

Ultrasonic Signal Competition Between Male Wax Moths

Feng-You Jia,^{1,2} Michael D. Greenfield,¹ and Robert D. Collins¹

Accepted June 6, 2000; revised August 2, 2000

*Pair formation in the lesser wax moth, *Achroia grisella* (Lepidoptera: Pyralidae), is effected by male ultrasonic signals that are attractive to receptive females within 1–2 m. The males typically aggregate in the vicinity of the larval food resource, honeybee colonies, and signal for 6–10 h each night. Females are known to choose males on a relative basis and evaluate primarily three signal characters: signal rate (SR), loudness (peak amplitude; PA), and asynchrony interval (AI), a temporal feature reflecting the time interval between signals produced by the left and right tymbals. We conducted a series of experiments to investigate whether and how *A. grisella* males modify their signals in the presence of neighboring signalers. When separated by <40 cm, males increase their SRs by 3–6% upon perceiving a neighbor's signals, but they do not alter their PAs or AIs. Increased SRs continue for 5–10 min and are more pronounced in males that are silent at the time they perceive their neighbor. By increasing its SR, a male improves the likelihood of matching or exceeding its neighbor's SR and may thereby compete more effectively for local females. SR increases are energetically demanding, though, and their brief duration and occurrence primarily at the beginning of signaling bouts may be the most prudent allocation of a male's limited energy reserves.*

KEY WORDS: *Achroia grisella*; acoustic communication; acoustic perception; sexual selection; signal energetics.

¹Department of Entomology, University of Kansas, Lawrence, Kansas 66045.

²To whom correspondence should be addressed at Department of Entomology, Kansas State University, Manhattan, Kansas 66506. e-mail: fjia@oz.oznet.ksu.edu.

INTRODUCTION

Darwin's (1871) theory of sexual selection is based on observations that males commonly compete to mate with a maximum number of females and that such competition leads to great variation in mating success among males. A consequence of this high variation is that those traits contributing to an individual male's mating or reproductive success will be strongly favored by selection. Darwin identified two categories of sexual competition or selection: (1) intrasexual (2) and intersexual. Intrasexual selection involves overtly agonistic encounters and other rivalries between individuals of the same sex, generally male, in which the "winners" gain access to reproductive females. Competition in this context favors traits such as greater male strength and specialized morphological weaponry. On the other hand, in intersexual selection males do not compete directly but vary in their opportunities to encounter sexually receptive females. Here, competition may favor male traits that attract females or influence their receptivity.

The evidence that reproductively mature males compete with one another for access to females is overwhelming (Andersson, 1994). Examples include direct fights between rival males in which large body size, relative to females, and specialized weaponry are often favored. But in many cases the contests involve only ritualized displays, which presumably reduce the risk of serious injury or death that might result from more overt aggression (Clutton-Brock *et al.*, 1982). Evidence that male features evolved under the influence of female choice has been more elusive, but many recent experimental studies have succeeded in separating inter- and intrasexual selection and clearly demonstrate that certain exaggerated morphological and behavioral traits attract or otherwise influence females (e.g., Gilburn and Day, 1994; Wilkinson *et al.*, 1998; Jang and Greenfield, 1998).

It has been traditional to regard male competition and female choice as two distinct processes. However, these two aspects of sexual selection are not mutually exclusive, and both may act in the same direction on the same trait. For example, in the house sparrow, *Passer domesticus*, the size of the black throat patch represents both a signal of dominance status in competitive interactions between rival males and an adornment that is attractive to females (Møller, 1988). Moreover, rival males normally compete for mating sites, and these interactions may involve an element of female choice because females are more likely to arrive at certain sites (Balmford *et al.*, 1992).

When the male traits are behavioral in nature, both intra- and intersexual selection may lead to significant trait modifications in the presence of neighboring males. These modifications are most notable among male advertisement signals. Here, male-male competition may result in males escalating the intensity, rate of delivery, length, or complexity of their signals in a

program of sequential assessment (Clutton-Brock *et al.*, 1982). Female choice may also drive such escalations in cases wherein females choose males on a relative basis, thereby demanding that successful males at least match their neighbors' values for critical signal characters. Lekking species are expected to be especially subject to this effect, as males in a dense congregation may perceive, and possibly assess, their neighbors' signals and then adjust their own signals accordingly. Because attractive signaling may be energetically costly (e.g., see Reinhold *et al.*, 1998) and energy reserves might be limited, males may not be expected to enhance signal intensity, rate, length, or complexity except when necessary.

Here, we present a study investigating male signal competition in the lesser wax moth, *Achroia grisella* (Lepidoptera: Pyralidae). Unlike most moths, in which pair formation is accomplished by searching males that detect and locate pheromone-emitting females (Silberglie, 1977; Greenfield, 1981), male *A. grisella* produce acoustic signals that attract sexually receptive females (Greenfield and Coffelt, 1983). Signaling males are normally clustered in a high density, and laboratory experiments show that females choose among neighboring males based on relative values of their signal characters (Jang and Greenfield, 1998). Observations that males often begin a nightly signaling bout merely seconds after their neighbors begin indicate that they both perceive and respond to their neighbors' signals. We therefore conducted a series of tests to determine whether males modify their signals in more specialized ways when in the presence of signaling neighbors. Our findings indicate that male *A. grisella* significantly modify one critical signal character and that this modification probably occurs in the context of competition driven by female choice.

Natural History and Acoustic Behavior of *A. grisella*

Lesser wax moths are symbionts of the honeybee (*Apis mellifera*; Hymenoptera: Apidae) and are found in or associated with honeybee colonies during most of their life (Künike, 1930). Immediately following adult eclosion, both males and females usually exit the colony, but they may remain nearby if the colony continues to represent a valuable larval food resource. Males typically congregate in the vicinity, where they broadcast ultrasonic signals that attract receptive females within 1–2 m. Such congregations may represent “resource-based leks” (*sensu* Alexander, 1975). The males signal for 6–10 h each night during their brief (2-week) adult life spans. Adults have an atrophied proboscis and neither feed nor drink. Because signaling males display at sites likely to be visited by females, competition among males for prime female encounter sites close to honeybee colonies

is expected to be intense. Both laboratory and field observations showed that while males generally remain stationary during signaling, agonistic interactions with neighboring signalers do occur (Greenfield and Coffelt, 1983; Cremer and Greenfield, 1998).

Signaling male *A. grisella* generate a series of ultrasonic pulses by fanning their wings, which causes the pair of tymbals on the tegulae at the bases of each forewing to buckle in and out (Spangler *et al.*, 1984). The tymbals buckle once on the upstroke and once on the downstroke. Each tymbal buckling yields a highly damped 100- μ s pulse of ultrasound. Due to slightly asynchronous wing movements, the two tymbals produce a pair of pulses during each upstroke and downstroke that are usually separated by a brief (100- to 1000- μ s) silent gap. The sound pulses are loud [amplitude, \cong 95-dB sound pressure level (SPL) at 1 cm; 0 dB = 20 μ Pa], are broadcast rather omnidirectionally, and include frequencies from 70 to 130 kHz (Spangler *et al.*, 1984; Snedden *et al.*, 1994). At 25°C, production rates of pulse pairs range from 70 to 140 s⁻¹; i.e., wingbeat frequencies range from 35 to 70 s⁻¹ (Jang and Greenfield, 1996; Jang *et al.*, 1997). Wing-fanning males also release an odor (combination of two aldehyde compounds) from glands on the base of the front wings, but its function remains unclear in intrasexual and intersexual interactions (Greenfield and Coffelt, 1983). A loudspeaker broadcasting the ultrasonic signals is as effective as a wing-fanning male in attracting females (Spangler *et al.*, 1984).

Previous playback experiments indicated that females prefer males whose advertisement signals have a higher amplitude [peak amplitude (PA), defined as the maximum SPL measured during a pulse], are delivered at a faster rate [signal rate (SR), defined as the wingbeat frequency (see Jang and Greenfield, 1998)], and include longer silent gaps [asynchrony interval (AI), defined as the elapsed time between the onset of the first pulse and the onset of the second within a pulse pair produced by one wing upstroke or downstroke] within pairs of pulses (Jang and Greenfield, 1996, 1998). Breeding and selection experiments demonstrated that two of these three signal characters, PA and SR, are repeatable, have substantial additive genetic variance, and are heritable (Jang *et al.*, 1997; Collins *et al.*, 1999).

MATERIALS AND METHODS

Experimental Insects and Recordings

The stock *A. grisella* population used for our experiments was derived from approximately 300 insects collected on abandoned beeswax at a single location in Lawrence, Kansas, in July 1997. The insects were maintained

in a rearing chamber at 25.5°C under a 12:12 L:D photoperiod, and larvae were provided a standard diet composed of cereals, beeswax, yeast, honey, water, and glycerol [a modification of the *Galleria* diet described by Dutky *et al.* (1962)]. Under these conditions and at the density established (approximately 200 eggs per 50 g diet), the generation time was approximately 45 days (Jang and Greenfield, 1996; Jang *et al.*, 1997). We maintained a breeding protocol that minimized inbreeding and the loss of genetic variation from the stock population.

One-day-old virgin males held individually in cylindrical screen cages (1-cm diameter, 1.5-cm height) were used for all experiments. The screen did not affect the quality of male acoustic signals (Jang *et al.*, 1997). To avoid exposure of experimental insects to other males or male signals, we placed each cage in a small plastic cup with a closed lid prior to testing. All tests were conducted in a semianechoic room with temperature and photoperiod conditions equivalent to those of the chamber used for rearing the stock population. Experimental insects, within the individual cages, were placed in a circular screen arena (80-cm diameter) in the center of the room. Observations and measurements were made under 25-W incandescent red light. Because *A. grisella* activity peaks during the first half of the scotophase, we completed all tests 1–4 h after its onset.

Male signals were recorded with a condenser microphone (ACO Pacifica Model 7016; frequency response, ± 6 dB from 10 to 160,000 Hz) whose output was amplified 40 dB and sent to a soundcard (SoundFX Engineering Version; Silicon Soft, San Jose, CA) in a desktop computer. To standardize recordings, the microphone was always placed 10 cm distant from the focal moth. We sampled the microphone output at 398 kHz for 230 ms and saved the samples to computer files using a custom signal-processing program. Thus, seven complete cycles of wing movement were selected and analyzed from each male. A separate signal-processing program was used to determine mean PA, SR, and mean AI for the recorded signals in each file.

Experiment 1: Do Males Modify Their Signal Characters with Competitors Present?

We measured the signal characters of males both in acoustic isolation and in the presence of a neighboring signaler to determine if signal quality was affected by competition. In each trial, we tested two *A. grisella* males randomly chosen from the stock population. The individually caged males were placed in the arena 20 cm apart, and a 10 × 10 × 10-cm block of acoustic insulation foam was situated between them. We recorded the signals of each male after it began signaling. These recordings are termed “basal signals.”

We assumed that when a male was producing its basal signals (and separated from its neighbor by the foam block), it did not hear the other male's pulses or at most just barely perceived them. To verify this assumption, we placed a single male on one side of the foam block and recorded its signals from the other side, where the second male would normally be located. We repeated this procedure on 15 males and never recorded detectable signals. Because the microphone, amplifier, and soundcard gain settings used would ordinarily detect an *A. grisella* male's signals 1 m distant, we inferred that the foam block attenuated the signals severely. Any perception by one test male of the other's signals would be equivalent to hearing an average neighbor at least 1 m away. As reported under Results, behavioral responses are not observed between males separated by such distances.

We next removed the foam block immediately after recording the basal signals and recorded "interactive signals" produced by the two males. However, we recognized that a focal male's perception of a neighbor's signals may be influenced by whether or not the focal male is itself signaling (see Greenfield, 1997). Both behavioral and neurophysiological tests on various acoustic invertebrates and vertebrates indicate that hearing sensitivity may decrease markedly during signaling. Such impairments may arise from simple masking (Hedwig, 1990) or from mechanical alteration of peripheral auditory structures (Henson, 1965; Narins, 1992) during signal production. Therefore, we interrupted the signaling of each male following removal of the foam block and then recorded their interactive signals within 1 min after both moths had resumed signaling following interruption. We interrupted signaling with a weak air current from a squeeze blower held 30 cm distant from the focal male. Moths normally stopped signaling for 1–5 min in response to this stimulus. Thus, the male that resumed signaling first, the "leader," may not have been afforded unimpaired perception of the other's signals, whereas the male resuming second, the "follower," should have clearly perceived the first male.

Using the above procedures, we recorded the basal and interactive signals of 20 pairs of moths. In each pair the leader and follower roles during interactive signaling were identified. We repeated these recordings for another two sets of 20 pairs using intermoth separation distances of 40 and 60 cm, respectively. Each test moth was recorded only once, and the differential (Δ value) between its basal and its interactive signals was determined for PA, SR, and AI; e.g., $\Delta\text{PA} = \text{interactive PA value} - \text{basal PA value}$.

Because the air current stimulus might change the quality of a male's subsequent acoustic signaling in addition to interrupting its signaling, we conducted a control test on solo males. Using the above procedures, we recorded signals of males placed singly in the arena before and after interruption by the stimulus ($n = 20$).

We conducted a second control test on paired males to examine further how a focal male responds to a neighbor's signals when the focal male is signaling at the time the neighbor begins. Again, we followed the procedures outlined above except that signaling was not interrupted prior to removing the foam block; interactive signals were then measured approximately 2 min (maximum delay = 5 min) after removing the block. We recorded the signals of 10 pairs at a 20-cm separation distance and compared the Δ values for signal characters of these 20 males with the corresponding Δ values of leaders and followers in the trials wherein signaling was interrupted.

Experiment 2: How Long Does Signal Modification Last?

Because trials in Experiment 1 clearly showed that males did modify one signal character in the presence of a signaling neighbor (see Results), we conducted an additional series of trials to determine the duration of the effect. We followed the basic protocol of Experiment 1 and separated paired males by 20 cm. Basal and interactive signals of each male were recorded as before, but we continued to record interactive signals at 5-min intervals for 20 min following resumption of signaling.

Results in both experiments were analyzed with appropriate nonparametric statistics.

RESULTS

Modifications of Signal Characters

When 20 cm apart, individuals designated as followers significantly elevated their interactive SRs over their basal values ($P < 0.001$, Wilcoxon matched-pairs signed-ranks test, two-tailed) (Fig. 1a). These males exhibited a mean Δ SR of $+3.0$ wingstrokes s^{-1} , a 6.2% increase. Leaders also significantly elevated interactive SRs over basal values ($P = 0.017$), although their mean Δ SR was only $+1.3$ s^{-1} , a 2.6% increase and significantly less than that of followers ($P = 0.03$, Wilcoxon matched-pairs signed-ranks test, two-tailed). We detected no significant modifications in PA or AI for either leaders or followers (Figs. 1b and c). At separation distances of 40 and 60 cm, no significant modifications of in SR (Fig. 2), PA, or AI (data not shown) were found for either leaders or followers. These results justified the pooling of leaders and followers in Fig. 2.

The elevated interactive SRs exhibited by followers and leaders did not result from simple responses to the air current stimulus. In the first set of control trials, wherein only single males were tested, we recorded

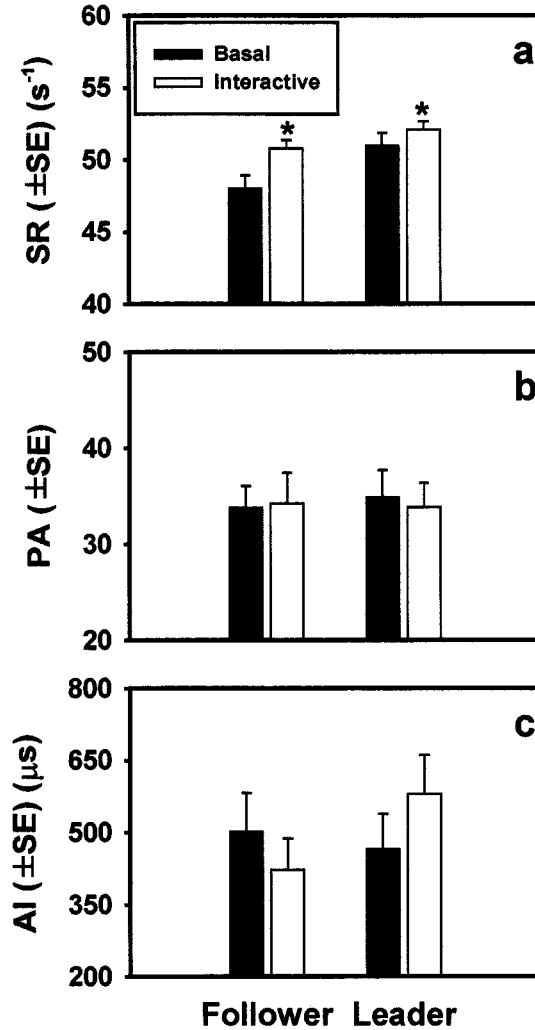


Fig. 1. Modification of signal characters of *A. grisella* males separated by 20 cm. (a) Modification of signal rate (SR). (b) Modification of peak amplitude (PA). (c) Modification of asynchrony interval (AI). See text for definitions of signal characters. Black bars indicate mean basal signal characters (\pm SE), measured in the absence of a neighboring male. White bars indicate mean interactive signal characters (\pm SE), measured in the presence of a neighboring male signaler. Leaders are males that resumed signaling first after interruption during a trial; followers are males that resumed signaling second. *Interactive signal character is significantly different from basal character ($P < 0.05$, Mann-Whitney U test).

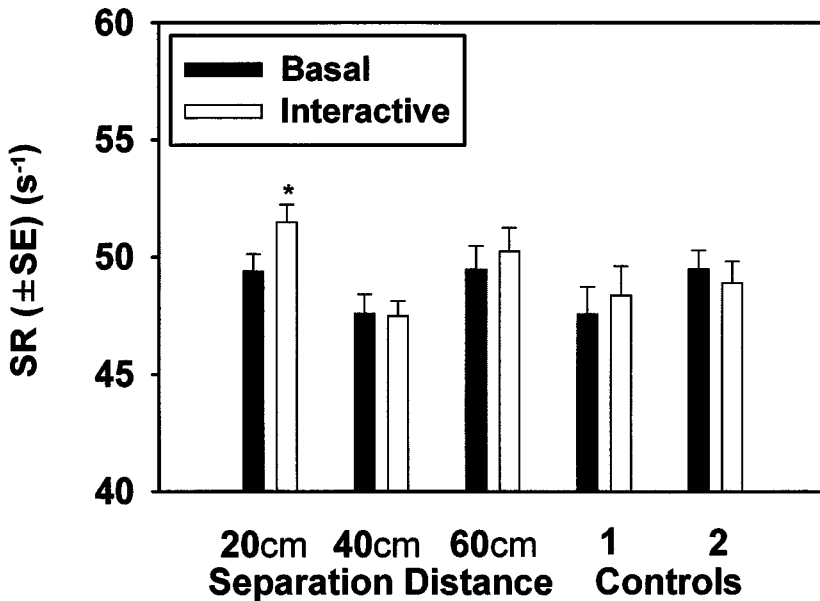


Fig. 2. Modification of the signal rate (SR) of *A. grisella* males separated from their neighbor by different distances (20, 40, and 60 cm) or subject to various treatments (controls 1 and 2). Control 1: Only one male was used in a trial; the interactive SR value was measured after the blower stimulus was presented. Control 2: Two signaling males were used in a trial, but they were not interrupted by the blower stimulus prior to removing the foam block. Black bars indicate mean basal signal characters (\pm SE), measured in the absence of a neighboring male. White bars indicate mean interactive signal characters (\pm SE), measured in the presence of a neighboring male signaler. Followers and leaders are pooled. *Interactive SR is significantly different from basal SR ($P < 0.05$, Mann–Whitney U test).

no significant modifications in SR (Fig. 2), AI, or PA after interruption of signaling ($P \geq 0.22$, Wilcoxon matched-pairs signed-ranks test, two-tailed). In the second set of control trials, wherein signaling was not interrupted, both males in a pair had comparable Δ SRs, and the differences between the Δ SR values of paired males were significantly less ($P = 0.0046$, Mann–Whitney U test) than those differences when the males were interrupted prior to measurement. Presumably, that interruption allowed one male, the follower, to perceive its neighbor more clearly.

Although our test males varied considerably in their basal SRs, we found no relationship ($P = 0.08$, Mann–Whitney U test) between a male's basal SR and his leader vs follower role at the onset of interactive signaling at the 20-cm separation. Similarly, we found no relationship between a male's basal SR and his Δ SR [followers, $r = 0.148$, $P = 0.06$ (t test for slope of least-squares regression); leaders, $r = 0.014$, $P = 0.62$] (Fig. 3). Thus, the possibility that

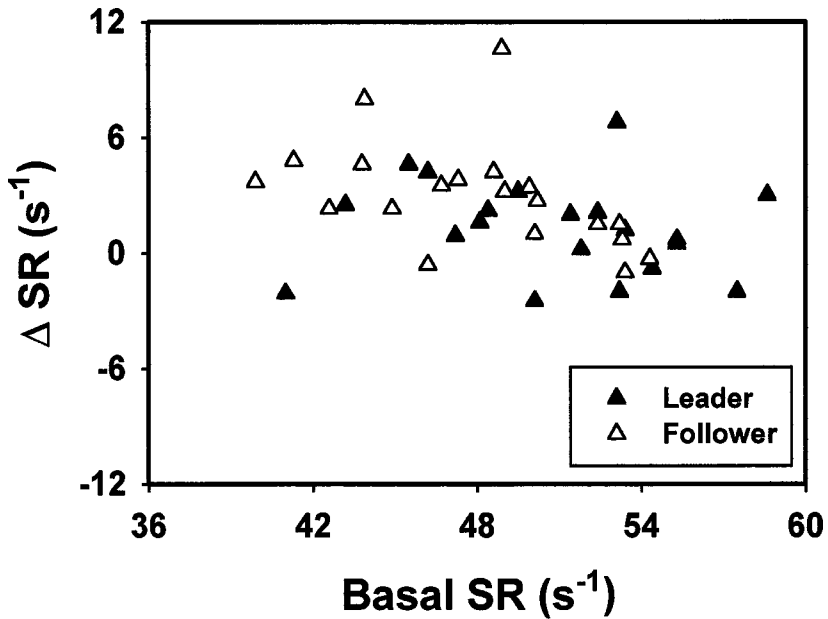


Fig. 3. ΔSR (interactive SR value – basal SR value) versus basal SR for trials conducted with a 20-cm separation between males. Both leader and follower roles of each tested individual are shown. Leaders: $r^2 = 0.0002$, $P = 0.62$ (t test for slope of least-squares regression). Followers: $r^2 = 0.0219$, $P = 0.053$.

followers had higher ΔSR s because they started from lower values seems unlikely. To determine whether males modified their SR in accordance with the difference between their signaling and that of their neighbor, we examined the regression of ΔSR vs $(basal SR_{leader} - basal SR_{follower})$ within a trial. Again, we found no relationship for either the leader's or the follower's ΔSR at the 20-cm separation ($P \geq 0.08$).

Persistence of Signal Modification

We evaluated the length of time during which interactive SRs in followers remained elevated by comparing a male's interactive SR values recorded at 5-min intervals with its basal value. These comparisons showed that the males modified their SRs for less than 10 min following interruption and resumption of signaling ($P < 0.01$, Wilcoxon matched-pairs signed-ranks test, one-tailed) (Fig. 4). Only 4 of 20 followers sustained an SR higher than their basal value for 15 min. Leaders were less persistent and most sustained their slightly elevated SRs for less than 5 min.

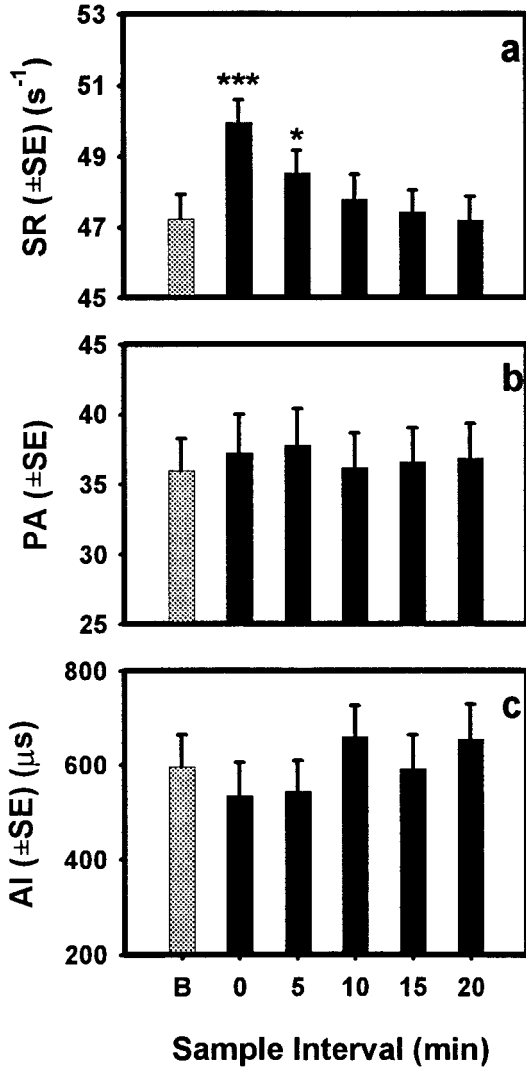


Fig. 4. Persistence of modification of three signal characters, signal rate (SR), peak amplitude (PA), and asynchrony interval (AI), of *A. grisella* males. Bars indicate mean signal character (\pm SE) measured before removal of foam block (B, basal signal character measured in the absence of a neighboring male) and at 5-min intervals beginning when the block was removed (interactive signal character measured in the presence of a neighboring male signaler). Followers and leaders are pooled. *Interactive signal character is significantly different from basal signal character: $P < 0.05$ (Mann-Whitney U test). *** $P < 0.001$.

DISCUSSION

In trials where males were spaced 20 cm apart, both leading and following individuals significantly increased their signal rates (SRs). Because these increases occurred only when the acoustic insulation was removed and another male was present, we presume that they represent responses to the acoustic signaling of the neighboring male. Signal modification did not occur when males were separated by distances of 40 cm or more, however, implying that a threshold sound pressure level (SPL) for the signaling response, which may exceed the threshold for basic acoustic perception, exists in *A. grisella* males. This interpretation is consistent with our finding that followers modified their signals by a significantly greater Δ SR than leaders did. If the hearing of *A. grisella* males is less sensitive during their own signal production, as is known in various acoustic invertebrates (Hedwig, 1990; Greenfield, 1997) and vertebrates (Narins, 1992), leaders would have perceived their (following) neighbor's signals to be lower in SPL than vice versa. Consequently, leaders would have been subject to acoustic stimuli closer to their thresholds for the signaling response, and their smaller Δ SRs may reflect the reduced stimulation they received during interactive signaling.

Because signal modification involves a character critical for female attraction and occurs only when males are close to one another, the phenomenon may be considered a form of signal competition (*sensu* West-Eberhard, 1984): When another male signals nearby, a male adjusts its signals in an attempt at least to match that neighbor's attractiveness to females or threat to other males. Failure to match competing males would greatly reduce mating opportunities both directly and indirectly. In *A. grisella*, SR predicts a significant proportion of the variance in male attractiveness to females, and females assess the SRs of local males on a relative basis prior to orienting toward and choosing one (Jang and Greenfield, 1998). Thus, males ≥ 40 cm distant may not elicit a signaling response because they are not perceived as direct competitors for females. A male's SR is strongly correlated with his energy expenditure during signaling (Reinhold *et al.*, 1998), and SR might also reliably indicate the amount of energy a male has available for intermale aggression should an escalated encounter arise. Thus, the elevated SRs observed during interactive signaling could represent a means of indirect competition for mating opportunities. That is, the males might use a graded signal to indicate their ability or willingness to defend a calling site or to attack an intruder (e.g., see Wagner, 1989). While previous experiments failed to show any relationship between a male's signal characters and his success in intermale agonistic encounters (Cremer and Greenfield, 1998), those trials measured only signaling prior to the encounters and ignored potential modifications during interactive signaling. Therefore, we cannot dismiss the

possibility that the positive Δ SRs mediate potentially agonistic encounters between neighboring males.

Why do *A. grisella* modify only SR, while holding peak amplitude (PA) and asynchrony interval (AI) at basal levels? This restriction may simply reflect their inability to control the other signal characters. PA is correlated with body weight, which may be correlated with tymbal dimensions, and an adult may not be able to increase the loudness of its signals by expending more energy. AI is much less repeatable than the other two critical signal characters (Jang *et al.*, 1997), and a male's control over it is unclear. Additionally, if mediation of intermale agonistic encounters is a major function of signal modification, SR would be the most likely character to modify because it the only one graded reliably with energy expenditure.

If SR modification is advantageous in competing for mating opportunities as outlined above, why do males make the adjustments for a mere 5–10 min? Can increases in SR for such brief intervals be of any value? The limited persistence of elevated SRs during interactive signaling probably reflects the increased energy required [a Δ SR of +3 wingstrokes s^{-1} demands elevation of net metabolic rate by $3.3 \mu\text{l O}_2/\text{h}$, an 11% increase (Reinhold *et al.*, 1998)] and the limited energy budget of adult *A. grisella*. Because these insects do not feed or drink as adults, they are constrained to use energy acquired during larval development for all of their activities. Thus, they may be selected to allocate their stored energy with extreme care, as it cannot be replaced. In this regard, increasing one's attractiveness at the onset of a signaling bout may be the most judicious use of scarce energy, particularly in light of the brief duration of female orientation and courtship in *A. grisella*. While females might arrive at a male at any time during the nightly signaling period, they may be most likely to be attracted and initiate orientations and pair formation at the beginning of the night or when a signaling bout first starts (see Walker, 1983). Would allocation of one's limited energy reserves to a significant increase in attractiveness at these times be more worthwhile than spreading them out over the course of many hours? Only careful behavioral observations and field data can provide a definitive answer.

ACKNOWLEDGMENTS

We thank Dr. Ralph Charlton and Dr. David Margolies for their valuable criticisms of an early version of the manuscript and several anonymous referees whose criticisms led to improvement of the paper. This research was supported by National Science Foundation Grants IBN-9407304 and IBN-9807915.

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