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Orthopteran Mating Systems

Sexual Competition in a Diverse Group of Insects

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Chapter 3

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3. Diel Patterns of Calling in Nocturnal Orthoptera

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The nightly timing of calling in crickets and katydids is a neglected aspect of orthopteran mating strategies, perhaps because orthopterists are fundamentally diurnal. Recent studies of a few warm-climate species have revealed patterns drastically different from what seemed typical on the basis of previous cool-temperate observations (Cade 1979; Forrest 1980, 1982; Walker 1980; Walker and Whitesell 1981).

This paper identifies factors that shape 24-hour patterns of calling, interprets existing data on nocturnal calling times in crickets and katydids, and spotlights the paucity of quantitative studies, there apparently being no detailed field data to document what are probably the most typical patterns.

In this paper, **calling** means the production of a long-range species-characteristic sound that mediates the coming together of potential mates. In crickets and katydids, and nearly all other acoustically advertising animals, males are the principal or only callers. In most cases the female moves toward the caller (by **phonotaxis**) until detected by the male. In some katydids (e.g. Spooner 1968) the female answers to the male's call with a nondescript sound after a species-characteristic delay, thereby shifting to the male the burden of crossing the final gap between them.

WHEN SHOULD MALES CALL?

Males should call when calling is reproductively more profitable than other activities (including rest). To the extent that the function of calling is acquiring sexual partners, the availability of sexually receptive phonotactic females is of primary importance.

Availability of females

The temporal availability of females may be influenced by maturation, weather, predation, other female activities, and number of males calling.

Maturation. The numbers of sexually ready, song-responsive females should depend to a large degree on temperature-dependent maturation processes. Several days generally elapse between a female's final molt and the onset of response to song, and between one mating (or bout of matings) and the next. Rates of physiological processes during these periods are dependent on ambient temperatures: cricket and katydid females are never endothermic for more than brief periods (e.g. in flight). **Ceteris paribus,** the numbers of females becoming sexually ready should relate directly to temperature: when females are exposed to the diel cycle of temperature (as for tree- or herb-dwelling species), more females should mature during the day than during the night (Fig. 1A, line b). Females that spend most of their time in burrows, where diel cycles of temperature are damped or absent, should mature at an approximately constant rate (Fig. 1A, line a).[1]

In nocturnal species, females that mature during the day must postpone their susceptibility to the calls of males until dark. This delay should cause at least 50% of the females maturing during a 24-hour period to become available for the first time at evening twilight. If these females are quickly serviced by calling males, the potential rewards per hour of calling during the remainder of the night are sharply reduced, i.e. by more than 90% (Fig. 1B).

Weather. As temperatures drop during a night, reaction times and escape behaviors of females moving toward calling males may become sluggish, putting them in greater danger from predators, especially warm-blooded

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[1] The temperature dependence of physiological processes in poikilotherms is powerful (Chapman 1971) but not absolute, as attested by physiological clocks that run at nearly uniform rates in a range of temperatures (Bunning 1967) and by the effects of temperature on diapause development (e.g. Masaki 1980). Nonetheless, if for no other reason than increased complexity, there are costs to producing biochemical tricks that override the fundamental temperature dependence of chemical reactions. Compensating benefits are therefore required to maintain such tricks, making deviations from the lines in Fig. 1A worthy of study.

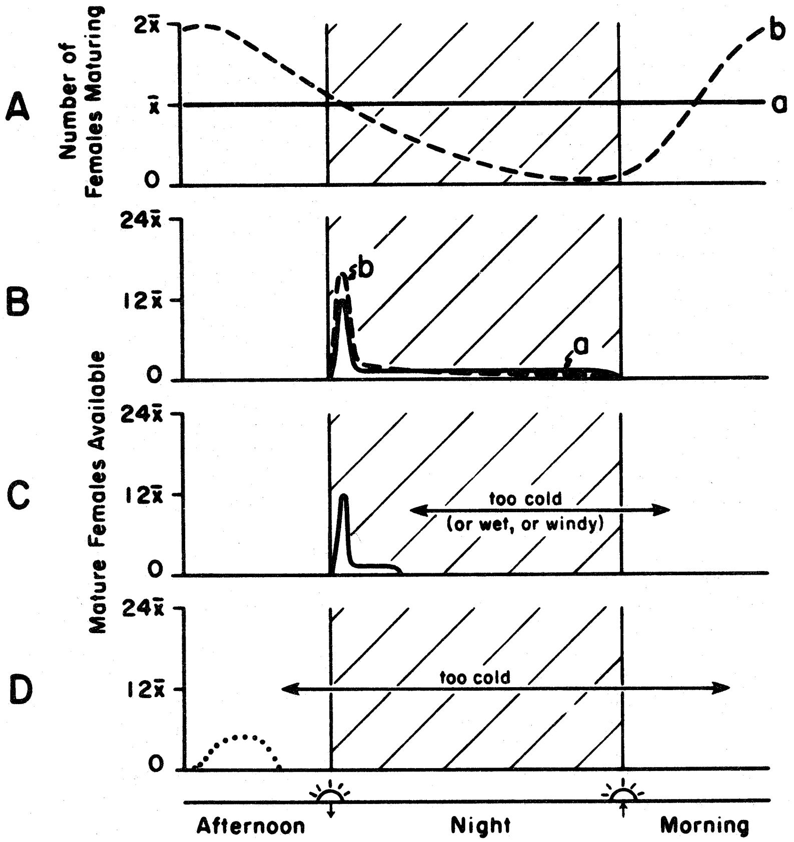

Fig. 1A. Number of females maturing (i.e. reaching a physiological state permitting phonotaxis and mating) as a function of time. (a, solid line) When temperature is uniform, as in a deep burrow, number of females maturing each unit time is the same as the average number of females maturing per unit time ($\bar{x}$). (b, dashed line) When temperature fluctuates daily, females mature at a higher than average rate when warm and at a lower than average rate when cool. B. Availability of mature females if strictly nocturnal and if temperature (and other weather factors) are uniformly favorable. Lines a and b as in A. (Assumes that mature females mate within an hour of becoming available and that unit time is 1 h.) C. As in B, but 3 h after sunset, temperature drops below the minimum favorable to female mating activity. (If females continue to mature, early evening peak on the following day will be greater.) D. As in C, but by late afternoon, temperature is below the minimum favorable to female mating. If nocturnal temperatures remain cold for several days, females may switch mating activities to mid-afternoon (dotted curve).

ones. If females fly endothermically during phonotaxis, their warm-up costs increase. At some level of cooling, the price of phonotaxis will exceed the price of delaying mating (Fig. 1C). This temperature should be higher than the minimum permitting female locomotion or male stridulation. Its value should depend on a variety of intrinsic and extrinsic factors, including how many previous nights have been too cold for phonotaxis. Field studies suggest threshold values ranging from -4 to 23°C (**Cyphoderris strepitans,** Dodson et al. 1982; **Anurogryllus arboreus,** males calling from perches, Walker 1980). During cold spells, some species that are strictly nocturnal when nights are warmer apparently shift some or all of their phonotaxis to mid afternoon (e.g. **Oecanthus fultoni,** Snodgrass 1924; **Tettigonia viridissima,** Nielsen and Dreisig 1970) (Fig. 1D). Other weather conditions, such as rain or high wind, may reduce female availability by increasing the risks of moving toward the male's call. They may also reduce the distance over which the call can function.

Predation. The probability of being killed or maimed by predators should be an important determinant of when females are available. Unlike pheromone-mediated systems of pair formation, in acoustical systems the female is generally the sex that makes the hazardous gap-closing journey (Greenfield 1981a). Sharp-eyed diurnal predators, especially birds, are probably a major reason that most crickets and katydids mate at night. In support of this contention is the fact that crickets and katydids that live in relatively open, predator-accessible places, such as trees and bushes, are generally strictly nocturnal in their acoustically mediated pair formation (e.g. **Oecanthus fultoni, Orchelimum minor).** Closely related species (e.g. **Oecanthus nigricornis, Orchelimum agile)** that live in dense herbaceous vegetation call and mate during daylight hours as well as at night.

Nocturnal predators can modify the pattern of female availability illustrated in Fig. 2A. The ones of greatest influence are probably insect-eating mammals, including aerially foraging and surface-gleaning bats (Griffin et al. 1965, Vaughan 1976). Nocturnal birds may also be important (Horner et al. 1974).

Predators may affect nightly availability of females in ways that have opposing consequences. If a predator is effective throughout the night in capturing females on their ways to calling males **and** has a low maximum rate of capture, a female may decrease her risk by moving at the same time as other females, a temporal analog of Hamilton's (1971) selfish herd. A predator population that was saturated during its prey's early-evening peak of availability (Fig. 2A) would cause females that matured after the early evening peak to benefit by delaying phonotaxis until the following evening (Fig. 2B). On the other hand, if the predator population is not rendered less lethal by synchronous phonotaxis, females exposing themselves during a peak of availability (e.g. Fig. 2A, B) would increase their risk of capture, because the predators could temporarily specialize in catching that type of prey. For instance, some bats are capable of detailed discrimination of echolocated targets, permitting them to concentrate on a particular type of prey that is delectable and abundant (Griffin et al. 1965, Simmons et al. 1974). In this circumstance individual females are safest when they move toward males unaccompanied (Fig. 2C).

If a predator threatens only for a short period (e.g., during evening twilight), its effect would be to reduce female activity during that period thereby increasing the numbers available at the next 'safe' time; for example, the evening peak might be postponed and slightly heightened or, if the dangerous time came later, a secondary peak might be formed.

Other (female) activities. If females move about during the night for reasons other than mating (e.g. egg laying, dispersal to new habitats), they may make a short side trip to a calling male, thereby avoiding a prolonged trip devoted solely to male seeking. Such behavior would have the effect of spreading out female availability, if the other activity occurs throughout the night, or of concentrating it, if the other activity is brief.

Number of males calling. Females may benefit by mating not with the first-heard or closest conspecific male but with the **best** calling male, i.e. with the one that has genes that will maximize the fitness of her progeny (e.g. Blum and Blum 1979, Thornhill 1980). She may also select a male having the best nuptial gift (e.g. the largest spermatophylax, Gwynne 1982; or the safest burrow) but these are likely to be evaluated only after phonotaxis. Females that select a mate at a time when maximum numbers of males are calling should on average get a better male than females that select at quieter times. If females make themselves available when most males call, and if males call when females are most available, the outcome could be that all phonotaxis and mating occur in a brief period in which all males call. This would be the temporal equivalent of a **lek**,

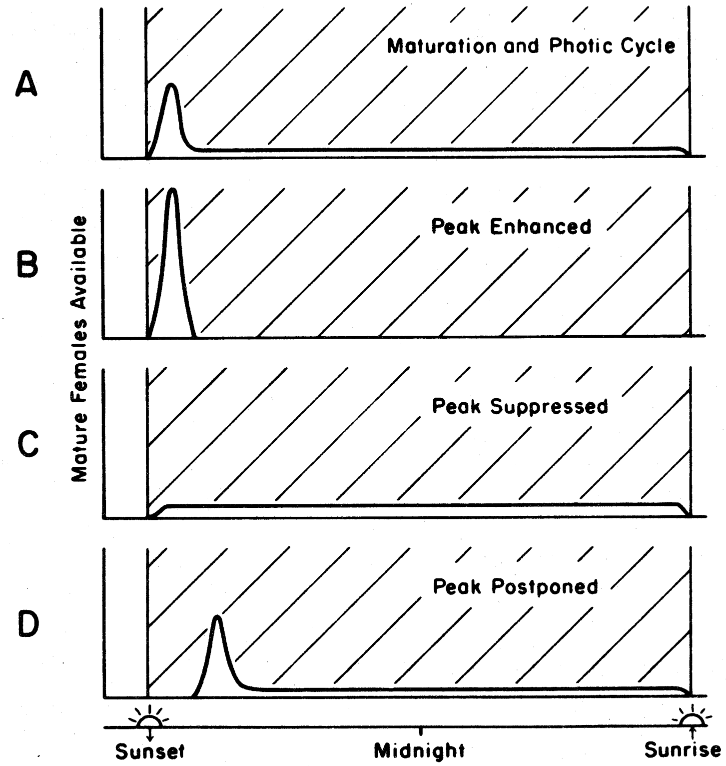

Fig. 2 Mature females available as a function of time, assuming uniform rate of maturing (as in Fig. 1A, line a), weather uniformly favorable for mating, and female phonotaxis and mating only at night. A. No complications. B. Peak enhanced--e.g. predators cause high percent mortality when low numbers of females are moving (see text). C. Peak suppressed--e.g. predators cause high percent mortality when high numbers of females are moving (see text). D. Peak postponed--e.g. first hour after sunset unsuitable for female mating activity (see text).

a place where males gather and compete for females, or, in R.D. Alexander's (1975) usage, any mating aggregation or assembly. Alexander proposes that in lekking species females have forced males to assemble by doing all or most of their mating where they have numerous males to choose among.

The duration of a 'temporal lek'[1], henceforth called a **spree,** could be short (e.g. Fig. 2B); but if females judge quality by how long a male calls during an evening, it would be long. For a female to select a male on the basis of duration of his call, she must keep track of males she is comparing (otherwise a male could cheat by calling only near the end of the spree or by somehow taking over the credits accumulated by a long-calling male). If a female has the ability to keep track of individual males during a spree, she might even keep track of them one night to the next, suggesting a variety of intriguing possibilities (Lloyd 1981).

Alternative (male) activities

If phonotactic females are available, males should call, unless calling is incompatible with some other activity that has greater reproductive payoff. Alternative activities may be of a maintenance nature, for example, digging a shelter for the coming day, finding food, or even resting. Or they may be alternative mate-finding behaviors, for example, satelliting (Cade 1979), searching within a habitat (Walker 1982), or seeking a habitat more favorable for females (Forrest 1981). The number of song-responsive females during a night probably seldom if ever approaches the number of calling males, but if it should, mating itself could become an alternative activity significantly reducing the number of calling males. (Males of at least one species, **A. arboreus,** continue to call as they mate -- Walker 1982.)

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[1] Campanella and Wolf (1974) used the term **temporal lek,** in a very different sense, to denote the mating system of the dragonfly **Plathemis lydia.** They reported that a sequence of males dominated a particular territory during a day, with the males and the sequence varying from day to day. At high densities as many as five males (one dominant, the rest subordinates) occurred on a territory at once. The dominant male was much more successful in mating incoming females than were subordinates. However, most females arrived during the same 3-h period each day. Consequently to be successful a male had to be dominant during the optimal times for mating, rather than in the optimal spaces (cf. Kob leks, Buechner and Schoeth 1965).

Conditions affecting acoustical transmission. The profitability of calling can be reduced, changing the diel pattern, by conditions that reduce the likelihood that the call can be transmitted in a recognizable form to a distant available female. For instance, daytime thermal gradients often create sound shadow zones in which calls are inaudible at distances they easily traverse at night (Michelsen 1978, Wiley and Richards 1978). Propagation along the ground is always difficult, but at night some ground-dwelling crickets and katydids increase their range, without substantially increasing their vulnerability to visually hunting predators, by ascending to a height of ca 1 m (Michelsen 1978, Paul and Walker 1979).

Calling range can be reduced by acoustical interference from other species using similar frequencies, especially if the interfering individuals occur in large numbers and produce intense sounds. For instance, the concentrated calling of many cicada species at evening twilight may delay the start of calling in nocturnal crickets and katydids; similarly, acoustical interference among synchronously emerging species of periodical cicadas may have contributed to their chorusing at different times of day (Alexander and Moore 1962).

Phonotactic enemies. Calling can summon lethal predators and parasitoids as well as nubile conspecifics (Bell 1979, Cade 1979, Burk 1982). The diel pattern of prey- or host-finding activities of phonotactic enemies should influence the diel pattern of calling. Cade (1979) monitored the diel pattern of phonotaxis in a **Gryllus**- attacking parasitoid fly, **Euphasiopteryx ochracea.** It was attracted in largest numbers at sunset, whereas maximal numbers of males called at sunrise.

Caloric costs. Calling males draw upon their metabolic reserves at rates up to 35 times those of resting males (Heath and Josephson 1970, Prestwich and Walker 1981). Experimentally starved males reduce their calling until they are fed again (Nielsen and Dreisig 1970; Walker, unpublished, **Scapteriscus** spp.).

The degree to which energy restraints influence male calling patterns should depend on energetic requirements of calling, the availability of food, and the time required to find and consume it. Prestwich and Walker (1981) concluded that energetic costs of calling, per unit body weight, can be roughly estimated from the number of wing strokes. Table 1 shows energy costs calculated on this basis. Approximate wing strokes per minute of calling vary from 173 for **Orocharis luteolira** to 12,000 for **Neoconocephalus robustus** (i.e. X 69); yet the number of wing strokes per 24 h varies only from

100,000 to 670,000 (i.e. X 6.7): species that use energy at the highest rates during calling have short calling durations.

Distribution of calling times among males

If females are available all night but males do not call all night, males should time their calling to take advantage of maximum acoustical transmission and female availability as well as minimum risk and male competition. If all males optimize their reproductive chances in this manner, no male can benefit by shifting its calling time (all equal males that call for the same duration will have the same average return) and the timing behavior will be evolutionarily stable. The pattern of calling achieved is the temporal counterpart of Fretwell's (1972) ideal free distribution, in which animals occupy habitats in inverse proportion to habitat suitability, resulting in all individuals occupying space that provides the same average resources. In an ideal free (spatial) distribution highly suitable habitats have high densities; poor habitats have low densities; and no individual can do better by moving, since each has freely occupied the space that has the best available combination of suitability and freedom from competition.

An ideal free (temporal) distribution of calling is simple in principle but predicting its exact form (Fig. 3) requires making assumptions about the pattern of female availability, amount of calling per male each 24 h, and choosing-and-travelling time required by the female (i.e. the time between a female's first hearing a male and reaching him). The longer this time is, the more a male may lose by breaking his total calling into isolated segments. For example the particular values assumed for Fig. 3 (no choosing time; travel time 0.5 ± 0.3 h, $\bar{x}$ ± SD) mean that a male that quits calling 30 min after starting has only a 50% probability of receiving a female that started toward him when he began calling. By calling 30 min longer, his chances increase to 95%. Fig. 3B illustrates an ideal free distribution of calling times in which all males call during the time of maximum female availability (54% of the night's total are assumed to be available during the first hour; cf. Fig. 1B, line a). During the rest of the night, few males (8 or 7; $\bar{x}$ = 15.3%) are calling at any one time, but all males total 3 additional hours of calling. Average payoff during the first hour of calling is more than thrice the average payoff during each subsequent hour.

Fig. 3C illustrates an ideal free distribution of calling times in which some males call at time of maximum female availability and others do not. Because each male can call only 1 h during the night, males calling at the

Table 1. Energetic costs of calling in ten species of crickets and katydids estimated from numbers of acoustically effective wingstrokes.

Species	Wingstroke rate[a] (no./sec, 25°C)	Wing stroking as a proportion of calling[b]	Wingstrokes per min of calling	Aver. time calling/ 24 h (min)	Aver. no. wingstrokes 24 h (100,000's)
Gryllidae					
Anurogryllus arboreus [c]	75	1.0	4,500	33	1.5
Anurogryllus muticus [d]	130	1.0	7,800	83	6.5
Scapteriscus acletus [e]	54	1.0	3,240	52	1.7
Scapteriscus vicinus [e]	137	1.0	8,220	56	4.6
Teleogryllus commodus [f]	(21)	(1.0)	1,260	300	3.8
Orocharis luteolira [g]	72	.04	173	600?	1.2
Anaxipha sp.[h]	6	1.0	360	600?	2.2
Tettigoniidae					
Neoconocephalus robustus [i]	200	1.0	12,000	56	6.7
Neoconocephalus caudellianus [j]	210	.45	5,670	60?	3.4
Neoconocephalus affinis [k]	12	.01-.60	<432	240	<1.0

[a] Wingstroke rate is the maximum rate at which the wings are moved during calling. It varies little for a species at a temperature.

[b] In some species wing stroking during calling is discontinuous—i.e. the proportion of calling that is wing stroking is <1.0.

[c] Walker 1973, 1980; Prestwich and Walker 1981.

[d] Walker 1973, Walker and Whitesell 1981.

[e] Forrest 1981.

[f] Bentley and Hoy 1972, Loher 1972; calling male alternates groups of wingstrokes at 32 and 19/s.

[g] Walker 1969; calling consists of 5- to 7-pulse chirps emitted at a rate of ca 5/10 sec.

[h] Walker 1964, **Anaxipha "exigua"** slow tinkler.

[i] Heath and Josephson 1970, Walker et al. 1973.

[j] Walker unpublished; calling is a 0.5-sec. chirp every 1.1 sec.

[k] Greenfield 1981b, and pers. comm.; calling is irregularly broken to continuous.

time of maximum female availability cannot call later. As diagrammed (Fig. 3C, D), the 13 males (54% of the total) that call during the first hour have the same average chance of receiving a female as the 11 males that take their turns at calling for an hour during the rest of the night.

Singing that does not call

The above analysis of determinants of diel calling patterns is based on the assumption that the sounds in question are functioning in bringing together distant potential mates. When such an assumption is false, the analysis is inappropriate. For example, males of **Orchelimum** spp. studied by Feaver (1977, 1982) sing for at least 1-2 h prior to the time that females apparently start responding to potential mates. During this time, males are using 'calling' songs to lay claim to singing territories needed for later reproductive success.

WHEN DO MALES CALL?

Although millions of males of thousands of species call each evening, biologists spend little time noting exactly who is calling when, especially after midnight. From more than 20 yr of field work I conclude that most nocturnal species call in greatest numbers early in the evening and that a few hours later the number of callers starts to drop rapidly or slowly and reaches zero at dawn (Fig. 4, lines a and b) (also Alexander 1960, p. 43). However, many of my observations were in cool seasons or in northern localities where temperatures dropped steeply after sunset, making it difficult to be certain that the fall-off in numbers of callers was not temperature induced (Fig. 1C). For many reasons, especially fatigue and a lack of compelling questions, I seldom extended field work through the last few hours of darkness even on warm nights, making the last portion of Fig. 4A, lines a and b, even less reliable than the first.

The most important feature of typical calling patterns, other than their lack of support by hard data, is that maximal calling lasts longer than predicted by the most parsimonious assumptions (Fig. 4A, line c). If this difference is real, one likely cause is that females take more than an hour to judge which male is the best potential mate (i.e. line b represents a prolonged spree; indeed the duration of calling could be used by the female to judge the quality of a male. Following the same reasoning, line a could represent an all-night spree, an oxymoron that is a temporal parallel of Gilliard's, 1963, **exploded lek** or Marshall and Alcock's, 1981, **dispersed lek).** Another likely cause is that

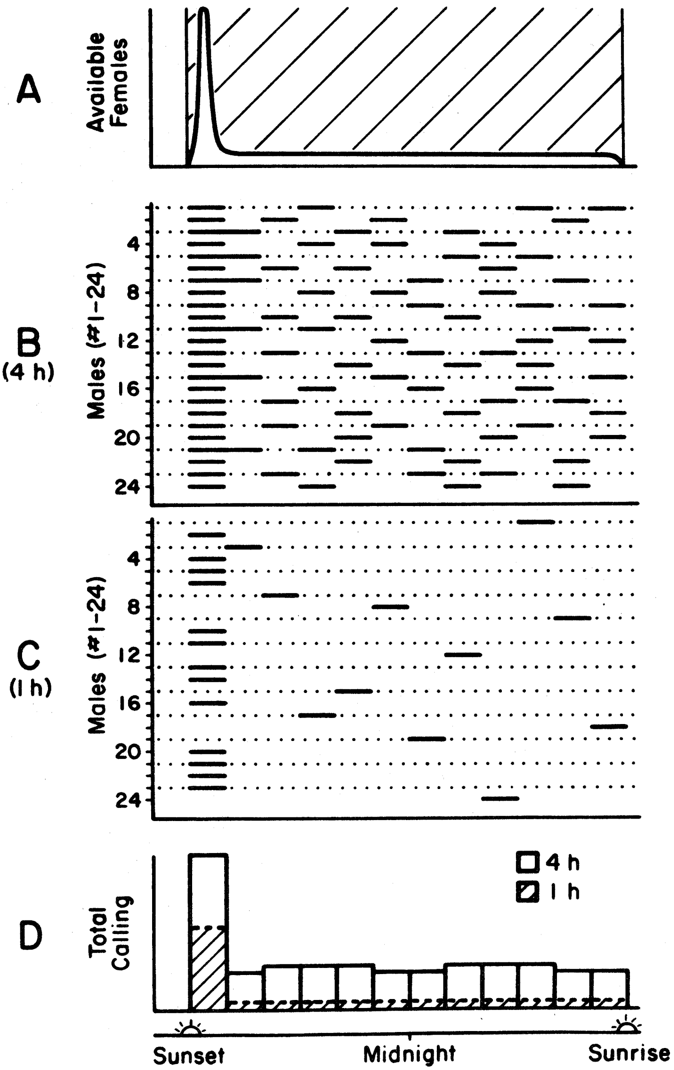

Fig. 3. Ideal free distributions of calling times. Acoustical transmission and risks from phonotactic enemies are assumed to be constant throughout the night. A. Expected total payoffs of calling when sexually receptive females go to calling males as soon as darkness and travel time ($\bar{x} \approx 0.5$ h, SD $\approx$ 0.3h) permit. (Temperature uniform and favorable; cf. Fig. 1B, line a). B. Expected distribution of individual calling times when males call ≈4 h per night. All males call during the time of maximum total payoff and at intervals during the rest of the night. No male can do better by

females go to males as side trips from other activities, making their availability fit lines a or b.

The three species most intensively monitored for diel calling patterns in the field are two mole crickets, **Scapteriscus vicinus** and **S. acletus** (Fig. 4B; Forrest 1980, 1982), and a short-tailed cricket, **Anurogryllus arboreus** (Fig. 4C; Walker 1980, 1982). Their patterns are alike in that practically all males call at once and calling ends by 2 h after sunset. The three patterns deviated so greatly from what I'd assumed to be typical (Fig. 4A, lines a and b) and from expected patterns of female availability (Fig. 1B) that they prompted the ruminations leading to this paper.

The biology of the two mole cricket species contrasts with the biology of **A. arboreus** in ways that led Forrest (1982) and Walker (1982) to somewhat different conclusions as to the causes of the similar deviations from expected. The most relevant difference among the reproductive behaviors of the short-tailed cricket and **S. vicinus** and **acletus** is that only in the latter two species do females fly to calling males. Flight is exceptionally hazardous and energy consuming in mole crickets, which weigh 0.6-1.2 g and are built for tunneling. Safety and energy concerns are optimally met in early evening, when darkness handicaps visually hunting predators and the temperature differential that mole crickets must overcome in preflight warmups has barely begun its nightly increase.

In **S. vicinus** and **acletus** (Fig. 5) and in **A. arboreus** (Fig. 6), females that go to calling males have maximal numbers of males to choose among, since all males that call during a night, call during one brief period. In the two mole crickets the existence of positive feedback between maximal female choice and synchrony of female availability (Fig. 5, dashed arrow) is less certain because the synchrony may be viewed alternatively as a byproduct of temperature- and predator-imposed restraints on female flight. However, for brief synchronous calling by males to be entirely a byproduct

(Fig. 3 continued) altering its calling times. (Dots help trace calling patterns of individual males.) C. Expected distribution of individual calling times when males are limited (e.g. by energy costs) to ≈1 h of calling per night. Some others call at other times during the night, yet no male can do better by altering its calling time. D. Total calling in B and C plotted at hourly intervals. In B, calling during the first hour has a higher average payoff (see A); in C, calling at any hour during the night has the same average payoff.

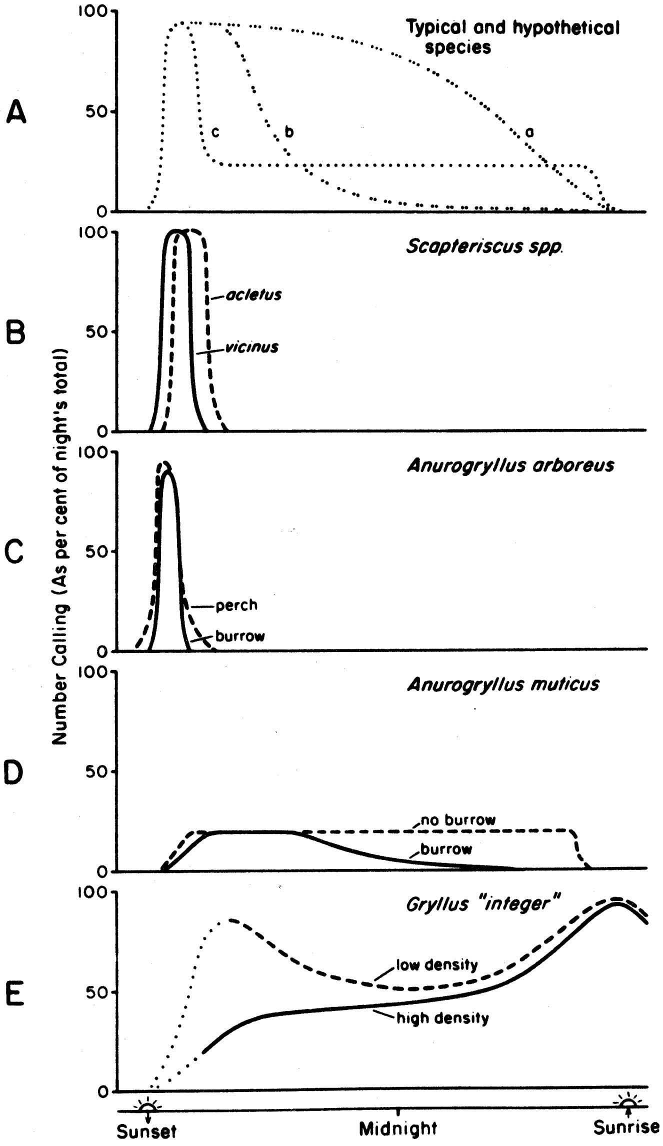

Fig. 4. Nocturnal changes in individual and population calling activity during favorable weather (i.e. calling

of constraints on flight, females should go to calling males only at the end of a flight. That female mole crickets need not resort to flight or even to phonotaxis to acquire sperm is proved by **S. abbreviatus,** a flightless, call-less species (Walker, unpub.). Likewise, Ulagaraj (1975) reported that more than 20% of **vicinus** females and more than 80% of **acletus** females had already mated when spring flights began. Since males call prior to the flight season (by ca 2 months in **acletus),** it seems likely that females crawl or tunnel to calling males, activities that lack the constraints of flight. The fact that both virgin and previously mated females fly to calling males may be a result of their benefiting from choosing among a large array of males. When a female mates without flying, her choice of males is limited to those within a few meters, and she may have difficulty finding (or being found by) more than one or two of them. On the other hand, a female in flight may easily have a choice of more than 60 males in 5 min (Forrest 1980). Forrest (1982) has proved that flying females land at males producing the most intense calls and ignore those producing calls only slightly less intense. Given the degree of sperm precedence known for other Orthoptera (W. Walker 1980), it seems likely that intensely calling males father most mole cricket

(Fig. 4 continued) not curtailed by low temperature, rain, or strong wind). Ordinate is the number calling during a 5-10 min census period as a percent of the total number of males calling during that night. A. Typical and hypothetical species. a and b curves based on extensive field work but no systematic censuses. In some species (a), numbers remain high through most of the night; in others (b), numbers of callers drop sharply a few hours after sunset. Curve c is generated by theory illustrated in Fig. 3A, B. B. **Scapteriscus acletus** and **S. vicinus,** Gainesville, Fla., males caged in soil-filled buckets outdoors (Forrest 1981 and pers. comm.). C. **Anurogryllus arboreus,** Gainesville, Fla. (Walker 1980, 1981). Since burrow-calling males were in the open and perch-calling males were in a wooded area, peaks for the two types of calling may come at the same light intensity. D. **Anurogryllus muticus,** Ft. Sherman, Panama (Walker and Whitesell 1981; based on data from one favorable night). Burrow-calling males were apparently calling chiefly to flying females whereas males calling away from any burrow were apparently calling to terrestrial females. E. **Gryllus** sp., Austin, Texas (Cade 1979).

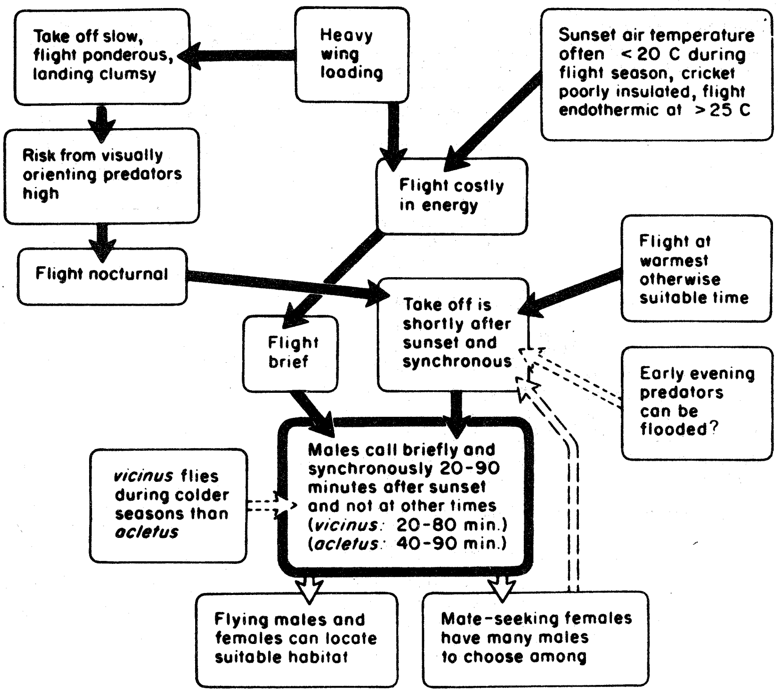

Fig. 5. Major forces contributing to diel pattern of calling in the mole crickets, **Scapteriscus vicinus** and **S. acletus** (partly from Forrest 1981). One of the two effects of brief synchronous calling is hypothesized to feed back positively to one of the causes (dashed arrow). The limit to such a feedback is all males that will call during a night, call during the same limited period.

offspring. If this be so, females should be choosing fathers for their sons during their early evening flights; and since females are making most of their important mate choices on the wing, males that call had best join the evening sprees.

A. arboreus females have no associated activity, comparable to flight in **vicinus** and **acletus**, that can be charged with synchronizing phonotaxis. The chief synchronizer is evidently the positive feedback between most males calling at once and all females benefiting from making their choices when most males call (Fig. 6). Walker (1982) discusses other possibilities but attributes to them no more than supporting roles.

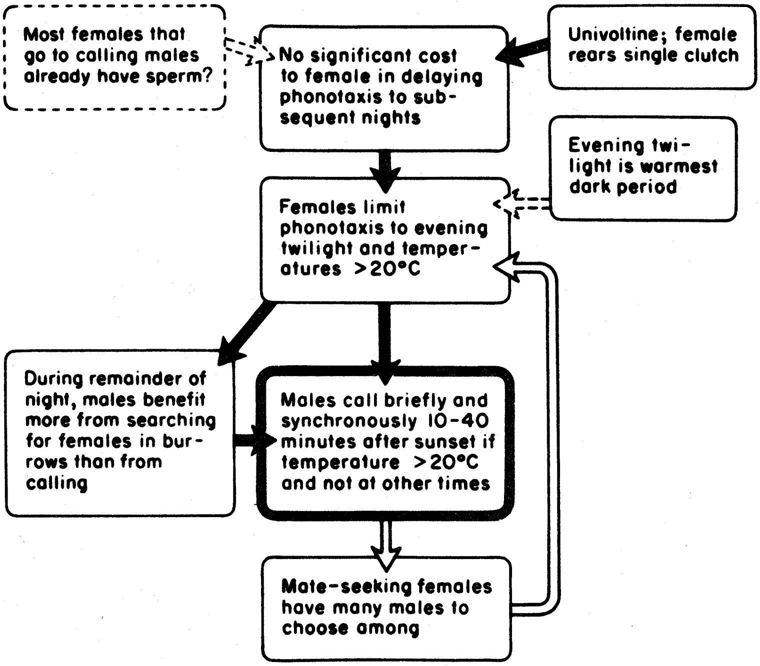

Fig. 6. Major forces contributing to diel pattern of calling in the short-tailed cricket, **Anurogryllus arboreus** (Walker 1980, 1981). The effect of brief synchronous calling feeds back positively to one of its causes.

The three species discussed above deviate from the hypothetical 'typical' patterns by calling during one brief period. The fourth species that has been critically studied in the field deviates in the opposite direction, there being no apparent peak and no period when most males are calling (Fig. 4D). Walker and Whitesell (1981) monitored a Panamanian short-tailed cricket, **Anurogryllus muticus**, for 4 nights and found that only ca 20% of calling males called during any 10-min period. Since **A. muticus** uses energy faster than other crickets (Table 1), it is not surprising that males call for short periods. What is surprising is the lack of an early evening peak (Fig. 3D). The lack of a peak for males calling at burrows was attributed to circumstances different from those for males calling away from any burrow. Males calling without burrows are apparently searching for females ensconced in burrows.

By calling as they search they consecutively call to different land-bound females that come within acoustic range as a result of the male's movement. As long as the male is searching an area not already covered that night, payoffs of calling should remain approximately constant throughout the night (Fig. 4D, dashed line). On the other hand, males calling at burrows are stationary and direct their songs upward toward flying females. New females become available by flying to within acoustic range. The expected early evening peak of female flight is apparently lacking, perhaps suppressed, as discussed above (Fig. 2C), by aerially foraging bats.

A final substantial data set relative to outdoor nocturnal calling in Orthoptera is for a Texas field cricket, **Gryllus** sp. (formerly **"integer"**; now nameless) (Cade 1979). Unlike the observations on the previous species, individual males were not identified, making uncertain the vertical placement of the curves in Fig. 4E. If sunrise callers do not include the males that called earlier, the curves should be substantially lower (cf. Fig. 4D). Whatever the correct positions of the curves, the increase in calling between midnight and sunrise fits none of the simple models proposed above. One hypothesis is that most of the sound production at dawn is not calling, i.e. it does not function in attracting distant females. The fact that many males that produce sound at sunrise 'call' at low intensity supports this thesis (Cade 1979). Sunrise 'calling' could, for example, be in response to pheromones produced by nearby females. The lack of an early evening peak of calling coincides with the highest probability of attacks from phonotactic parasitoid flies (Cade 1979). The flies have another activity peak at sunrise, but they may have difficulty hearing low intensity calling.

Other published field data on nocturnal calling of Orthoptera are not analyzed here because no numbers are given, because they are for one or two individuals, or because they are for seasons or places having cold nights (e.g. Dumortier 1963, Alexander and Meral 1967, Nielsen and Dreisig 1970).

Laboratory studies of diel patterns of calling (and of female availability) have exciting potential for resolving some of the questions raised by field observations and by speculations about ecological functions. Thus far such investigations have employed light and temperature regimes that do not easily relate to field conditions, and their focus has been on physiological mechanisms (e.g. Nielsen 1972, Loher 1972, Sokolove 1975, Sokolove and Loher 1975). Recent papers (e.g. Loher 1979, Loher and Wiedenmann 1981) reveal increasing concern with ecological implications, and more fruitful interactions between field and laboratory studies are imminent.

DISCUSSION

Other groups that call

The analysis applied above to diel calling patterns in nocturnal Orthoptera is also appropriate to diurnal Orthoptera and to other taxa, such as cicadas and anurans.

Cicadas are of special interest because their calls are as intense as those of crickets and katydids, yet their mating is nearly always diurnal. If the logic of Fig. 1 is applied to cicadas, the peak of female availability every 24 h should occur at dawn; nonetheless, few cicadas, at least in eastern United States, call before mid morning. Lack of calling at dawn is attributable to low temperatures and endothermic, breakfast-seeking, cicada-eating birds. When a male cicada calls or a female cicada flies, it should be warm enough to evade avian attacks; cicadas are coldest at dawn (Fig. 1A, line b). The only cicada that choruses at dawn in eastern United States is **Neocicada hieroglyphica,** and it does so during the warmest months of the year in Florida. (It also calls throughout the day, choruses again at dusk, and rarely, calls at night -- unpub.). In the tropics, where dawns are always warm, the diel patterns of cicada calling have not been quantified, but Young (1981) reported that the majority of species exhibit "intense bursts of dawn-dusk chorusing".

Temperatures reach their peaks at mid day and some cicadas call in greatest numbers during that time (Heath and Wilkin 1970, Heath et al. 1972). Most species, however, call in greatest numbers at evening twilight, and the two largest eastern U.S. species, **Tibicen auletes** and **T. resonans,** do almost all of their calling then (Alexander 1956, 1960; see also, Crawford and Dadone 1979). Females that have become sexually mature during the previous 23 h have apparently delayed their availability until that time. Both the nocturnal **A. arboreus** and the diurnal **Tibicen** spp. time their sprees the same, i.e. at the warmest, nearly dark period. Alexander (1960) pointed out that two advantages of mating at evening twilight for diurnal species are that fewer insectivorous birds are active and pairs remaining in copula for long periods are less vulnerable.
(Heath and Wilkin, 1970, proposed that calling during mid day, when temperatures exceed 35°C, enables the desert cicada, **Diceroprocta apache,** to escape bird and wasp predators that are inactivated by the heat.)

Anuran females lack the options as to time and place of mating that insects have: they do not store sperm, making mating futile except when the sexual pair is at a site suitable for concurrent oviposition. For example, in species that lay their eggs in temporary pools, males should only call after heavy rains or flooding and from the pools. In such "explosive breeders" (Wells 1977), female availability may be compressed into one or a few nights and stable diel calling patterns would not be expected. Species that oviposit over longer periods and in relatively stable habitats, such as permanent ponds and bromeliads, should manifest diel calling patterns that are shaped by restraints and feedbacks similar to those for crickets and katydids. Wells (1977) discusses seasonal patterns of anuran reproduction, but apparently no one has reviewed diel patterns of calling (M.L. Crump, pers. comm., 1981) nor are the exact times of calling known for many species. Treatments of individual species reveal interesting variations: for example, **Rana catesbiana** calls all night or midnight to dawn (Howard 1978), and **Hyla versicolor** starts shortly after dusk and stops 2-4 h later (Fellers 1979).

Leks and sprees

Spatial aggregations of sexually displaying males, i.e. **leks,** are of special interest because of the difficulty in explaining why males competing for females should assemble (Alexander 1975, Bradbury 1981). Group displays are likely to be more imposing than solitary displays, and a group would be expected to attract more females. However, even if groups of males attract more females **per male,** the oft-observed concentration of matings among a very few of the grouped males raises the question of why the unsuccessful males bothered to assemble. The answer should be that they would do even worse by themselves. As Alexander (1975) points out, if females restrict their matings to groups of competing males (because of the advantage of selecting among many males), males should aggregate. Assembled males may be a bonanza for predators, but predation could also have a positive role in the evolution of leks, either because groups of males are more likely to detect predators or because predators may be saturated or thwarted by large numbers of prey. Finally, assemblies of males can be resource based or purely for mating (Alexander 1975). In resource-based mating aggregations, the competing males gather at resources valuable to the female, e.g. feeding or oviposition sites.[1]

Temporal assemblies of sexually displaying males have features that parallel those of spatial assemblies: they can be forced by females acting to maximize their selection of potential mates; predation can be either a threat or a contributing cause; and they may coincide with a (temporal) resource needed by the female (e.g. a warm dark time for flight).

Since phenomena are more likely to be discussed if they have labels, I proposed above a name for a temporal equivalent of a lek:

spree (n.) Concurrent display by most or all sexually active males in a population.

A spree, like a lek, has the effect of giving females increased opportunity to compare males. Males in a lek often display only when a female is present. Males in a spree must display whether they detect a female or not. Spreeing does not require spatial aggregation of males and hence need not involve dominance or territoriality (Fig. 7). If females are highly mobile, as in **Scapteriscus** spp., or if the population is dense but females are unaggregated and relatively sedentary, as in **Anurogryllus arboreus,** spreeing without lekking can greatly increase opportunity for comparison of males.

The most compelling examples of sprees among calling insects were discussed above: the brief choruses of **Anurogryllus arboreus, Scapteriscus vicinus, S. acletus,** and dusk-calling cicadas. Sprees should also occur among animals that display on other channels, e.g. swarming Diptera (Sullivan 1981), bioluminescent beetles (Lloyd 1966, **Photinus collustrans, Photinus tanytoxus)** and moths in which males are the pheromone-releasing sex (Greenfield 1981).

Temporal patterns of calling on a finer scale than considered here have been analyzed by Greenfield and Shaw (1982).

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[1] **Leks** are sometimes defined to exclude resource-based assemblies (e.g. Bradbury 1981), but unless individual males control female access to the resource, the opportunity for females to select among males is unchanged.

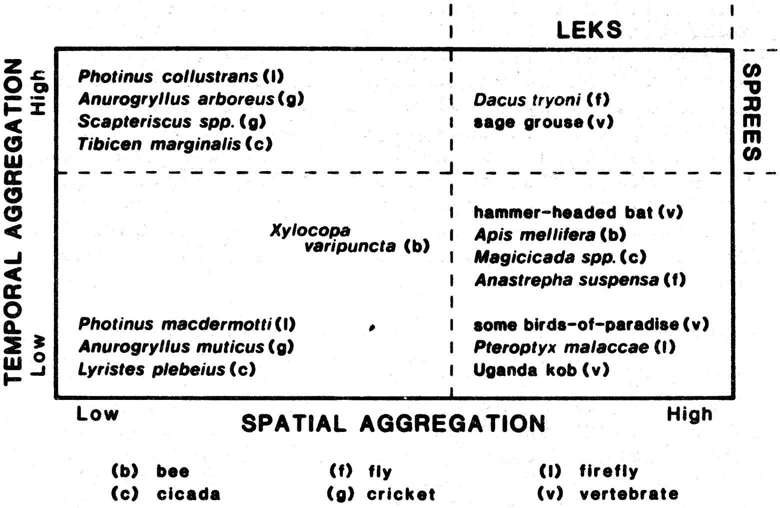

Fig. 7 Scatter diagram illustrating the independence of temporal and spatial aggregation of sexual displays. Lekking and spreeing occur together as well as independently. Placement of the species is based on the proportion of seemingly suitable time or habitat that is utilized for their displays. Data were from Marshall and Alcock (1981), Strang (1970) (bees); Claridge et al. (1979), Crawford and Dadone (1979), Alexander and Moore (1962) (cicadas); T.E. Burk (pers. comm.), Nielsen and Nielsen (1953) (flies); Lloyd (1966 and pers. comm.) (fireflies); Bradbury (1977), Buechner (1961), Gilliard (1969), Patterson (1952) (vertebrates).

SUMMARY

Males should call when calling is reproductively more profitable than other activities. The prime determiner of profitability is female availability. In nocturnal species, females maturing throughout the day should result in an early evening peak of numbers available. Other determinants of females' availability are weather, predation, and other activities. If females restrict their phonotaxis to times when high numbers of males call (thereby enhancing choice of mates), even higher proportions of males should call during the time of maximum calling, producing a concentration of calling termed a spree, the temporal analog of a lek.

Profitability of calling is also influenced by transmission conditions, risk from phonotactic enemies, and caloric costs. When calling by single males covers less than the entire period of female availability, population calling should approximate an ideal free distribution, with no male able to improve his returns by shifting his calling time(s). The diel patterns of sexual advertising on nonacoustical channels should be shaped by forces similar to those influencing patterns of calling.

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