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## Evolution of male mating behavior: male spadefoot toads preferentially associate with conspecific males

Received: 20 December 1999 / Accepted: 18 March 2000

**Abstract** The evolution of male breeding aggregations is difficult to explain because males may reduce their reproductive success by associating with their closest competitors. We examined aggregative behavior by male New Mexico spadefoot toads, *Spea multiplicata*, which form breeding choruses in rain-filled pools. We specifically asked whether males are attracted to conspecific calls and, if so, whether they preferentially associate with those male calls that are also attractive to females. Field observations revealed that males showed significant clustering with conspecifics within breeding ponds, whereas laboratory phonotaxis experiments revealed that males preferentially associated with conspecific male calls. Moreover, when males were presented with conspecific calls that differed in call rate, smaller males associated with the stimulus preferred by females (average call rate). Thus, males appear to evaluate the attractiveness of competitors using the same trait employed by females to assess potential mates, and males adjust their positions relative to competitors depending on their size. We discuss these results in the light of several current

hypotheses on the adaptive significance of male breeding aggregations.

**Key words** Male aggregations · *Spea multiplicata* · Chorus behavior

### Introduction

Males of many species form mating aggregations, and within such assemblages only a small proportion of males may mate successfully (Arak 1983; Bradbury et al. 1985; Wiley 1991; Höglund and Alatalo 1995). Thus, the evolution of aggregative behavior is difficult to explain, because, by associating with their closest competitors, males potentially reduce their reproductive success.

At least five evolutionary hypotheses have been proposed to explain the adaptive significance of male breeding aggregations (Höglund and Alatalo 1995). First, males may be attracted independently to patchily distributed environmental resources (Thornhill and Alcock 1983; Höglund and Alatalo 1995), which results in patchy distributions of the males. Second, males may cluster in areas where females tend to be found (Bradbury and Gibson 1983; Thornhill and Alcock 1983; Bradbury et al. 1986; Höglund and Alatalo 1995). For instance, males may aggregate in areas where females' home ranges overlap or where females aggregate to feed. Third, males may aggregate to reduce individual predation risk (Thornhill and Alcock 1983; Höglund and Alatalo 1995). Fourth, breeding aggregations may result when low-quality males cluster around high-quality males in order to intercept females attracted to the latter (Beehler and Foster 1988; Höglund and Robertson 1990). Fifth, females may prefer aggregations of males (Shelly and Greenfield 1991; Alatalo et al. 1992; Lank and Smith 1992; Höglund et al. 1993), thereby selecting for male aggregative behavior (Bradbury 1981; Gibson et al. 1990; Höglund and Alatalo 1995; Kokko 1997). For example, if females are attracted to male groups in order to compare alternative males more effectively,

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Communicated by R. Semlitsch

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those males that attend aggregations may have a higher mating success than males that do not attend aggregations.

One way to tease apart the above hypotheses is to examine individual male behavior. If, for example, males are attracted to other males, such behavior provides support for hypotheses three through five above. Only these hypotheses predict that males will be attracted to other males and can account for such behavior. The alternative hypotheses, that males are independently attracted to resources or females, would not necessarily predict that males should seek out other males. Similarly, if low-quality males preferentially associate with those males that females find attractive, then this provides strong support for the fourth hypothesis, because only this hypothesis predicts such behavior. Thus, examining how males respond to cues produced by other males can be a tool for evaluating the above hypotheses.

Many anuran species are ideal for examining the proximate and evolutionary causes of male aggregative behavior, because they form large choruses where males call to attract mates (Wells 1977; Arak 1983). Males often greatly outnumber females entering aggregations, so that many males are unlikely to mate successfully (Wells 1977; Arak 1983). Although in many species males aggregate in ponds required for breeding, males often appear to associate with other conspecifics rather than being randomly or regularly distributed throughout the ponds (Emlen 1976; Howard 1978; Sullivan 1982; Arak 1988; Cherry 1993).

We examined male aggregative behavior in New Mexico spadefoot toads, *Spea multiplicata*. Males call to attract mates in rain-filled pools, and they appear to be distributed non-randomly within breeding ponds: males call from floating positions and often form one to several clusters (Simovich 1985; K. Pfennig, personal observation). To examine aggregative behavior in *S. multiplicata*, we addressed the following questions: (1) are males distributed randomly within ponds, or are they clumped with other conspecific males? (2) do males respond preferentially to the calls of conspecific males when given a choice of conspecific and heterospecific calls (of a sympatric congener)? and (3) do males preferentially associate with those male calls that are also attractive to females? In answering these questions, we determined if *S. multiplicata* males were attracted to conspecifics and, if so, whether they were attracted to males that females find attractive. Our results were used to assess the factors that might contribute to aggregative behavior by *S. multiplicata* males.

## Methods

### Field observations of male aggregations

To assess whether *S. multiplicata* males aggregate within breeding ponds, we mapped the positions of calling *S. multiplicata* males at two breeding ponds near Portal, Ariz. We sampled the first pond by collecting the males in each of five equal-size regions. Using

“super-glue,” we affixed a small white letter to each male’s dorsum (to prevent resampling), and released each male where he was initially collected. Marking did not affect the behavior of the males, and marks fall off in about 5 days (K. Pfennig, personal observation). All but 3 of 18 males were collected and marked. We calculated the coefficient of dispersion for these males as the sample variance divided by the mean number of males in the samples (Sokal and Rohlf 1995). To determine if males were clustering with conspecifics, we calculated a  $\chi^2$ -value as the sum of squares of the samples divided by the sample mean (Zar 1999). Our null expectation was that the males would be distributed randomly in the pond.

At the second pond, we placed flags next to all 27 calling males located in an area 5.7 m wide by 330.9 m long. We measured the distance between flags, and calculated a nearest-neighbor distance for each male. We used a goodness-of-fit test to determine whether males were randomly distributed (Campbell and Clarke 1971; Krebs 1989). To do so, we established five classes of nearest-neighbor distances: 0–5.0 m, >5.0–10.0 m, >10.0–15.0 m, >15.0–20.0 m, and >20.0 m. Using the methods of Campbell and Clarke (1971), we calculated the expected number of nearest-neighbor distances that would be found in each class if the males were randomly distributed. We compared these expected values to the number of nearest-neighbor distances observed in each class using a  $\chi^2$ -test (Campbell and Clarke 1971; Krebs 1989). The last two classes were pooled so that the expected value in each class was greater than three (Krebs 1989).

### Phonotaxis experiments

To determine whether *S. multiplicata* males are attracted to calls produced by conspecifics, we conducted phonotaxis experiments. Males were collected from four natural breeding aggregations near Portal, Arizona, and transported to the University of North Carolina, where they were housed in dirt-filled buckets and fed nutrient-dusted crickets ad libitum. The males were maintained under a light-dark cycle of 14L:10D. During the fall months, the temperature in the room was cooled from 25.5°C to approximately 17°C. The cooler temperature was maintained for approximately 3 months, then returned to 25.5°C. Phonotaxis experiments were conducted following this period. The males used in the experiments were in reproductive condition, showing nuptial pads.

We used a two-speaker choice test design to determine whether males preferentially associate with calls produced by conspecific males. Males were initially placed on a plastic block in the center of a water-filled wading pool, equidistant between two speakers set 180° and 1.4 m apart. The speakers were set on plastic blocks placed against the side of the pool and flush with the water level. From each speaker, we broadcast one of two stimuli (see below). Each male was initially placed in an opaque container for an acclimation period of 15 min. We began playing the stimuli at the start of this period. At the end of 15 min, the male was released and allowed to move freely about the pool while the stimuli continued to play. A hidden observer then continuously recorded the male’s location in the pool for a 30-min interval.

We considered a male as associating with a stimulus when he was within an area surrounding the speaker that was approximately rectangular in shape (it was flush with the circular side of the pool) and which measured 95 cm by 53 cm (at its deepest point). This area was marked with a string grid hung over the top of the pool and corresponds to approximately the minimum distance that separates males in a natural situation (K. Pfennig, personal observation). The block supporting the speaker was centered at the back of this area. We designated the area of the pool outside these regions as “neutral.” This neutral area contained two additional blocks set 90° from those supporting the speakers. If a male did not leave the neutral area during the 30-min observation period, he was considered non-responsive and excluded from analysis.

We conducted three experiments to determine whether *S. multiplicata* males are attracted to conspecific males. First, we presented *S. multiplicata* males with *S. multiplicata* and *S. bombi-*

*frons* calls. By presenting *S. multiplicata* males with conspecific versus heterospecific calls, we determined whether they are specifically attracted to conspecifics as opposed to calling males in general. We used *S. bombifrons* calls as our heterospecific signal because *S. bombifrons* is sympatric with *S. multiplicata* in southeastern Arizona where the males were collected. The two species often co-occur in breeding aggregations, and potentially hybridize where sympatric. Moreover, calls of the two species are distinct and are potentially used by both males and females to identify conspecifics (Forester 1973; Pfennig, 2000).

Second, we presented *S. bombifrons* males with *S. bombifrons* calls versus calls of *S. multiplicata*. The *S. bombifrons* males were collected from three breeding aggregations near Portal, Ariz., and were treated as the *S. multiplicata* males above. This experiment controlled for the possibility that *S. multiplicata* calls are generally attractive to spadefoot toads rather than to conspecifics in particular. If such were the case, *S. bombifrons* and *S. multiplicata* males would associate with *S. multiplicata* calls. If, however, *S. multiplicata* calls attract only conspecifics, then *S. multiplicata* males would be attracted to *S. multiplicata* calls, but *S. bombifrons* males would not be attracted to *S. multiplicata* calls.

Finally, we presented *S. multiplicata* males with conspecific calls played at a fast call rate (37 calls/min) versus an average call rate (31 calls/min). *S. multiplicata* females that are sympatric with *S. bombifrons* prefer conspecific calls at an average call rate versus a fast call rate (Pfennig, 2000). Thus, this experiment determined whether males associate with the stimulus that is attractive to females. Following the observation period for each male in this experiment, the male was patted dry, weighed, and measured for snout-vent length. We used the ratio of mass to snout-vent length as an indication of overall body size. Size can have important consequences for a male's tendency to associate with other conspecific males (Arak 1983; Howard 1984; Sullivan and Sullivan 1985; Beehler and Foster 1988). In particular, prior work on satellite behavior suggests that smaller males may associate with those males that females find attractive (reviewed in Arak 1983; e.g., Howard 1984; Sullivan and Sullivan 1985). We therefore examined if the tendency of a male to associate with the stimulus preferred by females (average call rate) is related to male size.

To create the sound stimuli for the two experiments in which males of both species were presented with *S. multiplicata* versus *S. bombifrons* call stimuli, we chose four *S. multiplicata* calls and four *S. bombifrons* calls from a set of male calls recorded at natural breeding aggregations where our experimental animals were collected (natural male calls are effective stimuli in phonotaxis experiments; e.g., Sullivan 1983; Schwartz and Wells 1985; Schwartz 1991; Wagner and Sullivan 1995; Pfennig, 2000). Recording methods and call analyses for both species are reported elsewhere (Pfennig, 2000). Each *S. multiplicata* call was randomly paired with an *S. bombifrons* call to create four pairs of *S. multiplicata* versus *S. bombifrons* calls. For each set of calls, the *S. multiplicata* call was repeated onto a single track of an audio tape at the average call rate for *S. multiplicata*, and the *S. bombifrons* call was repeated onto a second track of the audio tape at the average call rate for *S. bombifrons*. To create the sound stimuli for the average versus fast call rate experiment, five *S. multiplicata* calls were selected as above. Each call was repeated onto a track of an audio tape at either an average or a fast call rate, so that the stimuli of a single tape consisted of alternative repetition rates of the same male's call (e.g., Wagner and Sullivan 1995; Pfennig, 2000).

Males used in each phonotaxis experiment were randomly assigned to either four or five groups (corresponding to the number of tapes made for each experiment). Each male within a group was presented the same tape; each group was presented a different tape. Thus, all males in a given experiment were presented the same stimuli across the groups, but the calls used in making those stimuli differed between the groups. This procedure of using different representations of the same stimuli ensured that males were responding to the call stimuli per se rather than an uncontrolled variable in a natural male recording (Kroodsma 1989).

Before each male was tested, we switched the stimuli between speakers to control for position effects and equalized the speakers

for volume. No male was used more than once in a given experiment, but some *S. multiplicata* males were used in more than one experiment.

Because we used natural calls to create the stimulus tapes, different tapes may have elicited different responses from the test animals. We used analysis of variance to determine whether heterogeneity existed among the groups in their responses to the stimuli. We then analyzed the association data using paired *t*-tests to determine if males spent significantly more time with one stimulus versus the alternate stimulus. Our null expectation for each experiment was that there would be no difference in the time that males spent with each stimulus. To determine if size affected the males' tendency to associate with the conspecific call rate stimulus preferred by females (average call rate), we used a Spearman rank correlation analysis. We used this non-parametric test, because our data contained outliers and, therefore, did not meet the assumptions for parametric analysis (Sokal and Rohlf 1995; Zar 1999). Because the Spearman test uses ranks of data, however, outliers do not have undue influence on the strength or significance of the relationship (Sokal and Rohlf 1995; Zar 1999).

## Results

### Field observations of male aggregations

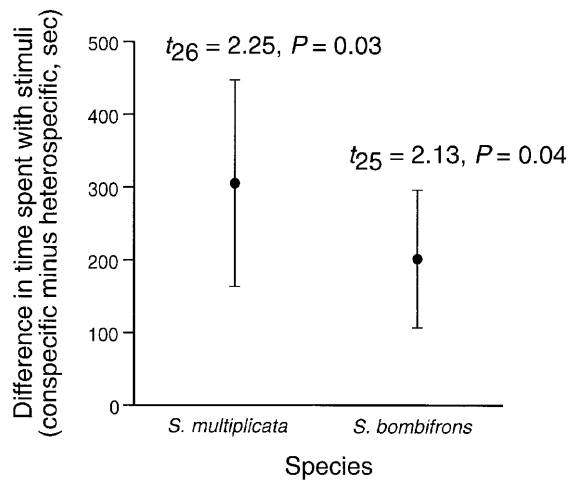
*S. multiplicata* males were significantly clustered within both ponds (pond 1:  $\chi^2_4=11.33$ ,  $P<0.03$ ; pond 2:  $\chi^2_3=32.51$ ,  $P<0.001$ ). In the first pond, the coefficient of dispersion was 2.8. If males were randomly distributed, the coefficient of dispersion would be 1. In the second pond, the mean ( $\pm$ SE) nearest-neighbor distance was 6.61 m ( $\pm$ 1.53 m) in a 1,886.1 m<sup>2</sup> area. Of the 27 males, 16 had nearest-neighbor distances less than 5 m. Only 5.44 males were expected in this nearest-neighbor distance class.

### Phonotaxis experiments

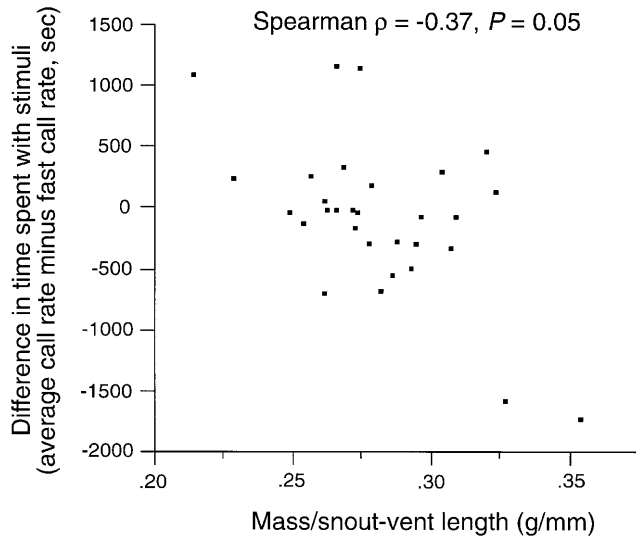
Of 29 *S. multiplicata* males presented conspecific calls versus heterospecific calls, two males did not respond. Of 27 males that responded, 22 spent more time in association with the conspecific stimulus and 5 spent more time in association with the heterospecific stimulus. Male responses to the stimuli were similar among groups ( $F_{3,23}=1.11$ ,  $P=0.37$ ): *S. multiplicata* males spent significantly more time in association with the speaker broadcasting the conspecific call (Fig. 1).

When 26 *S. bombifrons* males were presented conspecific versus heterospecific calls, all responded to the stimuli. Of these males, 15 spent more time with the conspecific stimulus and 11 spent more time with the heterospecific stimulus. Overall, the males spent significantly more time in association with the speaker broadcasting *S. bombifrons* rather than *S. multiplicata* calls (Fig. 1).

We found significant heterogeneity among the groups of *S. bombifrons* males in their responses to the stimuli sets ( $F_{3,22}=3.15$ ,  $P=0.05$ ), indicating that responses of *S. bombifrons* males to the stimuli varied depending on the stimulus set presented to them. When we examined the groups individually, we found that males in one of the



**Fig. 1** Mean ( $\pm$ SE) difference in time spent with conspecific versus heterospecific stimulus for two *Spea* species. A paired *t*-test was used for analysis. The null hypothesis was that there would be no difference in time spent with the conspecific versus heterospecific stimulus



**Fig. 2** Correlation of male mass/snout-vent length ratio and the difference in time spent between the average and the fast call rate stimulus. A non-parametric Spearman rank correlation coefficient is reported

four groups spent more time with the heterospecific stimulus, although this difference was not significant (mean $\pm$ SE time with conspecific stimulus minus heterospecific stimulus =  $-109.43 \pm 165.25$  s, paired  $t_6 = -0.66$ ,  $P = 0.53$ ). Males in the remaining three groups spent more time with the conspecific stimulus, although this difference was significant in only one group [mean $\pm$ SE time with conspecific stimulus minus heterospecific stimulus for group 1 =  $167.00 \pm 143.76$  s, paired  $t_3 = 1.16$ ,  $P = 0.33$ ; group 2 =  $125.00 \pm 142.00$  s, paired  $t_6 = 0.88$ ,  $P = 0.41$ ; group 3 =  $568.25 \pm 186.05$ , paired  $t_7 = 3.05$ ,  $P = 0.02$ ].

When 30 *S. multiplicata* males were presented conspecific calls played at an average versus a fast rate,

28 responded to the stimuli. Eleven of these males spent more time with the average call rate stimulus, whereas 17 spent more time with the fast call rate stimulus. We found no heterogeneity among the groups in their responses to the stimuli ( $F_{4,23} = 0.44$ ,  $P = 0.78$ ). We also found no significant difference in the amount of time these males spent with each stimulus (mean $\pm$ SE time with average stimulus minus fast stimulus =  $-58.89 \pm 124.23$  s, paired  $t_{27} = -0.47$ ,  $P = 0.64$ ).

When we examined the relationship between male size and the difference in time spent with the two stimuli, we found a negative correlation (Fig. 2). Males with lower ratios of mass to snout-vent length spent more time in association with the average call rate stimulus, whereas males with higher mass to snout-vent length ratios spent more time in association with the fast call rate stimulus (Fig. 2).

## Discussion

Our study helps illuminate the proximate and evolutionary causes of male aggregative behavior. *S. multiplicata* males showed significant clumping with conspecific males within breeding ponds. Such aggregative behavior can occur when males cluster independently around environmental cues (e.g., female oviposition sites; Thornhill and Alcock 1983; Höglund and Alatalo 1995) or when males preferentially associate with conspecifics. Our results suggest that formation of aggregations by *S. multiplicata* males occurs, at least in part, because they preferentially associate with calling conspecifics. Of the five evolutionary hypotheses for male breeding aggregations discussed in the Introduction, three predict that males will be attracted to one another as we observed for *S. multiplicata*.

Males may preferentially associate with conspecifics because it reduces an individual's risk of predation. The importance of predation in the evolution of male breeding aggregations remains unclear (Höglund and Alatalo 1995), but in several species, males suffer reduced predation risk as group size increases (Ryan et al. 1981; Trail 1987; Neems et al. 1992). In the case of spadefoots, snakes and birds visit breeding aggregations and feed on chorusing males (K. Pfennig, personal observation). Thus, reducing the risk of predation may explain why *S. multiplicata* males preferentially associate with conspecifics.

A second explanation for male aggregation with other males is that some males may cluster around others that are attractive to females (Beehler and Foster 1988; Höglund and Alatalo 1995). Previous work with spadefoots by Sullivan and Sullivan (1985) revealed that non-calling *S. multiplicata* males that sought to intercept females were smaller than calling males. Our finding that smaller males tended to associate with the average call rate stimulus, a stimulus preferred by females, suggests that male clustering may be due, in part, to aggregation of smaller males near attractive males. Smaller males

may behave as satellites if they are unable to attract females (Arak 1983; Howard 1984; Sullivan and Sullivan 1985). Indeed, *S. multiplicata* females at some breeding aggregations prefer males that are heavier for a given body size (Pfennig, 2000). Thus, smaller males may enhance their reproductive success if they intercept females attracted to larger, calling males. An unexpected aspect of the relationship between male size and association with the call rate stimuli was the finding that larger males tended to associate with the fast call rate stimulus. Further studies are required to understand this behavior.

Finally, males might be attracted to conspecifics because aggregative behavior by males is favored by female preferences for male groups (e.g., Shelly and Greenfield 1991; Alatalo et al. 1992; Lank and Smith 1992; Höglund et al. 1993). Female preferences for male groups could favor aggregative behavior by males if those that attend aggregations are more likely to mate successfully than those that fail to aggregate (Bradbury 1981; Gibson et al. 1990; Höglund and Alatalo 1995; Kokko 1997). Moreover, males that aggregate with conspecifics (as opposed to heterospecifics) may be more likely to mate with conspecific rather than heterospecific females. In the case of *S. multiplicata*, females may prefer groups of males to facilitate choice of conspecific mates. By preferring conspecific groups, females may reduce the risk of mistakenly mating with heterospecifics or of being intercepted by heterospecifics as they move through the breeding pond. Indeed, spadefoot species appear to segregate spatially at breeding aggregations: whereas *S. multiplicata* males tend to call from the center of ponds, *S. bombifrons* males tend to call from pond perimeters (Simovich 1985; K. Pfennig, personal observation). Thus, *S. multiplicata* females may use spatial cues to facilitate their choice of conspecific mates (e.g., Bush 1974).

We did not test the hypotheses that aggregative behavior by *S. multiplicata* males results from independent attraction to environmental factors such as resources or females but, as with other species (Bradbury and Gibson 1983; Thornhill and Alcock 1983; Bradbury et al. 1986; Höglund and Alatalo 1995), such factors may result in the formation of male aggregations. Our findings suggest, however, that male attraction to other conspecifics contributes, at least in part, to the formation of aggregations by *S. multiplicata* males. Predation pressure, attempts by smaller males to intercept females attracted to competitors, and female preference for conspecific groups may account for male attraction to other males. These hypotheses are not mutually exclusive and, taken together, suggest that *S. multiplicata* males may benefit by actively clustering with competing conspecifics.

**Acknowledgements** We thank David Pfennig, Tony Frankino, and the staff and volunteers at the Southwestern Research Station for their field support. Many thanks also to David Pfennig, Jeff Conner, Jeff Brawn, David Enstrom, Bob Podolsky, George Batzli, Scott Robinson, Ray Semlitsch, and two anonymous reviewers, for their comments on the manuscript, and to the Arizona Game and Fish Department for collecting permits. This research was supported by grants from the American Museum of Natural History Roosevelt and SWRS Student Support Funds, the Animal Behavior Society, the Francis M. and Harlie M. Clark Fund (University of Illinois), and Sigma Xi to K.S.P. All procedures were approved by our institutional animal care and use committees and conform to the laws of the USA.

## References

- Alatalo RV, Höglund J, Lundberg A, Sutherland WJ (1992) Evolution of black grouse leks: female preferences benefit males in larger leks. *Behav Ecol* 3:53–59
- Arak A (1983) Male-male competition and mate choice in anuran amphibians. In: Bateson P (ed) *Mate choice*. Cambridge University Press, Cambridge, UK, pp 181–210
- Arak A (1988) Female mate selection in the natterjack toad: active choice or passive attraction? *Behav Ecol Sociobiol* 22:317–327
- Beehler BM, Foster MS (1988) Hotshots, hotspots, and female preference in the organization of lek mating systems. *Am Nat* 131:203–219
- Bradbury JW (1981) The evolution of leks. In: Alexander RD, Tinkle DW (eds) *Natural selection and social behavior*. Chiron, New York, pp 138–169
- Bradbury JW, Gibson RM (1983) Leks and mate choice. In: Bateson P (ed) *Mate choice*. Cambridge University Press, Cambridge, UK, pp 109–138
- Bradbury JW, Vehrencamp SL, Gibson R (1985) Leks and the unanimity of female choice. In: Greenwood PJ, Harvey PH, Slatkin M (eds) *Evolution: essays in honour of John Maynard Smith*. Cambridge University Press, Cambridge, UK, pp 301–314
- Bradbury J, Gibson R, Tsai IM (1986) Hotspots and the dispersion of leks. *Anim Behav* 34:1694–1709
- Bush GL (1974) The mechanism of sympatric host race formation in the true fruit flies (Tephritidae). In: White MJD (ed) *Genetic mechanisms of speciation in insects*. Australia & New Zealand Book Company, Brookvale, pp 3–23
- Campbell DJ, Clarke DJ (1971) Nearest neighbour tests of significance for non-randomness in the spatial distribution of singing crickets [*Teleogryllus commodus* (Walker)]. *Anim Behav* 19:750–756
- Cherry MI (1993) Sexual selection in the raucous toad, *Bufo rangeri*. *Anim Behav* 45:359–373
- Emlen ST (1976) Lek organization and mating strategies in the bullfrog. *Behav Ecol Sociobiol* 1:283–313
- Forester DC (1973) Mating call as a reproductive isolating mechanism between *Scaphiopus bombifrons* and *S. hammondi*. *Copeia* 1973:60–67
- Gibson RM, Taylor CE, Jefferson DR (1990) Lek formation by female choice: a simulation study. *Behav Ecol* 1:36–42
- Höglund J, Alatalo RV (1995) *Leks*. Princeton University Press, Princeton, NJ
- Höglund J, Robertson JGM (1990) Female preferences, male decision rules and the evolution of leks in the great snipe *Gallinago media*. *Anim Behav* 40:15–22
- Höglund J, Montgomerie R, Widemo F (1993) Costs and consequences of variation in the size of ruff leks. *Behav Ecol Sociobiol* 32:31–39
- Howard RD (1978) The evolution of mating strategies in bullfrogs, *Rana catesbeiana*. *Evolution* 32:850–871
- Howard RD (1984) Alternative mating behaviors of young male bullfrogs. *Am Zool* 24:397–406
- Kokko H (1997) The lekking game: can female choice explain aggregated male displays? *J Theor Biol* 187:57–64

- Krebs CJ (1989) Ecological methodology. HarperCollins, New York
- Kroodsma DE (1989) Suggested experimental designs for song playbacks. *Anim Behav* 37:600–609
- Lank DB, Smith CM (1992) Females prefer larger leks: field experiments with ruffs (*Philomachus pugnax*). *Behav Ecol Sociobiol* 30:323–329
- Neems RM, Lazarus J, Mclachlan AJ (1992) Swarming behavior in male chironomid midges: a cost benefit analysis. *Behav Ecol* 3:285–290
- Pfennig KS (2000) Female spadefoot toads compromise on mate quality to ensure conspecific matings. *Behav Ecol* 11:220–227
- Ryan MJ, Tuttle MD, Taft LK (1981) The costs and benefits of frog chorusing behavior. *Behav Ecol Sociobiol* 8:273–278
- Schwartz JJ (1991) Why stop calling? A study of unison bout singing in a Neotropical treefrog. *Anim Behav* 42:565–577
- Schwartz JJ, Wells KD (1985) Intra- and interspecific vocal behavior of the Neotropical treefrog *Hyla microcephala*. *Copeia* 1985:27–38
- Shelly TE, Greenfield MD (1991) Dominions and desert clickers (Orthoptera: Acrididae): influences of resources and male signaling on female settlement patterns. *Behav Ecol Sociobiol* 28:133–140
- Simovich MA (1985) Analysis of a hybrid zone between the spadefoot toads *Scaphiopus multiplicatus* and *Scaphiopus bombifrons*. PhD thesis, University of California, Riverside
- Sokal RR, Rohlf FJ (1995) Biometry, 3rd edn. Freeman, New York
- Sullivan BK (1982) Sexual selection in Woodhouse's toad (*Bufo woodhousei*) I. Chorus organization. *Anim Behav* 30:680–686
- Sullivan BK (1983) Sexual selection in Woodhouse's toad (*Bufo woodhousei*). II. Female choice. *Anim Behav* 31:1011–1017
- Sullivan BK, Sullivan EA (1985) Variation in advertisement calls and male mating success of *Scaphiopus bombifrons*, *S. couchi* and *S. multiplicatus* (Pelobatidae). *Southwest Nat* 30:349–355
- Thornhill R, Alcock J (1983) The evolution of insect mating systems. Harvard University Press, Cambridge, Mass
- Trail PW (1987) Predation and antipredator behavior at Guianan Cock-of-the-Rock leks. *Auk* 104: 496–507
- Wagner WE Jr, Sullivan BK (1995) Sexual selection in the Gulf Coast toad, *Bufo valliceps*: female choice based on variable characters. *Anim Behav* 49:305–319
- Wells KD (1977) The social behaviour of anuran amphibians. *Anim Behav* 25:666–693
- Wiley RH (1991) Lekking in birds and mammals: behavioral and evolutionary issues. *Adv Stud Behav* 20:201–291
- Zar JH (1999) Biostatistical analysis, 4th edn. Prentice Hall, Upper Saddle River, NJ