A Mathematical Model of the Repopulation of southern high plains playas by Ambystoma Tigrinum following Antevs' Altithermal

Dorothy Wallace, Erin Dauson, Ben Bier, Clyde Martin

April 9, 2012

Abstract

The 20,000 ephemeral ponds, the *playas* of the southern high plains of the United States, were thought to have experienced a prolonged drought ending approximately 5,000 years ago, during which amphibians and other aquatic residents would have died out. A few permanent ponds are conjectured to be the source of repopulation of the entire region since then. We develop a series of mathematical models based on the tiger salamander, *Ambystoma tigrinum*, on rainfall data, and on field data, to test this hypothesis. We show that, under reasonable assumptions, the region could have been repopulated through migration within this time frame.

1 Introduction and Background

The ecological literature offers many examples of habitats that are only viable for certain species on a seasonal or irregular basis. We examine the effect of population growth due to reproduction and emigration, as well as loss due to predation, migration and local extinction, on populations in habitats where there is a strict limit on resources and high variation in habitability. In this paper we consider the southern high plains, the playa wetlands of West Texas, Oklahoma, Colorado, Kansas and New Mexico, described in [36].

In the playa wet lands of the Midwest there are about 20,000 isolated shallow lakes, called "playas", that fill with rain and then dry during periods without rain. In the playa system the primary resource is water and typically these wetlands are truly wet for only a small percentage of the time and the wet times occur in a seasonal but irregular manner [36]. Average annual rainfall across this region varies from 45 cm to 33 cm per year, of which over half occurs from May to September [6]. No permanent rivers or streams cross the region. These playas are ecologically important for eleven species of amphibians and a host of birdlife. Typically the amphibian populations of these habitats have communication on an irregular basis through migration during periods of high rainfall.

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The model that we develop is applicable to wide variety of vertebrates and invertebrates that live in these difficult habitats. As a test case we model the life cycle of the tiger salamander that is one of the eleven species of amphibians that inhabit the playas system. The particular subspecies is *Ambystoma tigrinum mavortium*, [Petranka, 1998], common to the playa wetlands [26].

There are other examples of such habitats around the world, including isolated transient wetlands in the great plains of Canada [15], parts of Spain [35], Africa [13], Australia [14] and India [28]. There are also examples of isolated habitats such as the Madrean Sky Islands of the Southwest United States and Mexico, [24], to which the models developed in this paper may also apply. In the case of salamanders, it is generally conceded that dispersal and recolonization of fragmented habitats is required for the persistence of these populations [32], [33], [34].

1.1 Spacial Distribution of Playas

A study based on 10,000 depressions in 20,000 square miles [23] gives .5 playas per square mile or about .2 playas per square km, or 1 playa per 5 square km for a distance between playas of about 3.13 km. However the paper also describes "innumerable small lakes" which are not part of that count.

A study on the ground of 40 quadrangles in Texas [29] counts 19,600 playas in 40 quadrants, each quadrant about 7 by 8 = 56 sq miles, gives about 8.75 per sq mile, which is 3.38 per square kilometer or one per .3 square kilometers, giving a distance between playas of about .55 kilometers.

1.2 Playa Biology

Playas, when wet, host a variety of plants and invertebrates, thirteen species of amphibian, one species of reptile, and no fish unless introduced by humans [36]. Additionally a large variety of bird species, including both shorebirds and waterfowl, populate playas and the shores around them, with the greatest abundance during migration periods [36]. Currently, no aquatic mammals inhabit the playas.

Amphibians feed on invertebrates and other amphibians, including their own species, have large clutch sizes, and are quick to mature [36]. All of these are useful adaptations to seasonal ponds. However, of the thirteen species found in playas, *Ambystoma* has a relatively low clutch size and slow maturation period. Yet this one species of salamander has established itself throughout the Southern High Plains playas. We choose this organism as a test case for the question of repopulation of playas through migration, as it represents the less fecund end of the amphibian species. If *Ambystoma* can repopulate a playa system in a given amount of time, it is very likely that the other amphibians found in playas can do so as well.

1.3 Antevs' Altithermal

In 1948 Antevs hypothesized a dry warm period in the playa region during the middle Holocene (7500-5000 B.P.) [2] [3]. Subsequent geomorphic data [11] and paleohydrologic data [30] have supported this hypothesis, as well as archeological evidence of well digging as an adaptation to drought [19]. There is also evidence that, prior to this period, aquatic mammals inhabited the playas [36].

Severe drought causes the disappearance of playas for extended periods and large scale extinction of amphibians in the region would have been the result of Antevs' Altithermal. However, groundwater held in the Ogallala aquifer was discharged along the eastern escarpment [42] and may have allowed permanent ponds for amphibian habitat, from which salamanders (and other amphibians) may have repopulated the playas since the end of the altithermal approximately 5000 years ago.

One goal of this study is to understand the time frame in which the salamanders could have populated the region. In [18] an elementary model was proposed that suggested that the time frame was best measured in a few thousand years. In this study we revisit this question.

1.4 Brief Overview of Paper

In this paper we develop mathematical models to test the hypothesis that the playas of the southern high plains could have been repopulated by *Ambystoma* through migration within 5000 years. Section 2 of this paper describes the basic biology of *Ambystoma*. Section 3 develops two continuous models for the its lifecycle during a single reproductive season. Section 4 describes two probabilistic models of 22,500 plays with repeated migration/extinction events. Section 5 reports the results of these models. Section 6 interprets the models in light of rainfall and field data. Section 7 summarizes the conclusions of the paper.

2 *Ambystoma tigrinum mavortium*

The general biology of the *Ambystoma tigrinum mavortium* has been well studied. The habitat of the Tiger Salamander in central North America ranges from southern Canada to the Chihuahua Desert, varying from forest to desert scrubland, although appearing to require an aquatic habitat at least sporadically. It is known that environmental influences can stimulate larvae to develop into sexually mature adults with aquatic rather than terrestrial adaptations [8], [22]. Courtship behavior depends on the presence of water, eggs are laid in water and larvae are aquatic [4], [8]. It is believed that salamanders and other amphibians survive the dry periods between playa filling through hibernation or estivation, although little is known about this because most studies are carried out on wet playas [36].

The western subspecies occurring in the playas region is genetically diverse in color patterns, size, rates of metamorphosis. Local populations of the species may differ morphologically more than completely separate species in other parts of the country [26] and are attributed to the adaptation this organism must make to semi-arid conditions.

Three morphs occur in the region: large, small, and cannibal. The large morphs mature sexually as larvae before metamorphosing into adult form. This is adaptive in a situation where the only viable habitat is aquatic. Most amphibians mature and reproduce on land. The small morphs are more common in ephemeral ponds and may or may not mature before metamorphosis. The ability to morph at a small size may prevent the immediate death of the salamander if the pond dries up [26]. These differ in other ways also: their reproductive cycles, metamorphosis rates and so on. Cannibal morphs are so called because the larva have larger mouths and longer teeth associated with cannibalistic feeding, which is their observed preference. Tiger salamanders are opportunistic feeders [26]. Thus, to a great extent, they provide their own predation.

2.1 Reproduction and Life Cycle

It is difficult to get good data about tiger salamanders in playas over the course of an exceptionally wet season because these do not occur every year or even frequently. For growth, maturation, emigration and other important rates we must use data from regions where ponds are permanent or at least predictable. The rates described below are gleaned from studies of the same or closely related species in Colorado, California and elsewhere.

Tiger salamanders lay eggs that hatch into a juvenile (or larval) stage, grow and eventually metamorphose into adults. A study in Colorado shows the rate of growth is higher in warmer habitats and the size at metamorphosis is smaller [5]. The same study shows an example of a cohort hatched in a warm pond growing an average .2 grams per day and achieving metamorphosis at about 7.6 grams, for an estimated time to maturity of around 38 days. In addition, metamorphosis may occur early if ponds begin to dry out [26]. One playa that had dried out was observed to fill on May 31, contain larva on June 18 and produce adults on July 16, 39 days later [26]. Thus a rainy season that lasts slightly over a month will bring one generation to maturity. In permanent ponds some remain in an aquatic, "paedomorph" state. Whether metamorphosed or paedomorph, females will be mature in about a year [26].

The observed rate of successful juveniles per female in a single breeding season of California tiger salamanders is 5.94 in a pond that did not dry out [16]. Thus the total successful juveniles per individual in that population was approximately 2.97, based on a population where the ratio of males to females is approximately 1:1. Over the course of a rainy season (one month) the increase in juveniles per day is approximately 0.099 new juveniles introduced into a population per adult per day. Although the habitat, predation rates and so forth would be different in a playa, the species is close enough that we might expect similar results in a playa that does not dry out.

A study of related species *Ambystoma maculatum* in a Michigan pond [12] gives similar results at about 207 eggs produced per female, egg mortality of 38% to 60%, larva survival to 120 days at 40-108 per 1000. Thus from 2 adults we get 200 eggs at 50% mortality to give 100 hatchlings of which 4 to 10 survive, giving 2-5 per adult. A third study [31] of tiger salamanders near the Savannah River in South Carolina finds the annual production of juveniles per adult to vary between zero and 23, depending on the year (and its particular environmental factors).

Ambystoma survive the dry season, including the potentially complete drying of the pond, through estivation [9]. They burrow into the mud, remaining encased in hardening mud until the next rainy season [9], or shelter in the cracks in the mud at the bottom of ponds [40]. This allows the pond to carry a viable population into the next season, although extremely prolonged multi-year dry periods, such as the Altithermal, would be fatal.

Tiger salamanders will emigrate from their pond under some circumstances. Requirements for emigration are maturity, wetness, and crowdedness of the pond. A study of *Ambystoma* in both permanent and temporary ponds in Colorado [41] finds that emigration is indeed dependent on food supply depletion, in particular dwindling supply of fairy shrimp in the ephemeral pond, whereas those in permanent ponds are more prevalent in the absence of competition from their own species. In [16] emigration ranged from 15% per day on a wet day down to less than 1% on an even wetter day that occurred at the start of metamorphosis.

Most of these studies are in relatively permanent ponds. In playa habitats, areas between ponds typically have little cover for terrestrial Ambystoma, so migration will necessarily depend more on favorable wet weather conditions. Thus, if rainfall is timed properly, high rates of emigration could occur. These have been observed in the region around Lubbock, TX, and reported, if not quantitatively, then at least anecdotally with gusto [38].

2.2   Movement and Speed

Studies of salamander motion on land involve either catching, tagging, releasing and then re-catching the animals or attaching a radio device to the animals that slows them down and often is the cause of mortality. All estimates from these studies therefore report the minimum amount of distance the animal has moved in some time frame. Thus all measurements of how far a salamander moves in a day are underestimates.

One paper studying migratory movements of tiger salamander in Long Island [17] found that although average motion was around 2 m per day, some salamanders moved 100 m in the course of a few days. These were permanent ponds and, unlike the habitat between playas, there was cover for amphibians on the land between ponds. Similarly, a study of related salamanders in Missouri found maximum single movements of as much as 75 m, (reported as 37.82 m +/- 41.71 m) [25].

If the average distance between playas is 600 m, as described in Section 1.1, then migration between two playas should take approximately 5-20 days.

3   *Ambystoma* Reproduction: Two Continuous Models

3.1   Patch Models in General

The term patch dynamics refers to an ecosystem made of many subsystems. In this section we look at two situations: a single patch and two patches connected through migration. These models will inform a subsequent probabilistic model of 20,000 patches. Both of the models in this section have an Allee effect directly attributable to predation.

There is of course considerable work in the literature on Allee effect in populations, [20], [1]. This effect is an observed phenomenon wherein a population that drops below a threshold goes extinct. The models we develop all display this effect, as the possibility of extinction is high in the habitat described above. Amphibians evade extinction during dry periods and emerge to breed during wet ones, yet the possibility always exists that a habitat can dry up too early or too quickly, leading to extinction due to shortage of adults, or that the population is overly depleted during vulnerable periods of migration. The interplay between migration and the Allee effect is an important feature of these habitats.

3.2   One playa

For this model we imagine a single species growing rapidly in a limited habitat with predation, corresponding to a breeding season in which the organism could easily outstrip its resources and a predator whose population is independent of the prey population. The second assumption fits the relationship of migratory bird populations to the prey density of a single playa.

$$x' = ax(1-x) - bx/(k+x) \tag{3.1}$$

The growth term is a simple logistic equation with units of the organism in percent of the capacity. Actual pond populations have been measured in a few instances, and found to range from 10,000 to 50,000 adults, although these were larger playas, [27]. Within pond dynamics of *Ambystoma* are quite complex, and all of that is ignored here. In the case of rapid breeders the constant a could be quite large. As our point of reference we use the observations from [26] and [5] to give time to adulthood at 38 days and number of juveniles produced per adult at 3, as in [16] and [12]. This gives a birth rate of .08 new adults per salamander per day.

The death term represents predation with predator satiation. This would represent predation from a source external to the pond itself, such as migratory birds in the case of playas. These birds feed on amphibians and invertebrates in the playas, but the sheer magnitude of biomass produced by amphibian breeding is thought to be the key to their survival through predator satiation [36]. The predator response function used here is O(bx/k) near zero, rising monotonically to a maximum rate of b. Thus when prey is small, predation is assumed to be roughly proportional to prey biomass, but as the prey population rises the capacity of the predator to remove prey reaches a finite limiting rate. The constant k is the prey population at which this capacity is half its maximum, also controlling the initial constant of proportionality. To make biological sense with regard to the units of population chosen, both b and k should be less than 1, with k fairly small to indicate an early rise to the limiting value.

Solving (1) for equilibria values is equivalent to finding the roots of a cubic. For this equation the cubic has 0 as one root that is stable if $b/k > a$ and unstable if $b/k < a$. It will have two other real roots if $k + 1 > \sqrt{4b/a}$ and both of these will be larger than 0 if

$b/k > a$. In this case 0 will be a stable equilibrium and the system exhibits an Allee effect, going to zero for starting values that are less than the smaller, unstable nonzero equilibrium. This simple model predicts that reduction of the maximum predation rate, b, can eliminate the Allee effect entirely. This result is consistent with various hypotheses in the biology literature connecting the Allee effect to the role of predation.

As the predation rate b increases the initial population of x required to evade the Allee effect rises. In the case of playas, a source of predation external to the pond is migratory birds, which may arrive when the population of salamanders is already fairly high. Realistic values of b and k are not known, nor are probabilities and timings of waterfowl arrival. Table 1 shows the timing of population growth in a few cases. Note that $b/k = 1$ represents a massive rate of predation at low prey density, as when flocks of waterfowl are present. We are checking a case of high predation, to compare with the case of zero predation.

Table 1: One playa, populations at 30,60,90 days

Runs at $a = .08$	x_0	b, k	30 days	60 days	90 days
1, logistic	.01	0,0	.09	.53	.92
2, logistic	.02	0,0	.18	.72	.96
3	.02	.01,.01	Allee		
4	.2	.01,.01	.37	.66	.81
5	.3	.02,.02	Allee		
6	.4	.02,.02	.405	.415	.425

Although a simple model, Table 1 illustrates a few important points. If the starting density of salamanders is low, it will take at least one and possibly two months of breeding before population pressure would be likely to drive migration. If predators arrive early in this process they could drive the population to extinction but if they arrive later, when the population has grown to a substantial percent of capacity, they will do no harm although they may prevent the population from rising to the point where population pressure becomes a factor.

Table 1 suggests that about two months are required for a minimally populated pond to become fairly crowded. In addition, 5-20 days are required for migration to a nearby pond, as described in Section 2.2. These considerations are behind the assumption in Section 4 that it is unlikely that a population of salamanders would have time in a single rainy season to rise to necessary numbers, migrate to an adjacent pond, breed and rise in numbers in the second pond, and migrate a second time. Thus, in the probabilistic model in section 4, we assume that it is only possible to reach ponds that are nearby in a given iteration (representing a rainy season).
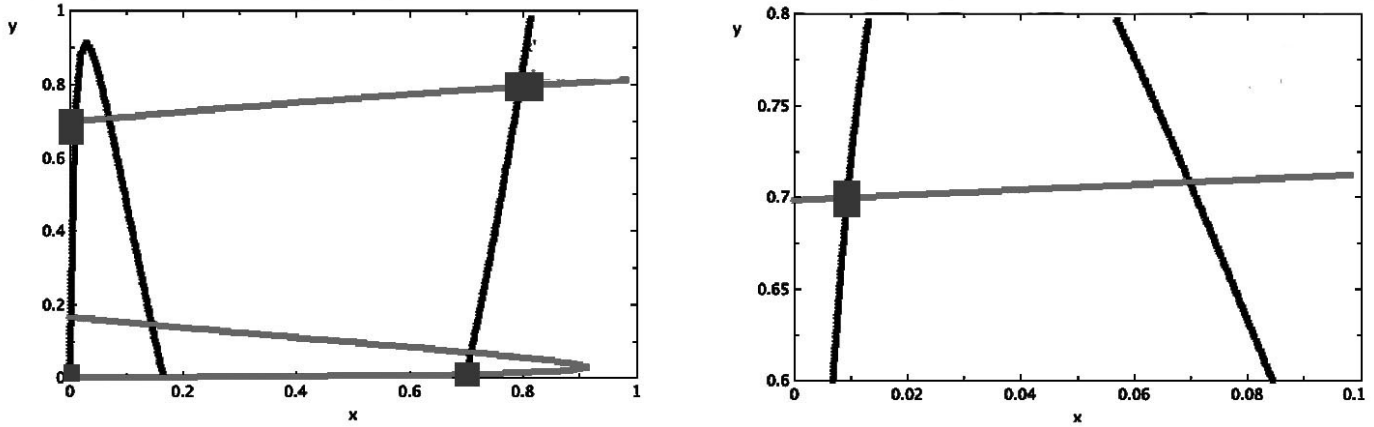
Figure 1: One example of nullclines for the two playa model. Boxes indicate stable equilibria. The left image is the 0-1 quadrant, and the right is zoomed in on a stable equilibrium.

3.3 Two Playas and the Role of Cyclic Disturbances

It is worth briefly considering a system of two playas with migration between them, based on the model in equation 3.1.

Two nearby habitats with migration are given by:

$$x' = ax(1 - x) - bx/(k + x) - ex + fy \qquad (3.2)$$

$$y' = ay(1 - y)by/(k + y) - ey + fx \qquad (3.3)$$

Here the quantity x represents the proportion of the carrying capacity occupied by individuals in habitat X, and similarly for y in habitat Y. The constant e will be the proportion of the whole emigrating per day, therefore less than one. The constant f should be interpreted (in the first of the two equations for example) as the proportion of individuals leaving habitat Y and successfully arriving at habitat X. Thus f should be much smaller than e, because the chance of losing organisms during migration is great. Based on the information given from [25], the survival rate during emigration is equal about 0.66 %, thus it would make sense to set $f = .66e$.
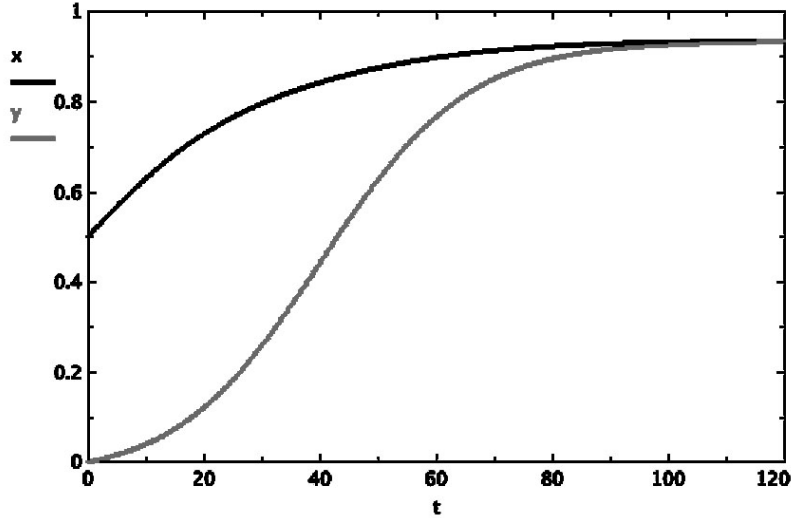
Figure 2: The two playa model where the first playa has had a chance to fill before migration, and where total predation is therefore a smaller percentage of the whole. $x_0 = .5, y_0 = 0, a = .08, b = .001, k = .01, e = .01, f = .006$

Because the equations are symmetric in x and y, it is possible to find the solutions where x=y. This system then reduces to a cubic, so for suitable choices of constants we will find three of these in the unit interval, one at zero and two distinct positive roots, as in the case of a single playa. Because of symmetry the basin of attraction for the (0,0) equilibrium (henceforth called the Allee basin) is also symmetric. It is also worth noting that the only equilibrium with one of the populations zero requires both to be zero.

Solving for all equilibria values requires finding roots of a pair of cubic equations in two variables. Such a pair may have up to 9 roots. The nullclines for one such system, chosen with biologically reasonable constants, are shown in Figure 1. Besides one stable equilibrium with equal populations, there are also two stable equilibria where one population is substantially lower than the other, as shown in the closeup view. For some parameter choices, a migration beginning with low quantities of x and zero y will stabilize at such a low equilibrium value in y that, when migration is turned off, the Allee effect causes y to drop to zero. In this model of a pair of playas, as with the model of a single one, removing the predation term removes the Allee effect.

For some organisms, such as Ambystoma inhabiting the playas, migration is a periodic activity occasioned by changes in weather or habitat. During one part of the cycle there may be no migration and even loss of life due to reduction of habitat. Another part of the cycle may allow the organism to grow in isolation. A third part may allow migration between habitats and a fourth stage may cut that migration off. This simple model of two patches with predation, emigration and immigration shows the efficiency of alternating periods of isolation with periods of migration. During periods of isolation, the population of an inhabited pond has the opportunity to grow to a substantial proportion of its carrying

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capacity. As pointed out in [36], the biomass of aquatic amphibians in playas can surpass all other fauna, particularly in Summer. During massive short term emigration the local predators of salamanders on land would reach satiation at a lower percentage take. The combination of these two factors (reduced b and increased x_0) result in a situation where both ponds quickly fill, as in Figure 2.

The model given by equations 3.2 and 3.3 thus illustrates the following points. Neighboring populations engaged in constant migration can achieve asymmetric equilibrium values, with one population maintained below its cutoff for viability in isolation. Alternating periods of isolation and migration allow populations to circumvent this possibility and full restocking of vacant habitats is more likely. In the case of the playas, alternate isolation and migration is exactly what happens.

We remind the reader that growth rates and survival rate in migration are values taken from the literature, whereas other parameters are not known. In the next section we will pass to a probabilistic model which, although coarser in detail, allows us to estimate relevant parameters. From continuous models we take two main points. One is that the probability of a salamander migrating to playas beyond its nearest neighbors in a single rainy season is negligible. The second it that alternating isolation and migration, far from being a detriment to an organism, may be a benefit or even requirement for repopulation of isolated habitats.

4   Two Probabilistic models Incorporating Migration and Extinction

In order to model the entire 20,000 playa region at once we represent it as a square 150 by 150 grid of vertices connected by edges. Two alternating probabilistic processes are constructed, one to represent migration with probability p and the other to represent extinction with probability q. Each vertex has a binary value of populated or extinct. An annual cycle is the result of two sequential processes. During the migration process each vertex is independently designated fit to migrate using a random variable with probability p. If a fit vertex is populated then the adjacent vertices will become populated also (if empty), otherwise there is no change. During the extinction process each vertex is independently designated unfit for habitation using a random variable with probability q. If an unfit vertex is populated then it becomes unpopulated, otherwise there is no change. The random variables assigned to all vertices are independent and identical, except for one corner vertex in the 150 by 150 grid, which remains continuously populated.

Thus one run of both processes in sequence simulates a rainy season in which there is probability p of migration, followed by a dry season in which there is probability q of extinction. The continuously populated corner vertex models those few playas at the edge of the eastern escarpment enjoying discharge from the Ogallala aquifer [42], thus remaining viable in all years.

In order to obtain statistics on the behavior of this model, for each pair of p and q chosen the simulation was carried out multiple times, and both the number of iterations required to

move populations across the grid and the final proportion of populated vertices was recorded.

4.1   Percolation Models in General and This One in Particular

The migration process taken alone is an example of a finite percolation model. These were originally invented to study fluid flow through porous media. In the case of porous media the number of vertices involved is so large that most models simply consider an infinite grid. There is body of literature about that situation, asking the basic question as to under what circumstances the fluid will cross an infinite space, as in for example [7], [10], or [37]. In this model we are considering a finite space, for which there is always some probability of crossing. A further difference is the presence of a source, that special vertex which remains forever populated. Finally, the alternating extinction process is not a percolation process and further complicates the model. So we apologize to percolation theorists that we found no theorems that clarified our question or answered it.

However, in the spirit of percolation theory a second model was also developed that, rather than tracking a binary variable, tracks the probability of each vertex being populated after N runs. We use this model to verify our experimental, numerical, binary results from the first model.

4.2   Numerical Methods

The playas are modeled as a 150 by 150 grid. Each node represents a playa and carries a binary value corresponding to populated or unpopulated (by *Ambystoma*) Based on the distribution of playas analyzed in Section 1.1 we will consider each playa to have eight neighbors as in Figure 3. The nearest are about 600 meters apart (adjacent grid cells) and the not so near are about 846 (600*$\sqrt{2}$) meters apart. Section 2.2 describes salamander movement speeds as ranging from a maximum of 30 to 70 meters per day. It could take as little as 9 days to as much as 28 days to reach these ponds. We assume, based on these estimates and the population model in Section 3.2, that in one season (represented by one time update of our model) there is not time to migrate to one of these eight neighbors, reproduce to the point of population pressure and migrate a second time.

4.2.1   Model 1

Using MatLab software, a program was developed to simulate migration and extinction on a grid of 150 by 150 vertices. The program employed a random number generator that determined updated states of each vertex based on probabilities chosen for migration (p and p_f) and extinction (q).
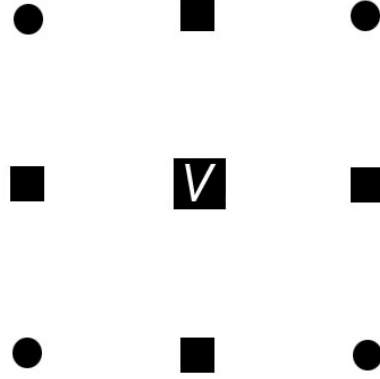
Figure 3: A playa in the grid (labeled V) and its nearby neighbors (squares) and not so near neighbors (circles).

At every time update, each node in the grid is updated. If the node is not populated, the program runs through the eight adjacent neighbors. If the neighbor is not populated, nothing changes. If the neighbor is populated, then a binary random variable decides whether the node will be populated with probability p for nearest neighbors, and $p_f = p/\sqrt{2}$ for not so near neighbors. The program runs through all neighbors of the given node and calculates the new state of the node for each neighbor.

The migration phase of the life cycle alternates with an extinction process that resets all nodes to unpopulated with probability q. Both migration and extinction processes are incorporated into a single step in the program.

The output of the algorithm is summarized in the equation below. Let v be a vertex in the grid. Let W be the set of nearest neighbors to v and let U be the set of not so near neighbors. Let p be the probability of migration, let $p_f = p/\sqrt{2}$, and let q be the probability of extinction. Let $S(v)$ be the state of vertex v.

If $S(v) = 1$ then $S(v)$ is updated to 0 with probability q. If $S(v) = 0$ then $S(v)$ is updated to 0 with probability P given by:

$$P = (1 - \Pi_{w \in W}(1 - pS(w))\Pi_{u \in U}(1 - p_f S(u))(1 - q) \tag{4.1}$$

Each simulation was run for 10,000 runs or twice as many cycles as it takes for the farthest lake to first have a population (if that time is less than 5000). The program reports the first occurrence of this, and then the proportion of the field that is populated at the end. For each pair of probabilities p, q, the program was run 100 times. These values were used to find standard deviations and means of both the time required to populate the grid and the final proportion of populated vertices.

4.2.2 Model 2

A second program calculates the new probability of population at each site for each year. It runs for twice as many years as it takes for the farthest corner to reach probability .1725, or to be within a tolerance of the previous year data, approximating an equilibrium state. It reports the time it takes for this to occur, and the average probability (over the entire grid of lakes except the one which is populated permanently) that a lake is populated. This average represents an expected percentage of populated lakes at the end of the run.

Both models were run for p and q ranging from .2 to 1 in increments of .1, and also a finer cut at low probabilities of p less than .2. Summary data for Model 1 are in Tables 8&9.

5   Results of the probabilistic model

For each choice of extinction probability in Model 1 we see in Figure 4 a sharp cutoff in migration probability, below which the program did not produce enough runs populating the system in less than 10,000 years to produce an average time. For example, when $q = .5$, p must be at least .2 in order to repopulate the system within 5000 years. On the other had, for low extinction probabilities of .1 or .2, the system always repopulates reliably even for p as low as .04, as we see in the expanded version in Figure 5. For extinction probabilities greater than .7 the system does not repopulate reliably within 10,000 years.
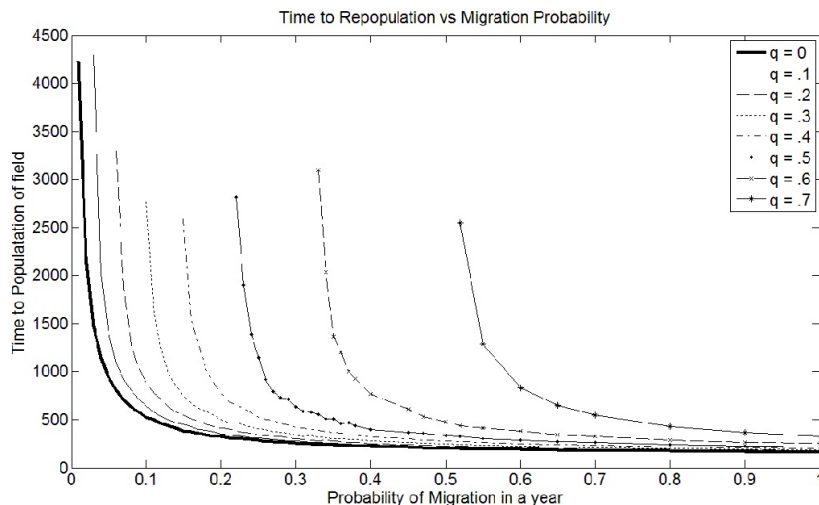
Figure 4: Model 1: Average time to repopulation as a function of migration and extinction probabilities for p between .1 and 1.

It is likely that, in the 5000 years since the Altithermal, the southern high plains experienced periods during which rainfall was fairly high. Suppose that there was a period where the probability of migration was fairly high and probability of extinction fairly low (such as $p = .3$ and $q = .2$). This period would only have to last a few hundred years in order to populate the region, far less than the 5000 since the Altithermal ended, as estimated from Figure 4.

We can compare the performance of Model 1 in Figures 4 and 5 with that of Model 2 in Figures 6 and 7. In Model 2 we are strictly computing probabilities and looking for the farthest pond to be populated with probability greater than .1725. We see that for $q = .5$, p must be at least .3 in order to achieve this, and it does so within 5000 years. In fact, it takes less than 500 years, which is consistent with results for Model 1 when $q = .5$ and $p = .3$. Similarly, at the low migration probability of .1 and low extinction probability of .8, both models give a time to repopulation of between 500 to 1500 years. Both models predict that for low p and high q repopulation within the 5000 year time frame is not likely.

Tables 2 and 3 show the cutoff values of q for a given p for both models. We can see that both models give similar although not identical results.
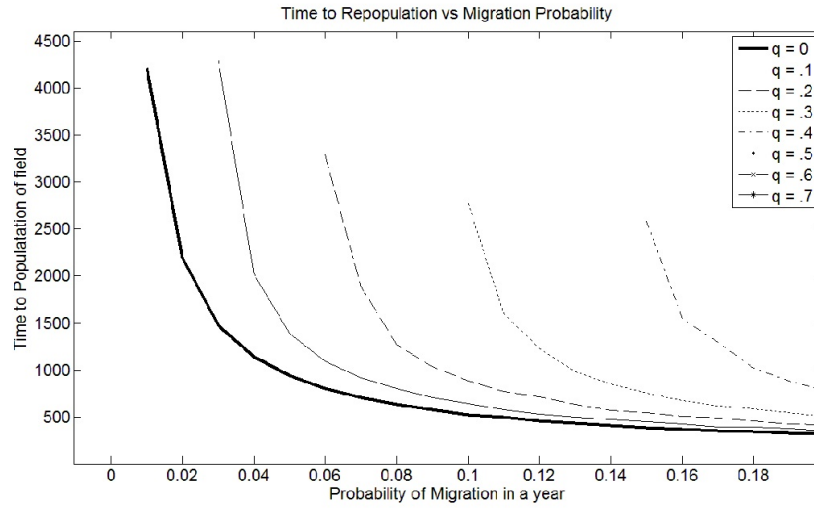
Figure 5: Model 1: Average time to repopulation as a function of migration and extinction probabilities for p between .02 and 2.

Table 2: Time to Repopulation for high p: q cutoffs

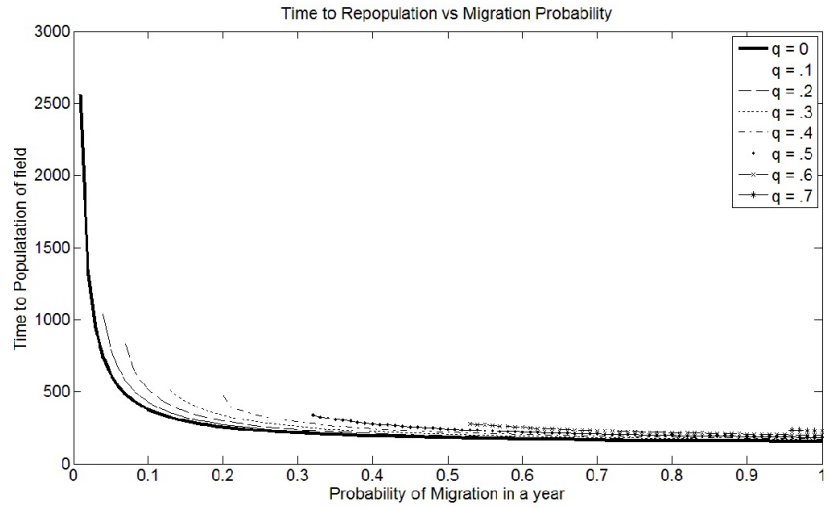| Migration p	Model 1: q cutoff	Model 2: q cutoff
.1	.3	.2
.2	.5	.4
.3	.6	.5
.4	.6	.5
.5	.7	.6

Figure 6: Model 2: Time until probability that the farthest pond is populated is .1725, for p between .1 and 1.

Table 3: Time to Repopulation for low p: q cutoffs

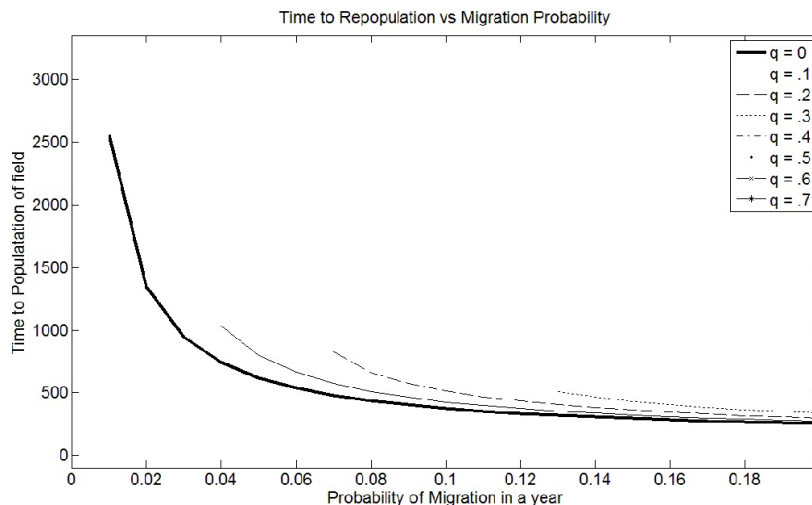| Migration p	Model 1: q cutoff	Model 2: q cutoff
.02	0	0
.04	.1	.1
.06	.2	.1
.08	.2	.2
.1	.3	.2
.12	.3	.2
.14	.3	.3
.16	.4	.3
.18	.4	.3
.2	.5	.4

Figure 7: Model 2: Time until probability that the farthest pond is populated is .1725, for p between .02 and 2.

We now turn to the question of what percent of ponds would be expected to be populated for given pairs of probabilities. Figures 8 and 9 show the percent of ponds populated at equilibrium (or at 5,000 years if equilibrium is not reached) in Model 1 for various migration and extinction probabilities. Note that at $p = 1$ the behavior of this percentage fits our intuition, coming close to $1 - q$. Note that for low p, the minimal percent populated ranges from 1 to 35 percent, depending on q. Similarly, Figures 10 and 11 show the average probability that a pond is repopulated, as computed from Model 2 (leaving out the continuously populated pond in the corner of the 150 by 150 grid). Note that each choice of q has a cutoff below which p fails to populate the grid at all. This is consistent with other results in percolation theory where the behavior of the system exhibits what is generally referred to as a "phase change" as a parameter is moved. Tables 2 and 3 summarize the values of p and q that give minimal repopulation in both models.
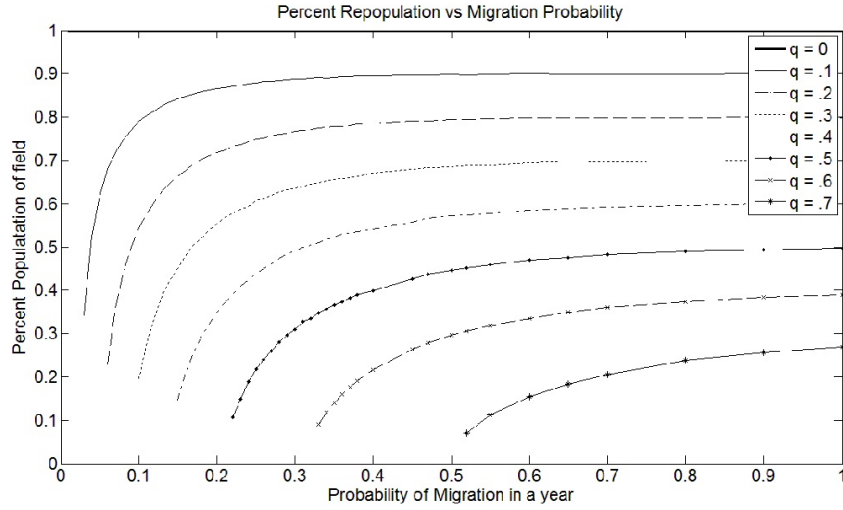
Figure 8: Model 1: Average percent of ponds repopulated at equilibrium for p between .1 and 1.

Table 4: Minimal criteria for repopulation for high p: q cutoffs

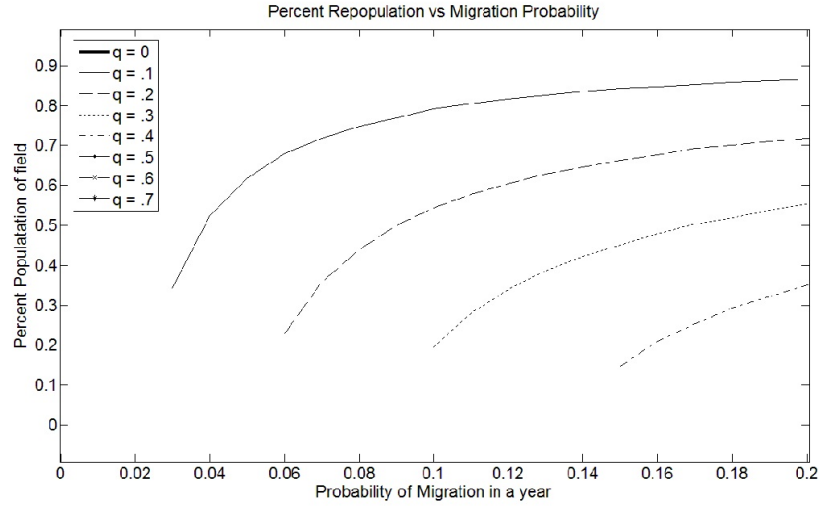| Migration p	Model 1: q cutoff	Model 2: q cutoff
.1	.3	.4
.2	.5	.5
.3	.6	.5
.4	.6	.7

Figure 9: Model 1: Average percent of ponds repopulated at end of run for p between .02 and 2.

Table 5: Minimal criteria for repopulation for low p: q cutoffs

Migration p	Model 1: q cutoff	Model 2: q cutoff
.02	0	.1
.04	.1	.2
.06	.2	.3
.08	.2	.3
.1	.3	.4
.12	.3	.4
.14	.3	.4
.16	.4	.5
.18	.4	.5
.2	.5	.5

Note that the q cutoff values for Model 1 in Tables 4 & 5 match those of Tables 2 & 3, respectively. However the q cutoffs for Model 2 are slightly higher in Tables 4 & 5. This is because, for Tables 2 & 3, Model 2, only runs where the farthest node reaches probability .175 are included, whereas in Tables 4 & 5 all runs are included.
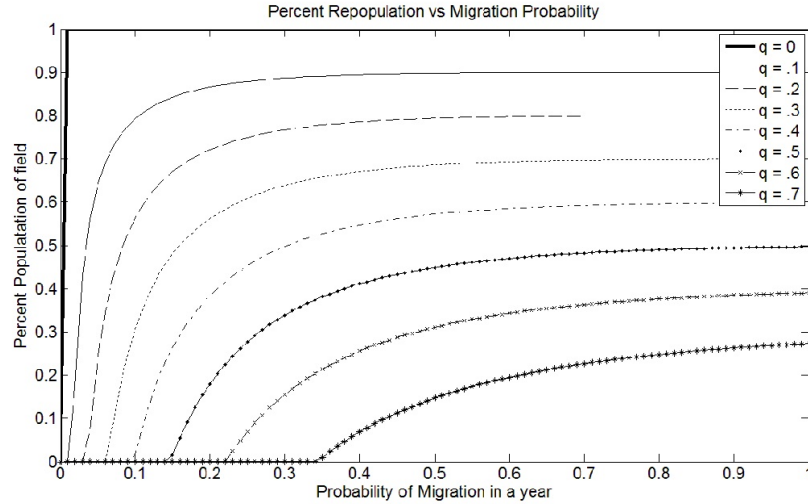
Figure 10: Model 2: Average probability a pond is populated at end of run, for p between .1 and 1.

The results from the two models are reasonably consistent with each other. Finer detail for Model 1 could have been obtained by running each simulation longer. Those choices of p and q for which Model 1 does not return an answer included many where some runs were not populated after 10,000 iterations even though other runs were, and thus a true average of times and population distributions could not be computed. Model 2 also had criteria for termination that could have been adjusted. But generally both models show similar behavior.

6   Discussion of the Probabilistic Models

In this section we compare the results of our probabilistic models to data from the area around Lubbock, Texas. We look at likely ranges for migration frequency and also at a study of twenty ponds over a two year period.
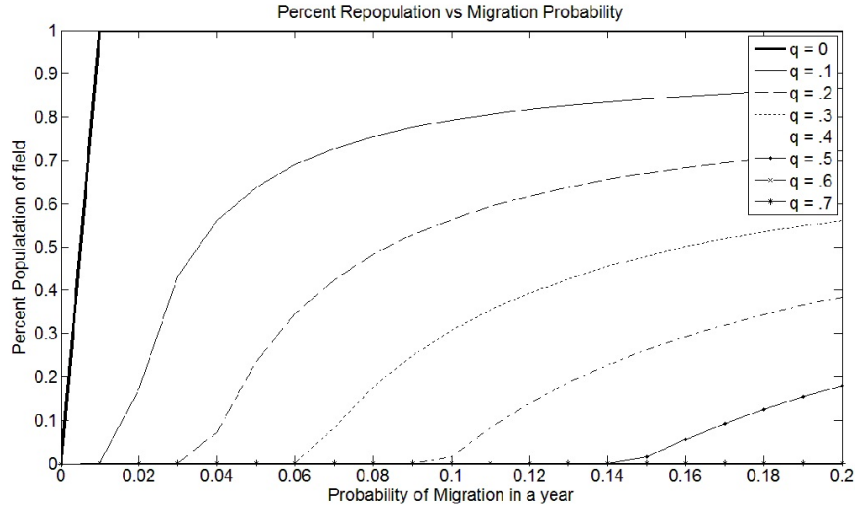
Figure 11: Model 2: Average probability a pond is populated at end of run, for p between .02 and 2.

6.1 Migration Frequency

Our estimates for migration probabilities are based on 100 years of monthly rain records for Lubbock, Texas [43]. Dry months are characterized not only by little rainfall but also by little variation in rainfall over the 100 year period for which we have data. On the other hand rainy months are far more variable. Summary data for March, a dry month, and July, a wet month, are shown in the histograms in Figure 12 as an illustration.

Table 6 shows summary data from one hundred years of monthly records. Frequently (58% of the time) we see a year in which one month exceeds normal rainfall by one standard deviation. Migrations are certainly not observed this frequently. Similarly, a single month will exceed normal rainfall by two standard deviations around 25% of the time, still too frequent to be believable. On the other hand, measures of one month exceeding 3 std, 2 consecutive months exceeding 1 std, and so forth all run a bit higher than 10%. So it seems reasonable to assume a migration probability of 5-25% based on this data.

Based on the estimated time required for a pond to become crowded (60 days, Section 3.2) and the estimated time required for migration from one pond to the next (5-20 days, Section 2.2), one or two months of normal rain followed by a particularly rainy month would suffice for migration. Two particularly rainy months with some normal months before or after, or other combinations such as these, would also suffice. Table 6 suggests a probability of around 12-14% for this kind of weather. A migration probability of around 12% is slightly more frequent than once every ten years, which corresponds to the anecdotally reported ten year "cycle" of playa-swelling rains [38].
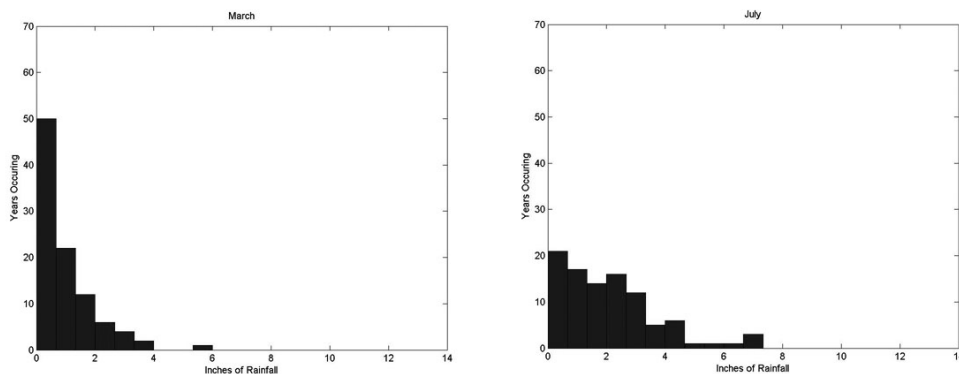
21

Figure 12: Rainfall is both higher and has greater variation in the summer months. On the left is summary data for 100 years of rainfall in March. On the right is July. Both are for Lubbock, TX.

There is also the suspicion that climate change in the last hundred years has resulted in drier habitats [36], and studies of habitats somewhat like playas that show drier habitats under conditions of higher temperature and even higher rainfall [21]. So the probability of migration over the last 5,000 years may actually be higher than Lubbock rainfall data suggests.

Years that stand out in local memory such as 1941 [38] may do so because not only was there migration locally, but the phenomenon was widespread and thus more noticeable than migrations affecting smaller or more remote regions. Our model does not take into account how weather correlates across a region but treats the state of the migratory region between any two playas as an independent random variable.

Table 6: Lubbock Rainfall Summary for Wet Years

rainfall criterion	fraction of years	percent of "wet" years
1 mo. exceeding 1std above normal	0.577	57
1 mo. exceeding 2std above normal	.278	27
1 mo. exceeding 3std above normal	.124	12
2 cons. mos. exceeding 1std above normal	.134	13
2 cons. mos. exceeding 2std above normal	.0103	1
3 cons. mos. exceeding 1std above normal	.0103	1
Annual exceeding 1std above normal	.144	14
Annual exceeding 2std above normal	.0515	5

6.2 Extinction Probabilities

Implicit extinction probabilities may be taken from a census of 20 ponds over one year, [39], in which 11 of 20 grassland ponds had tiger salamander in 2003 and only 8 had them in 2004. This gives an extinction probability of 3 in 11, which is quite high. If anything it is an overestimate because a pond with few salamanders may be categorized as empty. For example the same researcher found more ponds with Bufo in 2004 than 2003, indicating that habitat in general had not disappeared.

The statistics of particularly dry years from the Lubbock rainfall data gives a slightly different picture. As Table 7 shows, extremely dry years where rainfall is low for multiple months are relatively rare. About 10% of the years are one standard deviation drier than usual, about 7% of the years have two very dry months in a row, and about 45% of the time there is at least one unusually dry month.

One dry month is probably not enough to force extinction, since it happens about half the time. Such a high extinction probability is not consistent with [39], whose data is likely to represent an overestimate of extinction probability at approximately 30%.

Taken together, the rainfall data suggest an extinction probability of 7-10%, for a q value between 0 and .1 in our models.

Table 7: Lubbock Rainfall Summary for Dry Years

rainfall criterion	fraction of years	percent of "dry" years
1 mo. exceeding 1std below normal	0.453	45
1 mo. exceeding 2std below normal	0	0
2 cons. mos. exceeding 1std below normal	.072	7
2 cons. mos. exceeding 2std below normal	0	0
3 cons. mos. exceeding 1std below normal	0	0
Annual exceeding 1std below normal	.103	10
Annual exceeding 2std below normal	0	0

6.3 Current *Ambystoma* Prevalence

If [39] is representative of the playa system as a whole, then general prevalence of tiger salamander is around 50%. Of course it is possible the author chose to ignore completely dry playas for this study, which would lower the estimate considerably. This is the only data we have for prevalence of the tiger salamander in playas in general throughout the region.

6.4 Summary of Discussion

In Tables 8 and 9 we summarize the predictions of Model 1 for parameters in a range relevant to the particular situation of Ambystoma in playas of the southern high plains. Table 8 gives time to repopulation for all pairs of parameters for which repopulation was possible within 5000 years. Table 9 gives the percent of ponds repopulated for those same parameters.

Table 8: Time to Repopulation (years) estimated by Model 1, with observed standard deviation in 100 runs

Values of p	q = 0	q = .1	q = .2	q = .3	q = .4	q = .5
p = .01	4231 +/- 112	-				
p = .02	2195 +/- 74	-				
p = .03	1476 +/- 55	4289 +/- 511	-			
p = .04	1145 +/- 25	2017 +/- 91	-			
p = .05	942 +/- 25	1394 +/- 82	-			
p = .06	804 +/- 12	1090 +/- 59	3290 +/- 273	-		
p = .07	707 +/- 21	917 +/- 35	1879 +/- 194	-		
p = .08	635 +/- 14	804 +/- 24	1275 +/- 63	-		
p = .09	575 +/- 20	708 +/- 22	1034 +/- 48	-		
p = .1	528 +/- 15	644 +/- 20	886 +/- 41	2764 +/- 561	-	
p = .11	497 +/- 11	580 +/- 18	774 +/- 26	1601 +/- 158	-	
p = .12	461 +/- 14	530 +/- 13	715 +/- 30	1227 +/- 127	-	
p = .13	436 +/- 11	502 +/- 13	632 +/- 17	985 +/- 54	-	
p = .14	414 +/- 9	472 +/- 11	575 +/- 16	853 +/- 42	-	
p = .15	389 +/- 10	449 +/- 11	547 +/- 22	755 +/- 27	2588 +/- 333	-
p = .16	373 +/- 11	425 +/- 15	509 +/- 16	676 +/- 38	1549 +/- 168	-
p = .17	355 +/- 3	397 +/- 4	487 +/- 16	618 +/- 14	1292 +/- 175	-
p = .18	343 +/- 7	393 +/- 9	455 +/- 15	583 +/- 18	1021 +/- 108	-
p = .19	329 +/- 6	375 +/- 9	428 +/- 15		547 +/- 17	884 +/- 58
p = .2	324 +/- 7	352 +/- 7	415 +/- 13	502 +/- 17	777 +/- 41	

If we take 12% as our probability of migration, as discussed in Section 6.1, and 30% as our probability of extinction at the high end, as discussed in Section 6.2, Model 1 predicts the time to repopulation as 1500 years with about 30% of the ponds repopulated at the end of the process. For a range of parameters near these likely values, we see similar results.

Taken together, the models in this paper support the hypothesis that the entire network of playas were repopulated within the 5000 years since Antevs' Altithermal through migration alone.

7 Conclusions

The population model in Section 3.2 indicates that it is unlikely that the population of a single playa would grow to a crowded state and migrate successfully to a nearby playa two times in a single rainy season.

The two-playa model in Section 3.3 illustrates the value of isolation followed by migration as a mechanism for avoiding the Allee effect and undesirable local extinctions. Ponds that

Table 9: Percent of playas repopulated at end of run, estimated by Model 1, with observed standard deviation in 100 runs

Values of p	$q = 0$	$q = .1$	$q = .2$	$q = .3$	$q = .4$	$q = .5$
$p = .01$	100 +/- 0	-				
$p = .02$	100 +/- 0	-				
$p = .03$	100 +/- 0	34 +/- .3	-			
$p = .04$	100 +/- 0	53 +/- .5	-			
$p = .05$	100 +/- 0	62+/- .4	-			
$p = .06$	100 +/- 0	69 +/- .3	23 +/- .5	-		
$p = .07$	100 +/- 0	72 +/- .2	36 +/- .5	-		
$p = .08$	100 +/- 0	75 +/- .3	44 +/- .3	-		
$p = .09$	1100 +/- 0	77 +/- .3	50 +/- .5	-		
$p = .1$	100 +/- 0	79 +/- .2	54 +/- .3	20 +/- .8	-	
$p = .11$	100 +/- 0	80 +/- .3	58 +/- .3	28 +/- .6	-	
$p = .12$	100 +/- 0	82 +/- .3	60 +/- .5	34 +/- .3	-	
$p = .13$	100 +/- 0	83 +/- .2	63 +/- .4	39 +/- .6	-	
$p = .14$	100 +/- 0	84 +/- .2	65 +/- .3	42 +/- .6	-	
$p = .15$	100 +/- 0	84 +/- .3	66 +/- .3	45 +/- .6	15 +/- .4	-
$p = .16$	100 +/- 0	85 +/- .3	68 +/- .5	49 +/- .4	21 +/- .5	-
$p = .17$	100 +/- 0	85 +/- .2	69 +/- .4	50 +/- .5	25 +/- .4	-
$p = .18$	100 +/- 0	86 +/-.3	70 +/- .3	52 +/- .3	29 +/- .4	-
$p = .19$	100 +/- 0	86 +/- .3	71 +/- .4		54 +/- .5	32 +/- .6
$p = .2$	100 +/- 0	87 +/- .2	72 +/- .4	55 +/- .3	35 +/- .4	

have low populations at the start of migration can arrive at asymmetric equilibria values that force on population to extinction when migration is cut off. By contrast, a pond that is fairly full at the start of migration will successfully populate its neighbor, as illustrated in Table 1.

The process of population growth of Ambystoma, followed by migration, requires several successive months of good to above average rainfall, which appears to happen approximately 12% of the time according to rainfall data in Section 6.1. Likelihood of extinction is below 30% annually, as estimated from field data and rainfall data in Section 6.2.. Given these parameters, the results of the probabilistic models described in Section 5 predict that a 150 by 150 grid of playas would be repopulated in around 1500 years, with 30% of the ponds populated at the end of our simulation (equilibrium or 10,000 years).

Note, however, that this phenomenon is marginal. If extinction probabilities are raised to 40%, the network cannot repopulate in even 10,000 years. However some authors have suggested that the last 100 years have been somewhat drier than average, [36], so perhaps probabilities were in fact more favorable for parts of the last 5000 years. It is likely that favorable conditions would simultaneously raise the probability of migration and lower the

probability of extinction. With only slightly higher probability of migration (14%) and slightly lower probability of extinction (20%) the time to repopulation would be close to 600 years. So a relatively favorably period would only have to be sustained for 600 of the 5000 years since the Altithermal.

Although the percent of populated ponds (for migration probability 12% and extinction probability 30%) is less than reported in [39], that study did not appear to include playas that were actually dry for a summer season. Therefore the field data is reporting an artificially high percentage. If we use extinction probability of 10% as suggested by rainfall data in Table 7, the model predicts 82% percent of ponds repopulated. Our model is at least consistent with the data. Also, the slight improvement in climate discussed above would result in slightly over 50% of playas populated, completely consistent with the observations of [39].

In summary, our models support the idea that the playas could have been repopulated with *Ambystoma* since the Altithermal through the process of migration alone.

References

[1] Allen, L. J. S., J. F. Fagan, G. Hognas, and H. Fagerholm. . Population extinction in discrete-time stochastic population models with an Allee effect. *Journal of Difference Equations and Applications.* **11(4-5)** 273-293. (2005)

[2] Antevs, E. . The Great Basin with emphasis on glacial and postglacial times. *University of Utah Bulletin* **38**, 168-191. (1948)

[3] Antevs, E. Geologic-climatic dating in the West *American Antiquity* **20**, 317-335. (1955)

[4] Arnold, S. J. Sexual behavior, sexual interference, and sexual defense in the salamanders Ambystoma maculatum, Ambystoma tigrinum, and Plethodon jordani. *Zeit. Tierpsychol.* **42** 247-300. (1976)

[5] Bizer, J. R., Growth Rates and Size and Metamorphosis of High Elevation Populations of *Amysoma tigrinum, Oecologia* **34**, 175-184 1978

[6] Bolen, E.G., Smith, L. M., Schramm, H. L.,Playa Lakes: Prairie Wetlands of the Southern High Plains *BioScience*, **39 9**, 615-623 (1989)

[7] Bollobas, B. Riordan, O., Percolation, Cambridge University Press, (2006)

[8] Duellman and Trueb, Duellman, W. E. and L. Trueb. Biology of amphibians. McGraw-Hill Book Company, New York. (1986)

[9] Feder, M.E. & Burggren,W. W. Environmental physiology of the amphibians, University of Chicago Press, (1992)

[10] Grimmett, G., Percolation, Springer (1999)

[11] Holliday,V.T., Middle Holocene Drought on the Southern High Plains, *Quaternary Research* **31**, 74-82 (1989)

[12] Ireland,P.H., Larval Survivorship in two Populations of *Ambystoma maculatum*, *Journal of Herpetology*, **23 3** 209-215 (1989)

[13] Jones, B.F., Eugster , H.P., Rettig, S. L., Hydro-chemistry of Lake Magadi Basin, Kenya. *Geochim Cosmochim* **41** 53-72 (1977)

[14] Killigrew, L.P., & Gilkes, R. J., *Nature* **247**, 454 - 455 (1974) *Sediment Geol.* **64** 207-221 (1989)

[15] Last, W.M. Continental Brines and Evaporates of the NOrther Great Plains: An Overview, *Sediment Geol.*, **64** 207-221, (1989)

[16] Loredo, I., Vuren, D.V., Reproductive Ecology of a Populations of the California Tiger Salamander, *Copeia* **4** 895-901 (1996)

[17] Madison, D.M. & Livingston, F., Habitat Use during Breeding and Emigration in Radio-Implanted Tiger Salamanders, *Ambystoma tigrinum Copeia*, **2** 402-410 (1998)

[18] Martin CF, Hanlon,B., Zhou, Y., Models of extinction of genotypes in closed populations, *International Journal of Innovative Computing, Information, and Control: special issue on recent advances in stochastic systems theory and its applications*, **1**, 341-355 (2005)

[19] Meltzer, D.J. Altithermal Archaeology and Paleoecology at Mustang Springs, on the Southern High Plains of Texas,*American Antiquity* **56 2** 236-267 (1991)

[20] Odum, H.T. & Allee, W.C. *Ecology* **35**, 95-97 (1954)

[21] Poiani K.A., Johnson, W. C., & Kittel, T. G. F., Climate change and northern prairie wetlands, *Limnology and Oceanography* **41** 871-881 (1996)

[22] Pough, F. H., R. M. Andrews, J. E. Cadle, M. L. Crump, A. H. Savitzky, and K. D. Wells. 2001. Herpetology, 2nd edition. Prentice-Hall, Upper Saddle River, New Jersey. (2001)

[23] Reeves,C. C., Pluvial Lake Basins of West Texas *The Journal of Geology* **74 3** 269-291 (1966)

[24] , Ricketts, T.H., E. Dinerstein, D.M. Olson, C.J. Loucks, et al. Terrestrial Ecoregions of North America: A Conservation Assessment. World Wildlife Fund - United States and Canada. Island Press, Washington, D.C. pp. 258-260. (1999)

[25] Rittenhouse, T. & Semlitsch, R.D., Grasslands as movement barriers for a forest-associated salamander: Migration behavior of adult and juvenile salamanders at a distinct habitat edge, *Biological Conservation* **1 3 1** 1 4 2 2 (2 0 0 6)

[26] Rose, F. L, & Armentrout, D., Adaptive Strategies of *Ambystoma tigrinum* Green Inhabiting the Llano Estacado of West Texas *Journal of Animal Ecology* **45 3** 713-729 (1976)

[27] Rose FL & Armentrout, D., Population Estimates of Ambystoma tigrinum Inhabiting Two Playa Lakes, *Journal of Animal Ecology* **43 3** 671-679 (1974)

[28] Roy, P.D. Thermal characteristics of hte near-surface playa sediments from the Thar desert, Rajasthan, India, *J. Geol. Soc. India* **69** 781-788 (2007)

[29] Sabin, T. J., & Holliday, V.T., Playas and Lunettes on the Southern High Plains: Morphometric and Spatial Relationships,*Annals of the Association of American Geographers* **85 2** 286-305 (1995)

[30] Sanford, W., and W. W. Wood GEOLOGY, March 1995 229-232

[31] Semlitsch, R. D. Structure and Dynamics of Two Breeding Populations of the Eastern Tiger Salamander, *Ambystoma tigrinum Copeia* **3** 608-616 (1983)

[32] Semlitsch, R.D., Principles for management of aquatic-breeding amphibians. *Journal of Wildlife Management* **64** 615631 2000

[33] Semlitsch, R.D., Critical elements for biologically based recovery plans of aquatic-breeding amphibians, *Conservation Biology* **16** 619629 2002

[34] Semlitsch, R.D. (Ed.), Amphibian Conservation. Smithsonian Institution, Washington D.C., 324 (2003)

[35] Schutt, B., Reconstruction of palaeoenvironmental conditions by investigation of Holocene playa sediments in the Ebro Basin, Spain: Preliminary results *Geomorphology* **23** 273-283 (1998)

[36] Smith, L. M., Playas of the Great Plains, University of Texas Press, (2003)

[37] Stauffer, D. & Aharony, A., Introduction to Percolation Theory (2nd ed.), CRC Press, (1994)

[38] Steiert, J. & Meinzer, W., Playas, Jewels of the Plains, Texas University Press (1995)

[39] , Venne, L.S., Effect of Land Use on the Community Composition of Amphibians in Playa Wetlands, Thesis, Texas Tech University, (2006)

[40] Webb, R. G. Survival adaptations of tiger salamanders (*Ambystoma tigrinum*) in the Chihuahuan, Physiological systems in semiarid environments Hoff & Riedull (eds.). Univ. New Mexico Pr., Albuquerque. 256276 (1969)

[41] Whiteman, H.H., wissinger, S.Z., Bohonak, A. J., Seasonal movement patterns i a subalpine population of the tiger salamander, *Ambystoma tigrinum nebulosum*, Can. J. Zool. **72** 1780-1787. (1994)

[42] Wood,W.W., Role of Ground Water in Geomorphology, Geology and Paleoclimate of the Southern High plains, *Ground Water*, **40:4** 438-447 (2002)

[43] Lubbock rainfall data purchased from http://weathersource.com/past-weather/official-weather/product-2?location=79409&start-date=1913&end-date=2012&report-type=prcp&elements%5Btemp%5D=temp&type-daily=daily&search=1