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AMPHIBIAN UPLAND HABITAT USE AND ITS CONSEQUENCES FOR POPULATION VIABILITY

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Abstract. To predict the effects of habitat alteration on population size and viability, data describing the landscape-scale distribution of individuals are needed. Many amphibians breed in wetland habitats and spend the vast majority of their lives in nearby upland habitats. However, for most species, the spatial distribution of individuals in upland habitats is poorly understood. To estimate the upland distribution of subadult and adult California tiger salamanders (*Ambystoma californiense*), we used a novel trapping approach that allowed us to model the spatial variation in capture rates in the landscape surrounding an isolated breeding pond. As expected, we found that captures of adults declined with distance from the breeding pond. However, captures of subadults increased steadily from 10 to 400 m from the breeding site, but there were no captures at 800 m. A negative exponential function fit to the adult capture data suggested that 50%, 90%, and 95% were within 150, 490, and 620 m of the pond, respectively. For subadults, the quadratic function fit to the data similarly suggested that 95% were within 630 m of the pond, but that 85% of this life stage was concentrated between 200 and 600 m from the pond. To investigate the population-level consequences of reducing the amount of suitable upland habitat around breeding ponds, we used a stage-based stochastic population model with subadult and adult survival parameters modified according to our empirical observations of upland distribution. Model simulations suggested that substantial reductions in population size are less likely if upland habitats extending at least 600 m from the pond edge are maintained. Model elasticities indicated that quasi-extinction probabilities are more sensitive to reductions in subadult and adult survivorship than reproductive parameters. These results indicate that understanding the upland ecology of pond-breeding amphibians, especially the distribution and survivorship of subadults, may be critical for designing protective reserves and land use plans.

Key words: Ambystoma californiense; *California tiger salamander; declining amphibian; drift fence; matrix simulation model; pitfall trap; population viability analysis; reserve design; terrestrial; upland spatial distribution.*

Introduction

In the United States, wetland habitats are protected against draining and filling by state and federal regulations. A few states further require maintenance of a 30–60 m wide upland buffer of undeveloped habitat around some or all wetlands. These buffers capture silt and chemical pollutants before they reach the wetlands, and are generally recognized as effective in protecting water resources (e.g., Phillips 1989, Brosofske et al. 1997). An additional benefit of upland buffers is that they provide essential habitat for a variety of wildlife species. While the contribution of buffers towards the maintenance of viable populations is intuitively obvious, there has been relatively little quantitative evaluation of exactly how buffers may enhance the value of wetlands for wildlife. Recently there have been attempts to estimate the amount of ‘‘core upland habitat’’ needed to accommodate populations of semi-aquatic wetland-breeding amphibians (Semlitsch 1998, Semlitsch and Bodie 2003). Summarizing across 32 species, Semlitsch and Bodie (2003) estimated that the core upland habitat used by amphibians extends 159 to 290 m from the wetland edge, revealing that buffers designed to protect water quality encompass only a small fraction of the habitat used by most amphibians. While the Semitsch and Bodie (2003) review provides strong rationale for greater protection of upland habitat around wetlands to enhance habitat values for amphibians, it also emphasizes our rudimentary understanding of amphibian upland ecology.

Losses of wetland and upland habitats are recognized as key contributors to the widespread decline of amphibian populations (Semlitsch 2002, Collins and Storfer 2003). However, experimental research on amphibian declines has continued to focus on the aquatic embryonic and larval stages, while the equally important terrestrial stages are rarely studied (Storfer 2003). This research inequity between aquatic and upland amphibian ecology is not a new phenomenon, and is probably

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PLATE 1. An adult California tiger salamander (*Ambystoma californiense*). Photo credit: Bret Stewart.

due to the relative difficulty of terrestrial studies. Particularly for the diverse array of amphibians that breed in aquatic habitats but spend most of their lives in underground terrestrial retreats, even basic elements of upland ecology have remained essentially a ‘‘black box.’’ For example, we know almost nothing about interspecific interactions, density dependent effects on growth and maturation, and how these factors may influence dispersion in the uplands. Further, two recent papers indicate that amphibian population viability is often extremely sensitive to reductions in survivorship of upland stages (Biek et al. 2002, Vonesh and de la Cruz 2002). Clearly, additional experimental and observational studies of upland ecology are warranted (Storfer 2003).

Although population modeling studies have demonstrated that amphibian populations are sensitive to reductions in upland survival parameters, we know of no attempts to estimate the effects of upland habitat loss or modification on populations. For conservation planning, a model reflecting the likely population-level consequences of converting upland habitat to non-habitat or habitat where survival is substantially reduced, would greatly improve our ability to estimate the effects of human modification of landscapes. This would require both a demographic population model and a model describing the spatial distribution of individuals in the uplands. Unfortunately, either of these pieces is available for very few species, mainly due to the rarity of detailed upland distribution data.

The federally threatened California tiger salamander (*Ambystoma californiense*; CTS; see Plate 1) is a species for which there is a pressing need for a realistic analysis of the likely population-level effects of upland habitat conversion. Currently, the best available evidence suggests that this pond-breeding species has declined primarily due to the conversion of its aquatic and upland habitats to intensive land uses (Fisher and Shaffer 1996, U.S. Fish and Wildlife Service 2000, Davidson et al. 2002). In 2004, the U.S. Fish and Wildlife Service listed the CTS as a federally threatened species throughout its range, which includes parts of 22 California counties (U.S. Fish and Wildlife Service 2004*a*). Researchers have characterized many critical aspects of CTS life history, demography, ecology, and genetics (Shaffer et al. 1991, Austin and Shaffer 1992, Fisher and Shaffer 1996, Loredo and Van Vuren 1996, Trenham et al. 2000, 2001, Trenham 2001, Shaffer et al. 2004). We used data from those studies to parameterize a stage-based demographic population model that includes density dependent larval survival and environmental stochasticity. However, our knowledge of upland distribution, based two short-term studies that tracked metamorphosed CTS either visually (Loredo et al. 1996) or with radio transmitters (Trenham 2001), was inadequate to confidently project the population-level impacts of upland habitat loss.

We had two goals for the current study. First, we sought to collect field data that would allow us to derive an empirical model reflecting the distribution of salamanders in the uplands around an isolated breeding pool. Because CTS are usually at least four years old when they breed for the first time (Trenham et al. 2001), we sought to design a study that would yield relevant upland distribution data for adults and subadults. Rather than tracking individuals, we used an upland trap grid to capture salamanders. We modeled trap capture rates as a function of distance from the breeding pond, and based on those relationships estimated the width of surrounding upland habitat needed to encompass

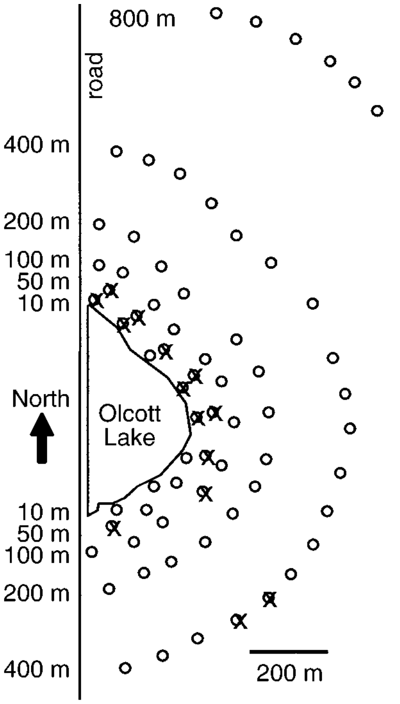

FIG. 1. Map of trap locations east of Olcott Lake, Solano County, California, USA (38.2712° N, 121.8224° W). Small circles indicate the location of each trap. An × is superimposed over traps consistently flooded and thus excluded from analyses.

specific proportions of CTS movements. Second, we used this newly derived model describing upland distribution and our demographic model to simulate the population-level effects of upland habitat loss/conversion around an isolated breeding pond. We explored the behavior of the model across a range of realistic parameter values and conducted an elasticity analysis to determine which parameters had the greatest incremental influence on the probability of quasi-extinction (Morris and Doak 2002). We discuss the implications of our results for the management and recovery of the CTS and other pond-breeding amphibians.

MATERIAL AND METHODS

Field methods

We collected field data at the Jepson Prairie Preserve, Solano County, California, USA. The site is essentially flat with less than 2.5 m of elevation variation across the entire 625-ha preserve. The uplands are dominated by grassland with a remnant stand of introduced blue gum (*Eucalyptus globulus*). The dominant feature in this landscape is Olcott Lake, a 36-ha playa vernal pool (Fig. 1). This pool fills with winter rainfall and runoff to a maximum depth of ~1 m, and dries every year, typically between May and July. In addition to harboring several endangered crustaceans (U.S. Fish and Wildlife Service 2002), this pool consistently contains large numbers of CTS larvae (H. B. Shaffer, *unpublished data*). Although CTS are known to use the burrows of both California ground squirrels (*Spermophilus beecheyi*) and pocket gophers (*Thomomys bottae*), only gopher burrows were present and abundant in all upland areas of the preserve. The pool is split by a north–south dirt road. We focused our trapping effort east of this road because there are no other suitable breeding pools for several kilometers to the east, whereas there are other breeding pools to the west. Based on prior tracking (Trenham 2001) and interpond movement (Trenham et al. 2001) studies at other sites, we assume that terrestrial salamanders captured east of the road originated exclusively from Olcott Lake.

We installed a total of 68 trap systems around the eastern half of Olcott Lake at locations 10, 50, 100, 200, 400, and 800 m away from the high-water line (hereafter, traps; Fig. 1). The distribution of traps was based on prior observations of CTS movements (Trenham 2001, Trenham et al. 2001). Each trap consisted of a 10 m long section of 0.9 m tall silt fence supported by wooden stakes. The bottom 15–30 cm of the silt cloth was buried in a shallow trench and anchored in place. Fence sections were oriented parallel to the perimeter of Olcott Lake. At both ends of each fence, one 3.8-L plastic bucket with 5 mm diameter drain holes was buried with its lip flush with the ground surface. To allow us to determine the direction of travel of captured animals, a tight-fitting piece of 4 mm thick plywood divided each bucket along the axis of the silt fence. A block of wood was attached to the top side of each bucket lid, such that when the lid was inverted it was supported 3 cm above the bucket lip, providing shade over the entire bucket. To allow the escape of nontarget animals, 15 cm long sections of rope were attached to the lids and hung in each bucket (Karraker 2001). When not in use, the bucket lids were closed to prevent the entry of animals.

Traps were spaced 90 m apart to achieve consistent fence coverage of ~10% at each distance. We shifted the spacing between some traps to avoid low areas subject to flooding. The portion of Olcott Lake east of the road is roughly half-circular with a radius of 240 m and a 754-m perimeter (Fig. 1). An arc 10 m beyond the high-water line has a radius of 250 m and a hemispherical perimeter of 785 m, so the eight 10 m long traps that we installed here encompassed just over 10% of that arc. Along the 50-, 100-, 200-, and 400-m arcs, we installed nine, 12, 14, and 19 traps, respectively, thus keeping coverage between 9.5% and 11.2% of each arc. The six traps installed at 800 m represent 1.8% coverage east of the road at this distance. We did not initially plan for traps at 800 m and only added them after we captured substantial numbers of CTS at 400 m. We constructed the 800 m traps northeast of Olcott Lake because initial captures were generally greater in this direction. We chose the 800 m distance to continue the pattern of doubling distances between

TABLE 1. Demographic information used to construct and parameterize the California tiger salamander population model.

Parameter	Estimate
Age of reproductive females	≥4 yr
Annual subadult survival probability	0.6†, 0.66
Annual adult survival probability	0.6†, 0.66
Probability of breeding in typical pond-filling years	0.5
Probability of breeding in late pond-filling years	0.1
Probability of late pond-filling years	0.0, 0.1, 0.3†, 0.5
Probability of complete reproductive failure	0.0, 0.1†, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9
Eggs deposited per breeding female	814
Survival from egg to metamorphosis	$0.131 \times (\text{no. eggs per m}^2)^{-0.6803}$; maximum = 0.20
Pond areas considered	700 m^2, 3500 m^2, 7000 m^2

Note: Where multiple parameter values are listed, daggers (†) indicate best estimates based on Trenham et al. (2000, 2001).

trap lines (Turchin 1998). The decision to construct all six traps in this area was purely for logistical reasons; we wanted to provide a reasonable probability of detection while not dramatically increasing the time to check all traps.

The first appreciable rain of the 2002–2003 season came on 13 December. We began installing traps on 14 December, and captured our first CTS that night. Traps 10 to 400 m from Olcott Lake were installed between 14 December 2002 and 4 January 2003; we added the 800-m traps on 20 January 2003. Beginning on 14 December, traps were opened each day prior to predicted rain, and kept open for several days thereafter. We installed a rain gauge to measure precipitation received between site visits. When open, we checked traps each morning by 07:30. Because we never caught more than one animal if no rain fell during the 24 hours prior, we closed traps after several days without rain or captures. Trapping of subadults and adults was terminated on 21 March 2003.

For each captured CTS, we noted trap number and direction of travel (i.e., moving towards or away from the pond). We also photographed each individual next to a metric ruler, clipped a single toe that was preserved in 70% ethanol, and recorded the sex of adult animals. Animals were immediately released into nearby dense vegetation or pocket gopher burrows. We measured the snout–vent length of each animal from the photographs.

Data analysis and modeling

The dependent variable that we modeled in our analyses was the capture rate of each trap, with the two buckets on each fence considered elements of the same trap. To determine capture rates for each trap we divided the number of adults or subadults captured by the number of nights the trap was open. We took this approach because there was some variability in the number of nights each trap was open. Capture rates were square root transformed prior to further analysis, and traps that were consistently flooded ($n = 14$; Fig. 1) and from which salamanders could easily escape were excluded from these analyses. We used linear and nonlinear regression to fit statistical models relating capture rates to distance from Olcott Lake. Based on these functions we estimated capture rate at 10 m intervals to the point where no further captures were predicted. We summed the capture rates across all distances, and then estimated the cumulative proportion of captures encompassed by upland habitat rings of increasing width.

To investigate the potential effects of increased mortality due to upland habitat loss on adult population size and population persistence, we used a stage-based matrix population model with six stages: new metamorphs, 1-yr-old subadults, 2-yr-old subadults, 3-yr-old subadults, new adults, and older adults (Caswell 2001). We parameterized the basic model with demographic data from our long term study of this species in Monterey County, California, USA (Trenham et al. 2000; P. C. Trenham, *unpublished data*; Table 1, Fig. 2). Because adult males are not presumed to be limiting, the model tracks only females. In the model, salamanders mature at four years old and, in each year, a fraction the surviving adults breed. Each breeding female lays a clutch of 814 eggs, half of which are assumed to be female, and survival from laying to metamorphosis depends on egg density in the pond (Fig. 2). After metamorphosis, upland survival of subadults and adults are fixed, but can be adjusted independently. In reality, subadult survival is poorly characterized. However, assuming that subadults survive at the same rate as adults (0.60) and mature at four years old, approximately 13% would survive to maturity, which matches the available data for this and related species (Scott 1994, Loredo and Van Vuren 1996, Trenham et al. 2000).

At the start of each model run, the population was composed of 100 new metamorphs, 50 1-yr-old subadults, 25 2-yr-old subadults, 13 3-yr-old subadults, seven new adults, and seven older adults. The model included two forms of environmental stochasticity to match observations from our long-term study (Trenham et al. 2000). First, because we found that in years when ponds fill late, females are much more likely to skip breeding, late pond-filling years occurred with a defined probability and the probability that an adult female bred in these years was reduced. Second, in some years model reproduction failed completely, as is com-

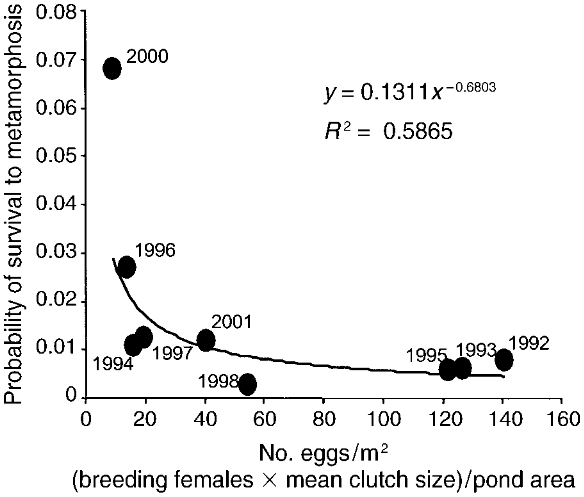

FIG. 2. Data from our long-term study in Monterey County, California, USA, suggest that larval survival is density dependent (Trenham et al. 2000). We fit a negative power function to these data to approximate this relationship. Symbols are labeled with the year for each data point; in 1999 California tiger salamander (CTS) breeding failed completely. Probability of survival to metamorphosis for each year was calculated as the number of newly metamorphosed salamanders emerging from the pond divided by the product of the number of breeding females and the average clutch size. Initial egg density was calculated as product of the number of breeding females and the average clutch size divided by 700 m², the area of our long-term study pond.

monly observed when ponds dry prior to metamorphosis (Gill et al. 1983, Semlitsch et al. 1996). Each year the program selected one random number to determine if pond-filling was late, and a second random number to determine if reproduction failed. Depending on the random values generated, the program used one of three alternate forms of the transition matrix—the first for typical pond-filling years, the second for late pond-filling years, and the third for years when reproduction failed completely—to project the population at the next time step. We initially evaluated model behavior with the probabilities of late filling and reproductive failure set to zero, and then with these probabilities set at a range of values (Table 1). For each set of parameter values considered we ran the model 100 times, recording for each the mean and variance in the number of adult females at 100 years, and the number of runs that went to zero. Because our model did not include random variation in upland survival probabilities and reproductive output, the probability of extinctions was underestimated.

To determine which parameters had the greatest proportional effect on modeled population viability, we used a simulation approach to estimate the elasticity values for cumulative quasi-extinction probabilities (Morris and Doak 2002). The quasi-extinction threshold was set at five adult females. To obtain elasticities we first ran the model with a baseline set of parameters, and then with each parameter reduced to 95% of its baseline value. For each parameter set, we made 1000 model runs of 100 years each, recording for each run where the adult population dipped to or below the quasi-extinction threshold, the year in which this occurred. Elasticities for each parameter were estimated based on the difference between the baseline and perturbed cumulative quasi-extinction probability at each year (Morris and Doak 2002).

After evaluating model behavior assuming intact upland habitat, we investigated the population-level consequences of maintaining increasingly narrow bands of unaltered upland habitat adjacent to 700-, 3500-, and 7000-m² breeding ponds. For these simulations, we fixed the probabilities of late pond-filling years and reproductive failures at 0.30 and 0.10, respectively, to match our long-term observations of environmental variation (Trenham et al. 2000; P. C. Trenham, *unpublished data*). We began with the same three alternative forms of the transition matrix described previously. However, based on the estimated cumulative distribution of subadults and adults in the uplands around Olcott Lake, survival parameters were adjusted accordingly. Because actual survival in altered habitat is unknown, we investigated two scenarios for animals moving beyond the protected habitats: (1) no survival and (2) survival reduced by 50%. For example, assuming that 10% of adults remain within 100 m of the breeding pond, an unaltered upland survival probability of 0.60 would be reduced to 0.06 for scenario one, or 0.33 (i.e., 0.06 + [0.54/2]) for scenario two. The first scenario approximates what we imagine occurs with intensive residential development, the second may be representative of some agricultural land uses or low-density housing. We assumed that movement is independent of habitat suitability. Because subadults do not migrate to and from the pond each year, the reduction in survival due to habitat alteration was assessed only once prior to maturity for each cohort. We also compared the effects of basing the cumulative distribution functions on different functional forms of the relationship between density and distance for the Olcott Lake data.

RESULTS

Upland trapping results

Between 14 December 2002 and 21 March 2003, we captured 74 female, 53 male, and 62 subadult CTS in 2696 trap-nights (see Appendix A for a complete listing of capture data). Only three salamanders were recaptured; for these individuals we used only their initial capture data in the analyses that follow. We captured at least one male, female, and subadult salamander in traps at each distance from 10 to 400 m from Olcott Lake. We captured no CTS in our traps at 800 m. Comparisons of the distributions of adult and subadult captures, however, indicate divergent relationships be-

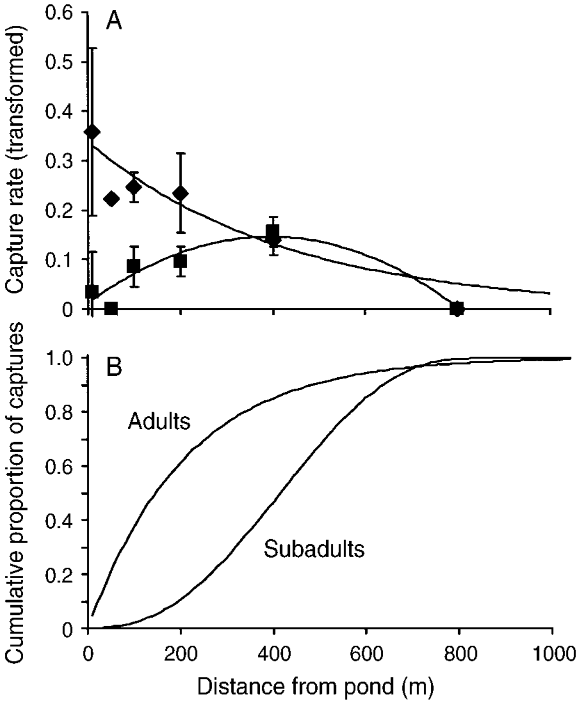

FIG. 3. Spatial distribution of California tiger salamander captures for all non-flooded traps. (A) Square-root-transformed number of adult (diamonds) and subadult (squares) captures per trap-night summarized for each distance (mean ± 2 SE). Lines represent exponential (adults) and second-order polynomial (subadults) regressions fit to the data; parameters are provided in *Upland trapping results.* (B) Using the regression functions represented in Fig. 3A, we estimated the cumulative proportion of subadults and adults encompassed within increasingly wide upland buffers around Olcott Lake.

tween capture rate and distance for these two groups. Adult capture rates declined from a maximum at 10 m, whereas subadult captures increased steadily from 10 to 400 m (Fig. 3A).

To make quantitative predictions about the distribution of adults in the uplands, we fit linear and exponential functions to the full adult data set. Although there was substantial heterogeneity in capture rates among traps at each distance, both the linear ($\sqrt{y} = 0.300 - 0.00039 \cdot x$; $F_{1,52} = 37.7$, $P < 0.0001$, $R^2 = 0.408$) and the exponential ($\sqrt{y} = 0.339 \cdot e^{-0.00236x}$; $F_{2,51} = 104.9$, $P < 0.0001$, $R^2 = 0.402$; Fig. 3A) fits were highly significant and explained roughly 40% of the variance in the data. Because there is a history of biological support for an exponential relationship between density and distance (Turchin 1998), we focus our further investigations on this form. Extrapolating from the exponential fit, we estimate that to encompass 50%, 90%, and 95% of the adults would require upland habitats extending 150, 490, and 620 m from the edge of Olcott Lake, respectively (Fig. 3B). A potential issue of concern with our sampling was the presence of only six traps at 800 m. To assess the influence of our lack of captures at 800 m on the predicted relationship we reanalyzed the data with those traps excluded. Extrapolating from the resulting function ($\sqrt{y} = 0.326 \cdot e^{-0.00205x}$; $F_{2,45} = 96.7$; $P < 0.0001$; $R^2 = 0.235$) the predicted upland habitat areas to encompass the same proportions of adults as above are roughly 13% wider: 170, 550, and 700 m, respectively.

Because subadult captures increased steadily from 10 to 400 m but declined to zero at 800 m we fit a quadratic function to the subadult dataset. Although the true shape of the function between 400 and 800 m cannot be determined from our data, quadratic regression provides a reasonable approximation. Fitting this function to the data resulted in a statistically significant relationship which explained only 18% of the variation ($\sqrt{y} = 0.084 + (1.8 \cdot 10^{-4}x) - (9 \cdot 10^{-7}(x - 290)^2)$; $F_{2,51} = 5.52$, $P = 0.007$, $R^2 = 0.178$; Fig. 3A). Extrapolating from this function the widths of upland habitat to encompass 50%, 90%, and 95% of subadults are 380, 590, 630 m, respectively (Fig. 3B). Upon further inspection, we noticed that very few subadults were captured in the traps south of Olcott Lake; dividing the traps into a northern and southern half there were 53 northern and nine southern captures. Reanalyzing only the northern trap data resulted in a substantially improved fit ($\sqrt{y} = 0.208 + (4.4 \cdot 10^{-5}x) - (1.3 \cdot 10^{-6}(x - 359)^2)$; $F_{2,26} = 10.12$, $P = 0.0006$, $R^2 = 0.438$). However, the predicted upland habitat widths to encompass 50%, 90%, and 95% of subadult CTS were nearly identical at 390, 600, 650 m, respectively.

Population model output

Before attempting to assess the population-level effects of upland habitat alteration for CTS, we investigated the model response to variation in parameters other than upland survival. With no stochastic elements, because larval survival was density dependent the number of adult females in the population rapidly reached an equilibrium determined by upland survival probabilities and pond area. With subadult and adult survival both set at 0.60, half of adult females breeding each year, and no stochastic reproductive failures, the equilibrium adult female population increased by one for each additional 8.1 m^2 of pond area.

Next, we investigated how population size and extinction risk responded to a range of stochastic conditions. Fig. 4A shows that, for a given pond area and probability of late pond filling, the average adult population size declines linearly as the probability of reproductive failure increases. Similarly, if the probability of reproductive failure is held constant while the probability of late pond-filling years is increased the mean adult population size declines linearly. Fig. 4B shows that the proportion of model runs going to zero within 100 years accelerates as the probability of reproductive failure increases. Because larvae may survive to metamorphosis in late pond-filling years, but not with reproductive failure, increasing the probability

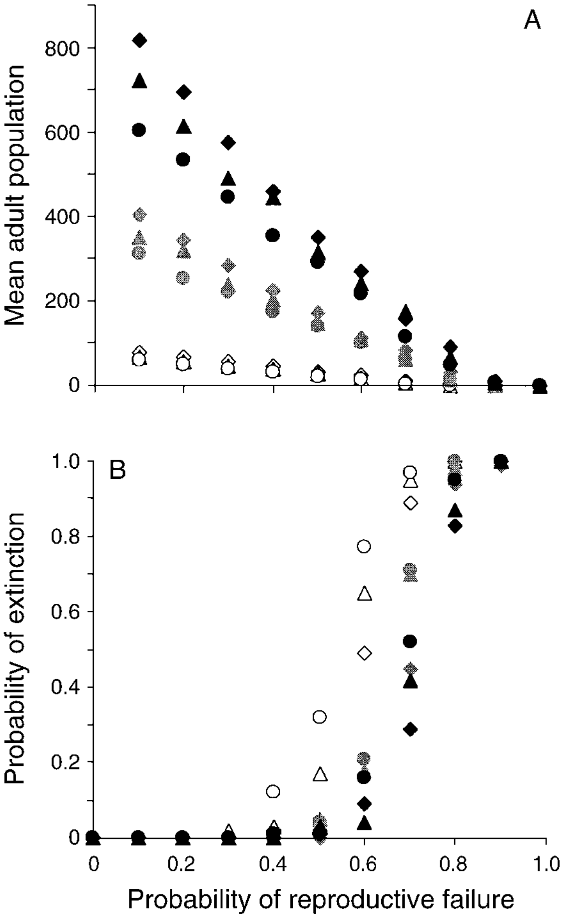

FIG. 4. Using our simulation model, we explored how (A) average California tiger salamander population size and (B) local extinction risk responded to increasing degrees of environmental stochasticity. Environmental stochasticity entered the model as (1) the probability of complete reproductive failure due to early pond drying (range 0–0.9; *x*-axis), and (2) the probability of late pond-filling years when only 10% of surviving females bred (diamonds = 0.1; triangles = 0.3; circles = 0.5). The probabilities of these perturbations were modeled as independent events. Symbol colors indicate the three different pond sizes modeled: 700 m^2 (open symbols), 3500 m^2 (gray symbols), and 7000 m^2 (black symbols). Upland survival of subadults and adults was set to 0.6. Females could breed beginning at four years old, and 50% of surviving females bred in each typical pond-filling year. Probability of survival to metamorphosis declined from a maximum of 0.2 in response to the density of eggs deposited in the pond (Fig. 2).

of the latter produced a larger effect on average population size and the frequency of runs that went to zero.

Fig. 5 summarizes the results of an elasticity analysis of the probability of quasi-extinction in model simulations. This analysis indicated that the probability of quasi-extinction was relatively insensitive to parameters influencing larval survivorship, but highly sensitive to small perturbations of upland survivorship. Of the two upland survivorship parameters, quasi-extinction probability was more than twice as sensitive to shifts in subadult as adult survivorship. Quasi-extinction probability was similarly insensitive to perturbation of each of the two parameters controlling larval survival.

The ultimate goal of this modeling exercise was to investigate the potential population-level consequences of converting upland habitat to nonhabitat or to habitat where survival is substantially reduced. Because there is uncertainty in the model parameters, we conducted simulations for a range of baseline survival parameters, mortality scenarios, and functional relationships between upland distribution and distance (see Table 1). In Fig. 6, we present model results illustrating the estimated effects on adult population size of maintaining increasingly wide areas of undisturbed upland habitat around a 700-m^2 pond; the results of model runs for 3500- and 7000-m^2 ponds were qualitatively identical (not shown). Consistent with the elasticity analysis results (Fig. 5), increasing annual subadult survivorship from 0.6 to 0.66 resulted in a larger average adult population than did similarly increasing adult survivorship (Fig. 6). Assuming a linear rather than an exponential decline in adult upland densities, resulted in small increases to estimated average population sizes of about 10–20% (Fig. 6).

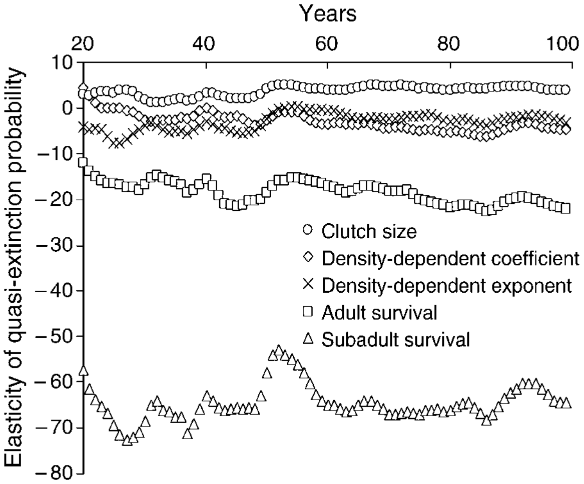

FIG. 5. Estimated elasticity values for cumulative quasi-extinction probabilities in response to perturbations of mean vital rates. Symbols represent elasticity in response to perturbation of various model parameters: subadult survival, adult survival, coefficient and exponent in larval density-dependent survival function, and number of eggs deposited per breeding female. Five adult females was the quasi-extinction threshold. The baseline model parameter values for this analysis were those indicated in Table 1. Elasticities for <20 years are not plotted because few extinctions occurred before this time, and as a result estimates of extinction probabilities and elasticities during this interval are highly variable and unreliable. Methods for elasticity analysis of density-dependent stochastic models are adapted from Morris and Doak (2002).

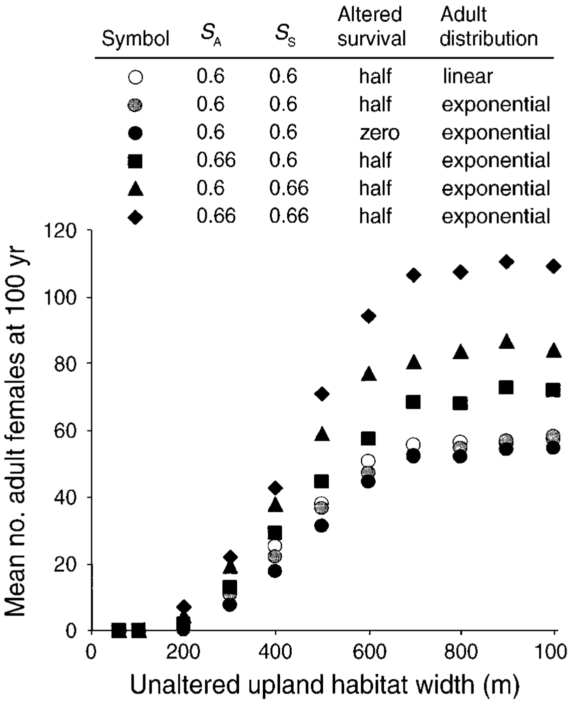

FIG. 6. Simulation model results showing the response of adult population size to the maintenance of increasingly wide bands of unaltered habitat around breeding ponds. Each point represents the mean number of adult females present in the simulated population at time step 100 based on a total of 100 runs with each set of parameter values. Different symbols represent different initial values for upland survival (i.e., with completely intact upland habitat), different mortality scenarios for animals moving into altered habitats (i.e., zero vs. halved survivorship), and adult survivorship (S_A) reduced either according to the cumulative distribution function in Fig. 3B (exponential) or a cumulative distribution function based on a linear relationship between adult captures and distance (linear; not shown). Subadult survivorship (S_S) was always reduced according to the subadult cumulative distribution function in Fig. 3B. Results shown are for a 700-m^2 breeding pond, with late pond-filling years and reproductive failures in 30% and 10% of years, respectively.

In general, as subadult and adult survival were reduced in response to simulated habitat loss, average population sizes declined, with accelerating declines when adjacent habitats extending less than 600 m from the pond edge were maintained (Fig. 6). Although estimated adult population sizes were sensitive to the particular set of parameter values, the proportional effects of a given amount of habitat loss were consistent. For example, under all scenarios considered, maintaining only a 400 m wide ring of upland habitat resulted in population declines of >50% when compared with the unaltered condition. Predicted declines approached 70% when animals moving into altered habitat all died. Leaving 200 m of upland habitat resulted in declines in average population size of 90–100%. Finally, if only 60 m of upland habitat was left intact, populations are generally predicted to go extinct within 100 years, or occasionally persist but at <1% of their estimated capacity in an intact landscape.

DISCUSSION

To confidently manage wetland habitats for viable populations of semi-aquatic animals requires a more detailed understanding of how these animals use upland habitats (Semlitsch and Bodie 2003). For researchers attempting to understand amphibian population ecology, penetrating the upland ecology of small, secretive, and often fossorial amphibians has remained a daunting empirical challenge (Taub 1961, Semlitsch 1998). While no single method or strategy will provide all of the critical data, our quantitative drift fence analysis of CTS at Jepson Prairie provides at least two novel results. First, adult dispersion appears to be far greater than indicated by earlier projections based on direct observations (Loredo et al. 1996) and radio tracking data (Trenham 2001), and is more in line with estimates based on observations of interpond dispersal over several years (Trenham et al. 2001). Second, the spatial distribution of subadults appears to be very different from that of adults.

To date, radio tracking has been the primary method used to obtain data on the distribution of adult amphibians in the uplands. Semlitsch (1998) and Trenham (2001) used tracking data to estimate the upland distribution ambystomatid salamanders. In a review of six eastern U.S. *Ambystoma* species, adults captured at breeding ponds and tracked directly via radio transmitters or radioactive implants moved an average of 125 ± 73 m (mean ± 1 SD) from ponds (Semlitsch 1998). Similarly, Trenham (2001) documented an average emigration distance of 114 ± 83 m for radio-tracked adult CTS. Assuming that movements are normally distributed, the means approximate the width of upland habitat required to encompass 50% of salamander movements. The means plus 1.645 standard deviations approximate the width of upland habitat needed to encompass 95% of movements (i.e., 245 and 250 m for these two studies). Our trapping results similarly suggest that 50% of adults are within 150 m of Olcott Lake. However, our analyses suggest that to encompass 95% of adults a 620 m wide upland habitat area is needed.

Although direct-tracking data provide valuable information on individual behavior and movements, we place more confidence in our trap-based projections of population distribution in the landscape for several reasons. First, there are always concerns that radio-equipped animals may not behave naturally, which is not an issue with our trap-based approach. Second, rather than assuming a normal distribution for salamander migration distances (Semlitsch 1998, Trenham 2001), we fit statistical models to the spatial distribution of actual capture rates. Finally, whereas radio tracking studies generally follow animals for only a few months after breeding, longer studies suggest that movement during these initial periods may not be representative of total adult displacement (e.g., Madison 1997, Madison and Farrand 1998). Because CTS adults frequently skip breeding for one or more years (Trenham et al. 2000), following post-breeding movements for just a few months is likely to underestimate overall movement patterns. Trap arrays, in contrast, register upland movements in proportion to their occurrence in the landscape. Interestingly, our projections in the current study closely resemble the spatial distribution of interpond dispersal events in our Monterey County study. In that system we observed adult and subadult dispersal among ponds separated by 60–670 m, but not farther (Trenham et al. 2001).

Because newly metamorphosed and subadult amphibians are generally too small to equip with radio transmitters, almost nothing is known about the upland ecology of these intermediate life stages. Whereas Semlitsch (1998) found tracking data for 265 individual adult *Ambystoma*, he found data for only 18 newly metamorphosed juveniles, and no data on subadults. CTS most commonly require three to five years to reach sexual maturity (Trenham et al. 2000; P. C. Trenham, *unpublished data*), and during this time they are completely terrestrial and rarely encountered. In contrast to the decline in adult capture rates at increasing distances from Olcott Lake, subadult capture rates increased from 10 to 400 m, and then declined to zero at 800 m. The apparent overall greater dispersion of subadults could potentially be a response to size-structured competition, which has been documented in related species (Smyers et al. 2002), or simply a consequence of diffusion-like movement over the lengthy subadult phase compared to the shorter interval between adult breeding events. Regardless of the cause, our data suggest that to encompass 95% of subadults an upland area on the order of 630 m wide would be required.

Although recommending upland habitat protection guidelines to encompass specific proportions of populations is a logical approach (Semlitsch 1998, Faccio 2003), this may not maintain population viability. We used a stochastic population model to evaluate this goal more directly. The results of our model, represented in Fig. 6, suggest that protecting at least 600 m of upland habitat would maintain populations with ~10% reduction in mean population size. Extrapolating from Fig. 3B, this translates to 90% and 92% protection of adults and subadults, respectively, and thus supports the protective value of the 95% protection benchmark. From a management perspective, this is a useful benchmark in situations where the goal is to maintain populations on lands containing one or a few breeding ponds isolated from immigrants. The upper bound on core upland habitat width of 290 m suggested by Semlitsch and Bodie (2003) may adequately protect other species, but our analyses suggest that if it were applied to CTS average population sizes would be reduced by >80% (Fig. 6). Therefore, for long-term preservation of individual CTS populations, the currently best-supported strategy is establishing protected landscapes with breeding ponds buffered by at least 630 m from incompatible upland land uses.

In many situations, due to historic habitat losses, protecting such broad areas of upland habitat will not be possible. Although breeding ponds nested in suboptimal uplands will be more likely to experience local extinctions, if linked to other ponds by dispersal they could contribute to the maintenance of a regional metapopulation (Sjögren-Gulve and Ray 1996, Marsh and Trenham 2001). Experimental metapopulation approaches to conservation may be the only viable option for CTS preservation highly fragmented regions and for the broader recovery of this species. Studies of a wide variety of amphibian species suggest that interpond distances of less than one kilometer should be maintained to avoid isolating breeding ponds (Marsh and Trenham 2001, Semlitsch 2002; but see also Smith and Green 2005). Strategies worth considering may include protecting corridors of marginal upland habitat between breeding sites, pond creation to enhance connectivity among distant sites, and even translocation of individuals to currently isolated unoccupied sites (Trenham and Marsh 2002, Seigel and Dodd 2002).

Ideally, before more detailed guidelines are drawn and predictions made, data from multiple sites and multiple years would be available to evaluate spatial and temporal variation in upland distribution, upland survival, and reproduction. Our model results suggest that obtaining additional data on upland survival should be a priority. In this and similar studies, pond-breeding amphibian populations are sensitive to upland survivorship of adults and subadults (Taylor and Scott 1997, Biek et al. 2002, Vonesh and de la Cruz 2002). Recognizing that upland survivorship of subadults is the parameter in which we have the least confidence and to which model results were most sensitive, this is an important area for additional study. Estimates of survivorship in different land use treatments would be of both basic and applied value (e.g., Rothermel and Semlitsch 2002).

Although we constructed our model as a tool to investigate the effects of upland habitat alteration, the results address some broader patterns of interest. Marsh and Trenham (2001), in reviewing the fit between theoretical metapopulations and pond-breeding amphibians, found little evidence that random extinctions of local populations are common as long as upland habitats were intact. This was also true of our model populations (Fig. 4B), and is due to strong density dependence in larval survivorship. In models where reproduction is enhanced at low densities, there is a strong tendency to recover from stochastic reductions in population size (Taylor and Scott 1997, Vonesh and de la Cruz 2002, Ferrer et al. 2004). From a practical perspective, our model results should also inform attempts to create breeding habitat for CTS or to assess the value of existing habitats. Our simulations emphasize the value of breeding habitats with large surface areas and those that hold water until metamorphosis in most years. In habitats where the probability of reproductive failure exceeds 0.50, simulations suggest that the result will be frequent local extinctions. However, it is important to note that, due to the potential for the establishment of fishes and other predator populations, reproductive failure is common in both permanent and highly ephemeral pools (Fisher and Shaffer 1996, Semlitsch 2002). Recent work indicates that even pond ''improvement'' that reduces the probability of annual drying, increases invasability by exotic fishes, crayfish and non-native tiger salamanders (*A. tigrinum*) decreasing the biological value of these sites (Fitzpatrick and Shaffer 2004).

The CTS was initially emergency listed as endangered in both Santa Barbara and Sonoma counties due to rapid conversion of its remaining habitat (U.S. Fish and Wildlife Service 2000, 2003). Because habitat loss was the main threat that brought about both of these actions and the statewide listing, a primary recovery objective should be the establishment of preserve areas with sufficient breeding and upland habitat for long-term persistence. To encompass a single isolated breeding pond with a 630 m wide ring of upland habitat (i.e., 95% protection) would require at least 125 ha. In Santa Barbara County, where all known CTS breeding ponds are on privately owned land, the U.S. Fish and Wildlife Service recently determined that about 4500 ha of critical habitat is needed to protect the salamander in perpetuity (U.S. Fish and Wildlife Service 2004*b*). In Sonoma County, confirmed breeding ponds existed on several preserves at the time of the emergency listing, but the largest of these protected areas is just 73 ha, and most are much smaller (U.S. Fish and Wildlife Service 2003). Thus, particularly in Sonoma County, experimental metapopulation approaches may be the only solution to the long-term viability of the remaining populations. Although the study of amphibians in the uplands remains challenging, new approaches are emerging that promise to yield further basic insights and data essential for improved conservation planning and management (Regosin et al. 2003, Rothermel and Semlitsch 2002). The pursuit of guidelines for upland habitat protection around wetlands will benefit from additional quantification of the consequences of habitat loss and appropriate data collection to reduce the assumptions required.

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APPENDIX A

A table showing raw trapping data is presented in ESA's Electronic Data Archive: *Ecological Archives* A015-031-A1.

APPENDIX B

A photograph of the study area and some representative traps is presented in ESA's Electronic Data Archive: *Ecological Archives* A015-031-A2.