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A Monte Carlo model simulating factors affecting migration in insular populations of *Peromyscus*

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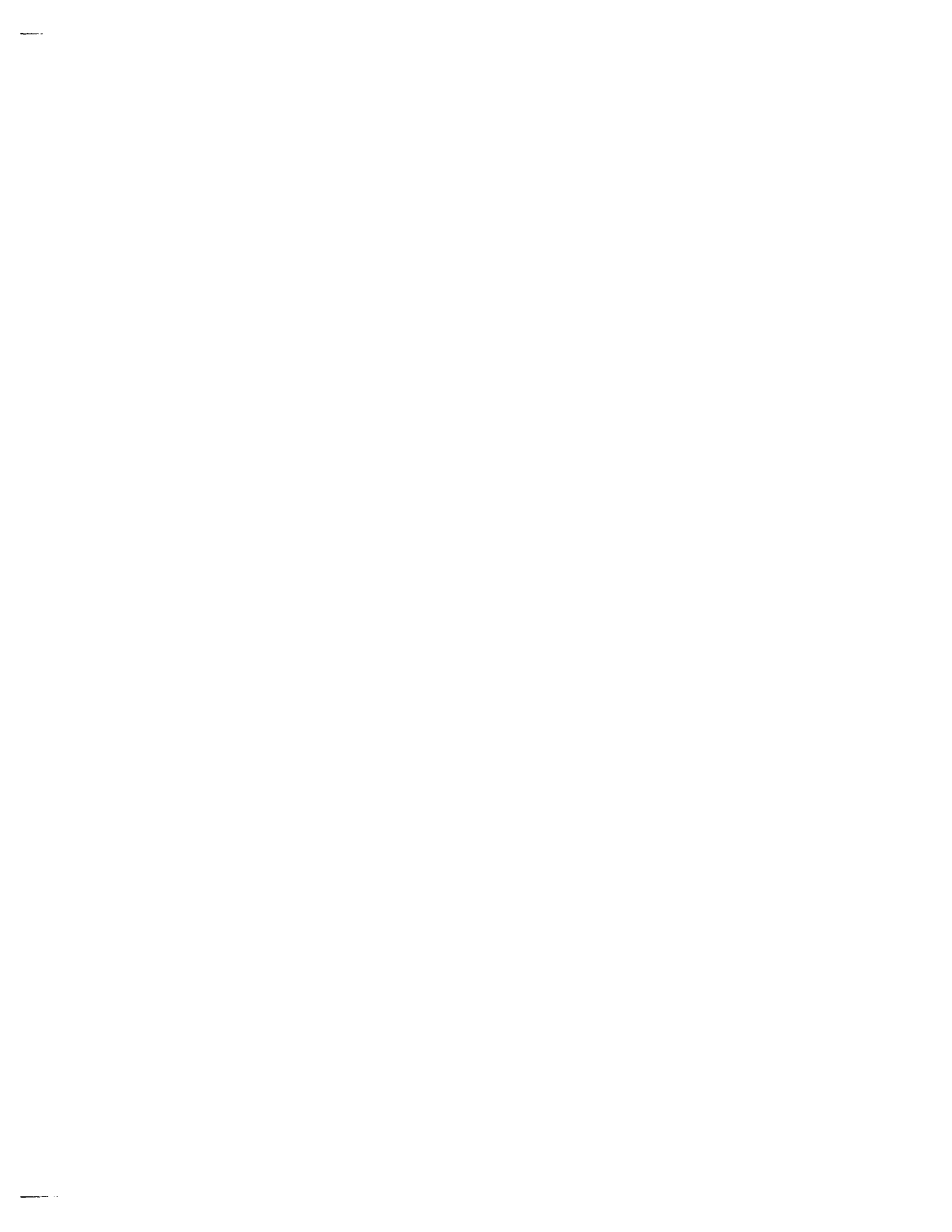
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insular populations of *Peromyscus***

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San Jose State University, 1992

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**A MONTE CARLO MODEL SIMULATING FACTORS AFFECTING
MIGRATION IN INSULAR POPULATIONS OF PEROMYSCUS**

A Thesis

Presented to

The Faculty of the Department of Biological Sciences

San Jose State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Arts

By

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May, 1992

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ABSTRACT

A MONTE CARLO MODEL SIMULATING FACTORS AFFECTING MIGRATION IN INSULAR POPULATIONS OF PEROMYSCUS

By Elaine K. Harding-Smith

Monte Carlo modelling was used to determine if spatial factors influenced emigration and immigration patterns of insular Peromyscus maniculatus and Peromyscus californicus populations. Movements among six vegetation islands were measured over a period of 5 months in 1990 within a 248 ha study area. Nine stochastic models simulating either emigration or immigration were developed. Five of the models contained simple probabilities and four utilized a Markovian random walk procedure. The modelled factors included population size, density, island size, distance between islands, proximity to island, and sand dune morphology. Each model's output, averaged over 1000 runs, was compared statistically to the actual migration pattern.

In this system population size, island size and density did not influence emigration. Two principal factors influencing immigration emerged: completely random movement and distance between islands. Although random movement provides the simplest explanation, additional modelling of increased inter-island distance would ultimately predict a distance at which stochastic movement is improbable.

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INTRODUCTION

The movement of individuals into or out of a small mammal population is motivated by a complex set of innate and externally driven responses, and its function may change temporally and spatially within a population. This movement, whether it be temporary (migration) or long-term (dispersal), is a key component of population regulation, perhaps operating at the genetic level (Lidicker and Patton 1987, Lidicker 1985, Fairbairn 1978, Sullivan 1977). Understanding the roles and interactions of the biological and environmental factors stimulating such movement is a necessary prerequisite for the management of rare or fragmented populations (Gilpin 1987, Brown 1986, Schonewald-Cox 1983).

Studies of the mechanisms responsible for small mammal migration and dispersal have typically utilized systems containing distinct zones of habitat and non-habitat, e.g., between actual islands or fragmented habitats. Through these studies, many theories have been proposed to explain the mechanism of migration. Island populations of rodents studied by Gliwicz (1988), Lidicker (1985), and Fairbairn (1978) suggest that limiting factors may increase social density and lead to heightened aggression and dispersal of non-optimal individuals (saturation or density-dependence theory). Dispersal "sinks," or areas of sub-optimal habitat, are often used by dispersing individuals after preferred habitats have filled (Gottfried 1982, Extine and Stout 1987). Adler et al. (1986) found that distance between isolated populations of Peromyscus was positively correlated with density, although Gottfried (1982) concluded that the largest and least isolated islands

contained the highest densities. The theory of island biogeography proposed that the rate of immigration is negatively correlated with distance of an island from a source population and positively correlated with island size (MacArthur and Wilson 1967). Unfortunately, few studies have addressed the extent that spatial factors may influence small mammal migration, and they are often of a qualitative rather than quantitative nature (Extine and Stout 1987, Smith and Vrieze 1979).

The objective of the present study was to use Monte Carlo modelling to examine the hypothesis that spatial factors were a primary influence on both emigration and immigration rates within a population of Peromyscus maniculatus (deer mouse) and Peromyscus californicus (California mouse) inhabiting six vegetation islands. Monte Carlo models are frequently used to test hypotheses concerning ecological systems through the replication of modelled stochastic processes (Service and Walters 1991, Weishampel 1990, Porter and Dueser 1989, Metzgar 1979, Simberloff 1978). The basic premise of these models is that stochastic events are simulated using a random number generator. If the stochastic pattern fits the observed pattern, then the observed events can be considered stochastic. In the model, both stochastic and non-stochastic factors are examined for their effect on ecological processes.

The number of Peromyscus migrants among six vegetation islands in a 248 ha study area at Pismo Dunes State Vehicular Recreation Area (PDSVRA) was recorded from June through October 1990. Turbo Pascal was used to create two model types: a simple probability model and a Markovian random walk model simulating complex spatial components. The probability model simulated those factors which had a simple

correlative relationship with migration. The more complex spatial factors were simulated using two dimensional space and a Markovian random walk procedure. Each of nine models simulated a different spatial condition(s), and ultimately produced an average of the expected number of emigrants or immigrants for each island. The expected pattern was compared statistically to the observed number of emigrants or immigrants. Each model simulated the effects of one or more of these spatial factors: population size, density, island size, distance between islands, proximity to island, and sand dune morphology.

STUDY AREA AND CAPTURE METHODS

Pismo Dunes State Vehicular Recreation Area (PDSVRA) contains 809 hectares of beach and sand dunes on the coast of San Luis Obispo County, California. Over the last 50 years the habitat of PDSVRA has been fragmented by shifting sand and recreational vehicle use into over a dozen vegetation islands (Fig. 1). The study area was located in the center of the park's off-highway vehicle riding area and consisted of six vegetation islands surrounded by barren sand. The islands, referred to as Islands 1 through 6, were located about 600 m inland from the Pacific Ocean and were relatively isolated; the nearest vegetation was approximately 270 m to the south (Fig. 2). The study area was delimited by the ocean, a vegetation mainland in the east, and the nearest vegetation islands in the north and south. The entire study area was approximately 1220 m by 2035 m, or 248 ha, in size. Area of the islands ranged from 0.43 to 2.0 hectares, with a minimum distance between any two islands of 19 m and a maximum of 153 m. The

major habitat types included riparian complex (Salix lasiolepis, Myrica californica, and Populus trichocarpa), dune scrub (dominated by Happlopappus ericoides and Baccharis pilularis), and wet meadow (dominated by Juncus leseurii). Off-highway vehicles, including ATVs and trucks, were driven on the sand dunes, but not through the vegetation areas as they were fenced to restrict riding.

To obtain an observed pattern of Peromyscus emigration and immigration, the populations were trapped, ear tagged, and recaptured over a five month period. During June, July, and August 1990, all six islands were trapped simultaneously for four consecutive nights each trapping session, and for five trapping sessions (except for Island 6 during the first trapping session). The islands were also trapped in September and October for two nights each month. Fifteen to 35 Sherman live traps, baited with wild birdseed and walnut oil and supplied with cotton bedding, were placed approximately 10 meters apart around the perimeter of each island. Dense foliage in the middle of each island precluded trapping the entire island, and most islands were small enough to warrant placing the traplines along only the perimeter. The islands were trapped for 3000 trap nights in the summer and 600 trap nights in the fall, for a total of 3600 trap nights during the study.

Each captured rodent was tagged with a numbered, metal Fingerling ear tag. Information on species (Ingles 1965) and trap location of each individual was recorded upon first capture. Recaptures of the same individual were reexamined for tag number and trap location. Trapping, over a period of 5 months, resulted in a total of 22 migrants, belonging to 4 species: Peromyscus maniculatus (13), Peromyscus californicus

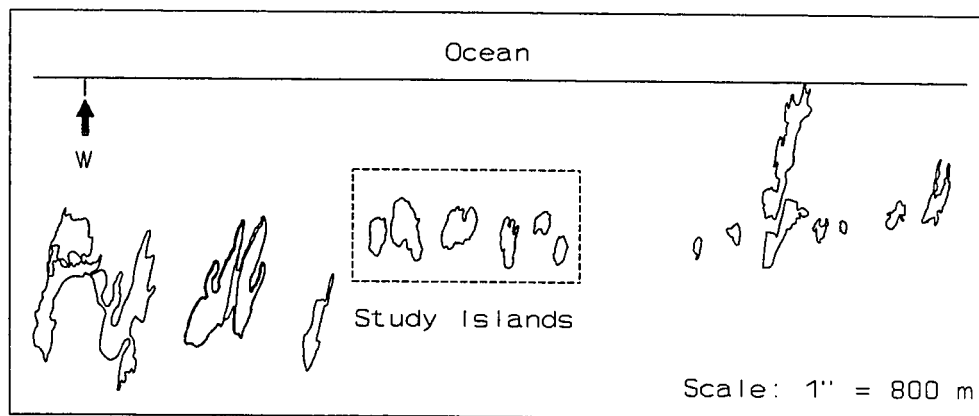


Figure 1. Study islands and nearby vegetation islands in the riding area of Pismo Dunes State Vehicular Recreation Area, Pismo Beach, California.

(5), Dipodomys heermanni (3), and Microtus californicus (1). Only the data for P. maniculatus and P. californicus were used in the model because they constituted the majority of migrants and were considered similar in physiology and niche (Table 1). All islands were inventoried for plant species present at each trap site and the major habitat types determined. Areas and distances were determined by digitizing aerial photos of PDSVRA taken in 1989 (Fig. 1).

MODELLING METHODS

The observed emigration and immigration patterns of Peromyscus (Table 1 and Fig. 2) were compared to the expected outcomes of various stochastic models to determine if the modelled factors provided a migration pattern comparable to the actual. One thousand runs were made for each of nine models. The number of emigrants or immigrants for each island was averaged across runs to produce an expected distribution. A G-log Likelihood test (Zar 1984) was used to compare observed and expected distributions. All nine stochastic models, of varying complexity, were created in Turbo Pascal, version 5.0.

Two groups of models were developed: the first group modelled factors affecting emigration and the second modelled factors affecting immigration. The former group included simulations of emigrant pool size, population size, density, and area. The immigration models were concerned with random immigration, distance between islands, island size, proximity to island, and dune morphology. Models simulating simple spatial factors were simulated by probabilities. Complex factors were simulated by a Markovian random walk procedure operating in a two-dimensional area. The Markovian random

Table 1. Emigrants and immigrants of Peromyscus between study islands at Pismo Dunes SVRA from June through October, 1990.

Island	Number of Emigrants			Number of Immigrants		
	Deer	Calif.	Total	Deer	Calif.	Total
	Mouse	Mouse		Mouse	Mouse	
1	0	0	0	8	0	8
2	4	0	4	1	4	5
3	6	2	8	1	0	1
4	0	0	0	1	1	2
5	2	3	5	1	0	1
6	1	0	1	1	0	1
Total	13	5	18	13	5	18

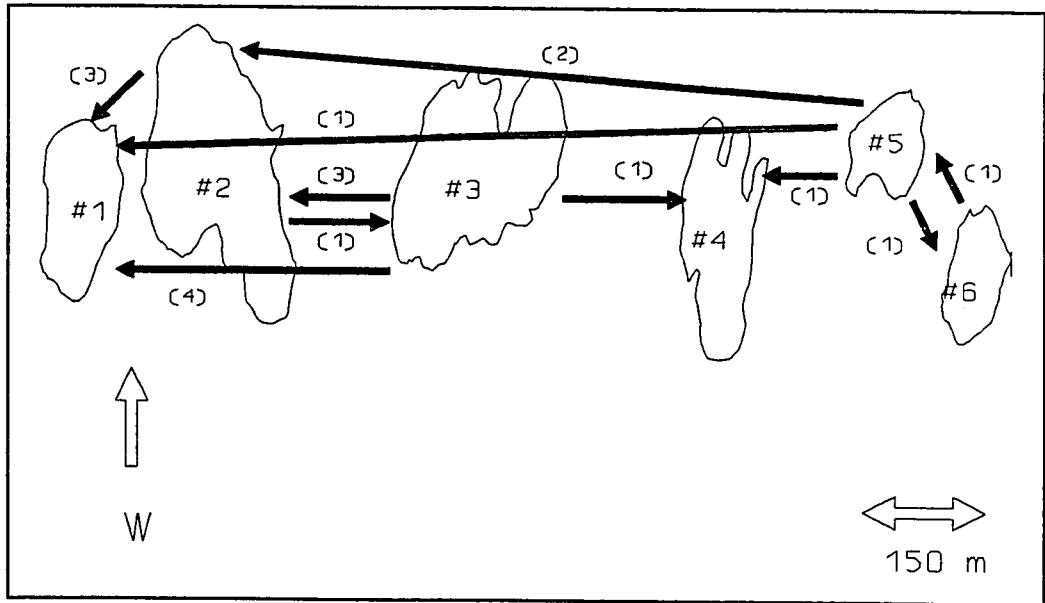


Figure 2. Movement of *Peromyscus* between the six study islands. The number of migrating individuals from each island is listed in parentheses.

walk consisted of movement of an individual by incremental steps, where the direction of each step was influential in determining the ultimate direction of movement.

Emigration

Four simple probability models were generated to simulate the factors affecting emigration. Each model examined one spatial factor: population size, emigrant population size, density (estimated population/hectares), or island size (perimeter to area ratio). All models shared these general assumptions: (1) all islands were equally available for immigration, except the home island; (2) a random number generator from 1 to 6 chose an island for immigration; and (3) the number of emigrants and immigrants was limited to 18, the actual number of migrants. A function was created to describe the influence of a factor on the probability of emigration from an island, e.g., an island with high density would have a high probability of emigration. During a run, emigrants were chosen from an island via the particular function, and were randomly assigned to a new island. The arrival of the new immigrant then changed the probability function of future emigration from that island. Each model allowed 18 mice to migrate from the six islands for each run. After 1000 runs, an average number of emigrants was calculated to produce an expected pattern.

A description of each emigration model and its probability function follows. The **POPSIZEPOOL** model simulated emigration by positively correlating population size and the number of emigrants. This function increased the probability of emigration with increased population size. The beginning population was based on the August 1990 MKA

(minimum known alive) of P. maniculatus and P. californicus at each island. If the simulated emigration pattern was similar to the actual, then this function was used in the complex models.

The EMIGRANTPOOL model was similar to the above model except it used the actual number of emigrants as the total population. Large emigrant populations therefore had a higher probability of producing emigrants in this function. Immigration and emigration changed the probability of emigrating by changing the population size. If the simulated emigration pattern was similar to the actual, then this function was used in the complex models.

The AREAEMIGRANT model simulated movement within the initial island prior to emigration. The probability of emigrating was a combined function of a changing emigrant population (as in the EMIGRANTPOOL model) and a function of the perimeter to area ratio. This ratio was representative of the area traveled by an emigrant before leaving the island. The higher the ratio (as in smaller islands), the greater probability of emigration.

The DENSITY model simulated emigration by positively correlating density and emigration. The probability of emigration was a function of the density of an island. The beginning population was based on a modified Peterson estimate of the average population in June-July, 1990. The area used to calculate density was the hectares of preferred Peromyscus habitat (willow/wax myrtle/cottonwood complex) on each island.

Immigration

Five immigration models were created, comprising four Markovian models and one simple probability model. The Markovian models included a scaled, two-dimensional graphics simulation of the spatial representation of the island system (Universe). Each model incorporated an additional degree of "reality" representing the geography of the Universe. The purpose of each model was to determine if the factor(s) modelled produced an immigration pattern similar to the observed pattern.

The Markovian models were more complex than the emigration models and contained these assumptions. (1) The probability of emigrating was a function of a changing emigrant population with a beginning population based on the actual emigrants at each island (Table 1). (2) Each island was represented by a square or rectangle proportional to the actual area (Fig. 3). For the DISTANCE model, the average size of the six islands was used. (3) The distance between islands was proportionally scaled. (4) The Universe consisted of a scaled rectangle 1220 m by 2035 m and delimited by the ocean in the west (top), a vegetation "mainland" to the east (bottom), and the nearest "islands" to the south (left) and north (right) (Fig 3). (5) Each emigrant randomly left the island from one of eight directions: north, northwest, west, southwest, south, southeast, east, or northeast. The exception was DUNEMORPH, which only allowed initial movement from 5 directions. (6) After the initial departure from the island, the emigrant randomly moved 15 meters at a time, in one of eight possible directions, until it encountered another island or the edge of the Universe (Fig. 3). An emigrant which returned to its home island simply continued random movement until it left again.

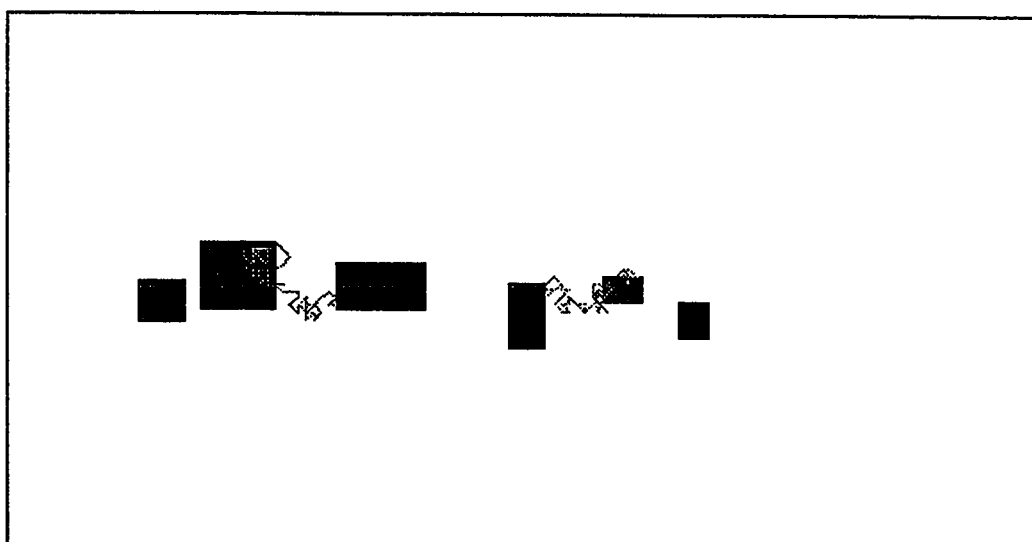


Figure 3. A graphic display of the Universe and random migration from two islands in the DISTSIZE model.

(7) When an emigrant encountered the edge of the Universe, it was considered "dead" and was not counted as an immigrant. (8) When an emigrant encountered another island it was considered "safe" and was considered an immigrant. (9) Every simulation allowed 18 safe immigrants. Therefore, it was possible to have more emigrants than immigrants because some emigrants died. (10) The number of safe immigrants per island per run was recorded, with 1000 runs per model.

Each of the five models simulated a different, but cumulative, spatial factor. **TOTALSTOCHASTIC** was a simple probability model which simulated the case in which immigration was strictly a function of chance. All actual emigrants left their home island and migrated to a new island (not the home island). This assumed that immigration did not affect emigration, and the probability of emigrating did not change temporally.

The **DISTANCE** model simulated the actual distances between islands to determine if distance was a primary factor. The distances (m) were scaled, with area of each island represented by a square 100 m² (average island size). The Markovian random walk was used to simulate an individual's movement, 15 meters at a time, from the home island to the new island. Therefore the probability of an individual randomly finding a new island was dependent on the distance between islands. The **DISTSIZE** model included the actual distances, and area and approximate shape of each island to test the factor of island size (Fig 3). The probability of immigration to an island was dependent on the distances between islands and the perimeter of the island as determined by island area.

The **PROXIMITY** model simulated the increased probability that an individual in close proximity to an island will immigrate to it. To simulate this factor, an island's area

was increased by 15 meters in each direction to create a "proximity" zone. All characteristics previously mentioned were also incorporated. The probability of immigration was determined by distances and increased island perimeter. DUNEMORPH was a model which determined the influence of dune morphology on immigration. The same cumulative parameters were included, but initial movement was not allowed from the northwest, west, and southwest sides of each island to simulate dunes 5 to 30 meters high that may have blocked initial movement. The probability of immigration was therefore a combination of restricted initial movement, distance, and increased island perimeter.

Statistical Analysis

Each model produced 1000 sets of 6 numbers each (immigrants or emigrants per island). These data were stored in an ASCII file and then transferred to SYSTAT, a statistical analysis program, where the mean values were computed for each model. These means became the expected number of emigrants or immigrants at each island. This was compared against the observed distribution using a G Log-Likelihood test (Zar 1984). This G value was adjusted using Williams correction for small samples (Sokal and Rohlf 1981). The alpha level for significance was set at 0.05.

RESULTS

Of the nine models created, six produced migration patterns in which the expected patterns were similar to the actual pattern (accepted the null hypothesis of no difference) and three did not (Table 2). Both the EMIGRANTPOOL and AREAEMIGRANT models produced expected patterns which did not differ significantly from the actual. The low G value of 3.6 for EMIGRANTPOOL confirms the validity of using this function to simulate emigration. The G value for AREAEMIGRANT, simulating intra-island movement via the perimeter to area function, also was not significant ($G=6.5$). However, because the AREAEMIGRANT model included the EMIGRANTPOOL function, it appears that the simpler model, EMIGRANTPOOL, is sufficient to explain the emigration pattern. The other emigration models, measuring the effects of population size (POPSIZEPOOL) and density (DENSITY), produced emigration patterns which were significantly different from the observed ($0.01 > p > 0.001$).

Four of the five immigration models produced patterns similar to the actual and one was significantly different. The G value of 10.3 for TOTALSTOCHASTIC, the completely random model, showed that the expected and observed immigrant distributions were not significantly different. Thus, the immigration pattern appears to be completely stochastic. The results of the DISTANCE model, which simulated distance and used average island size, were not significant with a G value of 9.5. This suggests that distance also provided a partial explanation for the actual immigration pattern. The G value of DISTSIZE, simulating actual distances and island size, was significant ($G=11.8$, $0.05 > p > 0.01$). The PROXIMITY model, simulating the increased probability of

Table 2. The factors modelled and resulting G values for each model.

Model Type	Model Name	Factor Modelled	G value
Emigration	POPSIZEPOOL	Population Size	19.8 **
Emigration	EMIGRANTPOOL	Emigrant Pop. Size	3.6
Emigration	AREAEMIGRANT	Area of Island	6.5
Emigration	DENSITY	Population Density	20.2 **
Immigration	TOTALSTOCHASTIC	Random Selection	10.3
Immigration	DISTANCE	Island Distances	9.5
Immigration	DISTSIZE	Size of Islands	11.8 *
Immigration	PROXIMITY	Proximity to Island	11.1
Immigration	DUNEMORPH	Dune Morphology	10.7

Significance levels: * = $0.05 > p > 0.01$, ** = $0.01 > p > 0.001$

locating an island by "proximity zones", provided a G value of 11.05 which was narrowly accepted. Model DUNEMORPH, simulating the effect of dune barriers on immigration patterns, was not significant at a G value of 10.7. The G value is similar to that of the completely random model and therefore the dunes may only provide only minimal influence on movement.

CONCLUSIONS

The pattern of Peromyscus emigration at Pismo Dunes SVRA was not influenced by the factors of population density or population size. However, the estimates of density in this study may be low because trapping was restricted to the perimeter of the islands. The results also indicated that the area of an island did not inhibit or improve an individual's possibility of eventual emigration. The emigration and immigration of individuals from an original population of observed emigrants, did not change the emigration pattern significantly from the observed pattern. The original emigrant population on each island was therefore used as the basis for a function which allowed greater emigration from a larger emigrant population.

Although larger islands are predicted to have increased immigration (MacArthur and Wilson 1967), island size did not appear to influence immigration in this system. This outcome may be due to the lack of very small or large islands, as island size ranged only from 0.43 to 2.0 hectares. Also, gross simulation of dune morphology and island proximity did not improve the accuracy of the immigration model over the "distance only" model, although both were still considered similar to the actual. Large dunes on

the west side of the islands seemed to have minimal effect on immigration. Because any initial movement in the western direction would lead to the ocean, immigration success was generally lower in that direction.

Random selection of an island without any consideration of distance or island size provides the simplest explanation for the immigration pattern observed at PDSVRA. The completely stochastic model produced an immigration pattern that was not significantly different from the actual pattern. This result implies that each island had a similar probability of immigration. This may be explained by Peromyscus' known ability to colonize areas rapidly (Kirkland and Layne 1989, Simberloff 1978).

However, the model simulating distance between islands also provided an immigration pattern which matched the observed pattern. Distance may therefore be an alternative explanation for the immigration pattern in this system. In this system, the greatest distance between two islands (153 m) may not be a substantial barrier to migration. Therefore, the probability of locating another island was not severely restricted by distance in this system. Because the immigration pattern was measured over 5 months, with two weeks or more between trappings, mice may have moved in a stepping stone fashion. Over time, additional movement occurred among the closest islands, producing a greater "crowding" on these islands. This explanation would account for the greater number of immigrants on the two closest islands, Islands 1 and 2.

To distinguish between distance as the primary factor or migration as purely stochastic, further data must be collected. Information from additional studies, or existing data, on immigration rates between islands at distances greater than 160 m would be of

primary importance. Using the methods described in this study, a stochastic model and a distance model simulating this system could be developed and the expected outcome of immigration produced. One model should produce a more accurate pattern of immigration in systems with increased inter-island distances.

Logically, there exists a distance at which immigration becomes improbable. Through additional modelling of distant islands in multi-island systems, it may be possible to determine this "critical" distance for reduced movement. If this distance were known, then insular populations of these species could be assessed to predict the gene flow among demes and ultimately assist in determining their genetic viability (Weishampel 1990).

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