ANIMAL BEHAVIOUR, 2001, **61**, 431–438
doi:10.1006/anbe.2000.1597, available online at http://www.idealibrary.com on IDEAL®

Evidence of convergent character displacement in release vocalizations of *Bufo fowleri* and *Bufo terrestris* (Anura; Bufonidae)

CHRISTOPHER J. LEARY
Department of Zoology and Wildlife Sciences, Auburn University, Auburn, Alabama

*(Received 22 February 2000; initial acceptance 4 May 2000;
final acceptance 25 July 2000; MS. number: A8718)*

Anuran release vocalizations prevent prolonged amplexus of males by conspecific and heterospecific males, whereas advertisement vocalizations potentially act as a premating isolation mechanism. Selection favouring prompt release during heterospecific amplexus should result in convergent character displacement in release vocalizations. Conversely, selection should produce divergent character displacement in advertisement vocalizations. I examined call properties important to mate recognition from release and advertisement vocalizations of allopatric and sympatric populations of *Bufo fowleri* and *B. terrestris* to determine whether the two calls exhibit opposing patterns of character displacement. Results indicated convergent character displacement in the periodicity of release vocalizations (a measure equal to the inverse of pulse rate and an estimate of release vibration rate). The periodicity of advertisement vocalizations was significantly displaced from the allopatric character state resulting in greater divergence in sympatry. However, this parameter was already largely divergent in allopatry and, therefore, results were not consistent with the pattern expected for divergent character displacement. The dominant frequency of sympatric advertisement vocalizations was not significantly displaced from allopatry. Results for advertisement vocalizations provided evidence that convergence of release vocalizations was not the result of hybridization. There was no evidence that clinal variation accounted for displacement of call characteristics. Convergent character displacement in the periodicity of release vocalizations may facilitate interspecific communication during heterospecific amplexus, whereas divergent advertisement vocalizations promote species isolation.

Grant (1972) defined character displacement as ‘the process by which a character state of a species changes under natural selection arising from the presence, in the same environment, of one or more species similar to it ecologically and/or reproductively’. To clarify the direction and outcome of such selection, the terms ‘divergent character displacement’ and ‘convergent character displacement’ were proposed (Grant 1972).

Divergent character displacement of male courtship behaviours that serve as premating isolation mechanisms has been documented in a wide variety of organisms (see Grant 1972; Waage 1979; Butlin 1989; Howard 1993; Hostert 1997), mostly involving advertisement vocalizations of frogs (Gerhardt 1994a). Accentuated differences of premating isolation mechanisms in zones of sympatry ultimately reinforce prezygotic barriers thereby reducing hybridization (Dobzhansky 1937, 1940; W. F. Blair 1955; Brown & Wilson 1956). Conversely, depending upon the social context and function of species signals, the character states of sympatric species may be selected to converge (see reviews by Moynihan 1968; Cody 1969, 1970, 1973; Cody & Brown 1970; Grant 1972; Vadas 1990; Scott & Foster 2000). Convergent character displacement is not as well documented as the former (Grant 1972; Vadas 1990; Scott & Foster 2000), but has been reported in visual cues and vocalizations used by birds to defend territories (Cody 1969, 1970, 1973; Cody & Brown 1970; Rice 1978). Greater similarity between territorial signals among syntopic species presumably facilitates interspecific communication during heterospecific bouts (Cody 1969, 1970, 1973; Cody & Brown 1970).

Advertisement and release vocalizations of anurans (frogs and toads) differ in function and are potentially subject to opposing patterns of character displacement. Male advertisement vocalizations serve to attract conspecific females and often act as a premating isolation mechanism where two or more ecologically similar species coexist (Blair 1974; Gerhardt 1994b). Reinforcement (divergent character displacement) of the signal in zones of sympatry is well documented for several anuran species (e.g. W. F. Blair 1955, 1974; Littlejohn 1965;

Correspondence and present address: C. J. Leary, The University of Oklahoma, Department of Zoology, 730 Van Vleet Oval, Norman, OK 73019-0235, U.S.A. (email: leary@ou.edu).

Fouquette 1975; Loftus-Hills & Littlejohn 1992). Release vocalizations, on the other hand, are produced by male anurans in response to male mating attempts (Aronson 1944; Blair 1947; Bogert 1960; Brown & Littlejohn 1972). Production of release calls by an amplexed male signals an amplexing conspecific or heterospecific male to dismount (Aronson 1944; Blair 1947; Bogert 1960; Brown & Littlejohn 1972). Calls that are not effective result in prolonged amplexus of two males (e.g. Blair 1947; Sullivan & Wagner 1988). Rapid release of an amplexing male would be advantageous in conserving energy, preventing gametic wastage, reducing exposure to predation, and providing more time available for breeding opportunities (Blair 1968). Therefore, release vocalizations should be under selective pressure to converge in areas of sympatry (Rand 1988).

This study examines the advertisement and release vocalizations of males in allopatric and sympatric populations of *Bufo fowleri* and *B. terrestris* under the premise that these two signals should exhibit divergent and convergent character displacement, respectively. Although numerous studies have demonstrated divergent character displacement of anuran advertisement vocalizations (W. F. Blair 1955, 1974; Littlejohn 1965; Fouquette 1975; Loftus-Hills & Littlejohn 1992), convergent character displacement in anuran release vocalizations has not been investigated.

Bufo fowleri and *B. terrestris* belong to an assemblage of 10 closely related bufonids (the '*Bufo americanus* group': Blair 1963a, b, 1972a, b; Sullivan et al. 1996; Gergus et al. 1997). Isolating mechanisms among sympatric members of this group, including structural and temporal preferences in breeding sites, call discrimination, morphological differences and chemoreceptory cues, are apparently insufficient in preventing genetic exchange between species (A. P. Blair 1941, 1942, 1955; Volpe 1952, 1959; Cory & Manion 1955; Blair 1956, 1958, 1972a, b; Mount 1975). However, experimental crosses between *B. fowleri* and *B. terrestris* indicate that hybrids show higher levels of embryonic abnormality and mortality than crosses between other members within the group (Blair 1963b, 1972b).

Numerous studies have established that female preference within the *B. americanus* group is based upon the dominant frequency and periodicity of male advertisement vocalizations (Blair 1956, 1958; Sullivan 1982, 1992; Sullivan & Leek 1987; Gerhardt 1988; Howard & Palmer 1995; Howard & Young 1998). I focus on these two call parameters to test for divergent character displacement of advertisement vocalizations. Release calls consist of a release chirp (acoustic component) accompanied by muscular vibrations of the flanks (mechanical component) (Aronson 1944; Blair 1947; Bogert 1960; Brown & Littlejohn 1972). Aronson (1944) and Blair (1947) determined that the mechanical component of the release signal is of primary importance for initiating dismount among males within the *B. americanus* group. Release vibrations characteristically accompany release vocalizations and are directly responsible for the periodicity (a measure equal to the inverse of the pulse rate, see Gerhardt & Davis 1988) of the vocalization (Martin 1971, 1972). I test for convergent character displacement of release vibration rates by measuring the periodicity from release vocalizations.

METHODS

Distinct allopatric and sympatric populations exist for *B. fowleri* and *B. terrestris*. *Bufo terrestris* is allopatric to *B. fowleri* throughout most of Florida, U.S.A. but is sympatric with *B. fowleri* in the northwestern-most panhandle and the zone of overlap with *B. fowleri* extends throughout southern Alabama, U.S.A. (Mount 1975; Conant & Collins 1991; Fig. 1). *Bufo fowleri* is allopatric to other members of the *B. americanus* group throughout a narrow zone in central Alabama extending along the Fall Line Hills (Mount 1975; Fig. 1).

I recorded 188 release vocalizations and 108 advertisement vocalizations from *B. fowleri* and *B. terrestris* in 1994, 1995 and 1996 (Table 1, Fig. 1). To evoke release calls I grasped male toads behind the forelimbs and held them within 20 mm of a microphone and recorded one to five vocalizations (Leary 1999). I obtained recordings of advertisement vocalizations by placing a microphone within 30 cm of advertising males. Vocalizations were recorded in the field using a Uher 4000 Report IC open-reel recorder (recording speed 19 cm/s), Ampex 631 1.5 MIL polyester 6.35-mm magnetic tape and a Uher (Model M136) Dynamic Microphone. I recorded substrate temperature where males produced advertisement calls to the nearest 1.0°C by placing a quick-read thermometer immediately adjacent to advertising toads. Substrate temperatures were also recorded near individuals prior to grasping to evoke release calls. Release calls were recorded immediately upon capture to minimize temperature effects associated with handling. Temperatures were used to test for effects on vocal parameters (see Zweifel 1968; Brown & Littlejohn 1972).

I measured dominant frequency and periodicity from spectrograms and waveforms of advertisement vocalizations and periodicity from waveforms of release vocalizations using Canary 1.1.1, Cornell Bioacoustics Workstation software (settings: frame length 256 points, time 5.752 ms, 50% overlap, fast Fourier transform size 256 points, Hamming filter and amplitude logarithmic). I measured dominant frequency of advertisement calls at the midpoint of the dominant frequency band to the nearest 0.1 kHz. I calculated periodicity (used here also to reflect release vibration rate, see Martin 1971, 1972) by measuring the interval between the onset of rise in amplitude in successive pulses to the nearest 1.0 ms (a measure equal to the inverse of the pulse rate, see Gerhardt & Davis 1988). A single pulse was defined as any amplitude modulation where the depth of amplitude fell to 50% or less before the onset of a subsequent pulse.

I measured periodicity of release vocalizations from the first, middle (one of two middle chirps for even-numbered chirp vocalizations) and last release chirp. I then averaged the measures of the three chirps for each vocalization. I measured periodicity of advertisement vocalizations in a similar manner but calculated it from a

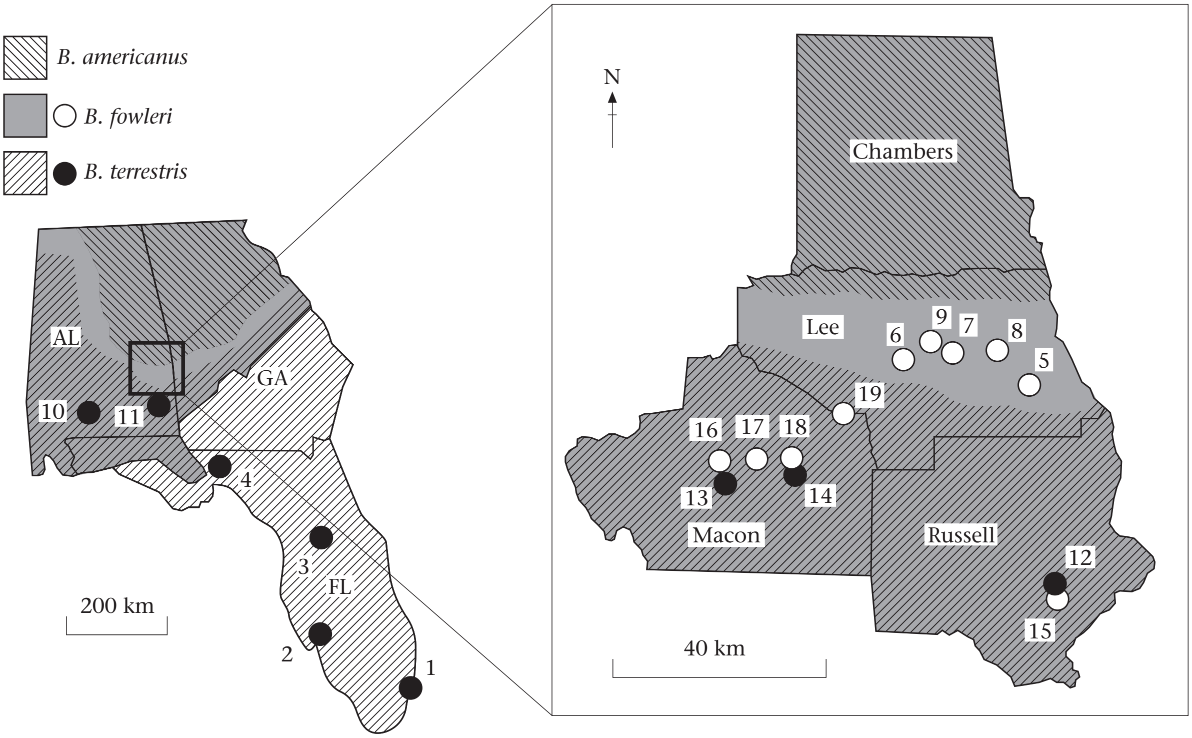

Figure 1. Distribution of *Bufo fowleri* and *B. terrestris* in Alabama, Georgia and Florida, U.S.A. (Mount 1975; Conant & Collins 1991). Populations are designated with numbers that correspond to sample localities in Table 1.

middle 192-ms segment of the call (the largest segment that allowed clear resolution of pulse rate).

Statistical analyses were performed utilizing JMP IN version 3.0 (SAS Institute, Cary, North Carolina, U.S.A.).

RESULTS

Release Vocalizations

I subjected mean periodicity for the combined populations of each species to nested analyses of covariance to determine whether call attributes were significantly displaced from the allopatric character state. I assigned temperature as the covariate, location (allopatry and sympatry) as the grouping factor, and nested population within location. Recording temperatures ranged from 16 to 24°C for allopatric *B. fowleri*, 21 to 27°C for allopatric *B. terrestris*, 21 to 27°C for sympatric *B. fowleri*, and 19 to 26°C for sympatric *B. terrestris*. To test for homogeneity of slopes between locations for the effects of temperature on periodicity of release calls, I first ran the models with locality and temperature as interaction terms. No significant differences in slopes were found (NS; Table 2). I then ran the models without interaction terms (Table 2). There was no significant effect for population nested within area (NS; Table 2). The effect of location was significant for the periodicity of *B. terrestris* (P=0.04; Table 2).

I then conducted linear regression analyses of the periodicity for each species in allopatry and sympatry with temperature as the independent variable (Table 3). I adjusted periodicity to the grand mean sample temperature of both species (23°C) (see Appendix).

Temperature-adjusted data for each locality are presented in box plots to show convergent character displacement in the periodicity of release calls (Fig. 2). Quartile distributions for this parameter did not overlap in allopatry. However, displacement from the allopatric character state resulted in greater similarity (overlap) of the calls in sympatry (Fig. 2). Displacement was unilateral (i.e. only the periodicity of *B. terrestris* was significantly displaced from the allopatric character state; see Grant 1972).

To test whether clinal variation accounted for displacement of release vocalizations, I regressed the periodicity for allopatric populations of *B. terrestris* against latitude (see Benedix & Howard 1991). There was no evidence of a significant latitudinal trend (b=0.224, N=38, P=0.2, r^2=0.033).

Advertisement Vocalizations

Recording temperatures for advertisement vocalizations ranged from 22 to 24°C for sympatric *B. fowleri*, 20 to 22°C for sympatric *B. terrestris*, and 16 to 24°C for allopatric *B. fowleri*. Allopatric males of *B. terrestris* were all recorded at 21°C. Only the periodicity for calls of allopatric *B. fowleri* was adjusted for the effects of temperature ($b=-0.263$, N=38, P<0.0001, r^2=0.471). The dominant frequency of allopatric *B. fowleri* was not significantly affected by temperature (b=0.008, N=38, P=0.1, r^2=0.049) and was not adjusted. Recording temperatures for other localities deviated no more than 2°C from the grand mean recording temperature of 23°C and,

Table 1. Locations of recording sites and sample sizes (number of individuals recorded) for release vocalizations (R) and advertisement vocalizations (A) of *B. terrestris* and *B. fowleri* in allopatry and in sympatry

Population	Species	Sample size		Condition	Locality (~latitude and longitude)
		R	A		
1	*B. terrestris*	8		Allopatric	Miami, Dade Co., FL (25°37′23″N, 080°24′17″W)
2	*B. terrestris*	10	11	Allopatric	Tampa, Hillsborough Co., FL (28°01′19″N, 082°25′26″W)
3	*B. terrestris*	9		Allopatric	Ocala National Forest, Marion Co., FL (29°10′00″N, 081°47′30″W)
4	*B. terrestris*	11		Allopatric	Tallahassee, Leon Co., FL (30°27′00″N, 084°21′30″W)
5	*B. fowleri*	9	9	Allopatric	0.4 km E of Co. Rd 054 on Co. Rd 433, Auburn, Lee Co., AL (32°32′55″N, 085°25′50″W)
6	*B. fowleri*	5	8	Allopatric	1.2 km E of Co. Rds 137 and 152 junction, Auburn, Lee Co., AL (32°34′45″N, 085°31′50″W)
7	*B. fowleri*	11	7	Allopatric	0.8 km N of Co. Rd 137 on Co. Rd 053, Auburn, Lee Co., AL (32°35′30″N, 085°30′50″W)
8	*B. fowleri*	7	12	Allopatric	3.2 km E of State Highway 147 on Glenn Ave, Auburn, Lee Co., AL (32°36′15″N, 085°26′45″W)
9	*B. fowleri*	9	2	Allopatric	4.8 km NW of State Highway 147 on U.S. 280, Auburn, Lee Co., AL (32°41′45″N, 085°31′10″W)
10	*B. terrestris*	10		Sympatric	Conecuh National Forest, Covington Co., AL (31°07′35″N, 086°45′10″W)
11	*B. terrestris*	7		Sympatric	Eufaula National Wildlife Refuge, Barbour Co., AL (31°59′03″N, 085°04′55″W)
12	*B. terrestris*	4		Sympatric	Junction U.S. Highway 431 and State Highway 169, Russell Co., AL (32°17′50″N, 085°10′00″W)
13	*B. terrestris*	11		Sympatric	Tuskegee Lake, Macon Co., AL (32°25′36″N, 085°40′48″W)
14	*B. terrestris*	21	14	Sympatric	Tuskegee National Forest, Macon Co., AL (32°26′30″N, 085°38′10″W)
15	*B. fowleri*	7		Sympatric	Junction U.S. Highway 431 and State Highway 169, Russell Co., AL (32°17′50″N, 085°10′00″W)
16	*B. fowleri*	17	19	Sympatric	Tuskegee Lake, Macon Co., AL (32°25′36″N, 085°40′48″W)
17	*B. fowleri*	17	6	Sympatric	Tuskegee National Forest, Macon Co., AL (32°25′50″N, 085°39′30″W)
18	*B. fowleri*	6	11	Sympatric	Uphapee Creek, Macon Co., AL (32°26′30″N, 085°38′10″W)
19	*B. fowleri*	9	9	Sympatric	U.S. Highway 29 at Lee and Macon Co. border, AL (32°30′45″N, 085°31′35″W)

Populations are arranged from the southern-most to the northern-most allopatric/sympatric population and correspond with designated numbered localities in Fig. 1.

Table 2. Results of nested analyses of covariance for the periodicity of release calls for *Bufo fowleri* (N=97) and *B. terrestris* (N=91)

Species	Location	Population	Temperature	Homogeneity of slopes
B. fowleri	$F_{1,8}$=0.830 P=0.3	$F_{8,86}$=1.055 P=0.4	$F_{1,86}$=0.172 P=0.6	$F_{1,85}$=0.003 P=0.9
B. terrestris	$F_{1,7}$=4.669 P=0.04	$F_{7,81}$=1.505 P=0.1	$F_{1,81}$=1.871 P=0.1	$F_{1,80}$=0.497 P=0.4

Temperature is the covariate and population is nested within location. See text for analytical procedure.

therefore, were not adjusted for temperature effects (see Appendix).

Nested analyses of variance, using the temperature-adjusted data where appropriate, indicated that there were significant effects for populations nested within location (allopatry and sympatry) for the dominant frequency and periodicity of *B. fowleri* advertisement calls (P≤0.02; Table 4). However, the effect of location was not significant (NS; Table 4). Analysis of variance indicated that the dominant frequency was not significantly displaced from the allopatric character state for calls of *B. terrestris* ($F_{1,23}$=0.763, N=25, P=0.4) while the periodicity for calls of sympatric *B. terrestris* was significantly displaced from those of conspecific males in allopatry ($F_{1,23}$=6.61, N=25, P=0.02). Box plots revealed that displacement resulted in greater divergence in the periodicity of the calls in sympatry (Fig. 3). However, calls were already divergent in allopatry (Fig. 3). Therefore, results were not consistent with the pattern expected for divergent character displacement (see Grant 1972).

DISCUSSION

Blair (1962) provided evidence that the periodicity of advertisement vocalizations for *B. fowleri* and *B. terrestris* is subject to divergent character displacement. However, he did not examine allopatric and sympatric populations of *B. fowleri* and vocalizations were not adjusted for temperature effects. Although my results indicate that sympatric *B. terrestris* and *B. fowleri* show a greater degree

Table 3. Results of linear regression analyses for the periodicity of release calls of *Bufo fowleri* and *B. terrestris* with temperature as the independent variable

Species	Locality	N	b	P	r^2
B. fowleri	Allopatry	41	−0.472	0.03	0.104
	Sympatry	56	−0.556	0.4	0.014
B. terrestris	Allopatry	38	−0.652	0.0001	0.357
	Sympatry	53	−0.639	0.01	0.11

Species are divided into allopatric and sympatric populations with sample size (N), regression coefficient (b), significance of slope (P) and the coefficient of determination (r^2).

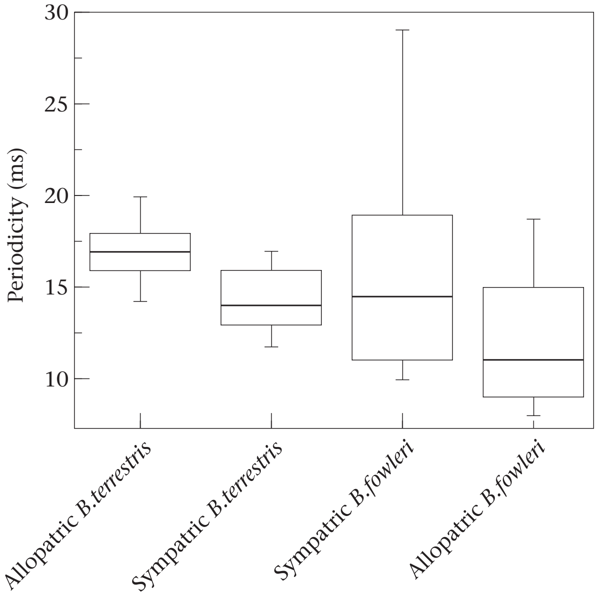

Figure 2. Box plots of the periodicity of release vocalizations adjusted for temperature for *B. fowleri* and *B. terrestris* in allopatry and sympatry showing convergent character displacement. See McGill et al. (1978) for information on box plots.

Table 4. Results of nested analyses of variance for the dominant frequency and periodicity of advertisement vocalizations for *Bufo fowleri* (N=83)

Call parameter	Location	Population
Dominantfrequency	$F_{1,7}$=0.019 P=0.8	$F_{7,74}$=2.500 P=0.02
Periodicity	$F_{1,7}$=0.0003 P=0.9	$F_{7,74}$=3.329 P=0.004

Population is nested within location (allopatry and sympatry) and temperature-adjusted data are used for the periodicity of allopatric *B. fowleri* (see text).

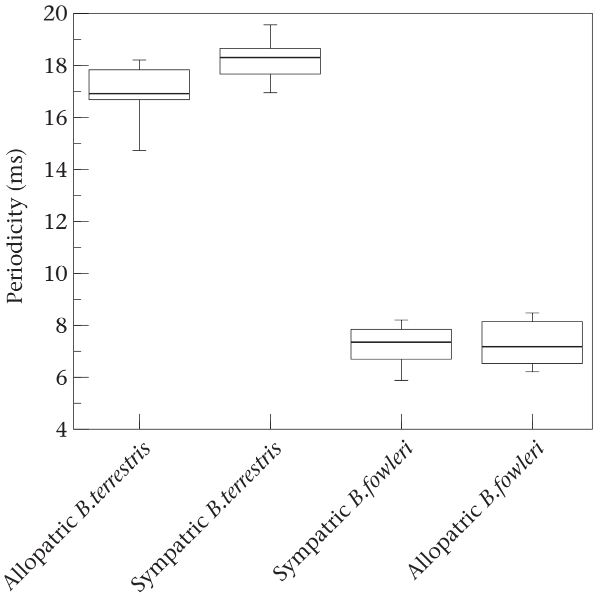

Figure 3. Box plots of the periodicity of advertisement vocalizations adjusted for temperature where appropriate (see text) for *B. fowleri* and *B. terrestris* in allopatry and sympatry. Plots show displacement in allopatry and sympatry for *B. terrestris*. Displacement results in greater divergence of the calls in sympatry. See McGill et al. (1978) for information on box plots.

of divergence in the periodicity of advertisement vocalizations than allopatric populations, displacement should not be considered biologically significant for species isolation. This is because a greater than two-fold difference in the mean periodicity of advertisement vocalizations already exists in allopatry (7.3 ms for *B. fowleri* versus 16.8 ms for *B. terrestris*), and an average 1.5-ms increase (divergence) of the periodicity in sympatry (7.2 ms for *B. fowleri* versus 18.3 ms for *B. terrestris*) is not likely to contribute significantly to the effectiveness of advertisement vocalizations as an isolating mechanism.

Box plots revealed that the quartile distributions for the periodicity of release vocalizations of *B. fowleri* and *B. terrestris* do not overlap in allopatry but do overlap in sympatry. Therefore, results are consistent with convergent character displacement. Investigations by Blair (1947) provide strong evidence that differences in the vibratory rates (periodicity) have a significant effect on the speed at which amplexing males dismount. Blair recorded the duration of amplexus among heterospecific and conspecific amplexed toads and determined that those species with the greatest divergence in release vibration rates spent the greatest time in amplexus. Field observations corroborate these results (Sullivan & Wagner 1988). Because of the nondiscriminating amplectic behaviour of male *B. fowleri* and *B. terrestris* (Volpe 1959; personal observation) and other sympatric bufonids (Aronson 1944; Blair 1947; Sullivan & Wagner 1988; Marco et al. 1998), similar signals are probably necessary to facilitate interspecific communication during heterospecific amplexus. Rapid release of an amplexing male through similar calls would conserve energy, prevent gametic wastage, and reduce exposure to predation (Blair 1968). Further investigations should compare the effectiveness of sympatric and allopatric release signals in initiating heterospecific dismount among these species.

Grant (1972) contended that convergence of character states in sympatric species often results from hybridization but is frequently misinterpreted as convergent character displacement. In this study, I used advertisement vocalizations as indicators of hybridization (see Zweifel 1968). If convergent release calls resulted from hybridization, then advertisement vocalizations of *B. fowleri* and *B. terrestris* would be expected to be more similar in sympatry (see Zweifel 1968). However, the periodicities of advertisement calls have diverged in sympatry while dominant frequencies were not significantly displaced from the values for allopatric populations. Although advertisement vocalizations were not obtained from all populations where release vocalizations were recorded, Weatherby (1982) reported *B. fowleri* × *B. terrestris* hybrids to be rare in Alabama. Thus, evidence suggests that convergent character displacement of release vocalizations is not the result of hybridization.

Clinal variation may also account for displacement of characters in allopatry and sympatry (reviewed by Grant 1972). However, results revealed that there was no significant latitudinal cline for call attributes that were significantly displaced from the allopatric character state.

The results presented here, accompanied by analysis of release and advertisement vocalizations of *B. americanus* and *B. fowleri* (unpublished data), indicate that convergent character displacement of release vocalizations and divergent character displacement of advertisement vocalizations are unlikely to co-occur. Convergent character displacement requires that the allopatric character states (presumed to be the precontact state) of the species are significantly different from each other, and the sympatric character states (presumed to be the postcontact state) are not significantly different (Grant 1972). The antithesis is true for divergent character displacement. Given the relatively conservative nature of release calls (Brown & Littlejohn 1972), it would be unlikely for release vocalizations to diverge while advertisement vocalizations remained unchanged during an allopatric speciation event. However, this scenario would be necessary for release calls and advertisement calls to be subject to convergent and divergent character displacement, respectively. Further investigations of other anuran species are likely to reveal that convergent character displacement of release vocalizations is not accompanied by divergent character displacement of advertisement vocalizations because advertisement vocalizations are already divergent in the precontact state (as reported here). It follows that divergent character displacement of advertisement vocalizations is not likely to be accompanied by convergent character displacement of release vocalizations because release calls are already similar in the precontact state. Further studies are necessary to investigate patterns of character displacement in anuran vocalizations with disparate functions.

Acknowledgments

This manuscript was completed in partial fulfillment of a Master's degree at Auburn University. I thank members of my advisory committee, J. L. Dobie, R. S. Lishak, M. T. Mendonça and C. Guyer for their assistance and guidance in completing this investigation. I thank R. H. Mount for sharing his extensive knowledge on the distribution and natural history of toads in Alabama. Special thanks to D. L. Leary and R. S. Lishak for their advice and assistance with sound interpretation and analyses, and M. West for assistance with statistics. B. K. Sullivan, R. D. Howard and M. J. Fouquette provided substantial logistical advice and comments on an early version of the manuscript. H. C. Gerhardt, M. Bee and J. P. Caldwell also provided valuable insight that greatly improved the final version. This study was funded by Grants-In-Aid of Research through the Sigma Xi Scientific Research Society. The research presented here was evaluated by the Animal Behavior Society's Animal Care Committee and approved on 25 July 2000.

References

Aronson, L. R. 1944. The mating pattern of *Bufo americanus, Bufo fowleri* and *Bufo terrestris*. *American Museum Novitates*, **1250,** 1–15.

Benedix, J. H. & Howard, D. J. 1991. Calling song displacement in a zone of overlap and hybridization. *Evolution*, **45,** 1751–1759.

Blair, A. P. 1941. Variation, isolation mechanisms and hybridization in certain toads. *Genetics*, **26,** 398–417.

Blair, A. P. 1942. Isolating mechanisms in a complex of four species of toads. *Biological Symposia*, **6,** 235–249.

Blair, A. P. 1947. The male warning vibration in *Bufo*. *American Museum Novitates*, **1344,** 1–7.

Blair, A. P. 1955. Distribution, variation and hybridization in a relict toad (*Bufo microscaphus*) in southwestern Utah. *American Museum Novitates*, **1722,** 1–38.

Blair, W. F. 1955. Mating call and stage of speciation in the *Microhyla olivacea–M. carolinensis* complex. *Evolution*, **9,** 469–480.

Blair, W. F. 1956. Call difference as an isolation mechanism in southwestern toads (genus *Bufo*). *Texas Journal of Science*, **8,** 87–106.

Blair, W. F. 1958. Mating call in the speciation of anuran amphibians. *American Naturalist*, **92,** 27–51.

Blair, W. F. 1962. Non-morphological data in anuran classification. *Systematic Zoology*, **11,** 72–84.

Blair, W. F. 1963a. Evolutionary relationships of North American toads of the genus *Bufo*: a progress report. *Evolution*, **17,** 1–16.

Blair, W. F. 1963b. Intragroup genetic compatibility in the *Bufo americanus* species group of toads. *Texas Journal of Science*, **15,** 15–34.

Blair, W. F. 1968. Amphibians and reptiles. In: *Animal Communication* (Ed. by T. A. Sebeok), pp. 289–310. Bloomington: Indiana University Press.

Blair, W. F. 1972a. *Bufo* of North and Central America. In: *Evolution in the Genus Bufo* (Ed. by W. F. Blair), pp. 93–101. Austin: University of Texas Press.

Blair, W. F. 1972b. Evidence from hybridization. In: *Evolution in the Genus* Bufo (Ed. by W. F. Blair), pp. 196–233. Austin: University of Texas Press.

Blair, W. F. 1974. Character displacement in frogs. *American Zoologist*, **14,** 1119–1125.

Bogert, C. M. 1960. The influence of sound on the behavior of amphibians and reptiles. In: *Animal Sound and Communication* (Ed. by W. W. Lanyon & W. N. Tavolga), pp. 137–320. Washington, D.C.: American Institute of Biological Sciences.

Brown, L. E. & Littlejohn, M. J. 1972. Male release call in the *Bufo americanus* group. In: *Evolution in the Genus Bufo* (Ed. by W. F. Blair), pp. 310–323. Austin: University of Texas Press.

Brown, W. L. & Wilson, E. O. 1956. Character displacement. *Systematic Zoology*, **5,** 49–64.

Butlin, R. K. 1989. Reinforcement of premating isolation. In: *Speciation and Its Consequences* (Ed. by D. Otte & J. A. Endler), pp. 158–179. Sunderland, Massachusetts: Sinauer.

Cody, M. L. 1969. Convergent characteristics in sympatric species: a possible relation to interspecific competition and aggression. *Condor*, **71,** 222–239.

Cody, M. L. 1970. Chilean bird distribution. *Ecology*, **51,** 455–464.

Cody, M. L. 1973. Character convergence. *Annual Review of Ecology and Systematics*, **4,** 189–211.

Cody, M. L. & Brown, J. H. 1970. Character convergence in mexican finches. *Evolution*, **24,** 304–310.

Conant, R. & Collins, J. T. 1991. *Reptiles and Amphibians of Eastern/Central North America*. New York: Houghton Mifflin.

Cory, B. L. & Manion, J. J. 1955. Ecology and hybridization of the genus *Bufo* in the Michigan–Indiana region. *Evolution*, **9,** 42–51.

Dobzhansky, T. 1937. *Genetics and the Origin of Species*. New York: Columbia University Press.

Dobzhansky, T. 1940. Speciation as a stage in evolutionary divergence. *American Naturalist*, **74,** 312–321.

Fouquette, M. J. 1975. Speciation in chorus frogs. I. Reproductive character displacement in the *Pseudacris nigrita* complex. *Systematic Zoology*, **24,** 16–23.

Gergus, E. W. A., Sullivan, B. K. & Malmos, K. 1997. Call variation in the *Bufo microscaphus* complex: implications for species boundaries and the evolution of mate recognition. *Ethology*, **103,** 979–989.

Gerhardt, H. C. 1988. Acoustic properties used in call recognition by frogs and toads. In: *The Evolution of the Amphibian Auditory System* (Ed. by B. Fritzsch, M. J. Ryan, W. Wilczynski, T. E. Hetherington & W. Walkowiak), pp. 455–484. New York: J. Wiley.

Gerhardt, H. C. 1994a. Reproductive character displacement of female mate choice in the grey treefrog, *Hyla chrysoscelis*. *Animal Behaviour*, **47,** 959–969.

Gerhardt, H. C. 1994b. The evolution of vocalization in frogs and toads. *Annual Review of Ecology and Systematics*, **25,** 293–324.

Gerhardt, H. C. & Davis, M. S. 1988. Variation in the coding of species identity in the advertisement calls of *Litoria verreauxi* (Anura: Hylidae). *Evolution*, **42,** 556–565.

Grant, P. R. 1972. Convergent and divergent character displacement. *Biological Journal of the Linnean Society*, **4,** 39–68.

Howard, D. J. 1993. Reinforcement: origin, dynamics, and fate of an evolutionary hypothesis. In: *Hybrid Zones and the Evolutionary Process* (Ed. by R. G. Harrison), pp. 46–69. Oxford: Oxford University Press.

Howard, R. D. & Palmer, J. G. 1995. Female choice in *B. americanus*: effects of dominant frequency and call order. *Copeia*, **1995,** 212–217.

Howard, R. D. & Young, J. R. 1998. Individual variation in male vocal traits and female mating preferences in *Bufo americanus*. *Animal Behaviour*, **55,** 1165–1179.

Hostert, E. E. 1997. Reinforcement: a new perspective on an old controversy. *Evolution*, **51,** 697–702.

Leary, C. J. 1999. Comparison between release vocalizations emitted during artificial and conspecific amplexus in *Bufo americanus*. *Copeia*, **1999**, 506–508.

Littlejohn, M. J. 1965. Premating isolation in the *Hyla ewingi* complex (Anura: Hylidae). *Evolution*, **19,** 234–243.

Loftus-Hills, J. J. & Littlejohn, M. J. 1992. Reinforcement and reproductive character displacement in *Gastrophryne carolinensis* and *G. olivacea* (Anura: Microhylidae): a reexamination. *Evolution*, **46,** 896–906.

McGill, R., Tukey, J. W. & Larsen, W. A. 1978. Variations of box plots. *American Journal of Statistics*, **32,** 12–16.

Marco, A., Kiesecker, J. M., Chivers, D. P. & Blaustein, A. R. 1998. Sex recognition and mate choice by male western toads, *Bufo boreas*. *Animal Behaviour*, **55,** 1631–1635.

Martin, W. F. 1971. Mechanics of sound production in toads of the genus *Bufo*: passive elements. *Journal of Experimental Zoology*, **176,** 273–294.

Martin, W. F. 1972. Evolution of vocalization in the genus *Bufo*. In: *Evolution in the Genus* Bufo (Ed. by W. F. Blair), pp. 279–309. Austin: University of Texas Press.

Mount, R. H. 1975. *The Reptiles and Amphibians of Alabama*. Auburn, Alabama: Agricultural Experiment Station.

Moynihan, M. 1968. Social mimicry: character convergence versus character displacement. *Evolution*, **22,** 315–331.

Rand, A. S. 1988. An overview of anuran acoustic communication. In: *The Evolution of the Amphibian Auditory System* (Ed. by B. Fritzsch, M. J. Ryan, W. Wilczynski, T. E. Hetherington & W. Walkowiak), pp. 415–433. New York: J. Wiley.

Rice, J. 1978. Ecological relationships of two interspecifically territorial vireos. *Ecology*, **59,** 526–538.

Scott, R. J. & Foster, S. A. 2000. Field data do not support a textbook example of convergent character displacement. *Proceedings of the Royal Society of London, Series B*, **267,** 607–612.

Sullivan, B. K. 1982. Significance of size, temperature and call attributes to sexual selection in *Bufo woodhousei australis*. *Journal of Herpetology*, **16,** 103–106.

Sullivan, B. K. 1992. Sexual selection and calling behavior in the American toad (*Bufo americanus*). *Copeia*, **1992,** 1–7.

Sullivan, B. K. & Leek, M. R. 1987. Acoustic communication in Woodhouse's toad (*Bufo woodhousei*) II. Response of females to variation in spectral and temporal components of advertisement calls. *Behaviour*, **103,** 16–36.

Sullivan, B. K. & Wagner, W. E., Jr. 1988. Variation in advertisement and release calls, and social influences on calling behavior in the gulf coast toad (*Bufo valliceps*). *Copeia*, **1988,** 1014–1020.

Sullivan, B. K., Malmos, K. B. & Given, M. F. 1996. Systematics of the *Bufo woodhousii* complex (Anura: Bufonidae): advertisement call variation. *Copeia*, **1996,** 274–280.

Vadas, R. L. 1990. Competitive exclusion, character convergence, or optimal foraging: which should we expect? *Oikos*, **58,** 123–127.

Volpe, E. P. 1952. Physiological evidence for natural hybridization of *Bufo americanus* and *Bufo fowleri*. *Evolution*, **6,** 393–406.

Volpe, E. P. 1959. Experimental and natural hybridization between *Bufo terrestris* and *Bufo fowleri*. *American Midland Naturalist*, **61,** 295–312.

Waage, J. K. 1979. Reproductive character displacement in Calopteryx (Odonata: Calopterygidae). *Evolution*, **33,** 104–116.

Weatherby, C. A. 1982. Introgression between the American toad, *Bufo americanus*, and the southern toad, *B. terrestris*, in Alabama. Ph.D. thesis, Auburn University, Auburn, Alabama.

Zweifel, R. G. 1968. Effects of temperature, body size, and hybridization on mating calls of toads, *Bufo a. americanus* and *Bufo woodhousei fowleri*. *Copeia*, **1968,** 269–285.

Appendix

Table A1. Mean ($\bar{X}$), standard error (SE) and range for the periodicity of release vocalizations and dominant frequency and periodicity of advertisement vocalizations prior to and after adjustment for the effects of temperature (where appropriate, see text) for *B. fowleri* and *B. terrestris* in allopatry and sympatry

	Allopatric *B. fowleri*		Sympatric *B. fowleri*		Allopatric *B. terrestris*		Sympatric *B. terrestris*	
	Unadjusted	Adjusted	Unadjusted	Adjusted	Unadjusted	Adjusted	Unadjusted	Adjusted
Release call								
Periodicity (ms)								
$\bar{X}$	13.9	12.9	15.3	16.6	16.1	16.9	5.2	14.5
SE	0.84	0.78	1.01	0.99	0.44	0.34	0.40	0.39
Range	7.5–28.2	7.0–28.0	6.9–37.9	8.0–38.0	12.1–22.7	12.0–22.0	10.2–24.6	10.0–24.0
Advertisement call								
Periodicity (ms)								
$\bar{X}$	8.2	7.3	7.2		16.8		18.3	
SE	0.22	0.16	0.11		0.51		0.29	
Range	5.6–12.2	5.6–10.6	5.6–8.5		12.1–18.5		16.4–20.8	
Dominant frequency (kHz)								
$\bar{X}$	1.9		1.9		2.0		2.0	
SE	0.02		0.12		0.04		0.04	
Range	1.6–2.2		1.6–2.1		1.6–2.2		1.8–2.3	