INFLUENCE OF LAND USE ON POSTMETAMORPHIC BODY SIZE OF PLAYA LAKE AMPHIBIANS

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Abstract: Agricultural land use may indirectly affect the body size of amphibians by altering the hydroperiods of nearby wetlands and influencing amphibian densities—both factors which can limit the larval and postmetamorphic growth rates of amphibians. We measured postmetamorphic body size for 4 species (*Spea multiplicata, S. bombifrons, Bufo cognatus, Ambystoma tigrinum mavortium*) and 3 age classes (metamorph, subadult, adult) of amphibians captured at playa wetlands surrounded by one of 2 general land-use types (cultivation, grassland) in the Southern High Plains. Sixteen playas (4 per land-use type in 1999 and 2000) were partially enclosed with drift fence and pitfall traps, and mass and snout-vent length (SVL) were measured from a subsample of captured individuals. Mass and SVL were 10–148% greater for amphibians captured at grassland wetlands than at cropland wetlands for most species and age classes. Mass and SVL also were 3–124% greater in 1999 than in 2000 for most species and age classes. We attribute differences in body size between land-use types to differences in the hydroperiods of the associated wetlands, and potentially to variation in the density of terrestrial conspecifics and aquatic predators. We attribute differences in body size between years to differences in rainfall. Body size is positively related to the probability of survival, reproduction, and evolutionary fitness in amphibians. Thus, if cultivation of landscapes surrounding wetlands negatively influences postmetamorphic body size of amphibians, restoration of native grasslands surrounding playa wetlands may help prevent local amphibian declines.

Anthropogenic land use of areas surrounding wetlands may affect larval and postmetamorphic amphibians (Hecnar and M'Closkey 1996; Bonin et al. 1997a,b; Dodd 1997; Alford and Richards 1999; Semlitsch 2000) by influencing many ecological mechanisms that regulate the growth and mortality rates of individuals in aquatic and terrestrial environments (Werner 1986). Agricultural cultivation (i.e., arable cropland) may confine amphibians to wetlands, resulting in species associations and population densities different from those that are found in similar, undisturbed ecosystems (Knutson et al. 1999, Kolozsvary and Swihart 1999, Gray et al. 2004a). Consequently, landscape cultivation may influence postmetamorphic body size of amphibians by affecting density of conspecifics (Oldham 1985). Cultivation of the watershed also can increase sedimentation in wetlands, which decreases hydroperiods (Martin and Hartman 1987, Corn and Bury 1989, Luo et al. 1997), and may reduce the duration of larval development (Brady and Griffiths 2000). Agricultural chemicals (nitrates, ammonia, organophosphates) can bioaccumulate and reduce food densities, foraging activity, and growth of larval amphibians (Hall and Kolbe 1980; Baker and Waights 1993, 1994; Freemark and Boutin 1995; Hecnar 1995; Semlitsch et al. 1995), with possible negative effects on postmetamorphic body size.

No studies have been conducted in North America examining the influence of general agricultural land use on postmetamorphic body size of amphibians. Understanding this possible relationship is important because body size positively influences survival, reproduction, and recruitment of amphibians (Wilbur 1984, Semlitsch et al. 1988). Research has shown larger amphibians within a species are better at acquiring food resources, escaping predators, withstanding dehydration, and attracting mates than are smaller individuals (Berven 1981, Newman and Dunham 1994, Newman 1999, Beck and Congdon 2000). Also, larger female amphibians have greater fecundity than smaller females (Berven 1982, Semlitsch 1985, Krupa 1986). Thus, amphibian populations composed of larger individuals may be less likely to experience demographic declines than those composed of smaller individuals.

As anthropogenic disturbance generally negatively affects wildlife populations (Primack 2000), we hypothesized that cultivation of terrestrial landscapes surrounding wetlands would negatively influence body size of amphibians. We tested for this relationship in 4 species (New Mexico spadefoot, *Spea multiplicata*; plains spadefoot, *S. bombifrons*; Great Plains toad, *Bufo cognatus*; and barred tiger salamander, *Ambystoma tigrinum*

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mavortium) and 3 age classes (metamorph, subadult, and adult) of amphibians using playa wetlands surrounded by either cropland or uncultivated grassland in the Southern High Plains. These species are the most abundant in this region (Rose and Armentrout 1974, Anderson 1997, Gray 2002).

STUDY AREA

Our study was conducted in the Southern High Plains (SHP) of Texas, USA. The SHP are on the largest continuous plateau in the United States (the Llano Estacado), encompassing ca. 8.9 million ha (Haukos and Smith 1994). Primary land uses in the SHP are agricultural cultivation (2.7 million ha, 46%) and grassland (2.9 million ha, 49% [native and replanted lands combined], Haukos and Smith 1994). The most important amphibian habitat in the SHP is playa lakes (Bolen et al. 1989). Playas are small depressional wetlands with erratic and often ephemeral hydroperiods; they typically receive surface runoff from precipitation between May and September (Smith 2003).

We randomly selected 8 inundated playas (4 per land-use type per year) in March 1999 and March 2000. We considered playas to be in grassland if ≥75% of the surrounding landscape (i.e., area ≤3 km from the playa center) was uncultivated and vegetated, and to be in cultivation if ≥75% of the surrounding landscape was arable cropland (Anderson et al. 1999:760). We chose the 3 km threshold for land-use treatment designation because it was similar to the maximum dispersal distance for our species (Gehlbach 1967; Gehlbach et al. 1969; Sinsch 1990, 1997; Miaud et al. 2000).

Playas that were inundated and available for sampling in each land-use type were geographically separated ($\bar{x}$ = 97 km, SD = 11). Grassland playas were located in Castro County northeast of Dimmitt, Texas, USA (Gray 2002:12). Playas surrounded by cropland were located in Hale and Floyd counties near Plainview, Texas, in 1999 and north of Ralls, Texas, in Crosby County in 2000 (Gray 2002:12). Some variables that may differ geographically and influence amphibians (e.g., vegetation, temperature, rainfall) were measured during amphibian sampling and did not differ statistically between the land-use types (Gray 2002).

METHODS

Sampling Techniques

Terrestrial capture.—We partially enclosed playas with continuous 60-cm high drift fence ($\bar{x}_{length}$=

330 m per playa, 25% of circumference) (Dodd and Scott 1994). Pitfall traps (19-L volume) were placed on alternate sides of the fence at 10-m intervals with openings flush to the ground (Dodd and Scott 1994). We checked pitfall traps in each land-use type on alternate days for captures from 16 May–17 October 1999 and 19 April–18 August 2000. Pitfall traps at 4 playas within 1 land-use type were opened near dusk (1800–2100 hr) before the night of intended capture, and captures were processed the next afternoon (1400–1800 hr). As we closed pitfall traps in 1 land-use type, we opened pitfall traps at the 4 playas in the other land-use type.

Biological processing.—We classified individuals by species and age as metamorph (juveniles <1 yr), subadult (>1 yr but not displaying secondary sexual characteristics), and adult (>1 yr and possessing reproductive morphology such as vocal sacs, nuptial excrescences, or eggs [anurans], and enlarged cloaca [salamander]; Duellman and Trueb 1994:33–38, 52–60). We did not designate a subadult category for barred tiger salamander because distinction is based on color (Webb and Roueche 1971), which can depend on hydroperiod in playas (Rose and Armentrout 1976). Snout-vent length (SVL) and mass were measured for the first 5 individuals captured per playa per species per age class per day. It was not possible to measure all individuals captured at each playa, because number of captures exceeded 14,000 individuals on some days (Gray 2002). Our total sample sizes of measured individuals were 2,816 and 2,372 in cultivation and grassland, respectively. Individuals were toe-clipped; recaptured individuals were not measured. Sampling techniques followed approved Texas Tech University Animal Care and Use Committee protocol (#99843).

Statistical Analyses

Independent factors were arranged as a 3-way factorial-nested design (Montgomery 2001:569–573). Land uses and years were crossed factors and considered fixed effects. Playas were nested within land uses and years and treated as a random effect. The unit of replication was the individual. Interdependencies among individuals nested within playas were expected and modeled in the response using an unrestricted mixed model (Hocking 1973, Montgomery 2001:526–527).

We used multivariate analysis of variance (MANOVA) to test for differences (α = 0.05) in body size within species and age classes between land-use types and years and among playas. Gen-

ders were not analyzed separately, because a priori analyses indicated gender did not interact with land-use type. We assumed the matrix of SVL and body mass response vectors represented a multivariate description of body size. We used an unrestricted mixed MANOVA model with an unstructured covariance matrix for factorial-nested designs to account for between- and within-subject heterogeneity (Littell et al. 1991:120–126; Littell et al. 1996:269, 293; Montgomery 2001:526–527). Consequently, it was not necessary to assume sphericity or other covariance structures (Littell et al. 1996:99). Because sample size generally was large (i.e., $n \geq 30$ individuals per level per effect), we assumed average body size per effect approximated a bivariate normal density (Milton and Arnold 1995:241, Johnson and Wichern 1998:187). We also used the Pillai-Bartlett trace test statistic, because it can be more powerful and robust than other statistics (e.g., Wilk's likelihood ratio) if multivariate assumptions are violated (Olson 1974, 1976, 1979). We tested additivity of fixed main effects by including an interaction term in the mixed model (Montgomery 2001:526); analyses were separated into simple main effects (i.e., land-use type by year and year by land use) when this assumption was violated. Westfall-Young's (1993:113–121) multivariate multiple comparison method was used to test for simple effect differences in body size between levels of fixed effects when a MANOVA was significant (Westfall et al. 1999:227–239). We used the SAS® system to perform all analyses (Littell et al. 1991, 1996; Westfall et al. 1999).

RESULTS

Land-use Type and Year Interaction Effects

Land-use and year effects interacted significantly for all species and age classes except adult plains spadefoot (Table 1). Tests with significant interactions were analyzed separately by land-use and year effects (see next 2 sections). Multivariate tests with main-effect interactions could not be performed for metamorph Great Plains toad and plains spadefoot, and subadult plains spadefoot, because no individuals were captured in grassland in 2000 and cropland in 1999, respectively. Thus, we separated these analyses immediately by land use and year. Also, no analyses were performed for subadult barred tiger salamander, because there was no subadult category for this species.

Body size of adult plains spadefoots was 7% greater at grassland playas than at cropland playas

Table 1. Inferential statistics for multivariate analysis of variance tests on differences in body size of amphibians between land-use types (cultivation vs. grassland), years, and their interaction at 16 playa wetlands in the Southern High Plains of Texas, USA, 1999 and 2000.

Species[a]	Age class[b]	Effect[c]	df[d]	F	P
GPT	adult	land use × year	593	12.6	<0.001
	subadult	land use × year	325	19.4	<0.001
NSF	adult	land use × year	1,541	49.8	<0.001
	subadult	land use × year	383	12.3	<0.001
	metamorph	land use × year	577	12.2	<0.001
PSF	adult	land use	240	15	<0.001
		year	240	4.1	0.02
		land use × year	240	2.5	0.09
BTS	adult	land use × year	361	7.5	<0.001
	metamorph	land use × year	462	7.8	<0.001

[a] Abbreviations: GPT, Great Plains toad; NSF, New Mexico spadefoot; PSF, plains spadefoot; and BTS, barred tiger salamander.

[b] Tests with main-effect interactions could not be performed for metamorph GPT and PSF, and subadult PSF, because no individuals were captured in grassland in 2000 and cropland in 1999, respectively.

[c] Land-use and year effects presented only for adult PSF because land use and year interacted for all other species-age combinations.

[d] df = denominator degrees of freedom; numerator df = 2 for all tests.

and 5% greater in 1999 than in 2000 (Table 2). The differences in both SVL and mass were significant ($P \leq 0.001$) according to Westfall's multiple comparison method; this was true in all subsequent tests unless otherwise noted.

Land-use Type Main Effect

Adults.—Body size was 23%, 10%, and 15% greater at grassland playas than at cropland playas for adult Great Plains toad, New Mexico spadefoot, and barred tiger salamander, respectively, in 1999 (Tables 2, 3). Body size also was 24%, 22%, and 14% greater at grassland playas than at cropland playas for adult Great Plains toad, New Mexico spadefoot, and barred tiger salamander, respectively, in 2000.

Subadults.—Body size was 54%, 32%, and 46% greater at grassland playas than at cropland playas for subadult Great Plains toad, New Mexico spadefoot, and plains spadefoot, respectively, in 2000 (Tables 3, 4). Body size did not differ between land uses for subadult Great Plains toad and New Mexico spadefoot in 1999.

Metamorphs.—Body size was 148%, 23%, and 35% greater at grassland playas than at cropland playas for metamorph Great Plains toad, New Mexico spadefoot, and plains spadefoot, respectively, in 1999 (Tables 3, 5). Body size was not different between land uses for metamorph barred

Table 2. Adult body size of New Mexico spadefoot (NSF), plains spadefoot (PSF), Great Plains toad (GPT), and barred tiger salamander (BTS) between land-use types and years at 16 playa wetlands in the Southern High Plains of Texas, USA, Apr–Sep 1999 and 2000.

Size metric	Species	Year[a]	Cultivation				Grassland			
			n	$\bar{x}$	SE	$P \leq 0.05$[b]	n	$\bar{x}$	SE	$P \leq 0.05$
Snout-vent length (mm)	NSF	1999	536	42.1	0.1	Aa	409	44.4	0.2	Ba
		2000	401	38.7	0.2	Ab	206	43.7	0.2	Bb
	PSF	1999	45	46.1	0.6	Aa	57	49.2	0.7	Ba
		2000	77	43.9	0.4	Ab	72	46.9	0.4	Bb
	GPT	1999	256	72.4	0.5	Aa	164	80.2	0.6	Ba
		2000	76	64.9	0.9	Ab	108	75.3	0.8	Bb
	BTS	1999	63	92.6	1.8	Aa	107	101.4	0.9	Ba
		2000	66	81.3	0.9	Ab	100	86.5	1.2	Bb
Mass (g)	NSF	1999	536	8.5	0.1	Aa	409	9.8	0.1	Ba
		2000	401	7.2	0.1	Ab	206	9.4	0.2	Bb
	PSF	1999	45	11.4	0.5	Aa	57	12.2	0.4	Ba
		2000	77	9.7	0.3	Ab	72	11.5	0.3	Bb
	GPT	1999	256	51.5	1.1	Aa	164	70.1	1.7	Ba
		2000	76	40.5	1.7	Ab	108	53.8	1.8	Bb
	BTS	1999	63	39.7	2.8	Aa	107	48.1	1.6	Ba
		2000	66	22.3	0.9	Ab	100	27.1	1.4	Bb

[a] Analyzed by year because land-use and year main effects were not additive ($P \leq 0.001$, Table 1) for all species except PSF ($P = 0.09$); PSF statistics presented by year for tabular parsimony.
[b] Within-species means in the same row with unlike uppercase letters are different; means in the same column within size variables and species with unlike lower case letters are different.

tiger salamander in 1999. However, body size was 16% greater at grassland playas than at cropland playas for metamorph barred tiger salamander in 2000. Body size was 27% greater at cropland

Table 3. Inferential statistics for multivariate analysis of variance tests on differences in body size of amphibians between land-use types (cultivation vs. grassland) for each year at 16 playa wetlands in the Southern High Plains of Texas, USA, 1999–2000.

Species[a]	Age class[b]	Year	df[c]	F	P
GPT	adult	1999	411	47.2	<0.001
		2000	175	18.3	<0.001
	subadult	1999	62	0.7	0.49
		2000	256	13.7	<0.001
	metamorph	1999	335	114.1	<0.001
NSF	adult	1999	936	9.4	<0.001
		2000	598	90.6	<0.001
	subadult	1999	80	2.9	0.07
		2000	298	112.2	<0.001
	metamorph	1999	494	19.2	<0.001
		2000	78	7.9	<0.001
PSF	subadult	2000	64	24.8	<0.001
	metamorph	1999	156	21.9	<0.001
BTS	adult	1999	161	12.5	<0.001
		2000	157	5.4	0.005
	metamorph	1999	267	0.5	0.62
		2000	188	18.4	<0.001

[a] Abbreviations: GPT, Great Plains toad; NSF, New Mexico spadefoot; PSF, plains spadefoot; and BTS, barred tiger salamander.
[b] Tests were not performed for metamorph GPT and PSF in 2000 and subadult PSF in 1999 because no individuals were captured in grassland and cropland, respectively.
[c] df = denominator degrees of freedom; numerator df = 2 for all tests.

playas than at grassland playas for metamorph New Mexico spadefoot in 2000.

Year Main Effect

Adults.—Body size was 19%, 13%, and 46% greater in 1999 than in 2000 for adult Great Plains toad, New Mexico spadefoot, and barred tiger salamander, respectively, at cropland playas (Tables 2, 6). Body size also was 18%, 3%, and 47% greater in 1999 than in 2000 for adult Great Plains toad, New Mexico spadefoot, and barred tiger salamander, respectively, at grassland playas.

Subadults.—Body size was 41% and 5% greater in 1999 than in 2000 for subadult Great Plains toad and New Mexico spadefoot, respectively, at cropland playas; only the difference in SVL was significant ($P = 0.04$) for New Mexico spadefoot (Tables 4, 6). Body size was 13% and 14% greater in 2000 than in 1999 for subadult New Mexico spadefoot and plains spadefoot, respectively, at grassland playas. Body size did not differ between years for subadult Great Plains toad at grassland playas.

Metamorphs.—Body size was 18%, 28%, and 23% greater in 1999 than in 2000 for metamorph New Mexico spadefoot, plains spadefoot, and barred tiger salamander, respectively, at cropland playas (Tables 5, 6). Body size did not differ between years for metamorph Great Plains toad at cropland playas. Body size was 124% and 8% greater in 1999 than in 2000 for metamorph New Mexico

Table 4. Subadult body size of New Mexico spadefoot (NSF), plains spadefoot (PSF), and Great Plains toad (GPT) between land-use types and years at 16 playa wetlands in the Southern High Plains of Texas, USA, Apr–Sep 1999 and 2000.

Size metric	Species	Year[a]	Cultivation				Grassland			
			n	$\bar{x}$	SE	$P \leq 0.05$[b]	n	$\bar{x}$	SE	$P \leq 0.05$
Snout-vent length (mm)	NSF	1999	26	34.1	0.9	Aa	61	36.2	0.5	Aa
		2000	221	32.5	0.2	Ab	86	39.1	0.4	Bb
	PSF	1999	0	0	0	NT	15	38.1	0.8	a
		2000	55	34.2	0.5	A	18	43.2	0.7	Bb
	GPT	1999	41	58.4	0.9	Aa	30	56.5	1.3	Aa
		2000	64	47.1	0.8	Ab	201	59.0	0.6	Ba
Mass (g)	NSF	1999	26	4.8	0.3	Aa	61	5.3	0.3	Aa
		2000	221	4.6	0.2	Aa	86	6.6	0.2	Bb
	PSF	1999	0	0	0	NT	15	6.5	0.4	a
		2000	55	4.7	0.2	A	18	7.8	0.4	Bb
	GPT	1999	41	23.3	0.9	Aa	30	24.4	1.8	Aa
		2000	64	14.7	0.7	Ab	201	26.9	0.7	Ba

[a] Analyzed by year because land-use and year main effects were not additive ($P < 0.001$, Table 1) for NSF and GPT; PSF analyzed for 2000 only.
[b] Within-species means in the same row with unlike uppercase letters are different; means in the same column within size variables and species with unlike lower case letters are different; NT indicates no test performed because SE = 0 for >1 level of the effect.

spadefoot and barred tiger salamander, respectively, at grassland playas; only mass was significant ($P = 0.002$) for barred tiger salamander.

DISCUSSION

Land-use Effect

For most age classes (metamorph, subadult, and adult) and species of amphibians in the Southern High Plains, body size was 10–148% greater at grassland playas than at playas surrounded by cultivation. This range of statistical differences likely was biologically significant as well. Goater (1994) and Scott (1994) found that a 10% increase in amphibian body size could result in approximately 4% and 80% increases in individual survival and fecundity, respectively. Morey and Reznick (2001) documented that average

Table 5. Metamorph body size of New Mexico spadefoot (NSF), plains spadefoot (PSF), Great Plains toad (GPT), and barred tiger salamander (BTS) between land-use types and years at 16 playa wetlands in the Southern High Plains of Texas, USA, Apr–Sep 1999 and 2000.

Size metric	Species	Year[a]	Cultivation				Grassland			
			n	$\bar{x}$	SE	$P \leq 0.05$[b]	n	$\bar{x}$	SE	$P \leq 0.05$
Snout-vent length (mm)	NSF	1999	384	28.1	0.2	Aa	119	31.9	0.4	Ba
		2000	51	24.5	0.4	Ab	34	22.9	0.4	Bb
	PSF	1999	76	31.8	0.4	Aa	89	36.5	0.4	B
		2000	27	25.9	0.4	b	0	0	0	NT
	GPT	1999	142	25.1	0.7	Aa	202	38.2	0.7	B
		2000	39	25.5	1.1	a	0	0	0	NT
	BTS	1999	103	77.4	1.0	Aa	173	78.5	0.6	Aa
		2000	76	72.4	0.7	Ab	121	79.4	0.7	Ba
Mass (g)	NSF	1999	384	2.8	0.1	Aa	119	3.7	0.1	Ba
		2000	51	2.3	0.1	Ab	34	1.2	0.1	Bb
	PSF	1999	76	3.6	0.2	Aa	89	5.6	0.2	B
		2000	27	2.7	0.1	b	0	0	0	NT
	GPT	1999	142	2.5	0.2	Aa	202	8.6	0.5	B
		2000	39	2.8	0.3	a	0	0	0	NT
	BTS	1999	103	21.4	0.9	Aa	173	22.0	0.6	Aa
		2000	76	15.4	0.9	Ab	121	18.8	0.8	Bb

[a] Analyzed by year because land-use and year main effects were not additive ($P < 0.001$, Table 1) for NSF and BTS; PSF and GPT analyzed for 1999 only.
[b] Within-species means in the same row with unlike uppercase letters are different; means in the same column within size variables and species with unlike lower case letters are different; NT indicates no test performed because SE=0 for >1 level of the effect.

Table 6. Inferential statistics for multivariate analysis of variance tests on differences in body size of amphibians between years for each land-use type at 16 playa wetlands in the Southern High Plains of Texas, USA, 1999 and 2000.

Species[a]	Age class[b]	Land use	df[c]	F	P
GPT	adult	cultivation	323	15.6	<0.001
		grassland	263	6.3	0.002
	subadult	cultivation	96	12.4	<0.001
		grassland	222	0.2	0.78
	metamorph	cultivation	174	0.3	0.73
NSF	adult	cultivation	928	110.6	<0.001
		grassland	606	3.1	0.05
	subadult	cultivation	293	3.7	0.03
		grassland	139	3.2	0.04
	metamorph	cultivation	427	17.9	<0.001
		grassland	145	16.4	<0.001
PSF	subadult	grassland	24	3.5	0.05
	metamorph	cultivation	96	37.5	<0.001
BTS	adult	cultivation	120	22.5	<0.001
		grassland	198	65.1	<0.001
	metamorph	cultivation	170	10.8	<0.001
		grassland	285	20.7	<0.001

[a] Abbreviations: GPT, Great Plains toad; NSF, New Mexico spadefoot; PSF, plains spadefoot; and BTS, barred tiger salamander.

[b] Tests were not performed for metamorph GPT and PSF in grassland and subadult PSF in cropland because no individuals were captured in 2000 and 1999, respectively.

[c] df = denominator degrees of freedom; numerator df = 2 for all tests.

body size of surviving amphibians was approximately 50% larger than individuals that experienced mortality. In general, larger amphibians use a greater range of microhabitats (Newman and Dunham 1994), consume a greater range of prey sizes (Flowers and Graves 1995, Newman 1999), are more efficient foragers (Newman 1999), and have lower specific metabolic rates (Hutchison et al. 1968; Ultsch 1973, 1974) than small individuals. Large individuals also can withstand dehydration more than small individuals (Newman and Dunham 1994). Larger amphibians have greater sprint speeds, jumping ability, and endurance than small individuals (Taigen and Pough 1981, John-Alder and Morin 1990, Goater et al. 1993, Beck and Congdon 2000), which can increase their chance of escaping predators. Mating success of male and female amphibians is positively related to body size (Berven 1981, Verrell 1982, Howard and Young 1998). Large females also exhibit greater fecundity than small females and may spawn multiple times (Clarke 1974; Berven 1982; Krupa 1986, 1994; Fontenot 1999). Large amphibians within a species also may reproduce at an earlier age than small individuals (Berven and Gill 1983, Berven 1990, Scott 1994). All these factors suggest that

amphibian populations composed of larger individuals (as occurs at grassland playas) have greater recruitment and thus probability of population persistence (Semlitsch et al. 1988).

To our knowledge, this is the first documentation of the possible correlation between agricultural cultivation and body size of amphibians in North America. Smaller body size at cropland wetlands may be related to amphibian density. Beebee (1983) and Oldham (1985) found that body size of *Bufo bufo* and two species of newts (*Triturus vulgaris*, *T. helveticus*) was greater at wetlands with lower terrestrial conspecific density. Total amphibian density at our cropland playas was 196–247% greater than at the grassland playas both years (Gray et al. 2004*a,b*). Density of conspecifics, and possibly congeners, can negatively influence postmetamorphic growth rate and body size of amphibians (Goater 1994, Pechmann 1994, Morey and Reznick 2001) by increasing competition for food resources. Runoff or aerial drift of insecticides and scarification of vegetation associated with cultivation also can negatively affect terrestrial food resources (Freemark and Boutin 1995, Smith et al. 2004) and possibly limit the body size amphibians can attain.

Postmetamorphic body size also may have been related to conditions in the larval environment (Wilbur and Collins 1973, Werner 1986, Brady and Griffiths 2000, Morey and Reznick 2001). Hydroperiod can negatively influence postmetamorphic body size by reducing duration of larval development (Newman 1988, 1989; Denver 1997). The mean hydroperiod of the grassland playas in one study ($\bar{x}$ =139 d, SE=14) was greater than that of the cropland playas ($\bar{x}$ = 89 d, SE = 22) in 1999 and 2000 (Gray 2002). Because mean monthly rainfall at all playas was similar for the 2 land uses in both years (Gray 2002), reduced hydroperiod in cropland playas may be related to higher rates of sedimentation, which decreases volume and hydroperiod (Luo et al. 1997).

Postmetamorphic body size also may have been related to differences in the density of the primary aquatic predator of amphibians, larval and neotenic barred tiger salamanders, in playas (Rose and Armentrout 1976, Collins and Holomuzki 1984, Skelly 1996). Mean daily abundance of barred tiger salamander larvae and neonates in seine-net samples was 208–492% greater in grassland playas than in cropland playas in both years (Gray 2002). Predators can positively influence postmetamorphic body size of anurans by reducing density of conspecific larvae (Gray et al.

2004*a*), thus decreasing competition for food resources (Wilbur 1984). Alternatively, predators may negatively affect postmetamorphic body size of prey by restricting their foraging activity and limiting their size at metamorphosis (Skelly and Werner 1990). However, this effect may be species-dependent (Werner 1991, Werner and McPeek 1994) and secondary. We speculate that the primary effect of predation on postmetamorphic body size of amphibians in playas occurs through a reduction in competition (Morin 1983). This would result in large postmetamorphic body size of amphibians associated with predator-rich wetland, which was observed at the grassland playas.

Although we did not quantify the abundance of aquatic plant (e.g., nektonic algae) and animal (e.g., anostracan shrimp) foods in the 2 land-use types, densities may have been lower in cropland playas because increased mortality of these organisms is associated with agricultural runoff or drift (Freemark and Boutin 1995). Reduced aquatic food resources can negatively influence larval growth (Wilbur 1977, Steinwascher 1979, Newman 1994, Walls 1998), and consequently limit postmetamorphic body size. Agricultural chemicals also can directly reduce foraging activity and growth of larval amphibians, which can decrease body size at metamorphosis (Semlitsch et al. 1995, Fioramonti et al. 1997, Boone and Semlitsch 2001).

Year Effect

Postmetamorphic body size of amphibians was 3–124% greater in 1999 than in 2000 for most species and age classes. The influence of land use and year on body size generally was non-additive. Differences in body size between land uses increased 33–545% between 1999 and 2000 for adult and subadult New Mexico spadefoots and Great Plains toads, and metamorph barred tiger salamanders. Yearly differences in body size likely were related to rainfall, because average monthly precipitation at our playas during sampling was 107% greater in 1999 than in 2000 (Gray 2002). Although a cause-and-effect relationship was not tested, the non-additivity of land-use and year effects suggests that cultivation may negatively influence body size to a greater extent during drier years. Rainfall can positively influence postmetamorphic growth rates (Tinsley and Tocque 1995) and presumably body size (Bruce and Hairston 1990, Reading 1990) by reducing probability of desiccation (Newman and Dunham 1994) and

increasing opportunities for foraging (Jaeger 1980) and movement (Hurlbert 1969, Semlitsch 1985, Sinsch 1988). Rainfall also can positively affect postmetamorphic body size by influencing duration of larval development (Reading and Clarke 1999, Camp et al. 2000). Mean larval duration at all playas was 13% greater in 1999 than 2000 (Gray 2002).

Yearly differences in adult postmetamorphic body size could have occurred because a greater proportion of large individuals (mostly females) were active, and thus captured and measured, during the wet year (Trenham et al. 2000, 2001). However, when gender was included as a main effect in the linear model (Gray 2002), it did not interact with land-use or year effects, suggesting that sex ratios were similar among levels of the effects and sexual dimorphism did not influence body-size results.

MANAGEMENT IMPLICATIONS

Our results suggest that amphibians in playas surrounded by cultivated land may be smaller than those in playas in uncultivated landscapes. Many factors may contribute to this correlation, such as wetland hydroperiod, conspecific density of amphibians in the terrestrial landscape, and predator density in the aquatic environment. Larger body size of individuals at grassland playas may afford these populations increased probability of persistence, because of the positive relationship between amphibian body size and survival, reproduction, and recruitment. Most of the grassland playas we studied were immediately surrounded by native pasture (Gray 2002). Land-use managers may consider restoring grassland surrounding playas in the Southern High Plains with native grasses to positively influence body size, and possibly demographics, of amphibians, as described by Smith (2003) and Semlitsch and Bodie (2003).

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