Metapopulation Processes or Infinite Dispersal?: Habitat Patch Occupancy by Toads (*Bufo punctatus*) in a Naturally Fragmented Desert Landscape

David F. Bradford[1], Anne C. Neale[1], Maliha S. Nash[1], Donald W. Sada[2], and Jef R. Jaeger[3]

1 U.S. Environmental Protection Agency, Landscape Ecology Branch, Las Vegas, NV 2 Desert Research Institute, Reno, NV 3 Biological Sciences Department, University of Nevada, Las Vegas

ABSTRACT

Amphibians are often thought to have a metapopulation structure, which may render them vulnerable to habitat fragmentation. The red-spotted toad (*Bufo punctatus*) in the southwestern USA and Mexico commonly inhabits wetlands that have become much smaller and fewer since the late Pleistocene. This study tests two predictions based on metapopulation theory ó the incidence of habitat patch occupancy is directly related to patch size and inversely related to patch isolation ó and a third, potentially competing hypothesis that patch occupancy is influenced by local environmental conditions. In a 20,000 km^2 area of the eastern Mojave Desert, 128 potential habitat patches (primarily springs) were identified and surveyed for local environmental characteristics and presence/absence of *B. punctatus*. Patch isolation metrics were based on nearest-neighbor distances, calculated both as Euclidian distance and distance via connecting drainage channels. *B. punctatus* was found at 73% of the sites, including all of the 15 historic (pre-1970) sites. Based on stepwise multiple logistic regression, the incidence of patch occupancy increased significantly with patch size, and was also significantly related to elevation, latitude, and four metrics that were associated with rocky terrain, periodic scouring water flows, and ephemeral water. In contrast, incidence of patch occupancy was not significantly related to patch isolation. These findings are consistent with a ìpatchy populationî model, rather than the classical equilibrium metapopulation model, implying frequent dispersal among patches and virtually no local extinctions. Implicated dispersal distances of many kilometers are large for an amphibian.

Fig. 1. Red-spotted toad (*Bufo punctatus*)

INTRODUCTION

Amphibians are often thought to occur in metapopulations, in which individual populations may go extinct but then be recolonized from other populations. This trait may render amphibians especially vulnerable to anthropogenic processes that result in fragmentation of habitat. This study tests two common predictions based on metapopulation theory for an amphibian inhabiting a highly patchy environment, the red-spotted toad (*Bufo punctatus*; Fig. 1) in wetlands of the Mojave Desert of the southwestern USA: (1) incidence of patch occupancy increases with patch size, and (2) incidence of patch occupancy decreases with patch isolation. We also tested a third hypothesis that local environmental factors (patch quality) are important determinants of patch occupancy for *B. punctatus*. Patch quality is often assumed to be uniform in metapopulation studies.

METHODS

The study area corresponds roughly to the northeastern quarter of the Mojave Desert, ~20,000 km^2 in area (Fig. 2). Potential habitat patches were identified as a spring or natural catchment shown on USGS 7.5í topographic maps, plus 12 other spring sites identified from other information, all below 1735 m elevation. Sites within the major valleys (i.e., Las Vegas, Pahrump, and Indian Spring Valleys, Nevada) were excluded because they lack any historic records for the species, and all natural aquatic habitat in these valleys has been destroyed by urban or agricultural development.

A total of 153 sites met the criteria for the study; data were obtained for 128 that were not dry or otherwise unavailable (Fig. 2). Toads were surveyed by a visual and audio search for adults, tadpoles, and eggs along all aquatic habitat (up to 400 m linear extent) by two individuals. Sites were surveyed during both the day and night during favorable conditions, and on a second night if the species had not been found previously. Example sites are shown in Fig. 3.

Thirty-three metrics were included in analyses (Table 1), reflecting three spatial scales. Stepwise multiple logistic regression was used to test the hypotheses that patch size, patch isolation, and environmental variables influence patch occupancy by *B. punctatus*.

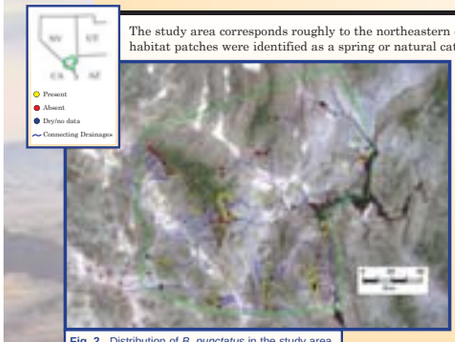

Fig. 2. Distribution of *B. punctatus* in the study area. Las Vegas is in the center of the study area; Lake Mead is on the right.

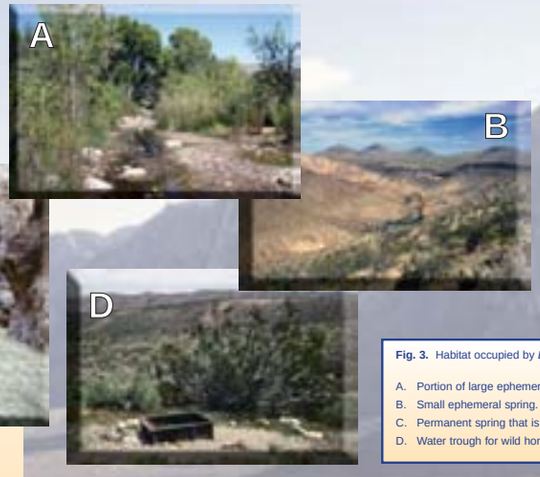

Fig. 3. Habitat occupied by *B. punctatus*

A. Portion of large ephemeral spring.
B. Small ephemeral spring.
C. Permanent spring that is scoured, eliminating most vegetation.
D. Water trough for wild horses.

Table 1. Metric types used as independent variables in analysis to predict patch occupancy.

Isolation Distance (Euclidian & via drainage network; 4 metrics):
- Distance to nearest site
- Distance to nearest occupied site

Patch size (7 metrics)
- Extent of water
- Extent of riparian vegetation

Habitat (18 metrics)
- Variables for elevation, substrate, vegetation cover, water chemistry, exotic species, long-term persistence of water

Spatial distribution (2 metrics)
- Latitude, longitude

Temporal (2 metrics)
- Year and date of sampling

RESULTS

- ***Bufo punctatus*** was present at a large fraction (73%) of the 128 sites at widespread locations throughout the study area (Fig. 2). For the stepwise multiple logistic regression, seven variables were retained in the final model for patch occupancy (Table 2).
- ***Patch size hypothesis*** ó Patch occupancy increased significantly with increasing patch size as measured by either extent of water (Table 2) or extent of riparian vegetation (separate analyses). Patches were generally small and narrow; the median linear extent of surface water was only 200 m.
- ***Isolation hypothesis*** ó Patch occupancy was not significantly related to any of the isolation metrics. Distance to the nearest patch ranged from 0.4 to 22.0 km (median 1.8 km) for Euclidian distance and 0.5 to 64.9 km (median 6.8 km) for drainage distance (Fig. 4).
- ***Environmental hypothesis*** ó Patch occupancy was significantly related to five environmental metrics. Patch occupancy decreased with increasing elevation, increased with extent of bedrock substrate, decreased with increasing conductivity of the water, and decreased with vegetation cover over both water and adjacent land. The latter four variables suggest that the species favors rocky terrain, ephemeral water (low conductivity), and little vegetative cover resulting from scouring or ephemeral water.
- ***Geographic metrics*** ó Patch occupancy was also significantly related to latitude, apparently because the edge of the range of the species passes through the northwestern portion of the study area.

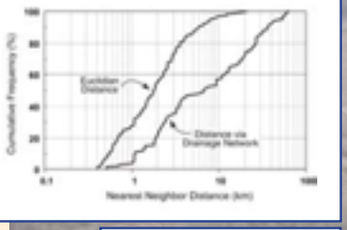

Fig. 4 Cumulative frequency distribution for nearest-neighbor distances between sites, measured in two ways (n = 128 sites).

Table 2. Final stepwise logistic regression model for habitat patch occupancy by Bufo punctatus (n = 122 sites). Wald χ^2 for the model was significant (P = 0.0027); model correctly classified population presence/absence at 95.4% of the sites.

Variable	Relationship to patch occupancy	*P*
Elevation	Neg.	<0.0001
Latitude	Neg.	<0.0001
Water electrical Conductivity	Neg.	0.0006
% bedrock substrate	Pos.	0.0033
% vegetation cover over water	Neg.	0.0004
water area	Pos.	0.0109
% vegetation cover on bank	Neg.	0.0125

DISCUSSION

The study supports the hypothesis that the incidence of patch occupancy increases with increasing patch size, but does not support the hypothesis that the incidence of patch occupancy is related to patch isolation. An obvious possible explanation for not finding the predicted isolation-occupancy relationship in *B. punctatus* is that populations in the study area may not represent a classical metapopulation at equilibrium in which local extinction and recolonization are operating.

An alternative metapopulation model, Harrisonís patchy population model, appears to be more applicable to the *B. punctatus* system in this study. In this model, dispersal among patches is sufficiently frequent so that local extinctions virtually never occur, and the system effectively consists of a single large population occupying many habitat patches, or a complex of several such populations. This model is consistent with our findings that the frequency of patch occupancy is high, and that occupancy is determined primarily by local conditions (i.e., habitat quality and patch size) rather than the spatial distribution of patches relative to each other.

The application of the patchy population model in the *B. punctatus* system, however, leads to a perplexing situation. The model requires that dispersal among patches is frequent, yet most of the nearest-neighbor distances in this system (Fig. 4) are far greater than the 0.8 km maximum movement distance observed for the *B. punctatus* and the 2.6 km maximum observed for other temperate-zone *Bufo* species. A possible scenario for explaining this discrepancy is that the limited data on *B. punctatus* movements may greatly underestimate the potential dispersal distance of the species. A quadrupling of the maximum known movement distance for *B. punctatus* (0.8 km) to 3.2 km would represent an increase from the 23rd to the 74th percentile for nearest-neighbor Euclidian distances and an increase from the 4th to the 35th percentile for distance via drainage channels (Fig. 4). Conceivably, such dispersal events could occur during extended El Nino/Southern Oscillation events that occur at intervals of many years to decades.

CONCLUSIONS

1. **W**etland patches in the Mojave Desert vary in their suitability for *B. punctatus*, indicating that patch quality metrics should be included in analyses addressing patch dynamics.
2. **T**he patchy population model is appropriate for the species in the Mojave Desert, rather than the classical population model, implying frequent dispersal and virtually no local extinctions.
3. ***B**ufo punctatus* appears to be a weedy species in the Mojave Desert, perhaps dispersing much greater distances than previously thought (e.g., many kilometers).

Note: Further details are available in:

- Bradford, D.F., A.C. Neale, M.S. Nash, D.W. Sada, and J.R. Jaeger. 2003. Habitat patch occupancy by toads (*Bufo punctatus*) in a naturally fragmented desert landscape. Ecology 84: 1012-1023.
- Nash, M.S., and D.F. Bradford. 2001. Parametric and nonparametric logistic regressions for prediction of presence/absence of an amphibian. EPA/600/R-01/081, U.S. Environmental Protection Agency, Office of Research and Development, Washington, D.C.

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