HABITAT PATCH OCCUPANCY BY TOADS (Bufo punctatus) IN A NATURALLY FRAGMENTED DESERT LANDSCAPE

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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 United States 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, that the incidence of habitat patch occupancy is directly related to patch size and that it is inversely related to patch isolation, and a third, potentially competing hypothesis, that patch occupancy is influenced by local environmental conditions. In a 20,000 km² 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 size metrics reflected extent of water and riparian vegetation of several types. 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 16 historic (pre-1970) sites. Patches were generally quite small, with water extending a median distance of only 200 m and median area of 72 m². Median nearest-neighbor distances among patches were 1.8 km Euclidian distance (range: 0.4–22.0 km) and 6.8 km via drainage channels (range: 0.5–64.9 km). 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 “patchy population” model, rather than the classical equilibrium metapopulation model, implying frequent dispersal among patches and virtually no local extinctions. We speculate that B. punctatus in the Mojave Desert today occurs primarily in a patchy population or populations within mountain ranges that are isolated from patchy populations in other ranges. The influence of local environmental characteristics on patch occupancy demonstrates the importance of including patch quality metrics in tests of predictions for patch occupancy based on metapopulation theory.

Key words: amphibian; Bufo punctatus; desert; habitat fragmentation; isolation; metapopulation; Mojave Desert; patch occupancy; patch size; patchy population.

INTRODUCTION

Amphibians are often thought to occur in metapopulations, a trait that may render them especially vulnerable to anthropogenic processes that result in fragmentation of habitat (Blaustein et al. 1994, Hecnar and M’Closhkey 1996, Alford and Richards 1999). A metapopulation, in the classical sense of Levins (1969), can be defined as “a network of semi-isolated populations with some level of regular or intermittent migration and gene flow among them, in which individual populations may go extinct but then be recolonized from other populations” (Meffe and Carroll 1994:562). The presumed tendency for amphibians to occur in such metapopulations derives largely from the often patchy distribution of suitable habitat, such as wetlands (Gibbs 1993), and traits of amphibians that limit the recolonization of sites following local extinction, such as physiological constraints for evaporative water loss, low vagility, and site fidelity (Blaustein et al. 1994). These attributes have been implicated as contributing to the dramatic declines in many amphibian populations that have occurred around the world in recent decades (Blaustein et al. 1994, Green 1997, Houlanahan et al. 2000). This is because many potential stressors on amphibian populations result in fragmentation of suitable habitat which, among other effects, can dramatically alter key metapopulation processes by increasing extinction rates in local populations and reducing recolonization rates following local extinction (Saunders et al. 1991, Hanski 1994, 1998, Green 1997).
The primary purpose of this study is to test two common predictions based on metapopulation theory for an amphibian inhabiting a highly patchy environment, the red-spotted toad (*Bufo punctatus*) in the Mojave Desert of the southwestern USA. Aquatic habitat in this region has been dramatically reduced and fragmented by the natural process of climatic drying since the late Pleistocene (Grayson 1993). At the beginning of this study, we postulated that *B. punctatus* in this area has a classical equilibrium metapopulation structure because preliminary observations indicated that habitat patches are generally quite distinct, interpatch distances are often large relative to the known movement distances for this species, and thousands of years have elapsed since fragmentation occurred. The predictions (hypotheses) tested are those represented by Hanski’s (1994, 1998, 1999) incidence function model for a metapopulation at equilibrium: (1) incidence of patch occupancy increases with patch size and (2) incidence of patch occupancy decreases with patch isolation. The rationale for the first prediction is that extinction rate should decrease as patch size increases, because population size generally increases with increasing patch size. The rationale for the second prediction is that immigration rate should decrease with increasing patch isolation; hence, the more isolated a patch is, the more likely it will remain unoccupied after local extinction (Wilcox and Murphy 1985, Sjogren 1991, Hanski 1994, 1998, 1999). One or both of these predictions have been substantiated for some amphibians (e.g., Sjogren 1991), but not others (see Discussion).

We also tested a third hypothesis, that local environmental factors are important determinants of patch occupancy for *B. punctatus*. The ecological literature is replete with examples of local environmental conditions influencing an organism’s distribution, yet patch quality is often assumed to be uniform in metapopulation studies (Hanski 1991, 1999). The inclusion of local factors in analyses may facilitate the detection of associations among patch occupancy, patch size, and patch isolation. Alternatively, local environmental factors, rather than patch size or isolation, may be found to predominate in determining patch occupancy. In some systems, both metapopulation and local effects are evident. For example, in studies of the Granville fritillary (*Melitaea cynthia*) in northern Europe, patch occupancy is significantly affected positively by patch size and host-plant density and negatively by patch isolation and livestock grazing (Moilanen and Hanski 1998, Hanski 1999). For the pool frog (*Rana lessonae*) in Sweden, pond occupancy is influenced primarily by pond isolation and springtime water temperature (Sjogren 1994).

*Bufo punctatus* commonly occurs at springs and rain pools (catchments) in rocky portions of desert and semiarid regions (Stebbins 1951, 1985, McClanahan et al. 1994, Degenhardt et al. 1996). It has a wide geographic range, occurring roughly from central Mexico to southern Oklahoma and west to southern Nevada, southern California, and Baja California (Stebbins 1985). In the study region of the northeastern Mojave Desert, *B. punctatus* evidently colonized most sites after the Pleistocene, within the past 8000 years. Prior to this time, a dominant plant species of this area was big sagebrush (*Artemisia tridentata*), a species associated with cooler and more mesic climatic conditions than the current ones (Thompson 1988, Grayson 1993). Today, this plant occurs primarily north of the Mojave Desert and at higher elevations (MacMahon 1985), areas not inhabited by *B. punctatus* (Stebbins 1985). Whether *B. punctatus* colonized the study area early during the period of drying, when conditions were moister than those of today, or later, when conditions were similar to those at present, is unknown.

The dispersal capability of *B. punctatus* is unknown, but adults in relatively arid regions are thought to reside throughout the year in the vicinity of breeding sites (Sullivan, in press). *B. punctatus* has no known mechanism to retard dehydration and must have access to moist substrate year-round to maintain water balance (Shoemaker et al. 1992). Nevertheless, *B. punctatus* can travel on dry land by using bladder water for rehydration and by occasionally tolerating substantial dehydration (Shoemaker et al. 1992, McClanahan et al. 1994). Known maximal movement distances for *B. punctatus* in three studies are in the range of 0.4–0.8 km, all of which were observed along drainage channels (Turner 1959, Tevis 1966; L. McClanahan, unpublished data). For six other temperate zone *Bufo* species, movements range up to 2.6 km (Sinsch 1992, Dodd 1996), whereas the tropical, introduced cane toad (*Bufo marinus*) expanded its range in northern Australia at a mean rate of 27 km/yr over a 4-yr period (Freeland and Martin 1985).

The breeding season for *B. punctatus* in the Mojave Desert is primarily April through June, although breeding may occur through August, usually in association with rain storms (Tevis 1966; D. F. Bradford, unpublished data). Individual males may call for several months although oviposition generally takes place infrequently (Tevis 1966). In a population in the Sonoran Desert in central Arizona, males matured in their first or second full season following metamorphosis, the average age of adult toads was 2 yr for both males and females, and the maximum age of 30 individuals aged by skeletochronology was 6 yr (Sullivan and Fernandez 1999; Sullivan, in press).

We tested the above three hypotheses concerning patch size, isolation, and quality by surveying for *B. punctatus* and habitat characteristics at sites with potentially suitable habitat throughout a contiguous area. We evaluated the presence/absence of *B. punctatus* as a function of variables selected to reflect habitat patch size and isolation and a number of local environmental metrics that may reflect patch quality. We included in the analyses geographic metrics to represent spatial pat-
terns of distribution that may not be explained by the other variables. We also compared the historic and current distributions of the species to detect any local population change in recent decades.

METHODS

Study area and site selection

The study area corresponds roughly to the north-eastern quarter of the Mojave Desert (MacMahon 1985), consisting of an ~20,000-km² area in Nevada, California, and Arizona (Fig. 1). The study area was delineated to include areas near and remote from the Colorado River system (i.e., Colorado, Virgin, and Muddy Rivers), which was suspected to represent a post-glacial dispersal network for the species. The area includes a number of mountain ranges. The area drains primarily to the Colorado River system, but also includes several enclosed basins. Land use in recent de-
decades has been mostly low-density livestock grazing, although military, urban development, agriculture, and recreation are represented. Elevations range from 210 m along the Colorado River to over 3600 m in the Spring Mountains (Fig. 1).

Potential habitat patches were identified as a spring or natural catchment shown on USGS 7.5' topographic maps, plus 12 other spring sites identified from other information. Sites located within 350 m linear distance of each other or within 1.6 km via a drainage channel were combined as one site. Sites >1735 m in elevation were omitted because surveys above this elevation failed to reveal any occupied locations. Sites within the major valleys (i.e., Las Vegas, Pahrump, and Indian Spring Valleys, Nevada) were also excluded because they lack rocky terrain preferred by *B. punctatus* and also lack any historic records for the species. Moreover, all natural aquatic habitat in these valleys has been destroyed by urban or agricultural development.

A total of 153 sites met the criteria for inclusion in analyses. Data for *B. punctatus* presence/absence were obtained for 128 of these sites. Of the sites in which presence/absence was not determined, 11 were dry over 2 yr of repeated visits (including 1 yr with above-normal precipitation) and 14 were either inaccessible because of private property or physical limitations, not reached during the proper season, or destroyed by urban development. Complete environmental data were obtained at 122 of the 128 sites. The other six sites lacked some environmental data because of access limitations due to private property, inaccessibility of aquatic habitat, agency habitat restoration activities, or equipment failure.

**Amphibian surveys**

Each survey consisted of a visual and audio search for adults, tadpoles, and eggs along all aquatic habitat (up to 400 m linear extent) by two individuals. All sites were searched during daylight and again at night except at some sites where the species had already been detected during the day. Night surveys, conducted using headlamps and a 50,000-lx light, included this aquatic habitat plus adjacent terrestrial habitat within several meters of water. Second night surveys were conducted at most (35/41) sites where the species had not been found during the previous day and night surveys; night surveys proved to be more reliable than daylight surveys for detecting this species. Although *B. punctatus* was found at 26% of these sites during the second night survey, this finding was invariably associated with more favorable conditions (i.e., wetter and/or warmer) on the second survey. Given that at least one night survey was conducted at a time of favorable conditions at all sites where the species was not found, we feel that our determinations for species absence are reasonably sound.

Most surveys were conducted in 1997 (58.6%) and 1998 (37.5%), with a few in 1999 (3.9%). In 1997 and 1999 the previous winter precipitation was below average, whereas in 1998 it was above average. In the few cases where only tadpoles were seen, they were identified to species following the morphological key of Altig et al. (1998). Historic localities for *B. punctatus* in the study area were determined from specimen records obtained by a search of 35 museums with significant holdings in the western USA.

**Independent variables**

Definitions and sampling methods are provided for 33 metrics in Appendix A. Metrics were selected to reflect patch size (7 metrics), patch isolation (4 metrics), local environmental conditions (17 metrics), long-term persistence of water (1 metric), geographic position (2 metrics), and temporal variation in sampling (2 metrics). Metrics reflect three spatial scales: regional scale, corresponding to multiple patches or the entire study area; survey-area scale (400 m), corresponding roughly to the size of most patches; and plot scale (≤30 m), corresponding to the size of individual breeding pools or stream reaches.

Patch size metrics, all sampled at the survey-area scale, were comprised of two metrics reflecting extent of water (area and linear extent) and five reflecting extent of riparian vegetation (area and linear extent for vegetation in four categories). The four vegetation categories were defined to represent a gradient in persistence of water at or near the ground surface (Appendix A).

Patch isolation was represented by nearest-neighbor metrics commonly used in habitat fragmentation studies: distance to nearest patch and distance to nearest occupied patch (Vos and Stumpel 1995). Each was calculated in two ways, Euclidian (straight-line) distance and distance via the drainage network, resulting in four patch isolation metrics (Appendix A). Distance via the drainage network was included because toads are closely associated with moist environments in this otherwise xeric landscape and may disperse primarily by following moist environments along drainage channels or by flooding (Tevis 1966, McClanahan et al. 1994). Concentric isolation metrics, i.e., those reflecting number of patches within a given distance from a site (Vos and Stumpel 1995), and Hanski’s (1999) metric for isolation, which incorporates distances to all occupied patches in the study area, were not used because of concerns about independence of observations in logistic regression analyses. No metrics were included for the quality of habitat adjacent to wetlands (i.e., landscape complementation; Pope et al. 2000). Although *B. punctatus* can forage beyond the wetland boundaries in arid desert habitats, there is no evidence that the species depends on nonwetland-associated habitat for part of its life cycle (McClanahan et al. 1994).

Eight environmental metrics were sampled at the survey-area scale, representing elevation, channel substrate type, channel overgrowth by vegetation, exotic
plants and animals, and water chemistry (Appendix A). Nine environmental metrics were sampled at the plot scale, representing substrate type, extent of water, extent of aquatic vegetation, vegetation cover over water and bank, and water temperature (Appendix A).

The long-term persistence of water at a site was assessed by surveying for presence/absence of macroinvertebrate taxa associated with continually flowing water believed to have persisted for thousands of years (Appendix A). These taxa are characterized as extremely low in vagility, endemic to the Great Basin/Mojave Desert area, and known to have relictual populations in springs. They are generally absent at sites characterized by ephemeral water or periodic scouring flooding (D. W. Sada, personal observation).

Two geographic metrics (corresponding approximately to latitude and longitude) were included to identify potential spatial patterns of patch occupancy within the study area that may reflect processes unrelated to the other variables. Two temporal metrics, year and day of year, were included to test for temporal effects in the sampling regime.

**Statistical analysis**

Univariate logistic regression (LOGISTIC procedure, SAS 1998) was used to evaluate simple associations between patch occupancy and each independent variable. As a more comprehensive, multivariate approach, stepwise multiple logistic regression was conducted to provide a best-fit model explaining patch occupancy and to test the hypotheses that patch size, patch isolation, and environmental variables influence patch occupancy. The dependent variable was presence/absence of *Bufo punctatus*; independent variables are listed in Appendix A. Details for the analysis, including evaluation of collinearity between independent variables, influence of individual observations (i.e., sites), interaction terms, and effects of spatial clustering of the observations, are provided in Appendix B. For the final multiple logistic regression model, the magnitude of the effect of each independent variable on the dependent variable was represented by the odds ratio (Allison 1999). The odds ratio indicates the change in the odds of the dependent variable (i.e., probability of presence/probability of absence) for a one-unit increase in the independent variable, when all other independent variables are held constant.

**Results**

**Distribution of amphibians**

*Bufo punctatus* was present at a large fraction (93; 73%) of the 128 sites (Fig. 1). The species was widespread, occurring in six of the seven mountain range groups in the study area and in 8 of the 10 drainage systems (Fig. 1). It was absent from the two smallest drainage systems, which lie on the edge of the study area (i.e., watersheds 5 and 10 in Fig. 1). No evidence was found for a decrease in incidence of patch occupancy in the study area during recent decades. Specimen records for *B. punctatus* prior to 1970 were obtained for 16 sites farther than 1.0 km apart, dating between 1936 and 1966. The species was found at all 16 of these sites. Other amphibians observed during surveys were the Pacific treefrog (*Pseudacris regilla*), Woodhouse’s toad (*Bufo woodhousii*), American bullfrog (*Rana catesbeiana*), and relict leopard frog (*R. onca*; Jaeger et al. 2001).

**Factors affecting patch occupancy by *B. punctatus***

Logistic regression analyses.—In univariate logistic regressions, 15 of the 33 variables were significant (*P* < 0.10; Appendix A). For the stepwise multiple logistic regression, seven variables were retained in the final model (Table 1, Appendix B). The Wald χ² for the model was significant (*P* = 0.0027), and the Hosmer-Lemeshow goodness-of-fit test did not indicate lack of fit (*P* = 0.87). The model correctly classified (i.e., concordance) population presence/absence at 95.4% of the sites. All seven variables were significant at *P* < 0.05. Spatial dependency among observations was not found to be a concern (Appendix B).

<table>
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<tr>
<th>Variable</th>
<th>β</th>
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<th>P</th>
<th>Standardized estimate</th>
<th>Odds ratio</th>
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<tr>
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<td>0.0033</td>
<td>1.3399</td>
<td>1.205</td>
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<tr>
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<td>0.0004</td>
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<td>0.0153</td>
<td>0.0125</td>
<td>-0.6486</td>
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</tr>
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</table>

Notes: The dependent variable is patch occupancy by *B. punctatus*. Variables are arranged in order of importance in influencing patch occupancy (i.e., by absolute value of the standardized estimate). β is the parameter estimate, and the odds ratio is exp(β). Wald test for overall model significance: χ² = 21.8, df = 7, *P* = 0.0027; Hosmer-Lemeshow goodness-of-fit test: χ² = 3.91, df = 8, *P* = 0.87. Metric definitions may be found in Appendix A.
**Patch size metrics.**—Patches were generally small and narrow. The median area of surface water (LOGWATER) was only 72 m² (Fig. 2a). The linear extent of surface water (SITESURF) was <40 m in 25% of the sites, and the median extent was only 200 m. The median area of riparian vegetation (LOGRIPAR) was 1480 m² (Fig. 2b), and the median linear extent of the vegetation defining this metric was 320 m.

Patch occupancy increased significantly with increasing patch size as measured by either extent of water or extent of riparian vegetation. Water area (LOGWATER) was the only patch size variable retained in the final model (Table 1, Fig. 2a). However, when this variable was removed and the regression rerun, another patch size metric would be retained. Proceeding in this fashion, a total of four patch size metrics were significantly (P < 0.10) related to patch occupancy in the following priority: LOGWATER (P = 0.0109), SITESURF (P = 0.0165), linear extent of riparian shrubs/herbs (SITERIPA; P = 0.0704), and LOGRIPAR (P = 0.0909). The magnitude of the effect of patch size on patch occupancy is shown by the odds ratio for LOGWATER in the final model (Table 1). That is, for an increase in one log₁₀ unit of water area (i.e., a 10-fold increase in area), the odds of patch occupancy increase by a factor of 6.157. In contrast, in univariate logistic regressions, patch occupancy did not increase significantly with water area (Appendix A, Fig. 2a). Only two of the seven patch size metrics (SITERIPA, LOGRIPAR) were significant (P < 0.10) in univariate analyses (Appendix A, Fig. 2b). Percentage of occupancy increased from ~45–55% to ~80% between the low and high values for these two patch size metrics (Fig. 2b).

**Isolation metrics.**—Patch occupancy was not significantly related to any of the isolation metrics in the stepwise multiple logistic regression (Table 1). In univariate logistic regression, however, patch occupancy decreased with increasing distance to the nearest occupied patch (Euclidian distance [LOGNEAR1] and drainage distance [LOGNEAR2]; P < 0.0006; Appendix A, Fig. 2c), but showed no relationship to distance to the nearest patch (Euclidian distance [LOGSITE1] and drainage distance [LOGSITE2]; Appendix A, Fig. 2d). Distance to the nearest occupied patch ranged from 0.4 to 34.0 km (median 2.4 km) for Euclidian distance (Fig. 2c) and 0.5 to 104.6 km (median 11.2 km) for drainage distance (Fig. 3). 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.

**Environmental metrics.**—Patch occupancy was significantly related to five environmental metrics in the stepwise multiple logistic regression analysis, three at the survey-area scale (ELEV, PER_ROCK, and LOGEC) and two at the plot scale (PLOTSCANP and P_CANV) (Table 1). Elevation (ELEV) was the most important of all the metrics in explaining patch occupancy in the stepwise multiple regression (Table 1). Patch occupancy decreased with increasing elevation; the odds of patch occupancy decreased by a factor of 0.991 for each increase in elevation of 1 m. Elevation was also significant in the univariate logistic regression (Fig. 2h). Patch occupancy increased with extent of bedrock substrate (PER_ROCK); the odds of patch occupancy increased by a factor of 1.205 for each increase of 1% in PER_ROCK (Table 1). This effect was also evident in univariate logistic regression (Appendix A, Fig. 2e). Patch occupancy decreased with increasing conductivity of the water (LOGEC) in the multiple logistic regression analysis. For each log₁₀ unit increase in LOGEC (i.e., a 10-fold increase), the odds of patch occupancy decreased by a factor of 0.002, a 500-fold effect. This effect, however, was not evident in univariate logistic regression (Appendix A). Median conductivity was 0.835 mS/cm, ranging from 0.089 to 9.110 mS/cm. Patch occupancy decreased with vegetation cover over water (PLOTSCANP) and with cover over adjacent land (P_CANV); odds of patch occupancy decreased by factors of 0.942 and 0.962, respectively, for each 1% increase in cover for the two variables. Both of these effects were evident in univariate logistic regressions (Fig. 2f and g). Five other environmental metrics were positively related to patch occupancy in univariate logistic regressions (P < 0.10). These were extent of Tamarix spp. (SITETAMA), pH (PH), water temperature (WATTEMP), submerged or floating vegetation cover (PLOTFLSL), and plot bedrock substrate cover (PLT_ROCK; Appendix A). Patch occupancy was not significantly related to presence/absence of exotic predators and competitors (i.e., bullfrogs, crayfish, and fishes; PREDAT) in either multiple or univariate logistic regressions. Relatively few sites contained these exotics (11 sites), however, and B. punctatus inhabited 7 (64%) of these sites.

**Long-term persistence of water.**—Patch occupancy was not significantly related to the presence/absence of taxa indicative of long-term persistence of water (PERS_TAX) in either multiple or univariate logistic regressions; however, only 18 (14%) of the sites contained these taxa. Thirteen of these 18 sites (72%) contained B. punctatus, which is nearly identical to the frequency of site occupancy among the other 110 sites. Indicator taxa found were springsnails (family Hydrobiidae: Pyrguliopsis deaconi, P. coloradensis, and/or P. turbaria) at 15 sites, caddisflies (families Lepidostomatidae and Hydropsychidae) at three additional sites, and a number of indicator taxa (families Hydrobiidae, Dryopidae, and Naucaeridae; see D. W. Sada and D. B. Herbist, unpublished manuscript) at two other sites.

**Geographic metrics.**—Patch occupancy was significantly related to the metric reflecting latitude (i.e., Y) in both the stepwise multiple logistic regression and univariate logistic regression (Appendix A, Table 1). Latitude was the second-most important of the seven
metrics explaining patch occupancy (Table 1). Odds of patch occupancy decreased by a factor of 0.917 for each increase in latitude of 1 km. With latitude representing the region scale, all three spatial scales were represented in the final model of the stepwise multiple logistic regression (Appendix A, Table 1).

**Discussion**

**Patch size and patch occupancy**

The study supports the hypothesis that the incidence of patch occupancy increases with increasing patch size, although the patch size metric was not among the most important metrics determining patch occupancy. Nevertheless, the association between patch occupancy and patch size was robust, based on the diversity of patch size metrics that were significant when entered separately into the multiple logistic regression. Significant metrics reflected the areal and linear extents of water, which vary substantially within and between years at most sites, and the areal and linear extents of riparian vegetation, which are essentially constant over years. This association between patch size and patch occupancy has been demonstrated for several other amphibians (Loman 1988, Laan and Verboom 1990, Sjogren 1991).

Interestingly, the vegetation-based patch size metrics that were significant predictors of patch occupancy (i.e., SITERIPA and LOGRIPAR) are dominated by indicator plants associated with ephemeral surface water and water at shallow depth (i.e., indicator taxa listed for SITERIPA in Appendix A). These taxa contrast to those associated with long-standing surface water (i.e., indicator taxa for SITEEMER and SITENATI) and water at substantial depth (i.e., meters; indicator taxa for SITEMESQ; Appendix A). This may reflect the importance of the ephemeral nature of surface water to toads (see Environmental attributes and patch occupancy) and the year-round need for moist sites for adults.

**Isolation and patch occupancy**

The study does not support the hypothesis that the incidence of patch occupancy is related to patch isolation. Although metrics for patch isolation based on distance to the nearest occupied site (i.e., LOGNEAR1 and LOGNEAR2) were significant in univariate analyses, these metrics were not retained in the multiple regression. This effect may result from correlations between the isolation metrics and environmental and geographic metrics. For example, a site near an occupied site may tend to have similar characteristics to those of the occupied site. Indeed, these two isolation metrics were significantly correlated with water area and elevation, factors that were retained in the multiple regression. Moreover, the lack of occupied sites in portions of the study area results in high values for LOGNEAR1 and LOGNEAR2 for sites in these areas, yet latitude, rather than isolation metrics, “explains” this pattern of occupancy in the multiple regression (see Geographic metrics and patch occupancy).

Some studies with other amphibian species have found support for the predicted relationship between patch isolation and patch occupancy (Sjogren 1988, 1991, Laan and Verboom 1990, Vos and Stumpel 1995, Edenhaan 1996 cited in Vos and Chardon 1998, Skelly and Meir 1997, Skelly et al. 1999), whereas others have not (Gill 1978, Hecnar 1997, Skelly and Meir 1997). 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. Indeed, such metapopulation structure may not be common in natural systems (Harrison 1991, Harrison and Taylor 1997), although there is evidence for these metapopulations among amphibians (Hecnar and M’Closkey 1996, Alford and Richards 1999).

Two alternative metapopulation models conceivably explain the distribution of B. punctatus within the study system: the nonequilibrium and patchy population models (Harrison 1991, Harrison and Taylor 1997). In a nonequilibrium model, a species is undergoing a region-wide decline because recolonization is not keeping pace with extinction or perhaps dispersal between sites does not currently occur at all. Thus, long-term fragmentation of habitat results in little or no dispersal among habitat patches, and extinctions accumulate over time. For B. punctatus in the study system, this model implies that this species has been generally isolated within most spring sites since some previously favorable climatic period when dispersal was possible. We do not favor this model because it implies a high rate of local extinction and a low rate of recolonization and hence predicts a low frequency of occupied sites. Patch sizes are generally small (median length of aquatic habitat is only 200 m), and population sizes appear to be quite small (limited mark-recapture data indicate...
that the number of adults occupying many patches may be on the order of tens of individuals). Most patches are likely to have been isolated from one another since the post-Pleistocene increases in aridity, thousands of years ago (Thompson 1988, Grayson 1993). If non-equilibrium dynamics were governing this system, then we would expect relatively few sites to be occupied rather than the majority (73%) observed.

A patchy population model (Harrison 1991, Harrison and Taylor 1997) appears to be most 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. A patchy population dynamic appears to be common among species that exploit patchy habitats (Harrison 1991, Doak and Mills 1994).

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 are far greater than the 0.8 km maximum movement distance observed for the *B. punctatus* (Tevis 1966; L. McClanahan, unpublished data) and the 2.6 km maximum observed for other temperate-zone *Bufo* species (Sinsch 1992, Dodd 1996). Relative to the nearest-neighbor distances among patches in this study (Fig. 3), the 0.8 km distance represents the 23rd percentile for Euclidian distances and only the fourth percentile for drainage distances (Fig. 3).

Two possible scenarios may explain the discrepancy between the apparent patchy population dynamics in *B. punctatus* and the large distances between habitat patches. The first possibility is that our nearest-neighbor distances may be overestimated because we restricted our analysis primarily to water sources shown on USGS 7.5' maps. We know of other water sources from literature and agency databases that we did not sample, although these sites are generally much smaller than neighboring ones included in our study and they are more likely to be continually dry for many years at a time. Consequently, we would expect many of these sites to constitute unsuitable habitat for *B. punctatus*. Moreover, these other water sources occur primarily in spring-rich areas; thus, the inclusion of these sites would not greatly reduce most of our nearest-neighbor distance estimates. Even if the unmapped and unknown sites were evenly distributed relative to sites included in the study, it would take an increase in site density of 4.5-fold to yield a reduction in nearest-neighbor Euclidian distance from the 80th percentile level (3.6 km) to the maximum movement distance known for *B. punctatus* (0.8 km), and the increase in site density would have to be even greater to effect the equivalent change in distances via drainage channels (Fig. 3).

The second possibility for explaining the discrepancy between the apparent patchy population dynamics and the large nearest-neighbor distances is that the limited data on *B. punctatus* movements may greatly underestimate the potential dispersal distance of the species. Marsh and Trenham (2001) argue that long-distance dispersal of amphibians is notoriously difficult to detect, such that amphibian dispersal abilities are considerably larger than observed movements. 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. 3). Conceivably, such dispersal events could occur during extended El Nino/Southern Oscillation events that occur at intervals of many years to decades (Andrade and Sellers 1988). During exceptionally moist years, pools, seeps, springs, and streams can form in otherwise dry areas, and flooding may

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**Fig. 3.** Cumulative frequency distribution for nearest-neighbor distances between sites (log_{10} scale), measured as Euclidian distance ($n = 128$ sites) and via the network of connecting drainage channels ($n = 126$ sites).
facilitate downstream dispersal. In any event, we retain our interpretation that toads periodically disperse among most sites in our study area (i.e., patchy population dynamics) and recognize that the distances between sites may be overestimated by our nearest-neighbor distances while the movement distances reported for this species may be underestimates of their dispersal capabilities.

Environmental attributes and patch occupancy

The present study and others (e.g., Vos and Stumpel 1995, Sjogren-Gulve and Ray 1996, Hanski 1999) demonstrate that patch quality metrics can strongly influence patch occupancy by amphibians. Indeed, for *B. punctatus*, the magnitude of the influence of five metrics for local environmental conditions exceeded that for patch size (Table 1). Elevation was the most important variable affecting patch occupancy. Patch occupancy decreased significantly with increasing elevation, which may reflect climatic effects such as the temperature regime. Sites included in this study ranged up to the highest observed elevations for *B. punctatus* in the study area (1735 m); the known elevational limit for the species is about 1980 m in Colorado (Stebbins 1951, 1985). Patch occupancy was also related to environmental variables that reflect rockiness of the terrain, periodic occurrence of scouring water flows, and ephemeral water. Four significant variables in the multiple logistic regression model are consistent with this interpretation (PER_ROCK, PLOTCANP, P_CANY, and LOGEC). Scouring water flows in rocky terrain result in exposed bedrock along stream channels, and patch occupancy was positively related to the extent of bedrock substrate in the stream channel (PER_ROCK). Such rocky habitat often provides trapped water for breeding and crevices for sheltering of metamorphosed individuals (Degenhardt et al. 1996) and forces groundwater to near the surface in some places. Periodic scouring also reduces or removes vegetation within the stream channel, providing an open surface for toad movements on land and open water for tadpoles. Patch occupancy was negatively associated with the extent of vegetation cover over water (PLOTCANP) and over adjacent land (P_CANY). Maintenance of open habitat may also be facilitated by the ephemeral occurrence of surface water, which minimizes the establishment of aquatic plants that typically overgrow small, undisturbed, permanent patches of water in this area.

The influence of electrical conductivity (LOGEC) on patch occupancy is less obvious. Patch occupancy was negatively related to LOGEC, yet *B. punctatus* was found over the range of conductivity values, including the lowest (0.09 mS/cm) and the highest (9.11 mS/cm). The influence of conductivity appears to be operating on a local scale as evidenced by an analysis using generalized estimating equations (GEE, Appendix B) for patch occupancy vs. LOGEC. In GEE, with sites grouped by mountain range, LOGEC was significant ($P = 0.0148$), whereas it was not in the univariate logistic regression ($P = 0.68$). This finding suggests that if all other factors are equal, a site with higher conductivity may indicate a greater retention time for water in its groundwater basin, resulting in more time for mineral leaching. Such a difference may be associated with more permanent water and less scouring flows, features that appear not to be preferred by *B. punctatus*.

Interestingly, patch occupancy was not related to the presence/absence of macroinvertebrate taxa associated with persistent water, such as springsnails (PER_TAX). This may be due in part to the relatively small number of patches containing indicator taxa (18 of 128), and perhaps the conditions associated with these taxa are irrelevant to *B. punctatus*. Indicator taxa are associated not only with water that has persisted for thousands of years, but also the lack of scouring floods (D. W. Sada, personal observation). Despite not being scoured, many of these sites have variable water flows, meaning that portions of the spring brook are ephemeral, and we often found *B. punctatus* associated with these areas.

Geographic metrics and patch occupancy

One geographic metric (latitude, $Y$) strongly influenced patch occupancy. The relationship between patch occupancy and latitude is associated with the general absence of the species in the more northerly sites and appears to describe an anomaly in the distribution of *B. punctatus* in the study area (Fig. 1). That is, *B. punctatus* was absent from the more northerly sites on both the western and eastern slopes of the Spring Mountains (Fig. 1, Area A), yet conditions appeared to be favorable for the species in many of these sites. In contrast, the absence of *B. punctatus* from the Sheep Range (Fig. 1, Area G) is not surprising because these sites are all quite small and precipitation in this range is limited by the rainshadow cast from the nearby Spring Mountains. The northwest portion of the study area appears to define a northern range limit for the species in the region, which continues to the west to the Death Valley/Saline Valley area (Macey and Penning 1991; D. Threlfof, personal communication).

Conclusion

This study does not support the classical metapopulation model for *Bufo punctatus* in the northeastern Mojave Desert. The prediction derived from the classical model that patch occupancy would be inversely related to patch isolation was not supported, although the other prediction that patch occupancy would be directly related to patch size was supported. A model more consistent with these findings is the patchy population model, in which 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. In this case, the finding that patch occupancy is significantly related to patch size could occur due to the inclusion in the study of sites smaller than the minimum patch size or because suitable environmental conditions may occur less frequently for smaller patches than larger patches.

We pose as a scenario for further investigation that *B. punctatus* spread throughout most of the study area when climatic drying began after the Pleistocene, perhaps expanding from Refugia at low elevation along the Colorado River and the Amargosa River. The former drains most of the eastern and central portions of the study area, whereas the latter drains the western portion of the study area, terminating in Death Valley. Subsequently, further drying resulted in isolation of groups of populations from one another, with such groups often manifested as clusters of springs within mountain ranges. Thus, *B. punctatus* in the Mojave Desert today may occur primarily in a patchy population or populations within mountain ranges that are isolated from patchy populations in other ranges.

The present study and others demonstrate that patch quality metrics can strongly influence patch occupancy by amphibians. Indeed, for *B. punctatus*, local environmental characteristics predominated as determinants of patch occupancy. Had local environmental factors been excluded from the study, the analysis would have erroneously indicated that patch isolation was important in determining patch occupancy. Thus, variation in patch quality should be considered when applying incidence function models in tests of patch occupancy.

**Acknowledgments**

We are grateful for the conscientious efforts of several individuals in conducting the often arduous field surveys: C. Grant, M. Vermey, D. Browning, and A. Gianantonio. We also thank J. Norman and T. Rash (U. S. Bureau of Land Management) for assistance in locating sites, M. Burrell (Nevada Division of Wildlife) for providing boat transportation, D. Ebert and T. Wade (US. Environmental Protection Agency (EPA)) for GIS support, and others who helped in many ways: C. Douglas and K. Longshore (US. Geological Survey), B. Riddle (University of Nevada, Las Vegas), B. Land (The Nature Conservancy), S. Mayben (US. Forest Service), and D. Heggem, N. Tallent-Halsell, K. Feldman, and T. Roach (EPA). EPA, through its Office of Research and Development, funded and collaborated in the research described here under inter-agency agreement No. DW14937587 and DW14937926 to the U. S. Geological Survey, Biological Resources Division. This manuscript has been approved for publication by the EPA. The manuscript benefited from critical reading by C. Cross, C. Davidson, R. Knapp, P. Trenham, and three reviewers.

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APPENDIX A

A description of independent variables, the sampling methods used, and results of univariate analyses are available in ESA’s Electronic Data Archive: Ecological Archives E084-022-A1.

APPENDIX B

Procedures for the stepwise multiple logistic regression used in this study are available in ESA’s Electronic Data Archive: Ecological Archives E084-022-A2.