Effects of Agricultural Cultivation on Demographics of Southern High Plains Amphibians

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Abstract: *Anthropogenic disturbance of landscapes surrounding wetlands is considered a factor in local and global amphibian declines. Few data exist on the effects of agricultural cultivation of wetland watersheds on amphibians, and results from previous studies are contradictory. Our objective was to test the effects of general anthropogenic land use (cultivation vs. grassland) on the demographics of seven species and three age classes of amphibians in the Southern High Plains of Texas. We partially enclosed 16 playa wetlands (4 per land use per year) with drift fences and pitfall traps and monitored relative daily abundance and diversity from 16 May to 17 October 1999 and 19 April to 18 August 2000. In general, relative abundance (i.e., average daily capture) of New Mexico and plains spadefoots (Spea multiplicata, S. bombifrons) was greater at cropland than grassland playas; the abundance of other species and diversity of the amphibian assemblage was not affected by land use. Also, abundance generally was greater in 1999 than 2000 for metamorph spadefoots and barred tiger salamanders (Ambystoma tigrinum mavortium). Differences in spadefoot abundance between land-use types may have been related to low species-specific vagility, resulting in increased nestedness within disturbed landscapes and reduced abundance of a potential keystone intraguild predator in cropland playas. The yearly difference in amphibian abundance was likely related to annual precipitation, which influenced wetland hydroperiod. Agricultural cultivation surrounding wetlands is associated with the increased abundance of some amphibian species, but other demographic and fitness parameters—such as temporal demographics, body size, and diet diversity—may be negatively affected.*

Key Words: amphibian populations, anthropogenic disturbance, land use, playa wetlands, Texas

Efectos de Cultivos Agrícolas sobre la Demografía de Anfibios de Llanuras del Sur (E. U. A.)

Resumen: *La perturbación antropogénica de paisajes circundantes a humedales es considerado un factor en la declinación local y global de anfibios. Existen escasos datos de los efectos de la agricultura en cuencas de humedales sobre anfibios, y los resultados de estudios previos son contradictorios. Nuestro objetivo fue probar los efectos del uso de suelo antropogénico general (cultivo vs. Pastizal) sobre la demografía de siete especies y tres clases de edad de anfibios en las llanuras del sur de Texas (E.U.A.). Parcialmente cercamos 16 humedales de playa (4 por uso de suelo por año) con cercos de desvío y trampas de foso y monitoreamos la abundancia relativa y diversidad diaria del 16 de mayo al 17 de octubre de 1999 y del 19 de abril al 18 de agosto de 2000. En general, la abundancia relativa (i.e., captura diaria promedio) de Spea multiplicata y S. bombifrons fue mayor en las playas con cultivos que con pastizales; la abundancia de otras especies y la diversidad del ensamble de anfibios no fue afectada por el uso de suelo, También, la abundancia generalmente fue mayor en 1999 que en 2000 para metamorfos y Ambystoma tigrinum mavortium. Las diferencias en la abundancia de Spea spp. entre tipos de uso de suelo pueden haberse debido a baja vagilidad especie-específica, lo que resulta en mayor anidamiento en paisajes perturbados y en reducida abundancia de un depredador intragremial potencialmente clave en las playas cultivadas. Probablemente, la diferencia anual en la abundancia de anfibios se relacionó con la precipitación anual, que influyó en el hidroperíodo del humedal. Los cultivos agrícolas*

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circundantes a humedales están asociados con el incremento de la abundancia de algunas especies de anfibios; sin embargo, otros parámetros demográficos y de adaptabilidad (como demografía temporal, tamaño corporal y diversidad de dieta) pueden ser afectados negativamente.

Palabras Clave: humedales de playa, perturbación antropogénica, poblaciones de anfibios, Texas, uso de suelo

Introduction

Anthropogenic disturbance of landscapes surrounding wetlands can affect resident organisms (Findlay & Houlahan 1997). Amphibian populations are declining globally, and identifying factors associated with their declines is a necessary prelude to conservation efforts (Houlahan et al. 2000). Landscape disturbance may affect amphibian populations by physically altering aquatic and terrestrial environments (Wilbur 1980; Semlitsch 2000). For example, agricultural cultivation can increase sedimentation and decrease hydroperiod in wetlands (Luo et al. 1997), which can reduce the developmental time of larvae (Gray 2002). Agricultural chemicals and pesticides can influence wetland productivity (Hanson et al. 1994; Freemark & Boutin 1995) and thus food web and community structure (Wilbur 1997), and they can directly affect the motility and survival of amphibian larvae (Bridges 1997; Bridges & Semlitsch 2000; Relyea & Mills 2001). Mechanical disturbance of the uplands can affect the connectivity of spatially structured amphibian populations by influencing permeability to movement (Turner et al. 1989; Wiens 1997; Gibbs 1998*a*). Landscape disturbance also can reduce live and detrital vegetation, which can be important foraging, retreat, and burrowing sites for amphibians (Dodd 1996; deMaynadier & Hunter 1998; Herbeck & Larsen 1999; Naughton et al. 2000). Agricultural cultivation also may negatively influence the postmetamorphic body size of amphibians (Gray & Smith 2004).

Several studies have been conducted in North America examining the effects of forest disturbance (e.g., clearcutting, timber thinning) on amphibian populations (e.g., deMaynadier & Hunter 1995; Gibbs 1998*b*; Herbeck & Larsen 1999; Naughton et al. 2000). However, few data exist (cf. Knutson et al. 1999; Kolozsvary & Swihart 1999) on the effects of agricultural cultivation (Dodd 1997:178), though it is generally assumed that agriculture negatively influences amphibian populations (Semlitsch 2000). Recent evidence suggests that some amphibian assemblages may become nested in wetlands within disturbed landscapes (Hecnar & M'Closkey 1997; Wright et al. 1998) and thus may be positively associated with agricultural cultivation on a local scale (Knutson et al. 1999; Kolozsvary & Swihart 1999).

Two primary land-use types exist in the Southern High Plains of Texas: cultivation and intact grassland (Haukos & Smith 1994). Because playa wetlands are numerous, are similar structurally, and exist in their own watershed (Smith & Haukos 2002), they are ideal systems in which to test the effects of anthropogenic landscape disturbance on amphibians. Our objective was to determine whether the relative daily abundance and diversity of seven species and three age classes of amphibians residing in playa wetlands in the Southern High Plains was different between two general agricultural land-use types (cultivation vs. grassland) and between years (1999 vs. 2000).

Methods

Our study was conducted in the Southern High Plains of Texas (Sabin & Holliday 1995). We used playa wetlands as experimental units of land-use and year effects (Bolen et al. 1989; Smith 2003). Playas are small depressional wetlands with variable and often ephemeral hydroperiods that typically receive surface runoff from precipitation between May and September (Smith 2003). Playas located in grassland and cropland were surrounded (i.e., ≤3 km from the playa center) by >75% natural or replanted grass and agricultural vegetation, respectively (Gray 2002). We chose the ≤3 km threshold for land-use treatment designation because it probably was the near-maximum dispersal distance for our species (cf. Gehlbach 1967; Gehlbach et al. 1969; Sinsch 1990, 1997; Miaud et al. 2000). Cropland landscapes were primarily cotton (*Gossypium hirsutum*) and sorghum (*Sorghum vulgare*; Gray 2002). Normal farming practices in the Southern High Plains, such as herbicide and pesticide application and center-pivot irrigation, existed in cultivated landscapes (Gray 2002). Grassland landscapes were uncultivated and vegetated with native or replanted grasses and forbs (Gray 2002). Low grazing intensity (i.e., <1 head/ha) existed in all grassland landscapes (M.J.G., unpublished data).

We randomly selected 16 playas (4 per land use per year) in March 1999 and 2000. Average study playa size in cropland and grassland landscapes was 11.5 ha (SE = 2.3) and 9.4 ha (SE = 2.4); mean size was not statistically different between land-use types ($t_{14,0.05} = 0.62$, $p = 0.55$). Mean hydroperiod (i.e., measured from the date amphibian sampling started until playas dried) of grassland playas ($\bar{x} = 123$ days, SE = 10) was greater than that of cropland playas ($\bar{x} = 79$ days, SE = 13, $t_{14,0.05} = 2.52$, $p = 0.02$).

Playas were partially enclosed (i.e., 25% of the circumference) with continuous 60-cm-high drift fences and 19-L pitfall traps prior to anuran breeding (Dodd & Scott 1994). A cardinal quadrant was randomly selected for placement of fence and pitfalls. Fence and pitfalls were placed approximately 10 m upslope from and parallel to the playa edge (i.e., the clay-silt loam line; Luo et al. 1997). One 10-m perpendicular lead centered at the main fence existed at each end. Vegetation underneath the main fence and leads was removed, and bases were covered with soil to reduce the probability of trespass. Pitfalls were placed on alternate sides of the fence at 10-m intervals, with openings flush to the ground (Dodd & Scott 1994). Water and sponges were placed in pitfalls to reduce desiccation of captured individuals (Daoust 1991). Pitfall traps were checked alternate days in each land use for captures from 16 May to 17 October 1999 and 19 April to 18 August 2000. Sampling was terminated when no individuals were captured at ≥75% of the study playas for 2 consecutive weeks.

Captured individuals were enumerated by species and age: metamorph (juveniles <1 year), subadult (>1 year but not displaying secondary sexual characters), adult (>1 year and possessing reproductive morphology such as vocal sacs, nuptial excrescences, or eggs for anurans, and enlarged cloaca for salamanders) (Duellman & Trueb 1994). We did not designate a subadult category for the barred tiger salamander (*Ambystoma tigrinum mavortium*) because distinction is based on color (Webb & Roueche 1971), which can be dependent on hydroperiod in playas (Rose & Armentrout 1976). Individuals were toe-clipped uniquely with sterilized scissors (i.e., soaked in 0.01% chlorhexidine gluconate) and released on the opposite side of the fence after marking (Dodd & Scott 1994). All sampling techniques followed the approved protocol of the Texas Tech University Animal Care and Use Committee (permit 99843).

We used mean daily capture per playa as an estimate of relative daily abundance (Dodd & Scott 1994). Mean daily diversity of the amphibian assemblage was also calculated with the Shannon-Weaver algorithm (Hair 1980). We assumed that these demographic parameters were estimates of amphibian population size and composition and meaningful for relative comparison between land-use types and years. Mean total capture (adjusted for playa size) was compared between levels of main effects (M.J.G., unpublished data); these results are not presented, however, because numerical trends were identical to mean daily abundance results.

Our experiment was arranged as a three-factor factorial design (Montgomery 2001) in which land use, year, and species captured were crossed-fixed effects. We analyzed demographic parameters for seven species: *Spea multiplicata* (New Mexico spadefoot, NSF), *S. bombifrons* (plains spadefoot, PSF), *Bufo cognatus* (Great Plains toad, GPT), *B. woodhousii* (Woodhouse's toad,

WHT), *Pseudacris clarkii* (spotted chorus frog, SCF), *Rana blairi* (plains leopard frog, PLF; Mecham et al. 1973), *Ambystoma tigrinum mavortium* (barred tiger salamander, BTS). These amphibians are explosive breeders (i.e., complete simultaneous breeding in 1–3 days; Sullivan & Fernandez 1999) and generally complete larval development in 2–6 weeks (Degenhardt et al. 1996). We captured two additional species—*B. debilis* Girard (green toad) and *Gastrophryne olivacea* (Great Plains narrowmouth toad)—but there were insufficient capture data for analysis.

We used a three-factor analysis of variance (ANOVA) model with days as subsamples to test for differences ($\alpha = 0.05$) in the relative abundance of individuals between land-use types and years and among species (Montgomery 2001:194–196). We used a two-factor ANOVA model (land-use and year main effects) with days as subsamples to analyze diversity because species were combined to calculate the Shannon-Weaver index. Nonadditivity was tested by including all two- and three-way interactions in the models (Montgomery 2001:194). When nonadditivity was violated (i.e., ≥1 interaction significant), analyses were separated by species to test for differences between land uses and years (i.e., two-way ANOVAs) and by land use and year to test for a species effect (i.e., one-way ANOVAs). For species that differed in response between levels of land use or year, we performed a post hoc set of two-way ANOVAs with land use and year as crossed factors but by age class to discern which age category was responsible for the observed abundance differences. Age was not included as a factor in the initial analyses, because there was no subadult category for the barred tiger salamander (i.e., design was unbalanced) and levels of age likely were not independent. Also, this analytical approach conserved the experiment-wise error rate at the lowest probability for main effect ANOVAs because only significant species were analyzed in post hoc tests. Tukey's honest significant difference multiple-comparison test was used to test for differences among species when the main effect ANOVA was significant (Westfall et al. 1999:179). We natural log–transformed all data to meet linear model assumptions of normality and homoscedasticity; means and standard errors were back-transformed for presentation.

Results

The mean daily abundance of amphibians was different between land uses and years and among species (Table 1). Cropland playas ($\bar{x} = 71.5$, SE = 1.4) had greater abundance of amphibians than grassland playas ($\bar{x} = 22.4$, SE = 1.4), and abundance was greater in 1999 ($\bar{x} = 67.8$, SE = 1.4) than 2000 ($\bar{x} = 23.5$, SE = 1.4). However, the species effect interacted with land use and marginally interacted with year (Table 1); therefore, analyses were separated by species.

Table 1. Inferential statistics for analyses of variance (ANOVAs) testing differences in relative daily abundance and diversity of amphibians between land-use types (cropland vs. grassland) and years and among species at 16 playa wetlands on the Southern High Plains, Texas, May–October 1999 and April–August 2000.

Variable	Test and effect[a]	df[b]	F	p
Abundance	*three-way ANOVA*			
	land use	1	11.97	<0.001
	year	1	10.54	0.002
	species	6	55.67	<0.001
	land use × year	1	0.80	0.375
	land use × species	6	8.36	<0.001
	year × species	6	2.52	0.051
	land use × year × species	6	1.40	0.223
	two-way ANOVA			
	NSF			
	land use	1	20.33	<0.001
	year	1	2.63	0.131
	land use × year	1	2.34	0.152
	BTS			
	land use	1	1.26	0.283
	year	1	8.08	0.015
	land use × year	1	0.02	0.895
	GPT			
	land use	1	0.01	0.913
	year	1	2.35	0.152
	land use × year	1	0.11	0.747
	PSF			
	land use	1	7.94	0.016
	year	1	0.51	0.489
	land use × year	1	3.30	0.094
	SCF			
	land use	1	0.23	0.639
	year	1	1.99	0.184
	land use × year	1	0.11	0.751
	PLF			
	land use	1	0.156	0.156
	year	1	0.289	0.289
	land use × year	1	0.151	0.151
	WHT			
	land use	1	0.33	0.576
	year	1	1.00	0.338
	land use × year	1	0.97	0.345
	one-way ANOVA			
	cropland species	6	34.20	<0.001
	grassland species	6	18.74	<0.001
	1999 species	6	20.06	<0.001
	2000 species	6	15.56	<0.001
Diversity[c]	*two-way ANOVA*			
	land use	1	0.91	0.359
	year	1	0.29	0.602
	land use × year	1	1.04	0.329

[a] *Overall three-way ANOVA on abundance was separated by species to test for differences between land uses and years (two-way analyses) and then by land use and year (one-way analyses) to test the species effect because species interacted with land use and year in the three-way analysis. Abbreviations: NSF, New Mexico spadefoot; BTS, barred tiger salamander; GPT, Great Plains toad; PSF, plains spadefoot; SCF, spotted chorus frog; PLF, plains leopard frog; and WHT, Woodhouse's toad.*

[b] *Error (denominator) df for three-way ANOVA, two-way ANOVAs, and one-way ANOVAs were 84 (2 land uses × 2 years × 7 species × 3 playas), 12 (2 land uses × 2 years × 3 playas), and 49 (7 species × 7 playas), respectively.*

[c] *Diversity was calculated with the Shannon-Weaver algorithm (Hair 1980:273).*

Mean daily abundance of NSF and PSF was greater at cropland than grassland playas, and abundance was greater in 1999 than 2000 for BTS (Table 2). Mean daily abundance also differed among species across and within levels of land-use and year main effects. The New Mexico spadefoot was the most abundant species at cropland playas. Mean daily abundance of BTS, GPT, and PSF was greater than that of SCF, PLF, and WHT at cropland playas. New Mexico spadefoots, BTS, GPT, and PSF were more abundant than SCF, PLF, and WHT at grassland playas. Mean daily abundance of NSF was greater than that of all other species except BTS in 1999 and 2000. Barred tiger salamanders were more abundant than all other species except NSF and GPT in 1999, and they were more abundant than all other species except NSF, GPT, and PSF in 2000. The mean daily abundance of GPT was greater than that of SCF, PLF, and WHT in 1999 and 2000. Plains spadefoots were more abundant than PLF and WHT in 2000. No differences were detected in amphibian diversity between land uses and years (Table 2).

The mean daily abundance of adult NSF was greater at cropland than grassland playas. Land-use and year effects interacted for metamorph and subadult NSF; therefore, analyses were separated by main effects (Tables 3 & 4). Metamorph NSF were more abundant at cropland than grassland playas in 1999, and they were more abundant in 1999 than 2000 at cropland playas. The mean daily abundance of subadult NSF was greater at cropland than at grassland playas in 2000, and abundance was greater in 2000 than 1999 at cropland and grassland playas. Abundance of metamorph PSF was greater in 1999 than 2000, and adult PSF were more abundant in 2000 than 1999. Land-use and year effects interacted for subadult PSF; therefore, analyses were separated by main effects. The mean daily abundance of subadult PSF was greater at cropland than grassland playas in 2000, and abundance was greater in 2000 than 1999 at cropland playas. Metamorph BTS were more abundant in 1999 than 2000. No additional differences were detected between land-use types and years in mean daily abundance for age classes of significant species (Table 2).

Discussion

The mean daily abundance of spadefoots was generally greater at playa wetlands surrounded by cultivation than at grassland playas, and abundance of barred tiger salamanders was greater in 1999 than 2000. In general, the New Mexico spadefoot was the most abundant species, followed by the barred tiger salamander and Great Plains toad. No difference in mean daily diversity of the amphibian assemblage was detected between land-use types and years.

Table 2. Relative daily abundance and diversity of amphibians between land-use types and years and among species at 16 playa wetlands on the Southern High Plains, Texas, May–October 1999 and April–August 2000.

| Variable | Species[a] | Land use[b] | | | | | | Year[b] | | | | | |
| | | cropland | | | grassland | | | 1999 | | | 2000 | | |
		x̄	SE	p ≤ 0.05	x̄	SE	p ≤ 0.05	x̄	SE	p ≤ 0.05	x̄	SE	p ≤ 0.05
Abundance	NSF	53.2	1.5	Aa	6.1	1.4	Ba	26.5	1.9	Aa	12.1	1.5	Aa
	BTS	7.1	1.3	Ab	10.3	1.3	Aa	13.7	1.2	Aab	5.4	1.3	Bab
	GPT	5.1	1.3	Ab	5.4	1.4	Aa	7.2	1.3	Abc	3.8	1.3	Ab
	PSF	4.1	1.3	Ab	2.0	1.2	Ba	2.6	1.2	Acd	3.1	1.3	Abc
	SCF	1.3	1.1	Ac	1.2	1.1	Ab	1.4	1.1	Ad	1.1	1.0	Acd
	PLF	1.2	1.1	Ac	1.1	1.0	Ab	1.2	1.1	Ad	1.1	1.0	Ad
	WHT	1.2	1.0	Ac	1.1	1.0	Ab	1.2	1.1	Ad	1.1	1.0	Ad
Diversity		1.3	0.2	A	1.1	0.1	A	1.2	0.1	A	1.3	0.1	A

[a] *Abbreviations: NSF, New Mexico spadefoot; BTS, barred tiger salamander; GPT, Great Plains toad; PSF, plains spadefoot; SCF, spotted chorus frog; PLF, plains leopard frog; WHT, Woodhouse's toad; all species used in estimation of Shannon-Weaver diversity index.*

[b] *Playa wetlands per land use and year, n = 8. The x̄s and SEs were back transformed from natural logs for presentation. Land use and year means within rows (species and diversity) followed by unlike uppercase letters are different by two-way analysis of variance (Table 1); land use and year means within columns (among species) followed by unlike lowercase letters are different by Tukey's honest significant difference.*

Land-Use Effect

Abundance of spadefoots may have been elevated at cropland playas because landscape disturbance confined individuals to the remnant available habitat (i.e., the playa; Kolozsvary & Swihart 1999). Spadefoots may have become more nested in cropland wetlands than other species because of their relatively low vagility and individual perception of patch viscosity and edge permeability in adjacent agricultural fields (Wiens 1997). Indeed, geometric complexity and edge density were greater in cropland than grassland landscapes (Gray 2002). Road density was also greater in cropland than grassland landscapes, which can decrease permeability (Yanes et al. 1995). Thus, dispersing spadefoots may have been unable to penetrate complex cropland landscapes, resulting in increased nestedness and abundance at their natal wetlands (Kolozsvary & Swihart 1999).

Table 3. Relative daily abundance for each age class of amphibian species that differed significantly in relative daily abundance between land-use types and years (see Table 1) at 16 playa wetlands on the Southern High Plains, Texas, May–October 1999 and April–August 2000.

| Species[a] | Age | Year[b] | Land use[c] | | | | | |
| | | | cultivation | | | grassland | | |
			x̄	SE	p ≤ 0.05	x̄	SE	p ≤ 0.05
NSF	metamorph	1999	100.5	1.7	Aa	3.1	1.8	Ba
		2000	1.6	1.5	Ab	2.2	2.1	Aa
	subadult	1999	1.2	1.0	Aa	1.3	1.2	Aa
		2000	11.8	1.4	Ab	2.1	1.1	Bb
	adult	1999	8.9	1.2	Aa	3.5	1.5	Ba
		2000	12.2	1.2	Aa	3.2	1.5	Ba
PSF	metamorph	1999	2.6	1.2	Aa	1.9	1.3	Aa
		2000	1.3	1.2	Ab	1.0	1.0	Ab
	subadult	1999	1.0	1.0	Aa	1.1	1.0	Aa
		2000	3.3	1.4	Ab	1.2	1.0	Ba
	adult	1999	1.3	1.2	Aa	1.3	1.1	Aa
		2000	2.9	1.3	Ab	1.6	1.1	Ab
BTS	metamorph	1999	8.9	1.7	Aa	14.5	1.1	Aa
		2000	2.6	1.2	Ab	4.7	1.5	Ab
	adult	1999	2.2	1.2	Aa	2.4	1.3	Aa
		2000	2.7	1.3	Aa	3.2	1.4	Aa

[a] *Abbreviations: NSF, New Mexico spadefoot, PSF, plains spadefoot, and BTS, barred tiger salamander.*

[b] *Analyzed by year for metamorph NSF and subadult NSF and PSF because land-use and year main effects interacted (Table 4); statistics for remaining species and ages are presented by year for tabular parsimony.*

[c] *Playa wetlands per land use per year, n = 4; x̄s and SEs were back transformed from natural logs. Within-species means in the same row (within ages and years) with unlike uppercase letters are different (land-use effect); means in the same column within species and ages with unlike lowercase letters are different (year effect).*

Table 4. Inferential statistics for analyses of variance (ANOVAs) for species (by age class) that differed significantly in relative daily abundance between land-use types (cropland vs. grassland) or years (see Table 1) at 16 playa wetlands on the Southern High Plains, Texas, May–October 1999 and April–August 2000.

Species[a]	Test and effect[b]	df	F	p
two-way ANOVA				
NSF	metamorph			
	land use	1,12	6.79	0.023
	year	1,12	13.99	0.003
	land use × year	1,12	10.19	0.008
	subadult			
	land use	1,12	17.18	0.001
	year	1,12	50.06	<0.001
	land use × year	1,12	21.26	<0.001
	adult			
	land use	1,12	14.02	0.002
	year	1,12	0.10	0.758
	land use × year	1,12	0.48	0.499
PSF	metamorph			
	land use	1,12	1.93	0.189
	year	1,12	12.1	0.005
	land use × year	1,12	0.001	0.966
	subadult			
	land use	1,12	6.74	0.023
	year	1,12	11.69	0.005
	land use × year	1,12	8.66	0.012
	adult			
	land use	1,12	3.71	0.078
	year	1,12	7.88	0.016
	land use × year	1,12	2.79	0.121
BTS	metamorph			
	land use	1,12	2.07	0.176
	year	1,12	10.50	0.007
	land use × year	1,12	0.01	0.909
	adult			
	land use	1,12	0.22	0.648
	year	1,12	0.76	0.399
	land use × year	1,12	0.01	0.907
one-way ANOVA				
NSF	metamorph			
	land-use effect in 1999	1,6	17.46	0.006
	land-use effect in 2000	1,6	0.17	0.698
	year effect in cropland	1,6	34.84	0.001
	year effect in grassland	1,6	0.11	0.747
NSF	subadult			
	land-use effect in 1999	1,6	0.36	0.570
	land-use effect in 2000	1,6	22.55	0.003
	year effect in cropland	1,6	43.66	<0.001
	year effect in grassland	1,6	6.96	0.039
PSF	subadult			
	land-use effect in 1999	1,6	1.96	0.211
	land-use effect in 2000	1,6	7.79	0.032
	year effect in cropland	1,6	10.59	0.017
	year effect in grassland	1,6	1.27	0.302

[a] *Abbreviations: NSF, New Mexico spadefoot; PSF, plains spadefoot; and BTS, barred tiger salamander.*
[b] *Overall two-way ANOVA on abundance of significant species was separated by land use and year for metamorph NSF, subadult NSF and PSF (one-way analyses) because land-use and year main effects interacted.*

Spadefoot vagility may have been less than that of other species in the Southern High Plains because of their relatively small postmetamorphic body size (With & Crist 1995; Gray et al. 2004). Species-specific perception of landscape context and migration distance is positively correlated with body size for various organisms (e.g., Peters 1983:89–91; Crist et al. 1992; With 1994). Excepting the spotted chorus frog, spadefoots were smaller physically than other species we monitored. We would expect the spotted chorus frog to be affected similarly by landscape disturbance if amphibian demographics in playa wetlands were exclusively dictated by the relative connectivity between them. Differences may not have been detected in demographics between land-use types for the spotted chorus frog because they have relatively low abundance in the Southern High Plains (Anderson et al. 1999). Alternatively, other proximate factors may be responsible for demographic responses to anthropogenic land use.

Elevated spadefoot abundance in cropland playas may have been a consequence of changes in the trophic structure of the aquatic environment. The barred tiger salamander may function as a keystone intraguild predator (sensu Paine 1969; Polis & Holt 1992) in playas, as do different species in other wetland systems (e.g., *Ambystoma opacum*; Walls & Williams 2001) because they can establish neotenic populations prior to anurans if water is present during winter or early spring (Rose & Armentrout 1974, 1976). Indeed, the density of larval and neotenic barred tiger salamanders was greater in seine-net plots from our playas surrounded by grassland than in cropland playas, presumably because of longer hydroperiods in grassland playas (Gray 2002). Grassland playas generally have greater volume and longer hydroperiods than cropland playas because of differential sedimentation (Luo et al. 1997).

Spadefoot larvae may have been more susceptible to predation in grassland playas than other species because of their relative palatability and escape probability (Alford 1999:260–264). Spadefoots typically inhabit semiarid environments worldwide and exploit ephemeral water sources with few vertebrate or invertebrate predators (Bragg 1965; Dimmitt 1975). Spadefoots also have physiological mechanisms for rapid growth (Richmand 1947; Newman 1992) but lack the tools, such as toxicity, cryptic coloration, or altered microhabitat use, to efficiently escape predators (e.g., *Spea bombifrons*; Kruse & Francis 1977). For example, spadefoot tadpoles are more active than tadpoles of certain *Bufo*, *Rana*, and *Pseudacris* species, so they are more conspicuous and vulnerable to predation (Morin 1983; Woodward 1983; Dayton & Fitzgerald 2001). Spadefoot tadpoles also lack dermal toxins and cryptic coloration unlike many species of *Bufo*, *Rana*, and *Pseudacris* (e.g., Walters 1975; Formanowicz & Brodie 1982; Peterson & Blaustein 1991; Smith & Van Buskirk 1995).

Spadefoots also may have been the most abundant species in cropland playas because of their relative competitive or predatory ability (Morin 1983; Wilbur 1987; Dayton & Fitzgerald 2001). In the absence of significant top-down predatory control (as likely existed in cropland playas because of reduced abundance of aquatic barred tiger salamanders), spadefoots can outcompete other amphibian species for food and other resources, resulting in increased recruitment (Woodward 1982; Wilbur 1987; Dayton & Fitzgerald 2001). Several laboratory experiments have documented that spadefoot tadpoles are competitively dominant in anuran communities when aquatic predators are absent (e.g., Morin 1981, 1983; Wilbur 1987). Moreover, spadefoots may be predators on the eggs and larvae of other species (Petranka & Kennedy 1999).

Other modifications of the aquatic and terrestrial environments may have positively influenced spadefoot populations at cropland playas. Smith and Haukos (2002) noted that plant diversity and structure could be greater in cropland playas, which could increase food resources and escape cover for larvae. Nitrogen influx from fertilizers may have increased food resources for larval amphibians in cropland playas (Leibold & Wilbur 1992). Pesticide drift and runoff into cropland playas also may have reduced the density of aquatic insects (Boone & Semlitsch 2001), which can compete with amphibian larvae for food resources (Morin et al. 1988). If any of the aforementioned suggestions were strictly true, however, we should have observed similar demographic responses by species other than spadefoots. Thus, these factors probably were not the ultimate reasons for the observed demographics between our disturbed and undisturbed landscapes.

Year Effect

Yearly differences in abundance occurred because of a greater number of metamorph New Mexico and plains spadefoots and barred tiger salamanders in 1999 than 2000. Abundance differences between years were likely related to precipitation (Berven 1995; Semlitsch et al. 1996). Average monthly rainfall at our playas was two times greater in 1999 ($\bar{x}$ = 15.1 cm, SE = 1.6) than 2000 ($\bar{x}$ = 7.3 cm, SE = 3.5). Rainfall stimulates amphibian emergence (Dimmitt & Ruibal 1980*a*) and positively affects intra- and interdemic movement (Hurlbert 1969; Sinsch 1988). Amphibian survival can also be positively related to rainfall (e.g., Berven 1990), presumably because the density of food resources increases (Dimmitt & Ruibal 1980*b*) and the probability of desiccation decreases (Jaeger 1980; Newman & Dunham 1994). The probability of breeding, larval survival, and juvenile recruitment also increases with rainfall because wetland hydroperiod is positively correlated with rainfall (Pechmann et al. 1989; Sinsch & Seidel 1995; Semlitsch et al. 1996). Indeed, the mean duration of hydroperiod at our study wetlands was greater in 1999 than 2000 (Gray 2002).

Conservation Implications

Agricultural disturbance around wetlands may positively influence the abundance of some amphibian species. Less vagile amphibians that explosively breed and are competitively dominant in the absence of predation, such as spadefoots, may benefit most by landscape cultivation. An elevated abundance of individuals in cropland landscapes, however, does not necessarily imply better conditions for amphibian populations (Yeargers et al. 1996). Populations with elevated abundance may be less stable, particularly if they exceed their carrying capacity or have a high intrinsic rate of increase (Edelstein-Keshet 1988). Pathogenic incidence can also be positively correlated with population density (Hastings 1996). Additionally, landscape disturbance may negatively affect the interdemic movement and genetic structure of populations (Reh & Seitz 1990). Research in the Southern High Plains also indicates that the postmetamorphic body size, temporal demographics, and diet diversity of amphibians can be negatively affected by agricultural cultivation (Gray 2002; Gray & Smith 2004; Smith et al. 2004). Amphibian assemblages at playa wetlands in cultivated landscapes also may function as ecological sinks more often than sources (Gray 2002). Thus, amphibian assemblages in disturbed landscapes may have a greater probability of local or metapopulation extinction than those positioned in natural landscapes, despite the elevated abundance of some species.

Additional research is needed to discern proximate and ultimate mechanisms driving population responses to landscape cultivation. For example, the effects of chemical and mechanical disturbance in and around wetlands on the trophic structure of invertebrate and amphibian communities needs to be investigated. Pathogenic incidence in amphibians (i.e., viruses, fungi, bacteria, and parasites) should also be quantified in disturbed and undisturbed wetland systems. Estimates of land-use type and boundary permeability to amphibian movement are needed as well (e.g., Rothermel & Semlitsch 2002). Such estimates would enable conservation biologists to assign permeability and hardness indices to cover types and boundaries in spatial analysis programs and subsequently estimate the relative connectivity of habitat patches and extinction probabilities for local populations. Finally, our results suggest that annual rainfall may be an important variable to include in population viability models for amphibians.

Acknowledgments

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