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Conservation Implications of a Marbled Salamander, *Ambystoma opacum*, Metapopulation Model

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**CONSERVATION IMPLICATIONS OF A MARBLED SALAMANDER,
AMBYSTOMA OPACUM, METAPOPOPULATION MODEL**

A Thesis Presented

By

ETHAN B. PLUNKETT

Submitted to the Graduate School of the
University of Massachusetts Amherst in partial fulfillment
of the requirements for the degree of

MASTER OF SCIENCE

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Wildlife and Fisheries Conservation

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ABSTRACT

CONSERVATION IMPLICATIONS OF A MARBLED SALAMANDER, *AMBYSTOMA OPACUM*, METAPOPOPULATION MODEL

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Amphibians are in decline globally and a significantly greater percentage of ambystomatid salamander species are in decline relative to other species; habitat loss contributes significantly to this decline. The goals of this thesis is to better understand extinction risk in a marbled salamander (*ambystoma opacum*) population and how forestry effects extinction risk. To achieve this goal we first estimated an important life history parameter (Chapter 1) then used a metapopulation model to estimate population viability and determine what aspects of their life history put them most at risk (Chapter 2) and finally predicted extinction risk in response to hypothetical forestry scenarios (Chapter 3).

In Chapter 1 we estimated one of the requisite parameters for the model, juvenile survival, based on 8 years of field data. We estimated juvenile survival probabilities (to first breeding) at 17% for males and 11% for females. To our knowledge, these are the first estimates for marbled salamanders that include both returning and dispersing individuals.

In Chapter 2 we used a metapopulation model to estimate extinction risk and sensitivity of extinction risk to changes in vital rates and other model parameters. We

found that although there is considerable uncertainty in our estimate it is likely that extinction risk is low at our study site. Sensitivity analysis revealed that small changes in adult survival lead to relatively large changes in persistence and the presence of an apparent threshold in reproductive failure probabilities beyond which extinction risk rapidly increased.

In Chapter 3 we used the extinction risk and sensitivity estimates to model the effects of forestry on the metapopulation. We parameterized several different levels of impact of forestry on salamander survival; for each parameterization we calculated the extinction risk for 20 different forestry scenarios involving buffer size (30 to 300 meters) and complete or partial restrictions on cutting (5 different levels). We found for all but the most optimistic parameterizations large buffers (around 200 meters) with high restrictions on cutting within the buffer were necessary to maintain a low extinction risk.

Overall we show that although the population at our intensively studied field site is unlikely to go extinct under present conditions small decreases in adult survival, small increases in catastrophe rate, and intensive forestry can all make extinction likely.

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CHAPTER 1
JUVENILE SURVIVAL OF MARBLED SALAMANDERS IN WESTERN
MASSACHUSETTS

1.1 Abstract

Metapopulation and population viability models depend on vital rates for all stages of a population. However, estimates of juvenile survival (defined for this paper as survival from metamorphosis to sexual maturity) and upland survival in general are scarce for seasonal pond-breeding amphibians. Those estimates that do exist often ignore dispersing individuals. Here we use eight years of data from 14 ponds encompassing a single metapopulation to estimate juvenile survival of Marbled Salamanders (*Ambystoma opacum*). Juvenile survival estimates were 17% for males and 11% for females. Additionally we show variations in survival among ponds within the metapopulation were weakly correlated with a land-cover based measure of habitat quality and uncorrelated to variation in size at metamorphosis.

1.2 Introduction

Amphibian declines and the role of metapopulation dynamics in these declines has received considerable research attention (Stuart et al., 2004; Storfer, 2003). To model these population dynamics effectively requires estimates of survival rates for all life stages. For many amphibian species, including the Marbled Salamander (*Ambystoma opacum*), the post-metamorphic stages are less studied than the pre-metamorphic. However, changes in post-metamorphic vital rates may have greater impact on population

viability than changes in pre-metamorphic vital rates among pond-breeding amphibians (Biek et al., 2002; Vonesh and De la Cruz, 2002).

Obstacles to obtaining accurate life history data for post-metamorphic (both juvenile and adult) ambystomatid salamanders include fossorial habitat selection (Montieth and Paton, 2006), multiple year delays to first breeding (Scott, 1994; Trenham et al., 2000), females not breeding every year (Gamble, in press), and dispersal (Gamble et al., 2007). Trenham et al. (2000) encountered many of these problems measuring survival in the California Tiger Salamander (*A californiense*).

Studies examining survival often use enclosures (e.g., Rothermel and Luhring, 2005; Rothermel and Semlitsch, 2006), which may not completely represent factors affecting survival in natural environments. Finally, those studies that have estimated juvenile survival in natural environments have generally ignored dispersing individuals (e.g., Semlitsch et al., 1988; Scott, 1994). In this study, we estimate juvenile survival, defined as survival from emergence to first breeding, from eight years of population monitoring at 14 seasonal ponds constituting all the potential breeding sites in a presumed closed metapopulation.

1.3 Methods

1.3.1 Study Organism

In Massachusetts, the Marbled Salamander is at the northern extent of its range and is state-listed as “threatened” under the state Endangered Species Act (M.G.L c.131A and regulations 321 CMR 10.00). Marbled Salamanders breed in the late summer and fall and oviposit their eggs in dry basins of seasonal ponds. Eggs hatch within 24 hours of

pond flooding (Dunn, 1917), which generally also occurs in the fall. Young overwinter in the ponds as larvae, metamorphose the following spring, and emerge from ponds as juveniles in late May, June, and early July (Timm et al. 2007).

Mark recapture techniques estimate the annual survival of breeding females at our field site at 58% and suggest 56% of breeding females will not breed the following year (Gamble, in press) Estimated annual survival of adult non-breeding females is 66% and 97% breed the following year. Adult males generally return to breeding ponds every year and their estimated annual survival rate is 58% (Gamble, In Press); Gamble et al. (2007) estimated 9% of juveniles in this population disperse to breed at ponds other than their natal pond.

1.3.2 Field Site

Our study site contains a cluster of 14 seasonal ponds on the south side of the Holyoke Range in S. Hadley, Massachusetts USA and has been the focus of an intensive long-term research project designed to monitor Marbled Salamanders at the metapopulation level (Gamble et. al., 2007; Gamble, 2007). Half the ponds support persistent populations of breeding Marbled Salamanders, while sporadic breeding efforts have been observed in most of the other ponds. The largest interpond distance is 1.4 km. We believe that these 14 ponds are largely isolated from other breeding sites; the Holyoke Range bounds them to the north and a heavily traveled road (Route 116) and dense residential development bounds the study area to the east and south. To the west, the nearest seasonal pond is approximately 800 m away and no Marbled Salamander breeding activity has been observed in two years of larval surveys at this pond (L.

Gamble, unpubl. data). The site consists largely of contiguous mixed deciduous-hardwood forest, but is bisected by a powerline and a brook.

1.3.3 Field Methods

We enclosed ponds 2, 3, 4, 5, 6, 9, 11, 12, and 14 in drift fence prior to the 1999 spring juvenile emergence and the remainder of the ponds prior to 2000 spring emergence. We maintained all fences through the end of the fall 2006 breeding season. The drift fence was either 0.36 m tall aluminum flashing or, in especially wet areas, 0.90 m plastic silt fencing buried in the ground. We placed pairs of pitfall traps made from number 10 cans every 10 m along the fence on both sides. Whenever the water table rose above the bottom of the cans we temporarily replaced individual pitfall traps with aluminum screen funnel traps. We checked all traps daily from the middle of May until the end of the outward migration of post-breeding adults, which occurred in October or November. During the winter and early spring the traps were closed and gates opened in the fence to allow free passage of animals. To minimize the time animals spent in traps we also checked traps on rainy nights when large movements of animals were expected. Emerging juveniles received a pond specific (but not year specific) toe-clip consisting of a pair of adjacent digits (Ott and Scott, 1999) and a subsample were weighed and measured. We photographed adults in the population entering and exiting the drift fence arrays and matched photographs of individuals from 1999 to 2006 with the aid of a computer algorithm (Ravela and Gamble, 2004; Gamble et al., 2008). We also recorded the sex, weight, and any toe-clip marks of adults.

1.3.4 Data Analysis

For each of the eight years of capture data, we used trespass rate estimates (Gamble et al. 2006, Gamble in press) to calculate the total number of breeding adults from the outside-of-fence adult captures and the total number of emerging juveniles from the inside-of-fence unmarked juvenile captures. We assumed sexual parity, which has been demonstrated for Spotted Salamanders, *A. maculatum* (Shoop, 1974) and previously assumed for Marbled Salamanders (Scott, 1994), and multiplied the total number of juveniles captured by 50% to estimate the total number of juveniles emerging for each sex. We calculated a survival-based estimate of the number of first-time breeding adults (FTBA) for each year by subtracting from the observed number of breeding adults the number expected to have survived and returned from prior years based on Gamble's (2007) estimates of adult survival and breeding state transition probabilities (to account for year skipping), as follows:

Females:

$$FTBA_t = BA_t - [BA_{t-1} * S_{BA} * (1 - T_{BA}) + BA_{t-2} * S_{BA} * T_{BA} * S_{NBA} * T_{NBA}] \quad (1)$$

Males:

$$FTBA_t = BA_t - BA_{t-1} * S_{BA} \quad (2)$$

where BA represents breeding adults, NBA represents non-breeding adults, t is time (in years), S is annual survival, and T is the probability of transitioning out of the subscripted state.

For a subset of years (2000-2004 for males, and 2001-2004 for females), we validated our survival-based estimate of FTBA by comparing it to an image-based estimate of FTBA, which was the count of individuals breeding in a given year with no

prior occurrence at the field site. The image-based estimate is a more direct estimate of FTBA but is not available for the last 2 years of the study and is not accurate for the first 2 years (2 for females, 1 for males) because many experienced breeders still had not yet been observed and thus would bias FTBA estimates.

In the absence of year-specific marks, we determined time lags between emergence and first breeding by documenting how long it took for the initial marked cohort of 1999 juveniles to be recaptured at a breeding pond as marked FTBA adults. This was facilitated by the fact that the 1999 emergence was large and the 2000 emergence was almost a complete failure.

We used two models to estimate juvenile survival. First, the *time-implicit* model assumed that most female FTBAs from the last 5 (of 8) years originated as juveniles in the first 5 years of the study, that most male FTBAs from the last 6 years originated as juveniles in the first 6 years, and that juvenile survival is the ratio of number of adults to juveniles. This is essentially a hybrid between two methods of generating life history data: (1) tracking a cohort through time and (2) assuming a stable state and estimating the distribution of age classes at a single snapshot in time. Thus, to calculate male juvenile survival, we divided the number of male FTBA immigrating to ponds in the last six years of the study by the number of male metamorphs emigrating in the first six years (incorporating a two year lag). For females, we made the same calculation, but with a three year lag. To the extent that the assumptions are not met and some individuals take shorter or longer to reach sexual maturity, we do not expect this estimate to be significantly biased as long as the population size is stable. For example, if some percentage of females took longer than three years to mature, then some juveniles we

observed emigrating from ponds in the fifth year would not have bred by the last (eighth) year, which would negatively bias survival estimates. In addition, juveniles who had emerged prior to the initiation of the study who, due to their long maturation times, did not breed for the first time until after the third year of the study, would introduce a positive bias to survival estimates. These two biases would tend to cancel each other out as long as the variability in fecundity in the years preceding the study was similar to the variability during the study.

Second, we estimated juvenile survival rates using a *time-explicit* model, which assumed that the majority of individuals matured in one of two time lags to breeding (two and three years for males, three and four years for females) and estimated components of survival for each lag that best predicted the number of FTBA, as follows:

$$FTBA_t = JuV_{t-L1} * P_1 + JuV_{t-L2} * P_2 \quad (3)$$

$$(FTBA_t - JuV_{t-L1} * P_1 + JuV_{t-L2} * P_2)^2 \quad (4)$$

where P_1 represents the proportion of emerging metamorphs that both survive and return to breed after the first time lag, Juv represents the number of emerging juveniles, t represents the year, and $L1$ represents the number of years in the first lag. To find the maximum likelihood value for P_1 and P_2 , we minimized the value of expression (4).

To estimate how well the *time-explicit* estimate of juvenile survival fit the data, we used the *time-explicit* juvenile survival rates to predict FTBA from juvenile emergence. We then calculated the coefficient of determination (R^2) of those predicted FTBA against observed FTBA. To measure the significance of the observed R^2 , we compared it to 10,000 similar R^2 values derived from repeating both the parameter estimation and regression process with Monte Carlo permuted data (both juvenile

emergence and FTBA were resampled without replacement). This estimated how likely the observed R^2 would randomly occur given the variability in the data and the potential for over fitting that occurs with small sample sizes, and in particular indicates how much better than random the time lags we chose to model perform. It does not give us an estimate of error or guarantee that there are no biases in our estimates.

In addition to conducting the two estimates of juvenile survival on the pooled data, we also used the same techniques to estimate juvenile survival individually for four ponds that had sufficient numbers of juveniles (ponds 2, 4, 5, and 12). For the pond-specific calculations of FTBA, we used all adults found with the given pond's mark as well as all adults found at the pond with no mark. Thus, if we knew an adult originated from a certain pond, we assign it to that pond. Where we were not certain of its origin, we would assign it to the most likely pond.

We tested several hypotheses that might explain differences in juvenile survival estimates among ponds including: (1) size at metamorphosis varied among ponds and was driving differences, (2) unaccounted for dispersal varied among ponds and was driving differences, and (3) differences in habitat connectivity among ponds was driving differences. The null hypothesis in all cases was that differences were representative of the error in our estimate of juvenile apparent survival. In all the tests we used the mean of the *time-explicit* and *time-implicit* estimates of juvenile apparent survival. To test hypothesis (1) we regressed the juvenile survival estimate at each pond against the ponds' mean metamorph total length, snout-vent length, and weight. The basis for hypothesis (2) is our assumption that unmarked adults had returned to their natal pond to breed. This assumption holds for 91% of individuals that do not disperse to other breeding ponds

(Gamble et. al., 2007). However, we expect the error from the other 9% of unmarked adults to introduce a bias in survival rate estimates: negative for ponds that are a net source of dispersers and positive for ponds that are net recipients. This is because unmarked adults, or ones that lose their mark, that disperse from the source ponds would be counted as if they had originated in the destination pond. To test for this bias, we regressed juvenile survival estimates against the net number of dispersers produced. To test hypothesis (3), we regressed habitat connectivity as measured with a resistant kernel estimator (Compton et al. 2007) against juvenile survival. The resistant kernel integrates habitat quality, quantity, and accessibility around a pond into a single number. It calculates the connectivity of each point in the landscape to the focal pond as a Gaussian function of the least cost path between the two. In a minimally resistant landscape (pure forest) it yields a Gaussian surface. Resistance in part or all of the landscape reduces the connectivity to the pond and depresses the surface downward. The volume of the realized surface relative to the maximum possible volume is the habitat connectivity estimate. We used the same resistance values and kernel bandwidth as Compton et al. (2007).

We performed all calculations using the program R version 2.7.0 (R-Development-Core-Team, <http://www.R-project.org>).

1.4 Results

1.4.1 Time to First Breeding

Most juvenile females returned to breed either 3 or 4 years after initial emigration based on the timing of marked adults showing up to breed after the large emergence in 1999 (Fig. 1.1). For juvenile males the time lag was less distinct, but almost certainly less

than that of females. Marked juvenile males from 1999 bred for the first time in 2001 and 2002, an apparent two or three year time lag. However, some of the large numbers of marked juveniles emerging in 2003 appeared to breed one year later in 2004, although greater numbers returned after either two or three years in 2005 and 2006. Monte Carlo tests showed that time lags were significant for overall juvenile survival estimates for both males and females as well as most individual pond estimates (Table 1.1).

1.4.2 Female Juvenile Survival

Using the *time-explicit* model, we estimated that 7% of emerging juvenile females returned to breed after three years and that an additional 4% returned to breed for the first time after four years. Thus, we estimated that 11% of the emerging females survived from metamorphosis to first breeding. The *time-implicit* model also yielded an estimate of 11% of females surviving to breed. FTBA numbers predicted from juvenile emergence based on our *time-implicit* estimate of juvenile survival were similar to the both the image-based and adult survival-based FTBA estimates (Fig.1.2) and fit the adult survival-based estimates, with an adjusted R^2 of 0.91. Only 478 of the 10,000 Monte Carlo samples yielded better fits ($P > 0.05$) than the observed data, implying that the time lags we defined were significant.

Female juvenile apparent survival rates at individual ponds (Table 1) varied from 8% at pond 2 to 12% at ponds 4 and 12. *Time-implicit* and *time-explicit* survival estimates were similar (Pearson's correlation = 0.96). Adult-survival-based estimate of FTBA fit the image-based measure of FTBA, with an adjusted R^2 of 0.82.

1.4.3 Male Juvenile Survival

Males generally had higher apparent survival rates to first-time breeding than females, with 10% surviving to breed in two years and an additional 7% surviving to breed for the first time in three years. Both *time-explicit* and *time-implicit* models predicted 17% percent survival to first-time breeding. As with females, FTBA numbers predicted from juvenile emergence and survival rates closely matched the adult survival-based FTBA estimates (adjusted $R^2 = 0.97$). Only 284 of the 10,000 Monte Carlo samples yielded higher adjusted R^2 values. Male juvenile survival rates ranged from 11% at pond 2 to 20% at ponds 4 and 12 (Table 1). The Pearson's correlation between the two estimates of survival at individual ponds was 0.65. This was much lower than for the females largely because of a large discrepancy between the two estimates at pond 12. Adult-survival-based estimate of FTBA for males fit the image-based estimate with an adjusted R^2 of 0.81.

1.4.4 Differences Among Ponds

There was no clear relationship between juvenile survival for either males or females at each pond compared to the ponds' mean metamorph length, snout-vent length, and weight (total length females: $R^2_{\text{adj}} = -0.40$, $b = -0.04$, $P = 0.74$; other results were similar: $R^2_{\text{adj}} < -0.031$, $P > 0.65$ in all cases). Ponds that supplied net sources of dispersing juveniles generally also had higher estimated juvenile survival (females: $R^2_{\text{adj}} = 0.93$, $b = 9.8e-5$, $P = 0.02$ males: $R^2_{\text{adj}} = 0.74$, $b = 2.7e-4$, $P = 0.09$), which was direction opposite that expected from the bias. There was a trend showing higher juvenile apparent survival estimates for both genders in more connected habitats (female: $R^2_{\text{adj}} = 0.95$, $b = 0.15$, $P = 0.02$; male: $R^2_{\text{adj}} = 0.31$, $b = 0.34$, $P = 0.27$).

1.5 DISCUSSION

We had two primary conclusions. First, we estimated juvenile survival across a metapopulation of 17% for males and 11% for females. In general, our estimates were slightly higher than estimates from other studies on pond-breeding amphibians. The one other study to estimate juvenile survival of Marbled Salamanders (Scott, 1994) reported survival rates of 15% and 10% for males and females, respectively. However these results were from ponds with artificially manipulated larval densities. It is somewhat surprising that our estimates of juvenile survival were higher, as our population is at the northern end of the species' range and individuals here take longer to reach sexual maturity. Both dispersal and mark loss are accounted for in this study but, if present, would reduce Scott's (1994) estimates. If dispersal at Scott's site was equivalent to the 9% we observed, after correction for dispersal Scott's survival rates would be 16.5 % and 11%. There are few estimates of juvenile survival in other Ambystomatids; Trenham et al. (2000) report that 3.4% of their 1992 cohort of Tiger Salamanders was recaptured breeding sometime in the following five years, but they noted that both dispersal and long maturation times made it challenging to accurately estimate survival. Smith (1987) estimated survival in the Chorus Frog (*Pseudacris triseriata*) at 12.8 % for large (>11 or 12 mm depending on when they emerged) and 6.6.% for small metamorphs. Bevins (1990) reported juvenile survival of 37.9 % for male Wood Frogs (*Lithobates sylvaticus*), which generally bred eight months after emerging; 7.8% for females, which generally bred at two years of age; and corresponding annual apparent survival rates of 24 and 21.6%.

Second, we observed considerable variation in juvenile survival across the four ponds for which we were able to estimate survival independently. Differences in mean metamorph size among ponds did not explain differences in survival among ponds despite the fact that Scott (1994) showed through experimental manipulations that increasing larval density decreased both size at metamorphosis and juvenile survival in Marbled Salamanders. Trenham et al. (2000) found no relationship between size at emergence and either age or size at maturity in Tiger Salamanders. It is possible that size at metamorphosis does effect juvenile survival of Marbled Salamanders at our study site but was not revealed in our analysis either because of the small sample size or, more likely, because it was confounded with other differences among the ponds such as habitat connectivity. We did detect a trend towards higher juvenile survival in ponds with greater habitat connectivity. However, our estimate of habitat connectivity relied only on a relatively coarse classification of landcover (e.g., road, forest, field, or stream) due to the paucity of information on the specific upland habitat requirements of Marbled Salamanders. A greater understanding of upland habitat requirements, for example how slope, soil moisture, soil type, rodent burrow density, and tree species effect habitat quality, might allow us to explain more of the differences in juvenile survival among ponds.

In summary to our knowledge, estimates of juvenile survival of Marbled Salamanders within and across this metapopulation in Massachusetts are the first published estimates that include both individuals known to have dispersed as well as site faithful individuals. These basic demographic estimates are critical to metapopulation and population viability modeling. In addition, our results indicate that variation in juvenile

survival among ponds in our metapopulation is not clearly related to variation in size at metamorphosis and appears to be driven by upland habitat connectivity, although this finding needs further investigation.

Table 1.1. *Time-implicit* and *time-explicit* estimates of juvenile apparent survival in Marbled Salamanders pooled across 14 seasonal ponds (all) and within the four individual ponds containing the largest populations in South Hadley, Massachusetts between 1999-2006. In the *time-explicit* estimates, the P1 and P2 represent the proportion of the juveniles surviving and returning to breed in two different time lags, 2 and 3 years for males and 3 and 4 years for females, respectively.

Sex	Pond	Mean	Time Implicit	Time Explicit	Lag 1	Lag 2	P
m	All	0.17	0.17	0.17	0.10	0.07	0.02
m	2	0.11	0.10	0.11	0.08	0.04	0.009
m	4	0.20	0.20	0.20	0.09	0.11	0.03
m	5	0.18	0.19	0.18	0.05	0.12	0.03
m	12	0.20	0.16	0.23	0.22	0.02	0.07
f	All	0.11	0.11	0.11	0.07	0.04	0.05
f	2	0.08	0.08	0.08	0.04	0.04	0.09
f	4	0.12	0.11	0.13	0.06	0.07	0.01
f	5	0.10	0.10	0.11	0.09	0.02	0.1
f	12	0.12	0.11	0.12	0.09	0.03	0.08

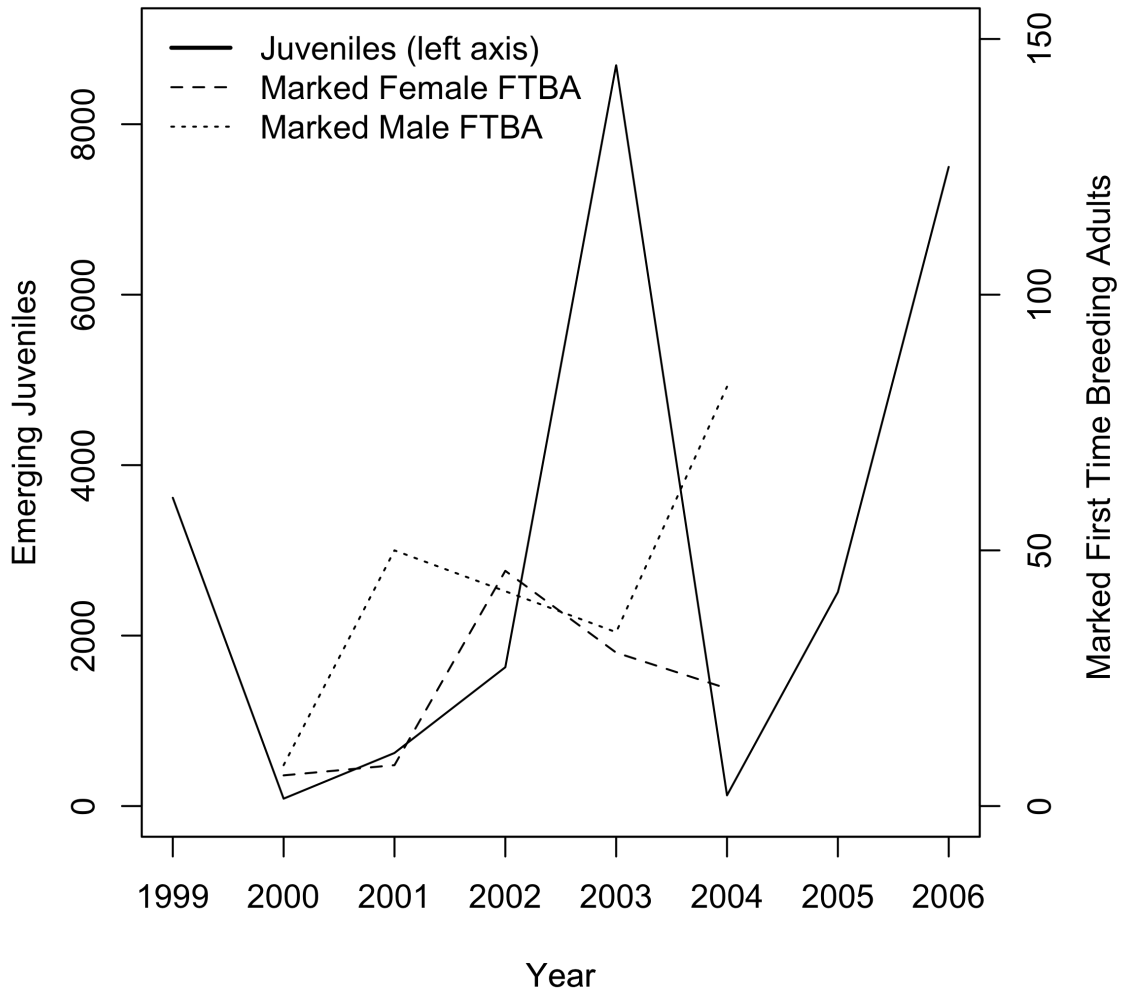


Figure 1.1. Number of juvenile Marbled Salamanders emigrating from 14 seasonal ponds in South Hadley, Massachusetts between 1999-2006 (solid line and left axis), and the estimated number of first-time breeding adults (FTBA) with marks (dashed line and right axis). Time lags to first breeding were different between genders. For females (A), the initial wave of marked emerging juveniles released in 1999 returned as marked FTBA three and four years later. For males (B) there appears to be a two to three year delay to first breeding.

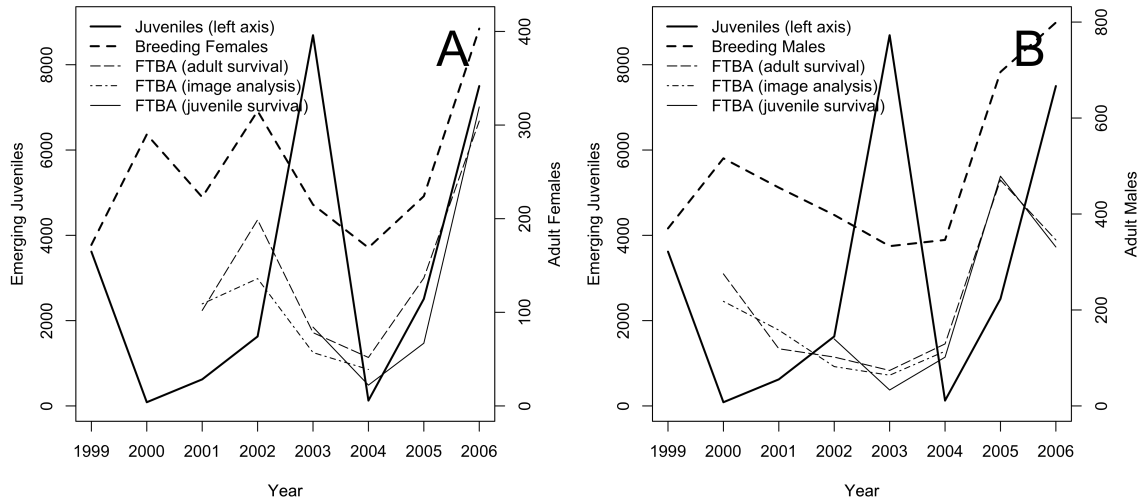


Figure 1.2. Number of juvenile Marbled Salamanders emigrating from 14 seasonal ponds in South Hadley, Massachusetts between 1999-2006 (solid line and left axis), and the corresponding number of breeding adults (dashed line and right axis) and estimated number of first-time breeding adults (FTBA) based on three different methods (see text). The peaks in juvenile production in 1999 and 2003 resulted in an increase in marked FTBAs three and four years later for females (A) and two and three years later for males (B) for all three methods of estimation.

CHAPTER 2
POPULATION VIABILITY ANALYSIS OF A MARBLED SALAMANDER
METAPOPULATION

2.1 Abstract

We investigated marbled salamander demography and movements at 14 seasonal ponds in Massachusetts over eight years to parameterize a spatially-realistic metapopulation model. Our results suggest that there is a low probability of extinction risk in this metapopulation. However, there is considerable uncertainty in this estimate due to our inability to predict reproductive failure. A sensitivity analysis suggested small changes in adult survival lead to relatively large changes in persistence. In addition, there was an apparent threshold in reproductive failure probabilities, beyond which extinction risk rapidly increased. Given the importance of reproductive failure to metapopulation persistence and the strong relationship between climate and reproductive failure, climate change could have a major impact on this metapopulation. In addition, given the importance of adult survival, conservation of upland habitat at multiple scales will be necessary to protect viable metapopulations of this species.

2.2 Introduction

Many amphibian populations are currently threatened by the loss, fragmentation and/or degradation of habitat caused by human land use. The problem is especially acute for pond-breeding amphibians, which are suffering dramatic declines worldwide (Stuart et al. 2004). Ambystomatid salamanders are experiencing significantly more rapid decline than other amphibian families, apparently due to habitat loss (Stuart et al, 2004).

It is essential that we identify factors influencing extinction risk to develop and implement effective conservation and management strategies for these pond-breeding amphibians.

Population viability analysis is one successful modeling approach to examine extinction risk by identifying specific factors that could affect populations (Morris & Doak 2002). Spatially-realistic models have a number of advantages over nonspatial models and are especially important for spatially-structured populations or metapopulations. Previous efforts to model demographics of amphibians have largely focused on individual populations (e.g., Vonesh & De La Cruz 2002, Beik et al. 2002). While much can be learned from individual populations, they may not be adequate to address population processes that occur at broader spatial scales (e.g., dispersal) and their implications for viability. Metapopulation models incorporate larger scales and can be used to predict extinction risk (Hanski & Simerloff 1997). However, most amphibian metapopulation models have largely focused on modeling patch occupancy (Marsh & Trenham 2001) rather than populations and thus usually are unable to draw conclusions about demographic processes (but see Hels & Nachman 2002).

Our objective was to develop a spatially-realistic metapopulation model to conduct a population viability analysis of a northern population of marbled salamander (*Ambystoma opacum*). Specifically, we used a population-based model parameterized from eight years of empirical data to determine the sensitivity of extinction risk to changes in adult survival, juvenile survival, dispersal rates, reproductive failure rates, or fecundity given the specific landscape context of our long-term study site.

2.3 Methods

2.3.1 Case Study Landscape

We conducted fieldwork at 14 seasonal ponds on the south side of the Holyoke Range in South Hadley, Massachusetts USA (Fig. 2.1). These ponds have been the focus of an intensive long-term research project designed to monitor marbled salamander demographics at the metapopulation level (Gamble et. al. 2007; Gamble 2007; Gamble et al. 2009). Half the ponds support persistent populations of breeding marbled salamanders, while sporadic breeding efforts have been observed in most of the other ponds. The largest interpond distance is 1.4 km. These 14 ponds are largely isolated from other breeding ponds; the Holyoke Range bounds them to the north and a heavily traveled road (Route 116) and dense residential development bounds the study area to the east and south (Fig. 2.1a). To the west, the nearest seasonal pond is approximately 800 m away and no Marbled Salamander breeding activity has been observed in two years of larval surveys at this pond (L. Gamble, unpubl. data). Vegetation at the site was dominated by contiguous mixed deciduous-hardwood forest, and bisected by a powerline and a brook. The landscape was 363 ha, with landuse classified at a 10 m resolution (Fig 2.1b).

2.3.2 Model Design

Our model had two major components: 1) a spatial representation of the modeled area, and 2) a population projection matrix. The spatial component summarized the effect of land use on the population vital rates. Inputs were the location of all the potential breeding sites (seasonal ponds) and the land use throughout the study area. Land use was fixed for all analyses presented in this paper but the model also supports

dynamic landscapes (i.e., that change over time). The spatial component of the model estimated dispersal rates from the landscape based on a Gaussian function length of the least cost path between ponds.

The second part of the model was a stage and location (population) structured projection matrix (Caswell, 2001), which in this case included 56 rows and columns, one for each unique combination of four stages (juveniles, two sub-adult stages, and adults) and 14 populations (ponds). Cells in the transition matrix represented fecundity, survival of each age class at each location, and dispersal between locations (Table 2.1). We generated a new transition matrix for each time step, incorporating stochasticity in the fecundity and survival rates (details below). In this case, we did not model survival probabilities of eggs or larval stages, as we had not monitored these stages in our fieldwork. Instead, we modeled juveniles, which were youngest stage and represent metamorphs that have successfully emerged from ponds. Moreover, we presumed females to be limiting in the population and only modeled females. Juvenile survival represented the cumulative survival from emergence to first breeding (juvenile and two sub-adult year classes). The sub-adult stages were included in the model to ensure the correct delay of 3-4 years to sexual maturity (Chapter 1).

To implement this in the matrix format, we populated the cell for transitions out of the juvenile stage with the juvenile survival rate and assign a value of 1 to the transitions out of the two sub-adult stages (Table 2.1). We sampled juvenile survival and adult survival from uncorrelated normal distributions based on parameters which set both the survival rate (`adult.surv`, `j.to.a.surv`) and the coefficient of variation in survival rates (`cv.adult.surv`, `cv.j.to.a.surv`).

We defined fecundity as the number of female metamorphs produced per breeding female. We assigned fecundity, the most variable parameter in the model, at every time step in the following manner. First, we created a set of correlated uniform random numbers, one for each pond. Second, if the random number was below the observed pond-specific catastrophe rate, it was considered a catastrophe and the fecundity for the pond was set close to zero; as the random number varied from 0 to pond's catastrophe rate, the fecundity ranged from 0 to cat.cutoff – a low fecundity which represented the threshold for reproductive failure (Fig. 2.2a). Otherwise the random number was rescaled by subtracting the pond-specific catastrophe rate and dividing by 1 minus that rate. This produced a scaled fecundity that ranged from 0 to 1 for each successful pond. Third, the scaled fecundity was multiplied by the height of a Gaussian curve, which we fit to the observed distribution of pond-specific fecundities and hydroperiods, sampled at the pond's hydroperiod (Fig. 2.2b). This approach, although slightly cumbersome, allowed for correlations in fecundities and catastrophes, incorporated a hydroperiod-dependent limit on fecundity, allowed catastrophe rate to vary by pond, and generated fecundities similar to those observed at our field site. Before insertion into the transition matrix, the fecundities were multiplied by the proportion of females that breed each year (breeding.rate) to account for the fact that not all females breed every year.

In each time step, the transition matrix was modified with an Allee effect to suppress fecundity in ponds where very few animals are breeding, and a density dependence function that reduced fecundity to account for diminished larval survival under high densities. The Allee effect multiplies the fecundity by $n/(n+A)$, where A is

the allee parameter and n is the number of breeding adults (Morris & Doak 2002). We used the larval density dependence function created for a southern population of marbled salamanders by Taylor and Scott (1997) and applied it to the number of juveniles that would be produced in the model at each pond in the absence of density dependence. Finally, at the end of each time step we multiplied the transition matrix by the prior population state to generate the next population state, set to zero any component of the population that was less than one, saved the population state, and then repeated the whole process a user-specified number of times.

The initial population structure was user-specified. We generated the initial population by setting the number of adults equal to the 2000 field data and filling in the other stages (i.e., the juvenile and two sub-adult stages) to match the stable state stage distribution of each sub population. To calculate the stable distribution, we first created a representative transition matrix for the entire metapopulation by averaging 50 different possible transition matrices each of which reflects the deterministic and stochastic effects of the model parameters and the landscape at the first time step. Then, for each population we calculated the primary eigenvector of the 4 by 4 portion of the representative matrix which contained all the within population transitions; the primary eigenvector is the stable state distribution of the population (Morris & Doak 2002).

2.3.3 Model Parameterization

In this section we provide a brief description of the model parameterization, focusing only on the most important aspects of key parameters. A complete description of the model parameterization is provided in Appendix A.

We set annual adult survival at 0.62 (*adult.surv*) and breeding probability at 0.67 (*breeding.rate*) based on Gamble et al.'s (2009) estimates, although for adult survival we excluded one pond with a low survival outlier. We calibrated juvenile survival (*j.to.a.surv*) to account for the effective boost in survival due to successful dispersers; we set the parameter to 0.092 so that the sum of the survival rate (determined by the *j.to.a.surv* parameter) and all the dispersal rates out of each pond (determined by the dispersal parameters and the landscape) was on average (across ponds) equal to a target juvenile survival of 0.11 (Chapter 1). Most juvenile mortality likely occurs shortly after metamorphosis in the spring and summer (Rothermel & Semlitsch 2006) and most annual variation in adult survival occurs during the fall breeding period (Gamble et al., 2009); consequently, we did not correlate juvenile and adult survival to each other.

We calculated a coefficient of variation in adult survival (*cv.adult.surv*) of 0.08 from Gamble et al.'s (2009) year-specific estimates of adult survival. Because we had no estimate of the yearly variation in juvenile survival for our population, we set it proportionally equal to that of adults ($cv.j.to.a.surv = 0.08$). We assumed that variation in both juvenile and adult survival is driven largely by climate variables experienced by the entire metapopulation, so we made them correlated among ponds (within years). This assumption was verified by Gamble et al.'s (2009) finding that the best model of survival probabilities grouped most ponds but estimated survival separately for each year.

We estimated fecundity parameters from field data. First, we fit a segmented linear regression model (Muggeo 2003) to the fecundities plotted in rank order (Fig. 2.2a) and set the cutoff point below which a fecundity is considered a reproductive failure (*cat.cutoff*) to 1.2 based on the fecundity of the breakpoint in this model. Next, we

calculated each pond's reproductive failure probability as the percentage of observed annual fecundities that were below the cutoff at that pond. Third, we used the `quantreg` library in the R program to perform non-linear quantile regression (Koenker 1994) on reproductive failure in response to hydroperiod; we fit a Gaussian curve that encompassed 95% of the non-catastrophe fecundities (Fig 2.2b). The mean and SD of the curve defined two model parameters: `optimal.hp = 264`, and `hp.fec.sd = 35`, while a third parameter, `hp.fec.v.scale = 1891`, was the height of a curve relative to a unit area Gaussian curve of the same SD.

To estimate dispersal, we used landscape resistance values generated by Compton et al. (2007). The bandwidth of the dispersal kernel, `h.disp = 440m`, was estimated by Gamble et al. (2007) using data from our field site. We calibrated `disp.factor`, which sets the height of the dispersal kernel, so that the overall percentage of dispersers (successful dispersers divided by all first time breeding adults) calculated from the land use and observed emergence at our field site matched the percentage observed at our field site.

We performed all simulation and statistical analyses in program R version 2.8.1.

2.3.4 Extinction Risk

We estimated extinction risk by conducting 100 repetitions of the model on each of 1000 different parameterizations. To generate the parameterizations, we sampled the pond-specific catastrophe and adult survival probabilities based on our uncertainty in these parameters: adult survival from a normal distribution based on Gamble's (2009) standard error of the parameter estimate; and reproductive failure probabilities based on bootstrap resampling of the seven years of catastrophe data (sampling years with

replacement after filling in missing data by sampling observations from the same pond). We chose these two parameters because of the high uncertainty associated with our estimates and because initial model results indicated high sensitivity of extinction risk to these parameters. For each of the 1000 model parameterizations, we calculated extinction risk as the percentage of the 100 runs that went extinct. Lastly, we calculated quantiles in the distribution of extinction risks across the 1000 parameterizations to represent our confidence that extinction risk is below a specified quantile (Fig. 2.3).

2.3.6 Sensitivity Analysis

To determine how changes in each parameter are likely to affect model outcome we conducted a sampling-based sensitivity analysis (Cacuci et al. 2005) with two response variables: (1) extinction risk and (2) metapopulation size. For the sensitivity analysis, we varied all the model parameters slightly among model repetitions by sampling the parameters from a normal distribution with a mean set to the nominal value of the parameter and a coefficient of variation of 0.10. We then regressed the outcome (one of the response variables) against the realized parameter values for a set of 1000 repetitions. Lastly, we multiplied the slopes and confidence interval of each parameter by the mean value of the parameter and 0.01, thus calculating the expected absolute change in the response variable per percentage change in the parameter (the sensitivity to that parameter). This is similar to a procedure described by Bartell et al. (1986), although it differs in that Bartell et al. use the partial R² value for each parameter to determine its significance in the model, and they used the technique with deterministic models. We found that it was easier to interpret and estimate the standard error of the adjusted

coefficients than the adjusted R² values and that the results were highly correlated to the adjusted R² values.

To evaluate the robustness of the parameter sensitivities, we conducted sensitivity analysis on a number of alternative points in parameter space. More specifically, we individually varied: (1) the reproductive failure rates of all ponds from 0.2 to 0.7, and (2) the adult survival rate by increasing adult survival between 0.4 to 0.75 (in which case each pond's reproductive failure rate was set to the observed rate for that pond).

2.3.7 Bernoulli Trial Simulation

Extinction risk is likely to increase with the number of consecutive reproductive failures and given enough consecutive failures will increase to 100%. Each year, reproductive failure at each pond is a Bernoulli trial: a random experiment that results in one of two outcomes (success or failure). To examine how the probability of getting a string of at least n consecutive failures (within a series of 100 trials, where each trial represents a year) changes in response to the probability of failure we simulated 5000 series of 100 Bernoulli trials for each of 21 probabilities of failure (ranging from 0 to 1) and calculated the percentage in which n consecutive failures occurred (with n ranging from 2 to 20).

2.4 Results

2.4.1 Extinction Risk and Metapopulation Structure

The extinction risk was low given the current climate and habitat types in the landscape of this metapopulation and our uncertainty in pond-specific catastrophe rates; in 95% of the simulations the extinction risk was below 92%, in 90% of the simulations it

was below 37%, and in 60% of the simulations it was zero (Fig. 2.3). Pond 4 was by far the largest and most persistent population (Fig. 2.4). Ponds 2, 3, 5, and 12 also supported relatively persistent populations, but they were roughly an order of magnitude smaller in population sizes than pond 4. Occupancy rates and population sizes were generally higher for the ponds closest to pond 4 suggesting that it is acting as a source to nearby populations. The exception is pond 12 which despite being far from pond 4 and had a high occupancy rate.

2.4.2 Sensitivity Analysis

Extinction risk and metapopulation size were most sensitive to changes in adult survival, but they were also sensitive to juvenile survival, fecundity, and the reproductive failure probability (Fig. 2.5). These trends held true across a range of adult survival and reproductive failure probabilities. However, when the adult survival probability dropped below 0.5, relative sensitivity to changes in adult survival were similar to juvenile survival and fecundity (Fig. 2.5c). When adult survival dropped below 0.55 or reproductive failure probability exceeded 0.4, the extinction risk increased dramatically (Fig. 2.6). In addition, the sensitivity of extinction risk to both adult survival and reproductive failures peaked when adult survival was at 0.6 and when all reproductive failure probabilities were set to 0.5 (Fig. 2.5).

Figure 2.5a shows the sensitivity of extinction risk of several parameters across a range of reproductive failure rates. At any reproductive failure rate, the height of the line corresponding to each parameter indicates the expected change in extinction risk per percent change in the parameter. Under low reproductive failure rates, the sensitivity to changes in reproductive failure is relatively low (Fig 2.5a). This remains true until

reproductive failure increases to 0.45 at which point the sensitivity to failure jumps and then, above failure rates of .55, begins to decline again (Fig. 2.5a). Higher adult survival decreases the extinction risk so the sensitivity to adult survival is negative. However, as in sensitivity to reproductive failure, the magnitude of the sensitivity to adult survival peaks with reproductive failure rates around 0.5 (Fig 2.5a). Extinction risk and metapopulation size were relatively insensitive to dispersal, the allee effect (not shown), and the correlation in fecundities (Fig 2.5).

2.4.3 Bernoulli Trial Simulation

The probability of a n consecutive failures increases with the probability of each individual failure (p) monotonically but not uniformly (Fig. 2.7). For any given n , there tends to be a threshold in p near which the probability of n consecutive failures rapidly increases; above and below the threshold changes in p have little effect (Fig. 2.7). The probability of failure (p) at which the threshold occurs increases as n increases (Fig. 2.7). In biological terms p and n are analogous to reproductive failure and adult survival (the ability of adults to survive through a string of failures), and the probability of n consecutive failures represents extinction risk. Thus the Bernoulli trials suggest that as reproductive failure probability increases, the extinction risk will be unaffected until a threshold is reached beyond which extinction risk rapidly increases. Increasing adult survival shifts the threshold towards higher reproductive failure probabilities but also tends to make the threshold more abrupt.

2.5 Discussion

Using a spatially-realistic metapopulation model parameterized for a marbled salamander metapopulation in western Massachusetts, we found that both extinction risk and metapopulation size are highly sensitive to adult survival. This is not surprising given that only adults contribute to fecundity and the ability of adults to survive through periods of low fecundity is clearly beneficial. These results concur with models of individual populations. Several authors have concluded that survival of upland life stages were most important to extinction risk (Vonesh & De La Cruz 2002; Beik et al. 2002; Harper et al. 2008). Taylor et al. (2006) modeled a southern population of marbled salamanders and concluded that extinction risk increases dramatically either with increased rates of catastrophic breeding failure or decreased adult survival. Thus, despite the inclusion of multiple populations in our model, we reach similar conclusions to models based on single population. This is likely due to the fact that the single population at pond 4 is much larger and most persistent than the other populations and is a source bolstering nearby population persistence. Thus pond 4 likely drives metapopulation persistence in the whole model.

We found that extinction risk is most likely very low or near zero in this metapopulation, but there was considerable uncertainty in this estimate (Fig. 2.3). One striking aspect was that the distribution of extinction risks is not unimodal, but is instead concentrated in several bands (Fig. 2.3). This is likely due to the fact that reproductive failure rates were generated by bootstrap resampling only 7 years of data. Thus, for each pond breeding failure rate could only take on a small set of discrete values. A subsequent regression tree analysis (not shown) revealed that the variation in catastrophe rate at Pond

4 was responsible for most of the variation in extinction risk shown in Fig 2.3. The impact of these discrete steps was exacerbated by the fact that there appears to be a non-linear relationship between breeding failure rate, adult survival, and extinction risk, which appears to be driven by the behavior of Bernoulli trials. Just as the probability of a string of n consecutive failures in a series of 100 Bernoulli trials shows a very clear threshold behavior (Fig. 2.6) there appears to be a threshold in reproductive failure below which extinction risk rapidly increases. We see evidence for this threshold in the increased sensitivity to breeding failure rates near 0.5 (Fig. 2.5a) and in the rapid increase in extinction risk as breeding failure probabilities are reduced below 0.5 (Fig 2.2, Fig 2.6b).

Ultimately, predicting extinction risk with greater certainty will depend on a better understanding of the catastrophe rates at our study ponds. Unfortunately, our current estimates are akin to flipping a coin seven times to determine its odds. Harper et al. (2008) solved a similar problem by first building a model to relate reproductive failure in wood frogs (*Lithobates sylvaticus*) and spotted salamanders (*A. maculatum*) to precipitation and, second, applying that model to historical precipitation data. In doing this, they leveraged a small number of observations by combining them with historical data to estimate reproductive failure more precisely. However, because marbled salamanders breed in the fall, larval survival is probably influenced by more factors than in wood frogs and spotted salamanders which breed in the spring.

Previous analyses of breeding failures at our site showed that several variables related to climate were useful in predicting reproductive success or catastrophe, including the timing of pond basin inundation (either too early or too late) relative to oviposition

and spring hydroperiod (Gamble 2004). However, due to complex interactions among different variables (e.g., effects of extreme cold in years when inundation was later than normal) and limited data, Gamble (2004) was unable to develop models with predictive power. As we collect additional data in the future, we hope to be able to fit a climate-based model of catastrophe and use it to solidify our estimate of catastrophe rate and extinction risk and relate it more clearly to environmental variables.

One implication of the high uncertainty in catastrophe rate relates to the potential for climate change impacts. The Intergovernmental Panel on Climate Change (Meehl et al. 2007) has predicted increasing extreme events with global warming that might include extended dry periods or more frequent big storms. Breeding failure in our system appears to be linked to extreme climatic events such as early heavy rains which fill ponds before breeding; unusually dry fall conditions which delay inundation and leave the eggs more susceptible to desiccation, predation and freezing; or dry, cold winters in which ponds are more likely to freeze solid. Therefore, there is the potential for climate change to increase the frequency of reproductive failure. This, coupled with the apparent threshold nature of the response to catastrophe rates, suggests that climate change might not only increase the extinction risk of this species, but that extinction risk is likely to increase dramatically beyond some threshold in climate change. It is also possible that generally milder winters might improve conditions for marbled salamanders, especially in Massachusetts where they are at the northern end of their range by, for example, increasing upland survival or reducing the chance of pond freezing. However, if warming trends are coupled with more variability and more extreme weather events we

believe that the end result will be greater breeding failure rates, which we have demonstrated leads to higher extinction risk.

2.6 Model Limitations

We are forced as modelers to make tradeoffs between parsimony and realism. This tradeoff is further influenced by the state of our knowledge and ignorance. Adding complexity, even if it is likely to be ecologically meaningful, is folly if we are unable to estimate the required parameters with accuracy. Two of our greatest concerns are as follows:

(1) We are limited by the time span of our data and are forced to assume that the 8 years of data this model is parameterized from is a representative sample of the next 100 years. Eight years is less than the life span of some of the longer-lived adults in our population and much shorter than the time scales metapopulation dynamics play out on (e.g. Skelly et al. 1999). The reproductive failure rate of each pond is a particularly important parameter that we needed to estimate with at most seven fecundity observations; in some ponds where the animals have rarely attempted to breed this data is even sparser. Additionally, in the course of our field work, we have observed an explosion of the population at Pond 4 and a decline at several other ponds. Our model reflects these data in the dominance of Pond 4 in the metapopulation (Fig. 2.4), but we are left wondering how accurately 8 years of data represent the mean and variability of demographic parameters in general and pond specific reproductive failure probabilities in particular.

(2) We currently model dispersal rates between two ponds as a Gaussian function of the cost length of the least cost path between the ponds without considering either (a)

the quality of the source or destination ponds or (b) the population size at the source or destination ponds. The result in the model is many dispersing individuals arriving at all ponds. However, in the real metapopulation, while distance does drive dispersal rates (Gamble et al. 2007), we also observe more dispersal to ponds with breeding salamanders than without. These also appear (based on hydroperiod) to be the better quality ponds in the system, so it is unclear whether dispersers are selecting destinations based on the presence of other salamanders or by selecting ponds with higher habitat quality.

Unfortunately we lack sufficient data to parameterize a more complex dispersal model and as a result our model probably distributes dispersers more evenly than the salamanders are distributing themselves in the natural population. This could potentially lead to an overestimation of colonization, because most of the ponds in question function as ecological traps in the model our parameterization may actually be lowering the number of effective dispersers to ponds that matter. Most ponds in the model are regularly visited by potential colonizers (Fig. 2.4), and it appears that success is largely driven by pond quality (hydroperiod and breeding failure rate). However, because the model is dominated by a single pond and is insensitive to small changes in dispersal rates, it is unlikely that this concern has much effect on the model results.

2.7 Conservation Implications

The great sensitivity of the model to changes in the frequency of breeding failure and survival (both juvenile and adult, but especially adult) suggest that conservation efforts should focus on maintaining or decreasing the breeding failure rate and maintaining or increasing adult survival. Juveniles and adults spend most of their annual cycle away from breeding ponds, therefore their survival is dependent on the quantity,

quality and accessibility of upland habitat (e.g. Raymond & Hardy 1991; Rothermel & Luhring 2005). However, currently most protection of pond-breeding amphibian populations has focused on the wetlands themselves. Massachusetts regulations provides some protection up to 30 m (100 ft) beyond the edge of the ponds (310 CMR 10.00). However, as others have noted, this is insufficient to protect the majority of the upland habitat critical to adult and juvenile survival (Semlitch 1998; Gamble et al. 2006; McDonough & Paton 2007).

We believe that the best way to mitigate the potential impacts of habitat loss and climate change is to adopt a multi-scale approach (e.g., Compton et al. 2007). Buffers are an important tool for preserving the pond itself, but a 30 m buffer is an order of magnitude too short to protect the uplands used by amystomatid salamanders. When the area is considered a 30 m buffer is even less adequate: the area encompassed by a 30 m buffer is several orders of magnitude smaller than the area of uplands used by salamanders. So in addition to buffers to protect the breeding habitat, we think that conservation should also focus on proactively targeting collections of pools with forested uplands for conservation.

Global climate change is difficult to address through local management; however, again we believe that a cluster of ponds in close proximity is more likely to be able to sustain a population than a single pond because the cluster will tend have a variety of hydroperiods. That variety offers some insurance against the possibility that climate change will (1) alter individual pond hydroperiods or (2) shift the ideal hydroperiod for the species. In either case, if there is a variety of hydroperiods as some ponds' hydroperiods move away from the ideal others will move towards it. If the ponds are

close together it is likely that the population will be able to shift from one pond to another as conditions change. In conclusion a reserve that encompasses a collection of pools is likely to capture at least a few larger, more robust populations, to have a diversity of pond characteristics and to include much of the uplands around the ponds all of which will make salamanders more likely to persist in the reserve.

Table 2.1. The transition matrix is structured first by populations and then by stages. Transitions within each population fall within 4x4 sections of the matrix while transitions among subpopulations (dispersal) sparsely fill the rest of the matrix. Columns and rows are labeled by the stage they represent: juvenile (J), sub-adult 1 (S1), sub- adult 2 (S2), and (A) and their subscripts correspond to population number. Transitions within the matrix correspond to fecundity (F), dispersal (D), and survival (S) and their subscripts represent the stages and populations involved. For example $S_{J-A,2}$ represents survival from juvenile to adult within the second population.

	Population 1				Population 2			
	J ₁	S1 ₁	S2 ₁	A ₁	J ₂	S1 ₂	S2 ₂	A ₂
J ₁	F ₁							
S1 ₁	S _{J-A,1}				D ₂₋₁			
S2 ₁	1							
A ₁			1	S _{A,1}				
J ₂					F ₂			
S1 ₂	D ₁₋₂				S _{J-A,2}			
S2 ₂					1			
A ₂							1	S _{A,2}

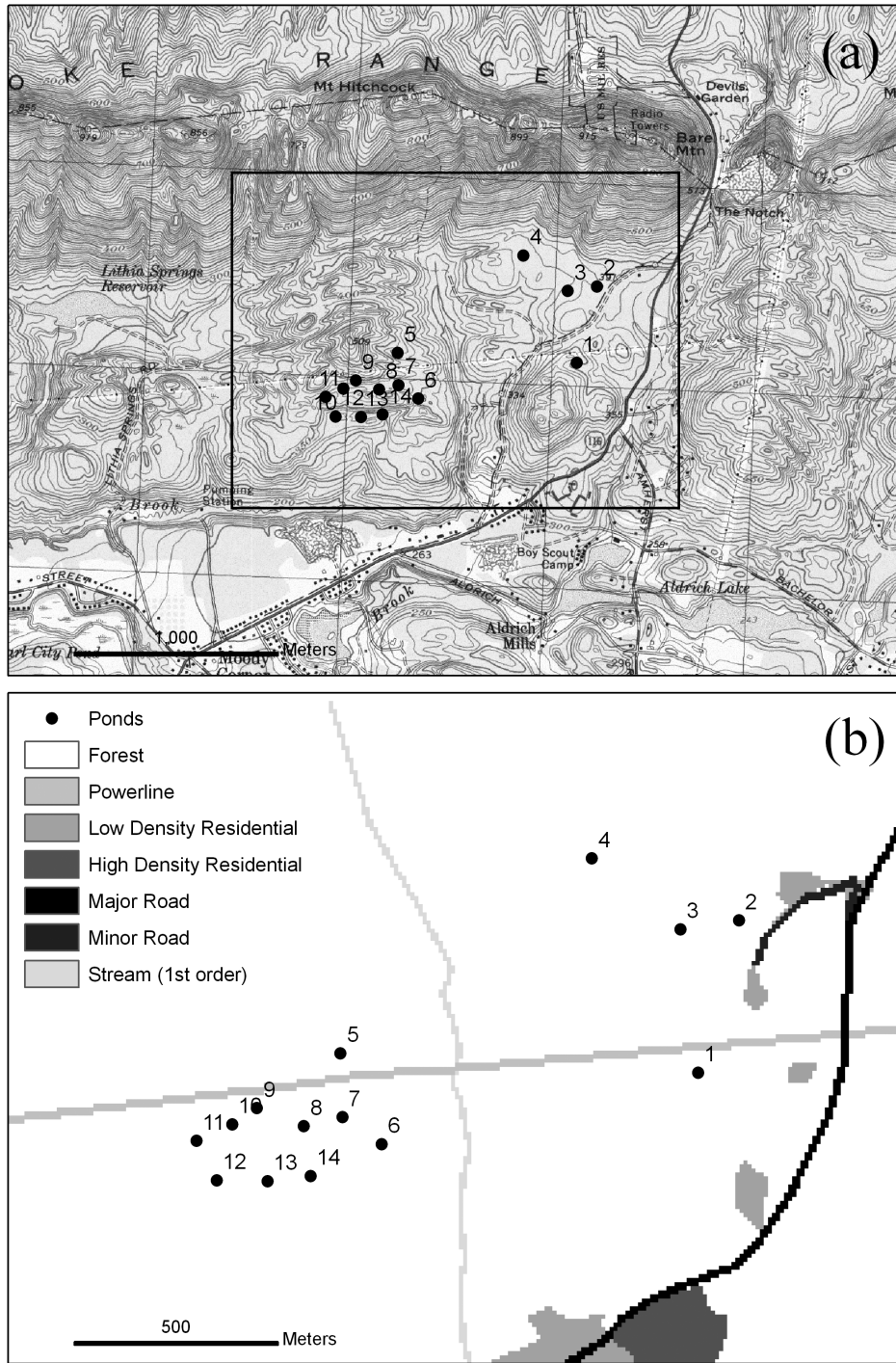


Figure 2.1. The study site (a) consists of 14 seasonal ponds bounded to the north by the Holyoke range and to the east and south by Route 116. We classified land use at the study site at a 10 m resolution (b) from 0.5 m/pixel digital orthophotos. The rectangle in (a) represents the extent of the landcover map (b) that was submitted to the model.

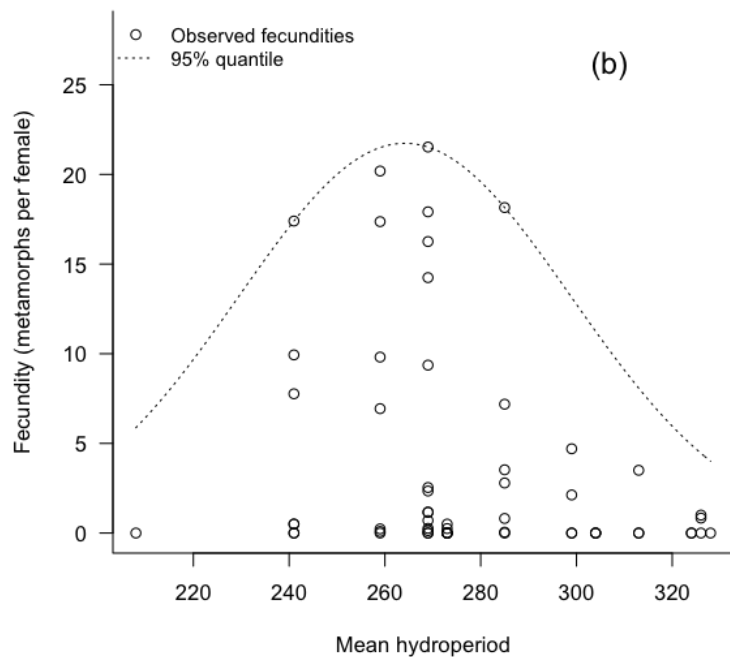
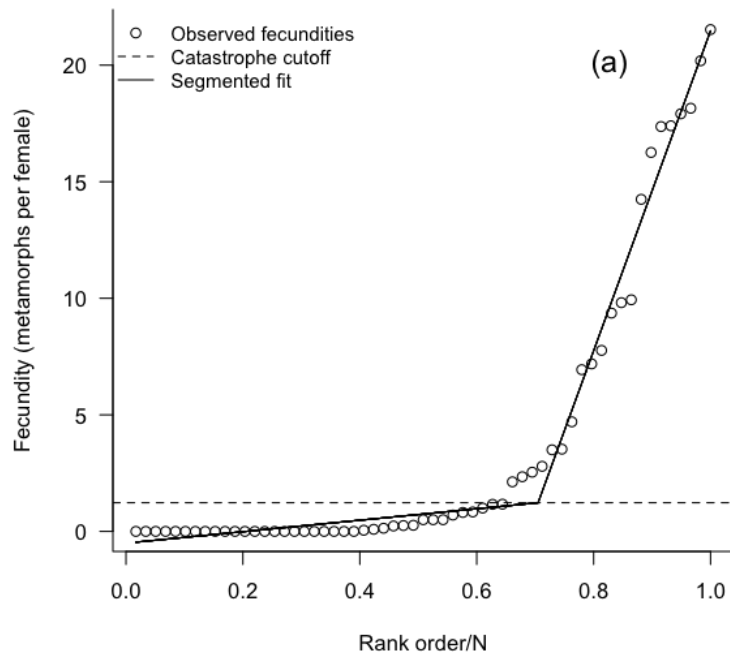


Figure 2.2. We fit a segmented linear model to the rank-ordered fecundities to determine the point below which a fecundity would be called a catastrophe (cat.cutoff) (a) and a Gaussian curve to the 95th quantile of observed non-catastrophe fecundities to determine how hydroperiod relates to fecundity (b).

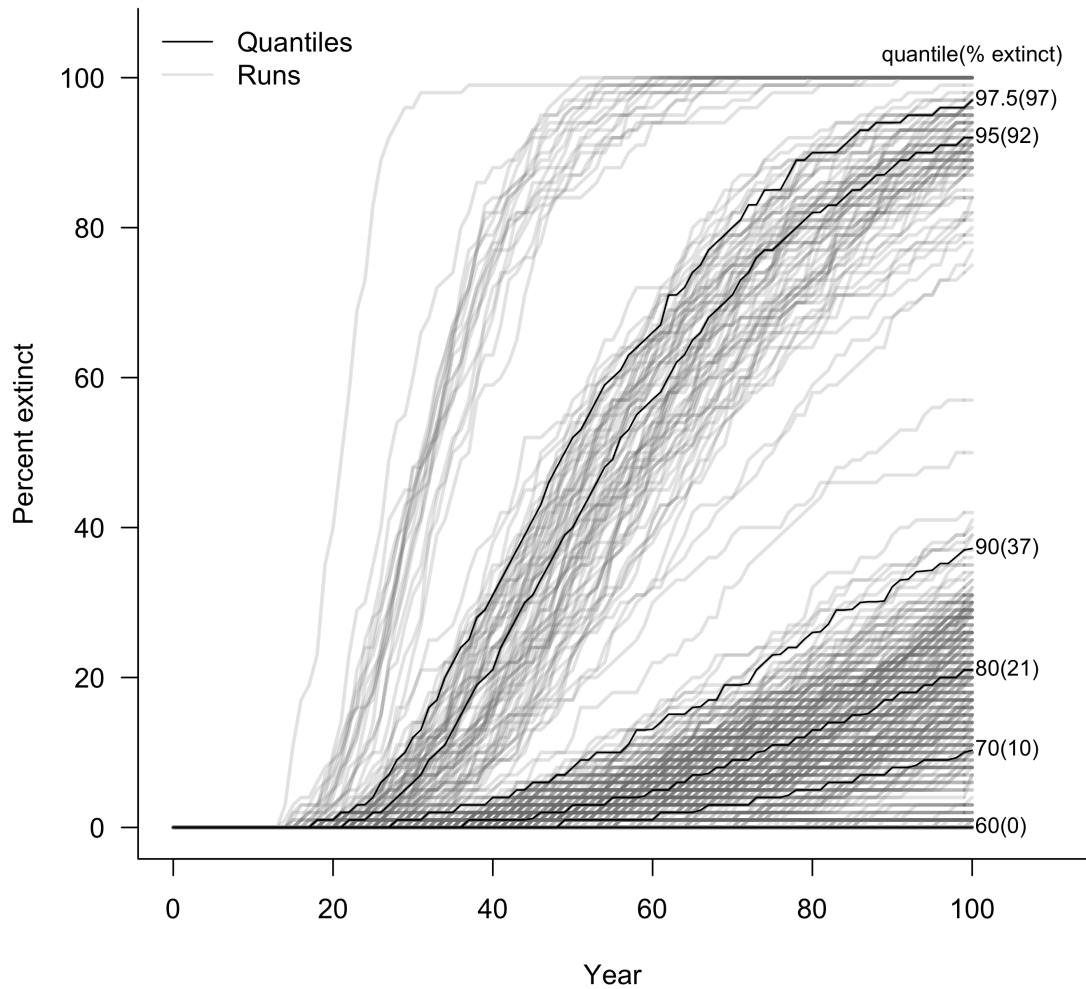


Figure 2.3. Extinction risks for 1000 parameterizations of the model (grey lines) reflect the distribution of our uncertainty in reproductive failure and adult survival rates. Quantiles of these lines reflect probabilities that the extinction risk is at or below the height of the quantile. For instance, based on the 90th quantile, we are 90% certain that the extinction risk within 100 years is below 37%.

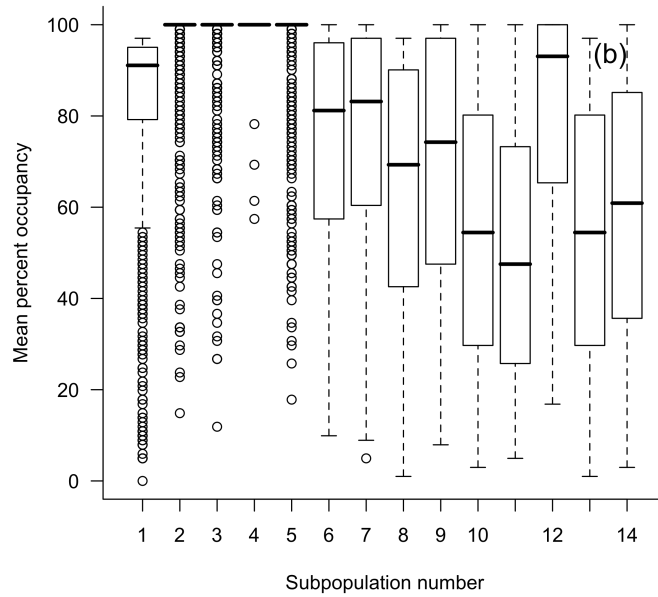
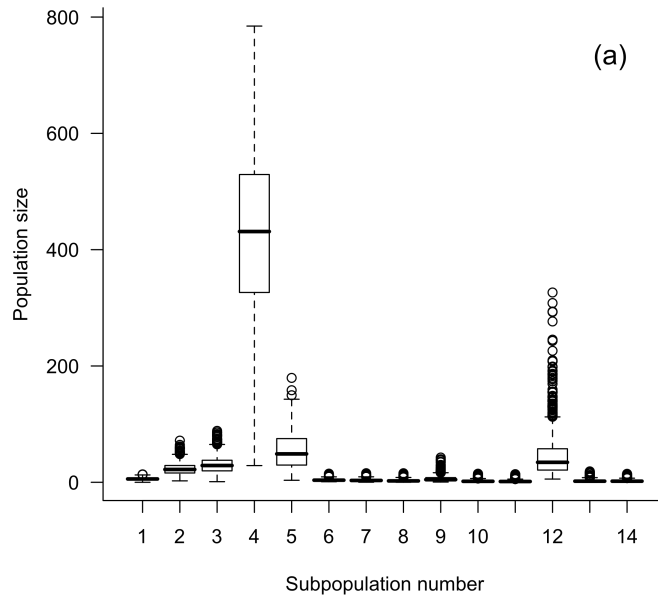


Figure 2.4. Mean subpopulation size across model runs (a) reveals the dominance of pond 4 which functions as a relatively persistent source in the metapopulation. Ponds 2, 3, and 5 are relatively close to pond 4 and are likely maintained by their proximity to pond 4. The ponds were considered occupied if any adults were present; thus, for many ponds occupancy (b) seems to be maintained via dispersal and occupancy rate seems to be a function of proximity to pond 4. Pond 12 is interesting in that it is one of the farthest ponds from 4 yet has a reasonably high mean population size and moderate occupancy rates.

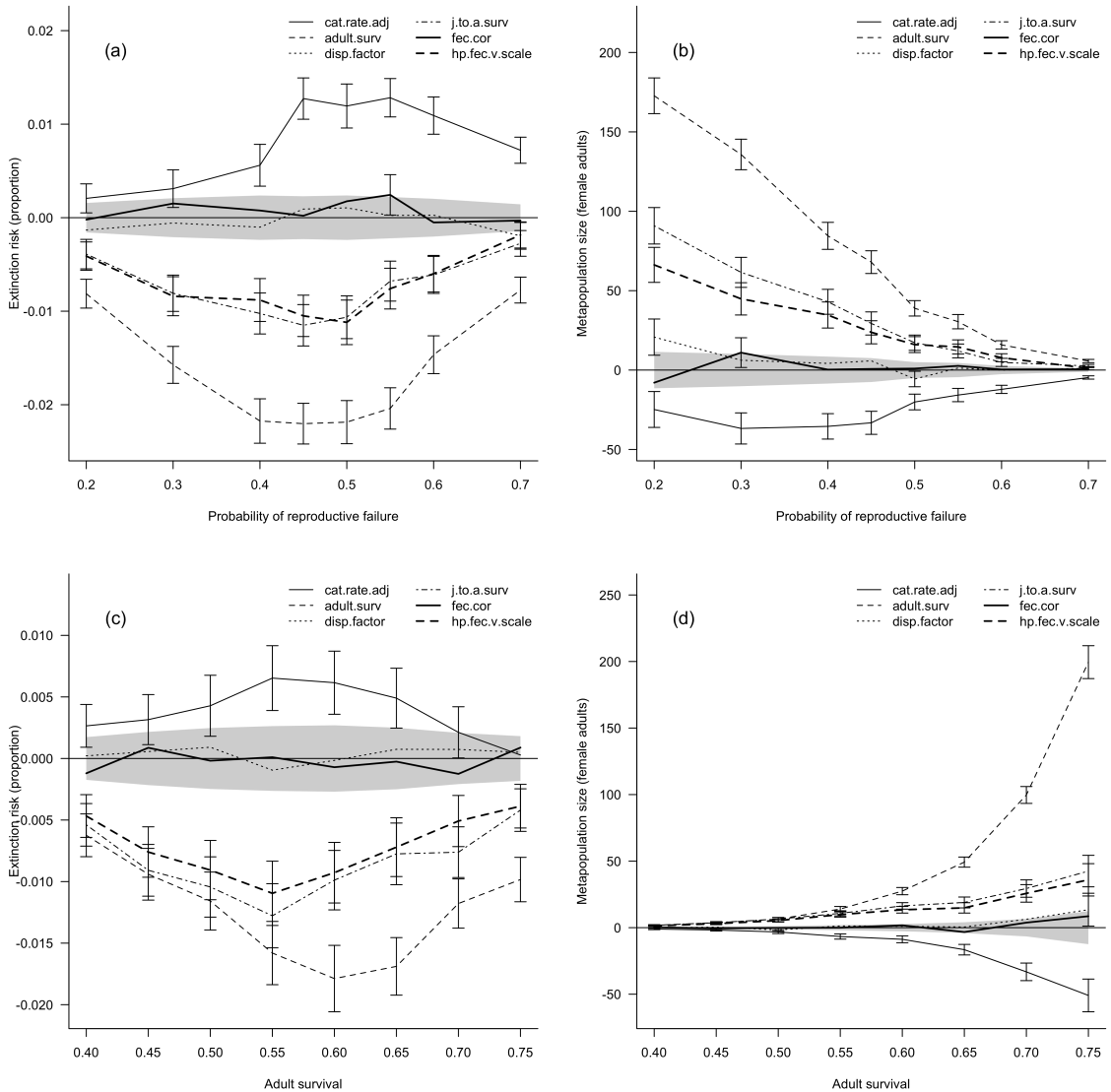


Figure 2.5. Error analysis shows that extinction risk (a and c) and metapopulation size (b and d) are most sensitive to adult survival (adult.surv) but roughly equally sensitive to the breeding failure rate (cat.rate.adj), fecundity (hp.fecundity.v.scale), and juvenile survival (j.to.a.surv). These trends hold true across a broad range of breeding failure rates (b and c) and for most adult survival rates (a and b). The y-axis represents the expected change in the response per percent change in each parameter. Error bars indicate 95 % confidence intervals and are not shown within the grey region that represents points whose confidence intervals span zero.

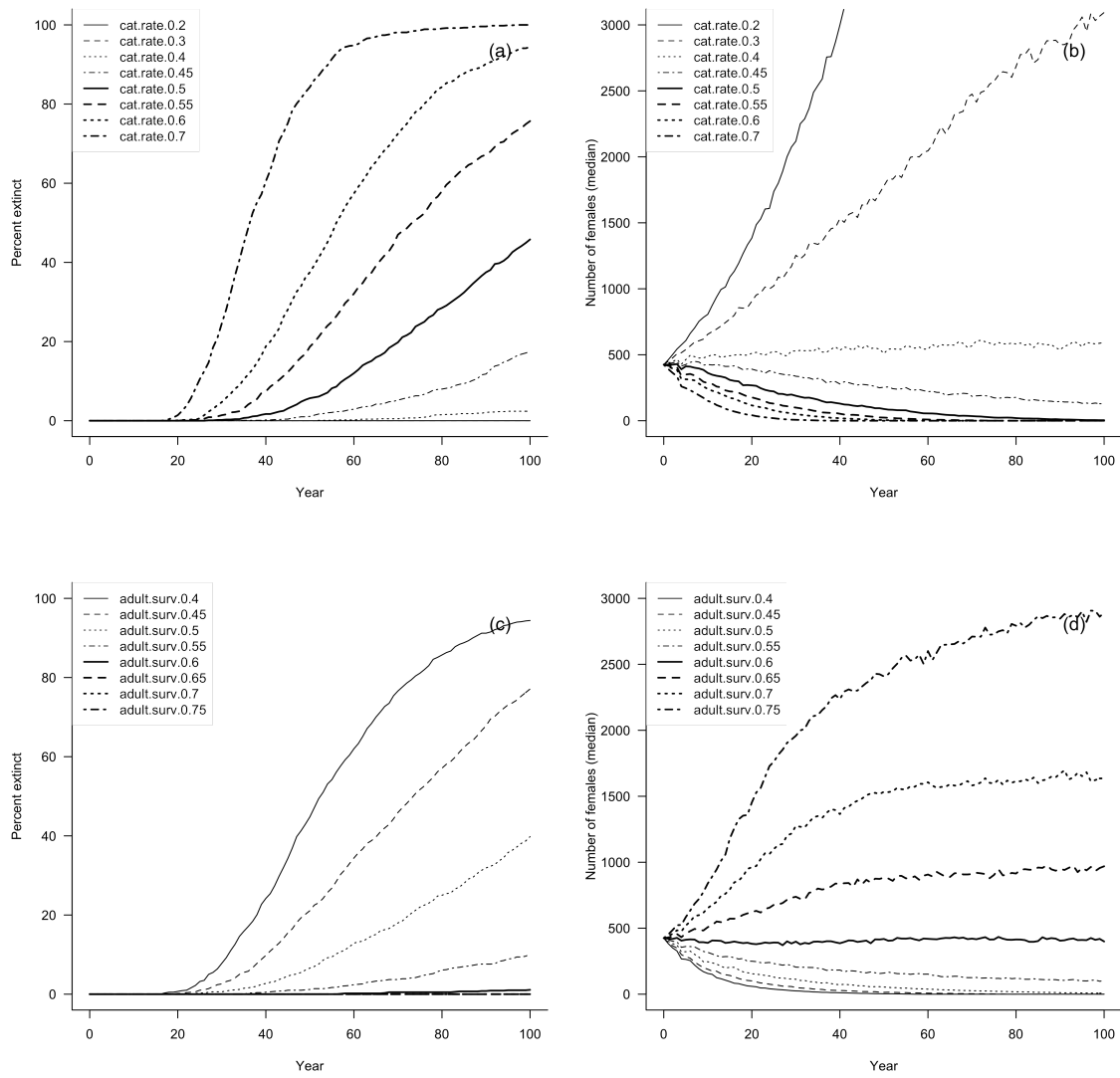


Figure 2.6. Modeled extinction risk (a and c) and mean metapopulation size (b and d) under varying breeding failure probabilities (a and b) and adult survival rates (c and d).

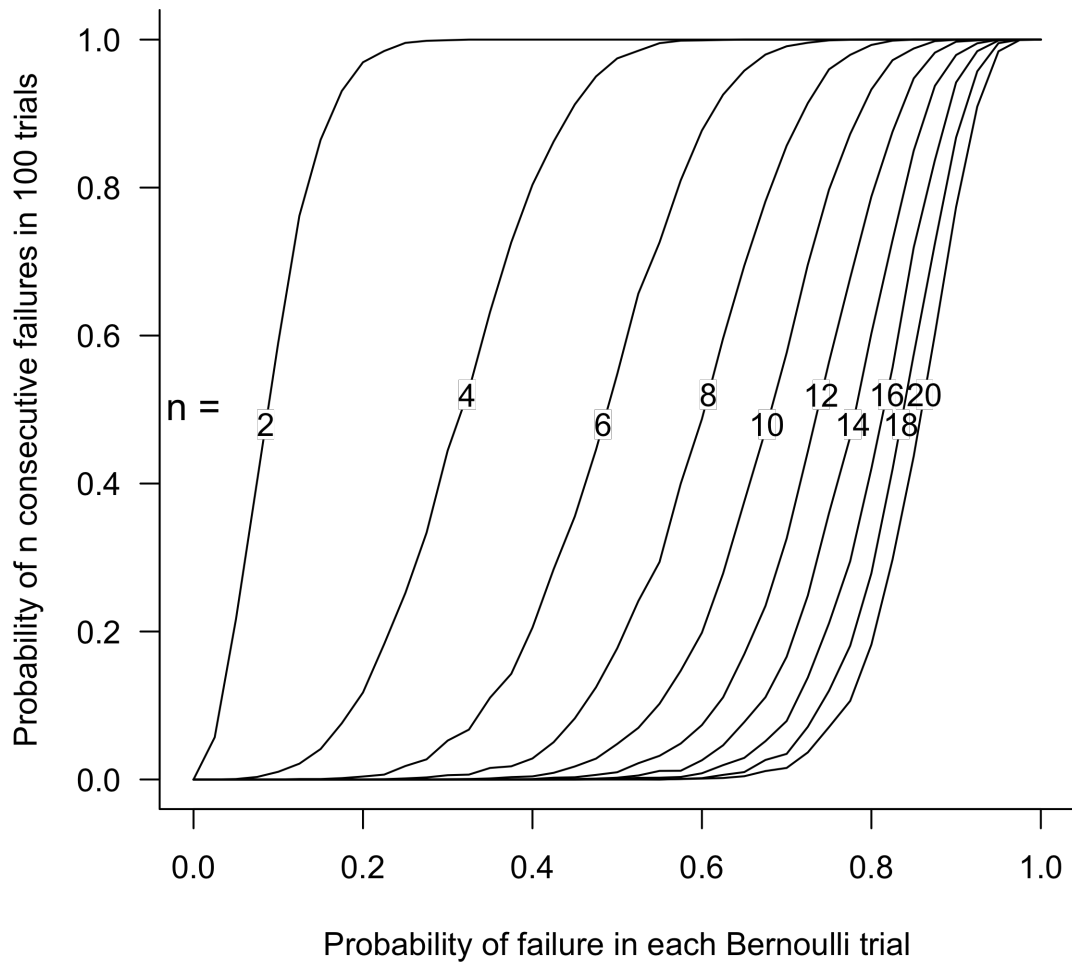


Figure 2.7. The relationship between the probability of failure, p , and the probability of n consecutive failures in 100 Bernoulli trials is a simplistic model for the relationship between breeding failure, adult survival, and extinction risk. For any given n , as the probability of failure p increases, the probability of n consecutive failures stays low until a threshold is reached, at which point it rapidly increases and then stays high. The probability of failure at which the threshold occurs and the sharpness of the threshold both increase as n increases.

CHAPTER 3

MODELED IMPACTS OF FORESTRY BUFFER SIZE AND RESTRICTION LEVEL ON A MARBLED SALAMANDER METAPOPOPULATION

3.1 Abstract

We present a model which integrates our understanding of population dynamics in marbled salamanders with a range of assumptions about the impacts of forestry to predict how a suite of different forestry practices encompassing a range of buffer radii and cutting restriction levels would impact extinction risk of marbled salamander population. We based vital rates in our model on eight years of demographic data from 14 ponds and tested the impacts of forestry under several parameterizations that reflect the range of impacts reported in the literature. We show that under most parameterizations buffers, of at least 200 m and restrictions of at least 80% (within the buffer) were necessary to keep extinction risk below 5%.

3.2 Introduction

Many amphibian species are at risk; worldwide, 43% of species are in decline and 7.4% are listed as critically endangered by the International Union for Conservation of Nature (Stuart et al. 2004). Ambystomatidae (mole salamanders) are under significantly more rapid decline than most amphibian families and the biggest cause of the decline is habitat loss (Stuart et al. 2004). Three of the four ambystomatid salamanders that occur in Massachusetts are listed on the Massachusetts List of Endangered, Threatened and Special Concern Species; *Ambystoma jeffersonianum* and *A. maculatum* are both listed as species of special concern while *A. opacum* is listed as threatened (M.G.L c.131A and

regulations 321 CMR 10.90). All of these pond-breeding amphibians breed in seasonal ponds where larvae develop, but spend most of their lives in nearby wooded uplands. The Massachusetts Forest Cutting Practices Act Regulations (304 CMR 11.00) restricts cutting to 50% of the trees within 15 m (50 ft) of a certified vernal pool. However, mole salamanders are known to reside much farther into the uplands (Semlitsch 1998; Gamble et al. 2006; McDonough & Paton 2007).

Many studies have found impacts of forestry on salamanders. Movement preferences towards mature forests from the breeding ponds has been repeatedly demonstrated in ambystomatid salamanders (Raymond & Hardy 1991; Rothermel & Semlitsch 2002; Semlitch et al. 2008; Patric et al. 2006); although one study failed to find preferences (Morris & Maret 2007), and one study found preference for juveniles but not adults (Patrick et al. 2008). Several studies have claimed reduced survival or fitness in ambystomatids in response to forestry (Raymond & Hardy 1991; Rothermel & Luhring 2005), while others have failed to find differences (Rothermel & Semlitsch 2006; Chazal & Niewiarowski 1998).

Both deMaynadier and Hunter (1995) and Semlitch et al. (2008) suggest that displacement or increased mortality would lead to reduced abundance in response to forestry. Consequently, there is extensive evidence of reduced densities of salamanders in response to forestry. deMaynadier and Hunter's (1995) review concluded that on average, the density of amphibians in forested plots was 3.5 greater than in clearcut plots. If just salamanders are considered, the density in controls plots was 4.3 times in forested plots; the review, however, did not include any studies of ambystomatid salamanders. Since that review, several studies have found differences in abundance in response to forestry in ambystomatid (deMaynadier & Hunter 1998; Perkins & Hunter 2006; Patrick

et al. 2006) and other salamander species (Grialou et al. 2000; Homyack & Haas 2009), while only one study that we are aware of found no differences (Morris & Maret 2007). Homyack and Haas (2009) attributed the difference in abundance to the impact of extraction (i.e., mortality caused by the logging activity).

Taken as a whole, the evidence suggests that both reduced survival in harvested stands and displacement into nearby undisturbed forest, if available, are likely to occur in response to forestry. We expect that even when animals are able to relocate out of harvested stands into nearby undisturbed forest that there are costs, either because the new habitat is of lower quality (Raymond & Hardy 1991) or simply because movement and searching for new habitat has costs (Rothermel 2004). There is indirect evidence for these costs: much of the mortality during the first two years after metamorphosis occurs in the first few months (Rothermel & Semlitsch 2006) and much of the adult mortality over a year occurs during the breeding season (Gamble 2009). Several studies have also shown greater forestry impacts on juvenile salamanders than adults (Patrick et al. 2006, Patrick et al. 2008). Finally, we should note that some researchers suggest that reduced abundances after forestry may be due to mortality caused by the timber extraction itself rather than reduced habitat quality of harvested forests (Grialou et al. 2000; Morris & Maret 2007; Homyack & Haas 2008).

Despite a surge in research on forestry impacts on amphibians in recent years, most studies have been at scales of a single pond or smaller; we know of no studies that have examined how salamander metapopulations respond to forestry. This is undoubtedly due to the coarse scales (both spatial and temporal) necessary to characterize metapopulations. Yet, because forestry is likely to affect migration between ponds at the

same time as it affects survival at local populations, it is important to understand how forestry impacts play out at scales larger than single ponds. Population viability modeling (Morris & Doak 2002) and matrix models (Caswell 2001) are useful tools for assessing how populations are likely to respond to different management strategies. In particular, they allow for a better understanding of how the amount and distribution of habitat influence population dynamics (Cushman 2006).

In this paper, we use a spatially-realistic population viability model to predict how a metapopulation responds to different intensities and spatial arrangements of forestry. Our goal was to determine what size of buffer and level of restriction within the buffer are necessary to maintain metapopulation persistence on the landscape and to determine which combinations of buffer and restriction produce the greatest reduction in extinction risk for the amount of timber yield sacrificed. To achieve these goals, we modeled three impacts of forestry on the metapopulation: (1) forestry in the upland habitat around a pond, which acts to reduce local survival, (2) forestry between ponds, which acts to reduce dispersal between ponds, and (3) forestry around ponds, which acts to increase the hydroperiod of the pond (by reducing evapotranspiration and increasing water yield), which in turn impacts the peak fecundity that can be achieved at that pond.

3.3 Methods

3.3.1 Study Area

Our study site contains a cluster of 14 seasonal ponds on the south side of the Holyoke Range in S. Hadley, Massachusetts USA (Fig 3.1) and has been the focus of an intensive long-term research project designed to monitor marbled salamanders at the

metapopulation level (Gamble et al. 2007; Gamble 2007; Gamble et al. 2009). In half the ponds we have observed consistent breeding effort over eight years while sporadic breeding efforts have been observed in most of the other ponds. The largest interpond distance is 1.4 km. We believe that these 14 ponds are largely isolated from other breeding sites; the Holyoke Range bounds them to the north and a heavily traveled road (Route 116) and dense residential development bounds the study area to the east and south (Fig. 3.1a). To the west, the nearest seasonal pond is approximately 800 m away and no Marbled Salamander breeding activity has been observed in two years of larval surveys at this pond (L. Gamble, unpubl. data). The site consists largely of contiguous mixed deciduous-hardwood forest, but is bisected by a powerline and a brook. The landscape we modeled was a 2200 by 1650 m (363 hectare) portion of the landscape with landuse classified at a 10 m resolution (Fig 3.1b).

3.3.2 Model Design

This model is a modification of the model presented in Chapter 2 with several additions and modifications that allow for modeling the effects of forestry on the metapopulation. It has a matrix and a spatial component. The matrix component consists of four stages for each of the 14 populations and is used to project the metapopulation forward one year at a time. It is populated with values that represent dispersal, survival, and fecundity within or between populations. The matrix is updated each timestep to reflect both deterministic and stochastic changes in parameters. The spatial component of the model summarizes the effect of land use on the population vital rates and thus affects the matrix.

The inputs to the spatial component are the location of all the potential breeding sites (seasonal ponds) and the land use throughout the study area. Land use consists of a broad cover classification and, in the case of forested cells, a designation of a treatment type. For each treatment type, we specified a trajectory of forest biomass over time under that treatment as a percentage of mature forest biomass. For each time step we extract from the spatial environment three sets of metrics which influence the matrix model for that time step: (1) dispersal rates, (2) upland habitat quality, and (3) delta hydroperiod. The following discussion focuses on these three metrics and how they affect the model, with special attention to how forestry influences them; see Chapter 2 for details on the rest of the model. Appendix B provides a complete description of model parameters.

3.3.2.1 Dispersal rates

We based dispersal rates on a Gaussian function of the length of the least cost path between ponds. For most landcover types, resistance was fixed. However, for forested cells it varied linearly with the amount of forest biomass from one (the lowest possible resistance) when biomass is that of an undisturbed forest to *max.forest.resistance* when forest biomass is zero (a clearcut).

3.3.2.2 Upland habitat quality

We estimated habitat quality around each pond by first assigning a habitat quality value to each cell in the landscape and then using a Gaussian kernel centered on the pond to calculate weighted mean of habitat quality at each pond. We used three functions to predict the impact of upland habitat quality on annual survival; they represent different abilities of salamanders to compensate for habitat degradation and loss by either moving

away from low-quality habitat areas or using additional habitat. In all three functions, survival was set at its nominal and highest value when the habitat quality was at its highest (one) and zero when the habitat quality was zero. We modeled low compensatory ability as a linear function, and moderate and high compensatory ability as monomolecular (Bolker 2008) functions (Fig 3.2): $y = a(1 - e^{-bx})$.

We added temporal variation to survival by sampling survival at each time step from a normal distribution with coefficient of variations specified by *cv.adult.surv* and *cv.j.to.a.surv* and a mean value set for each pond according to the habitat quality at that pond as outlined above. Adult and juvenile survival were sampled independently from each other but were both correlated across ponds (within years). Thus survival has both a deterministic, habitat-driven component and a stochastic component.

3.3.2.3 Delta hydroperiod

We modeled the relationship between hydroperiod and forest biomass by assigning a delta hydroperiod (DHP) value based on the change in forest biomass. DHP represents the number of days hydroperiod would increase if the pool was surrounded by forest of that (reduced) biomass instead of mature forest and varied linearly from *max.d.h.p* when there was no forest biomass (clear cut) to zero with full biomass (mature forest). The model calculated the DHP of each pool by averaging the DHP values of each cell within a circular catchment with a radius specified by *watershed.r*. At each time step, we determined the hydroperiod of each pond by adding the DHP to the base hydroperiod of the pond (a model input). The hydroperiod then influenced the peak fecundity that could be achieved at the pond, as explained in Chapter 2.

3.3.3 Model Parameterization

We set catchment size (*watershed.r*) to 100 m. Brooks (2005) reviewed basin morphology and hydrology of isolated wetlands and concluded that there was very little published data on catchment size. Driscoll and Parizek (2003) examined the hydrology of a series of 17 karst pools in Pennsylvania and found that they were perched above the water table, had catchments significantly smaller than the surface topography suggested, varied in catchment size as the water table rose and fell, and at its maximum extended 150 m from the ponds. Brooks (2005) also cited a study in Florida in which the authors found that ground water levels 81 m from an ephemeral cypress pond were uncorrelated with levels in the pond suggesting a catchment radius of less than 81 m.

We set the parameter *max.d.h.p*, which determines the maximum change in hydroperiod length (in days) that would be achieved if the entire catchment was converted from forest to clear-cut, to 17. The effect of forestry on water yield of streams is well documented. Bosch and Hewlett (1982) conducted a review of 94 experiments relating changes in vegetation type to changes in water yield and concluded that in general a 10% reduction in deciduous cover increased annual water yield by 25 mm. However, there is comparatively very little published on the effects of forestry on seasonal pond hydroperiod. Skelly et al. (1999) anecdotally reported that reforestation (over a 30-year time period) may have caused ponds to dry up to 2.5 weeks sooner (17 days). They do not state the change in forest cover necessary to achieve that shift, but do report that forest cover in their study landscape as a whole increased from 47% to 67% over the 30 years. It seems likely that the maximum shift they observed occurred at ponds

whose catchments went through a complete conversion from field to forest and we have parameterized the model accordingly.

We fixed $h.surv$, the bandwidth of the habitat quality kernel, to 124 m for all runs based on Compton et al's (2007) estimate of bandwidth from McDonough and Paton's (2007) data on radiotracked *A. maculatum*.

We assigned habitat quality values of zero to all non-forest landcover classes. Habitat quality of forest varied linearly in response to biomass. In all cases, the maximum habitat quality was one, and we modeled high, moderate, and low impacts of forestry by setting the minimum, zero-biomass habitat quality of adults to 0, 0.25, and 0.75. Thus, under the high impact scenario, habitat quality for adults decreased from 1 to 0 as forest biomass went from 1 (maximum) to 0 (clearcut) (Fig. 3.3). In each case, we set the minimum value of juveniles to half that of adults to simulate a greater susceptibility of juveniles to forestry.

We set adult survival equal to 0.62 based on Gamble et al.'s (2009) estimate for our study population. We calibrated juvenile survival to account for the effective boost in survival due to successful dispersers; based on a target juvenile survival of 0.11 (Chapter 1).

3.3.4 Forestry Scenarios

We simulated 20 different forestry scenarios involving a factorial combination of buffer zone widths around breeding ponds and intensity of harvesting within the buffers. Each scenario represented a different theoretical trajectory of forest biomass over time. To generate a trajectory, we used basal area as a proxy for biomass and calculated the percentage of peak basal area over time from the yield tables and management strategies

outlined by Hibbs and Bentley (1983) for a managed oak forest in southern New England (Fig 3.4a.) Each forestry scenario consisted of a stand regeneration clearcut followed by 30% thinning cuts at 60 and 80 years, at which point the stand was ready for harvest again. Hibbs and Bentley (1983) recommended this rotation because the clearcut promotes oak regeneration and yields a dense even-age stand that, during the first 60 years, promotes vertical growth and a long branchless bole. This is followed by the two thinning cuts to promote diameter growth. We simulated forestry scenarios in which this management strategy was applied to the matrix between ponds and less intensive management was conducted within buffers around the ponds (Fig 3.4b). We combined 30, 100, 200, and 300 m buffers (Fig 3.5) with 100, 80, 60, 40, and 20% restrictions on cutting to produce the 20 different forestry scenarios. The percent restricted designates the percentage of mature forest biomass that must be left standing on site; a 100% restriction represented no cutting and at 20% restriction allowed up to 80% of the biomass to be removed. We assumed that the cutting rotation within the matrix would drive the timing of cuts and that the restricted area (i.e., within the buffers) would simply be cut less during the harvest (Fig 3.3b).

We considered four model parameterizations by factorially combining high and low compensatory abilities (Fig 3.2) with high and low impacts of forestry on habitat quality (Fig. 3.3). We also produced a fifth parameterization that was intermediate with respect to both factors (i.e., moderate compensatory ability and medium forestry impact) and represented what we thought was a more likely parameterization. We simulated all 20 forestry scenarios (arrangements of buffers and restrictions) under each of these five model parameterizations for a total of 100 simulations and replicated each simulation

1000 times. For each scenario and parameterization we calculated the extinction risk (percent of runs resulting in metapopulation extinction) and median metapopulation size (median of mean population size during the last 10 years of each simulation).

3.3.5 Yield and Yield Optimization

We calculated the yield as the total biomass extracted from the entire study site in the 100 year forestry cycle. We then divided the yield in the 20 forestry scenarios by the yield when no restrictions were applied to forestry to calculate the percent of unrestricted yield associated with each scenario. We used four steps to plot how close each combination of buffer size and restriction was to the optimum. First we used local regression models (Cleveland et al. 1992) to smooth and interpolate the yield and extinction risk surfaces onto a grid of 200 by 200 cells. Second we set yield thresholds that spanned the entire range of the yields at 0.5, 0.25, and 0.075% increments when yield was high, moderate and low respectively (increments were adjusted so that number of cells in each inter-threshold range was roughly equal). Third, for each cell we determined the difference between the cell's extinction risk and the lowest extinction risk among all cells with similar yield (bounded by the same two thresholds). Fourth, we converted the difference to a greyscale with darker values indicating cells closer to the optimum (Fig 3.6).

3.3.6 Conditional Effects

To determine the relative importance of each of the three forest impacts on the metapopulation (impacts on upland habitat quality, landscape resistance, and pond hydroperiod) we calculated the conditional effect of each impact by running the model

with three additional parameterizations each of which excluded one of the three impacts. All three were based on the moderate compensatory ability and medium impact parameterization. For each of these three parameterizations we ran all 20 forestry scenarios 500 times each. To calculate the conditional effect of each of the three impacts of forestry we first calculated the mean response (extinction risk or metapopulation size) across all 20 forestry scenarios for each of the parameterizations. Second, we calculated the percentage of the mean response of the full model (all three mechanism present) achieved with each of the partial models (one response missing) to determine the conditional effect of each of the partial models.

3.4 Results

In all but the most optimistic parameterization, a combination of large buffers (200 – 250 m) and restrictions (80 to 100%) were necessary to keep the extinction risk below 5% (Fig. 3.6). The one exception was when we modeled a small effect of forestry on habitat quality and a large compensatory ability of salamanders (Fig. 3.6b), in which case there was little effect of forestry on extinction risk. As expected, increasing buffer size and restriction level both generally decreased extinction risk (Fig. 3.6), while timber yield decreased with increasing buffer radius and restriction level (Fig. 3.6f). The results for population size (not shown) were similar to extinction risk.

The optimal tradeoff between the size of the buffer and the level of restriction within the buffer depended on the impact of forestry on habitat quality, the compensatory ability of salamanders, and the amount of forestry (Fig 3.6). Consequently it is hard to make generalizations about the best tradeoff. However, in all parameterizations, if the buffer size exceeded 200 m, increases in restriction generally produced greater decreases

in extinction risk than comparable (in terms of yield sacrificed) increases in buffer size. Under most parameterizations (assumptions about impact and compensatory ability), there was an area of inefficiency when the restriction was high but the buffer size was small (Fig. 3.6, red shading); thus, if both the buffer size and restriction were small it was generally more efficient to increase buffer size than restriction. The low compensatory ability, high forest impact parameterization was the exception; under that scenario a high (100%) restriction was favored across the range of buffer sizes.

In the moderate parameterization the extinction risk averaged 46%. The conditional effects runs indicated that removing the impact of forestry on upland habitat quality reduced extinction risk by 99%; removing hydroperiod effects reduced extinction risk by 11% and eliminating the impact of forestry on landscape resistance decreased extinction risk by 2 %

3.5 Discussion

Our simulations demonstrate that forestry is likely to have a large, negative impact on salamander metapopulations. Salamanders may compensate for initial decreases in habitat quality around ponds by avoiding areas with lower habitat quality (Raymond & Hardy 1991; Rothermel & Semlitsch 2002; Patric et al. 2006; Semlitch et al. 2008). However as more habitat is eliminated or reduced in quality, the required movements would be further, the search times for good habitat could be longer, and the increasing concentration of animals in remaining habitat might lead to density dependent impacts. Thus, we expect a nonlinear relationship between habitat quality at the pond level and survival, but we do not know how far it should deviate from linear. However,

we believe that the compensatory abilities we modeled spanned the range of possibilities; the linear, low compensatory ability function represents no compensatory ability, while under the high compensatory ability initial decreases in habitat quality have almost no impact on survival.

When the effect of forestry on upland survival is dropped from the model, there is a 99% reduction in the effect of forestry on extinction risk. In contrast when hydroperiod or landscape resistance (dispersal) effects are dropped from the model, there are slight reductions in the mean extinction risk (by 11 and 2%, respectively). Thus it appears that most of the impact on forestry is due to the direct impact on survival. This is not surprising given that extinction risk in the model is more sensitive to changes in survival than to changes in hydroperiod or dispersal rate (Chapter 2). Although we modeled an impact of the changes in water yield on hydroperiod and thus peak fecundity realized at each pond, due to insufficient data we were unable to model the effect of altered water yield on catastrophe rates at each pond, which the model is more sensitive to than changes in hydroperiod (Chapter 2). Thus, it is possible that the hydrology mediated impact of forestry on the population is greater than we modeled.

3.5.1 Future Research.

To build better models we need to understand how individual salamanders respond to forestry. Modeling individual salamanders would allow for interplay between the spatial configuration of habitat, salamander behavior, and survival. Survival in such a model could reflect both the cost of moving through the environment and residing in different habitats. However, modeling individuals requires more data. That data could be produced by radio tracking animals leaving a pond in which the uplands have been

recently harvested. With sufficient animals such a study could examine mortality associated with moving through and residing in both harvested and mature forests as well as how forest state affects movement preference. McDonough and Paton (2007) used this approach to study *A. maculatum* in a landscape fragmented by a golf course and in addition to characterizing how far salamanders move from breeding ponds, they found that although spotted salamanders often crossed fairways the salamanders appeared to be subject to greater predation risk in a fragmented landscape than in a contiguously forested landscape.

3.5.2 Conservation Implications

Larger buffers are required to protect the uplands around seasonal ponds. In our study, we did not model any direct effects of forestry on pond basins (such as altered basin morphology) and it may be that the 15 – 30 m buffers protecting certified pools in Massachusetts from some impacts is sufficient to protect the basin itself. However, it is clear that a 30 m buffer is insufficient to protect upland habitat used by pond-breeding amphibians and our modeling shows that forestry with a 30 m buffer leads to large increases in extinction risk in all but the most optimistic parameterization we considered (Fig 3.6). We believe that conservation efforts should proactively target areas with known robust populations or clusters of ponds in minimally fragmented landscapes for protection. Within these protected areas, no forestry should take place within 250 m of ponds.

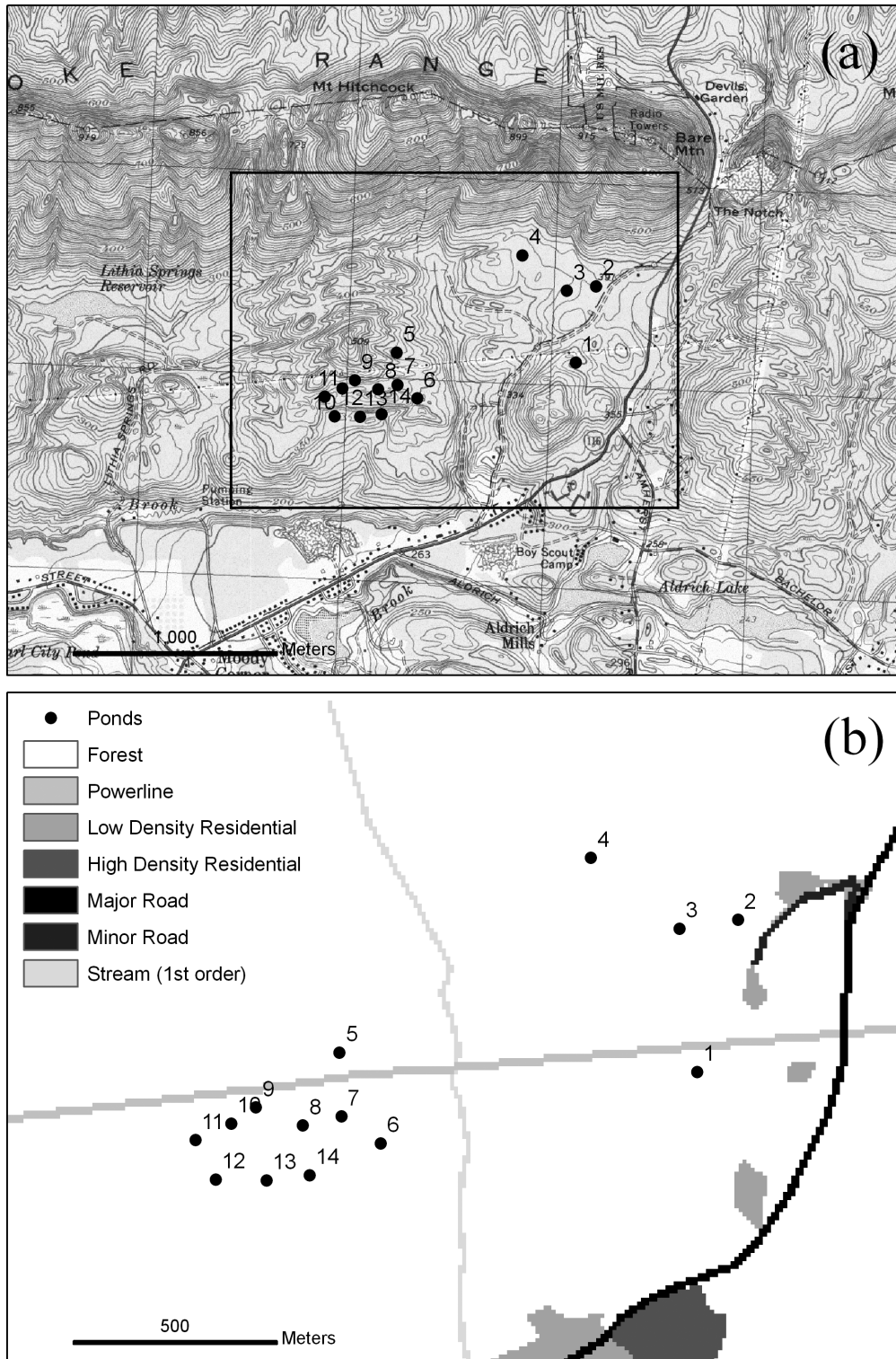


Figure 3.1. The study site, pond, numbers and locations, and land cover classification of the site (10 m resolution).

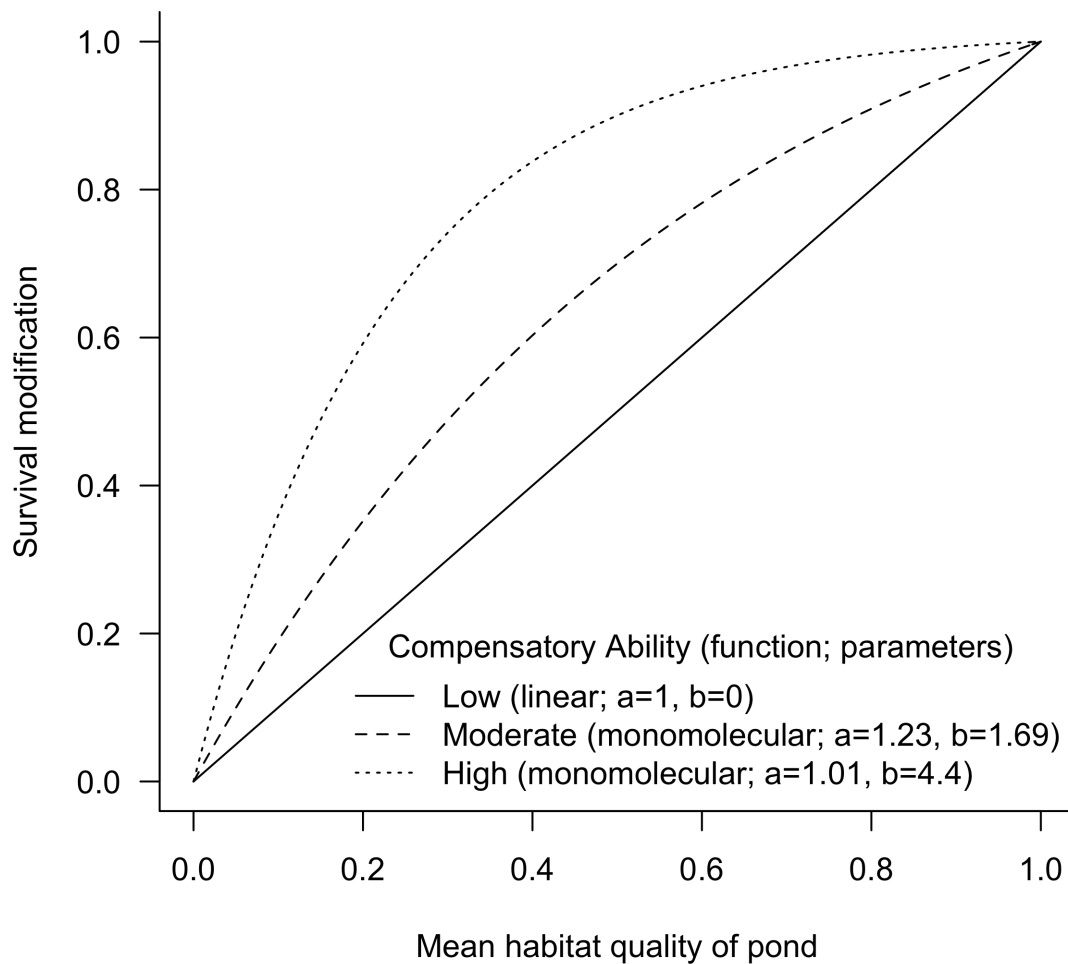


Figure 3.2. Modeled relationships between upland habitat quality around a breeding pond and the proportional modification of survival rate. We modeled three different relationships to represent low, moderate and high compensatory ability of salamanders. With low compensatory ability, there is a one-to-one relationship between habitat quality and survival. With a high compensatory ability, changes in habitat quality have little effect on survival when habitat quality is high and increasing effects as habitat quality approaches zero. Note, the y-axis represents the proportional reduction in the nominal survival rate.

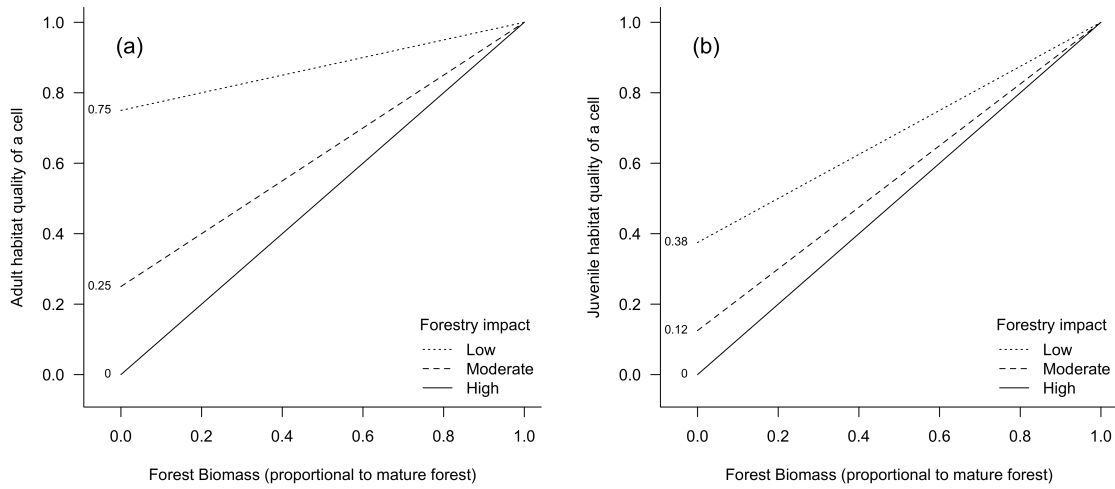


Figure 3.3. Three modeled relationships between forest biomass (expressed as a proportion of mature forest biomass) and the habitat quality of a 10 m cell in the landscape. The y-intercept corresponds to the habitat quality of a clearcut, which we made half as large for juveniles (b) than for adults (a).

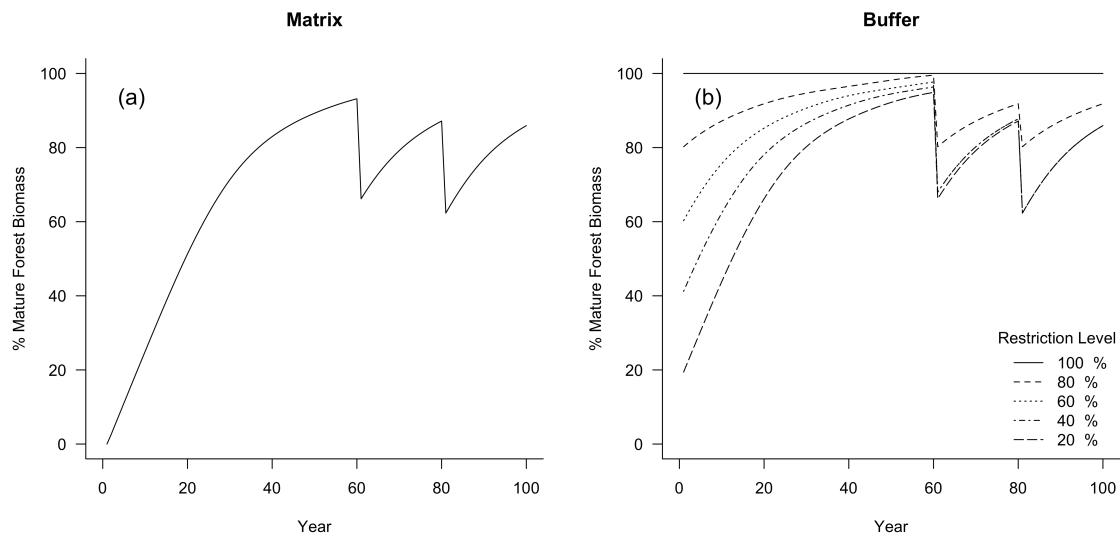


Figure 3.4. Simulated forest biomass trajectories under different forestry scenarios. We based the matrix biomass trajectory (a) on a 100-year rotation in which a stand regeneration clearcut at year 1 is followed by thinning cuts at 60 and 80 years which each remove 30% of the standing biomass. At year 101 (not shown) the stand is harvested again and reset to the condition at year 1. In the buffers (b), the restriction denotes the percentage of mature forest biomass that must be left standing. We assumed that cutting timing would be driven by the matrix so the timing of cuts is the same in the buffers and the matrix; the main difference is the intensity of the stand regeneration cut.

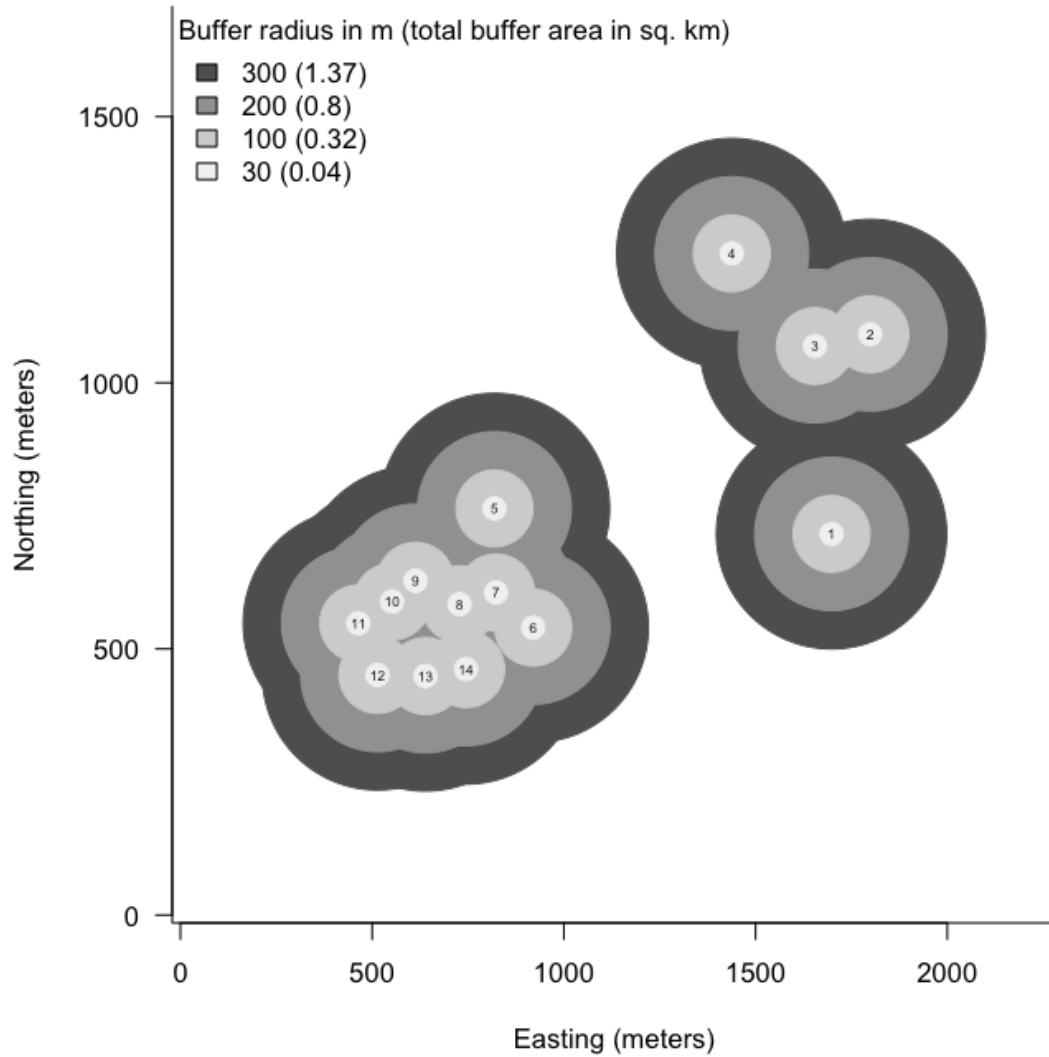
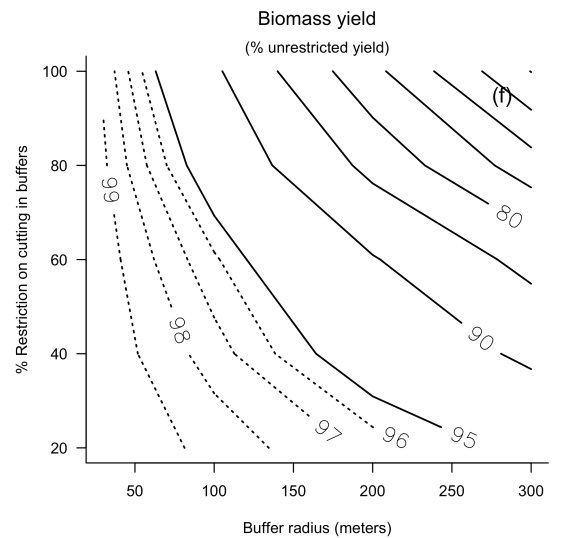
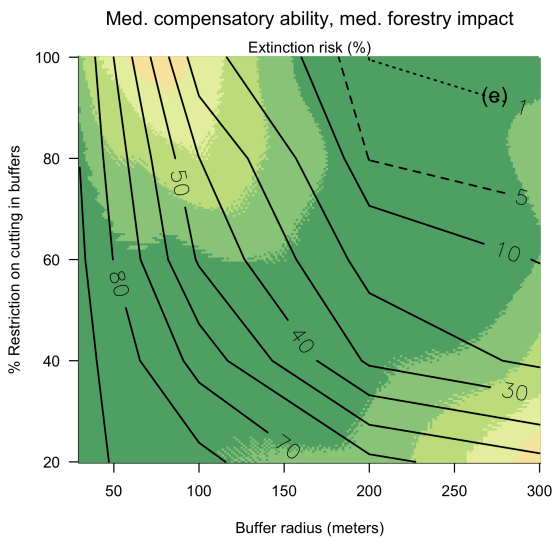
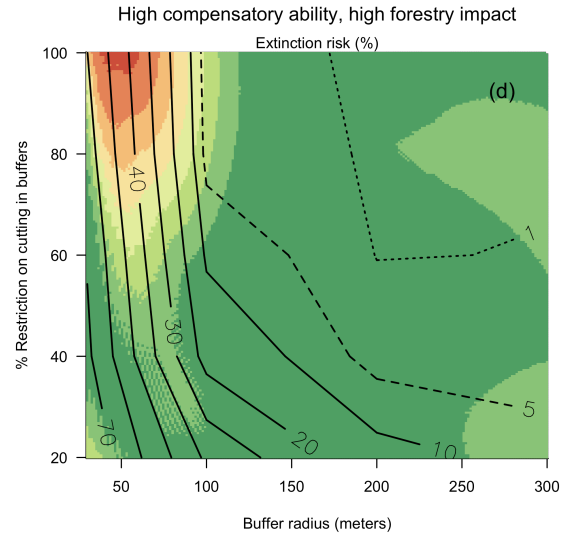
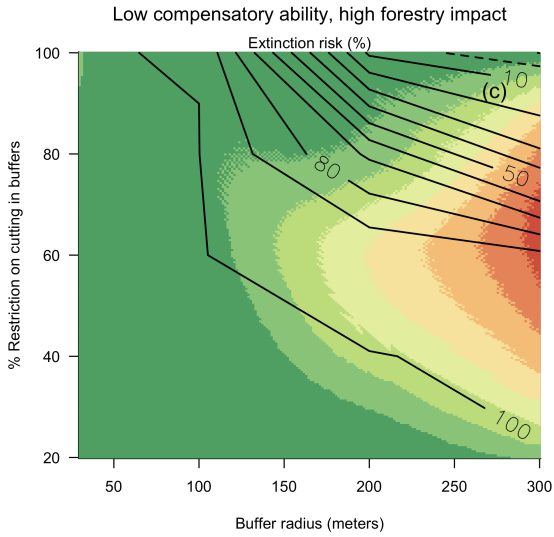
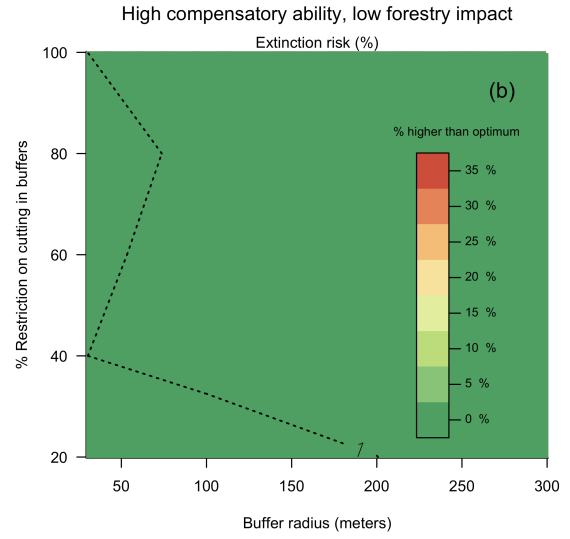
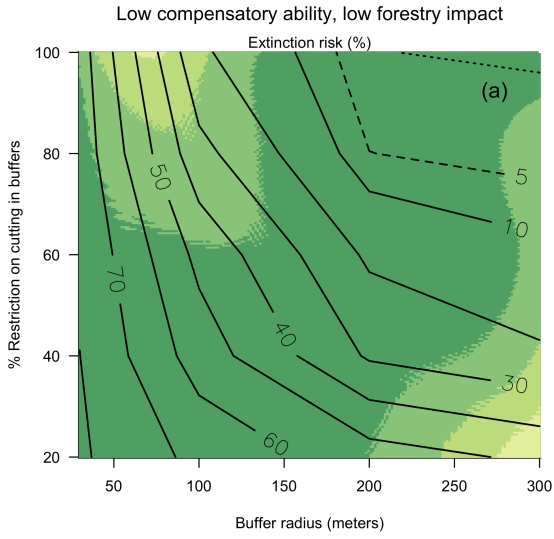


Figure 3.5. Spatial representation of the relationship between buffer radius (m) and the area encompassed by the buffers integrated across ponds. Note that increasing the buffer radius around ponds increases the area encompassed by the buffers, but due to overlap among the buffers, the increase is not as great as would be expected around a single pond.

Figure 3.6. Extinction risk contours under five model parameterizations (combinations of levels of salamander compensatory ability and levels of forestry effect on habitat quality) and 20 different forestry scenarios (30, 100, 200, 300 m buffers; 20, 40, 60, 80, 100 percent cutting restrictions within buffers). Shading represents the difference between the extinction risk of each cell and the lowest extinction risk among all cells with similar yield (the legend in b applies to a-e); green shading indicates cells closer to the optimum for the associated yield while yellow and red shading indicate inefficiencies. We also calculated biomass yield as a percentage of unrestricted yield (f) under each scenario based on the area that would be in each trajectory type given the configuration of pools and forest in our study.



APPENDIX A

ALL MODEL PARAMETERS RELEVANT TO CHAPTER 2, THEIR VALUES, AND A BREIF DESCRIPTION OF THEIR FUNCTION

Parameter	Value	Description
<i>adult.surv</i>	0.62	Survival of adults under habitat quality of 1 (Gamble 2009)
<i>allee</i>	1	The allee parameter. Fecundity is multiplied by $(N+allee)/N$ where N is the number of breeding adults.
<i>breeding.rate</i>	0.67	Percentage of females that breed each year (Gamble 2009)
<i>canopy.threshold</i>	100	Canopy cover (or biomass) value for mature forest.
<i>cat.cutoff</i>	1.2	The threshold below which a fecundity is considered a reproductive failure. In a reproductive failure fecundity is set to a low number that ranges between 0 and this parameter.
<i>cat.rate.adj</i>	1	Reproductive failure (catastrophe) probabilities are defined individually for each pond but are multiplied by this parameter before use. It was included to allow for error analysis.
<i>cell.size</i>	10	Cell size in meters (If there are input maps their cell size overrides this parameter)
<i>cv.adult.surv</i>	0.08	Adult survival in each time step is drawn from a normal distribution with this coefficient of variation. Calculated from data in Gamble (2009).
<i>cv.j.to.a.surv</i>	0.08	Juvenile (to adult) survival in each time step is drawn from a normal distribution with this coefficient of variation. (Assumed to be equal to adults)
<i>density.fun</i>	taylor.scott.1997	The name of the density depression function to use (Taylor & Scott 1997)
<i>disp.factor</i>	0.0029	Calibration parameter for dispersal. The height of the resistant kernel with a peak (center) of 1 is multiplied by this number to calculate dispersal rates.
<i>dp1</i>	1	Parameter passed to density functions (use depends on function) <i>taylor.scott.1997</i> only uses the first parameter which scales up and down the degree of depression.
<i>dp2</i>	0	Parameter passed to density functions (use depends on function)
<i>dp3</i>	0	Parameter passed to density functions (use depends on function)
<i>fec.cor</i>	0.64	Correlation in (scaled) fecundities among ponds
<i>forest.lc.code</i>	2	Landcover code of forest.
<i>h.disp</i>	440	Bandwidth (standard deviation) of the dispersal resistant kernel (Gamble et al. 2007)
<i>h.surv</i>	124	The bandwidth (SD) of the survival kernel (McDonough & Paton 2007; Compton et al. 2007).
<i>hab.based.surv</i>	FALSE	If TRUE the model adjusts survival based on the upland habitat quality around each pond. If FALSE survival is set by <i>adult.surv</i> and <i>j.to.a.surv</i> . (In both cases the cv parameters in survival still effect the variation in

Parameter	Value	Description
		survival).
<i>hp.fec.sd</i>	35	Standard deviation of the hydroperiod fecundity curve
<i>hp.fec.v.scale</i>	1891	Sets the height of the fecundity curve relative to a unit area Gaussian curve
<i>j.to.a.surv</i>	0.092	Juvenile survival when habitat quality is 1 (Chapter 1) See also Scott (1994), Pechmann (1995), and Rothermel and Semlitsch (2006).
<i>max.c.c.range</i>	500	Upper end of range used to represent canopy cover (biomass) values in matrix maps
<i>max.d.h.p</i>	17	Hydroperiod shift (in days) achieved by converting all of the watershed from 100 to 0 percent canopy cover (or biomass). (Bosch & Hewlett 1982; Skelly et al. 1999)
<i>max.forest.resistance</i>	3	Resistance of clearcut when there is 0 canopy cover (biomass)
<i>max.lc.range</i>	200	Upper end of the range assigned to landcover codes in maps
<i>max.scaled.fec</i>	1	Maximum value of the scaled fecundities. (This parameter is redundant as doubling it has the same effect as doubling <i>hp.fec.v.scale</i>).
<i>max.t.range</i>	300	Upper end of range used to represent forest management trajectories (in matrix maps)
<i>min.adult.forest.hq</i>	0.5	The habitat quality for adults of clearcut forest.
<i>min.c.c.range</i>	400	Lower end of range used to represent canopy cover values in maps
<i>min.juv.forest.hq</i>	0.25	The habitat quality for juveniles of clearcut forest.
<i>min.lc.range</i>	1	In matrix maps of the landscape this is the lower end of the range used to represent landcovers.
<i>min.t.range</i>	201	Lower end of range used to represent forest management canopy cover trajectories in matrix maps
<i>n.stages</i>	4	Number of stages in the transition matrix for each population.
<i>optimal.hp</i>	264	Hydroperiod at which fecundity is optimal
<i>pop.rounding</i>	floor.01	Type of rounding to be performed on the population structure between each time step. floor.01 means values between 0 and 1 are floored and all other values are left in decimal format.
<i>run.length</i>	100	Number of years to simulate.
<i>surv.hq.a</i>	1	The "a" parameter in the function used to relate habitat quality to survival
<i>surv.hq.b</i>	0	The "b" parameter in the function used to relate habitat quality to survival
<i>surv.hq.fun</i>	linear	The function used to relate habitat quality to survival (only relevant if <i>hab.based.surv</i> is TRUE)
<i>watershed.r</i>	100	The radius of the watershed around a pool in meters (used to determine Δhp). This is an educated guess but see Driscoll & Parizek (2003) and Brooks (2005)

APPENDIX B

ALL MODEL PARAMETERS RELEVANT TO CHAPTER 3, THEIR VALUES, AND A BREIF DESCRIPTION OF THEIR FUNCTION

Parameter	Value	Description
<i>adult.surv</i>	0.62	Survival of adults under habitat quality of 1 (Gamble, 2009)
<i>allee</i>	1	The Allee parameter (A). Fecundity is multiplied by (N+A)/N where N is the number of breeding adults.
<i>breeding.rate</i>	0.67	Percentage of females that breed each year (Gamble, 2009)
<i>canopy.threshold</i>	100	Canopy cover (or biomass) value of mature forest.
<i>cat.cutoff</i>	1.2	The threshold below which a fecundity is considered a breeding failure. Given a breeding failures fecundity is set to a low number that ranges between 0 and this cutoff.
<i>cat.hp.i</i>	9.31	The intercept term of the quadratic function that defines the relationship between hydroperiod and catastrophe rate. Only used when pond specific catastrophe rates are not input as part of the pond arrangement.
<i>cat.hp.res.sd</i>	0.2	Standard deviation in the noise added to the catastrophe rate as determined by the quadratic function.
<i>cat.hp.x</i>	-0.06575	The linear term of the quadratic function that defines the relationship between hydroperiod and catastrophe rate.
<i>cat.hp.x2</i>	0.00012337	Quadratic term of the function that defines the relationship between hydroperiod and catastrophe rate.
<i>cat.rate.adj</i>	1	Included solely to allow for error analysis. Cat rates can be produced in several ways but they are always multiplied by this parameter.
<i>cell.size</i>	10	Cell size in meters. Only relevant if no input maps are specified.
<i>cv.adult.surv</i>	0.08	Adult survival in each time step is drawn from a normal distribution with this coefficient of variation. Calculated from data in Gamble (2009).
<i>cv.j.to.a.surv</i>	0.08	Juvenile (to adult) survival in each time step is drawn from a normal distribution with this coefficient of variation. (Assumed to be equal to adults)
<i>density.fun</i>	taylor.scott.1997	The name of the density depression function to use.
<i>disp.factor</i>	0.0029	Calibration parameter for dispersal. The height of the resistant kernel with a peak (center) of 1 is multiplied by this number to get dispersal rates.
<i>dp1</i>	1	Parameter passed to density functions (use depends on function) taylor.scott.1997 only uses the first parameter which scales up and down the degree of depression.
<i>dp2</i>	0	Parameter passed to density functions (use depends on function)
<i>dp3</i>	0	Parameter passed to density functions (use depends on function)
<i>fec.cor</i>	0.64	Correlation in (scaled) fecundities among ponds
<i>forest.lc.code</i>	2	Landcover code of forest.
<i>h.disp</i>	440	Bandwidth (standard deviation) of the dispersal resistant kernel (Gamble et al. 2007)
<i>h.surv</i>	124	The bandwidth (sd) of the survival kernel (McDonough & Paton 2007; Compton et al. 2007)

Parameter	Value	Description
<i>hab.based.surv</i>	TRUE	If TRUE the model adjusts survival based on the upland habitat quality around each pond. If FALSE survival is set by <i>adult.surv</i> and <i>j.to.a.surv</i> . (In both cases the CV parameters in survival still effect the variation in survival).
<i>hp.fec.sd</i>	35	Standard deviation of the hydroperiod fecundity curve
<i>hp.fec.v.scale</i>	1891	Sets the height of the fecundity curve relative to a unit area Gaussian curve
<i>j.to.a.surv</i>	0.092	Juvenile survival when habitat quality is 1 (Chapter 1) See also Scott (1994), Pechmann (1995), and Rothermel and Semlitsch (2006).
<i>max.c.c.range</i>	500	Upper end of range used to represent canopy cover (biomass) values in matrix maps
<i>max.d.hp</i>	17	Hydroperiod shift (in days) achieved by converting all of the watershed from 100 to 0 percent canopy cover (or biomass). (Bosch & Hewlett 1982; Skelly et al. 1999)
<i>max.forest.resistance</i>	3	Resistance of clearcut when there is 0 canopy cover (biomass)
<i>max.lc.range</i>	200	Upper end of the range assigned to landcover codes in matrix maps
<i>max.scaled.fec</i>	1	Maximum value of the scaled fecundities. (This parameter is redundant as doubling it has the same effect as doubling <i>hp.fec.v.scale</i>).
<i>max.t.range</i>	300	Upper end of range used to represent forest management trajectories (in matrix maps)
<i>min.adult.forest.hq</i>	0.75, 0.25, 0	The habitat quality for adults of cleacut forest. (Values for low, medium, and high forestry impact on habitat quality)
<i>min.c.c.range</i>	400	Lower end of range used to represent canopy cover values in maps
<i>min.juv.forest.hq</i>	0.375, 0.125, 0	The habitat quality for juveniles of cleacut forest. (Values for low, medium, and high forestry impact on habitat quality)
<i>min.lc.range</i>	1	In matrix maps of the landscape this is the lower end of the range used to represent landcovers.
<i>min.t.range</i>	201	Lower end of range used to represent forest management canopy cover trajectories in matrix maps
<i>n.stages</i>	4	Number of stages in transition matrix for each (sub)population.
<i>optimal.hp</i>	264	Hydroperiod at which fecundity is optimal
<i>pop.rounding</i>	floor.01	Type of rounding to be performed on the population structure between each time step.
<i>run.length</i>	100	Number of years to simulate.
<i>surv.hq.a</i>	1, 1.23, 1.101	The "a" parameter in the function used to relate habitat quality to survival (Values for Low, Mod., and High Compensatory abilities.)
<i>surv.hq.b</i>	0, 1.23, 4.4	The "b" parameter in the function used to relate habitat quality to survival (Values for Low, Mod., and High Compensatory abilities.)
<i>surv.hq.fun</i>	linear, monomolecular, monomolecular	The function used to relate habitat qualit to survival (only relevant if <i>hab.based.surv</i> is TRUE)
<i>watershed.r</i>	100	(Values for Low, Mod., and High Compensatory abilities.) The radius of the watershed around a pool in meters (used to determine delta hp). This is an educated guess but see Driscoll & Parizek (2003) and Brooks (2005)

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