right).$$

Again we can apply Descartes' rule to have at least a positive root. This occurs for one root if we impose either one of the alternative conditions

$$c_2 < 0, \quad c_1 < 0; \qquad c_2 < 0, \quad c_1 > 0, \tag{19}$$

and we get two positive roots if

$$c_2 > 0, \quad c_1 < 0. \tag{20}$$

We do not write explicitly these conditions. For feasibility we must impose

$$\widehat{R}_5 > \frac{\omega}{(1-q)\lambda k} \tag{21}$$

and the condition

$$\widehat{R}_5 > \frac{dk + f\omega}{ek - f(1-q)\lambda}, \quad ek > f(1-q)\lambda, \tag{22}$$

since the opposite one $ek < f(1-q)\lambda$ would give a negative value for $\widehat{R}_5$.

For $\widehat{P}_1$ the eigenvalues are $-\omega$, d, a, showing its instability.

The eigenvalues of $\widehat{P}_2$ are $-(dk + f\omega)f^{-1}$, $-d$, $(af - cd)f^{-1}$, for which the stability condition is (6). Here again comparing (6) with (2) we observe the existence of a transcritical bifurcation, for which the same conclusions, using the healthy prey invasion number (7) can be drawn as for the model with refuge for the healthy prey (1).

The eigenvalues of $\widehat{P}_3$ are $(bd + ae)b^{-1}$, $[(1-q)\lambda a - b\omega]b^{-1}$, $-a$, thus it is unstable.

For $\widehat{P}_4$ one eigenvalue can easily be factored out, while the other ones are the roots of the quadratic (8). Thus, as found formerly, by feasibility (2) both its roots have negative real part, and stability depends only on the first eigenvalue, namely it is given by $(1-q)\lambda R_4 < kF_4 + \omega$, a condition that can also be explicitly written as

$$(1-q)\lambda \frac{af - cd}{bf + ce} < k\frac{ae + bd}{bf + ce} + \omega. \tag{23}$$

Figure 4 shows the result of a simulation with the same parameter values (11) as for Figure 1, but for $q = 0.1$, assessing the stability of the coexistence equilibrium $\widehat{P}_5$.

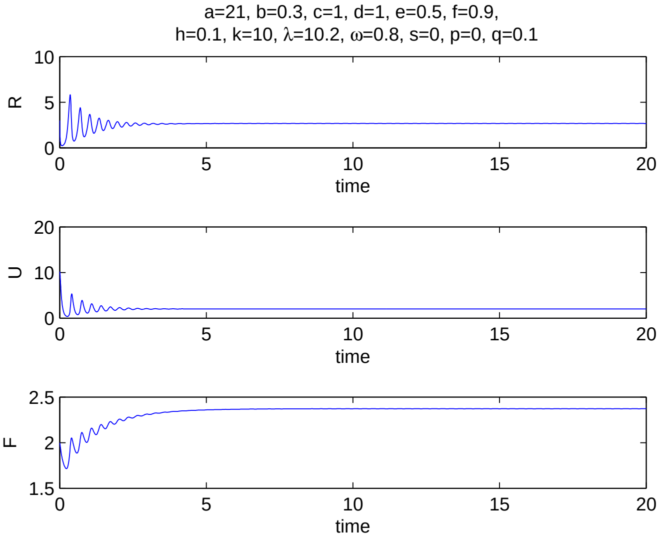

Figure 4: The coexistence equilibrium is attained $\widehat{P}_5$ for the same parameters (11) as in Figure 1 with $q = 0.1$.

5 Models Comparison

The classical predator-prey model underlying these ecoepidemic systems is obtained by eliminating the variable U and its corresponding equation in (18). The resulting system, which can be seen as the projection of the ones considered here onto the disease-free $R-F$ phase plane, has the following equilibria:

$$Q_1 = (0,0), \quad Q_2 = \left(0, \frac{d}{f}\right), \quad Q_3 = \left(\frac{a}{b}, 0\right), \quad Q_4 = \left(\frac{af-cd}{bf+ce}, \frac{ae+bd}{bf+ce}\right).$$

The latter is feasible when (2) holds.

Q_1 and Q_3 are both unstable, in view of their respective eigenvalues a, d and $-a$, $(ae+bd)b^{-1}$. For Q_2 we find $(af-cd)f^{-1}$, $-d$ showing that it is stable exactly when (6) holds. The eigenvalues of Q_4 are complex conjugate, with negative real part, so that Q_4 is unconditionally stable. Being the only such equilibrium, local stability implies global stability. This fact could be shown also via a suitable Lyapunov function.

Thus, the ecoepidemic system exhibits a similar range of behaviors as the demographic ecosystem: coexistence is allowed, both with and without infected, compare P_4 and P_5, and also the predators-only equilibrium P_2, recalling that other food sources for them are available. Evidently, in this prey-free environment, the role of the refuge for the prey is nonexistent. The same does not occur, not surprisingly either, for the disease-free equilibrium P_4. In fact the population levels are not affected by the size of the refuges in any model, but the stability of this equilibrium does in fact depend on this parameter. The way in which the refuges' parameters s and q appear in the stability conditions differs, compare (10) and (23). But both have a stabilizing effect for the ecoepidemic system, a result which as mentioned agrees with former findings in the literature for predator-prey models, [3]. In the case of the reduced contacts model, the refuge favors stability since, mathematically, the left hand side becomes smaller due to a positive q, while in the case of a refuge for the healthy prey it is the right hand side that gets increased by the presence of s. However, since q is a fraction, denoting the relative reduction in the frequency of contacts, while s represents the number of refuges, it is more likely that the latter has a more marked influence on stability.

Note further that the disease-free equilibrium P_4 does not exist per se if the infected find cover, i.e. in system (12). However, we have seen that this equilibrium is achievable when the infected population value falls below the threshold given by the size of the niche p. For the same model (12), however, in place of the disease-free equilibrium, we find an additional situation that does not arise in the other models, in which namely the predators get wiped out from the environment while the prey thrive with their disease becoming endemic. This predator-free environment can be achieved if the conditions (13) and (17) hold. In such situation note that the infected level is directly proportional to the size p of the niche available for their segregation. In particular, if the disease is unrecoverable,

$\omega = 0$, or if there is no intraspecific competition among the healthy prey, $b = 0$, the size of surviving infected is exactly p. If these situations are not met, then the resulting number of thriving infected is larger than p. Hence, the higher the refuges, the more endemic the disease remains, when the predators are wiped out. This is a somewhat counterintuitive result. It is true that the niches help the infected not to get in contact with the susceptibles, but then one would expect also an advantage for the healthy individuals. Instead we find them at the level ab^{-1} which would be attained at the unstable equilibrium P_2. Hence, another way of looking at this situation is to observe that in this case the niche stabilizes the otherwise unstable predator-free equilibrium, at the price of making the disease endemic.

The numerical experiments with the coexistence equilibria of the three models show that using the set of demographic parameter values in (11), i.e. those given by the first row, the system settles to the demographic disease-free equilibrium $(23.2475, 0, 14.0261)$, whose projection onto the $R - F$ phase plane corresponds of course to the equilibrium of the underlying classical predator-prey system, $(23.2475, 14.0261)$. If we now introduce the disease, with the related parameter values found in the second row of (11), we find the ecoepidemic equilibrium $(2.1133, 1.8658, 2.0819)$. As we can easily observe, the disease has a large impact on the system, reducing both its populations by an order of magnitude. Although the epidemics affects only the prey, its effect is felt also by the predators. This can easily be interpreted, because a reduced food supply, due to a lower prey population caused by the disease, must reduce also the predator population and, in addition, consumption of infected prey is harmful for the predators. In other words, diseases, as stated many times in ecoepidemiological research, affect the whole ecosystems, and therefore in environmental studies they cannot be easily neglected.

Coming back to the effects of our safety refuges, we have run simulations using the previous parameter values (11), with various sizes for the refuge coefficients s, p and q. As remarked earlier the proviso holds, that in the models (1) and (12) a check is implemented, for which when $U < p$ and $R < s$ the next to last term in the first equation and the first one in the second equation are set to zero in both (1) and (12). The results are reported in Figures 5-7.

Comparison of the results indicates that for the healthy refuge, the healthy prey and the predators at equilibrium increase in a linear fashion their numbers as s grows, while the infected appear to reach a plateau. When the infected prey have a cover, there is a threshold value of its size p beyond which the disease disappears and the other populations suddenly jump to the level of the corresponding demographic, disease-free, classical model and stay there independently of the value of p. A similar result holds also when it is the contact rate that gets reduced, i.e. for model (18). In this case the equilibria behavior before the threshold value of q is reached appears to be smoother than in the previous case of system (12).

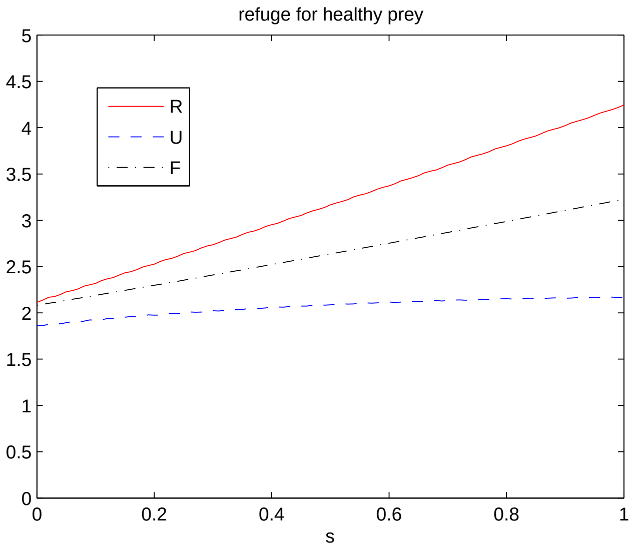

Figure 5: Equilibrium population values of system (1) as function of the refuge size s.

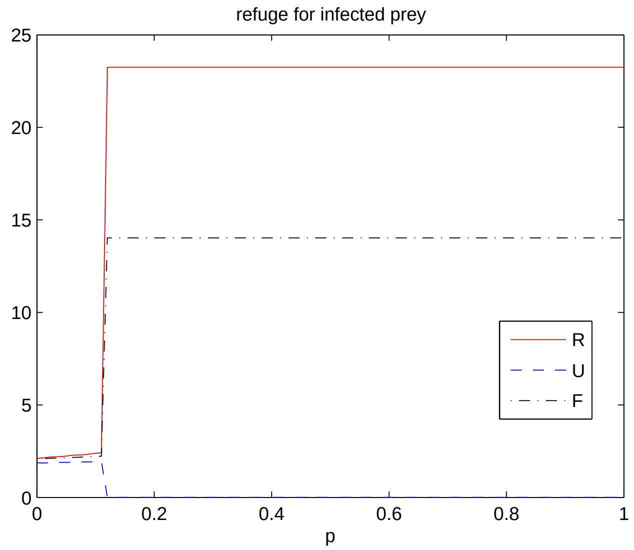

Figure 6: Equilibrium population values of system (12) as function of the refuge size p.

We also plot the equilibrium levels of the various populations as function of the disease parameters λ and ω versus the refuge parameters s, p and q in Figures 8-13

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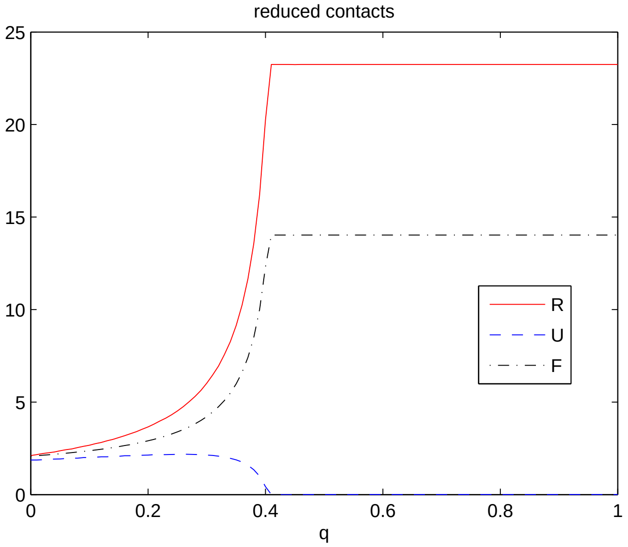

Figure 7: Equilibrium population values of system (18) as function of the contact rate reduction coefficient q.

Comparing the susceptible levels in Figure 8, when the contact rate is high, an improvement in the equilibrium value is obtained for larger value of the refuge s in model (1), while for (12) and (18) an increase in the refuge size is irrelevant, the equilibrium configuration is determined essentiall by the contact rate λ. A similar behavior holds for the predators as well, Figure 10. A corresponding opposite effect is noted among the infected, Figure 9. In (1) a larger s smoooths out the growth of the equilibrium value, which is much sharper for the other two models, once the contact rate crosses the critical threshold.

Considerations along the above lines can be also made when comparing the refuge usage versus the disease recovery rate ω. Comparing Figures 11-13, we see the marked similarities between the equilibrium surfaces of the models (12) and (18), for all the populations involved. Both healthy prey and predators show a linear increase as function of the recovery rate, while the niche apparently does not play any essential role. The infected prey instead seem to reach a plateau. Instead, for the model 1, we find again a linear increas in terms of ω, but what is more important, also a sharp increase of healthy prey and predators as function of the niche size s. A corresponding decrease of infectives can also be observed, which is more marked for high values of the niche size and of the recovery rate, as it should be expected.

Based on these overall considerations, it appears that the model (1) shows the best characteristics in terms of disease reduction. Thus in this type of predator-prey ecoepidemic system with disease just in the prey, for an endemic disease, the ecosystem with a place where some of the healthy individuals can be segregated from coming in contact with disease carriers would exhibit the best features to preserve the epidemics to spread. This result could possibly give some hints to field ecologists as how to fight diseases in wild populations, in case some artificial refuges, unreachable by the diseased individuals, can be provided in specific real-life situations.

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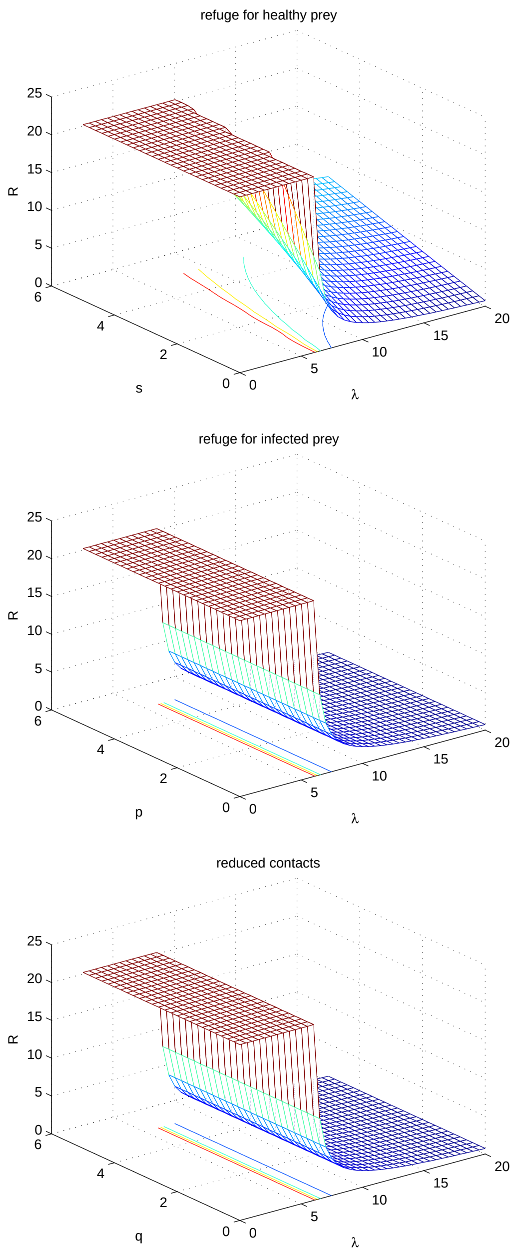

Figure 8: Equilibrium population value for the healthy prey as function of the disease contact rate λ and refuge size: top, refuge size s in model (1); middle, refuge size p in model (12); bottom, reduced contact rate q in model (18). Other parameter values as in (11).

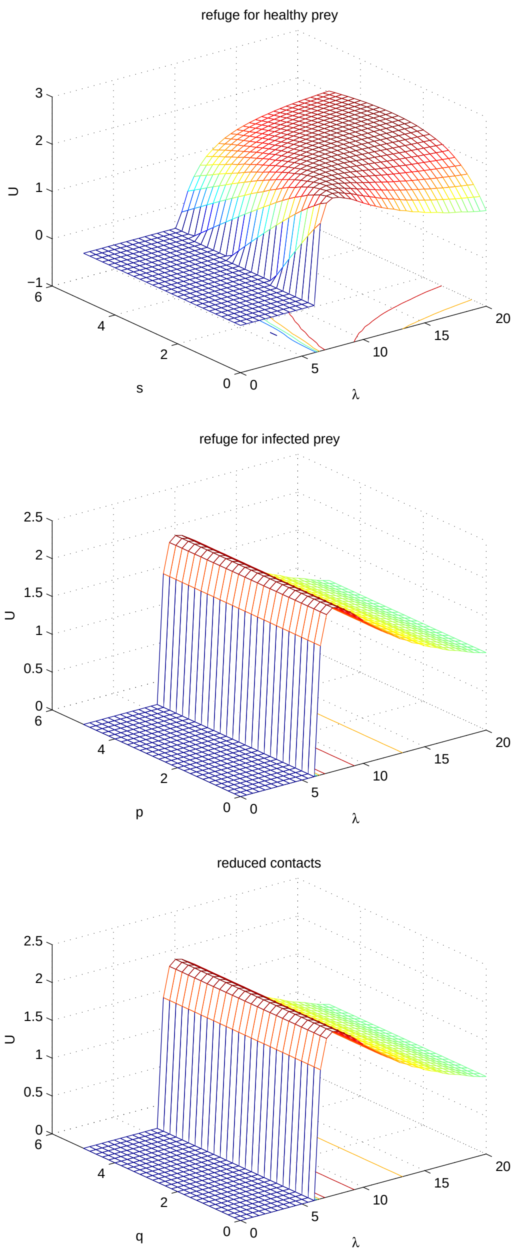

Figure 9: Equilibrium population value for the infected prey as function of the disease contact rate λ and refuge size: top, refuge size s in model (1); middle, refuge size p in model (12); bottom, reduced contact rate q in model (18). Other parameter values as in (11).

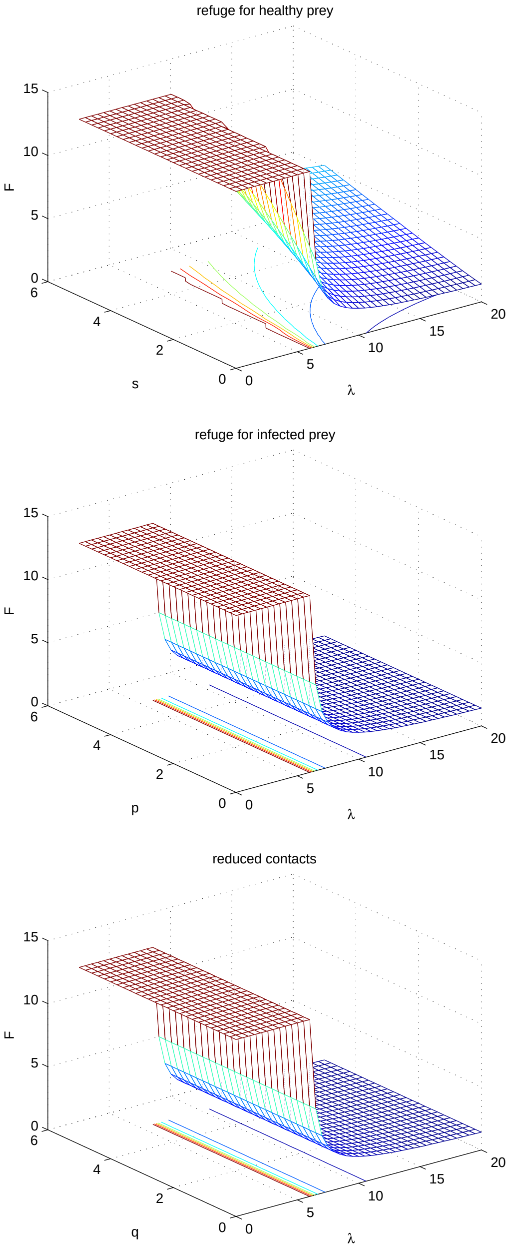

Figure 10: Equilibrium population value for the predators as function of the disease contact rate λ and refuge size: top, refuge size s in model (1); middle, refuge size p in model (12); bottom, reduced contact rate q in model (18). Other parameter values as in (11).

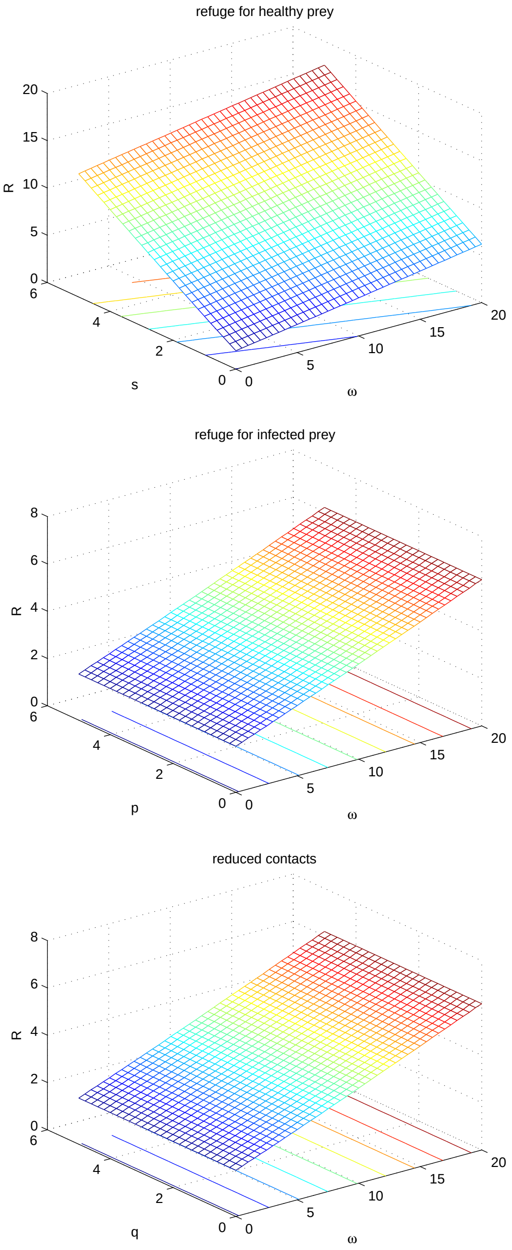

Figure 11: Equilibrium population value for the healthy prey as function of the disease contact rate ω and refuge size: top, refuge size s in model (1); middle, refuge size p in model (12); bottom, reduced contact rate q in model (18). Other parameter values as in (11).

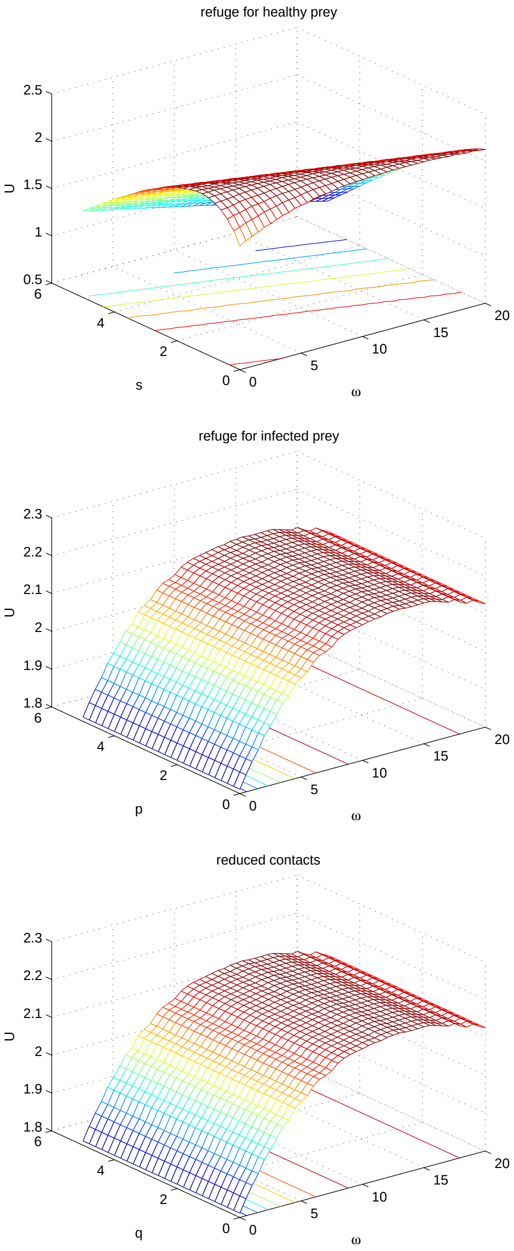

Figure 12: Equilibrium population value for the infected prey as function of the disease contact rate ω and refuge size: top, refuge size s in model (1); middle, refuge size p in model (12); bottom, reduced contact rate q in model (18). Other parameter values as in (11).

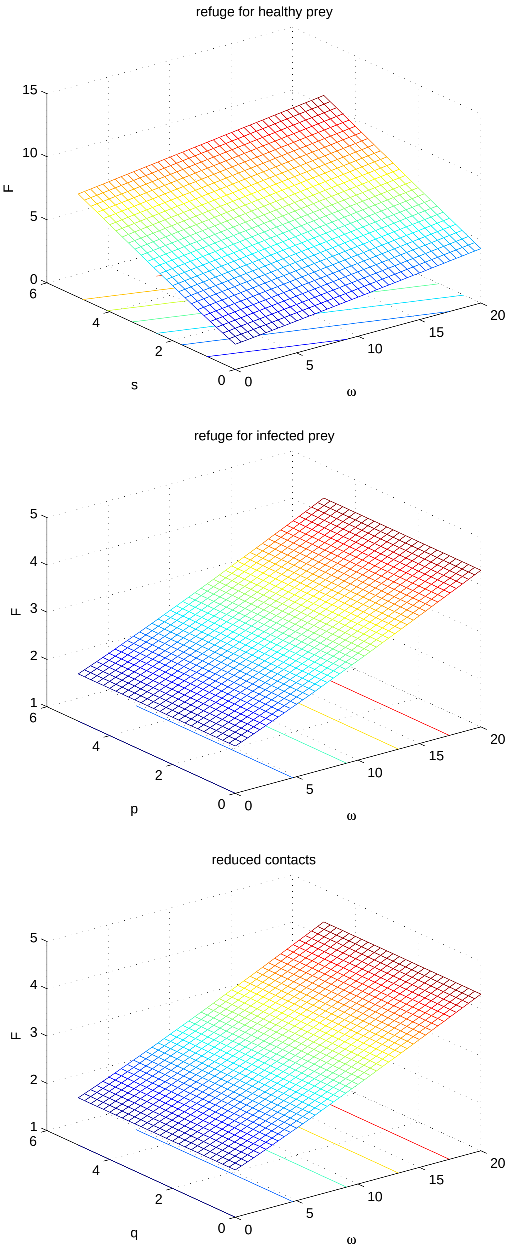

Figure 13: Equilibrium population value for the predators as function of the disease contact rate ω and refuge size: top, refuge size s in model (1); middle, refuge size p in model (12); bottom, reduced contact rate q in model (18). Other parameter values as in (11).