

ASSESSING THE POTENTIAL IMPACTS OF ALTERNATIVE
LANDSCAPE DESIGNS ON AMPHIBIAN
POPULATION DYNAMICS

By

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Assessing the Potential Impacts of Alternative Landscape Designs on Amphibian Population Dynamics

Abstract: I present a unique modeling approach to investigate the potential impacts of future land use alternatives on amphibian population dynamics in two agricultural watersheds in central Iowa. An individual-based spatially explicit population was used to predict the consequences of alternative landscape design and management for populations of four amphibian species. The model includes both breeding and upland habitat and incorporates the effects of prairie wetland hydroperiod and demographic stochasticity. Data requirements of the model included species' life history characteristics, dispersal behavior, and habitat affinities, and GIS maps of the landscapes. The future scenarios were ranked according to change in intrinsic rate of increase, and breeder abundance, saturation and distribution compared to baseline conditions. The sensitivity of results to changes in model parameters was also examined. Results of the simulations suggest the four species modeled will persist under present and future scenario conditions, assuming parameter estimates are correct. While the study species are all widespread generalists regarded as having a low conservation priority, they are dependent on wetlands and ponds, increasingly endangered habitats in agricultural landscapes. Broader conservation strategies in the region would ensure that these currently common organisms do not become the endangered species of the future.

Introduction

Amphibian population dynamics have been the subject of increased scrutiny in recent years in response to apparent widespread and often inexplicable declines, range reductions, and extinctions (Blaustein and Wake 1990; Wake 1991; Richards et al. 1993; Pounds and Crump 1994; Fisher and Shaffer 1996). Several potential causal mechanisms have been suggested, including increased UV-radiation, exotic predator introductions, disease, chemical contamination of habitats, habitat loss and fragmentation, and natural population fluctuations, as well as combinations of these factors (Moyle 1973; Pechmann

et al. 1991; Blaustein et al. 1994a; Blaustein et al. 1996; Laurance et al. 1996; Oldham et al. 1997; Lehtinen et al. 1999). Amphibians are considered to be integral components of many ecosystems and have been shown to constitute the most abundant group of vertebrates in both numbers and biomass in some forest ecosystems (Petranka et al. 1993; Blaustein et al. 1994b). Amphibians are known to occupy important positions in food webs, being important carnivores in some systems and prey species in others (Petranka et al. 1993; Blaustein et al. 1994b). The recent declines in amphibian populations are thought to be warning signals indicating that other organisms may also be facing imminent decline or extinction (Blaustein et al. 1995).

Agricultural practices, such as tilling and cropping, forest harvest, wetland draining, non-native species introductions, and agrichemical use have contributed to the loss of vertebrate biodiversity in agricultural regions (Erlich 1988; Risser 1988; Herkert 1991; Soule 1991; Freemark 1995; McNeely et al. 1995). More than 90% of Iowa's pre-European settlement landscape has been converted to agricultural and urban use (Farrar 1981). As a result, much of Iowa's original suitable amphibian habitat has been transformed from forest, prairie, pool, and marsh into farmland (Christiansen 1981). Over 95% of Iowa's natural wetlands have been drained, more than 98% of Iowa's pre-settlement prairie has been lost, and forest cover has decreased from 19% at the time of European settlement to 4% at present (Bishop 1981; Smith 1981; Thomson and Hertel 1981). Of the 23 amphibian species known to occur in Iowa, 12 (52%) are considered to be declining, threatened, or endangered within the state (Christiansen 1981). Christiansen (1981) forecasted that without a reversal in present trends, less than one third of Iowa's present amphibian and reptile fauna would remain in the next 50-100 years.

In response to serious concern about ecological and environmental degradation from modern agriculture, a collaborative study between Oregon State University, Iowa State University, and the University of Minnesota, funded by the U.S. Environmental Protection Agency was begun in 1997. This project aimed to develop an integrated, multidisciplinary approach linking: water quality, biodiversity, and socioeconomic considerations to predict the effects of land use decisions in central Iowa. Several modeling approaches were used to evaluate three future landscapes resulting from different land management scenarios (Santelmann et al. in preparation). As part of this collaborative effort, this study investigates the effects of the land use changes envisioned in these future scenarios on amphibian population dynamics.

Future scenario studies are being used in landscape ecology to explore potential ecological impacts of land management alternatives (Harms et al. 1993; Freemark et al. 1996; White et al. 1997; Ahern 1999; White et al. 1999). Harms et al. (1993), Freemark et al. (1996), White et al. (1997), and Santelmann et al. (in preparation) estimated potential risk to vertebrate biodiversity in future landscape scenarios in The Netherlands, a western Oregon watershed, Monroe County, Pennsylvania, and central Iowa watersheds respectively, by measuring possible changes in species richness and habitat abundance. While the approach of these studies proved useful in the discrimination of the effects of potential changes in land use on biodiversity, several important ecological factors were not incorporated, including differences in habitat quality and configuration, chance demographic events, and climatic variation (Freemark et al. 1996; White et al. 1999). Freemark et al. (1996) and White et al. (1997 and 1999) recommend improving the

assessment of risk by augmenting their approach with population viability analysis (PVA).

Spatially explicit population models (SEPMs), a type of demographic model used in PVA, are valuable tools in the evaluation of alternative land use and management scenarios (Turner et al. 1995; Lindenmayer and Possingham 1996; Beissinger and Westphal 1998). SEPMs differ from other landscape and demographic models by incorporating the movement of organisms among specific patches across the landscape (Dunning et al. 1995). These models synthesize animal demographic and dispersal information with the spatial distribution of habitat patches to predict changes in population size over time (Gibbs 1993). SEPMs incorporate both species-habitat relationships and the arrangement of the habitats in space and can therefore be used to investigate the effects of fragmentation, isolation, patch shape, and patch size (Turner et al. 1995).

SEPMs have been applied to spotted owls (McKelvey et al. 1992; Lamberson et al. 1994), Bachman's sparrow (Pulliam et al. 1992; Liu et al. 1995), possum (Lindenmayer and Possingham 1996), and butterflies (Fahrig and Paloheimo 1988; Hanski and Thomas 1994). Few attempts have been made to apply SEPMs to amphibians. Halley et al. (1996) used a stochastic population model to predict the necessary conditions for the persistence of two amphibian species in agricultural regions of Britain. The model generated extinction probabilities as a function of average pond carrying capacity and distance from a source pond. Space was not explicitly included in this model, but implied through the inclusion of an immigration term (Halley et al. 1996). Gibbs (1993) used a spatially structured metapopulation model to evaluate the effect of

loss of small wetlands on the extinction risk of metapopulations of frogs, salamanders and newts, and other wetland-associated animals in Maine. This study used artificial landscapes consisting of mosaics of large and small circular wetlands. No change in amphibian metapopulation extinction risk was found, possibly due to high rates of population increase and high population densities (Gibbs 1993).

Wetland-breeding amphibian species are challenging to model for several reasons. The paucity of life history and dispersal data for most amphibian species makes adequate model parameterization difficult (Doak and Mills 1994; Halley et al. 1996). These animals require both aquatic and terrestrial habitats and often are limited to areas where there is sufficient moisture for reproduction and survival (Blaustein et al. 1994b). Eggs are laid in water and larvae remain in water until metamorphosis. After metamorphosis, juveniles disperse from the breeding pond to terrestrial habitat. While the distribution of breeding sites is thought to be a major limiting factor in amphibian populations, the availability of adjacent terrestrial habitats in agricultural landscapes might be equally or more important (Jameson 1957; Wilbur 1987; John-Alder and Morrin 1990; Vos and Stumpel 1995). For these reasons, models of wetland breeding amphibian population dynamics should consider two largely independent habitats, aquatic and terrestrial (Doak and Mills 1994; Vos and Stumpel 1995; Halley et al. 1996).

To ensure the persistence of amphibian populations in the Midwest, a reliable method is needed predict the effects of landscape change in agricultural regions. This study applies a SEPM to assess the potential impacts of future land use scenarios on amphibian population dynamics in two agricultural watersheds in central Iowa. The goals of this paper are to quantify the consequences of alternative landscape design and

management for populations of four amphibian species, predict the necessary conditions for the persistence of populations of these species, and determine which, if any, parameter estimates have disproportionate impacts on the results.

Methods

Study Site and Future Scenarios

The Walnut Creek and Buck Creek watersheds are located in the Western Corn Belt Plains Ecoregion of the Midwestern US (Figure 1). Walnut Creek watershed is 5100 ha in area and located in Boone and Story Counties, in the Des Moines Lobe physiographic region of Iowa (Figures 2 and 3). Buck Creek watershed is 8790 ha in area and located in Poweshiek County, in the Southern Iowa Drift Plain physiographic region of Iowa (Figures 2 and 3).

Three prospective future scenarios each for Walnut and Buck Creek watersheds designed by Nassauer and Corry (in preparation) were used in this study. The scenarios were designed to portray land cover patterns in the year 2025 that might result from alternative policy choices. Scenario 1 is based on the assumption that profitable agricultural production is the dominant objective of landscape management (Figures 4a and 5a). In this scenario, woodlands have nearly disappeared as more land is converted to cultivation, riparian areas have narrow (3-6 m) grass buffers, corn and soybeans are grown with limited crop rotations, and there is little pasture or alfalfa (Nassauer et al. 1999; Nassauer and Corry in preparation).

Scenario 2 assumes that land cover patterns have evolved in response to federal policy that has enforced water quality performance standards (Figures 4b and 5b). In this

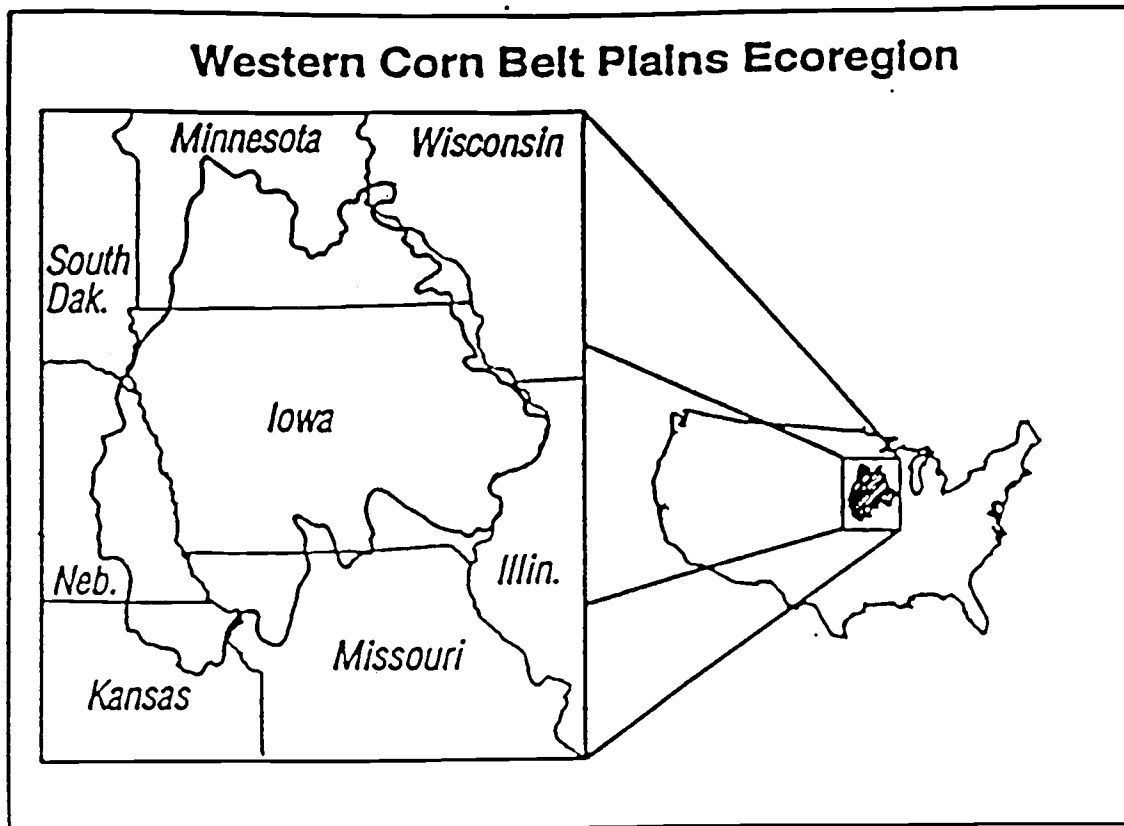


Figure 1. Location and outline of the Western Corn Belt Plains Ecoregion in the midwestern U.S. (from Prior 1991).

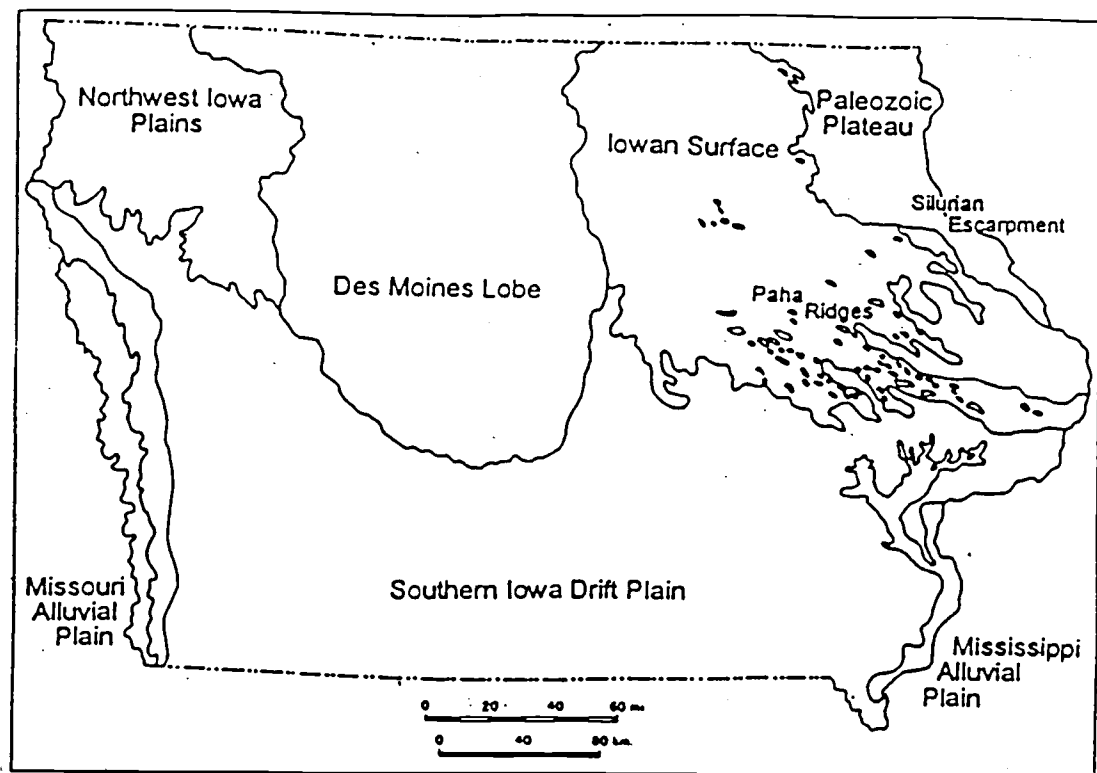


Figure 2. Depiction of the major landform regions of Iowa (from Prior 1991).

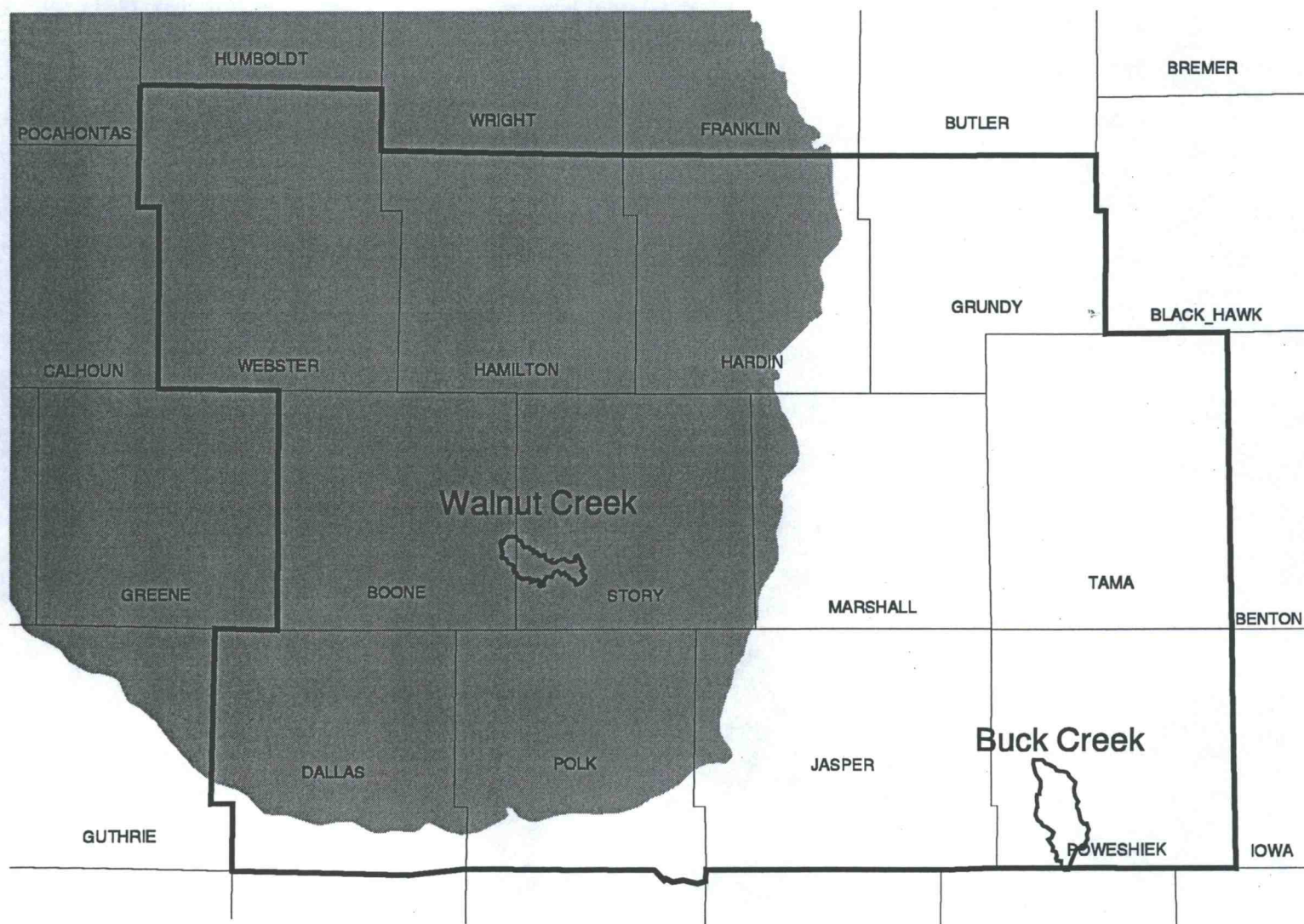
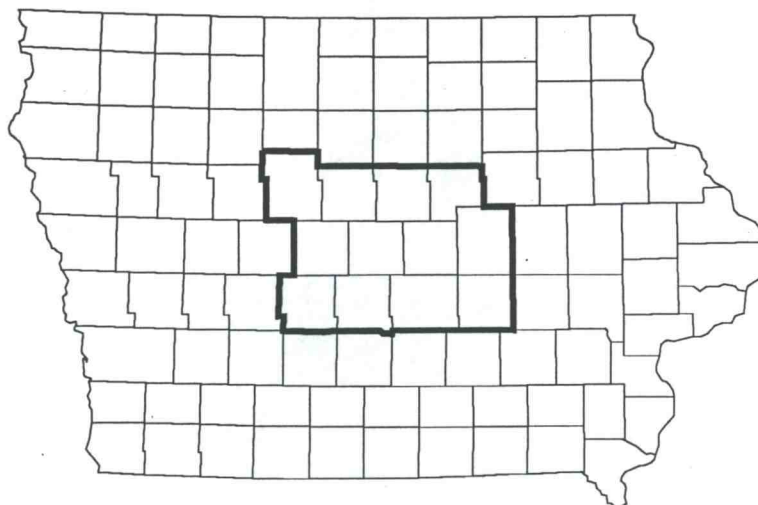
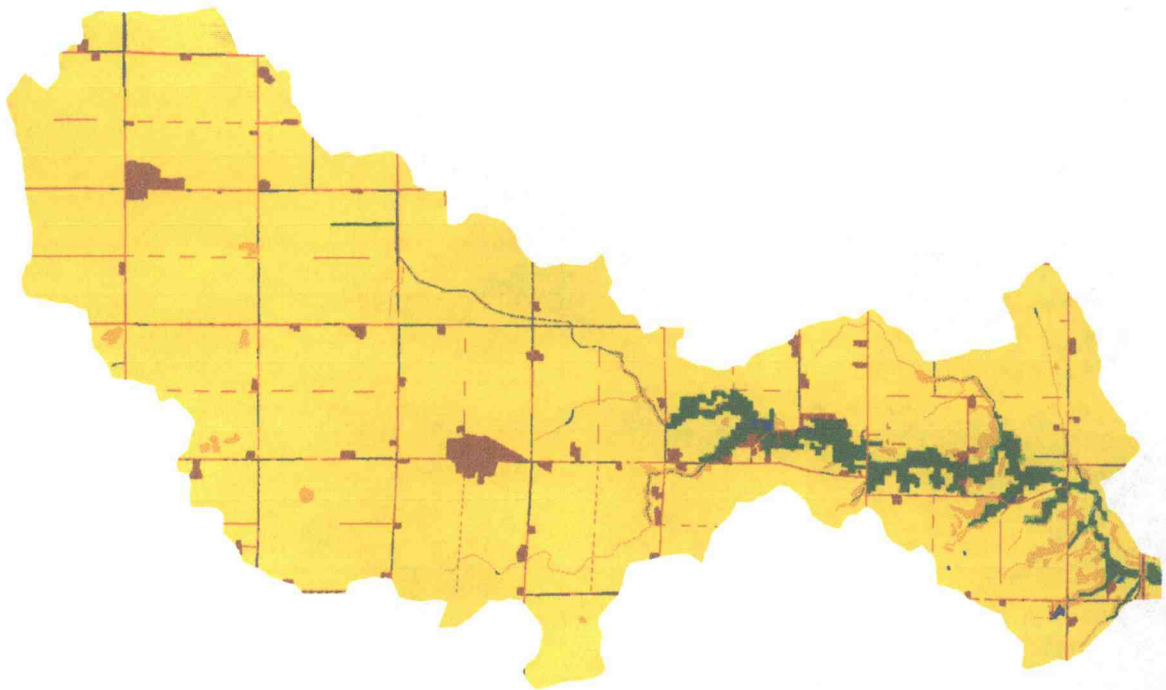


Figure 3. Location of Buck and Walnut Creek Watersheds in central Iowa.

a.)



b.)

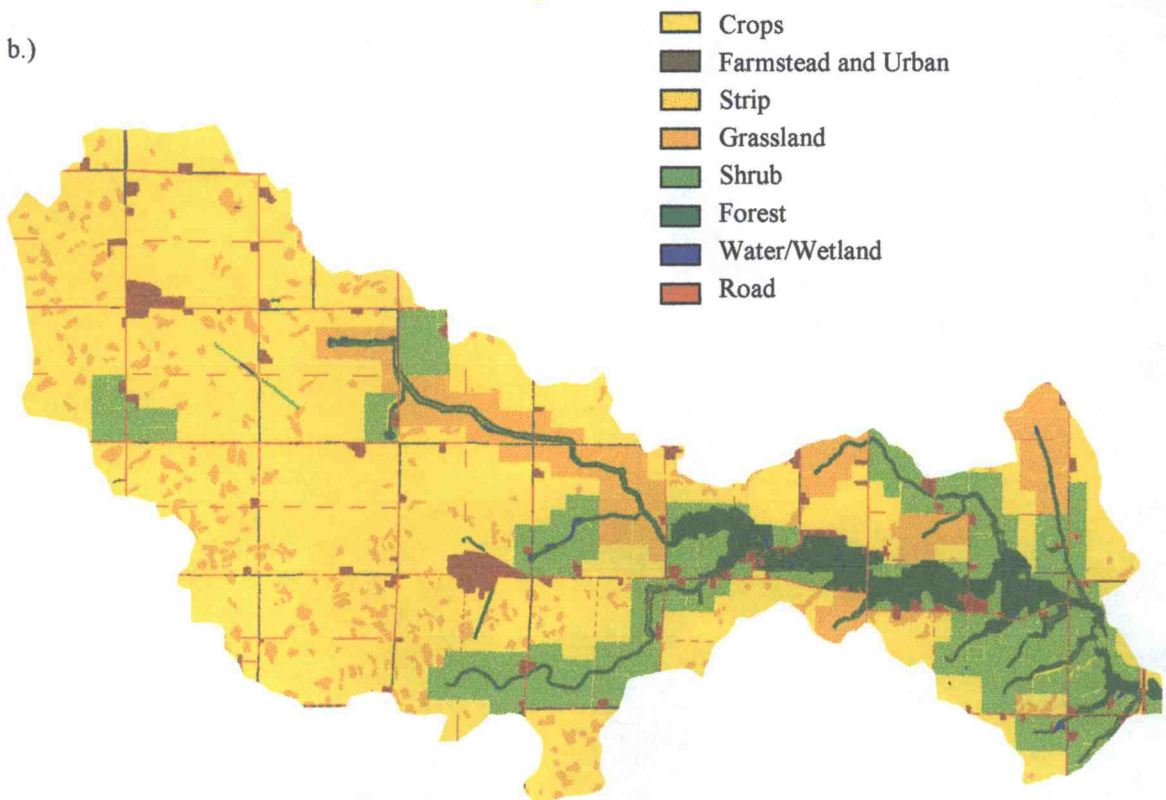


Figure 4. Walnut Creek watershed Scenario 1 (a), and Scenario 2 (b).

a.)

b.)

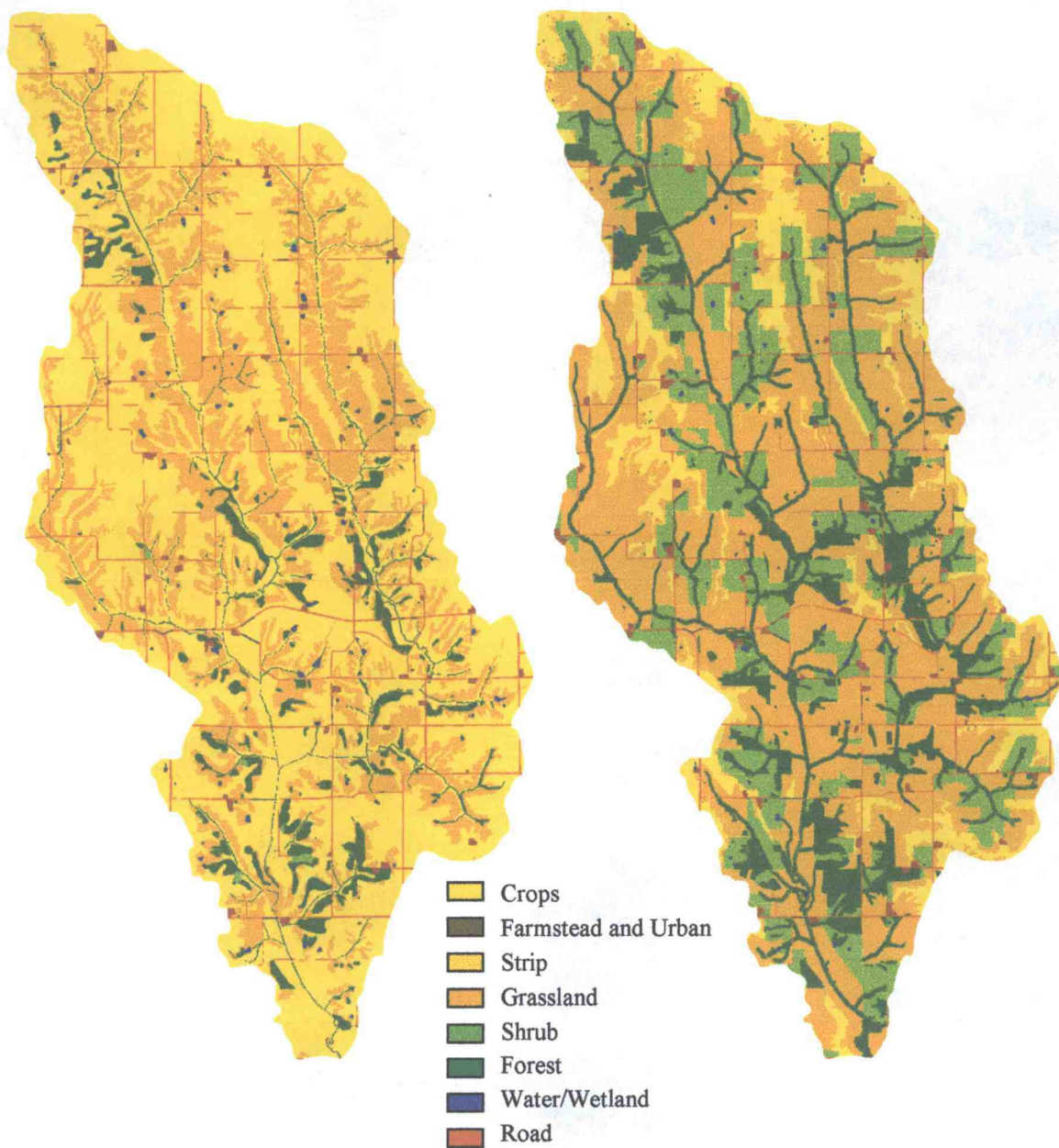


Figure 5. Buck Creek watershed Scenario 1 (a), and Scenario 2 (b).

scenario, woodlands have been maintained and are used for livestock grazing, riparian buffers have been widened (15 to 60 m), and alfalfa crop rotations have been adopted (Nassauer et al. 1999; Nassauer and Corry in preparation).

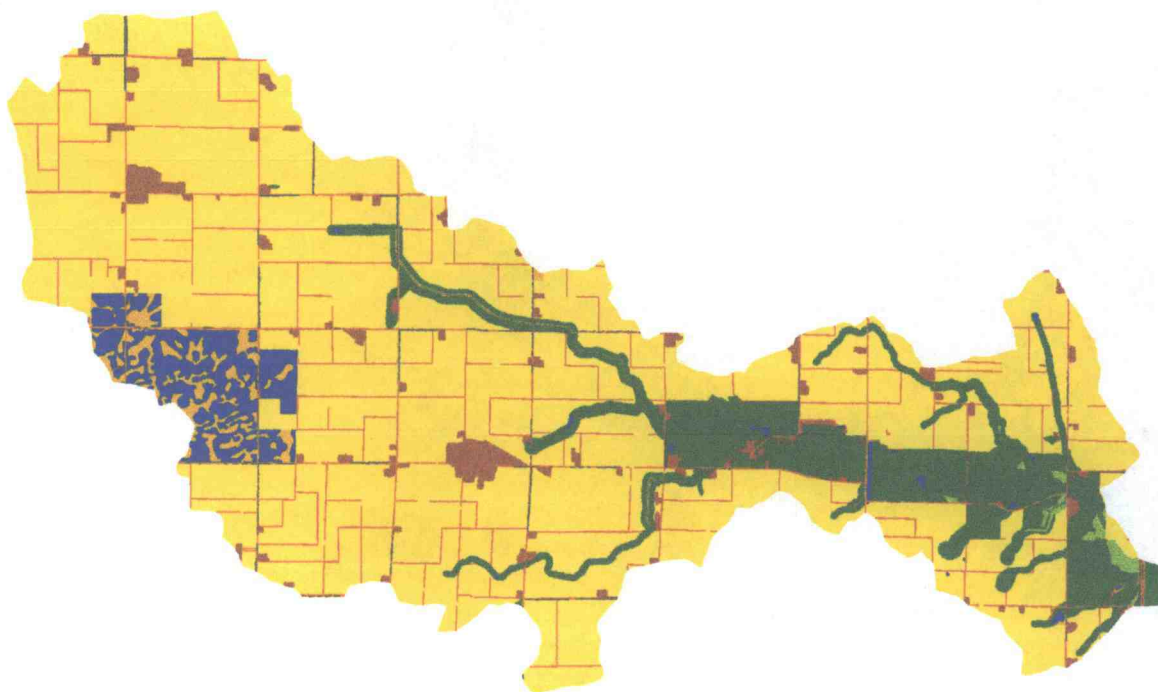
Scenario 3 is based on the assumption that land cover patterns have been dramatically changed by policy interventions to increase indigenous biodiversity and improve water quality (Figures 6a and 7a). In Scenario 3, at least 260 ha of each watershed has been set aside as permanent indigenous ecosystem core reserves. The reserve in Buck Creek watershed is wooded, while the reserve in Walnut Creek consists of a large wetland complex. In this scenario, riparian areas are widest (30 to 90 m), innovative farming practices have been adopted, such as native herbaceous strip intercropping and agroforestry (Nassauer et al. 1999; Nassauer and Corry in preparation).

GIS coverages of 1994 (called the "present" in our analysis) land cover were used for comparison, resulting in a total of 8 landscapes (Figures 6b and 7b). These coverages were derived from 1:20,000 aerial photographs taken in 1990 and ground-truthed in 1993-1994 (Santelmann et al. in preparation).

Study Species Selection

Of the 19 amphibian species known to occur in central Iowa, four species were chosen for modeling. These species (*Ambystoma tigrinum*, *Bufo americanus*, *Hyla versicolor*, and *Pseudacris triseriata*) were chosen because adequate natural and life history data were available. Constraints in the availability of such data precluded the inclusion of any rare and uncommon species.

a.)



b.)

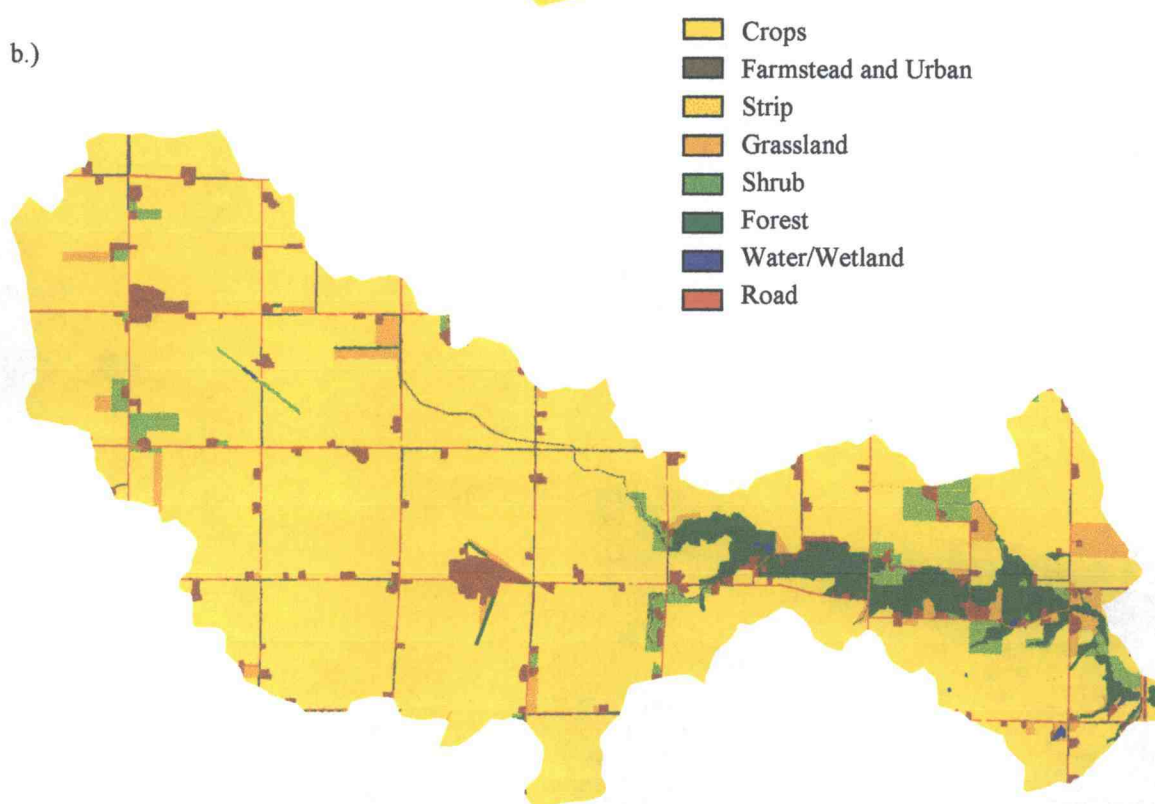


Figure 6. Walnut Creek watershed Scenario 3 (a), and present land cover (b).

a.)

b.)

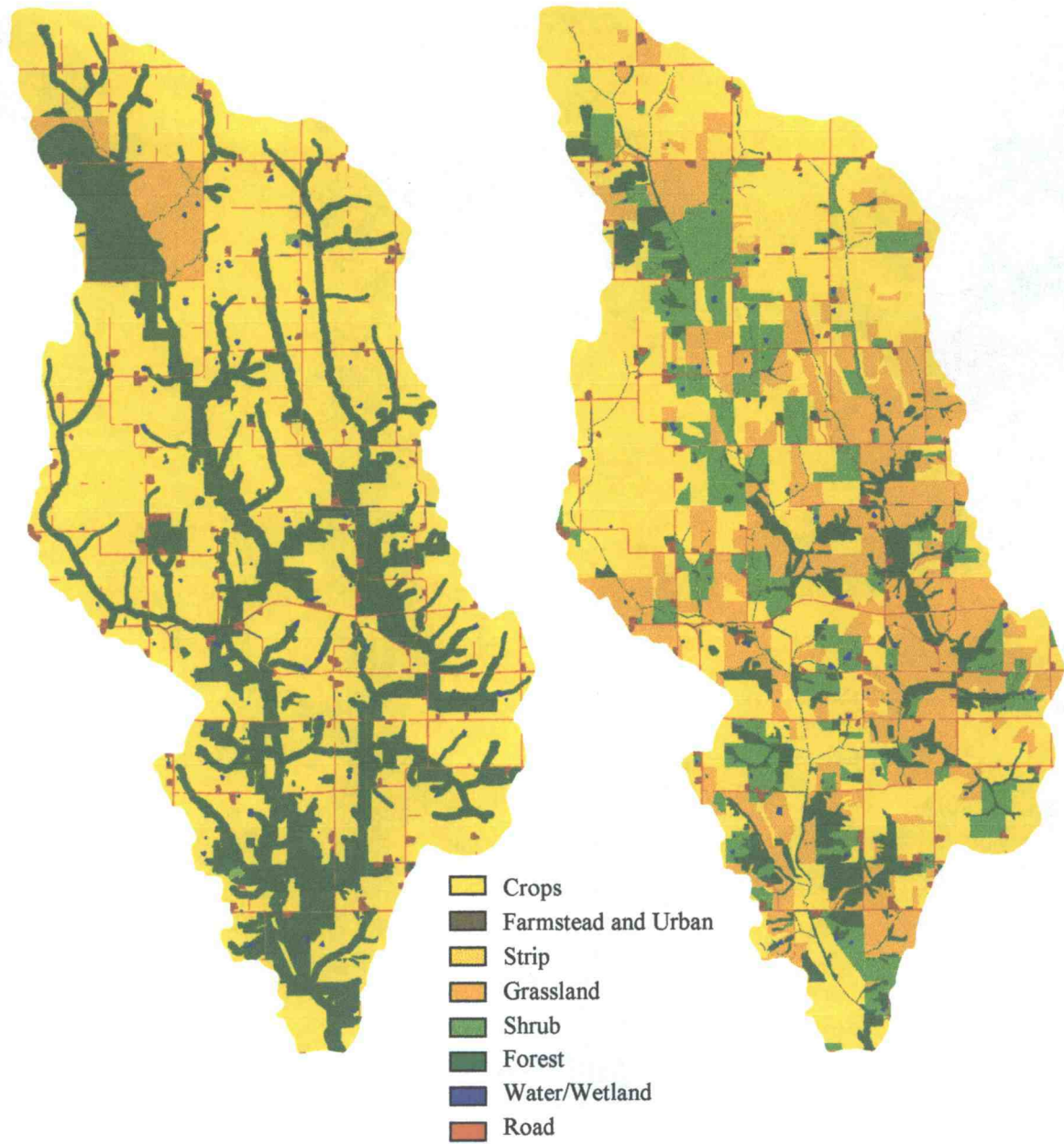


Figure 7. Buck Creek watershed Scenario 3 (a), and present land cover (b).

A. tigrinum, considered the most abundant salamander in Iowa, is thought to have increased in abundance or remained stable in the state as a result of human activities such as the creation of farm ponds (Christiansen 1981; Christiansen 1998). However, according to Lannoo et al. (1994) *A. tigrinum* larvae are less abundant and widespread than 70 years previously. *B. americanus*, considered to be abundant in Iowa, (Christiansen and Bailey 1991), also may have increased during this century (Lannoo et al. 1994). Yet, according to Christiansen (1998) this species has declined in Iowa due to loss of grassland habitat. *P. triseriata*, considered one of Iowa's most common anurans (Knutson et al. 1999), is thought by some to be more abundant now than early this century (Lannoo et al. 1994) and by others to be in decline (Christiansen 1998, Christiansen and Van Gorp 1998). *H. versicolor* populations are believed to have declined in Iowa since the early 1920s (Christiansen 1981; Lannoo et al. 1994).

Model Description and Parameterization

For this study, a customized version of PATCH (Program to Assist in Tracking Critical Habitat, Schumaker 1998), a females-only, individual-based demographic model, was used. Data requirements of the model include raster landscape maps, habitat-use patterns, maximum densities, maximum dispersal distances, and estimates of survival and fecundity.

A species-habitat association matrix was compiled from published literature for the Midwest (Smith 1961; Minton 1972; Vogt 1981; Christiansen and Bailey 1991, Collins 1993; Oldfield and Moriarty 1994; Casper 1996; Harding 1997) and local expert opinion (M. J. Lannoo, pers. comm.). For each species, 26 habitat types were assigned a

score ranging from 0 to 4 for both breeding and non-breeding habitat. For feeding habitat, scores were based on food abundance and quality and probability of survival while foraging in the habitat. Scores for breeding habitat were based on source/sink behavior, where source habitats are capable of sustaining a population without immigration and sink habitats require an influx from better quality habitats to sustain a population.

The introduction of predatory fish to breeding ponds has been found to be associated with reduced amphibian species richness and abundance, particularly in macrophyte-free ponds (Sexton and Phillips 1986; Hecnar and M'Closkey 1997; Leja 1998; Knutson et al. 1999). Furthermore, a positive relationship between the presence of non-predacious fish and amphibian species richness has been found recently in Minnesota (Lehtinen et. al. 1999). For the purposes of this study, ponds were assumed to be unstocked with fish.

Estimates of maximum adult and juvenile density, maximum dispersal distance, and average survival and reproductive rates were obtained from published literature (Table 1). In instances where necessary values were not reported, data from related species were used. Estimates of juvenile and adult survival rates and fecundity (measured by the number of juvenile females produced per year) were entered into a Leslie projection matrix for use in the model. For *H. versicolor*, *P. triseriata*, and *B. americanus*, the number of juveniles produced per female has not been published. Therefore, this parameter was derived from number of eggs produced, egg viability, and larval survival rates (Wright and Wright 1949; Calef 1973; Kramer 1978; Dash and Hota 1980; Vogt 1980; Ritke et al. 1990; Smith 1990; Skelly 1995; Ovaska 1997).

Table 1. Parameters of model used to simulate population dynamics of four amphibian species in response to landscape change in central Iowa.

Species	Fecundity ¹	Juvenile Survival ²	Adult Survival ³	Dispersal Distance ⁴ (m)	Breeder Density ⁵ (per 0.01 ha)	Juvenile Density ⁶ (per 0.01 ha)
<i>A. tigrinum</i>	4	0.20	0.72	250	10	10
<i>P. triseriata</i>	14	0.13	0.11	100	6	3
<i>H. versicolor</i>	130	0.13	0.29	125	6	3
<i>B. americanus</i>	65	0.11	0.50	600	2	8

¹ Wright and Wright 1949, Calef 1973, Kramer 1978, Dash and Hota 1980, Vogt 1981, Semlitsch 1983, Smith 1990, Skelly 1995, Ptacek 1996, Ovaska 1997

² Blair 1953, Jameson 1956, Organ 1961

³ Jameson 1955, Jameson 1956, Pearson 1955, Turner 1959, Sever and Dineen 1978, Ritke et al. 1990, Friedl et al. 1997

⁴ Oldham 1966, Kramer 1973, Illinois Department of Conservation 1995, Madison and Farrand 1998, Petranks 1998

⁵ Sever and Dineen 1978, Semlitsch et al. 1996

⁶ Pearson 1955, Kramer 1974, Douglas and Monroe 1981, Semlitsch 1983, Petranks 1998

GIS coverages of the future scenarios and present land cover were converted to grids with a 3 m pixel size for use in PATCH. Each landscape was divided into 12 pixel (0.01 ha) hexagonal units which were assigned breeding or non-breeding status according to the amount and quality of habitat contained. The number of individuals allowed to occupy a hexagon was based on estimates of maximum densities for each species (Table 1). Habitat quality and life history parameters were linked by linearly scaling survival and reproductive rates with habitat weighting values (Schumaker 1998).

The model incorporated the effects of both fluctuations in environmental conditions and demographic stochasticity. Northern prairie wetlands undergo a 10 to 20 year wet-dry cycle, resulting in prolonged (two to three year) droughts (Duvick and Blasing 1981; Karl and Riebsame 1984; Diaz 1983). Droughts have been linked to suppressed amphibian reproductive activity (Dodd 1993), decreased reproductive success (Seale 1982; Semlitsch 1983 and 1987; Wissinger and Whiteman 1992; Skelly 1995 and 1996), and localized extinctions and population declines (Blair 1957; Corn and Fogelman 1984). The effects of the prairie wetland hydroperiod were mimicked with the substitution of 'dry year' maps, which lacked ephemeral, seasonal, and semi-permanent wet habitats, into the model for 2 of every 15 (+/- a random number between 0 and 5) years. Demographic stochasticity was simulated with the use of a random number generator to evaluate the outcome of specific survival and reproduction decisions (Schumaker 1998).

The model's life history module began with a survival routine, followed by a terrestrial habitats, where they remained until they reached sexual maturity. Since no mortality is associated with adult dispersal in the model and because strong breeding site

fidelity in amphibians is well documented, adults remained in breeding sites, rather than disperse and return year after year (Jameson 1956; Dole 1965; Whitford and Vinegar 1966; Sinsch 1990; Ritke et al. 1991). There is convincing evidence documenting amphibian homing behavior, target-oriented dispersal, and non-random oriented movement between terrestrial habitats and breeding sites (Jameson 1957; Oldham 1966; Dodd and Cade 1998; Sjögren-Gulve 1998). Therefore, the model parameters were set to allow new adults to make an intelligent search for the nearest breeding site prior to the next breeding pulse. Adults unable to "find" available breeding sites prior to the next breeding pulse became non-breeding 'floaters' until the next year, when they again attempted to disperse to an unoccupied site. Lastly, the population was censused (Schumaker 1998).

Demographic and Landscape Analyses

All simulations were run over a period of 100 years for each of the four study species and ten landscapes. Each simulation was started with one female in every breeding site. Output data derived from PATCH included mean (from years 50 to 100): population size, number of breeding females, observed dispersal distances, lambda values (the dominant eigenvector of a Leslie matrix), and breeding site occupancy rates. The future scenarios were ranked according to change in intrinsic rate of increase (r or $\ln(\lambda)$, a predictor of exponential change in population size under constant conditions), mean number of breeding females (MNBF), saturation of breeding sites (mean number of breeding females relative to carrying capacity, defined as the number of breeding sites multiplied by the maximum number of breeding females allowed to occupy a site), and

breeding site occupancy (percentage of breeding sites with at least one breeding female during years 50 to 100), compared to the present.

Pattern-based metrics produced by PATCH and FRAGSTATS (McGarigal and Marks 1994) and one-tailed t-tests were used to quantify the landscape structure of the scenarios by assessing the amount, quality, and spatial arrangement of breeding habitat, and to compare occupied and unoccupied breeding sites.

Sensitivity Analysis

Sensitivity analyses are commonly conducted to compare the sensitivity of model results to quantitative parameters (Pulliam et al. 1992). Results of sensitivity analysis can be used to determine where future efforts are most needed to obtain accurate natural history information for model parameterization. Sensitivity analyses can also be invaluable tools for wildlife managers who need to evaluate the relative effectiveness of changes in demographic rates on population size (Heppell et al. in press).

To evaluate the sensitivity of the simulation results to parameter variation, changes in population size resulting from small changes in the values of the parameters of interest were recorded. The sensitivity of modeled results to parameter variation was investigated for the following parameters: fecundity, juvenile survival, adult survival, maximum dispersal distance, maximum breeder and juvenile density, habitat score, and the amount of breeding and non-breeding habitat. Due to time constraints and overlap in life history characteristics (Table 1), sensitivity analyses were not completed for *H. versicolor*. Sensitivity (S_x) was expressed as an index:

$$S_x = (\Delta x/x)/(\Delta P/P),$$

where $\Delta x/x$ is the observed change in the total population size resulting from a change in the parameter P ($\Delta P/P$) (Jørgensen 1986; Pulliam et al. 1992).

Results

Landscape Composition and Arrangement

The importance of habitat availability, quality, and connectivity to wildlife population viability has been well studied (reviewed in Andrén 1994). The amount of breeding and upland habitat, composition of breeding habitat, and mean nearest neighbor distance of breeding habitat patches in the future scenarios and present landscapes were compared to get a better idea of how the scenarios differed from one another with respect to amphibian habitat.

Ephemeral, seasonal, and semi-permanent wetlands; roadside ditches; ponds; and temporary pools were considered breeding habitat for all species. *P. triseriata* breeding habitat also included engineered wetlands, while *B. americanus* breeding habitat also included engineered wetlands and streams. Less than 1% of Walnut Creek watershed consisted of breeding habitat for the study species, except in Scenario 3, where breeding habitat increased to just over 4% of the landscape (Figure 8a). Breeding habitat made up between 0.42% and 1.06% of Buck Creek watershed (Figure 9a). In Walnut Creek present, Scenario 1, and Scenario 2, breeding habitat consisted primarily of roadside ditch, whereas in Scenario 3, breeding habitat consisted primarily of ephemeral, seasonal, and semi-permanent wetlands (Figure 10). In Buck Creek, ponds made up a far larger percentage of breeding habitat than roadside ditches (Figure 10).

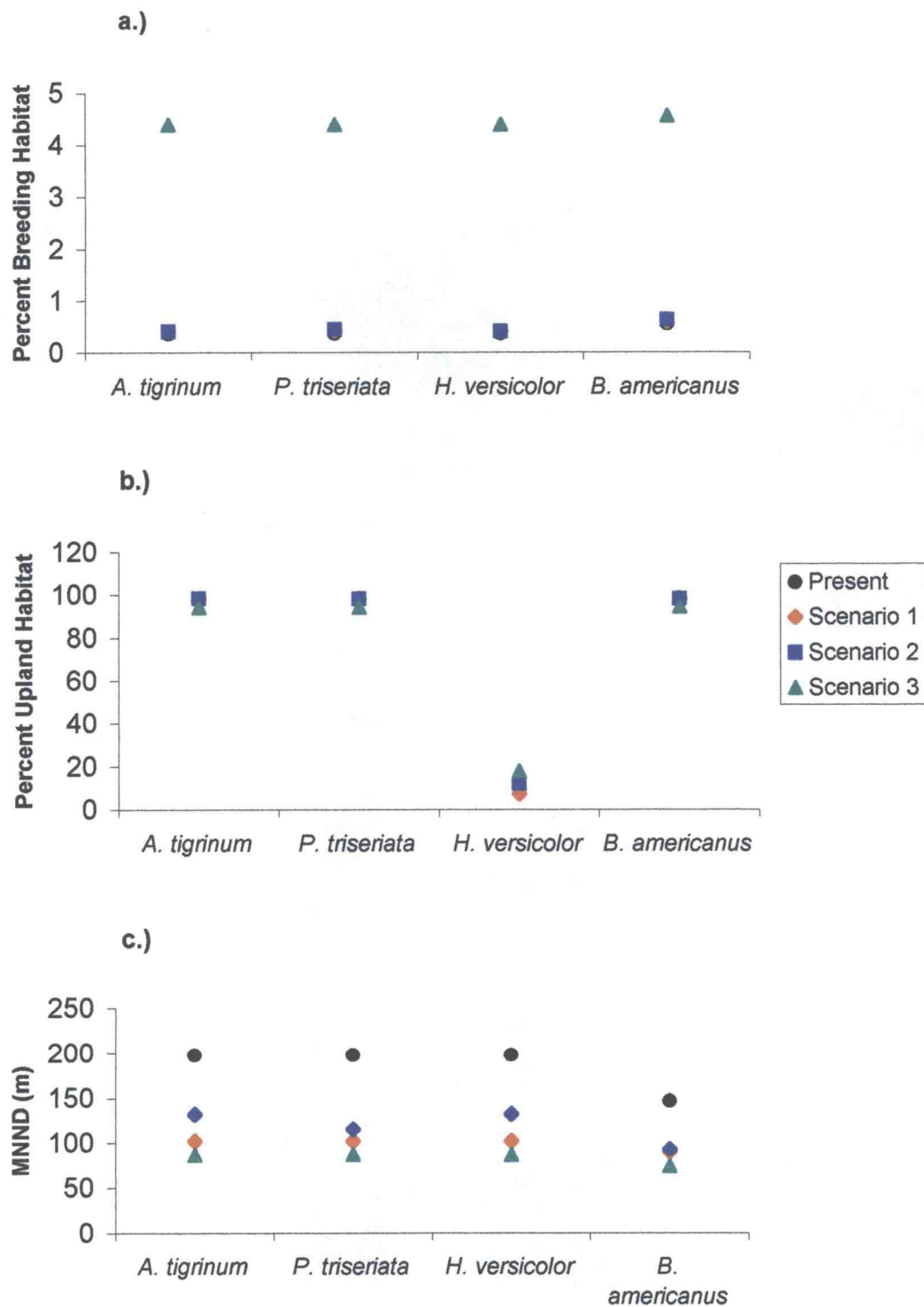


Figure 8. Percentages of Walnut Creek watershed present and future scenarios in breeding habitat (a) and upland habitat (b); and mean nearest neighbor distance of breeding habitat patches (c).

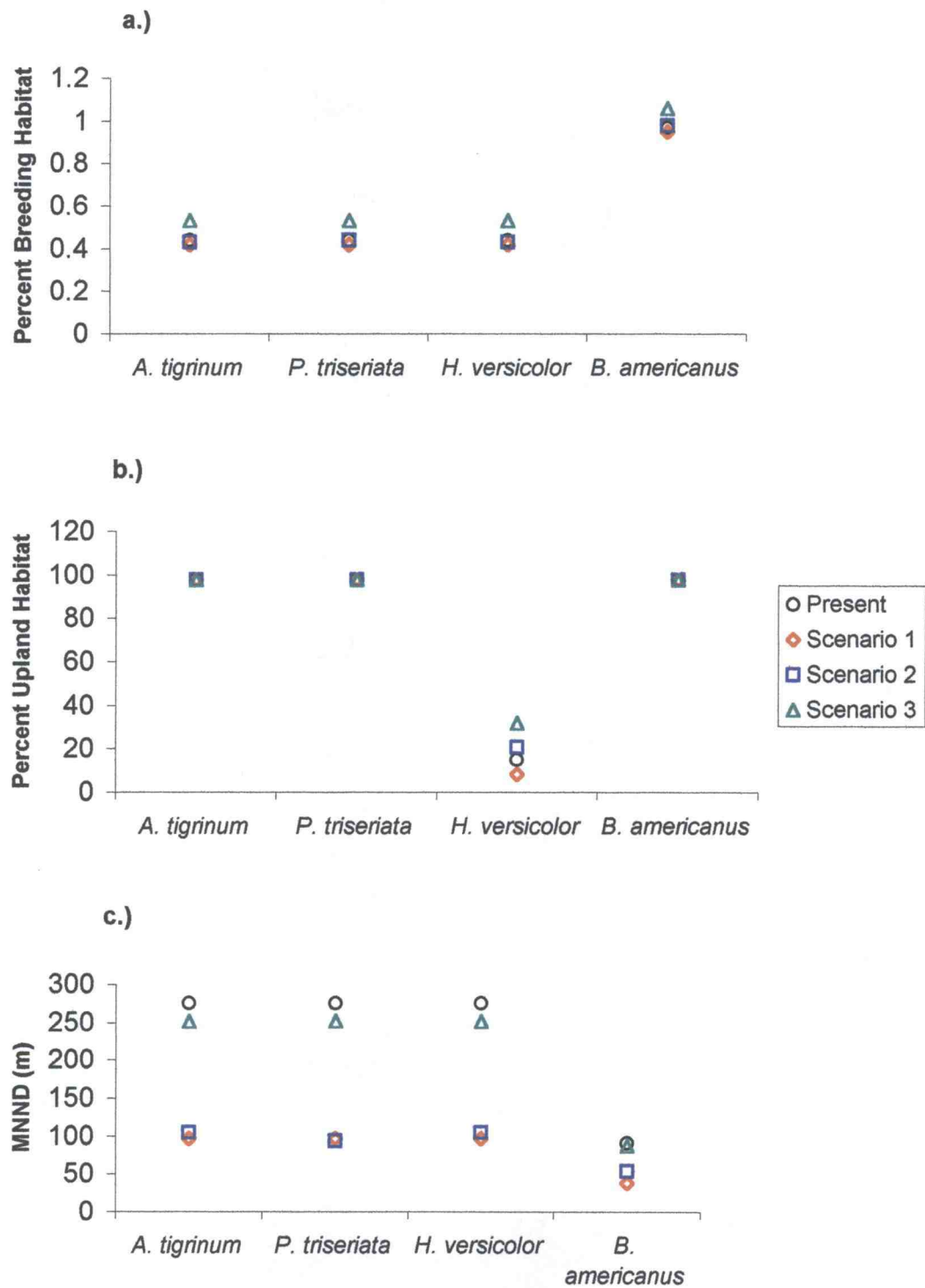


Figure 9. Percentages of Buck Creek watershed present and future scenarios in breeding habitat (a) and upland habitat (b); and mean nearest neighbor distance of breeding habitat patches (c).

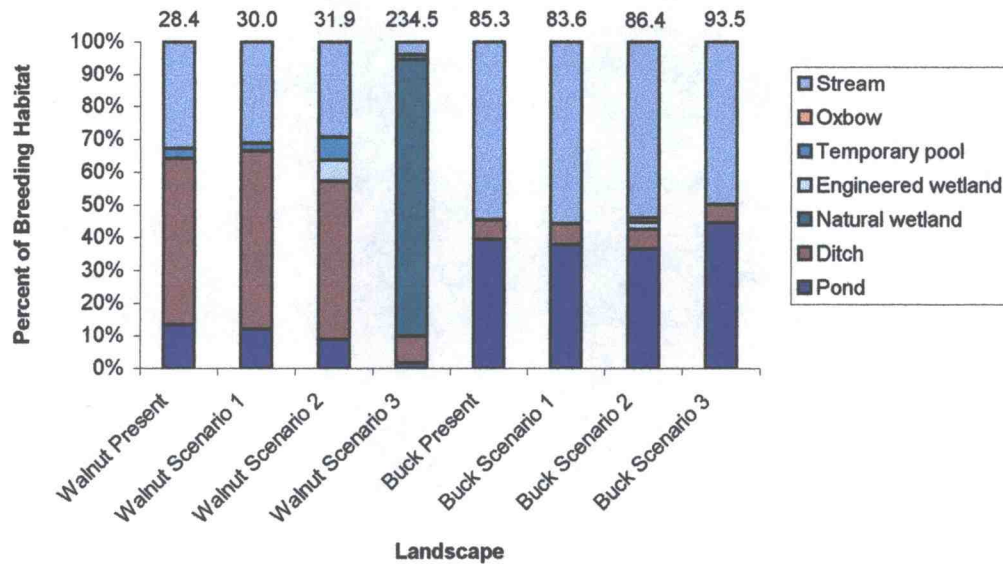


Figure 10. Breeding habitat composition of Walnut Creek and Buck Creek watersheds in the present and future scenarios. Values at top of columns indicate total area (ha).

Non-breeding habitat comprised over 94% of the landscape for *A. tigrinum*, *P. triseriata*, and *B. americanus* in both watersheds for the baseline and all scenarios. For *H. versicolor*, the only species for which agricultural land was not habitat, upland habitat ranged from less than 10% of the landscape in Scenario 1 in both Buck and Walnut Creeks, to 18% in Buck Creek Scenario 3 and 32% in Walnut Creek Scenario 3 (Figures 8b and 9b).

Mean nearest neighbor distance for breeding habitat patches in Walnut Creek watershed were greatest in the baseline and smallest in Scenario 3 for all species (Figure 8c). In Buck Creek watershed, mean breeding habitat nearest neighbor distance was greatest in the baseline for all species and smallest in Scenario 1 for *A. tigrinum*, *H. versicolor*, and *B. americanus*, and Scenario 2 for *P. triseriata* (Figure 9c).

Responses to Scenarios

Mean number of breeding females (MNBf) relative to the present showed little change in Walnut Creek Scenarios 1 and 2 for all species. In Scenario 3, where there was a nearly one hundred-fold increase in the amount of breeding habitat, MNBf increased from 3.5 (*B. americanus*) to 35 (*A. tigrinum*) times relative to the present (Figure 11a).

The response in breeder saturation and breeding site occupancy to the scenarios varied among species in Walnut Creek (Figure 11b). *A. tigrinum* populations were at less than 20% of carrying capacity in the baseline and Scenarios 1 and 2, but increased to over 55% of carrying capacity in Scenario 3, due to the addition of the large wetland complex within the biodiversity reserve. Low *A. tigrinum* breeder saturation in Walnut Creek Scenarios 1 and 2, where breeding habitat is predominantly ditch, can be explained by the

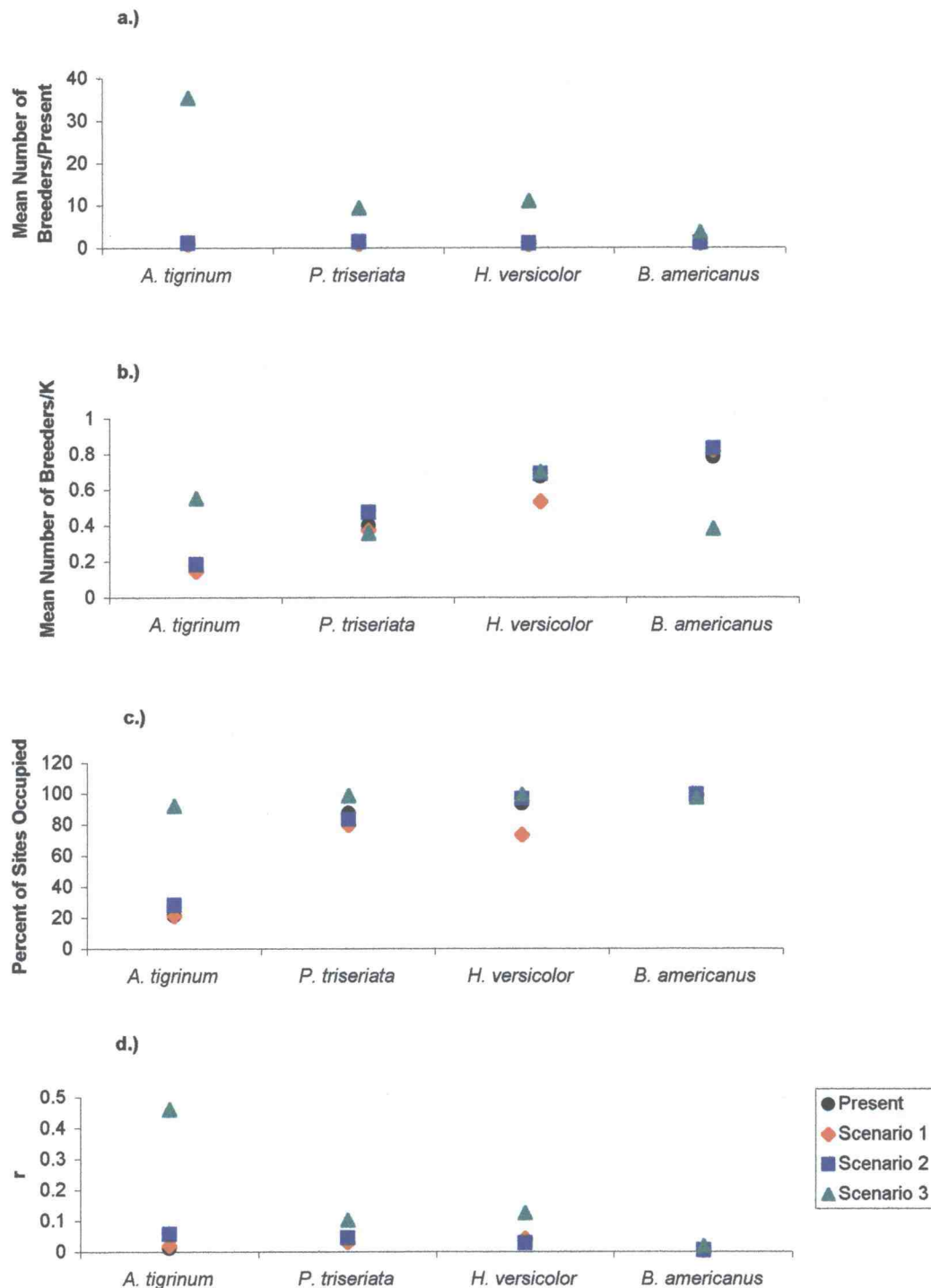


Figure 11. Response of mean number of breeding females in future scenario relative to the present (a), saturation of breeding sites (b), breeding site occupancy (c), and intrinsic rate of increase (d) to Walnut Creek future scenarios.

scoring of ditches as very poor sink habitat for this species. Nearly 80% of *A. tigrinum* Walnut Creek breeding sites were unoccupied during years 50 to 100 in the baseline and Scenarios 1 and 2 (Figure 11c). Most of the unoccupied *A. tigrinum* breeding sites in these landscapes were roadside ditches, whereas most occupied sites were large ponds clustered in the southeastern corner of the watershed, large temporary pools clustered in the northwest, and sections of the roadside ditches near these ponds and pools (Figure 12). The percentage of breeding sites occupied by *A. tigrinum* more than tripled in Scenario 3, where the proportion of breeding habitat that was roadside ditch decreased with the addition of the wetland complex in the southwestern corner (Figure 13).

H. versicolor populations were near 70% of carrying capacity in the present and Scenarios 2 and 3 in Walnut Creek, but decreased in Scenario 1 to 53% of carrying capacity, possibly due to the slight increase in the proportion of breeding habitat comprised by roadside ditches, which function as sink habitat for this species (Figure 11b). *H. versicolor* occupied over 90% of available Walnut Creek present, Scenario 2, and Scenarios 3 breeding sites, but only 73% of the breeding sites in Scenario 1 (Figure 11c).

Populations of *B. americanus* were near 80% of carrying capacity in Walnut Creek present and Scenarios 1 and 2, but dropped sharply to just 38% in Scenario 3 (Figure 11b). While this species occupied over 97% of available breeding sites in all Walnut Creek landscapes, it did not utilize a large portion of the wetland reserve in Scenario 3, explaining the low breeder saturation in this scenario (Figure 14).

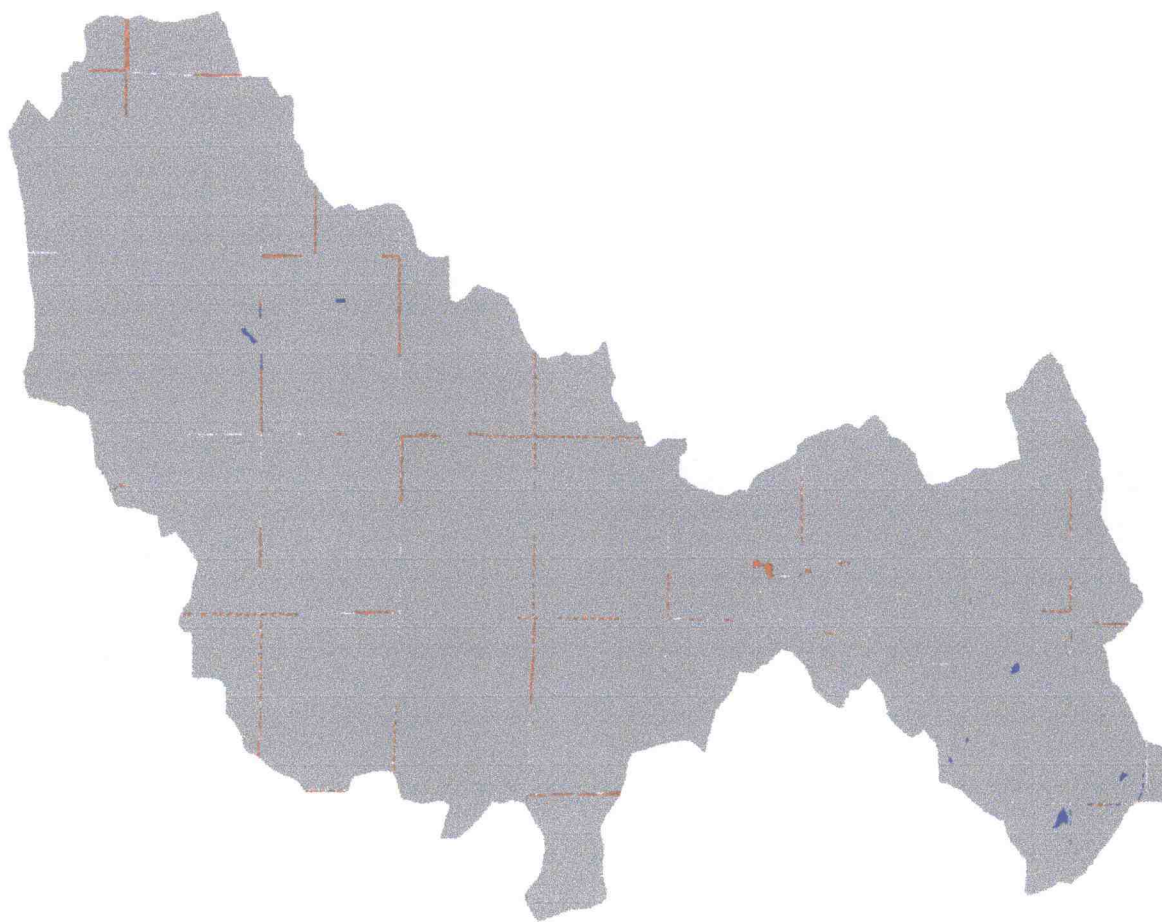


Figure 12. *A. tigrinum* breeding site occupancy in Walnut Creek present. Red indicates sites that were unoccupied during years 50 to 100. Blue indicates sites that were occupied by at least one breeder during that time.

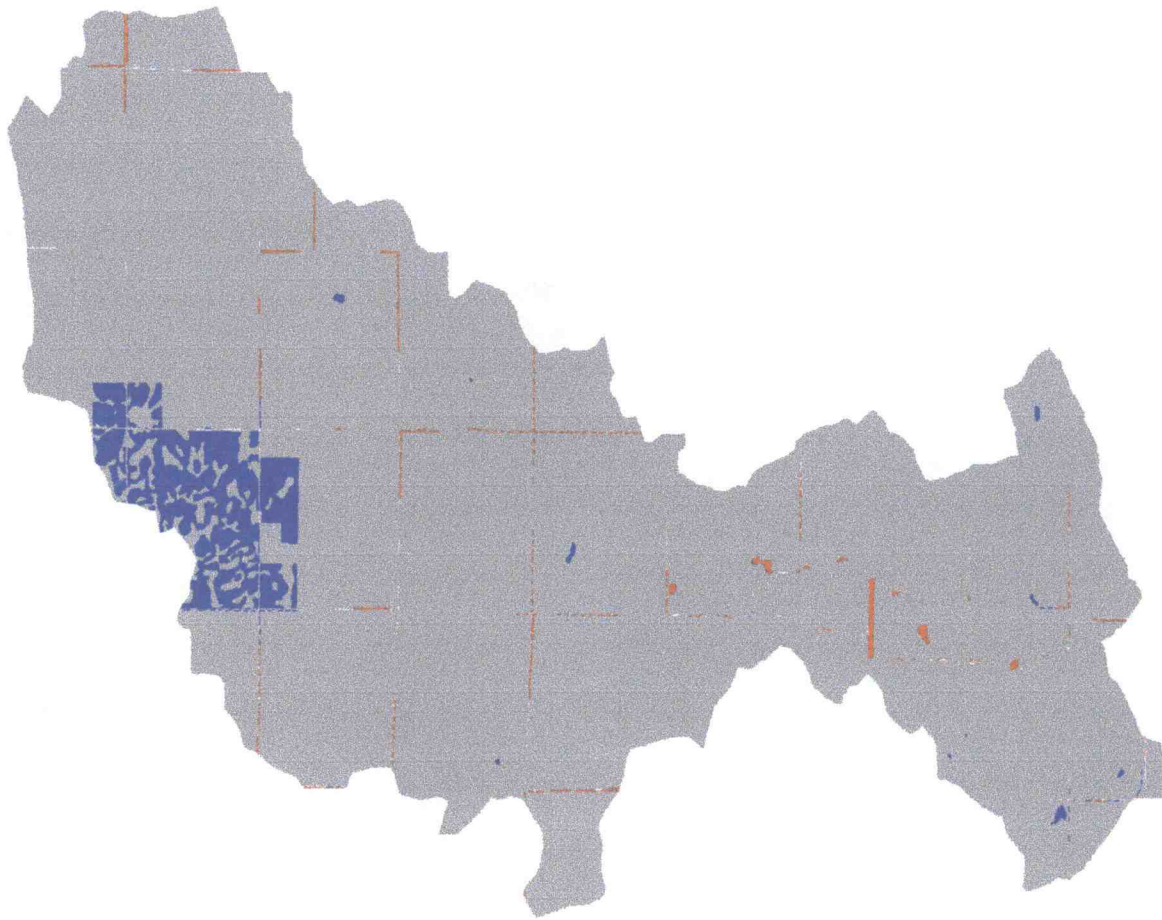


Figure 13. *A. tigrinum* breeding site occupancy in Walnut Creek Scenario 3. Red indicates sites that were unoccupied and blue sites that were occupied during years 50 to 100.

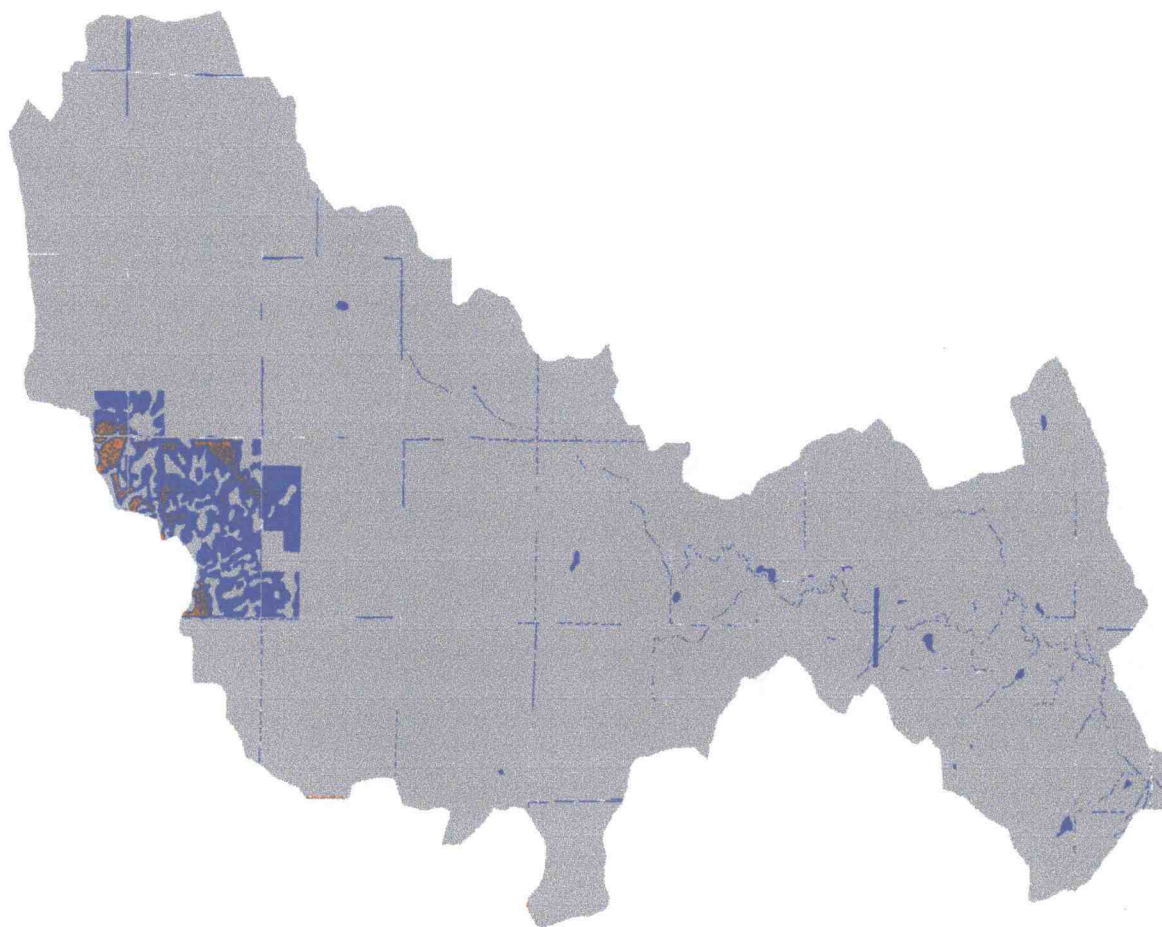


Figure 14. *B. americanus* breeding site occupancy in Walnut Creek Scenario 3. Red indicates sites that were unoccupied and blue, sites that were occupied during years 50 to 100.

P. triseriata populations were near 40% in all Walnut Creek landscapes (Figure 11b). While this species occupied over 75% of the breeding sites in these landscapes, the percentage of sites occupied was lowest in Scenario 1 (Figure 11c).

Population growth rates were greater than zero in all Walnut Creek simulations (Figure 11d). There was little variation in r (intrinsic rate of increase) for *B. americanus*, *P. triseriata*, and *H. versicolor* in Walnut Creek present and Scenarios 1 and 2. However, population growth rates for these species were 2 to 3 times greater in Scenario 3 compared to the present and Scenarios 1 and 2. The rate of *A. tigrinum* population growth in Walnut Creek was over 3 times greater in Scenario 2 and over 20 times greater in Scenario 3 than in the present and Scenario 1.

MNBF relative to the present landscape showed less variation among landscapes for all species in Buck Creek than Walnut Creek (Figure 15a). As in Walnut Creek, Buck Creek Scenario 3 ranked highest in MNBF for each species, with mean number of breeders ranging from 1.09 (*B. americanus*) to 1.27 (*P. triseriata*) times MNBF in the present landscape.

Buck Creek breeder saturation for *A. tigrinum* and *B. americanus* showed little variation among landscapes, with populations at over 82% and over 98% of carrying capacity, respectively (Figure 15b). Breeding site occupancy in Buck Creek showed little variation among landscapes for *A. tigrinum*, *H. versicolor*, and *B. americanus*, with over 90% of sites occupied in every simulation (Figure 15c). *P. triseriata* breeder saturation (74.2% of carrying capacity), and breeding site occupancy (81% of sites occupied) were lowest in Scenario 2, possibly due to infrequent utilization of the added engineered wetlands. *H. versicolor* breeder saturation was also lowest in Scenario 2, with

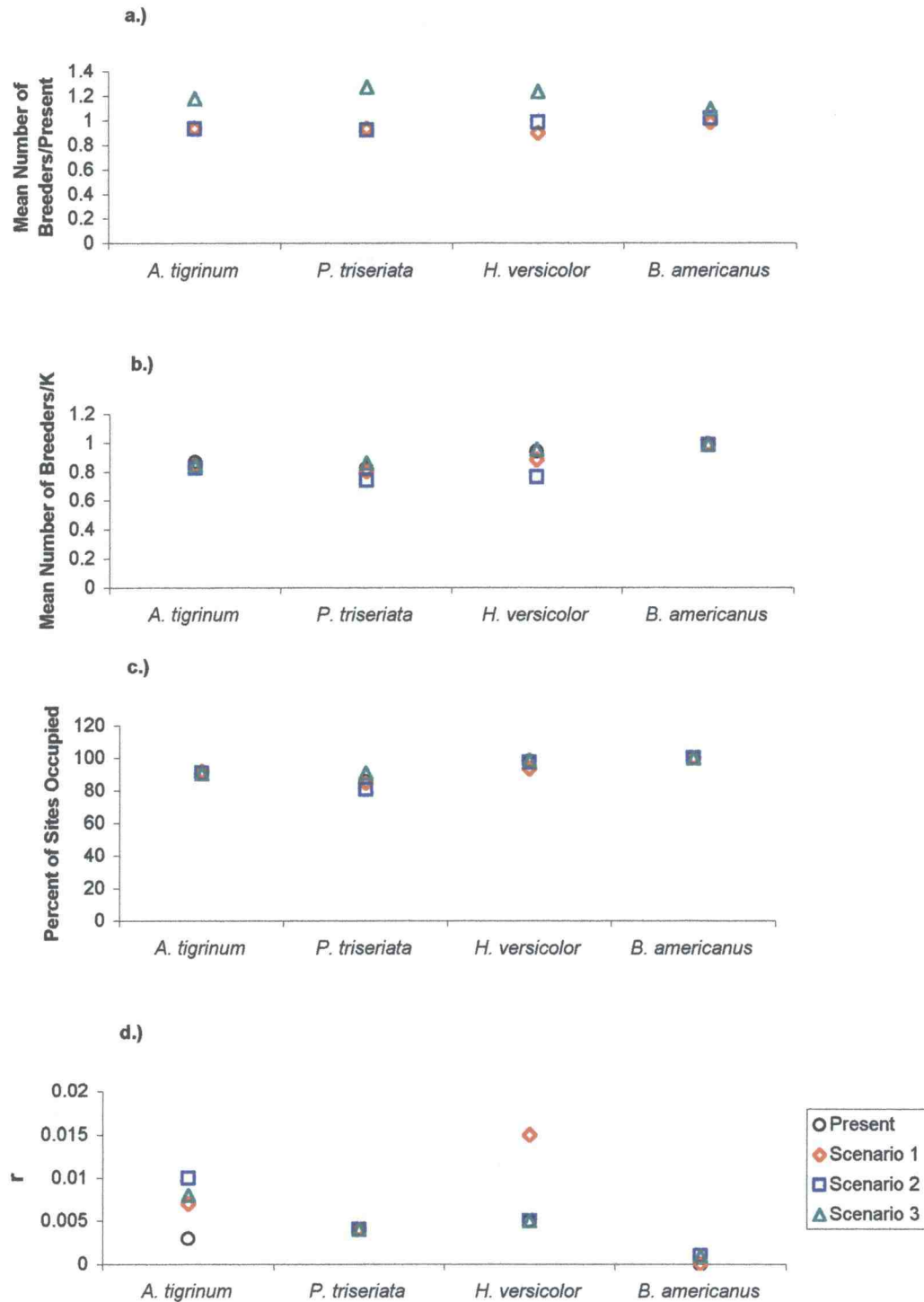


Figure 15. Response of mean number of breeding females in future scenario relative to the present (a), saturation of breeding sites (b), breeding site occupancy (c), and intrinsic rate of increase (d), to Buck Creek future scenarios.

populations at less than 80% of carrying capacity, in spite of the fact that there was no change in amount of breeding or upland habitat, proportion of source habitat, or mean nearest neighbor distance relative to Scenario 1.

Population growth rates were close to zero in all Buck Creek simulations (Figure 15d). There was little variation in r among Buck Creek landscapes for *P. triseriata* and *B. americanus* (Figure 15d). Contrary to expectations, the rate of *A. tigrinum* population growth was smallest (0.3%) in the present, and largest (1%) in Scenario 2, where there was less breeding habitat and a slightly higher proportion of breeding habitat was ditch, but a much smaller mean nearest neighbor distance for breeding habitat patches. Also unexpected, the rate of *H. versicolor* population growth in Scenario 1 (1.5%), which had the smallest amount of breeding habitat, highest proportion of ditch, but low breeding habitat patch mean nearest neighbor distance, was 3 times that in the other Buck Creek landscapes.

Landscape Analysis of Breeding Sites

P. triseriata was the only species to display relatively low occupancy rates that could not be explained by a lower habitat score. Mean patch size of breeding sites which were occupied by at least one breeding *P. triseriata* and those which were empty during years 50-100 were compared with one-tailed t-tests. For Walnut Creek Scenarios 1 and 2 and Buck Creek present and all scenarios there was convincing evidence that occupied patches were larger than unoccupied patches (Table 2). This may be due to the division by the model of large, individual ponds into many small, hexagonal breeding sites. This

Table 2. Influence of mean patch size (\pm SE) on *P. triseriata* breeding site occupancy. *P*-values from one-tailed t-tests.

Landscape	Patch Size (ha)		<i>P</i>
	Occupied	Unoccupied	
Walnut Present	0.057 \pm 0.140	0.019 \pm 0.010	0.2
Walnut Scenario 1	0.063 \pm 0.152	0.033 \pm 0.049	0.02
Walnut Scenario 2	0.075 \pm 0.147	0.030 \pm 0.030	0.001
Walnut Scenario 3	0.733 \pm 7.224	0.032 \pm 0.043	>0.2
Buck Present	0.265 \pm 0.295	0.072 \pm 0.079	0.0005
Buck Scenario 1	0.201 \pm 0.244	0.060 \pm 0.060	0.0005
Buck Scenario 2	0.181 \pm 0.233	0.051 \pm 0.057	0.0005
Buck Scenario 3	0.242 \pm 0.305	0.074 \pm 0.071	0.0005

creates small clusters of 'ponds', artificially increasing breeding site density and effectively reducing the distance between breeding sites.

Sensitivity Analysis

A. tigrinum, *B. americanus*, and *P. triseriata* differed in their responses in MNBF to changes in model parameters (Figure 16). Overall, model results were most sensitive to changes in fecundity, juvenile survival rates, amount of pond habitat, and scoring of breeding habitat.

Among demographic parameters, *P. triseriata* was most sensitive to change in fecundity, experiencing a 50% drop in MNBF in response to a near 25% decrease in fecundity (Table 3). A 25% decrease in juvenile survival resulted in extinction for *B. americanus* and an over 50% decline in MNBF for *P. triseriata*. *A. tigrinum* was far less sensitive to changes in fecundity and juvenile survival. All three species displayed only moderate sensitivity to changes in adult survival.

For all species, MNBF was relatively insensitive to changes in maximum dispersal distance and density (Figure 16). However, *P. triseriata*, which had the smallest dispersal distance (100 m) was the most sensitive, experiencing a 17% decrease in MNBF and 15% decrease in the number of breeding sites occupied in response to a 25% decrease in maximum dispersal distance. *A. tigrinum*, which had an intermediate dispersal distance (250 m), showed little change in MNBF in response to a 25% decrease in maximum dispersal distance. However, the number of breeding sites occupied by *A. tigrinum* dropped by 64%. MNBF and breeding site occupancy were relatively unaffected by change in dispersal distance for *B. americanus*, the best disperser of the

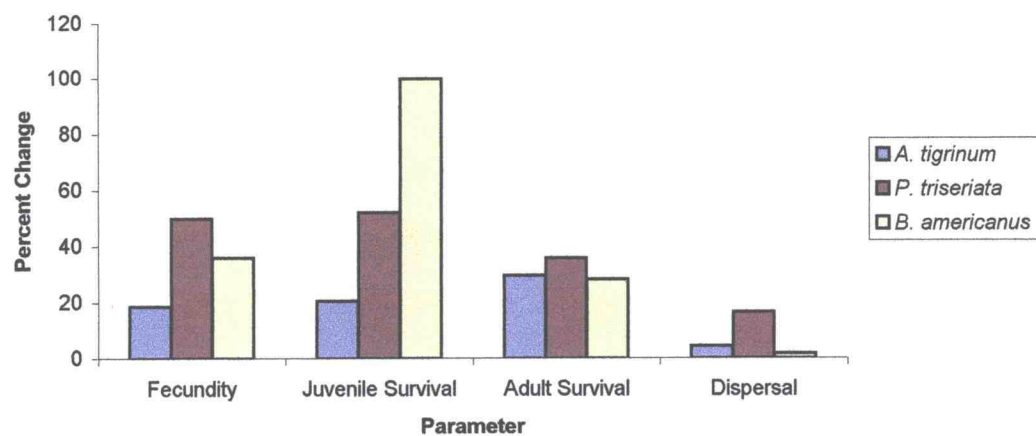


Figure 16. Percent change in mean number of breeding females in response to an approximate 25% decrease in parameters, relative to baseline conditions.

Table 3. Sensitivity of mean number of breeding females to change in model parameters ($S_x = (\Delta X/X)/(\Delta P/P)$).

Parameter	<i>A. tigrinum</i>			<i>P. triseriata</i>			<i>B. americanus</i>		
Varied	$\Delta X/X$	$\Delta P/P$	S_x	$\Delta X/X$	$\Delta P/P$	S_x	$\Delta X/X$	$\Delta P/P$	S_x
F ¹	627/3346	1/4	0.75	2444/4892	3/14	2.33	1780/4941	16/65	1.55
S _j ²	688/3346	0.05/0.20	0.82	2552/4892	0.03/0.13	2.27	4932/4941	0.03/0.11	3.66
S _a ³	994/3346	0.18/0.72	1.19	1752/4892	0.03/0.11	1.31	1394/4941	0.12/0.50	1.18
D ⁴	147/3346	6/23	0.17	811/4892	2/9	0.75	90/4941	14/54	0.07
Dn _b ⁵	682/3346	2/10	1.02	1020/4892	1/6	1.26	2486/4941	1/2	1.01
Dn _f ⁶	23./3346	2/10	0.03	-174/4892	1/3	0.12	51/4941	2/8	-0.04
Po ⁷	3279/3346	3.8/19.1	4.95	4886/4892	3.8/19.1	5.05	764/4941	3.8/28.5	1.16
Di ⁸	508/3346	14.5/19.1	0.2	2570/4892	14.5/19.1	0.70	2178/4941	14.5/28.5	0.87
Up ⁹	838/3346	4191/5046	0.3	2777/4892	4191/5046	0.69	1631/4941	4191/5046	0.40
Sc _{br} ¹⁰	1468/3346	1/4	1.75	3268/4892	1/4	2.67	24.3/4941	1/4	0.02
Sc _{up} ¹¹	166/3346	1/4	0.2	153.1/4892	1/4	0.12	-64/4941	1/4	-0.05

¹ Fecundity.

² Juvenile survival.

³ Adult survival.

⁴ Maximum dispersal distance.

⁵ Breeder density (number per 0.01 ha).

⁶ Floater density (number per 0.01 ha).

⁷ Amount of pond habitat.

⁸ Amount of ditch habitat.

⁹ Amount of upland habitat.

¹⁰ Breeding habitat score.

¹¹ Upland habitat score.

group (600 m). Change in maximum breeder density resulted in moderate sensitivity while change in maximum juvenile density resulted in low sensitivity (Table 3).

Simulations were conducted with the 6 ponds in Walnut Creek present land cover removed as breeding habitat to investigate the implications of the assumption that ponds are fish-free and therefore good source habitat. Loss of ponds as breeding habitat decreased the amount of available breeding habitat by nearly 20% for *A. tigrinum* and *P. triseriata*, and 13% for *B. americanus*. As a result, both *A. tigrinum* and *P. triseriata* went extinct, while *B. americanus* suffered a 15% decrease in MNBF (Table 3).

Simulations were also run with ditches removed as breeding habitat, testing the assumption that ditches actually serve as breeding sites. The loss of ditches as breeding habitat decreased the amount of breeding habitat by over 75% for *A. tigrinum* and *P. triseriata*, and over 50% for *B. americanus*. The elimination of ditches resulted in a decrease of MNBF of 53% for *P. triseriata*, 44% for *B. americanus*, and 25% decrease for *A. tigrinum*, for which ditches were classified as sink habitat (Table 3). Simulations were also conducted with row-crops designated as non-habitat, reducing the amount of non-breeding habitat in the Walnut Creek present by 83%, to investigate the implications of the characterization of agricultural land as high quality non-breeding habitat. In response, the MNBF *A. tigrinum* decreased by 25%, *B. americanus* by 33%, and *P. triseriata* by 57% (Table 3).

Breeding and non-breeding habitat scores were decreased separately by approximately 25% each to test the sensitivity of the model results to the habitat scores in the expert reviewed species habitat matrix. In response to decreased breeding scores, the *P. triseriata* breeding female population decreased by 67%, *A. tigrinum* by 44%, and *B.*

americanus by less than 1% (Table 3). Model results were far less sensitive to change in non-breeding habitat score for all species, resulting in change in MNBF ranging from a 5% decrease (*A. tigrinum*) to a 1% increase (*B. americanus*, Table 3).

Discussion

Present Predictions

H. versicolor and *B. americanus* were predicted by the model to maintain healthy populations in the present landscape in both watersheds, while *A. tigrinum* and *P. triseriata* were predicted to maintain healthy populations in the present landscape of Buck Creek. In the present Walnut Creek landscape, the model simulations estimate populations of *A. tigrinum* and *P. triseriata* to be at less than 50% of carrying capacity. However, the model also estimates populations of these species to be growing on average 1.3% (*A. tigrinum*) and 4.4% (*P. triseriata*) per year. While these results do not completely concur with reports that populations of *A. tigrinum* and *P. triseriata* may be in decline in Iowa (Lannoo et al. 1994; Christiansen 1998; Christiansen and Van Gorp 1998), they do suggest that these species may be more at risk to future landscape change than the other species modeled. Efforts to secure the continuance and improvement of present programs monitoring Midwestern amphibians, such as the Declining Amphibian Populations Task Force (DAPTF), the North American Amphibian Monitoring Program (NAAMP), and individual states' natural resource departments, will help to ensure the availability of important long-term data on population trends and distribution patterns in the region.

Evaluation of Scenarios

Scenario 3 consistently ranked above the present and other scenarios in mean number of breeders supported, while patterns in the other responses investigated were less clear. The obvious advantages of this scenario compared to the others were the increase in the amount of breeding habitat, the decrease of roadside ditches in the proportion of breeding habitat, and the reduced isolation of breeding sites. Scenario 1 and 2 had little benefit for amphibian species over the present landscape.

Influence of Breeding Habitat Patch Size

The results of *P. triseriata* breeding site analysis indicate the significance of breeding patch size in explaining patterns of *P. triseriata* breeding site occupancy. This contrasts with some studies that have shown breeding site area to be of minor importance compared to breeding site isolation in predicting the presence of certain species. Studies by Mann et al. (1991), Vos and Stumpel (1995), and Lehtinen et al. (1999) found amphibian species richness to be highest in areas with high wetland or pond density, or low isolation. However, Laan and Verboom (1990) found significant effects of both pool size and isolation on amphibian species richness. Our results may be explained by the fact that our model divided individual ponds into small, hexagonal breeding sites, which effectively may function as a small cluster of ponds, artificially increasing breeding site density. Future field studies should be done to explore the relative importance of breeding habitat patch size and degree of isolation.

Implications of Sensitivity Analysis

The results of our sensitivity analysis indicate that simulation results are sensitive to changes in fecundity, juvenile survival rates, amount of breeding and upland habitat, and the scoring of breeding habitat. These results point to the need for accurate habitat-specific demographic information. Assuming the model parameters were accurate, our results also indicate that future conservation efforts for these species will be most effective if they are directed at increasing the availability of high quality breeding and upland habitat, increasing the number of juveniles produced, and enhancing juvenile survival. The amount of high quality breeding habitat in the region can be attained through wetland restoration programs and the creation of unstocked farm ponds. Efforts to protect remaining forests and grasslands and reduce adverse farming practices, such as agrochemical use and mechanized reaping, may serve to improve the quality of upland habitat and increase juvenile survival rates. The number of juveniles produced may be increased by efforts to increase larval survival rates, such as removal of predacious non-native fish species from breeding ponds and prevention of chemical pollution of breeding ponds.

Limitations of Model

The model used (a modified version of PATCH), did not incorporate within breeding site variables, such as water chemistry, vegetation coverage, and biotic interactions. Lehtinen et al. (1999) found no significant associations between water chemistry (pH and total dissolved solids) or vegetation coverage and amphibian species richness in an agricultural prairie region of Minnesota. However, the presence of *A.*

tigrinum and predatory fish were found to be significant predictors of amphibian species richness (Lehtinen et al. 1999). The current study might be improved by making allowances for such biotic interactions.

The model's division of the landscape into hexagons and determination of hexagon status (breeding site or upland site) according to the number of pixels of habitat contained (Schumaker 1998) resulted in the conversion of narrow linear features, such as roadside ditches, streams, and roads, into discontinuous series of hexagonal patches. As a result, the model was unable to incorporate the effects of roads, which are widely regarded as having negative impacts on amphibian populations (Knutson et al. 1999). Increasing road density has been found to be associated with increased adult mortality during migration to and from breeding sites (Ashley and Robinson 1996), decreased species richness (Findlay and Houlihan 1997; Lehtinen et al. 1999), barriers to movement (Gibbs 1998), and decreased probability of occurrence (Vos and Chardon 1998). However, since road density was held constant among scenarios in both watersheds, this limitation did not effect scenario comparisons.

Limitations of Scenarios

The future scenarios were not designed specifically to investigate the effects of landscape change on amphibian populations. The future scenarios were not designed specifically to enhance amphibian biodiversity. Rather, the future scenarios had multiple purposes: to improve water quality, to maintain production of agricultural commodities, and to restore vertebrate biodiversity for many taxa, among which amphibians are but a minority. As a result, Scenarios 1 and 2 differed little from the present land cover in the

amount and arrangement of important amphibian habitat. In addition, the level of detail in land cover and land use specified by the design team far surpassed the current level of knowledge in amphibian habitat affinities and included innovative agricultural practices for which no data are available for use by amphibian species.

Extant amphibian species in Iowa must coexist with row crop agriculture because it is the dominant land use in the region. The effect of agriculture on amphibians has been the subject of an increasing number of studies. Knutson et al. (1999) found no negative association between anuran presence and agriculture. However, Hecnar (1997) found decreased amphibian diversity associated with agricultural landscapes in Ontario and Bonin et al. (1997) found an inverse relationship between anuran species richness and agricultural monocultures in Quebec. Furthermore, several studies have shown the toxic effects of pesticides and herbicides on amphibians (Berrill et al. 1997; Diana and Beasley 1998) and suggested the role of such agents in recent high prevalences of hindlimb deformities (Ouellet et al. 1997; Helgen et al. 1998). While some agricultural practices (such as haying or grazing) are thought to be more favorable to amphibians than others (such as row cropping) due to disturbances of lower intensity or less use of agricultural chemicals, there have been no studies conducted to support such theories (Knutson et al. 1999). Field-based studies to quantify amphibian use of different types of agricultural lands would vastly improve our level of knowledge about the impacts of various agricultural practices and help to refine population viability models.

Conclusions

In conclusion, the model used in this study provides a much-needed method to predict the effects of landscape change on terrestrial amphibians and the necessary conditions for the persistence of amphibian populations in agricultural regions of the Midwestern U.S. Several important factors set this investigation apart from those completed previously: the inclusion of both breeding and non-breeding habitat; the use of real landscapes; the spatially explicit nature of the approach; the incorporation of climatic variation; and the comparison of the relative effectiveness of different land management and policy scenarios.

This study suggests the four species modeled will persist under present and future scenario conditions, assuming the parameter estimates used in the simulations are correct. However, results of the sensitivity analysis show the strong influence that variation in fecundity, juvenile survival, definition of source habitat have on model results, emphasizing the need for more long-term field studies of amphibian life history to lessen parameter uncertainty. As a result, there is a need for caution when applying results of the model. Furthermore, it is also important to keep in mind the extinction debt concept, where abundant species experience time-delayed extinction as a result of moderate habitat destruction (Tillman 1994). The four species modeled are all successful, widespread generalists regarded as having a low conservation priority. However, these species are dependent on wetlands and ponds, increasingly endangered habitat forms in the agricultural landscapes of the Midwest. Broader conservation strategies, such as those implemented in Scenario 3, which focus on habitats or suites of species, in the region

would ensure that these currently common and widespread organisms do not become the endangered species of the future (Beebee 1996).

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