Sexual selection and mating system variation in anuran amphibians of the Arizona–Sonoran Desert

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SEXUAL SELECTION AND MATING SYSTEM VARIATION IN ANURAN AMPHIBIANS OF THE ARIZONA-SONORAN DESERT

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ABSTRACT.—Mating system variation in anuran amphibians of the Arizona-Sonoran Desert was reviewed. Male density and breeding period duration were negatively correlated in seven bufonids and pelobatids. Variation in male mating behavior and ability of females to freely select their mates unhindered by active-searching males also was related directly to male density. These observations support hypotheses relating ecological factors to mating system organization. It is suggested that male calling behavior, and anuran lek mating systems in general, may be significantly influenced by predation on vocalizing males.

The Arizona-Sonoran Desert boasts a surprising diversity of frogs and toads: seven bufonids, three pelobatids, three ranids, two hylids, one microhylid, and one leptodactylid. As expected, the breeding biology of these anurans is significantly influenced by the xeric climate. Most of these species have short, or "explosive," (Wells 1977) breeding periods during the summer rainy season, although a few have relatively extended, or "prolonged" breeding periods during the spring (Sullivan 1982a, 1983a, 1984, Sullivan and Sullivan 1985). As suggested by Wells (1977), the mating behavior of anurans such as those of the Arizona-Sonoran Desert appears related to breeding period duration. For example, Woodhouse's toad (*Bufo woodhousei*) forms low-density breeding aggregations at sources of permanent water throughout the spring, and all males within these choruses call to attract females (Sullivan 1982a). In contrast, the Great Plains toad (*B. cognatus*) forms high density aggregations at temporary rain pools for only a few nights each summer. Within these short-lived choruses some males adopt satellite positions near vocalizing males and attempt to intercept females approaching the calling males (Sullivan 1982b).

This diversity in breeding period duration and reproductive behavior provides an excellent opportunity for evaluating hypotheses of sexual selection and mating system theory (Trivers 1972, Emlen and Oring 1977, Wells 1977). It is generally hypothesized that duration of breeding period should directly influ-

ence opportunities for female mate selection and, hence, male behavior. Wells (1977) argued that for explosive-breeding anurans female choice should be restricted as a result of: (1) temporal constraints limiting time available for mate selection and (2) high male densities and corresponding alternative male mating tactics that typically reduce the ability of females to move freely in breeding aggregations. Conversely, in species with prolonged breeding periods and lower male densities, females should be capable of freely selecting their mates and constitute a potentially significant evolutionary force (e.g., Arnold 1983). The variation in breeding biology of anurans of Arizona allows direct test of these hypotheses. Here I summarize recent studies of sexual selection in pelobatids and bufonids of Arizona and, following Emlen and Oring (1977), document the existence of predictable relationships between the ecology, mating systems, and reproductive behavior of these species. I also examine species recognition and acoustic competition among these anurans. Lastly, I discuss the evolution of anuran lek mating systems.

GENERAL METHODS

Methods employed in the studies reviewed here have been described in detail elsewhere (Sullivan 1983c, 1984, Sullivan and Sullivan 1985); a brief summary follows. Observations at anuran breeding aggregations in southern Arizona were made with a six-volt headlamp

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TABLE 1. Mean male density (number of males) and breeding period duration (days) for seven anurans (*Bufo* and *Scaphiopus*) of southern Arizona (N = number of breeding aggregations).

Species	Density		Duration		Source
	$\bar{x}$	N	$\bar{x}$	N	
S. multiplicatus	43.6	7	1.6	7	Sullivan and Sullivan, 1985
S. bombifrons	26.7	6	1.8	6	Sullivan and Sullivan, 1985
B. cognatus	25.2	8	2.6	10	Sullivan, 1983c
S. couchi	23.3	3	1.0	3	Sullivan and Sullivan, 1985
B. debilis	11.4	5	2.6	5	Sullivan, 1984
B. woodhousei	5.4	5	19.8	10	Sullivan, 1982a
B. punctatus	3.0	5	20.0	5	Sullivan, 1984

during the evening in the spring and summer from 1980 to 1984. Toads were captured by hand at breeding aggregations and individually marked by toe-clipping. Snout-vent length was measured to the nearest mm with a plastic rule, and density of males at breeding aggregations was determined by direct count on each night of breeding activity. Male mating success was defined as the number of females a male was observed in amplexus with during a season since amplectant males were never displaced by single males (Sullivan 1983c, 1984, Sullivan and Sullivan 1985).

Focal animal sampling techniques were used to observe behavior of individual males and females in breeding aggregations (Sullivan 1983a, 1983b, 1984). Male advertisement calls were recorded in the field and analyzed in the lab with a Kay 6061B Sonagraph. Determination of pulse rate and frequency of individual calls followed standard methodology as outlined in Sullivan (1982c).

DENSITY, ALTERNATIVE MALE MATING TACTICS, AND FEMALE CHOICE

There is considerable range in breeding period durations of Arizona anurans (Table 1). Mean male density at breeding aggregations is negatively correlated ($\tau = -0.71$, $P = 0.01$) with duration of breeding period for seven bufonids and pelobatids. All the species with high density aggregations utilize temporary rain pools for breeding. Presumably, in these explosive-breeding forms the limited temporal availability of water restricts local populations to a pattern of more or less synchronous breeding.

Wells (1977) postulated that temporal constraints and high male densities should pro-

mote the adoption of alternative mate-locating tactics by males of explosive-breeding anurans. Sullivan (1982b) corroborated Wells' hypothesis: in breeding aggregations of *B. cognatus* the proportion of noncalling, satellite males "parasitizing" calling males is correlated with chorus size. These satellite males will begin vocalizing if male density decreases. Similar satellite, as well as active-searching behavior, has been observed in two of the pelobatids of Arizona (Sullivan and Sullivan 1985). It seems clear that density is the primary factor influencing male adoption of alternative tactics, especially in light of the intraspecific variation in *B. cognatus*. Furthermore, in those anurans that form low density breeding aggregations no noncalling male tactics have been observed independent of breeding period duration (Sullivan 1982a, 1984). Other bufonids and pelobatids of North America also exhibit active-searching and satellite behaviors (Wells 1977). As expected, all these forms are characterized by explosive breeding periods and high male densities.

Active-searching and satellite males have been observed successfully amplexing females in high density breeding aggregations of two Arizona anurans, *B. cognatus* (Sullivan 1982b), and *Scaphiopus multiplicatus* (Sullivan and Sullivan 1985). These observations support the notion that females are limited in their ability to freely select mates in high density aggregations in part as a result of some males adopting noncalling, mate-locating tactics. Another line of evidence suggesting that mating is random with respect to male phenotype in explosive-breeding anurans is the lack of relationship between male size and mating success among these forms (Table 2). Many investigators have suggested that female

TABLE 2. Relationships between male size and mating success in five anurans (*Bufo* and *Scaphiopus*) of southern Arizona.

Species	Snout-vent length (mm)								Source
	Mating males		Nonmating males			Positive assortative mating			
	$\bar{x}$	N	$\bar{x}$	N	P	r	N	P	
S. couchi	71.0	6	70.0	6	>.05*	0.07*	12	=.50	Sullivan and Sullivan, 1985
	74.1	10	71.1	18	>.05	0.07*	20	=.43	
	74.4	5	69.2	18	>.05*	−0.40*	10	=.24	
S. multiplicatus	50.9	21	51.3	28	>.05	0.05	21	>.05	Sullivan and Sullivan, 1985
	51.2	12	50.0	15	>.05	—	—	—	
	48.0	6	48.0	11	>.05*	—	—	—	
B. cognatus	78.6	24	77.2	150	>.05	0.09	24	>.05	Sullivan, 1983a
B. debilis	41.3	6	42.3	16	>.05*	0.20*	6	>.05	Sullivan, 1984
B. woodhousei	84.1	18	85.4	43	>.05	0.23	47	>.05	Sullivan, 1983b

*For small samples (<10) a Mann-Whitney *U* test or Kendal's tau was calculated

anurans should select large males as mates if size is an indicator of fitness (Wilbur et al. 1978, Fairchild 1981). Others have argued that females might benefit from selecting a male similar in size to themselves if fertilization success is related to the size difference between mating males and females (Licht 1976, Davies and Halliday 1979). Analysis of male size and mating success in four explosive-breeding anurans of Arizona has not supported either of these hypotheses (Table 2.)

Male size is positively correlated with mating success in some explosive-breeding bufonids and pelobatids of the United States (Gatz 1981, Woodward 1982). However, in these forms large males might achieve greater mating success as a result of size advantages during direct struggles for possession of females (Sullivan 1983a). Davies and Halliday (1979) and Lamb (1985) determined that large male bufonids are more successful in taking over females during male-male disputes. For these species a mating advantage for large males may be independent of any female preference. Woodward (1982) documented a large-male mating advantage in one of four *S. couchi* and one of two *S. multiplicatus* breeding aggregations in central New Mexico. This interspecific variation suggests that a number of variables such as density and alternative mating tactics of males influence the outcome of sexual selection in nature.

Male mating success in prolonged-breeding anurans is often correlated with the number of nights a male participates in chorus activity (Kluge 1981, Woodward 1981, Ryan 1983). For prolonged-breeding *B. woodhou-*

sei in Arizona male mating success is weakly correlated ($R^2 = 0-25\%$) with participation in chorus activity (Fig. 1). However, this result is expected since many males are only observed at a chorus for one night: a correlation occurs because any male who mates two or three times must be present at the chorus for at least as many nights. Further, many males who are unattractive as mates (low call rate males) are active at choruses for many nights without obtaining any matings. Hence, for this anuran male persistance in chorus activity is not an important determinant of mating success.

Female mate selection has been observed in breeding aggregations of the three Arizona bufonids with low-density choruses (Sullivan 1983a, 1984). In all of these forms, females initiate amplexus by making physical contact with a calling male and are able to move freely through breeding choruses to select their mates from among the calling males. In *B. woodhousei* male mating success is correlated with call rate, suggesting that females prefer high call rate males as mates (Sullivan 1983a). Males within a chorus retain a consistent, relative ranking in call rate within and between nights, and there is significantly more variation in call rate between than within males (Sullivan 1983a, Sullivan and Leek in review). Females prefer speakers broadcasting calls at the higher rate in simple two-speaker discrimination experiments, further supporting the female preference hypothesis. Proximately, female choice of high call rate males could be passive if they merely locate such males more readily, or active if genetically determined
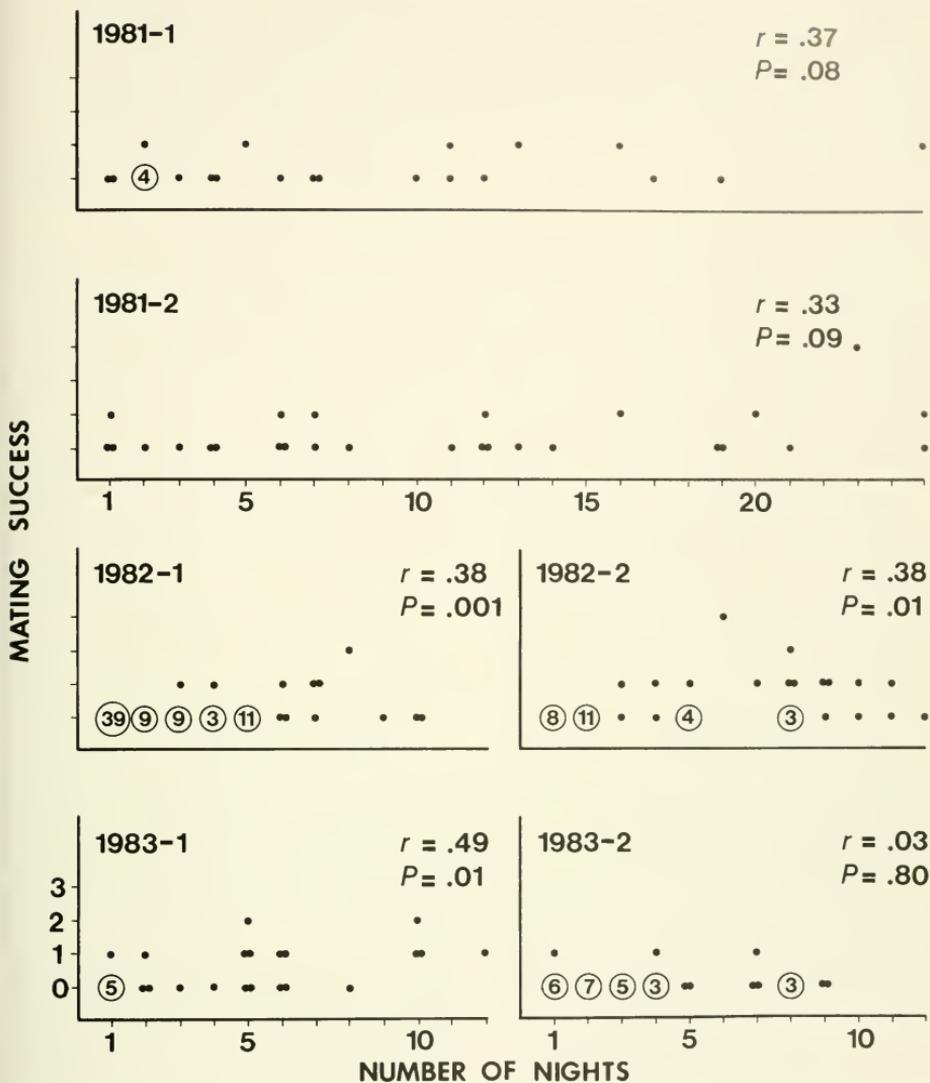
Fig. 1. Male mating success (number of matings) against number of nights of participation in chorus activity for six aggregations of *Bufo woodhousei* (number of concordant observations given inside circle).

preferences exist (Parker 1982, Arak 1983). In *B. woodhousei* female behavior is consistent with the latter alternative since they often pass by low call rate males when moving through a chorus toward a high call rate male (Sullivan 1983a). However, the ultimate significance of these alternatives is indistinguish-able: high call rate males derive fitness benefits through increased mating success, and females, although deriving no immediate benefits, may benefit via increased offspring survivorship or mating success, or both (Lande 1981, Kirkpatrick 1982, Arnold 1983). The importance of these benefits to females

would be determined by the heritability of male call rate and its relation to offspring sur vivorship and mating success. In any event, mating is clearly nonrandom with respect to male phenotype and female behavior in *B. woodhousei*.

These observations on male behavior and mate selection by females reveal that the pro longed-breeding species (*B. punctatus* and *B. woodhousei*), and at least some of the explo sive-breeding forms (*B. cognatus* and *B. de bilis*), have lek-like mating systems (Sullivan 1983c). Females typically select their mates freely from among aggregations of displaying males, and males provide only sperm to their mates. Females mate disproportionately of ten with males possessing high call rates in both *B. cognatus* and *B. woodhousei* (Sullivan 1983c); for the other species it is unknown whether females discriminate between con specific males on the basis of male phenotype (Sullivan 1984). The explosive-breeding pelo batids exhibit a typical male-dominance mat ing system in which mate selection by females is somewhat limited (Emlen and Oring 1977). Males may obtain multiple matings within a breeding season if they participate in breed ing aggregations following every rainstorm each summer (Sullivan 1983b). Although gen erally consistent with the hypothesis of Emlen and Oring (1977) concerning the significance of breeding period duration to mating system structure, these observations indicate clearly that male density, through its impact on fe male choice and regardless of breeding period length, influences sexual selection and the organization of the mating systems of these desert anurans.

SPECIES RECOGNITION
AND ACOUSTIC COMPETITION

An important component of female mate selection concerns proper species recogni tion. For anurans it is generally assumed that interspecific call differences allow sympatri cally breeding species to avoid hybridization (e.g., Hodl 1977, Drewry and Rand 1983, Duellman and Pyles 1983). For example, among hylid and bufonid forms, rate of ampli tude modulation (pulse rate) of the male ad vertisement call is apparently the primary call parameter separating closely related sym

patric species (Gerhardt 1982, Rose and Capranica 1983, Sullivan and Leek, in re view). Discrimination experiments have re vealed that female tree frogs (Hylidae) can discriminate between two acoustic stimuli dif fering only in pulse rate, and they prefer stim uli similar to advertisement calls of con specific males (Loftus-Hills and Littlejohn 1971, Straughan 1975).

All pelobatids and most bufonids occurring in southern Arizona have been observed in mixed-species breeding aggregations, provid ing the potential for heterospecific interac tions (Fig. 2). The ranges in pulse rate and dominant frequency of advertisement calls of these anurans are given in Figure 3. As ex pected, advertisement calls of the closely re lated forms, *S. bombifrons* and *S. multiplica tus*, and *B. microscaphus* and *B. woodhousei*, are clearly dissimilar in pulse rate but not frequency. In the pelobatids, hybrid offspring are sterile; hence, there is presumably strong selection against females who select het erospecific mates. The divergence in adver tisement calls of these two species in south eastern Arizona suggests that species recognition has been a significant selective force acting on female mate choice. Hy bridization has also been documented be tween the two bufonids, but nothing is known concerning the evolutionary significance of this interaction (Sullivan 1986b). Sympatri cally breeding bufonids in Texas have also been found to differ in pulse rate and fre quency (Blair 1956). Advertisement call varia tion in two other Arizona anurans is also com patible with the species recognition hypo thesis: the closely related but allopatric bu fonids *B. debilis* and *B. retiformis* do not differ dramatically in pulse rate. Presumably, selec tion has not favored divergence in advertise ment call structure in the absence of an oppor tunity for heterospecific interactions.

Aspects of intra- and interspecific acoustic competition between anuran males have re cently received considerable attention (re viewed by Sullivan, 1985). A number of work ers have argued that male anurans increase their locatability for selecting females by calling asynchronously with neighboring con specifics as well as heterospecifics. In Arizona *B. woodhousei* follows this pattern: males re duce their calling activity in response to play

SYMPATRICALLY BREEDING ANURANS IN ARIZONA

	Sb	Sc	Sm	Ba	Bc	Bd	Bm	Bp	Br	Bw
Sb	—									
Sc	•	—								
Sm	•	•	—							
Ba	•	•	•	—						
Bc	•	•	•	•	—					
Bd	•	•	•	•	•	—				
Bm							—			
Bp	•	•	•	•	•	•	•	—		
Br		•	•	•	•			•	—	
Bw		•		•	•	•	•			—

Fig. 2. Anurans (*Bufo* and *Scaphiopus*) observed breeding sympatrically (•) in southern Arizona (Sb = *S. bombifrons*, Sc = *S. couchi*, Sm = *S. multiplicatus*, Ba = *B. alvarius*, Bc = *B. cognatus*, Bd = *B. debilis*, Bm = *B. microscaphus*, Bp = *B. punctatus*, Br = *B. retiformis*, Bw = *B. woodhousei*).

back of conspecific advertisement calls as well as a variety of synthetic stimuli (Sullivan 1985, Sullivan and Leek, in review). Proximately, males avoid calling during playback of any acoustic stimuli with a freqency close to the mean frequency of the species-typical call (Sullivan and Leek, in review). However, male *B. punctatus* do not avoid overlap with broadcast of conspecific advertisement calls (Sullivan 1985). These bufonids possess relatively long calls ($\bar{x} = 7.0$ sec) and appear to prefer to call synchronously with nearby calling males. Such interspecific variation suggests that male calling behavior is influenced by factors other than those associated with locatability for females alone. It may be that males of some species call synchronously to reduce the risk of predation; predators who locate anurans acoustically have difficulty capturing synchronously chorusing forms (Ryan and Tuttle 1982). Below I develop the hypothesis that predation has shaped the evolution of anuran lek mating systems in general.

Evolution of Anuran Lek Mating Systems

The evolution of lek mating systems has recently received much attention (Bradbury 1981, Loiselle and Barlow 1978, Wrangham 1980). Lek mating systems, in which females select mates based on male phenotype or dominance position on a display arena, have been described for a variety of organisms, including two Arizona bufonids (Sullivan
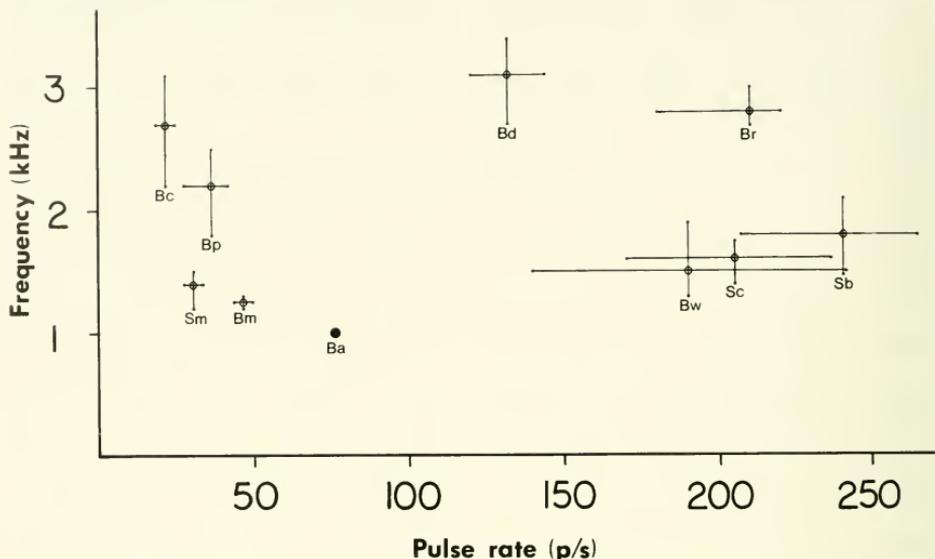
Fig. 3. Range in dominant frequency against range in pulse rate for bufonids and pelobatids of Arizona (see Fig. 1 for abbreviations).

1982a, 1983b). However, there has been considerable controversy concerning evolutionary origins of such female choice systems in which females receive no material benefits from their mates (Lambert et al. 1981, Taylor and Williams 1982). Most authors have argued that female preference for communally displaying males is a necessary condition for the evolution of a lek mating system (e.g., Alexander 1975, Bradbury 1981). It is suggested that when selecting a mate females save time and energy by sampling males in aggregations. Females might also benefit by selecting their mate from a group of males if a wider range of males (in terms of genetic quality) is available in larger aggregations (Bradbury 1981). A prediction of these hypotheses is that females should prefer the largest aggregation of males available since time and energy savings, and availability of high quality mates, should increase with aggregation size (Alexander 1975).

Many anurans have lek mating systems (Alexander 1975, Emlen 1976, Sullivan 1982a, 1983b, Wells 1977). Populations of *B. cognatus* and *B. woodhousei* in Arizona clearly possess lek mating systems (Sullivan

1982a, 1983b). In both of these bufonids, males aggregate in discrete areas of ponds, and females freely select their mates based on male behavior (calling activity). Males do not defend resources of interest to females or their offspring, because oviposition occurs away from the calling site of the male. Hence, females obtain no material benefits from their mates. These two toad species provide an opportunity for direct test of the hypothesis concerning female preference for larger aggregations because male choruses in both species often occur in close proximity to other conspecific aggregations. Models of lek evolution predict that female *B. cognatus* and *B. woodhousei* will visit large aggregations when selecting a mate. That is, the relationship between nightly operational sex ratio (OSR) or the proportional number of females available and number of males present (chorus size) should be positive.

For both *B. cognatus* and *B. woodhousei* OSR (no. of females/no. of males) and chorus size were not significantly correlated (*Bc*: $r = - 0.35$, $P > 0.05$, $N = 19$; *Bw*: $r = 0.04$, $P > 0.05$, $N = 144$). Females were afforded the opportunity to select between aggregations of

different sizes since for both species there were always from 1 to 4 choruses simultaneously active near the study chorus (<0.5 km) on the night of observation (some females even visited more than one chorus). It is important to note that in this analysis the assumption of independence of variables is violated since OSR is in part derived from chorus size; however, the results indicate clearly that for these aggregations OSR does not increase with chorus size. Hence, females do not prefer to visit larger choruses when selecting their mates. Observations on the intensity of sexual selection in *B. woodhousei* further support the hypothesis that anuran females do not prefer to visit larger aggregations of males when selecting a mate. Sullivan (1986a) documented that the intensity of sexual selection increases with chorus size (male density) in *B. woodhousei*. That is, the proportional number of females decreases as male density increases: proportionally fewer males obtain matings in larger choruses.

This result suggests that females do not derive any benefits by selecting their mate from among larger groups of displaying males. I suggest that benefits accruing to individual males who display communally are the primary factors influencing anuran lek behavior. For example, many authors have suggested that males who participate in aggregations suffer less predation than males who display in isolation (see reviews in Alexander 1975, Bradbury 1981, Loiselle and Barlow 1978, Wrangham 1980). Recently Ryan et al. (1981) substantiated this claim by showing that in a neotropical leptodactylid frog individual predation risk decreases for males as chorus size increases. Ryan et al. (1981) found that at least three predators located males acoustically; hence males might benefit greatly by displaying communally. Predation may only be important to males since they participate in choruses night after night: most anuran females visit choruses only on the night they oviposit and are inconspicuous while present in breeding aggregations (e.g., Sullivan 1982a, Wells 1977).

If males derive substantial benefits by displaying communally, and females incur no (or insignificant) costs by selecting their mate from among such groups, then it is conceivable that females play no active role in the evolutionary maintenance of lek behavior. Of

course, female choice of individual males within aggregations would remain an important aspect of sexual selection in species with lek mating systems.

Observations on mate selection by females also suggest that the spatial distribution of males within a chorus is unaffected by female behavior. For example, some workers have suggested that in lek breeding forms females prefer males positioned at the center of the display area. The linear, shoreline choruses of *B. woodhousei* can be readily partitioned into three equal areas with respect to the distribution of males within the aggregations to test this hypothesis. Analysis of mating success and chorus location for all males on 18 nights of chorus activity reveals there was no position effect: centrally located males did not achieve a disproportionate number of matings ($\underline{X}^2 = 0.33$, $\underline{P} > 0.05$, df = 2). Thus, within choruses females do not appear to favor the clustering of males.

Under the extremely arid conditions of the Arizona-Sonoran Desert the lek-like mating systems and acoustic courtship behaviors employed by anurans seem efficient means of rapidly bringing the sexes together. However, this review indicates that some diversity in mating systems can occur under these severe ecological constraints. It is clear that environmental factors influencing breeding period duration shape mating system organization as a result of corresponding variation in male density and behavior. Continued study will be necessary to further elucidate the precise action of sexual selection in relation to mating system variation in breeding aggregations of these desert anurans.

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