



The influence of age and size on temporal mate signalling behaviour

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I investigated how male size, condition and age influence both time spent calling and how signals are apportioned throughout the night (i.e. temporal calling pattern) in the Texas field cricket, *Gryllus integer*. I quantified male calling time and temporal calling pattern using an electronic apparatus that continuously monitored male calling/noncalling behaviour throughout the night. Male condition, measured using the residuals from an allometric regression of male mass on overall body size, did not explain any variation in either time spent calling or temporal calling pattern. However, some intrapopulation variation in time spent calling and temporal calling pattern was explained by differences in male size and age. Large males called more often than small males. Young and very old adult males called significantly less often than middle-age males. As males aged they initiated calling earlier in the evening, probably increasing their susceptibility to parasitism by the tachinid parasitoid *Ormia ochracea*. Overall, age and size differences explained 10–40% of signalling variation in male *G. integer*.

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An individual's mate attraction behaviour often changes throughout time because the best course of action in mating competition often depends on the individual's relative condition, size, strength and experience (e.g. Dawkins 1980; Austad 1984). Mate attraction behaviours that undergo ontogenetic shifts have been found in many species (Caro & Bateson 1986), while many other species display behaviours that vary with condition or size, rather than age (Dawkins 1980; Austad 1984; Waltz & Wolf 1984; Caro & Bateson 1986). Most research on size-, age- and condition-related shifts in mating behaviour has, however, focused on species with indeterminate growth (Andersson 1994), making it difficult to examine separately the effects of size and age, as they are, by definition, strongly correlated.

Research on determinate-growth species has allowed us to examine separately the effects of male size and age on mate attraction behaviour. However shifts in mating behaviour that correlate with age are also often correlated with improved condition, when foraging and other skills improve with age (e.g. Marchetti & Price 1989). Hence, even in species with determinate growth, examining separately the effects of male condition and age can be complicated.

Here I examine a Texas field cricket species, *Gryllus integer*, for evidence that differences in ontogenetic shifts,

size and/or condition explain some of the observed variation in mate signalling within this population. *Gryllus integer* is a determinate-growth species, and after its final moult, it ceases growth and becomes sexually mature. Furthermore, foraging in *G. integer* does not appear to improve with age postmaturity, thereby allowing examination of the effects of age, size and condition on mate attraction behaviour.

In *G. integer*, mating song plays an important role in male–male competition, female choice and risk of parasitism (Cade 1979; Simmons 1988). Mating song serves as an agonistic signal directed towards rival males. Male size, condition and previous fighting ability have all been shown to influence the outcome of a fight (Dixon & Cade 1986). Age, however, only appears to influence fighting ability between juveniles and adults, not between adults of different ages (Dixon & Cade 1986). Mating song also influences female choice as signals are used to attract receptive females. Females differentiate between male calls (Gray & Cade 1999a) and appear to select mates based partly on mating song (Cade & Cade 1992; Wagner et al. 1995; Gray & Cade 1999b). As with male–male competition, male size and condition also appear to influence female choice (Endler 1983; Simmons 1988; Milinski & Bakker 1990; Simmons 1995; Simmons & Ritchie 1996; Galeotti et al. 1997; Gray 1997), leading to the hypothesis that differences in male size and condition will correlate to differences in mating song. Finally, mating song influences the likelihood of being parasitized

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(Cade 1979) as mating signals can be intercepted by parasitoid flies (Diptera: Tachinidae, *Ormia ochracea*). Parasitoid females lay larvae on and around singing crickets. Larvae burrow into the host, feed and grow, and cause host death within a week (Robert & Hoy 1994). Mating song is therefore associated with benefits (mate attraction) as well as risks (male–male competition and parasitism). As old males may be more willing to risk the effects of male–male competition and parasitism in order to mate prior to their imminent death, I also hypothesized that mate attraction song would shift ontogenetically.

Gryllus integer males exhibit extensive continuous variation in many temporal and structural components of their song (Souroukis et al. 1992; Bertram & Johnson 1998; Gray & Cade 1999a, b). Here I focus on two temporal characteristics of mating song. The first, the amount of time spent calling per night (TSC), is highly variable among males (Cade & Wyatt 1984; Cade 1991). Some males never call, others call for a few minutes to a few hours a night, while others call for up to 10 h or more.

The second and recently described characteristic of male calling (Bertram & Johnson 1998) is temporal calling pattern (TCP). TCP is a family of parameters that depict how males partition their calls throughout the night (Bertram & Johnson 1998). The TCP family is especially important because male calls appear to vary in their daily calling patterning (Bertram & Johnson 1998), as well as in their temporal and structural components, yet the significance of substantial variation in male calling patterns has yet to be explored (Walker 1983). Because there is no simple relationship between a male's TSC and his mating success (Cade & Cade 1992), it is important to determine not only whether TCP influences male attractiveness, but what factors affect this distribution. In *G. integer*, TCP is of further importance because the mating song attracts both female crickets and parasitoids, although female attraction, mating and parasitoid attraction occur at different times. Female crickets begin to move towards calling males at dusk and continue to be attracted throughout the night (Cade 1988); most mating occurs at or after dawn (French & Cade 1987). *Ormia ochracea* orient to signals within several hours of dusk, and the number of parasitoids attracted diminishes after midnight (Cade et al. 1996).

Given that extensive variation in mate signalling behaviour persists in this population, I investigated how male age, size and condition could explain some of the observed within-population variation. The influence of age, size and condition on *G. integer*'s TSC are poorly documented. TSC does not appear to change with age after spermatophore production (Cade & Wyatt 1984), however, correlations with male body size are not so clear-cut. Body size, measured by male weight, was not correlated with TSC in laboratory or high-density field populations, but was positively correlated in low-density field populations (Cade & Wyatt 1984; Cade & Cade 1992). Male condition has never been examined to determine how it relates to TSC variation. The extent to which age, size and condition contribute to TCP variation is also unknown. Below, I ask whether age, size and condition

correlate with TSC and the family of TCP parameters in *G. integer*.

METHODS

I collected several hundred adult crickets from streetlight aggregations in Austin, Texas in the autumn of 1996 and spring of 1998. Crickets were raised in laboratory stock populations, housed in an environmental chamber for two generations under a 12:12 h light:dark cycle. To determine the extent of intra- and intermale variation in temporal components of calls, I monitored signals of adult males in the laboratory using adults from stock populations. I determined the effects of male age on mating song by monitoring male song parameters in males of known age. To minimize the influence of a communal rearing environment, 1 week prior to adulthood, I housed males individually and checked them daily for full wing development indicative of their final moult and maturity. I monitored 30 male adults for 20 nights after their final moult, the average adult life span (Murray & Cade 1995). I monitored 142 others ranging in age from 4 to 15 days postadulthood for at least 5 consecutive nights.

I measured each male's morphology using a dissecting microscope and optical micrometer. Following Simmons & Zuk (1992), body parts (total body length, widest points of the thorax and head, wing length and leg length) were measured three times and then averaged. I measured male body weight after acoustic monitoring was completed using an electronic balance (Denver Instrument Company, XE Series; Model 400). As all morphological body size measures were highly correlated, I used male head width as an overall measure of male size. Furthermore, I used the residuals from an allometric regression of male mass on size (head width) as a measure of male condition.

TSC and the TCP family of parameters were monitored using an electronic device that recorded each male's signalling/nonsignalling behaviour, six times/s, from 1800 hours to 1000 hours (see Bertram & Johnson 1998). This sampling rate ensured continuous courtship information, as cricket trills consist of a series of short calls ($N=686$, $\bar{X} \pm SD=450.3 \pm 7.96$ ms, range 98–1770) interspersed with silent intercall intervals ($N=686$, 164 ± 2.75 ms, range 23–563; S. Bertram & P. Montoya, personal observation). Males were housed in individual 250-ml glass jars with food and water. The jars were placed side by side and monitored at 25°C with the lights turned off at 1900 hours and on at 0700 hours. To ensure microphone accuracy, two microphones were hung in each container. The outputs of each container's microphones were strongly correlated (Bertram & Johnson 1998) and were averaged for all results.

I quantified TSC using the number of hours called per night. I described the TCP family using three parameters: start time, stop time and mean time. I quantified start time, the time a male was first observed to call within the night, by determining the time of the first 10-s calling score greater than zero. I quantified stop time, the last time a male was observed to call within the night, by determining the last 10-s calling score greater than zero. I

Table 1. Male temporal signaling pattern description

	Average	Minimum	Maximum	SD	N
Age first called	8.7	2	Never	5.50	30
Number of nights calling/20*	8.9	0	17	0.90	30
Number of breaks/20†	2.4	0	9	0.52	30
TSC‡	1.31	0	10.27	2.23	172
Start time (hour)	2230	1800	0815	3.10	107
Mean time (hour)	0245	2130	0845	2.50	107
Stop time (hour)	0700	0005	1000	2.40	107

Only 107 of the 172 males called and had their temporal calling patterns quantified.

*The number of nights a male was observed to call out of the 20 monitored.

†The number of nights he was not observed to call after he first called.

‡TSC: Time spent calling in hours per night.

calculated mean time as the normalized mean of the indicator function of time as follows. I transformed times first into numbers to eliminate the discontinuity of midnight. Next, I assigned every 10-s calling score greater than zero an indicator function value of one. Finally, I calculated the normalized mean value of the indicator function of transformed times as follows.

$$\text{Mean time} = \frac{\int_{1800}^{1000} I(t) t dt}{\int_{1800}^{1000} I(t) dt}$$

For example, three males (A, B and C) with an identical start time (1000 hours), stop time (1000 hours) and TSC (3 h) could have very different mean times. If male A called from 1000 to 1100 hours and again from 0800 to 1000 hours, his mean time would be 0530 hours. If male B called from 1000 hours to midnight and again from 0900 to 1000 hours, his mean time would be 0230 hours. Whereas, if male C called from 1000 to 1100 hours, from 0330 to 0430 hours and from 0900 to 1000 hours, his mean time would be 0400 hours

I tested results for normality using the Shapiro–Wilk statistic; I used non-parametric statistics when results were not normally distributed. I use $P < 0.05$ to indicate statistically significant differences, and provide exact probabilities when $P < 0.1$; otherwise, I indicate that results were not significant (NS).

To test the hypothesis that differences in male size and/or condition are correlated with differences in male mating song, I ran multiple regressions incorporating body size (head width measure) and condition (residuals measure) on TSC and average start time, mean time and stop time, the three TCP parameters.

I used repeated measures analysis of variance (ANOVA) on the 30 males monitored for the first 20 consecutive nights of adulthood to test the hypothesis that intra-population mating song variation is correlated, at least in part, with changes in male age. The 142 other males could not be included in this analysis as they were only monitored for 5–7 of the 20 possible nights and the analysis could not handle missing data. Also, because TCP

parameters do not exist for the nights when males had zero TSC, repeated measures analyses of variance could not be used on any of the TCP results. Therefore, I used a linear regression to determine whether age had an overall influence on the pooled population's TSC or TCP ($N=172$). I also used a multiple regression that incorporated age and an age class dummy variable (representing young males prior to spermatophore production: 1–5 days; males developing their signals: 6–8 days; males in the prime of their adult life: 9–17 days; and older males that may be experiencing senescence: 18–20 days). This multiple regression approach allowed me to determine whether signalling behaviour shifted with nonlinear, ontogenetic changes. These linear and nonlinear multiple regressions were used for TSC, start time, mean time and stop time.

RESULTS

Males differed in every aspect of their calling behaviour (Table 1). The number of nights a male called varied. Of the males monitored throughout their adult life ($N=30$), some called as early as 2 days after final moult, some never called, and average start date was 9 days. Once a male started calling, he took an average of 2.4 nights off from calling (breaks; $N=30$) over the 20-day period monitored. TSC for the entire population averaged 1.3 h/night ($N=172$) over all nights monitored, while individual male's average TSC ranged 0–10 h a night. The population's frequency distribution differed significantly from normal, being highly skewed to the right (Fig. 1; $N=172$). Thirty-eight per cent of males never called, 40% called for less than 2 h/night, while 22% averaged more than 2 h of calling time.

TCP parameters also varied between individuals. Average start times ranged from 1800 hours to 0820 hours ($\bar{X}=2240$ hours), mean times from 2130 hours to 0850 hours ($\bar{X}=0250$ hours), while males' average stop time ranged between midnight and 1000 hours ($\bar{X}=0700$ hours; Fig. 2). Six per cent of the males were early evening callers (stop time after 0200 hours), 77% called throughout the night (start time before 0200 hours, stop time after 0200 hours) and 17% were dawn callers (start time after 0200 hours).

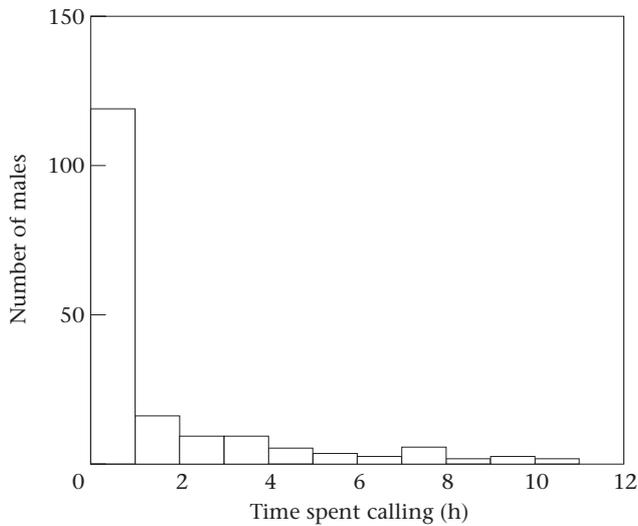


Figure 1. Histogram of the population's time (h) spent calling. Each of the monitored male's ($N=172$) average time spent calling is plotted. The population's time spent calling was not normally distributed but highly skewed to the right.

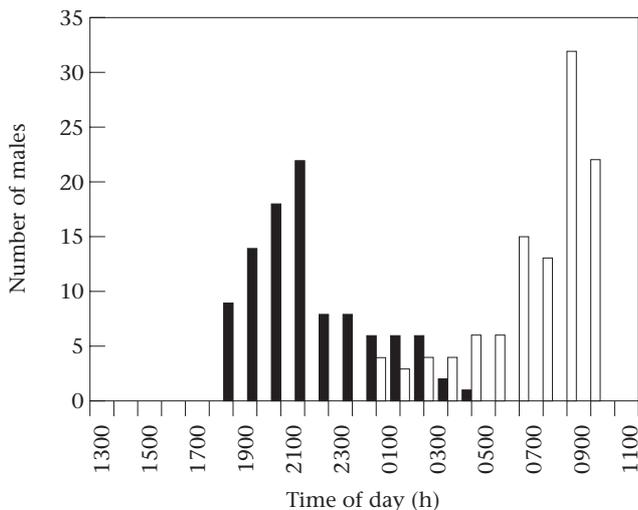


Figure 2. Histogram of the population's temporal calling pattern showing each calling male's ($N=107$) average start time (time each male initiated calling: ■) and average stop time (time each male stopped calling: □) throughout the night.

Results partially supported the hypothesis that size and condition correlate with mating song. Size affected mating song and explained 3–10% of the variation in the population. The larger the male, the more he called (Fig. 3a; multiple regression: $t_{103}=2.137$, $N=105$, $R^2=0.033$, $P=0.035$), the earlier he started calling (Fig. 3b; multiple regression: $t_{59}=-2.254$, $N=62$, $R^2=0.064$, $P=0.028$), with a corresponding shift to earlier mean calling times (Fig. 3b; multiple regression: $t_{59}=-2.731$, $N=62$, $R^2=0.097$, $P=0.008$). Size did not influence male stop time (Fig. 3b; multiple regression: $N=62$, NS). Male condition did not correlate with TSC or TCP (TSC: $t_{53}=0.491$, $N=54$, $R^2=0.000$, $P=0.626$; start time: $t_{40}=-0.015$, $N=41$, $R^2=0.000$, $P=0.998$; mean time:

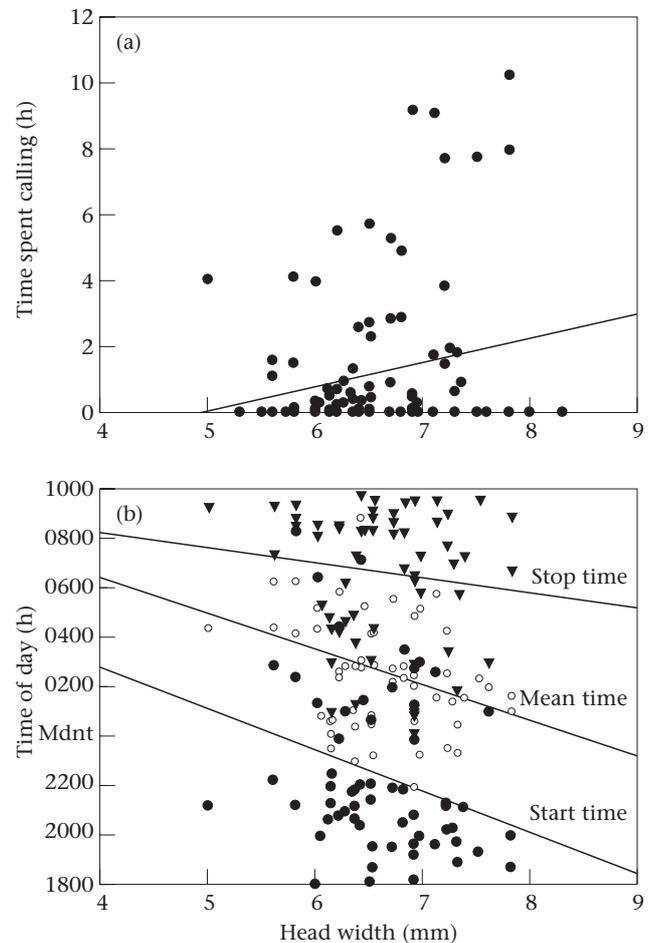


Figure 3. Influence of male size on time spent calling and temporal calling pattern. (a) The influence of male size (measured using head width, as all morphological measures were strongly correlated) on time spent calling. (b) Influences of male size on the family of temporal calling parameters. Stop time (▼) was not significantly influenced by size (solid line is the regression's line of best fit). Mean time (+) and start time (●) were significantly influenced by size.

$t_{40}=0.528$, $N=41$, $R^2=0.000$, $P=0.451$; stop time: $t_{40}=0.761$, $N=41$, $R^2=0.000$, $P=0.451$).

Male age influenced mate signalling, supporting my second hypothesis. On average, males started calling at a mean age of 9 days after final moult. However, one male started calling on his second day of adulthood, while others never called. The 30 males monitored throughout their first 20 days of adulthood showed significant age correlations with TSC (repeated measures ANOVA: $F_{20,29}=4.806$, $P=0.000$, $R^2=0.415$). Overall, the total population's ($N=172$) TSC was also influenced by age. For a few days after calling was initiated, the population's TSC averaged 40 min/day. TSC increased to a population average of 90 min/day by 9 days after final moult where it remained constant for several days. Eighteen days after final moult, the population's TSC average dropped to 40 min/day (Fig. 4a). A multiple regression incorporating age and an age-class dummy variable indicated male age class explained 8% of the population's variation in TSC (multiple regression, age: $t_{2,1206}=-0.877$, $P=0.381$; stage:

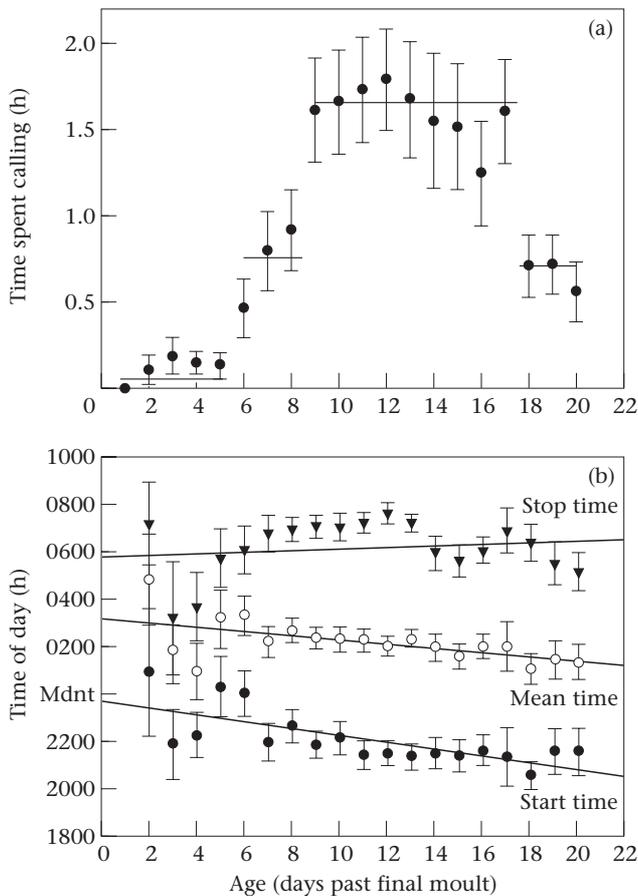


Figure 4. Influence of male age on time spent calling and temporal calling pattern. (a) The influence of male age on time spent calling (note horizontal lines represent different age categories). (b) Influence of male age on the family of temporal calling parameters. Stop time (\blacktriangledown) was not significantly influenced by age (solid line is the regression's line of best fit). However, mean time (\circ) and start time (\bullet) both became earlier with increasing age.

$t_{2,1206}=8.282$, $P=0.000$, $N=172$, $R^2=0.079$). Age explained a small portion (2%) of the variation in total population's TCP ($N=107$). Start time and mean time dropped linearly with age while stop time was not influenced (linear regression: start time: $t_{1,521} = -3.136$, $P=0.002$, $R^2=0.017$; mean time: $t_{1,521} = -2.616$, $P=0.001$, $R^2=0.011$; stop time: NS; Fig. 4b).

DISCUSSION

Male size accounted for a portion of the intrapopulation variation. Larger males called more often and their TCP's displayed earlier average start and mean times than those of smaller males. Overall, male size explained 3, 6 and 10% of the population's variation in TSC, start time and mean time, respectively.

There are many such examples of mating behaviours being conditional on body size (e.g. Thornhill 1981; Clutton-Brock et al. 1982), and behavioural differences associated with body size reflect genetic and/or environmentally based variation (Ryan et al. 1992). Genetically based differences have been shown to cause body size

variation in other *Gryllus* spp. Simmons (1988) found body size to be heritable in *G. bimaculatus*. A careful quantitative genetic study of both signalling behaviour and body size will determine whether conditional behavioural expression has evolved in this species (Travis 1994).

Although overall body condition has been shown to influence mate attraction displays in many species (Endler 1983; Milinski & Bakker 1990; Galeotti et al. 1997), results here indicate that male condition does not explain variation in TSC or the family of TCP parameters. However, residuals from an allometric regression of male mass on body size, may not be truly indicative of male condition in this species. To portray accurately how male condition influences mate attraction behaviour, individuals should be raised under high and low feeding regimes, matched for overall size and then tested to determine whether mating songs differ between the high and low feeding treatments (following Wagner & Hoback 1999).

Age explained some of the intrapopulation variation in male temporal mate signalling behaviour. Young and old males produced fewer calls than males in the prime of their life, and age class explained 8% of the total population's variation in TSC and 42% of the variation in the 30 males monitored for TSC throughout their complete adulthood. While TCP also changed with age, only 2% of intrapopulation variation was explained.

Young males signalled in a manner that may result in reduced risk of parasitism. Parasitoids are prevalent throughout the early evening hours and locate hosts using acoustic signals. Young males call less often than males in the prime of their life. Minimal signalling was observed within the first several days of adulthood, a result consistent with Cade & Wyatt's (1984) observations that males do not produce mate attraction signals until after they produce their first spermatophore. Furthermore, once young males initiated calling, they sang more in the morning hours, times that have minimal parasite activity (Cade et al. 1996).

These age differences in mating behaviours may represent a response to natural and sexual selection. In bullfrogs, older males that fight for territorial ownership are favoured in contests but are subject to increased snapping turtle predation relative to younger males and females (Emlen 1976; Howard 1981). Turtles may be attracted to the commotion of males competing for territorial ownership or males signalling to defend territories and attract mates may be more apparent to turtles than younger males or females.

If signalling entails a significant possibility of death, young males may have been selected to signal in a manner that reduces risk. Males live an average adult life span of 20 days in the field (Murray & Cade 1995). For young unmated males, the costs of being parasitized may outweigh the benefits of mating. For older males, the benefits of mating may outweigh the costs associated with a slightly shortened life span. Males in the prime of their life may therefore be more willing to risk signalling to attract a mate during times of parasitoid prevalence than younger males.

Adult males 18–20 days old called significantly less often than males in the prime of their life, a result that contradicts the second hypothesis. TSC reduction in old males has not previously been observed (Cade & Wyatt 1984). Apparent reduced TSC may be an artefact of sampling fewer individuals in the 18–20 age categories: the TSC distribution was highly skewed to the right and reduced sample sizes could result in lower population averages. Conversely, old males may show signs of senescence.

By not signalling, young males may also avoid competition with males in the prime of their adult life and save energy in the process (Wiley 1974, 1991). Sexual displays are energetically costly in a variety of species (Hoback & Wagner 1997; Wagner & Hoback 1999) and production of trilling song seems to be one of the most energetically demanding activities (Halliday 1987; reviewed by Prestwich 1994). Furthermore, competition in *G. integer* appears to have resulted in TSC reduction in other studies. Males in high-density populations experienced increased competition and as a result may have reduced their signalling behaviour (Alexander 1961; Cade & Cade 1992). Young males may be inefficient at competing with males in the prime of their life and as a result, signal significantly less often.

Overall, variation attributable to differences in male age and size results in some intrapopulation signal variation. Other hypotheses need to be explored to determine their role in the maintenance of signal variation in *G. integer*, including evolutionarily stable strategies, density-dependent selection, gene flow, antagonistic pleiotropy and balancing selection.

Future work should also focus on temporal components of male calls. Signal partitioning investigations have received limited attention despite their important implications for predator avoidance and mating success. In fact, this is the first intensive investigation of how males partition their calling behaviour throughout the evening. Field observations on Texas *G. integer* need to be completed to determine whether natural variation is similar to the observed laboratory variation. Furthermore, understanding how any acoustically signalling organism partitions its signals will increase our knowledge of how selection influences calling. Total calling time is positively correlated with mating success in many species (e.g. Cade 1979; Green 1990; Bertram et al. 1996), however, female preference is not solely based on total time of acoustic stimulation (Gerhardt et al. 1996). Correlating signal partitioning with when females mate may enhance our understanding of sexual selection.

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