THRESHOLDS OR COMPARISONS: MATE CHOICE CRITERIA AND SEXUAL SELECTION IN A PERIODICAL CICADA, MAGICICADA SEPTENDECIM (HEMIPTERA: CICADIDAE)

by

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Summary

Many insects possess life history characteristics that make them unlikely to use the kinds of relative mate choice criteria implicit in theoretical discussions of leks; thus, many insect mating aggregations are treated differently, as 'swarms' or 'choruses.' Yet periodical cicadas (*Magicicada* spp.) seem strong candidates for participating in lek mating systems. We present a series of observations and experiments designed to reveal whether there are mating biases in periodical cicadas and whether any biases are most consistent with flexible ('best-of-N'-choice) or fixed (threshold choice) mating criteria. We rule out postcopulatory choice by demonstrating that most females mate once, after which they become sexually unreceptive. In our study, patterns of mating success among actively chorusing males are indistinguishable from random mating, and we uncover no consistent differences between unmated and mated males on the basis of size and song pitch, two criteria that have been associated with *Magicicada* mating biases in other contexts. Because our results are most consistent with a fixed-threshold choice mechanism, we suggest that *Magicicada* mating aggregations do not function in a manner similar to vertebrate leks even though they fulfill Bradbury's (1981) lek criteria. Instead, features of *Magicicada* behavior suggesting female selectivity may arise incidentally from males' and females' unequal tendencies to mate multiply, the resulting superabundance of sexually receptive males, and the high frequency at which females are courted at the onset of mating readiness.

Introduction

Lek mating systems are characterized by (1) absence of male parental care, (2) a clumped distribution of males within the available habitat (forming 'leks'), (3) absence of special resources associated with leks, and (4) absence of mating outside the lek (Bradbury, 1981). Mate choice is of interest in lekking organisms because lekking females may potentially select the best among many available males ('best-of-*N*' or 'BN' choice of Janetos, 1980; 'sample-based' mate choice of Wiegmann *et al.*, 1996), and this choice may facilitate the evolution of extraordinary and apparently costly ornaments that characterize males of many lekking species (Höglund & Alatalo, 1995). BN choice requires either flexible choice criteria that can be revised as females gain experience about the pool of available mates, or indirect, simultaneous comparisons (Alexander *et al.*, 1997). Under BN choice, some skew in male mating success is expected, and, especially as lek size increases, extreme skew is possible because the highest quality males are able to monopolize mating opportunities. An alternative to BN choice is 'threshold' or 'minimal criteria' choice (MC choice) in which females accept the first mate encountered that meets or exceeds certain minimum standards (Janetos, 1980). Under MC choice, matings are expected to be randomly distributed among males meeting the acceptance criteria.

Many existing theoretical models of leks are based on examples in which vertebrates employ BN choice criteria (Bradbury, 1981, 1985; Bradbury & Gibson, 1983; Thornhill & Alcock, 1983; Wiley, 1991; Andersson, 1994; Höglund & Alatalo, 1995; Shelley & Whittier, 1997; for examples see Kruijt & Hogan, 1967; de Vos, 1979; Clutton-Brock *et al.*, 1989). Yet these vertebrate-based models are not necessarily applicable to insect mating aggregations because many insects have life-history characteristics that may reduce opportunities for BN mate choice (Alexander *et al.*, 1997). For example, most juvenile insects have minimal or nonexistent social contact with adult conspecifics before entering the mating pool, and thus have limited experiences that could influence the development of relative choice criteria. Relative mate choice also requires that females reject at least some mating opportunities even though insects' comparatively short adult lifespans may increase the significance of costs associated with mating delays.

Periodical cicadas (*Magicicada* spp.) have life history attributes that may offset constraints on female choosiness. Emergences are synchronized and extremely dense, with hundreds or thousands of cicadas routinely present in a single tree (Karban, 1982; Williams *et al.*, 1993). These high adult population densities appear to reduce predation risks (Karban, 1982) and could reduce the time needed for comparing potential mates. Some features of *Magicicada* behavior, such as routine rejection of male courtship attempts (Alexander & Moore, 1958, 1962; Dunning *et al.*, 1979) and unusually lengthy and complex courtship (Alexander & Moore, 1962; Williams & Simon, 1995; Cooley & Marshall, 2001) suggest that female periodical cicadas may be highly selective when acquiring mates. These aspects of periodical cicada life history and behavior suggest that periodical cicada mating aggregations may be more like classical leks than the aggregations of other insects; indeed, Alexander (1975) used *Magicicada* as a model in developing the non-resource based lek concept.

Direct experimental approaches for distinguishing BN and MC sampling strategies require information about the development of female preferences, the shape of female preference functions, and the characteristics of the potential mates a female is likely to encounter before mating. Although strong mating discrimination against heterospecifics (aggregations typically contain more than one *Magicicada* species) has been demonstrated in periodical cicadas (Marshall & Cooley, 2000; Cooley *et al.*, 2001), the study of within-species female choice has been hampered by the absence of information about within-species mating preferences, the impracticality of surveying such potentially enormous mating pools, and the possibility that females could use the teneral period to gather information about potential mates. Yet even in the absence of any *a priori* information about how or whether females discriminate among mates, patterns of male mating success should reflect underlying female choice criteria. This study is designed to reveal male mating patterns that are consistent with either BN or MC choice criteria, but not both.

The underlying null model of this study is that female periodical cicadas do not exercise choice among potential conspecific mates. First (Part I), to rule out postcopulatory choice, we establish that most females mate only once. We demonstrate that (A) mated females are unattractive to males, (B) normally mated females do not signal sexual receptivity (but mating-interrupted females do), and (C) females in a caged population tend to mate

once. Then (Part II), we present several approaches to uncovering evidence of mating bias: (A) we examined the degree of polygyny in a caged population and used computer simulations to determine if the observed variance in male mating success was greater than incidental biases expected to arise under random mating in a demographically similar population; (B) we examined the order in which males mated across trials, and again used computer-simulations to determined if male mating order (potentially reflecting female preferences) was significantly repeatable; and (C) we compared simple morphological and song characteristics of wild-caught copulating and chorusing males; in other contexts, both song pitch (Simmons *et al.*, 1971; Marshall & Cooley, 2000; English, 2001) and body size (Karban, 1983; English, 2001) have been shown to correlate with male success in *Magicicada*. Contrary to our initial expectations, we found little evidence consistent with BN choice criteria.

Materials and methods

Magicicada natural history

The periodical cicadas of eastern North America live underground as nymphs for 13 or 17 years before emerging for approximately three weeks of adult life (Marlatt, 1923; Maier, 1982a; Williams & Simon, 1995). Teneral (adult-immature) males and females mature for five or more days before beginning adult behaviors (Maier, 1982a; Cooley, 1999; Marshall, 2000). Since nymphal emergence is not perfectly synchronous, adults are present for 4-6 weeks. *Magicicada* populations are divided up into regional 'broods,' or year-classes, depending on their emergence schedule. Up to four sympatric, synchronous *Magicicada* species may be present in an emergence (Marshall & Cooley, 2000; Cooley *et al.*, 2001), often singing together in the same trees or shrubs. *Magicicada* adult populations are extraordinarily dense for such large insects, with estimates ranging from 8,355/ha (Maier, 1982b), to 272,000/ha (Whiles *et al.*, 2001) and 3,700,000/ha (Dybas & Davis, 1962). Individual trees routinely harbor hundreds or thousands of adult cicadas. Periodical cicadas, more so than other cicadas, are easily captured and eaten by predators because they are 'predator foolhardy,' or lacking overtly evasive or defensive behaviors, presumably an evolutionary response to the 'predator satiation' afforded by their periodicity and extraordinary population densities (Williams *et al.*, 1993; Lloyd & Dybas, 1966). After mating, females lay eggs in woody twigs. The eggs hatch after approximately eight weeks and the first instar nymphs immediately burrow underground (Williams & Simon, 1995).

We used the most well-studied periodical cicada species, *Magicicada septendecim*, for this study. *M. septendecim* males advertise and search for mates by 'chorusing,' or alternating bouts of 1-3 calls (typical) with short flights of a few centimeters to several meters (Alexander & Moore, 1958, 1962; Williams & Smith, 1991). These calls attract both male and female conspecifics to the chorus (Alexander & Moore, 1958). Sexually receptive females remain

relatively stationary within the chorus and respond by making wing flicks timed to conspecific male calls (Cooley & Marshall, 2001). Male periodical cicadas perceiving female wing flick responses to their own calls (or to those of other males) move toward the responding female; as the male approaches the female, the pair engage in a call/wing flick 'duet' and perform a courtship sequence that includes stereotypical movements and two distinct courtship signals in addition to the calling song (Alexander & Moore, 1958, 1962; Cooley & Marshall, 2001), an unusually complex acoustic repertoire for an insect. Pair-formation and courtship in natural and caged populations is brief (commonly less than a minute; Marshall, 2000; Cooley, Marshall & Hill, unpubl. observations). However, males sometimes persistently court females who apparently do not signal sexual receptivity; these attempts may last for several hours and may end with the female signaling sexual receptivity and mating, or with the female terminating the interaction by flying away or flapping her wings (Alexander, 1968; Dunning *et al.*, 1979; Marshall, 2000). Copulation usually lasts three to four hours (Cooley, 1999), and females have been observed ovipositing within 24 hours of mating (Cooley & Marshall, unpubl. observations).

General methods

Collection and storage of cicadas

Within *M. septendecim*, there are no known behavioral differences distinguishing different populations or broods (most of the modern brood structure appears to be Holocene in origin), so different aspects of this study were conducted in different years or locations to take advantage of cicada availability (Table 1). All females used in this study were initially unmated. Mating status was ensured by collecting females exclusively from low vegetation the morning after their emergence; such 'teneral' cicadas are easily recognized by their soft, dull exoskeletons and pale ovipositors. After collection, teneral females matured for several days in 'branch cages' (see below) placed on living, woody vegetation.

Except in Experiment C (below), males were collected from among those actively chorusing (*i.e.* calling and/or flying) in the area and were used immediately in experiments, or they were stored in the same manner as females before use. This manner of collecting males intentionally restricted the scope of our study to examining evolved mate choice mechanisms, or 'direct' mate choice, which consists of mating biases based on active discrimination among

TABLE 1. *Study Sites, 1995-2000*

Year	Brood	Life cycle	Location	County	State	Characteristics
1995	I	17	Alum Springs	Rockbridge	VA	Logged site
1996	II	17	Horsepen Lake SWMA	Buckingham	VA	Logged site
1997	III	17	Siloam Springs SP	Brown, Adams	IL	Old field
1998	XIX	13	Harold Alexander WMA	Sharp	AR	Recently cleared field
1999	V	17	Tar Hollow State Forest	Ross	OH	Recently cleared hillside
2000	VI	17	Private property	Burke	NC	Logged site

potential mates. Our methods exclude patterns resulting in 'indirect' mate choice, which is the restriction of the set of possible mates by all other aspects of behavior and morphology (Wiley & Poston, 1996). For *Magicicada*, this is not a trivial distinction; in any *Magicicada* emergence, some cicadas suffer apparent damage during ecdysis. These cicadas may have gross or subtle wing, leg, or other abnormalities that affect their mobility (*e.g.* White *et al.*, 1979). Because male and female *Magicicada* actively aggregate to mate (Alexander & Moore, 1958, 1962; Dunning *et al.*, 1979), males that fail to locate or remain within aggregations are effectively excluded from the mating pool; thus, 'indirect' mate choice discriminating against deformed cicadas always operates among *Magicicada.* The effects of indirect choice due to such phenotypic deformity are outside the scope of this study. No cicadas used in this study showed any signs of infection by the fungus *Massospora cicadina* (Soper, 1974; Soper *et al.*, 1976).

Experimental cages

We used three types of cages in our studies: (1) 'branch cages,' made by enclosing a living woody branch in a bag ($\approx$50 liter) constructed of window screen; (2) 'arena cages,' made of the same material as branch cages but larger ($\approx$150 liter) and placed upright over a deciduous stump sprout or small sapling; and (3) 'flight cages,' consisting of a $\approx$ 3 (width) $\times$ 3 (width) $\times$ 2.5 m (height) screened canopy placed over saplings or stump sprouts. All cages were placed in the sunlight. Branch cages were used for storage of unmated females collected as teneral individuals, while larger cages were used for observations or experiments. Cage types were not mixed within experiments, and, to the extent that it was practical, all cages used in any particular experiment were placed on vegetation that was similar in species, shape, size, and exposure.

Assessing female receptivity

The timed wing flick signals produced by sexually receptive female *Magicicada* generally lead to male/female signal 'duets' and mating (Cooley & Marshall, 2001). We used female wing flick signals as assays of mating receptivity in a series of playback experiments (described below). For all such experiments, we verified that weather conditions were appropriate for female wing flick signaling by playing the same calling song phrase to unmanipulated, mature, unmated females stored in nearby branch cages. We continued with the experiments only if some of the unmanipulated females responded with wing flick signals, demonstrating that conditions were appropriate for female responses.

Separating copulating pairs

In several of the experiments described below, we separated copulating pairs by quickly removing them from their cages, grasping the base of the male genitalia, and gently working male and female genitalia apart. No apparent damage is caused by this process. In all such experiments, we physically separated the copulating pairs before any significant ejaculate deposition, and before the formation of a visible 'sperm plug' (White, 1973; Cooley, 1999).

Statistical analysis

Some statistical analyses were conducted using Systat Version 5.2.1 (Macintosh). Statistical significance of other datasets was assessed by computer simulations of null models, as described below.

Experimental and observational procedures

I. Do female *M. septendecim* mate more than once?

Since most females mate only once (a finding corroborated by the rarity of mating pairs late in the emergence; Cooley & Marshall, unpubl. obs.), there is little opportunity for postcopulatory 'cryptic female choice' (Eberhard, 1985, 1997). However, if females revise their mate choice by remating, then the question of sexual selection imposed by female choice is more complex than if females mate singly. The observations described below are intended to determine whether males exhibit greater sexual interest in unmated females than mated ones, and whether females become sexually unreceptive following a normal mating.

Experiment A: Effect of mating status on recruitment of chorusing males.   In 1996, three arena cages were set up in a recently logged area 8 m from a woods edge in which *M. septendecim* males were actively chorusing. Males could be observed singing and flying in the surrounding vegetation. Thirteen mated, 10-day-post-ecdysis female *M. septendecim* were placed in one cage; these females had mated on the day prior to this experiment. Thirteen unmated females of the same age were placed into another cage, and the third cage was left empty.

  For one afternoon and the following morning, the exteriors of the cages were scanned approximately every half-hour for a total of 17 scans. In each scan the males present on the exterior of the cage were counted, and courtship behaviors were noted including wing flicking by the caged females, production of courtship songs by the males, or males mistakenly courting one another. After each scan all males were collected and removed to a distance of ten meters away from each cage on the side farthest from the woods edge, to reduce the possibility that they would visit the cage again. It is unlikely that females visiting the cages from the ambient chorus affected the experiment, since no females were observed on the exteriors of the cages, although on two occasions a perched cicada flew before its sex could be determined.

Experiment B: Effect of female mating status on wing flick response.   In 1997, we judged female postcopulatory sexual receptivity using playbacks of recorded male calling song. We allowed 22 individually-marked (Cooley *et al.*, 1998) adult female *M. septendecim* to mate without interference. After the mating pairs separated, we placed 11 into each of two branch cages. We also placed 11 marked, unmated females of the same age into each cage. Placing several females in the playback cage represents a compromise between processing an adequate number of receptive females (because after handling, some females are slow to return to sexual receptivity) and completing the experiments in a timely fashion (because female preferences may change as they age). In other, similar experiments (Marshall & Cooley, 2000, 2001), we have seen no evidence that females copy or imitate each other; rather, contact between females can inhibit responsiveness. Once the cages were stocked, we positioned a 3″ Radio Shack midrange speaker just outside each cage and played a recorded male *M. septendecim* calling song phrase repeatedly for two minutes at an intensity of ≈75 dB (at 25 cm). During this time we noted the number of mated and unmated females responding. We repeated the playbacks to the cage on each of the next four consecutive days.

Experiment C: Female remating in a large caged population.   In 1995, male and female mating was tracked in a large caged population to observe female remating tendencies and patterns of male mating success (the latter discussed under Experiment E below). The cage

was stocked progressively over 9 days (Table 2) with cohorts of recently emerged males and females. All cicadas were individually marked and no cicadas were ever removed from the population. Thus, like a natural population, the cage population generally consisted of unmated teneral, unmated adult, and mated adult cicadas. Approximately equal numbers of males and females were included, but male mortality reduced the population sex ratio to approximately 3 males : 4 females. The cage density was comparable to that of a natural population (approximately 1 cicada per 2 liters of cage space; Cooley, 1999). The cage was stocked such that all males were mature by the beginning of observations (the earliest cohorts of males were added before the females), while females matured progressively in accordance with their emergence date; thus, at any given time, the operational sex ratio in the cage was male-biased (see discussion of the highly male-biased operational sex ratio later in this paper). Beginning with the onset of adult activity in the cage (as indicated by male singing and flying) on 23 May and continuing until 3 June, we visually scanned the population for mating pairs continuously during hours of peak activity (10 AM-2 PM). During periods of lower activity (8-10 AM, 2-7 PM) we scanned the cages approximately every 15-30 minutes. At each scan, the time and identity of mating pairs were noted. At the end of each day, dead individuals were removed from the cage and their identities were recorded. The relatively short duration of the study excludes the possibility that females in the experiment remated to replenish sperm stocks depleted as a result of oviposition.

TABLE 2. *Phenology of* M. septendecim *female maturation and mating in the 1995 flight cage population (Experiments C, E), organized by date of female emergence (vertical axis)*

Female emergence date	Observation date															
	19	20	21	22	23	24	25	26	27	28	29	30	31	1	2	3
16	[9]				1	1										
17	[15]	[5]			1	2	2	*1*			*1*					
18		[7]			1	2	3	1								
21			[12]				1	6			5					
22				[15]				3			11	1				
23					[15]						12	3	1			
24						[16]						5	6			4
25							[10]	[15]			**1**	1	1			2
26																12
									Rain					Rain		

Numbers of females of a given age added 19-26 May are given in brackets. Numbers of matings observed 23 May - 3 June are given in plain text. The delay between addition (bracketed value) and first mating (plain text) is the 'teneral period'. Italicized values represent the second and third matings of a single May 17 cohort female that mated three times. The bold value represents a mating by a female that was likely not teneral when collected. Rain and cold temperatures suppressed cicada activity in the cage and surrounding woods on 27-28 May and on 1-2 June.

Experiment D: Mating interruption.   In 1997, we placed 5-10 individually-marked, mature, unmated *M. septendecim* females into branch cages and allowed them free access to mature males. To establish a starting time for each observed copulation, we monitored cages continuously or scanned them every 10-15 minutes, concluding each scan only when we had noted the location and activity of every cicada in the cage. We also *ad lib* scanned any cage in which we heard male courtship songs. The matings of 9 females were disrupted 15 minutes after commencing, those of 11 females were disrupted after one hour, those of 9 females were disrupted after two hours, and 17 females were allowed complete, undisturbed matings. After each mating (partial or complete), we placed the females in new cages without access to males. After interruption, and until the females showed signs of morbidity or mortality, we played model male calling songs to them twice daily and noted any wing flick responses.

II. Are patterns of male mating success biased?

Female choice using relative criteria should increase the variance in male mating success over that expected under random mating (defined as equal probability of mating among males). Further, females should show a consistent preference for the 'best' males, so the order in which males mate should be repeatable each mating opportunity. We tested both of these predictions and further sought evidence of female choice by examining correlations between male mating success and two male phenotypic attributes, size and song pitch. A correlation between male size and mating success has been shown in *M. cassini* (Karban, 1983), and song pitch has been shown to be important in mating discrimination against heterospecifics (Simmons *et al.*, 1971; Marshall & Cooley, 2000).

Experiment E: Male mating patterns in a large caged population.   Because *Magicicada* females emerge over a two-week period, and because males can mate on successive days, some degree of mating skew, or variance in mating success, is to be expected among males even in the absence of female choice. In order to determine the variance in male mating success expected under equal probability of mating across males (the null model), a computer program (available from the authors upon request) was designed in Think Pascal 4.0 (Macintosh) to simulate random mating in a model population of the same demographics and mating frequency as the flight cage population in Experiment C. In that experiment, males mated from 0 to 6 times (Fig. 1). The average number of days by which a copulation followed a prior copulation was 2.8 (range 0-7 days), though one male mated twice on the same day (Fig. 2). The computer simulation was designed around these parameters.

   The computer simulation design included only those males that could be accounted for as dead or that were in the cage at the end of our experiment (some males were never seen during scans and were not recovered at the end of the experiment; they either escaped or died, and may never have entered the mating pool). Two modifications of this program were used, one to simulate random mating across the entire male sample, and one to simulate random mating among males that mated. In all simulations, males at 5 days post-emergence were considered adult, males were assumed able to mate only once in a day (an assumption violated by only one male in the study), and mated males were available for remating the following day. A single simulation consisted of a number of simulated days corresponding to the number of days in the field experiment (in this case eight, because four of twelve days were rained out with little cicada activity). In each simulated day, a number of males were
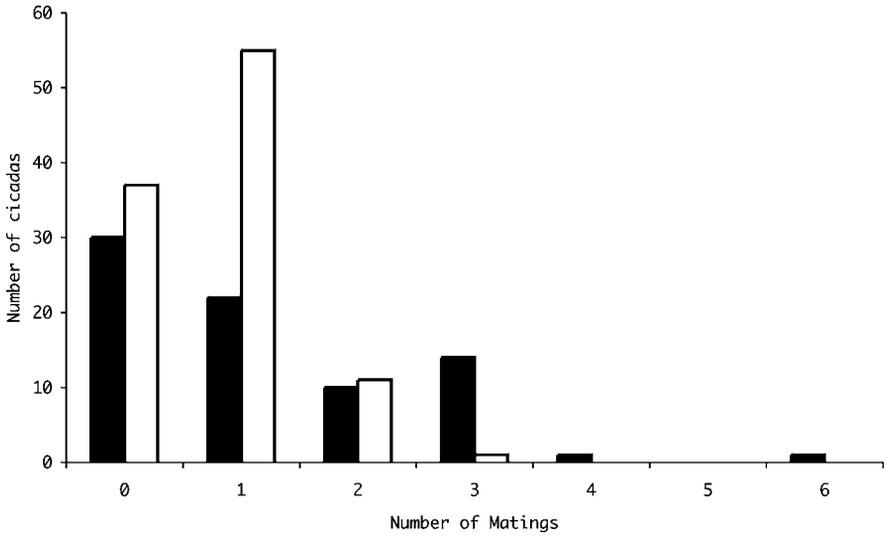
Fig. 1.   Mating frequency in male (black bars) and female (white bars) *Magicicada septendecim* in experiment E. Females that mated first on the last day of the experiment are excluded, since they did not have an opportunity to remate.
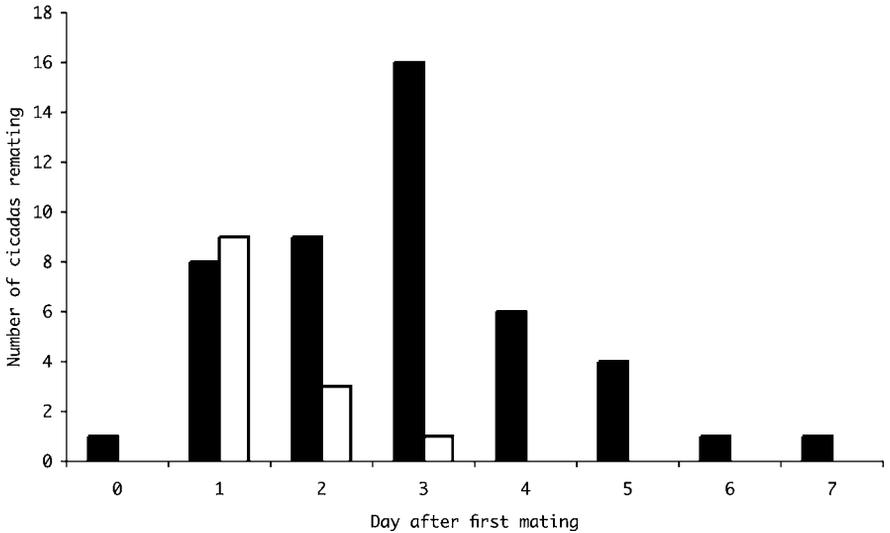

Fig. 2.   Histogram of delay, in days, between first and second matings in *M. septendecim* males (black bars) and females (white bars; Experiment E). Remating females tended to mate within a total period of 2-3 days, while males continued to mate throughout the study.

drawn at random without replacement from those available, with the number of drawings corresponding to the number of matings that occurred in the corresponding day of the field trial. Each time an individual male was drawn, it was marked as having mated. On each simulated day, the program also drew, at random, a number of males matching the number of additional deaths that had occurred up to the corresponding day in the actual population, and marked these males as 'dead'; males so marked were removed from the pool of available males.

After the completion of each simulation, the program calculated the variance in the total number of 'matings' across males, stored that value, reset the mating totals for each male to zero, and began again. The program repeated the simulation 10,000 times and generated a cumulative frequency distribution of the resulting variances. Comparison of the observed variance in mating success among the 1995 flight cage males to this simulated distribution allows testing of the random mating hypothesis. In addition, we explored the sensitivity of this simulation to detecting mating skew by analyzing simulated data sets.

Experiment F: Repeatability of male mating rank.   If females prefer some males over others and exercise at least partial control over the initiation of mating, the order in which the individual males in a sample mate should not be random; the highest quality males should mate first, and the lowest-quality males should mate last.

In 1996, we investigated the repeatability of male mating order by interrupting matings and allowing the same males and females opportunities to mate again. We used the following protocol, repeated four times: (1) Nine chorusing males were captured on the morning of a trial and marked individually; (2) Under conditions appropriate for mating, these males were placed into an arena cage with nine individually marked, mature, unmated females; (3) As individual copulating pairs formed, they were immediately removed from the cage, separated, and placed in single-sex holding cages; the identities of the cicadas and the time of mating were recorded; (4) At then end of the day the trial was terminated and all remaining cicadas were placed in the single-sex holding cages; (5) On the following day, the process was repeated with the same males and females; (6) Each male was assigned a first-day rank and a second-day rank reflecting his position in the mating order on the two different days of a complete trial. If the order of two or more matings could not be determined (because both began while the observer was temporarily absent) they were assigned an appropriate tied rank. Unmated males were also assigned a tied rank reflecting their position at the bottom of the hierarchy. In 1997, we conducted a similar experiment, using only one cage stocked with 20 individually-marked males. In this experiment, instead of allowing the same males and females opportunities for mating after interruption, we allowed all matings to proceed to completion, discarded the females after mating, and used new females each time we gave the males a mating opportunity. We allowed the males access to three separate groups of 20 females on three different days. As in the 1996 experiment, the order of male mating was recorded. Sixteen of the 20 males (fifteen that mated and one that did not) were given second and third mating opportunities on subsequent days. In effect, both of these protocols use a 'panel' of receptive females to rank the attractiveness of a collection of potential mates; if certain males are more desirable than others, and if females compete for the most desirable males, then the order in which males begin copulating will be repeatable.

Computer model simulations (available from the authors upon request) were used to determine if male mating order occurred with greater repeatability than expected by chance. For each trial, two simulation statistics were measured to quantify the repeatability of male rank.

The first statistic, FHLH (First-Half, Last-Half), quantified the degree to which individuals tended to mate in the same half of the rankings in both parts of a trial. To calculate FHLH, the summed first-day ranks of the last four males to mate on the second day were subtracted from the summed first-day ranks of the first four males to mate on the second day. On average, if first-day mating order does not predict second-day mating order, FHLH should be zero. If early-mating males tend to retain their high mating rank, FHLH will be negative. The second statistic, SRD (Specific Rank Difference), measured the tendency for males to mate in the same specific rank position on both days of a trial. To calculate SRD, the absolute difference between first-day rank and second-day rank was summed across all males. All values of SRD are zero or positive; SRD becomes smaller as male mating order becomes more repeatable.

For all experiments, a computer simulation was constructed to evaluate the expectations of FHLH and SRD under random mating. All simulations used the same general random model, adjusted to fit the population sizes in the various field trials. The males in the simulated population were assigned first-day rank values matching those assigned to the males in a given experimental trial; they were chosen again in random order for a second 'mating', and FHLH and SRD were calculated. The simulation repeated 10,000 times to generate the cumulative frequency distribution of FHLH or SRD. The values of SRD and FHLH observed in the experimental trials were compared to these simulated frequency distributions to determine if the null hypothesis of random mating could be rejected.

Experiment G: Correlates of male mating success.   In 2000 we compared the size and song pitch of male *M. septendecim* captured *in copula* with those captured flying in the chorus. Over a period of seven days, we located and captured mating pairs in a natural *M. septendecim* chorus; then, for each pair, we captured the nearest actively calling and flying male within a 1 meter radius. Mating males and females were separated, and each male was marked with a code indicating whether it had been captured mating or chorusing. All males were placed in a flight cage. Males that called in the cage were recorded using a Sony microphone and parabola, assigned a unique number, and preserved in 95% ethanol. At the end of the experiment, all remaining males were assigned a code and preserved in similar fashion. Once in the laboratory, we isolated one call (an individual male's calls do not vary significantly in dominant pitch; Marshall & Cooley, 2000) of each male and measured dominant pitch from a power spectrum (plot of sound intensity *vs* frequency) generated using Canary 1.1.1 (Cornell Bioacoustics Laboratory) for the Macintosh. Other song characteristics, such as duration or intensity of calling phrases, can vary depending on the context of the calling male, so they are not reliable indicators. Furthermore, call pitch, rather than temporal characteristics (pulse structure, *etc*.) is used in mate discrimination in the closely related species *M. neotredecim* (Marshall & Cooley, 2000; Cooley *et al.*, 2001). We also measured width horizontally across the abdomen at its widest point, the dorsal-ventral thickness of the abdomen at its widest point, the length from the tip of the head to the posterior margin of the first abdominal segment, and the head width between the eyes. All measurements were made to the nearest 0.1 mm using calipers.

Although our collection method suggests a paired design, we chose to treat the mating and chorusing males as independent samples. Our rationale for collecting males in pairs was to control any incidental sorting — such as would occur if individual characteristics (*e.g.* size) were nonrandomly associated with some characteristic of their chorus location (vegetation type, slope aspect, *etc.*). Because we did not collect our samples at the commencement of

copulation, the sample 'pairs' are less a representation of alternatives that were actually available to receptive females than independent samples of mating and chorusing males, with any locational effects controlled. One caveat of our choice of unpaired statistics is that we have sacrificed some statistical power. In addition to these tests, we performed a principal components analysis of all size data on male mating status.

Results

Experiment A: Effect of mating status on recruitment of chorusing males

Male *M. septendecim* were rarely observed on the surfaces of the empty cage or the cage containing mated females. In contrast, in nearly every scan males were observed sitting or walking on the surfaces of the cages containing mature, unmated females. When the number of scans with males present on cage exteriors is tabulated, the contrast between the cage containing mated (average 0.1 males/scan) and unmated (average 2.6 males/scan) females was significant (two-tailed Fisher's exact test, $p \leqslant 0.001$), as was the contrast between the cage containing unmated females and the empty cage (average 0.2 males/scan; two-tailed Fisher's exact test, $p \leqslant 0.001$). Both the empty cage and the cage containing mated females were equally unlikely to be visited by males (two-tailed Fisher's exact test, $p \geqslant 0.5$). The combined scan counts differed strongly across treatments (Kruskal-Wallis test statistic $= 48.729$, $p < 0.001$). In addition, the few males found on the empty cage or the cage containing mated females were never observed performing courtship-related behaviors, while such behaviors were repeatedly observed in association with the cages containing unmated females.

Experiment B: Effect of female mating status on wing flick response

Some mortality occurred between the day on which the cages were stocked and the day of the final playbacks. None of the mated females responded to playbacks, while at least half of the unmated females responded each day with wing flick signals (Fig. 3). This difference was significant in each of the four days ($p \leqslant 0.001$; two-tailed Fisher's exact test).

Experiment C: Female remating in a large caged population

Females mated most often on the fifth through seventh days after emergence (excluding cold rainy days) (Table 2). Fifteen females were excluded from
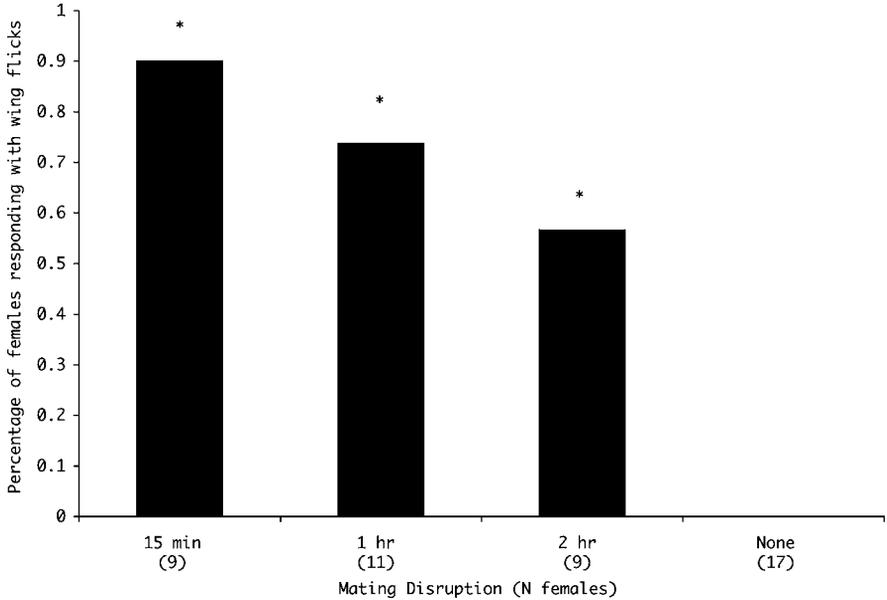
Fig. 3.   Comparisons of female *M. septendecim* wing flick responses to playbacks of male calls in response to mating disruption. Females were marked as responding if they made at least one timed wing flick signal in response to repeated playbacks of male calls. No females with uninterrupted matings responded. Disruption treatments marked with an asterisk were statistically distinguishable from no-interruption treatment ($p \leqslant 0.002$ in all cases, two-tailed Fisher's exact test, no Bonferroni correction).

our analyses because they mated for the first time on the last day of obser-vation and thus had no remating opportunities. The results of this experi-ment demonstrate that female mating motivation was not consistent over the course of the experiment; females stocked earlier in the experiment tended to have longer teneral periods, a trend likely attributable to changing weather conditions. However, regardless of when they first mated, all females in-cluded in the analysis had opportunities to remate in the final days of the experiment; thus inconsistent weather is unlikely to have constrained fe-male female remating opportunities. Of the females who mated before the last day of the experiment, 55 mated once (Fig. 1) despite the continuous availability of a dense male chorus. Eleven females mated twice, and one fe-male apparently mated three times. However, this particular female may have been physically incapable of normal copulation. All of her copulatory bouts lasted less than 30 minutes, and the copulating male in one bout appeared to have difficulty attaching despite an apparent lack of resistance by the female.

Three of the females that mated twice were observed *in copula* only briefly with one of their mates; the remainder engaged in two apparently normal matings. Because most rematings occurred on the day immediately follow-ing the previous copulation (mean 1.4 days after prior copulation, range 1-3; Fig. 2), and because the average mating occurred with 3.1 days remaining in the observation period (range 0-7, mode 3), most females had ample op-portunity to remate during the study. Excluding the female who mated three times and the three females who had atypically short first matings, approx-imately 10% of females in this cage remated. Given the absence of sexual receptivity among mated females in Experiment B, we suspect that some of the matings in the cage were forced, because caged females could not leave the chorus to oviposit and males were persistent in their attempts to force copulations.

Experiment D: Mating interruption

Most females whose matings were disrupted responded positively to the simulated male songs, while none of the normally mated females responded. All disruption treatments resulted in an equal likelihood of female response (Fig. 3).

Experiment E: Male mating patterns in a large caged population

Neither the variance in mating success among all males, nor the variance in success of mated males alone, differed significantly from random expec-tations (simulation results: for all males ($N = 60$), $p > 0.05$ if $1.21 <$ variance < 2.15; actual variance was 1.65; for mated males only ($N = 43$), $p > 0.05$ if $0.88 <$ variance < 1.72; actual variance was 1.2). The distri-butions of simulated data sets for all males and for mated males only, with critical values and actual values delineated, are shown in Fig. 4.

Experiment F: Repeatability of male mating rank

In the 1996 experiment, in each mating bout, the first matings typically began within minutes after the addition of the males. No evidence of forced copulations was seen. Over the course of the experiment, one male died, one male failed to mate at all, and one male was lost. Correction for this error and mortality reduced the total sample size for males in three of the
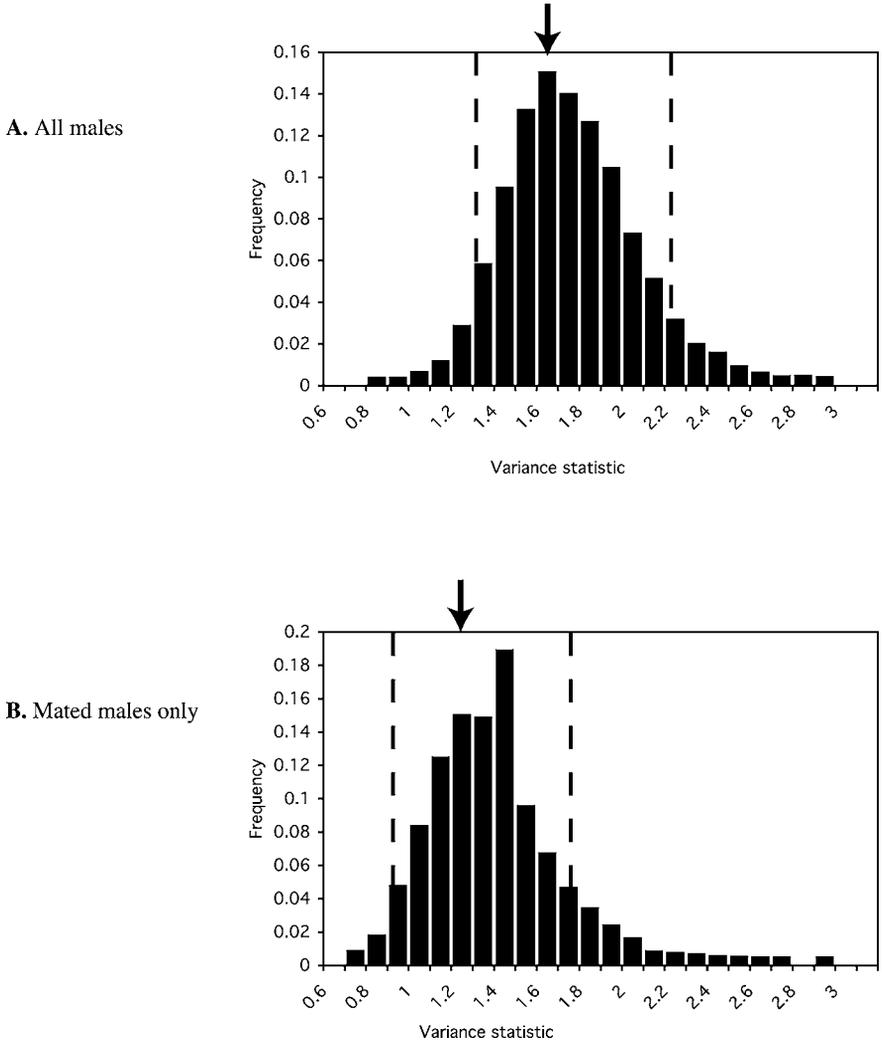
A. All males

B. Mated males only

Fig. 4.   The distributions of simulated data sets for all males (a) and for mated males only (b). Critical values are delineated by dashed lines, while experimental results are indicated with arrows.

experimental iterations from nine to eight. For the one iteration with nine surviving males and females, FHLH was calculated using the ranks of the first four and last four males, with male #5 not assigned to either half. Male mating order as measured by FHLH and SRD did not deviate significantly from random mating expectations (Table 3a), although there was a slight

TABLE 3. *Statistical tests of repeatability of* M. septendecim *male and female mating order in Experiment F*

Trial	FHLH	*p*	SR	*p*
(a) 1996 Trials 1A-1D				
Male mating order:				
All groups	−9	0.52-0.58	92	0.82-0.94
Group A	−2	0.68-0.86	26	0.28-0.46
Group B	−6	0.34-0.46	18	0.46-0.68
Group C	+3	0.58-0.82	22	0.82-1.00
Group D	−4	0.58-0.68	26	0.78-1.00
Female mating order:				
All groups	−32	0.02-0.04	62	<0.01
Group A	+8	0.20-0.34	24	0.64-0.77
Group B	−17	0.02	12	0.01
Group C	−9	0.20-0.26	16	0.10-0.15
Group D	−14	0.06-0.08	10	0.01
Groups B-D	−40	0.01	38	<0.01
(b) 1997 Trial 2				
2A-2B	−8	0.70	74	0.48
2B-2C	+5	0.80	75	1.0
2A-2C	−38	0.06	51	0.01

FHLH and SR values are empirical results of mating order experiments in (a) Trials 1A-D, 1996 and (b) Trial 2, 1997. *p* values or ranges are two-tailed significance levels of deviation of FHLH or SR from null hypothesis of random mating; the *p* values are derived from repeated computer simulation of random mating in model populations of the same composition. The FHLH statistic is negative when mating order tends to be repeated, positive when male mating order tends to be reversed. SR is always positive and becomes smaller as mating order becomes more repeatable.

tendency for FHLH values to be negative, which could result from a positive mating order correlation.

During the analysis of our 1996 data it became apparent (since females were allowed to mate again) that there was some repeatability in female mating order. We reworked the computer simulations to allow analysis of female mating pattern. Two experimental iterations showed a significant repeatability of female mating order across trials, while in a third, females showed a weak but nonsignificant correlation in the same direction (Table 3a). Females in the fourth group showed no indication of mating order repeatability between trials. Although we did not set out to address repeatability of fe-

TABLE 4. *Mann-Whitney One-Way ANOVAs comparing size (mm) and song pitch (kHz) for males captured while copulating or while chorusing*

Measure	Chorusing males	Mated males	U	p
Song Pitch	1.34 kHz $\pm$ 0.002, $N = 71$	1.34 kHz $\pm$ 0.002, $N = 65$	2329	0.925
Head Width	8.44 mm $\pm$ 0.049, $N = 77$	8.36 mm $\pm$ 0.045, $N = 78$	3530	0.04*
Abdomen Width				
Horizontal	11.04 mm $\pm$ 0.103, $N = 77$	10.91 mm $\pm$ 0.088, $N = 78$	3790	0.004*
Dorso-ventral	10.19 mm $\pm$ 0.138, $N = 77$	10.11 mm $\pm$ 0.124, $N = 78$	3342	0.212
Length	19.51 mm $\pm$ 0.375, $N = 77$	19.28 mm $\pm$ 0.284, $N = 78$	3648	0.02*

Fewer males were analyzed for song pitch than for size measurements, because not all males called after capture.

male mating order, the results help to validate the sensitivity of our statistical methodology.

In the 1997 experiment, most males mated in each of the three trials, and copulations appeared normal. Three of the sixteen males did not mate in Trial 2B, and one of the sixteen males did not mate in Trial 2C. As in the 1996 trials, neither simulation statistic revealed significant repeatability of male mating order between consecutive trials (Table 3b).

*Experiment G: Correlates of male mating status*

Although songs of males captured while mating did not differ in dominant pitch from those of males captured while chorusing, by several measures, mating males were significantly smaller than chorusing males (Table 4). These significant trends disappear when cicadas collected on the final 4 days of the study are excluded from consideration. Even given the low statistical power of our experimental design, it was sensitive enough to detect this trend. A principal components analysis of both covariance and correlation matrices failed to demonstrate any clustering of size data (Fig. 5).

Discussion

Mechanisms of mate choice in Magicicada septendecim

Patterns of female behavior and male mating success in *Magicicada septendecim* leks bear only superficial resemblance to those observed in many classical bird and mammal leks, where females appear to discriminate strongly

A. Plot of principal components correlation matrix.
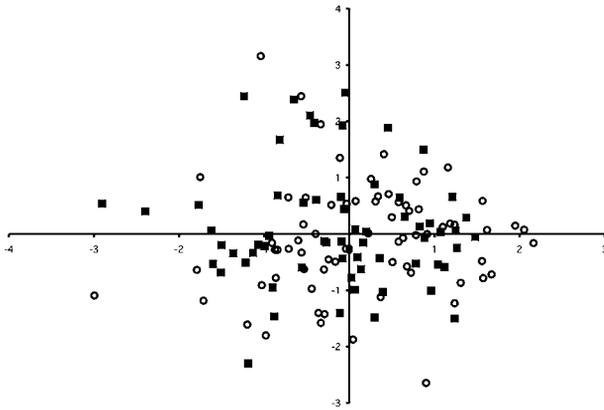
B. Plot of principal components covariance matrix.
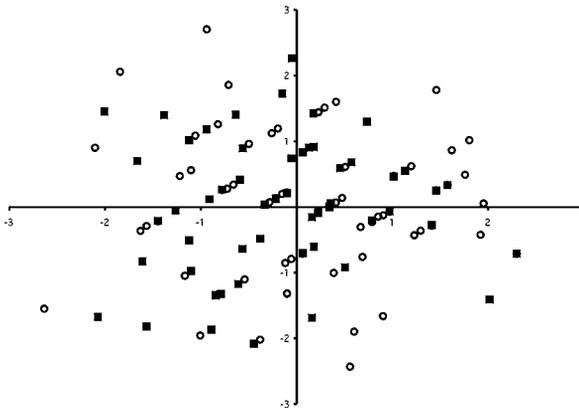

Fig. 5.   Principal components analyses of both correlation (A) and covariance matrices (B) for males captured while chorusing (diamonds) or mating (open circles). For the correlation matrix, PC1 accounted for 58% of total variation, and PC2 accounted for 21%. The values for the covariance matrix are 80% and 12%, respectively.

among males (Höglund & Alatalao, 1995). Except for the comparison of male size and mating status (see below), our experiments found little evidence of female discrimination among conspecific, chorusing males, even though females had opportunities to exercise choice. There is little evidence

of male mating skew or repeatable male mating order, and no evidence that male success correlates with song pitch. Most females mated only once, minimizing the potential for copulatory courtship or mate choice revision. Every copulation observed was preceded by species-typical male calling song, the stereotypical male courtship sequence and female acceptance signals. The one near-exception occurred in an experimental cage, when an opportunistic silent male mated with a female while another male on the outside of the cage completed the courtship sequence. These results are most consistent with the operation of a threshold, or MC, choice mechanism combined with a scarcity of unacceptable conspecific mates in our samples of chorusing males. Research demonstrating active female discrimination against heterospecifics (Marshall & Cooley, 2000) is also consistent with MC choice in which conspecifics meet the mating criteria while heterospecifics do not. Although a 'best-of-N' mechanism cannot be ruled out, if such a mechanism has evolved in *M. septendecim* then there appears be little variation in male quality among chorusing males.

The results of our size comparison of mating and chorusing males differ from those of Karban (1983), who found that males of the related species *M. cassini* collected *in copula* tended to be larger than males collected singly, and from similar results found by English (2001) for *M. cassini* and *M. septendecim*. While some differences in our results might be explained by differences in the species studied, our sampling methods also differed from Karban's and English's. We collected only males that were actively chorusing in order to exclude patterns arising from 'indirect choice' (Wiley & Poston, 1996; see General Methods, above) against cicadas that were unable to chorus due to faulty ecdysis (White *et al.*, 1979) or other developmental problems, while Karban and English apparently collected more at random from the population. These methodological differences may reveal different aspects of *Magicicada* mating discrimination: Comparison of mated and randomly sampled males will tend to reveal characteristics of males that are able to enter the mating pool (and therefore patterns of indirect choice), while comparison of mated males and single, actively chorusing males may reflect female discrimination (or lack thereof) among males within the mating pool.

We were initially surprised that, in our study, mating males were statistically smaller than chorusing males. While this tendency could be explained by mate discrimination, and this hypothesis remains viable until further analysis, we suspect that unanticipated biases in our collection methods could have been responsible. For example, one *post-hoc* explanation for

these results is related to daily patterns of *M. septendecim* activity, which typically peaks in the mornings and declines in the afternoon (Alexander & Moore, 1958). We made all of our collections at midday or in the early afternoon, which could have created a bias because mating males are, in effect, a delayed sample of males that were chorusing earlier in the day (copulation averages four hours; Cooley, 1999), while the chorusing males are an instantaneous sample of the ongoing chorus. If male size and stamina are correlated, then larger males might remain active later in the day than smaller males, so that larger males would have an increasing representation in the chorus over the course of a day. Even though our methods may have excluded some less vigorous or healthy males, our results remain consistent with the operation of MC choice criteria because we found little evidence of female discrimination among the sampled males. Additional research addressing the effects of size and vigor on male energetics and mating success (*e.g.* Gerhardt & Huber, 2002, p. 315) is needed to address this problem.

Magicicada septendecim mating aggregations meet Bradbury's (1981) lek criteria (absence of parental care, resources, or mating outside the lek; and males aggregated on the lek). However, if *M. septendecim* females are best characterized as using MC (threshold) choice criteria, then the sexual selection pressures in their leks should differ from those in vertebrate leks structured around BN (relative) choice criteria. Yet predicting how selection should differ remains a difficult task, especially since, as discussed below, other aspects of *Magicicada* mating aggregations may lead to the appearance (and perhaps functional equivalence, via indirect mate choice) of female choosiness of the sort found in vertebrate leks.

Biased operational sex ratio and the appearance of female choosiness

Magicicada have a combination of life-history characteristics (such as low predation risk, high population density and apparent female control of mating onset) that seem to make them good candidates for participation in 'best-of-*N*' female choice. Even so, *M. septendecim* do not appear to use relative criteria to choose among conspecific chorusing mates. Why, then, have some studies of *Magicicada* behavior (*e.g.* Dunning *et al.*, 1979) reported lengthy courtships, frequent rejections, and apparent female coyness, while other studies report no mating delays (this study, Cooley & Marshall, 2001)? Earlier studies of *Magicicada* mating behavior were conducted prior to the

discovery of the long, five-day teneral period. Most lengthy courtships in our studies occurred when males approached females that were teneral or already mated (therefore sexually unreceptive); fully mature females usually mate without delay (Cooley & Marshall, 2001; Marshall, 2000). Thus, the impression of female coyness may be more a manifestation of male strategies than of female mate choice.

Male courtship strategies leading to the appearance of female coyness may be fostered by an unusually competitive environment created by the interaction of a strongly male-biased operational sex ratio and high population density. Estimating the operational sex ratio in a *Magicicada* chorus is problematic because leks are large and because distinguishing receptive, mature females from teneral ones requires time-consuming playback experiments. But periodical cicada life histories suggest a male-biased operational sex ratio: If males mate multiply while most female *M. septendecim* emerge, mature, and mate only once within a short period, then at any given moment most females are either teneral or already mated, and for most of their lives *M. septendecim* males are confronted with a lack of receptive females. This bias is likely accentuated by emergence protandry (Graham & Cochran, 1954). Furthermore, given the high density of *Magicicada* leks, newly-receptive females are likely to be located and courted by one or more males during the transition from tenerality to maturity, while the female wing flick response and other behaviors needed for mating are only weakly or inconsistently produced. Under these conditions, a male's mating success may be strongly influenced by his ability to detect the earliest signs of mating readiness (*e.g.* weak or incomplete female signals) and his ability to attempt mating without causing the female to fly away if she is only marginally receptive, on the chance that she will become more receptive later.

Several observations are consistent with this view of *M. septendecim* mating behavior. Females that are only marginally mature, as well as those exposed to poor weather conditions or disturbances, produce weaker and less consistent wing flick responses (unpublished observations). Males appear extremely cautious when first attempting to touch or mount a female, instantly pulling back and waiting if the female makes any movement (receptive females remain stationary; Dunning *et al.*, 1979). Calling males can be induced to begin courting a nearby stationary cicada (any sex) if the experimenter makes a timed wing flick response nearby. Males even court and attempt to

mate with inanimate objects such as cast nymphal skins that could not possibly have responded to calls. Given these observations, the lengthy courtships and frequent rejections observed in *Magicicada* — characteristics that have been thought to imply adaptive female choice — may instead be byproducts of demographic realities that force males to (1) compete by locating and courting females at the earliest onset of mating readiness and (2) invest considerable courtship effort in any potential mate that gives even minor signs of receptivity, because such a target might be a rare female on the verge of sexual maturity.

The hypothesis that *Magicicada* males are forced into a scramble competition for marginally receptive females raises new questions about the nature of sexual selection in *Magicicada* leks. Marginally receptive females might incidentally favor males that are maximally stimulating in courtship (*e.g.* such males may be especially persistent, or their songs may be especially loud, pure-tone, or have accentuated downslurs). Even if such apparent choosiness has not resulted from direct selection on females for best-of-N preference, it may nonetheless create a similar form of sexual selection on males. More analyses of the ontogeny of female sexual receptivity and of the relationships between male vigor and courtship behavior are needed to understand this possibility.

If *Magicicada* females use threshold choice criteria, then why do males engage in complex acoustic courtship, with a stereotypical series of species-specific courtship signals prior to nearly every mating? Demonstrations of female choice against heterospecifics (Marshall & Cooley, 2000; Cooley *et al.*, 2001) suggest one possibility — that females require this courtship sequence in order to verify the species-identity of any potential mate. If so, then we would predict that females should refuse to mate with any male (of any species) that fails to complete all the courtship steps, and we might expect to find simplified courtship repertoires in locations where only one species is present (such as Michigan, northern Illinois, and the Finger Lakes region of New York, where *M. septendecim* is found alone). Another possibility is that the complex courtship repertoire is another manifestation of a general male strategy to persuade unreceptive or marginally-receptive females to mate. Under either of these scenarios, the structural characteristics of each courtship song may have less to do with female choice than with constraints on male activity, such as limitations in his ability to modulate his call by moving his abdomen while trying to mount and copulate. Neither of these

scenarios for the evolution of complex courtship in *Magicicada* is exclusive of the other, and both await further testing.

Many insect species have life history characteristics (such as protandry and brief periods of sexual receptivity) that appear to promote biased operational sex ratios and male scramble competition to locate females at or near the onset of mating readiness. In some, (*e.g.* red mason bees; Seidelmann, 1999), patterns of male mating success may be indistinguishable from random because pre-receptive females remain concealed and finding them involves some degree of chance. In other species, males compete among themselves to control access to female emergence sites (*e.g.* some Eumenid wasps; Smith & Alcock, 1980), and male mating success is nonrandom because it depends on the outcomes of male-male competitive interactions. Neither of these mating systems is likely to be confused with a lek mediated by female mate choice. But when insect species with these same life history characteristics (such as periodical cicadas) form mating aggregations, male efforts to persuade females on the verge of mating readiness may lead to the appearance of female choosiness. This apparent choosiness is of a different nature from sexual selection in classical leks: In classical leks, although males may compete among themselves to gain access to females, intense female choice and the coevolution of male and female mating strategies is an equal or greater selective influence than intrasexual competition. In contrast, the hallmark of periodical cicada leks appears to be intense intrasexual mating competition, which may play the greatest role in shaping the evolution of their mating system. If so, then the paradox of *Magicicada* leks is that, appearances aside, they are only superficially similar to vertebrate leks.

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