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SPATIALLY AUTOCORRELATED DEMOGRAPHY AND INTERPOND DISPERSAL IN THE SALAMANDER *AMBYSTOMA CALIFORNIENSE*

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Abstract. The regional dynamics of pond-breeding amphibians are often discussed in the context of metapopulations, under the assumption that individual ponds support distinct subpopulations. We used a combination of indirect and direct methods to assess the spatial population structure of California tiger salamanders (*Ambystoma californiense*) relative to two basic requirements of metapopulation models: (1) that patches support somewhat independent populations linked by dispersal, and (2) that interpatch dispersal probabilities decline as distance increases. Over three consecutive field seasons we captured, marked, and released adult California tiger salamanders at 10 breeding ponds. We observed interpond dispersal by these experienced breeders, and also by first-time breeders marked as newly metamorphosed juveniles at one pond. Spatial autocorrelation of pond-specific demographic parameters suggests that these ponds meet both of these requirements of metapopulation theory. Direct observations of interpond movement by marked individuals support the conclusions of the autocorrelation analyses but reveal relatively high probabilities of interpond movement by both first-time and experienced breeders. We conclude that the subpopulations utilizing these ponds are too closely linked by dispersal for classical extinction–colonization metapopulation dynamics to apply. High probabilities of dispersal are predicted to constantly supply less isolated ponds in this system with dispersers such that local extinctions will be rare. Based on population genetic theory, the high probability of interpond movement is also predicted to prevent significant genetic divergence among ponds over large areas.

Key words: Ambystoma californiense; *declining amphibian metapopulations; demography; dispersal; pond-breeding amphibian; rescue effect; salamander; spatial autocorrelation; spatial population structure.*

INTRODUCTION

Organisms that occupy discrete habitat patches exhibit a continuum of spatial population structures. These range from essentially panmictic populations, where individuals move freely among habitat patches, to isolated subpopulations, where interpatch movement occurs too infrequently to influence metapopulation persistence (Harrison 1994). Although the original model of metapopulation dynamics focused on the middle of this continuum (Levins 1970), metapopulation designation is now often applied to any species occupying a system of habitat patches connected by dispersal (Hanski and Simberloff 1997). The combined effects of juvenile and adult dispersal, demographic characteristics of the subpopulations, and subpopulation persistence, determine how metapopulation theory applies to a specific system.

Because pond-breeding amphibians utilize patchily distributed aquatic breeding habitats, it has been suggested frequently that spatial structure should influence patterns of pond occupancy and regional persistence (Gill 1978, Pechmann and Wilbur 1994, Sjögren-Gulve 1994). The first attempt to apply metapopulation theory to a pond-breeding amphibian found no evidence of interpond dispersal by red-spotted newts (*Notophthalmus viridescens*) over the course of 3 yr (Gill 1978). More recent studies indicate that in several species of frogs and toads, dispersal to nearby ponds occurs regularly with annual probabilities of 5–20%, and individuals occasionally disperse between ponds separated by distances as great as 1.0 to 2.5 km (Breden 1987, Berven and Grudzien 1990, Sinsch 1992). Although studies of ambystomatid salamanders have documented some interpond movement (Raymond and Hardy 1990, Scott 1994), Gill's (1978) newt work remains the only explicit study of spatial population structure in a pond-breeding salamander.

Here we used both indirect (analyses of demographic differentiation among patches) and direct (mark–recapture studies of interpatch dispersal) methods to evaluate the spatial population structure of California tiger salamanders (*Ambystoma californiense*) in a net-

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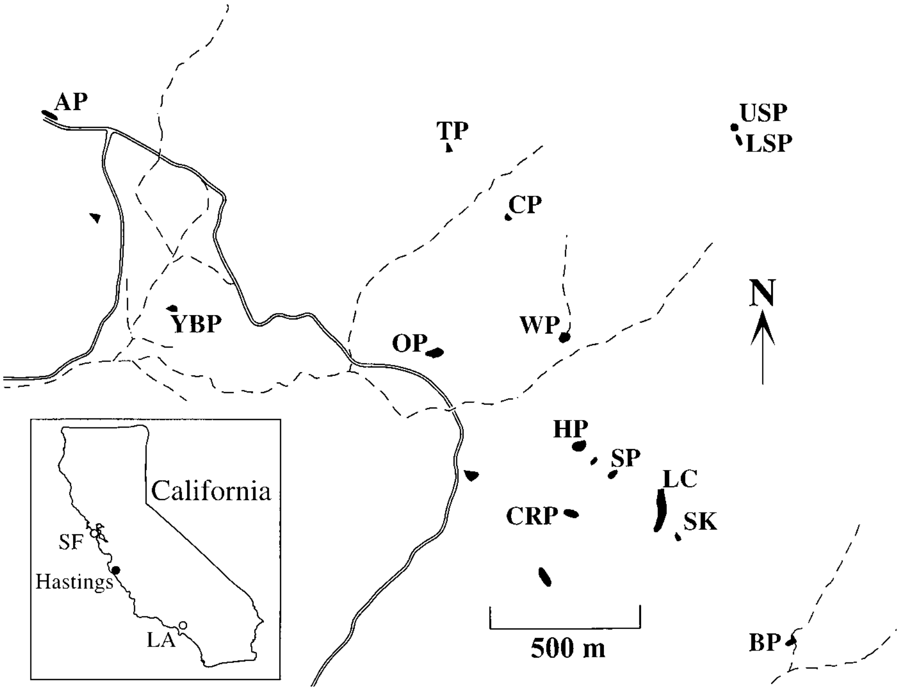

FIG. 1. Map of the study area in the upper Carmel Valley, Monterey County, California, USA. Ponds are represented by solid polygons. Ponds labeled with letter codes were used as breeding habitat by *Ambystoma californiense* during this study. Dashed lines = streams; double lines = paved roads. BP coordinates: 36° 23′ 09″ N; 121° 33′ 20″ W.

work of breeding ponds. The California tiger salamander is a species of conservation concern at state and federal levels, due largely to the fragmented condition of its remaining habitat (U.S. Fish and Wildlife Service 1994, 2000). To examine the spatial population structure of this species, we evaluated the validity of two requirements of metapopulation models by analyzing patterns of demographic spatial autocorrelation and observed interpond movements. First, relatively independent populations linked by occasional dispersal are required for metapopulation dynamics to play an important role in regional distribution and persistence. We evaluated population independence based on demographic correlation between groups of breeding adults captured at individual ponds. We also measured probabilities of interpond movement by marked individuals. Second, the spatial arrangement of habitat patches is important only if dispersal is spatially limited, and most modern metapopulation models assume that dispersal declines with distance (Akçakaya 1994, Hanski 1994). We tested whether demographic correlations and interpond dispersal probabilities are inversely related to distance. Finally, we discuss the implications of these results for the demographic ecology, population genetics, and conservation of the California tiger salamander.

METHODS

Study organism

The California tiger salamander (*A. californiense*) is an endemic member of the grassland community found throughout California’s Central Valley, the surrounding foothills, and coastal valleys (Fisher and Shaffer 1996). During the nonbreeding season, transformed juveniles and adults occupy mammal burrows and typically emerge only on rainy evenings (Loredo et al. 1996, Trenham 2001). Adults enter breeding ponds during storms, typically from November through January, breed, and return to the surrounding terrestrial landscape (Storer 1925, Loredo and VanVuren 1996, Trenham et al. 2000). Historically, natural ephemeral vernal pools were the primary breeding habitats, but ephemeral and permanent ponds created for livestock watering are now frequently used (Fisher and Shaffer 1996). Larvae grow to sizes capable of metamorphosis by late spring, and generally transform as ponds dry (Barry and Shaffer 1994). Newly metamorphosed juveniles move into the terrestrial habitat where they spend 2–6 additional years before returning to breed for the first time (Trenham et al. 2000).

Study site

We conducted field work at Hastings Natural History Reservation and adjacent Oak Ridge Ranch in upper Carmel Valley, Monterey County, California, USA (36° 23′ N, 121° 33′ W; Fig. 1). This site is located in the outer coast ranges of central California. The local terrain is steep (elevation 500–700 m) and the land cover is dominated by open grassland with scattered oaks and stands of mixed deciduous woodland. The ponds included in this study were both natural and modified

PLATE 1. Blomquist Pond (BP) where California tiger salamanders have been captured, marked, and released since 1991. The view is toward the northwest in April 1996.

ephemeral pools and constructed cattle-watering ponds, all of which are located on land grazed by cattle. We sampled all ponds ($n = 17$) for developing larvae each spring using minnow seines (Fisher and Shaffer 1996), and found California tiger salamander larvae in 14 ponds (Fig. 1; see Plate 1). Distances between study ponds, measured using a GIS map of the region, ranged from 60 m to 3 km with a nearest neighbor distance of 300 ± 236 m (mean ± SD). We captured, marked, and released breeding adults at BP, SK, LC, SP, CRP, HP, WP, CP, TP, and AP (abbreviations in Fig. 1). We also monitored annual hydroperiod, defined as the number of weeks a pond contained standing water, for each pond.

Census techniques

During the breeding seasons of 1995–1996, 1996–1997, and 1997–1998 (hereafter 1996, 1997, and 1998) we captured, marked, and released 1316 adult California tiger salamanders. Each year we trapped salamanders at ponds continuously from the first fall rains (October–December) through the end of the breeding season (March–May). At BP and LC, we captured salamanders using drift fences with pitfall traps. At all other ponds we used minnow traps. We completely encircled BP and LC with low drift fences with pitfall cans to capture immigrating and emigrating salamanders, and cattle fences to protect the drift fences from trampling (Dodd and Scott 1994, Trenham et al. 2000). Drift fences were 30 cm tall aluminum flashing with the bottom 5 cm buried in the soil, and pitfalls were 2-L metal cans. Pitfall cans were checked for salamanders each morning. At ponds without cattle fences, we used partially submerged minnow traps to capture salamanders (Shaffer et al. 1994). We placed two minnow traps on opposite sides of each pond and checked them at least every other day.

We used a combination of passive integrated transponder (PIT) tags and toe clipping to mark individuals, depending on the year and pond, and inspected all captured animals for any evidence of prior marking. Salamanders were sedated in a 0.03% solution of Benzocaine (Sigma-Aldrich, St. Louis, Missouri, USA) prior to measuring and marking (Vanable 1985), and mass, snout–vent length (SVL) to the anterior end of the cloacal opening, and total length (TL) were recorded for each animal upon its initial capture each breeding season. Animals captured at the drift fences were released on the opposite side of the fence near the point of capture, and minnow-trapped individuals were released in the ponds where they had been captured. Salamanders were released within 24–48 h.

We used the CAPTURE software (White et al. 1978) to estimate numbers of breeding adults in minnow-trapped ponds (Table 1). We estimated capture efficiency for males and females at each pond separately as: 1 − [(population estimate − number captured)/population estimate]. Because salamanders at the drift-fenced ponds were vulnerable to capture only as they entered or exited the ponds, we could not use CAPTURE to obtain population estimates for the fenced ponds. In drift-fence studies, trapping efficiency is estimated by calculating the probability that individuals that were present went uncaptured (Semlitsch 1983, Gill 1985). To estimate this probability, we calculated drift fence trespass probabilities (such as when an individual released inside the drift fence was next captured outside the fence) and the number of times individuals entered and exited the drift-fenced area. We then estimated the capture efficiency as: $1 - t^c$, where t = annual trespass probability and c = mean number of fence crossings per individual. Finally, we divided the census totals by the capture efficiencies to obtain population estimates (Trenham et al. 2000).

Whereas work at other ponds began in 1995, we erected the drift fence at BP in December 1991, and have monitored its traps daily since (Trenham et al. 2000). Prior to the first field season of this study, we had marked and released more than 1900 adult and

TABLE 1. Annual estimated numbers of breeding *A. californiense* at each sampled pond (see Fig. 1).

Pond	1996		1997		1998	
	Males	Females	Males	Females	Males	Females
BP‡	45 (0.99)	13 (0.95)	47 (0.96)	36 (0.99)	35 (0.99)	48 (0.99)
SK	8†	0†	14†	3†	11 (0.55)§ [8, 28]	0†
LC‡	89 (0.95)	32 (1.00)	325 (0.40)	216 (0.60)	168 (0.87)	150 (0.75)
CRP	1†	0†	8†	1†	⋯	⋯
SP	7†	1†	9†	2†	0†	1†
HP	0†	1†	20 (0.40)§ [13, 42]	6†	17 (0.59)‖ [12, 38]	1†
WP	43 (0.55)‖ [29, 77]	7 (0.71)§ [6, 25]	107 (1.0)¶ [107, 107]	44 (1.0)# [44, 52]	37 (0.95)¶ [36, 56]	8 (0.63)‖ [6, 25]
CP	17 (0.94)‖ [16, 22]	4†	36 (0.78)†† [31, 54]	12 (1.0)# [12, 12]	11 (1.0)# [11, 11]	5 (1.0)‖ [5, 5]
TP	27 (0.89)§ [25, 42]	6†	57 (1.0)¶ [57, 57]	39 (0.51)§ [28, 65]	35 (0.97)¶ [35, 44]	3†
AP	⋯	⋯	8†	4†	2†	0†

Notes: Capture efficiencies are reported in parentheses; where available 95% confidence limits are reported in brackets. Ellipses denote ponds that were not surveyed in that breeding season.

† Where we made no within-season recaptures we report the actual number of individuals captured.

‡ Breeding population estimates made using methods for drift fences (Trenham et al. 2000).

§ Program CAPTURE population estimator, Jacknife (White et al. 1978).

‖ Program CAPTURE population estimator, Null (White et al. 1978).

¶ Program CAPTURE population estimator, Burnham (White et al. 1978).

Program CAPTURE population estimator, Zippin (White et al. 1978).

†† Program CAPTURE population estimator, Chao's (White et al. 1978).

newly metamorphosed California tiger salamanders at BP. Thus, at the start of this study, BP was the only pond from which there were marked individuals available for recapture.

Catchability of males vs. females

Ponds that had large estimated breeding populations of males generally had large estimated breeding populations of females ($n = 3$ yr, all $r > 0.93$; Table 1). However, in minnow-trap surveys, we captured individual males nearly twice as many times per season as females (mean number of captures ± SD: males = 2.5 ± 2.5, females = 1.3 ± 0.7; Mann-Whitney U test, $Z = -4.5$, $N = 456$, $P < 0.001$). Ponds where we recaptured no females within a given breeding season were also common (Table 1). Due to sex-biased catchability in minnow-trapped ponds, females were sampled less completely and estimates of female population sizes are less reliable. We therefore compared pond demographics (i.e., age distributions, mass distributions, breeding population sizes) based on males only. We calculated interpond-dispersal probabilities for males and females both separately and combined, but limited our analysis of the relationship between dispersal probability and interpond distance to males because too few dispersing females were recaptured.

Age structure

We compared age structures among the study ponds based on age estimates from skeletochronology. Skeletochronology allows age estimation based on counts of lines of arrested growth (LAG) present in the bones of many amphibians and reptiles (Castanet and Smirina 1990). Nondestructive aging is possible in species where LAG are visible in the bones of the toes, and the timing of LAG deposition can be verified. During marking and measurement procedures in the 1997 season, we clipped toes from all individuals and preserved them in individually labeled 1.5-mL vials filled with 70% alcohol. We made skeletochronological preparations of all BP specimens (Trenham et al. 2000), while at other ponds where >20 males were captured we prepared a random subset of 20 specimens. For ponds where ≤ 20 males were captured, we prepared all specimens. See Trenham et al. (2000) for details of sample preparation and method validation.

Data analysis

We used Mantel tests to test for declining correlations and declining dispersal probabilities between ponds separated by increasing distances. This statistical method is used to test for association between two related matrices of values, such as matrices of biological

TABLE 2. Environmental characteristics of *Ambystoma californiense* breeding ponds.

Pond	Area (m^2)	Burrows (number/400 m^2)	Hydroperiod (weeks) 1995	1996	1997	1998
BP	700	26.0	31	23	24	32
SK	370	13.0	23	13	13	27
LC	3660	7.0	52	52	52	52
CRP	990	18.8	32	24	26	36
SP	640	9.8	23	19	22	36
HP	1250	14.0	22	10	13	22
WP	470	5.5	52	52	52	52
CP	360	6.3	38	52	52	44
TP	460	12.0	38	48	32	44
AP	400	29.7	27	19	23	32

Notes: Pond areas are based on digital aerial photographs of the region. Values for mammal burrows are means of counts along four transects extending 100 m from each pond. Hydroperiod is the number of weeks that each pond contained water between 1 November and 31 October.

similarities and linear distances between all possible pairings of study sites (Fortin and Gurevitch 1993, Sokal and Rohlf 1995). The significance of each observed Mantel Z statistic is evaluated by comparing the observed value with the Z statistics from 1000 randomization trials using the same data, but with one of the matrices randomly shuffled prior to each run (Fortin and Gurevitch 1993, Koenig 1999). The P value for each test is the proportion of the 1000 runs for which the randomized value was less than the observed Z. We used a significance level of $\alpha = 0.05$.

Spatial correlation of demography

Similarity in demographic parameters among locations may result from dispersal, correlated environmental parameters or disturbances, or a combination of both factors (Ranta et al. 1995, Bjørnstad et al. 1999, Koenig 1999). In systems where the probability of dispersal is high and dispersal occurs over long distances, demographic parameters should be strongly correlated over large regions. However, in systems where dispersal occurs with lower probability or on a limited spatial scale, demographic correlation should vary and generally decline as dispersal between locations becomes less likely (Hanski and Woiwod 1993, Sutcliffe et al. 1996). Because environmental similarity of nearby points also contributes to spatial patterns of correlation, it is generally difficult to isolate the unique contribution of dispersal. However, because all ponds along the 3-km transect of our study experience the same regional climate, local weather should have little influence on demographic correlation.

We also used Mantel tests to determine if similarity between other important features of these ponds declined with increasing interpond distances. For many pond-breeding amphibians, hydroperiod is considered to be the environmental feature with the strongest demographic influence (Semlitsch 1987, Semlitsch et al. 1988). We estimated hydroperiod dissimilarity for each possible pairing of ponds as the absolute value of the difference between their mean hydroperiods (Table 2). Because the availability of mammal burrows and pond size might also influence salamander demography, we calculated pairwise differences for mammal burrow densities and maximal pond surface areas. To estimate mammal burrow density, we walked four 100-m transects (north, south, east, west) from each pond, and counted all burrows within 2 m of the transect. We then averaged the total burrow counts for the four transects to obtain a regional mean for each pond. Maximal pond surface areas were estimated from aerial photographs (Table 2).

We used three types of data to analyze demographic autocorrelation between pairs of ponds: estimated numbers of breeding males ($n = 8$ ponds); frequency distributions of male masses from 1997 and 1998 ($n = 10$ ponds); and frequency distributions of male ages from 1997 ($n = 10$ ponds). We constructed mass-frequency histograms for each pond by dividing the pooled data into eight classes of equal width, and constructed age-class frequency histograms for each pond by totaling the number of individuals in each of 10 age classes from 2 to 11 yr. Then we calculated Pearson correlation coefficients for all possible pairwise combinations of ponds. We used the breeding population estimates to calculate the correlation of population fluctuations between pairs of ponds ($n = 3$ for each correlation). For the mass and age distribution data, we calculated correlations between the frequency histograms for each possible pair of ponds ($n = 8$ or 10 for each correlation, respectively).

Our interpretation of the above demographic analyses assumes that dispersers are a random subset of the total population with respect to demographic parameters such as age and mass. We evaluated this assumption for mass by comparing the predispersal mass of individuals recaptured at other ponds with the median mass of their total predispersal cohort (e.g., 1992 BP breeding males). Male breeders that later dispersed were equally likely to fall above or below the median body size of their predispersal cohort (sign test, $P = 0.69$, $N = 25$). We also detected no significant mass bias among female breeders (sign test, $P = 0.13$, $N = 7$) or new metamorphs (sign test, $P = 0.99$, $N = 9$) that later dispersed, although our power to detect significant biases is limited by the small sample sizes. Too few salamanders with skeletochronological age estimates were recaptured as dispersers to evaluate age biases.

Interpond dispersal

We classified recaptured individuals as dispersers or residents. Dispersers were individuals marked at one pond and recaptured in a subsequent breeding season at a different pond. Residents were individuals recaptured in the pond where they were originally marked. Each recaptured individual was counted only once per season. Because sex- and age-biased dispersal may influence spatial population structure, we report dispersal probabilities by sex and whether individuals were first-time breeders or experienced breeders. In calculating dispersal probabilities, we always adjusted the recaptured resident and disperser totals by dividing by the annual pond- and sex-specific capture efficiency (Table 1).

At the start of this study, BP was the only source of marked individuals; hence in 1996 and 1997 almost all observed dispersal was from BP. In 1998, male dispersers marked at BP and other ponds were detected in larger numbers. Thus, we limited our spatial analysis of the relationship between interpond dispersal probability and distance to 1998 recaptures of males previously captured in 1996 or 1997. Interpond dispersal probabilities were estimated as $(D_{\mathrm{A-B}} + D_{\mathrm{B-A}})/(R_{\mathrm{A}} + R_{\mathrm{B}} + D_{\mathrm{A-B}} + D_{\mathrm{B-A}})$, where $D_{\mathrm{A-B}}$ and $D_{\mathrm{B-A}}$ are the efficiency-adjusted numbers of dispersers from pond A to B and B to A, respectively, and R_{A} and R_{B} are the adjusted numbers of resident recaptures in each of these ponds. In cases where we could not estimate trap efficiency, we used the mean trapping efficiency for that sex at other minnow-trapped ponds. A Mantel test was used to evaluate the relationship between dispersal probabilities and interpond distances.

Finally, we estimated the spatial ranges over which dispersers might be expected to prevent the extinction of neighboring subpopulations (i.e., rescue effects), and to maintain genetic connectivity among subpopulations. These estimates were made using: (1) the pond-specific breeding population estimates and the negative exponential function describing the relationship between dispersal probability and distance, all derived from this study, and (2) the overall survival and breeding probabilities from our long-term study at BP (Trenham et al. 2000). We used a simple negative exponential function to model the relationship between movement and distance, because the functional form makes intuitive sense and shows a reasonable empirical fit to our data (Frampton et al. 1942, Turchin 1998). To estimate the distance to which rescue effects could extend from each study pond, we determined the maximum distance to which at least one male and one female are expected to disperse each year based on the functions

$$N_{\mathrm{males}}B_{\mathrm{males}}(ae^{-b\cdot\mathrm{distance}})$$

$$N_{\mathrm{females}}B_{\mathrm{females}}(ae^{-b\cdot\mathrm{distance}}) \quad (1)$$

where N = mean breeding population estimate, B = annual breeding probability, and a and b are the parameters of the negative exponential function relating dispersal probability to distance. We assume that these parameters do not vary annually, and that B, a, and b do not vary among ponds. Annual breeding probability is included because at BP surviving males and females frequently skipped breeding opportunities, reducing the number of potential dispersers.

In the literature of conservation genetics, considerable theoretical attention has been given to the levels of gene flow that will maintain a reasonable balance between population isolation (allowing for local adaptation) and connectivity (preventing deleterious effects of inbreeding). Although no absolute rules have been established, the ''one migrant per generation'' exchange rate is a useful benchmark that places a theoretically defensible lower bound on the optimal migration rate among subpopulations (Mills and Allendorf 1996, Hedrick 2000). While there is debate over what constitutes ''optimal'' connectivity under field conditions, and relaxing unrealistic model assumptions can affect the genetic consequences of any migration

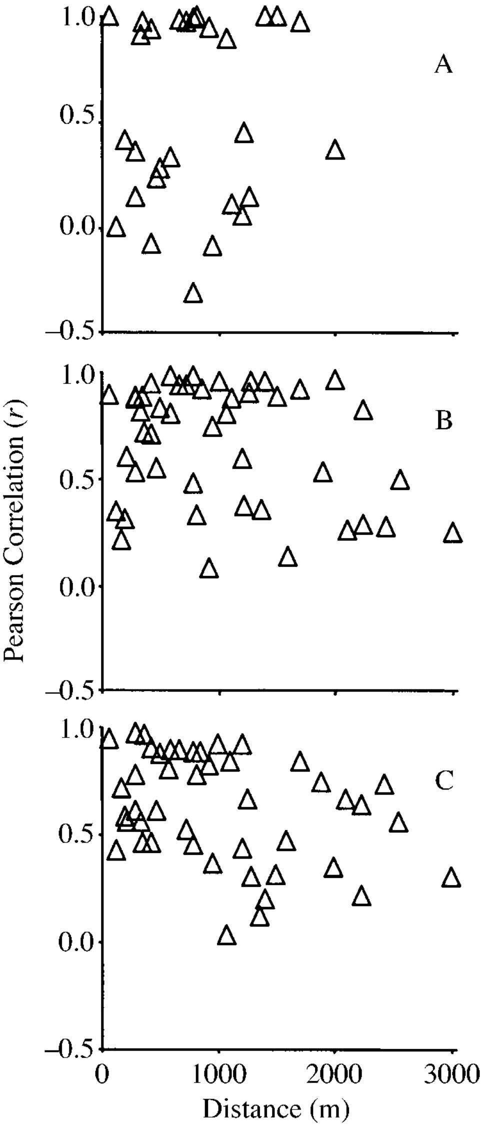

FIG. 2. Demographic autocorrelation between all possible pairwise combinations of ponds plotted against interpond distance for (A) breeding population sizes; (B) mass distributions; and (C) age distributions. Mean overall correlations are: population sizes, $\bar{x}$ = 0.54; mass distributions, $\bar{x}$ = 0.67; age distributions, $\bar{x}$ = 0.62.

TABLE 3. Summary of demographic autocorrelation analyses.

	Habitat variables analyzed			
Parameter	Interpond distance	Hydroperiod dissimilarity	Pond area dissimilarity	Burrow density dissimilarity
Population size	0.14	0.13	0.00	0.06
Mass distributions	−0.26*	0.08	−0.01	−0.13***
Age distributions	−0.34**	0.09	0.12	0.05

Notes: Values are Pearson correlation coefficients (r) between demographic correlations and interpond distances or habitat dissimilarities. A significant Mantel test indicates that demographic correlation coefficients decline as interpond distances or dissimilarity measures increase.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

rate (Mills and Allendorf 1996), the one migrant per generation benchmark is a reasonable starting point. We used this benchmark to predict the genetic effects of migration based on the following function:

$$\sum_{\text{year}=1}^{n} \{[N_{\text{males}}(S_{\text{male}})^{\text{year}-1}B_{\text{male}}] + [N_{\text{female}}(S_{\text{female}})^{\text{year}-1}B_{\text{female}}]\}(ae^{-b\cdot\text{distance}}) \qquad (2)$$

where S = annual survival probability from our long-term study at BP. We substituted increasing distances into the function to determine the maximum distance for which the function is ≥1 for each pond (i.e., at least one disperser over the entire lifetime of the cohort).

RESULTS

Spatial autocorrelation of demography

Although pairwise interpond correlations for male age distributions, mass distributions, and breeding population estimates were largely positive, divergent correlations between even nearby ponds indicate that the demographic features analyzed are not homogeneous throughout the study area (Fig. 2). Mantel tests indicated significant declines in correlation with increasing interpond distance for mass and age distributions, but not for population sizes of breeding males (Table 3). Correlations for both mass and age distributions declined and became more variable for ponds separated by >1 km (Fig. 2). In Mantel tests of the relationship between the dissimilarity of pond habitat features (hydroperiod, surface area, mammal burrow density) and interpond distances, mammal burrow densities was the only habitat variable that exhibited a significant increase in dissimilarity with increasing interpond distances (r = 0.47, Mantel test, P = 0.03).

Comparing demographic correlations with habitat dissimilarities, there was only one significant association: salamander mass correlations declined significantly with increasing dissimilarity of mammal burrow densities (Table 3). This suggests the possiblity that differences in mammal burrow abundance, rather than limited dispersal, is a plausible explanation for the decline in mass distribution correlations. However, the relationship between salamander mass correlations and mammal burrow densities was weaker than the correlation between mass correlations and distance (i.e., −0.13 vs. −0.26), and we found no evidence that the means or variances of masses were related consistently to mammal burrow density at individual ponds (Table 4). Rather, the only habitat variable significantly correlated with the means or variances of the demographic parameters was hydroperiod (Table 4), but Mantel tests revealed no significant relationship between hydroperiod dissimilarity and observed demographic correlations (Table 3).

Observed interpond dispersal

Although most recaptured individuals returned to the ponds where they were initially marked, overall an estimated 22% dispersed to different ponds (Table 5). Dispersers were of both sexes and included both first-time breeders (last captured as newly metamorphosed juveniles) and experienced breeders (last captured as breeding adults). Due to the extended subadult phase of California tiger salamanders at this locality (Trenham et al. 2000), individuals marked during the long-term study at BP provided the only opportunity for comparing dispersal probabilities between first-time and experienced breeders. Of the individuals marked at BP since 1992 and recaptured at BP and other ponds between 1996 and 1998, dispersers represented 30% of recaptured first-time breeders and 26% of recaptured experienced breeders. First-time breeder dispersal

TABLE 4. Spearman rank correlations between mean and variance in pond-specific demographic parameters and pond surface area, mean hydroperiod, and estimated mammal burrow density.

	Spearman rank correlations			
Demographic parameter	Pond area	Hydroperiod	Burrows	N†
N males (mean)	0.31	0.80*	−0.38	8
N males (variance)	0.23	0.83*	−0.45	8
Mass (mean)	−0.24	−0.40	−0.15	10
Mass (variance)	−0.13	0.52	−0.38	10
Age (mean)	0.50	−0.55	0.55	10
Age (variance)	0.03	−0.40	−0.09	10

* $P < 0.05$.

† N is the number of ponds used in calculating the correlation.

TABLE 5. *Ambystoma californiense* dispersal probabilities for experienced breeders from BP and all other ponds combined (OTHER), and first-time breeders from BP.

		Breeding season				
Origin	Sex	1996	1997	1998	Annual ± 1 SD†	Overall‡
Experienced breeders						
BP	M	0.10 (2)	0.43 (6)	0.33 (7)	0.29 ± 0.17	0.31 (15)
BP	F	0.11 (1)	0.23 (2)	0.13 (2)	0.16 ± 0.07	0.17 (5)
OTHER	M	NA	0.05 (2)	0.21 (10)	0.13 ± 0.11	0.15 (12)
OTHER	F	NA	0.00 (0)	0.41 (4)	0.21 ± 0.29	0.41 (4)
First-time breeders						
BP	M	0.00 (0)	0.40 (3)	0.36 (2)	0.25 ± 0.22	0.31 (5)
BP	F	0.49 (1)	0.19 (1)	0.31 (2)	0.33 ± 0.15	0.27 (4)

Notes: Dispersal probabilities were calculated for each breeding season as the number of recaptured dispersers divided by the total number of recaptured individuals (i.e., dispersers and residents combined). Numbers were corrected for annual pond-specific capture efficiencies. Raw numbers of observed dispersers are reported in parentheses.

† Mean ± 1 SD of "breeding season" values.

‡ Total number of dispersers divided by total number of recaptures for all years combined.

probabilities from BP were not significantly greater than those observed for experienced breeders (Wilcoxon signed- ranks test: $Z = -3.14$, $P = 0.75$), and overall first-time breeder dispersal probabilities were similar for males and females (Table 5). Of the adults that we captured in 1996 or 1997 and recaptured in 1997 or 1998, 15% (n = 2) of BP recaptures were dispersers compared with 17% (n = 15) of the recaptures from all other ponds combined.

All 29 dispersers from BP were recaptured 580 m away at LC. For the adult dispersers captured at all ponds including BP in 1996 or 1997 and recaptured in 1998, the distances between the pairs of ponds at which they were captured ranged from 60 to 670 m (mean ± SD distance: males = 452 ± 253 m [n = 11]; females = 373 ± 293 m [n = 4]). In 1998, estimated probabilities of interpond dispersal by adult males for all possible pairwise combinations of ponds ranged from 0% to 24%, and dispersal probabilities exhibited a significant inverse relationship with interpond distance ($r = -0.49$, Mantel test, $P = 0.04$; Fig. 3).

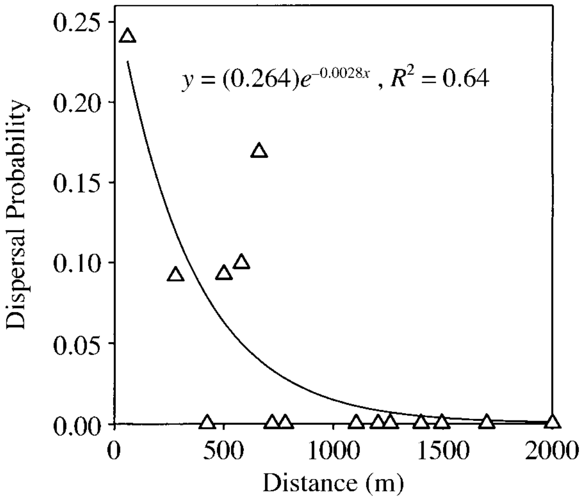

FIG. 3. Dispersal probabilities between all possible pairwise combinations of BP, SK, LC, WP, CP, and TP (based on males captured as breeding adults in 1996 or 1997 and recaptured in 1998). To estimate the relationship between interpond distance and dispersal probability, we fit a negative exponential curve to these data (Berven and Grudzien 1990, Turchin 1998).

DISCUSSION

Spatial population structure

To unravel the spatial population structure of any long-lived species, both direct and indirect measures of individual movements are useful. Direct data from marked individuals are preferable, but the time and effort needed to accurately characterize juvenile and adult movements over even one generation is often prohibitive. Indirect data, including molecular and demographic differentiation, can provide a summary of recent movement patterns, but the interpretation of among-patch variation requires a number of generally untested assumptions concerning environmental heterogeneity, local natural selection, and past frequencies of extinction and colonization.

For this network of California tiger salamander breeding ponds, the indirect and direct datasets suggest similar spatial population structures. The demographic autocorrelation data suggest that many ponds separated by <1 km exchange sufficient migrants to elevate levels of correlation for age and mass distributions. Because relatively small numbers of dispersers may have little effect on overall population sizes, the absence of a spatial pattern in the correlations of annual breeding population estimates was not surprising. While the effects of small numbers of dispersers on population size may be insignificant, they may have a larger effect on the mass and age distributions, particularly if they deviate significantly from the mean of the recipient pond. This appears to be the case in this system, and our results closely resemble the decline in correlations with increasing distances reported for butterfly population dynamics (Sutcliffe et al. 1996) and many other ecological processes (Koenig 1999). However, because it is impossible to rule out all other environmental factors that might produce similar clinal trends in demographic parameters, these results alone are not conclusive.

Our direct observations also support the hypothesis that California tiger salamanders commonly disperse among breeding ponds, and that interpond dispersal probability declines as interpond distances increase. Unlike the red-spotted newt system studied by Gill (1978), we observed high probabilities of dispersal by both first-time and experienced breeders. It might seem that a mean interpond dispersal probability of 20–25% per year in a long-lived animal would lead to virtual panmixia. However, because in our long-term study at BP the majority of individuals did not survive to breed a second time, most individuals will breed only in their natal ponds (Trenham et al. 2000). For example, if we assume a constant dispersal probability of 25% and a constant annual mortality rate of 50%, 25% of a given cohort would disperse as first-time breeders, but over all subsequent years only an additional 15% would survive to disperse and breed again. However, even if ponds support subpopulations composed predominantly of locally produced salamanders, interpond dispersal with these probabilities will strongly impact regional dynamics and population genetics.

As with any natural system, the local conditions in this network may limit the generality of our results. For example, if dispersal occurs in a stepping-stone fashion (as the frequent dispersal from BP to LC, but not further, suggests), the relative density of ponds might serve to limit the length of dispersal distances. Because we observed relatively high probabilities of dispersal between several ponds separated by 500 to 670 m, California tiger salamanders are probably capable of longer distance movements (Fig. 3).

Taken together, these data confirm that breeding ponds support somewhat independent populations linked by dispersal, and that dispersal declines with increasing interpond distance. Nonetheless, because of the high probabilities of interpond dispersal, this system should be considered a metapopulation only in the broadest sense of the term (Hanski and Simberloff 1997). Because interpond dispersal is relatively common, the persistence of this system will not depend on the subtle balance between colonization and extinction originally envisioned by Levins (1970). Instead, these ponds appear to support a nearly continuous, intermixed population. What are the implications of this spatial population structure for the demographic ecology, population genetics, and conservation of California tiger salamanders?

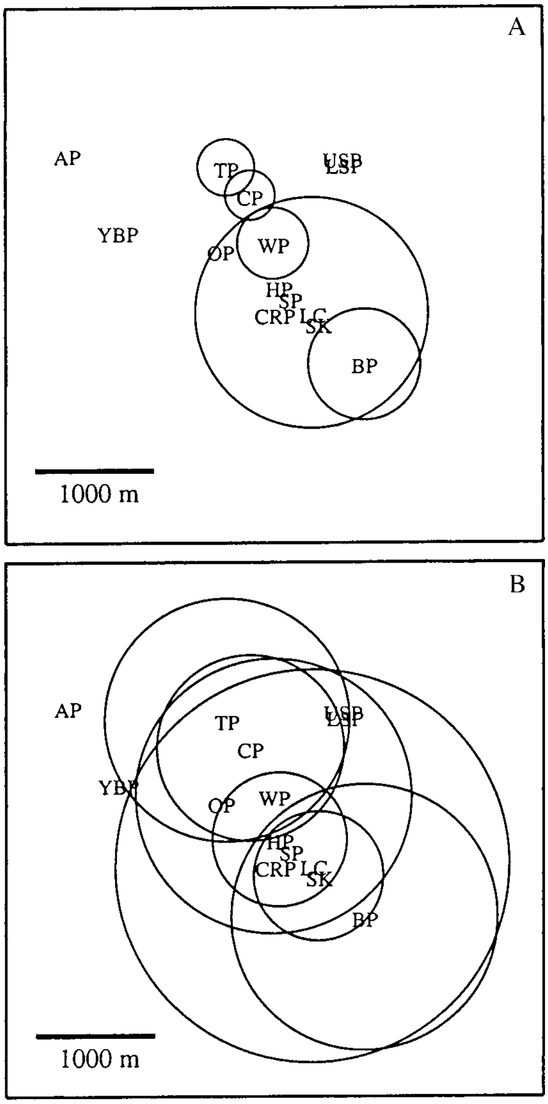

FIG. 4. (A) Estimated ranges for rescue effects and (B) apparent genetic homogeneity around *A. californiense* breeding ponds. Effects ranges and pond labels are centered over study ponds. Parameters used in Eq. 1 to calculate rescue effects ranges: N = mean numbers of breeding adults (Table 1); $B_{\text{males}} = 0.61$; $B_{\text{females}} = 0.44$ (Trenham et al. 2000); $a = 0.268$ and $b = 0.0029$ (Fig. 3). Additional parameters used in Eq. 2 to calculate genetic homogeneity ranges: $S_{\text{males}} = 0.50$; $S_{\text{females}} = 0.60$ (Trenham et al. 2000).

Demographic ecology

Rescue effects and source-sink dynamics are two recurring topics in discussions of the spatial population dynamics of pond-breeding amphibians (Stacey et al. 1997). In several amphibian systems, researchers have found that all study ponds, even unproductive ones, are occupied year after year due apparently to regular interpond dispersal (Gill 1978, Sinsch 1992). Unfortunately, because many amphibians have generation times of ≥2 yr, rigorously documenting source-sink dynamics is beyond the scope of most studies (Watkinson and Sutherland 1995). However, with knowledge of dispersal probabilities and population sizes, we can make reasonable predictions about the spatial scale at which the regular export of dispersers might prevent local extinctions.

As with many amphibians, a single pair of California tiger salamanders can produce hundreds of fertilized embryos. Thus it is reasonable to assume that a single pair can establish or rescue a local population. If we define rescue as one male and one female immigrant per year, we can estimate the maximum distance over which rescue effects could extend from each pond. Assuming that male and female dispersal are accurately described by the negative exponential dispersal curve for males in Fig. 3, that numbers of breeding adults are stable, and that our mean population estimates represent the potential numbers of breeding males and females from each pond (Table 1), our estimates of the range over which rescue effects are likely to extend from our study ponds are illustrated in Fig. 4A. Based on these estimates, the large population of LC is capable of rescuing ponds as far away as BP and CP. However, if dispersers typically stop at the first pond detected, the range of rescue effects would be diminished.

In any case, because most ponds in this region appear to be within the range of dispersers from the large population at LC, local extinctions should be rare and recolonization rapid. Based on Fig. 4A, the only ponds that appear likely to be demographically disjunct from the rest of this network are AP, YBP, USP, and LSP. The lower mass and age distribution correlations for AP, relative to those for all other ponds combined, also suggest the demographic isolation of this pond (mean mass correlations ± SD: AP = 0.38 ± 0.21, all others = 0.74 ± 0.25; mean age correlations ± SD: AP = 0.50 ± 0.23, all others = 0.66 ± 0.25). In addition USP contained *A. californiense* larvae in 1996 but not in 1997 or 1998, suggesting that it was the only pond where a local extinction may have occurred during this study (P. C. Trenham, *unpublished data*).

Population genetics

Because gene flow shapes regional patterns of genetic variation, understanding interpond dispersal is also important from the perspective of population genetics (Driscoll 1998, Rowe et al. 1998, Shaffer et al. 2000). If a single migrant per generation is sufficient to prevent the significant divergence of allele frequencies for selectively neutral traits (Mills and Allendorf 1996), only ponds that do not exchange regular dispersers will diverge genetically. Our results suggest that at least one disperser per generation from LC has the potential to reach all ponds from BP to TP, producing weak genetic differentiation throughout this network of ponds (Fig. 4B). Again, AP appears to reside outside of the influence of regular dispersers from the other study ponds, and is the most likely candidate for significant genetic divergence. Under a more realistic stepping-stone model of interpond migration, migrants will tend to be genetically more similar to the recipient pond than under the island model, and the homogenizing effect of a single migrant will be reduced. However, the general prediction that the migration probabilities observed in this study should result in very limited genetic subdivision across the landscape is still reasonable.

It should be emphasized that our estimates of the spatial extent of dispersal effects on demography and genetics depend critically on the shape of the dispersal function in Fig. 3. For example, if we fit a power function to the data, rather than a negative exponential, the extent of potential rescue and genetic effects for LC increase roughly 2 and 14 times, respectively. Although a body of empirical work supports the exponential decline of dispersal probabilities with distance, often the tails of these curves do not accurately represent rare but important long-distance dispersal events (Kot et al. 1996, Lewis 1997). Because we observed no dispersal events longer than 700 m, our projections of longer distance dispersal probabilities rely on the assumption of a continued exponential decline with distance. Better data on dispersal probabilities and responses to landscape features are needed before robust predictions of the spatial extent of rescue and genetic effects in this and other landscapes can be made.

Conservation

Contrasting with the common conception that pond-breeding amphibians represent classical metapopulations, the high probabilities of interpond dispersal by the California tiger salamanders in this system suggest that these ponds do not support distinct subpopulations that are likely to experience independent local extinctions. Rather, most of the ponds included in this study appear to represent an interconnected set of subpopulations where productive ponds will supply neighboring ponds with regular dispersers.

The greatest threat to the California tiger salamander is generally considered to be human habitat modification (Fisher and Shaffer 1996; C. Davidson, H. B. Shaffer, and M. R. Jennings, *unpublished manuscript*), resulting in loss of breeding ponds and fragmentation of the remaining occupied habitats (U.S. Fish and Wildlife Service 1994, 2000). Although the extinction risk for individual subpopulations is currently unknown, the high probability of interpond dispersal is probably an adaptation to the naturally variable recruitment potential of individual breeding ponds (Gill 1978, Gill et al. 1983, Trenham et al. 2000). Because the existence of multiple breeding ponds reduces the risk of extinction, and because the salamanders wander widely over the landscape, maintaining habitat connectivity for interpond dispersal should be a priority. Also, because ponds that support large subpopulations (e.g., LC) are less vulnerable to extinction and will export more dispersers over larger areas, their protection should be emphasized (Morey 1998). Finally, high dispersal probabilities and the colonization of created ponds throughout

California (Fisher and Shaffer 1996) also suggest that the restoration or creation of additional ephemeral ponds could enhance existing California tiger salamander populations.

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