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Author(s): Deanna H. Olson, Andrew R. Blaustein and Richard K. O'Hara
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Mating pattern variability among western toad (*Bufo boreas*) populations

Deanna H. Olson, Andrew R. Blaustein, Richard K. O'Hara
Department of Zoology, Oregon State University, Corvallis, OR 97331-2914, USA

Summary. Breeding ecology and mating patterns of the western toad, *Bufo boreas*, were examined in three large explosively breeding populations in the Oregon Cascade Mountains. Two mating patterns occurred variably within and among the three populations. First, a large male mating advantage was observed in two of the three populations when data from all the days of data collection were combined. When each day of breeding was analyzed separately, there was a large male mating advantage on 3 of 5 days at one population, and mating was random on all days at the two other populations. The second mating pattern, positive assortative mating by size, was observed at two of the three populations. This pattern was found on separate days of breeding as well as when data from all days were combined at one population, and on only one day of breeding at the second population.

In a survey of anuran amphibian mating patterns, intraspecific variation was found in 13 of 15 species, including the present study of the western toad. Intrapopulation variation in mating patterns among breeding years has been observed in 5 of 8 anurans, whereas within-site, within-year mating pattern variation has only been reported for the western toad. These results strongly suggest that anuran mating patterns are frequently neither species-specific nor population-specific attributes. Variable mating patterns were most commonly observed in explosively-breeding anurans. Explosive breeders may be susceptible to variable mating patterns because they may be more sensitive to fluctuations in environmental conditions, demographic parameters, and the intensities of intrasexual competition and mate choice.

Key words: Mating pattern – *Bufo* – Intrasexual competition – Mate choice

The factors that influence the mating behavior of animals is of central importance to evolutionary biology. Differential mating success of individuals during a single breeding season can contribute to variation in lifetime reproductive success, and this differential success is reflected in population patterns of nonrandom mating. Nonrandom mating patterns may result from competition for mates or mate choice, the two proximate components of sexual selection (Darwin 1871). Mating patterns presumably resulting from sexual selection have been observed in a variety of organisms (see reviews by Borgia 1979; Emlen and Oring 1977; Halliday 1978; Thornhill 1979; West-Eberhard 1983; see also a theoretical discussion by Arnold 1983).

Because anuran amphibian breeding aggregations are often conspicuous and easily observed in the field, they have been the subjects of several important mating system studies. Size dependent mating patterns have been described for a number of anuran species. Several studies have reported that males found paired with females are larger than unpaired males (e.g., Berven 1981; Fairchild 1981; Gatz 1981a; Howard 1978, 1980, 1983; Lee and Crump 1981; Ryan 1980; Wells 1979; Wilbur et al. 1978; Woodward 1982a, b), whereas other studies illustrate positive assortative mating by size (e.g., Arak 1983; Berven 1981; Davies and Halliday 1977; Howard 1978, 1983; Howard and Kluge 1985; Kagarise Sherman 1980; Lee and Crump 1981; Licht 1976). Both male-male competition and female choice of mates may result in these anuran mating patterns (e.g., Arak 1983; Howard and Kluge 1985; Lee and Crump 1981; Wells 1977a; Woodward 1982a).

We have studied mating patterns in three distinct populations of the western toad, *Bufo boreas boreas*. The large sizes of our three study populations provide us with an excellent opportunity to examine mating pattern variations both among populations as well as among different days of breeding within each population. Our findings suggest that *B. boreas* mating patterns vary extensively within and between populations. In addition, a review of studies of anuran mating patterns that were conducted at more than one natural breeding aggregation indicates that such variability may be common.

Materials and methods

We observed *B. boreas* breeding activity at three sites in the Cascade Mountains of Oregon, USA, from May to July 1982: (1) Lost Lake (site A, Linn County, elevation 1,220 m) on 5, 6, 8, 15 June; (2) Little Three Creeks Lake (site B, Deschutes County, elevation 1,950 m) on 1–4, 7, 8, 12 July; (3) Todd Lake (site C, Deschutes County, elevation 1,860 m) on 9, 12–14 July. Our observations spanned the entire breeding seasons at each site. Adult toads were captured, individually marked by toe-clipping and measured (snout-urostyle length) to the nearest mm (repeatable to within 2 mm). Amplexed pairs were not separated when marked; females were measured ventrally and males were

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Offprint requests to: D.H. Olson

measured dorsally. To estimate female dorsal lengths from ventral lengths, both were measured on a representative sample of 14 females and a conversion factor was calculated ($y = 0.97x + 0.76$, $r^2 = 0.82$).

The dorsal lengths of males and females were compared at each site using a *t*-test to assess the magnitude of sexual dimorphism in size. This test was also used to compare lengths of toads between study sites. Mean lengths (±SE) of newly captured toads on each day of data collection were determined to examine the relationship between toad size and arrival time at the breeding site. A chi-square test was used to determine whether newly caught males on each day at a site had equal probabilities of pairing. The expected pairing probability at each study site was obtained by dividing the number of paired males by the total number of males caught at each site throughout the breeding season. The observed number of newly caught paired males was compared with the expected number on each day at a study site.

Two size-related mating patterns were investigated. First, the relationship between male size and pairing success was examined by comparing paired male and unpaired male lengths using a two-tailed *t*-test, for each day of data collection separately and for all days combined at each study site. The combined-days analyses provided estimates of population mating patterns whereas daily tests illustrated patterns resulting from the pool of "available" males on each day. The classification of males as either paired or unpaired differed for the daily and combined-days analyses. For the combined-days tests, a male was classified as paired if he was observed clasping a female during the breeding season, whereas an unpaired male was never seen clasping a female. Each toad was entered into the tabulations only once in the combined-days analyses. For the daily analyses, paired males on any day were those caught clasping a new female. Therefore, paired males may have been previously captured unpaired or paired to another female, or they may have never been captured before. A male that was caught clasping a female on one day was excluded from analysis on subsequent days if it was found clasping the same female because that male was not part of the pool of "available" unpaired males at the site in that time period. Males designated as unpaired for the daily analyses may have been new captures or recaptures from previous days (either previously paired or unpaired), but were unpaired on the day considered. Individual males were included in tabulations only once for each day, but may have been included in the analyses for different days. The second mating pattern investigated, positive assortative mating by toad length, was examined by calculating the product moment correlation coefficient between lengths of males and females within pairs for each day of data collection separately and for all days combined. Pairs were included in a daily analysis on only the first day they were found, and they were included only once in each combined-days analysis.

Results

B. boreas is an "explosive" breeder, having a relatively short breeding season. The breeding period at each study site lasted from one to two weeks and more than 250 breeding adults were captured at each study site (Table 1). The sex ratios of breeding adults were male-biased at the three sites (male/female range: 1.5–2.6). Males actively searched for females on the water surface, clasped other toads regardless of sex, and neither defended territories nor gave mating calls. A male vocalized only when clasped by another male, after which the clasping male would release its grasp. Sixteen of 286 gravid females were captured individually (i.e., not paired with a male). We observed only one female (at site A) to pair with two males before spawning, and one male at each study site was observed to pair with two females. All other paired toads had only one known mate during the breeding period. Males were smaller than females at each site (Table 1). Male and female sizes varied significantly between study sites (Table 1). The sizes of newly caught males and females varied daily within sites, but only males at site B exhibited a significant size trend over the course of the breeding period (Fig. 1; mean male size was greater on 1, 2 July than on 8, 12 July, $t = 14.32$, $df = 92$, $P < 0.001$).

Table 1. Adult *B. boreas* body lengths (mm) at three breeding populations. Numbers given are mean ± SE, with *N* in parentheses

Study site	All females	All males	Paired males	Unpaired males
A	111.5±0.83 (113)	81.7±0.62 (171)	85.2±0.59 (113)	75.0±0.90 (58)
B	82.2±1.51 (74)	70.2±0.39 (186)	72.0±0.56 (73)	69.1±0.51 (113)
C	78.5±1.10 (99)	66.2±0.30 (223)	66.8±0.51 (85)	65.9±0.36 (138)

Male vs Female Length: Site A, $t = 19.57$, $df = 282$, $p < 0.001$; Site B, $t = 10.54$, $df = 258$, $P < 0.001$; Site C, $t = 14.33$, $df = 320$, $P < 0.001$
Female Length comparisons: Site A vs B, $t = 18.31$, $df = 185$, $P < 0.001$; B vs C, $t = 1.99$, $df = 171$, $P < 0.05$; A vs C, $t = 24.20$, $df = 210$, $P < 0.001$
Male Length comparisons: Site A vs B, $t = 36.58$, $df = 392$, $P < 0.001$; B vs C, $t = 8.26$, $df = 407$, $P < 0.001$; A vs C, $t = 27.09$, $df = 355$, $P < 0.001$

Newly caught males did not have equal probabilities of pairing throughout the breeding period at site A (Fig. 1; $X^2 = 16.2$, $df = 3$, $P < 0.005$). Males had a higher chance of mating if present at this breeding site early in the breeding period. In contrast, males at sites B and C had equal probabilities of mating throughout their breeding periods ($P > 0.05$). At site B, data from 1 July were excluded from analysis because unpaired males could not be sampled due to time constraints.

There were two size-related patterns of nonrandom pairing in two of the three breeding populations. First, paired males were significantly larger than unpaired males in the combined-days analyses at sites A and B (Fig. 2, and see Table 1 for mean body size values). Daily analyses showed mating was random with respect to size on all days at sites A and C, and paired males were larger than unpaired males on 3 of 5 days at site B (Table 2). Second, there was positive assortative mating by size at sites A and B. There were significant correlations between male and female sizes within pairs on each of the first three days of data collection at site A (Table 2), and on all days combined ($r = 0.43$, $N = 113$, $P < 0.01$). Mates were assorted by size on one of six days at site B (Table 2). Correlations of pair sizes from the other five days of data collection at site B, the combined-days correlations of pairs from B, and all separate and combined-days correlations of pairs from site C were random ($P > 0.05$).

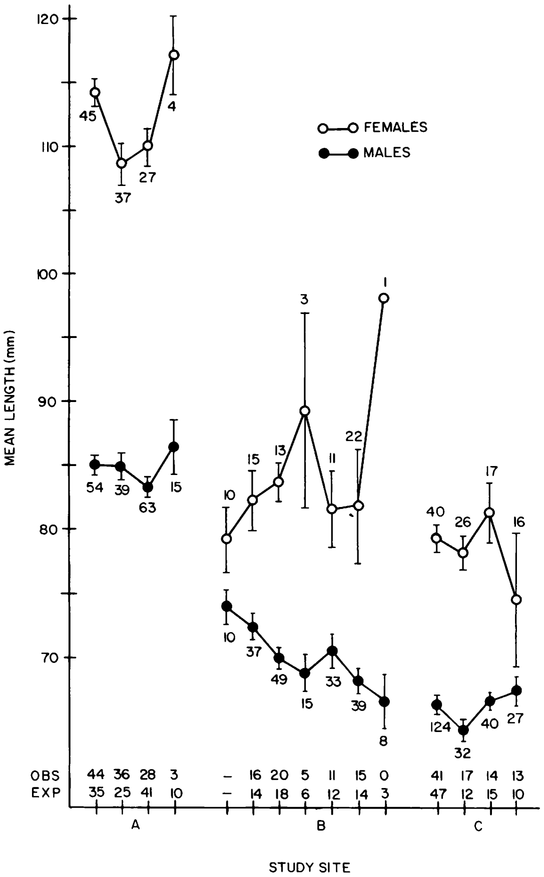

Fig. 1. Snout-urostyle lengths (mean ± SE, *N*) of newly caught males and females on each day of data collection (*A* 5, 6, 8, 15 June; *B* 1, 2, 3, 4, 7, 8, 12 July; *C* 9, 12, 13, 14 July) at the three *B. boreas* populations. The observed (*OBS*) and expected (*EXP*) numbers of newly caught males from each day that became paired over the breeding season at each site are given

Table 2. Results of the daily analyses of two mating patterns, a size-dependent male mating advantage (*t*-statistic) and size assortative mating (*r*)

Site	Date	N_{pr}	N_u	*t*-statistic	*r*
A	5 June	44	10	0.56	0.49*
	6 June	38	1	–	0.46*
	8 June	28	39	1.54	0.39*
	15 June	4	13	1.12	0.57
B	1 July	10	0	–	0.11
	2 July	14	23	2.14*	0.34
	3 July	13	38	2.15*	0.64*
	4 July	3	21	0.34	−0.06
	7 July	12	23	0.16	0.48
	8 July	21	26	2.37*	0.13
	12 July	1	8	–	–
C	9 July	37	85	1.31	0.14
	12 July	18	21	0.98	0.25
	13 July	16	31	0.17	−0.15
	14 July	15	17	1.06	−0.32

N_{PR} = number of pairs, N_u = number of unpaired males, $*P < 0.05$

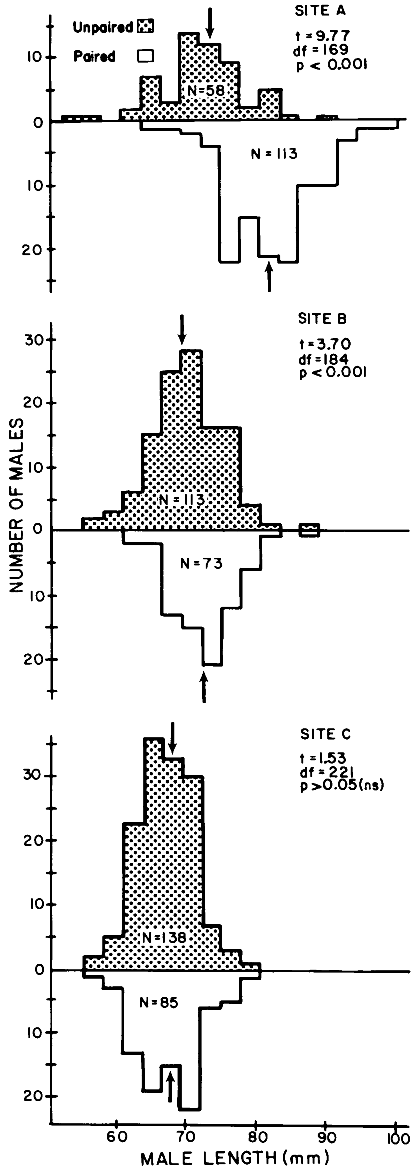

Fig. 2. Frequency distributions of paired and unpaired male lengths at three breeding locations (study sites *A, B, C*) in the Oregon Cascade Mountains. Means are indicated by *arrows*

Discussion

The two *B. boreas* mating patterns that we observed, a large male mating advantage and size assortative mating, varied between sites and between different days of the breeding season within some sites. Thus, our study suggests that these two size dependent mating patterns are general characteristics neither of the species *B. boreas*, nor of a single breeding aggregation or population.

A survey of the literature on anuran mating patterns suggests that intraspecific variability is common. Thirteen of 15 anuran species in which more than one natural breeding aggregation was studied display both random and nonrandom size dependent mating patterns (Table 3). Eleven of the 15 anurans have both a large male mating advantage and random mating with respect to male size (snout-urostyle or snout-vent length). Eight of the 12 species in which size assortative mating was examined in more than one

Table 3. Anurans for which size dependent mating patterns were studied in more than one natural breeding aggregation

Species	Large male advantage		Size assortative mating		Breeding season length	Reference
	Present	Absent	Present	Absent		
Bufo americanus		x		x	Explosive	Kruse (1981)
		x	x[a]	x		Wilbur et al. (1978)
		x	x			Licht (1976)
	x			x		Gatz (1981 a)
	x			x		Gatz (1981 a)
	x			x		Gatz (1981 a)
Bufo boreas	x		x		Explosive	this paper
	x		x[b]	x		this paper
		x		x		this paper
Bufo bufo		x		x	Explosive	Arak (1983)
	x[c]					Davies and Halliday (1979)
			x			Davies and Halliday (1977)
Bufo canorus	x			x	Explosive	Kagarise Sherman (1980)
		x		x		Kagarise Sherman (1980)
	x		x			Kagarise Sherman (1980)
	x			x		Kagarise Sherman (1980)
Bufo exsul	x		x		Explosive	Kagarise Sherman (1980)
		x		x		Kagarise Sherman (1980)
Bufo houstonensis	x				Prolonged	Hillis et al. (1984)
	x					Hillis et al. (1984)
Bufo quercicus	x			x	Prolonged	Wilbur et al. (1978)
	x			x		Wilbur et al. (1978)
				x		Wilbur et al. (1978)
Bufo woodhousei	x			x	Explosive	Fairchild (1981)
	x			x	(at times	Woodward (1982a)
	x			x	protracted)	Woodward (1982a)
	x			x		Woodward (1982a)
		x		x		Sullivan (1982)
		x		x		Sullivan (1983)
	x					Woodward (1982b)
Hyla versicolor	x			x	Prolonged	Gatz (1981 b)
		x		x		Gatz (1981 b)
	x			x		Fellers (1979)
Rana catesbeiana	x				Prolonged	Howard (1978)
	x		x			Howard (1978)
	x		x			Howard (1983)
	x			x		Howard (1983)
	x		x			Howard (1983)
Rana clamitans	x				Prolonged	Wells (1977b)
		x				Wells (1977b)
Rana sylvatica	x		x		Explosive	Berven (1981)
	x		x			Berven (1981)
	x			x		Berven (1981)
	x		x			Howard and Kluge (1985)
	x					Howard and Kluge (1985)
	x					Howard (1980)
Rana temporaria	x		x		Explosive	Arak (1983)
		x		x		Arak (1983)
Scaphiopus couchi	x			x	Explosive	Woodward (1982a)
		x		x		Woodward (1982a)
		x		x		Woodward (1982a)
		x				Woodward (1982a)
Scaphiopus multiplicatis	x				Explosive	Woodward (1982a)
		x				Woodward (1982a)

[a] Pers. Commun. from L.E. Licht to Wilbur et al. (1978)

[b] There was mating pattern variation within this breeding aggregation

[c] At the spawn site and spawning

breeding aggregation have variability in this pattern. Six of 12 anurans in which both a large male mating advantage and size assortative mating were investigated have intraspecific variability in both mating patterns. The separate breeding aggregations within each of these species represent either different study sites or different years at the same site (Table 3). Single site, multi-year studies were conducted with 8 species: *B. americanus* (Gatz 1981a), *B. bufo* (T. Halliday, personal communication), *B. canorus* and *B. exsul* (Kagarise Sherman 1980), *B. woodhousei* (Woodward 1982a), *R. catesbeiana* (Howard 1978, 1983), *R. clamitans* (Wells 1977b) and *R. sylvatica* (Howard and Kluge 1985). Of these, mating patterns varied among years in 5 species: *B. bufo, B. canorus, B. exsul, R. catesbeiana* and *R. clamitans*. In addition to our study of *B. boreas*, within breeding season variation in mating patterns was examined in two other species. Fellers (1979) compared the sizes of nine paired *Hyla versicolor* males to all males in the population and to males present on the night a male mated and found random mating in both comparisons. In *B. bufo*, pairing was random before pairs spawned, whereas size assortative pairing was recorded at spawning (Davies and Halliday 1977, 1979). Thus, in *B. bufo*, no variation in mating (= spawning) pattern was seen. Only Davies and Halliday (1977, 1979), Howard (1983) and Howard and Kluge (1985) followed all pairs through spawning, whereas other studies either assumed spawning occurred or were unclear as to whether pairs were spawning when sampled. If pairs are unstable and censused before spawning, the degree of nonrandom mating may be incorrectly estimated. In *B. boreas*, pairs seemed quite stable because only one of 271 females was observed to be clasped by more than one male before spawning. Within breeding season variation in mating patterns has thus been suggested only for *B. boreas*. Intrapopulation variation in mating pattern, either within or among breeding seasons, has been reported in 6 of 10 species studied.

A combination of factors might be involved in causing this variability. Although previous studies have focused on sexual selection as the primary cause of anuran nonrandom mating patterns (e.g., Arak 1983; Davies and Halliday 1977; Gatz 1981a; Howard and Kluge 1985; Wells 1977a; Woodward 1982a), widespread variability in these patterns suggests that they may be greatly influenced by other aspects of anuran ecology. For instance, mating patterns may vary with breeding season length (Lee and Crump 1981). Most of the anurans with variable mating patterns (Table 3) are explosive breeders, with breeding seasons lasting, at the most, a few weeks. A large male mating advantage is variable in 9 of the 10 explosive breeders in Table 3. In contrast, only 2 of the 5 species with prolonged breeding seasons have a variable incidence of a large male advantage. Size assortative mating occurs variably in 7 of 9 explosive breeders and 1 of 3 prolonged breeders (Table 3). Perhaps species with short breeding seasons are more prone to variable mating patterns due to a greater sensitivity to fluctuations in environmental and demographic conditions. Furthermore, the proximate components of sexual selection may be of variable intensity in explosive breeders, resulting in intermittent mating patterns (see also Wells 1977a; Sullivan 1986). In addition, the intensities of intrasexual competition or mate choice may change with the breeding sex ratio and the breeding density (Emlen and Oring 1977; Wells 1977a; Sullivan 1986), or breeding density and activity may be abruptly altered by local weather variations (personal observations).

What factors may influence *B. boreas* mating patterns? At our three study sites, female choice based on male vocalizations is unlikely because males do not produce mating calls. However, *B. boreas* males do sometimes exhibit intense intrasexual competition for mates (Black and Brunson 1971; personal observations), a characteristic of many explosive breeding anurans (Davies and Halliday 1979; Wells 1977a). In some explosive breeders, mating males frequently obtained their mates by aggressively displacing clasped males from females (Davies and Halliday 1979; Howard and Kluge 1985; Lamb 1984). Displacements of clasping males seems to be rare in *B. boreas* because only one of 271 paired females was observed to be clasped by two males before spawning.

Male-male competition, however, may not take the form of direct aggression. For instance, time of arrival at the breeding site may influence male mating success if early arriving males have a better chance of mating, either due to prolonged residence at the pond or if pairing occurs early (Gatz 1981a). Large male *B. americanus* (Gatz 1981a), *R. sylvatica* (Howard and Kluge 1985) and *R. catesbeiana* (Howard 1978) arrive at breeding sites earlier than small males. In *B. boreas*, early arriving males had a greater probability of pairing at site A, but early arriving males were not larger than males arriving later at this site. Conversely, male size decreased with time at site B and early arriving males did not have a better chance of pairing. In the populations we studied, the time when a toad's overwintering location is free of snow probably influences its time of arrival at the breeding sites and perhaps its mating success. If toad overwintering location or arrival time is size (or age) dependent, a size-related nonrandom mating pattern could result. The interactions among these ecological factors, the components of sexual selection, and the breeding demography of our three *B. boreas* populations are under further study to better understand the proximate mechanisms resulting in mating pattern variability.

Mating pattern variation seems to be common in anurans, yet has received little emphasis in the past. This may be a result of the number of anurans for which only a single mating pattern analysis has been reported, either due to studies conducted at one site for a relatively short time span or to the lumping of data from several breeding aggregations into a single mating pattern analysis. Information provided by multi-site or multi-year studies may provide a more accurate behavioral or ecological profile of the system (see Blaustein 1981; Hayne 1978; Wiens 1977; for discussion). Future emphasis on studies conducted at several breeding aggregations are needed to determine the causes of mating pattern variability and to more fully understand the dynamics of the anuran mating process.

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