

## PREDATION RISK CAN DRIVE CYCLES IN ZOO NOTIC DISEASE PREVALENCE

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### ABSTRACT

The recent increase in human cases of leishmaniasis in northern Israel has been accompanied by dramatic anthropogenic changes in the landscape that affect the behavioral ecology of one of its mammalian reservoirs, the rock hyrax, *Procapra capensis*. Hyraxes migrate from refuge to refuge, presumably following forage availability, but their migration patterns are strongly affected by the availability and spacing of the rock piles that form their den sites and give them protection from predators. We therefore expect changes in predation risk to influence the ability of hyrax groups to migrate from site to site. We combine mathematical metapopulation models of hyrax behavioral ecology, as well as compartmental models of disease dynamics, to investigate the effect of microhabitat alteration and varying perceived predation risk on disease incidence. Our models indicate that such fine-scale alterations in predation risk can have surprising effects on pathogen prevalence, leading to the emergence of epizootic cycles. Regular (predictable) cycles and chaotic (unpredictable) cycles may occur as predation risk is reduced. Under some conditions, cycles may result from very small changes in predation risk or environmental conditions. Our models show regions of sensitive dependence on environmental and predatory conditions, leading us to predict the possibility of the emergence of chaotic disease cycles as the result of small environmental disturbances.

*Keywords:* metapopulation, disease dynamics, leishmaniasis, hyrax, foraging, migration, predation risk

### INTRODUCTION

Risk of predation modifies the behavior of prey animals in many ways, even if lethal predation rarely occurs (Lima, 1998). Animals may alter their foraging habits to manage the risk of predation (e.g., Brown and Kotler, 2004), and environmental changes that

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alter risk are likely to have consequences for the movement behavior of prey. When the prey animal is a disease reservoir, changes in disease dynamics may also result from changes in the rates of mixing between the reservoir subpopulations, and also from altered contact rates with incidental disease hosts such as humans. For some disease systems, alterations in short-range movements may have an important impact on disease dynamics, even to the extent of disease outbreaks or extinctions.

Here, using a modeling approach, we investigate the effect of environmental change on pathogen prevalence via its effect on the behavioral ecology of the reservoir host. In particular, we examine the interplay between risk of predation, the availability of refuge sites, and reservoir migration. The models are inspired by a system of a zoonotic pathogen, the protozoa *Leishmania tropica*, and one of its mammalian reservoirs, the rock hyrax, *Procapra capensis*. They indicate that changes to the migration patterns of the hyrax can have significant effects on pathogen dynamics within reservoir host populations.

The rock hyrax is a medium-sized (~4 kg) herbivorous mammal that is widespread throughout Israel, the Middle East, and Africa. Jacobson et al. (2003) and Svobodova et al. (2006) showed that in at least one focal epidemic of leishmaniasis in northern Israel, hyraxes were the primary reservoir of the disease. The social structure and foraging behavior of hyraxes have been described previously (Meltzer, 1967; Barry and Shoshani, 2000). They live in small social groups (up to ~50 individuals) and use rock crevices and gaps between boulders as refuges. Hyraxes emerge to forage as a group on vegetation located up to ~50 m from their refuge (Druce et al., 2006), and remain alert for potential predators during the foraging period (Kotler et al., 1999). While foraging, the risk of predation probably increases with increasing distance from the refuge (Druce et al., 2006). They are central-place foragers, returning to their refuge after feeding, and do not hoard food. More than that, our preliminary observations suggest that hyraxes are *multiple* central-place foragers. That is, groups of hyraxes move together among multiple refuges. This means that whole subpopulations move from patch to patch, visiting the same patches repeatedly over a period of months. Such movement may be termed "migration" (sensu Dingle, 1996), though it is unlike the more familiar seasonal migration.

Cutaneous leishmaniasis (CL) is a protozoal disease causing lesions that heal slowly, leaving large disfiguring scars. Leishmaniasis persists in animal reservoirs such as rodents, dogs, and hyraxes (Ashford et al., 1973; Jacobson et al., 2003) and is transferred to humans by the bite of a sandfly (*Phlebotomus spp.*, *Lutzomyia spp.*) that became infected by biting an infected reservoir animal. CL is widespread in arid areas of Africa and the Middle East (Anon [World Health Organization], 2009). In Israel, notable outbreaks have occurred in the southern Negev Desert, and in the Jordan Valley (Wasserberg et al., 2003), hosted by the fat sand rat (*Psammomys obesus*). However, new foci of the disease have been emerging in the eastern Galilee, and the hyrax has been identified as the reservoir species in these outbreaks (Jacobson et al., 2003). Although CL foci have thus far been confined to a small area around the Sea of Galilee, it appears to be spreading (Israel Ministry of Health CL taskforce, pers. commun.). Since the sandfly is a poor flyer (Killick-Kendrick et al., 1986), hyrax migration may be key in the spread of infection among hyrax populations.

Migration corridors, as shown in mathematical metapopulation models, can be of crucial importance in determining the dynamics of disease among a species with a patchy distribution (Hudgens and Haddad, 2003). However, such models usually consider animal movement to be either a random process, or driven by simple resource gradients. Instead, migration in animals such as hyraxes may be highly directed. Although the motivation for hyrax migration is not yet understood, one possibility is that resource depletion drives the hyrax colony to sites with richer forage. Colonies typically return to previously occupied den sites after a period of a few weeks, during which time resource renewal can occur. This behavior will vary the distance between different subpopulations as they migrate, which may have significant effects on disease dynamics (Cully et al., 2010), as we demonstrate below. Since the animals are unlikely to spend any length of time away from the rock piles that offer shelter from predators, the spatial distribution of such refuges defines migration corridors and can be expected to exert a strong influence on the movements and behavior of the hyrax. Since we presume that refuges provide protection from predation, changes in predation risk are likely to influence the willingness of hyraxes to venture farther from rock piles, and thereby affect their ability to move between different den sites. A reduction in the number of natural predators might be expected to increase the range of hyrax foraging forays, and also the likelihood of moving from one rock pile refuge to the next. The Galilee region of Israel has recently seen a rise in the number of new residential neighborhoods, with three notable environmental effects. The first is a dramatic proliferation of the artificial rock piles that make suitable hyrax habitats, as an unintended side effect of construction programs that involve the leveling of areas for new residential neighborhoods. These rock piles, from ~2 to 20 m in diameter, provide ideal refuge sites for the hyrax (Fig. 1). Second, there



Fig. 1. Hyrax colonies can be found in artificial boulder piles created in close proximity to human residential areas from construction work. The difference between the unaltered Galilee habitat and the artificial boulder piles is primarily in the size and frequency of spaces between boulders and the existence of connected caverns beneath the boulder piles that do not exist in natural outcrops.

have been widespread changes in the distribution of the natural predators of hyraxes (Yom-Tov, 1988), in some cases, by an order of magnitude or more (Yom-Tov et al., 1995). These include common buzzards (*Buteo buteo*), golden jackals (*Canis aureus*), and marbled polecats (*Vormela peregusna*). This, too, could contribute to altered migration by hyrax colonies. Third, although natural predators are on the decline, residential areas bring with them new predators in the form of domestic dogs. Hyraxes are attracted to the forage in residential gardens, and domestic dogs may form a significant element of predation risk—the authors have observed several cases of hyraxes killed by free-ranging dogs.

We therefore investigated whether changes in the distribution of den sites, and changes in the predation risk (and the subsequent facilitation or restriction of migratory movements of hyrax colonies) were in themselves capable of producing epizootic outbreaks of disease.

## METHODS

Hyraxes migrate between den sites (i.e., rock pile refuges) every few weeks, moving distances of up to several hundred meters (Kershenbaum, unpubl. data), but the factors driving such migration are not known. In this model, we assume migration to be driven by food resource depletion, a likely assumption in the arid environment of Israel. However, the model should be valid for any simple dependence of migratory behavior on any environmental factor that causes a reduction in patch quality with occupancy time, e.g., parasite load (Allan et al., 2010). Movement from den to den is inhibited by the risk of foraging far from a refuge from predators, and we make a further assumption that this inhibition is related to perceived predation risk.

The model is designed to simulate the behavior of a multiple central-place forager such as the hyrax, where individuals feed at a distance from their refuge, and then return to the refuge after each feeding session. In addition, the colony moves from time to time, from one refuge site to another. Animal movement on two spatial scales (daily foraging and den-to-den migration) opens the possibility for complex dynamic behavior. When choosing how far from the refuge to feed, the model assumes that the animals must consider (a) the distance  $x$  of the feeding location from their current refuge, (b) the density and nutritional value  $F(x,t)$  of the food source available at distance  $x$  at time  $t$ , and (c) the distance  $y$  to the nearest safe refuge—which may or may not be their home refuge. The overall attractiveness  $Q$  of a particular feeding site  $x$  at time  $t$  is a function of these three factors, and we choose to define  $Q$  as a linear combination of them:

$$Q(x,t) = F(x,t) - \gamma x - \delta y$$

where  $\gamma$  and  $\delta$  are parameters that determine the animal's response to perceived danger.  $\gamma$  measures the “conservativeness” of the animals—their unwillingness to feed far from their home den.  $\delta$  measures the need for the animals to remain close to a safe refuge, whether or not it is their home den. Thus, the farther away the food is from either the

home or nearest refuge, the less attractive it is. Although the parameters  $\gamma$  and  $\delta$  cannot directly be related to real world predation risk, we can gain an intuitive indication by observing that the linear definition of  $Q$  means that doubling  $(\gamma + \delta)$  would half the distance at which animals would be prepared to forage.

The availability of food at location  $x$  and at time  $t$ , is specified by the function  $F(x,t)$  describing resource growth and consumption, where:

$$F(x,t+1) = L[F(x,t)] - \begin{cases} \epsilon & \text{if foraged} \\ 0 & \text{otherwise} \end{cases}$$

$$L(F) = \theta(1 - e^{-F\phi})$$

Here, resource growth is taken to follow an appropriate model such as logistic or exponential (defined by parameters  $\theta$  and  $\phi$ ), and the animal consumption is specified by  $\epsilon$ . The growth and feeding parameters  $\theta$ ,  $\phi$ , and  $\epsilon$  were given values ( $\theta = \phi = 10^{-3}$ ,  $\epsilon = 0.5$ ) that ensured a situation where food availability would show sufficient dynamic range to support the population of animals in the simulation: generating resource shortage after intense grazing (we assumed previously that migration is driven by food availability), but renewing within a reasonable timescale so that abandoned sites eventually become attractive again.

We consider foraging location choice to be reevaluated by the animals every morning, so the natural time unit for  $t$  is measured in days. Consider three potential refuges from which the animals must choose where to forage as shown in Fig. 2.

Allow the animals to deplete resources as they forage. We assume that the animals will return to the nearest refuge once they have finished foraging—this will often, but

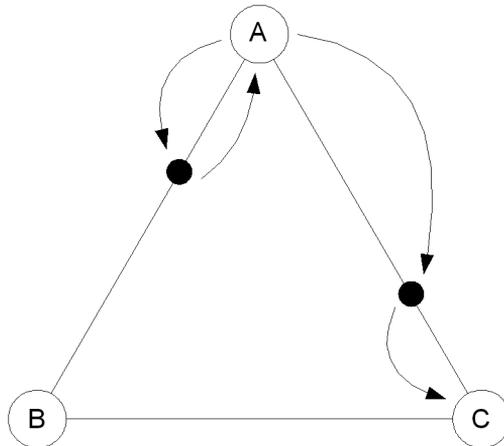


Fig. 2. Foraging choices with three potential dens. Central-place foragers will choose the optimum foraging location from the perspective of their current den. If they choose a point closer to their current den (as shown here between A and B), they will return to the same refuge. However, if the optimal foraging point is far from their current den (as shown here between A and C), the animals will choose to return to the alternative refuge.

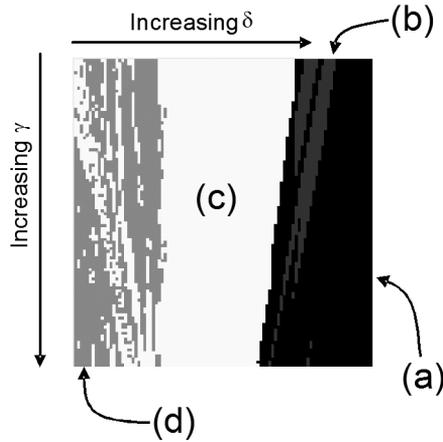


Fig. 3. Four different possible behaviors in  $\gamma$ - $\delta$  parameter space. As the animals become less fearful (moving from right to left), the behavior changes from remaining in a single den (a), through a small region where they alternate between two dens (b), and into a behavior of cyclic use of three dens, periodically (c) and aperiodically (d). The chart shows  $\gamma$  and  $\delta$  varying from 0 to 1.

not always, be the refuge from which they departed. As the hyraxes leave their refuge and move about to find and exploit resources, the optimal feeding point may at some time become one that is closer to a different refuge than it is to the initial home refuge. Thus, we can expect that under certain conditions, the animals will move from one refuge to another, i.e., migrate. This is a key feature of multiple central-place foragers: they are prepared to move from one den to another, using the new den as a base for future foraging forays. Solving for  $Q$  for a variety of parameter values for  $\gamma$  and  $\delta$ , we find four possible behaviors exist: (a) the animals stay in the same location, (b) they alternate between two locations, (c) they migrate between different locations in a cyclic manner, and (d) they migrate between different locations in an aperiodic manner. The distribution of these behaviors in  $\gamma$ - $\delta$  parameter space is shown in Fig. 3.

In some regions of parameter space (e.g., Region a), the animals behave in a conservative manner where they are unwilling to stray far from their dens and therefore unlikely to move from one den to another. However, if the animals show more willingness to forage at a distance, or if suitable dens are closer together, migration more often takes place (Regions b and c). Additionally, there are regions of parameter space (Region d) where the model is highly unstable, and a small change in the response to predation risk or refuge spacing may produce sudden and unexpected changes in movement patterns. These unstable regions indicate chaotic behavior, within which accurate predictions are impossible. Such changes in migratory behavior as demonstrated in the model will also affect the distribution of hyraxes across the landscape and the connectivity among subpopulations.

Our second model considers how migration affects infection dynamics. Two popula-

tions with enzootic infection may infect each other providing they are located close to each other physically, within the range of the disease vector. By combining the population migration model with a pathogen transmission model, we generate a set of patch populations with migration between them, thus generating a metapopulation system where the subpopulations can infect each other. Adapting a simple SIR (Susceptible–Infected–Recovered) model of infection within a reservoir population, we add a term for infection between the two populations that depends on the vector transmission between them:

$$\begin{aligned}\dot{S} &= b(S + I + R) - \beta SI - dS - \zeta\psi SI' \\ \dot{I} &= \beta SI - gI - dI + \zeta\psi SI' \\ \dot{R} &= gI - dR\end{aligned}$$

Here,  $\dot{S}$ ,  $\dot{I}$ , and  $\dot{R}$  represent the compartments of susceptible, infected, and recovered individuals, respectively,  $b$  is the birth rate,  $d$  the death rate,  $g$  the recovery rate, and  $\beta$  is the infection rate. In addition, we add the cross-infection term  $\zeta\psi SI'$ , where  $\zeta$  is a coefficient of infection between the two populations,  $I'$  is the number of infected individuals in the other population, and  $\psi$  a measure of the distance between them as a barrier to cross-infection. In the case of leishmaniasis, where infection is transmitted by a vector species, the nature of the infection term  $\zeta\psi SI'$  may be complex. We assume that transmission is caused by vector or host movement between den sites, and not by infected vectors remaining in a vacated site. This is consistent with what is known of the sandfly life cycle, in which the period from blood meal to oviposition, and the life expectancy of females, is short (Dye et al., 1987; Killick-Kendrick and Killick-Kendrick, 1999). Since the sandfly is a poor flyer, we assume that the probability of transmission via an infected sandfly is proportional to the inverse square of the distance  $r$  between the infected den and the non-infected one:

$$\text{Pr} \propto 1/r^2$$

The infection rate can be approximated as being proportional to  $SI$  since the sandfly vector is unlikely to show preference for individuals among the hyrax hosts. Each population is defined by the same set of equations and parameter values, since the cross-infection between them is symmetrical. However, we introduce a small amount of infection ( $I_0 \ll 1$ ) to just one population at the start of the simulation. The values used in these simulations were:  $b = d = 0.01$ ,  $\beta = 0.3$ ,  $g = 0.2$ ,  $\zeta = 0.2$ . The birth rate  $b$  of 1% per day, or 3.65 offspring per year, corresponds to a single annual litter size of  $\sim 7$ , rather higher than, but still in line with, the estimate of 3–4 given by Mendelsohn (1965). While the values for  $\beta$  and  $\zeta$  used for this part of the simulation are arbitrary, we later vary these parameters through their entire range (0–1) to explore their effect on the infection dynamics.

By combining the SIR model with the migratory model given above, we can see what happens when two reservoir populations move from den to den; we use the first

(migration) model to generate the movement patterns that are used as an input to the second (disease) model. We emphasize that our focal species forages and migrates as a unified group, so the flow of individuals can be treated in a simple manner. The distance between the populations varies with time, as we allow each population to move between den sites.

We simulated an artificial landscape and analyzed two scenarios. In the first, each group of animals moved between three sites that were in their exclusive territory (a total of six sites)—no den was used by both groups. This mirrors the three-site system described above and in Fig. 2. Simulations were repeated for (a) different values of the parameters  $\gamma$  and  $\delta$ , which describe the foraging and migrating behavior of the animals and the “willingness” of animals to expose themselves to risk of predation, and (b) different values of  $\beta$  and  $\zeta$ , which describe the epidemiological transmission of the pathogen. In the second scenario, we generated 100 den sites randomly located in a  $100 \times 100$  matrix, and allowed the two groups to move freely between all den sites, but disallowed simultaneous occupation of the same den by both groups. In the simulation, we varied the number of den sites, from 2 to 100. This simulates the effect of anthropogenic change, in which new den sites are generated as the result of building activity. Simulations in the  $100 \times 100$  matrix were replicated 30 times using random site locations. In each case, the differential equations were integrated numerically using Matlab 7.3.

A number of measurements of the resulting behavior of the model were taken. To describe the disease cycles, we measured:  $\mu$ , the mean pathogen prevalence in the reservoir population;  $M$ , the maximum prevalence in the population. In addition, we estimated the degree of periodicity of the disease cycles by measuring the relative strength of the strongest spectral component of the prevalence time series  $\Pi$  as determined by a fast fourier transform (FFT). FFT approximates the data as a mixture of sinusoidal signals of varying frequency and strength, so the strongest frequency should represent the overall cyclic nature of the series. A spectrum showing a large number of overlapping frequencies indicates chaotic or random variation, whereas a single strong frequency (or a small number of strong frequencies) indicates periodic cycles.

## RESULTS

In the first scenario with two territories of three sites each, the results shown in Fig. 4 are striking: from two populations, each with simple pathogen dynamics, sharp epidemic peaks occur. Subsequent peaks are of a consistent form and are synchronized to the migration movements of the populations. They result from the varying number of susceptible animals, which builds up during periods of low infective load (when the populations are far apart) and comprises the newly and rapidly infected animals when the populations move closer together. The increased prevalence among the reservoir species would lead to increased incidence among the vector and the human victims.

By varying the level of perceived predation risk, we see different regimes of constant, periodic, and aperiodic behavior in the pathogen prevalence. As  $\delta$  is reduced and animals venture further from refuge, we can see the transition from no migration and no

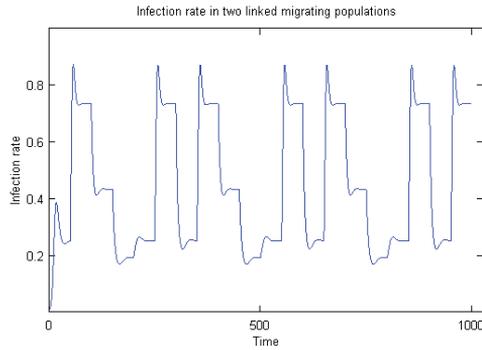


Fig. 4. Epidemic behavior of model with time, in region “c”. When the distance between the two dens varies regularly, the resulting pathogen prevalence dynamics show epidemic peaks when the populations approach each other.

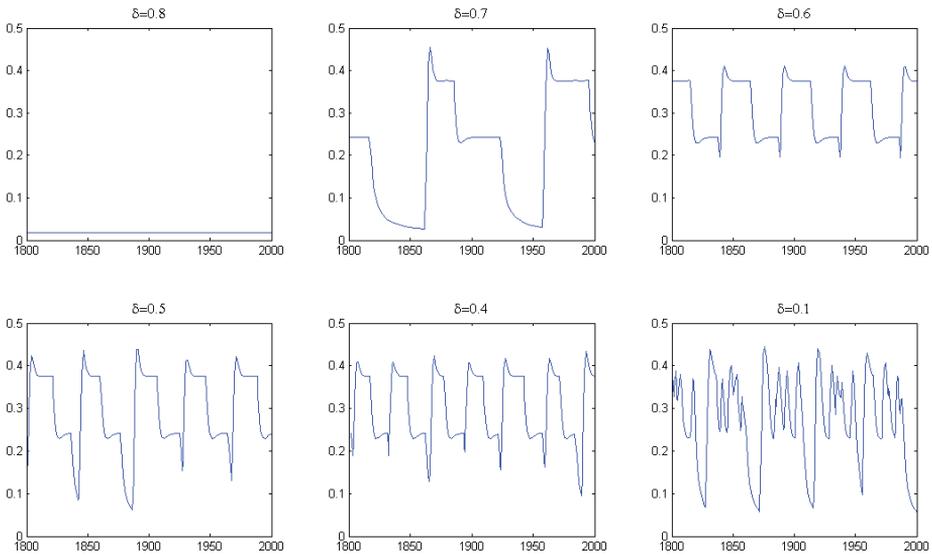


Fig. 5. Infection prevalence over time for varying values of  $\delta$ , with  $\epsilon = 0.6$ . As  $\delta$  falls, indicating reduced perceived predatory pressure, pathogen cycles appear (b), becoming more frequent (c–e), and eventually chaotic (f).

pathogen cycles (Fig. 5a), through periodic cycles of increasing frequency (Fig. 5b–d), to aperiodic or chaotic pathogen cycles (Fig. 5f). In this particular example, where  $\epsilon = 0.6$ , we can estimate that the transition to chaotic cycles (Fig. 5e–f,  $\delta = 0.4 \rightarrow 0.1$ ) occurs for an increase of approximately  $(0.4 - 0.1)/(0.6 + 0.4) = 30\%$  in the distance at which animals are prepared to forage from their dens.

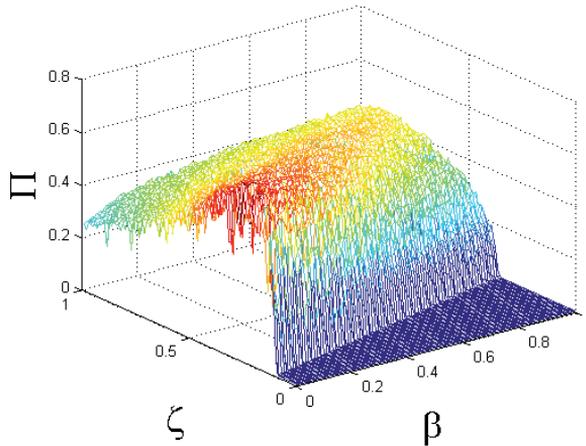


Fig. 6. Cycle power in epidemiological parameter space.  $\Pi$  indicates the power of the dominant frequency as determined by FFT. The axes of infectivity between populations  $\zeta$ , and the infectivity between individuals  $\beta$  are normalized units from zero (no infectivity) to unity (full infectivity). In regions of low  $\beta$  and  $\zeta$ , the power is zero. Beyond a sharp boundary, cycles exist and increase in intensity, before falling off at higher values of  $\zeta$ .

The existence of pathogen prevalence cycles is dependent both on epidemiological parameters and on behavioral ones. Where no migration occurs, there cannot be migration-induced prevalence cycles. This may correspond to situations with high risk of predation or refuges that are too far apart for movement. Within this migration regime, however, cycles only occur in a certain regime of epidemiological parameter space. Figure 6 shows the sharp boundary between cycles and enzoois/extinction as the infectivity ( $\beta$ ) of the pathogen and the cross-infection term ( $\zeta$ ) vary. At low infectivity and low cross-infection, cycles are not observed. Where cycles exist, their strength increases sharply, before falling off at higher  $\beta$  and  $\zeta$ .

In the  $100 \times 100$  matrix scenario, we also see consistent trends as the number of den sites are increased. At very low den density, migration does not occur. However, as more den sites are added beyond a critical density, cyclical migration begins, as evidenced by the sharp rise in the standard deviation of the distance between dens (Fig. 7a). Migration cycles continue as dens are added. A similar effect is observed with the spectral power  $\Pi$  of the prevalence, which indicates fluctuations of the pathogen prevalence with time (Fig. 7b). The mean prevalence  $\mu$  remains relatively invariant to an increasing number of dens, once the critical number has been surpassed, but the maximum prevalence  $M$  continues to increase as more den sites are added (Fig. 7c).

## DISCUSSION

These models demonstrate how small variations in the predator–prey balance, and fine-scale habitat disruption, can lead to a wide variety of possible outcomes of disease

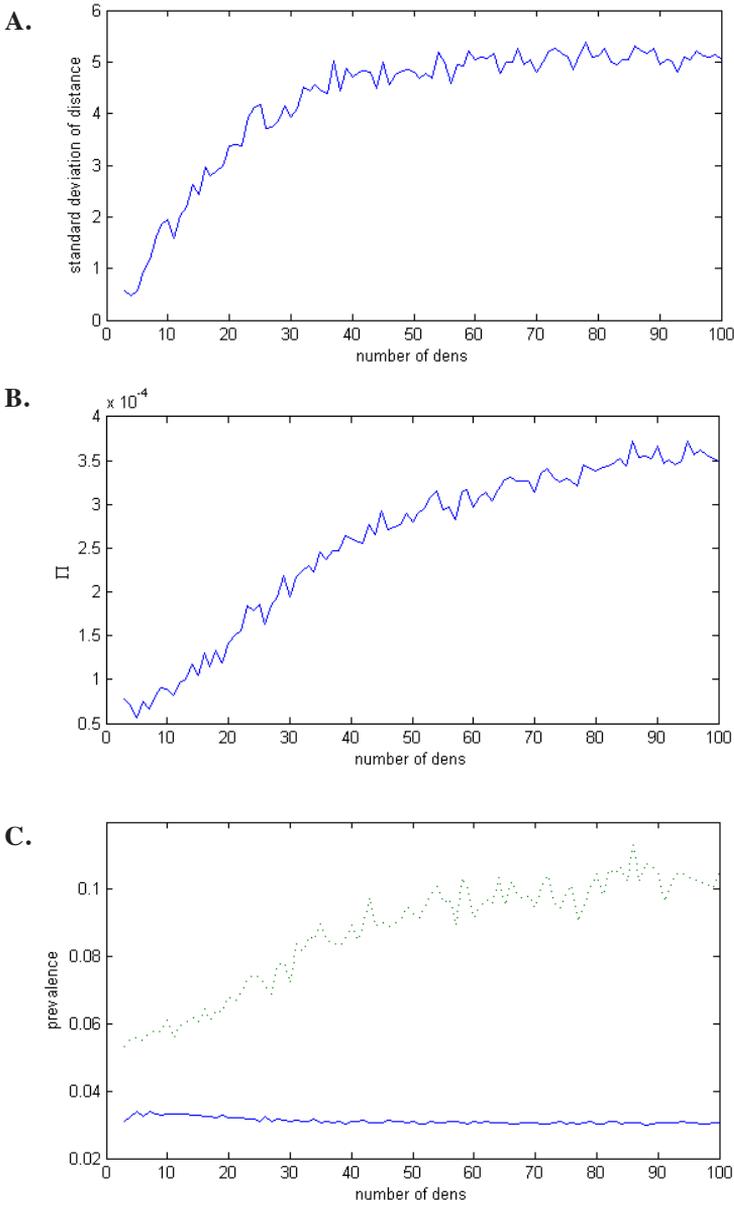


Fig. 7. Effect of adding new dens. As new dens are added to the virtual landscape, (a) the distance between the two migrating populations becomes more variable, and (b) so does the infection prevalence. (c) The mean prevalence changes little as more dens are added (solid line), but the maximum prevalence (broken line), i.e., the prevalence peaks, increases with more dens.

dynamics. In particular, the opening of migratory corridors for the reservoir species by the inadvertent construction of suitable habitats between existing populations, or the enabling of existing corridors by the reduction in perceived predation risk, can result in striking epidemic cycles, where a stable enzootic infection was previously observed. We used the models to explore two qualitative properties of this system. First, we showed that migration of the animals is sensitive to the spacing of suitable refuges, and to the willingness of animals to venture far from the refuges. At some spacing, migratory behavior may become complex, or even chaotic. Second, we showed that the complex migratory behaviors of two subpopulations are likely to produce epidemic peaks in each one due to the varying infective load from one population to the other.

Disease cycles are well known to be determined largely by epidemiological factors such as the basic reproductive rate,  $R_0$ . In the study of human epidemics, movements of populations and individuals are also well known to be of importance (Hufnagel et al., 2004). However, there has been a lack of emphasis on the importance of animal migrations in the generation of zoonotic cycles. This model illustrates that while disease cycles are dependent on epidemiological parameters such as cross-infection between populations, they are also sensitive to ostensibly minor changes in community interactions, leading to behavioral alteration among reservoir animals. In particular, foraging and movement behavior is often sensitive to risk of predation (e.g., Brown and Kotler, 2004). This may be affected by refuges from which to forage and their availability throughout the home range of the animals and throughout the landscape. More refuges will reduce the distance from any given location to the nearest refuge,  $y$ , and may lead to greater movement and larger home ranges. It may also be affected by the number of predators. More predators mean higher risk, which should reduce  $\gamma$  and  $\delta$  and lead to restricted movement (Berger-Tal et al., 2010). Thus, the physical structure of the landscape and the community context together determine the landscape of fear (Laundre et al., 2001) that in turn determines movement behavior and disease dynamics. We show that chaotic behavior both of reservoir animal movements and also of pathogen prevalence is potentially widespread. Under such circumstances, pathogen prevalence cycles persist, but they become irregular and unsynchronized with greater population movement, making the prediction of disease dynamics extremely difficult.

The models developed here are intended to capture the general nature of pathogen cycles in migrating populations, rather than make quantitative predictions about disease incidence. For that reason, the parameters are not specifically chosen for the case of hyraxes and leishmaniasis, and we do not have data to specify where in parameter space the real-world hyrax–leishmaniasis system exists. In addition, we do not consider factors such as seasonal variations in hyrax and sandfly populations. We have, however, illustrated that this parameter space is rich with contrasting behaviors, and transitions between such regions may result. We have also simplified certain aspects of the pathogen system—most notably the vector-based transmission of leishmaniasis. Any features of the transmission between individual hosts were incorporated into a general transmission term, and this is appropriate for our intention of illustrating qualitative behavior with striking results: all that is necessary to provoke an emergence of zoonotic disease

is an alteration of the spacing between suitable habitats for the reservoir species, or the willingness of animals to cross that spacing, because of risk of predation. Indeed, if the epidemiological parameters are appropriate, almost any migration activity is liable to destabilize an enzootic equilibrium and result in prevalence cycles. Furthermore, complex disease cycles that are difficult to predict may result from very simple periodic migratory movements of reservoir species.

The importance of metapopulation modeling for the understanding of disease dynamics has long been emphasized (Hethcote, 1978; Lloyd and May, 1996), and the mathematical basis of such systems has been closely examined (Keeling and Rohani, 2002; Colizza and Vespignani, 2008). However, these treatments place an emphasis on disease invasion thresholds, and rarely consider the factors behind the existence of disease cycles. In addition, the specific behavioral features of migration patterns are not usually incorporated into such models. We have shown that behavioral modifications can have a profound effect on disease dynamics, and should be incorporated into such metapopulation models, particularly where migration behavior may be strongly influenced by community dynamics. Our chosen focal species, the rock hyrax, shows particularly complex movement patterns because of its nature as a multiple central-place forager. While central-place foraging is commonplace, only a few species have so far been identified as foraging from multiple den sites; examples include the spider monkey *Ateles geoffroyi* (Chapman et al., 1989) and Atlantic salmon *Salmo salar* (Steingrímsson and Grant, 2008). For this reason, our model has importance beyond the specific instance of the hyrax–leishmaniasis system, and raises relevant issues where host species' migratory behavior is a complex result of multiple environmental influences.

In the specific case of leishmaniasis in Israel, the process of habitat alteration is already well advanced, with manmade boulder piles providing abundant and closely spaced refuges for the hyrax in close proximity to human habitation. Together with the spread of residential neighborhoods comes a decline in natural predators, and an increase in the occurrence of free-ranging domestic dogs, which may also act as significant predators on hyraxes. The spread of the disease is currently restricted to a small area of the eastern Galilee, but our models suggest that the recent environmental changes favoring high abundance of hyraxes in proximity to villages, combined with ease of migration due to the increase and spatial configuration of the artificial habitats, and a reduction in the number of natural predators, caution for ongoing research to understand the potential mechanisms of spread beyond the currently infected area.

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