subalpine fir. Soon after snowmelt, the breeding season is initiated by males as they secure calling perches in sagebrush and use tegminal stridulation to entice potential mates from dusk until midnight. Receptive females locate males acoustically and initiate mating by mounting a male and chewing on his fleshy underwings as an act of nonlethal sexual cannibalism (Figure 2). As the female ingests wing material and hemolymph, the male attempts to attach an external spermatophore to his mate. Although the damage incurred by males is permanent, this does not preclude them from securing additional instances of mating. Additionally, the post-copulatory degradation of male hindwings aids in determining their mating status in the field. The hindwings of virgin males are intact and milky-white while non-virgin male hindwings are tattered, withered, and visibly darkened (Figure 3).


Figure 3. Male *C. strepitans* underwings: virgin (left) versus old wounds (right) (Photos courtesy of S. Sakaluk.).

run along a series of teeth on the opposite wing. This generates sound in a fashion that is similar to raking a thumbnail along the teeth of a comb. Each closure of the forewings creates an individual acoustic pulse. A rapid series of pulses constitutes a train (Figure 4).

Our study was conducted on a population of sagebrush crickets at Lower Deadman's Bar, a level, four-hectare sagebrush meadow on the banks of the Snake River within Grand Teton National Park. The site's northern boundary is delineated by a gravel road while the east and west borders are defined by areas of lodgepole pine and subalpine fir accompanied by steep terrain. The southern limit of the site is defined by a copse of trees and a topographical narrowing of level ground (Figure 5).

Figure 2. A copulating pair of *C. strepitans*. (Photo courtesy of S. Sakaluk.).

Song is generated in *C. strepitans* when males stridulate their forewings, causing a plectrum to

The aim of our study was to investigate the relationship between aspects of male calling behavior and the amount of time it takes males to secure a mate. Multiple studies have indicated that calling is an
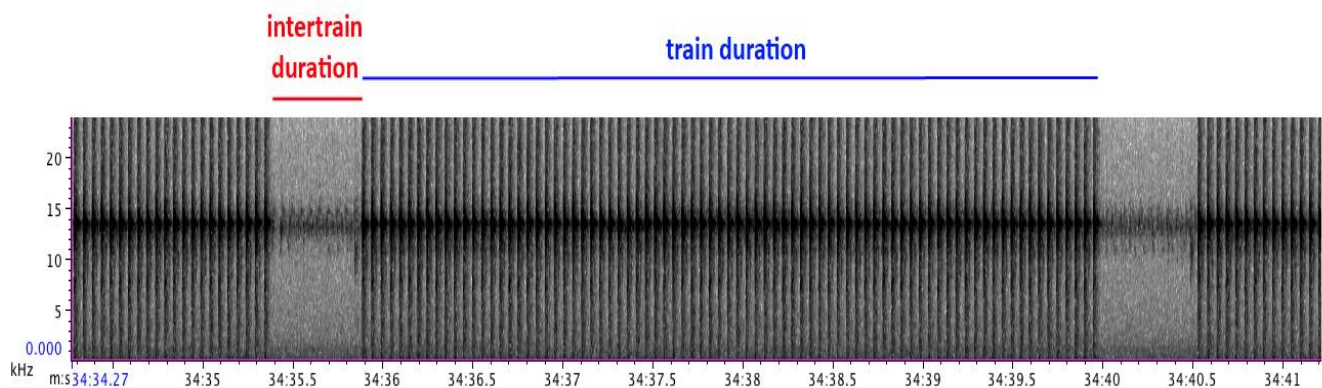
Figure 4. Male song is divided between periods of high and low activity. Each train is composed of multiple individual pulses bookended by periods of acoustic inactivity.

energetically expensive behavior and that males that invest more energy in calling have an advantage in securing mates (Sakaluk and Snedden 1990, Sakaluk et al. 2004, Leman et al. 2008, Ower et al. 2011). Based on these findings, we sought to determine if repeated measures of male calling behaviors in the field are predictive of mating success. More specifically, we hypothesized that high calling effort (time spent calling), long train durations, and short intertrain durations would decrease the time it takes for males to secure their first mate.

Figure 5. Lower Deadman's Bar

✦ **METHODS**

We were fortunate to have dry and reasonably warm weather during our 2014 field research window from May 23 through June 3. Additionally, we found that our study site was just coming into mating season when we arrived. From May 23 – May 25 we caught only virgin males. All males used in the study were captured on May 25.

On the morning following their capture, each male in our study was tagged by using Loctite® Superglue Gel to affix a unique number, printed on vinyl paper, onto his pronotum. Males were also marked with fluorescent, acrylic paint on their femora and pronotum, outside of the numbered area (Figure 6). The paint aided in recapturing males with the help of UV flashlights.

Repeated measures of each male's calling behavior in the field were made possible using pens fashioned out of aluminum flashing. The material for each pen measured approximately 3 m by 0.5 m. The ends of the flashing were joined together using duct tape to construct a circular pen approximately 0.5 meters in diameter. The pens were used to surround

the "home sagebrush" of the males and were buried several centimeters deep into the soil (Figure 7), very similar to a previous repeated measures study

Figure 6. Numbered and painted male *C. strepitans*.

Figure 7. Finishing the construction of a pen.

on *C. strepitans* (Johnson and Hupton 2011). Before dusk, flash drive microphones were sealed in plastic baggies and dropped into pens to record calling behaviors on three nights: May 26, 27, and 28. The microphones were collected as calling wound down each night.

On May 29, about an hour before calling began, males were released by disassembling the pens. Over the next five nights (May 30 through June 3), males were recaptured to determine mating status by examining their underwings for damage.

✦ **PRELIMINARY RESULTS**

Twenty-six of the thirty males were recaptured at least once. Time to mate was determined

as the number of nights from release until recapture as a non-virgin. Males that had not mated by their last recapture were included as "censored" observations. The fifteen males recaptured as non-virgins took from one to five nights to mate. Eleven males were last captured as virgins and were estimated to have taken from two to six nights to secure a mate.

Audio recordings were analyzed using the band limited energy detector function of Raven Pro 1.4 to determine the beginning and end time of each train. From these data, we determined nightly calling effort, mean nightly train duration, and mean nightly intertrain duration for each male.

Unfortunately, our intended sample size of 30 males was limited due to pen malfunctions (10 blew away), poor audio recordings (4), and failure to recapture males (4). This reduced our effective sample size to 17 males for whom we had good recordings all three nights, were released on May 29, and were recaptured following release. Adding to our data troubles, male calling behaviors were individually inconsistent over the three nights of recording (Figures 8 – 10).
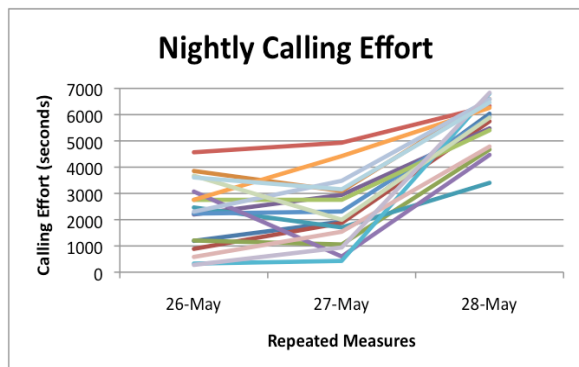
Figure 8. Individually inconsistent nightly calling effort.
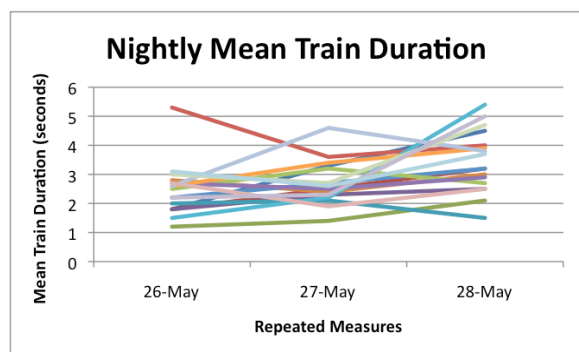
Figure 9. Individually inconsistent nightly mean train duration.
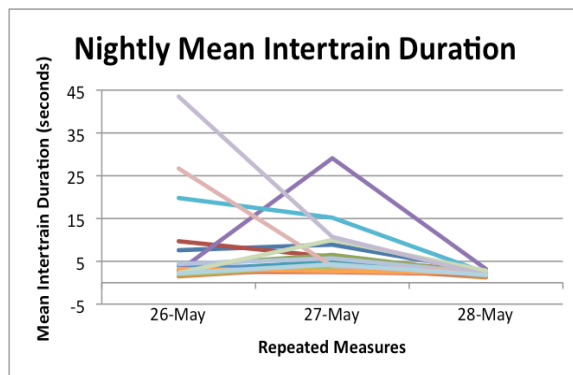
**Figure 10.** Individually inconsistent nightly mean intertrain duration.

Repeated measures ANOVA revealed statistically significant differences in mean nightly calling effort ($F_{2, 32}$ = 76.9, p < 0.001), mean nightly train duration ($F_{2, 32}$ = 7.7, p = 0.02), and mean nightly intertrain duration ($F_{2, 32}$ = 3.5, p = 0.04) over the three nights of recording (Figures 11 – 13). We tentatively attribute the abrupt differences in behavior on May 28 to progression of the mating season.

May 28 was the warmest day in more than a week of warm days (daily highs from 22˚C to 27˚C) with no recorded precipitation. Field conditions at Lower Deadman's Bar (LDB) ranged from 9˚C to 14˚C at 21:00 (onset of calling) from May 23 to May 27 which makes May 28 stand out with 16˚C at onset of calling. It is worth noting that all seventy-four males collected from LDB between May 23 and May 25 were virgins and that on May 30, our first night of recapturing, the proportion of non-virgin males in our study (22%) was close to the proportion of non-virgin males who were outside of our study (38%) and free to mate from May 26 through May 28.

Because of individually inconsistent calling behaviors and various indicators that suggest calling data gathered on May 28 best represents behaviors exhibited on nights with high mating activity, we chose to use the May 28 calling data alone for the failure-time analysis instead of combining it with calling data from May 26 and 27. Thus, failure-time analysis (PROC PHREG in SAS) was used to examine the effect of calling effort (X^2 = 1.75, p = 0.93), mean train duration (X^2 = 1.70, p = 0.53), and mean intertrain duration (X^2 = 2.06, p = 0.35) recorded on May 28 on time to mate. The analysis revealed no effect for any of the calling behaviors on time to mating success (Figures 14 – 16).

While these results were not anticipated, they are hardly surprising considering the lack of individual calling consistency coupled with a less than ideal sample size. This could still prove to be an interesting avenue of field research, but is fraught with multiple, uncontrolled variables in a tight window of opportunity. A similar study in which audio recordings are made over a series of nights in the lab prior to field release would help to determine if calling is individually consistent under controlled conditions and correlated with mating success in the field. It may also be interesting to record the calling behavior of penned males in the field for a week or more while monitoring mating status of the field at large.
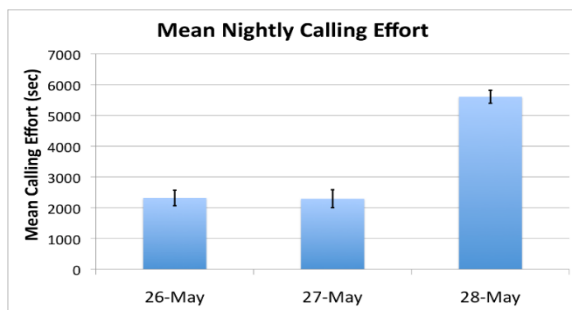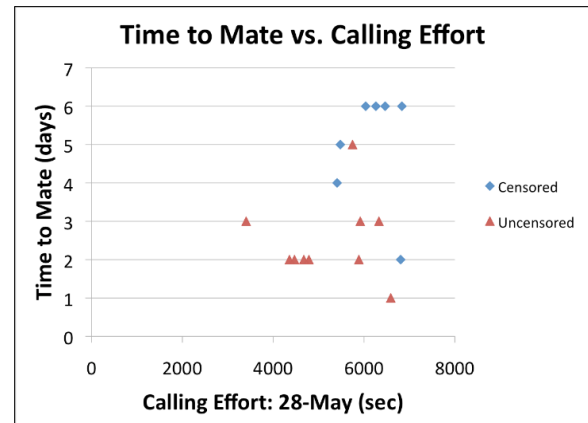

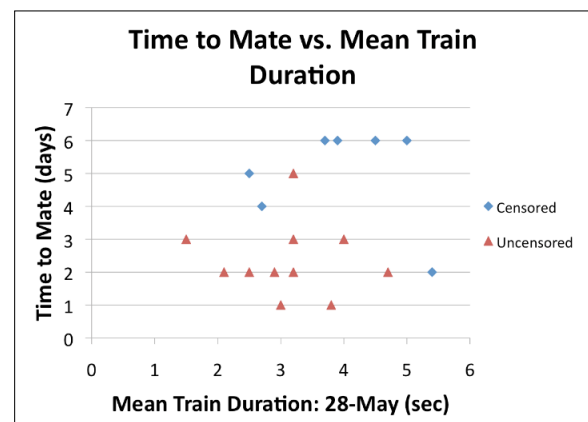**Figure 11.** Significant differences in mean calling effort by night.
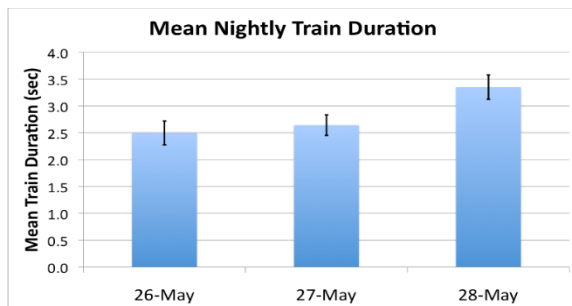
Figure 12. Significant differences in mean train duration by night.
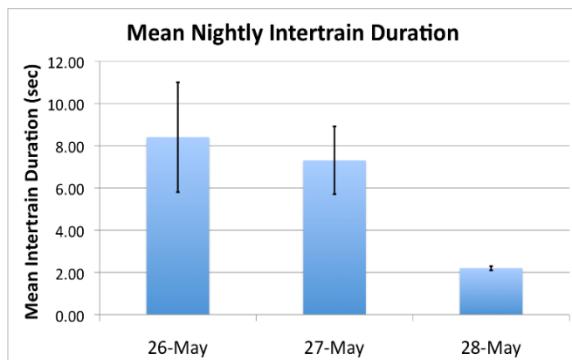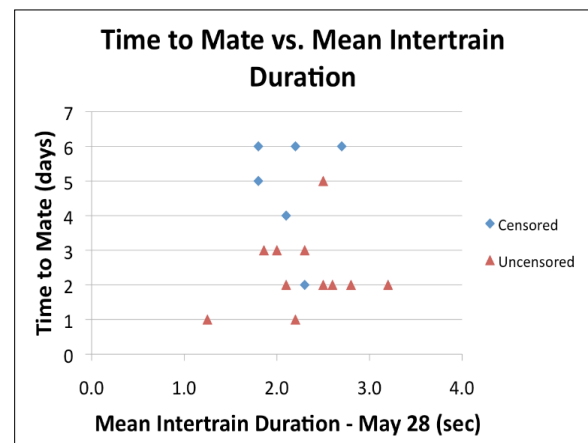

Figure 13. Significant differences in mean nightly intertrain duration.

Figure 14. No effect of calling effort on time to mate.

Figure 15. No effect of mean train duration on time to mate.

Figure 16. No effect of mean intertrain duration on time to mate.

✦ ACKNOWLEDEMENTS

✦ LITERATURE CITED

Johnson, J. Chadwick, and Gina Marie Hupton. 2011. Behavioral Syndromes in the Sagebrush Cricket: A Pilot Study to Quantify Individual Variation in Male Calling Behavior. University of Wyoming National Park Service Research Center Annual Report 34: 105-110.

Leman, J. C., et al. 2009. Lovesick: Immunological costs of mating to male sagebrush crickets. Journal of evolutionary biology 22(1): 163-171.

Steiger, Sandra, et al. 2013. Sexual selection on cuticular hydrocarbons of male sagebrush crickets in the wild. Proceedings of the Royal Society of London B: Biological Sciences 280(1773):2013.

Sakaluk, Scott K., et al. 2004. Hemolymph loss during nuptial feeding constrains male mating success in sagebrush crickets. Behavioral Ecology 15(5): 845-849.

Sakaluk, Scott K., and W. Andrew Snedden. 1990. Nightly calling durations of male sagebrush crickets, *Cyphoderris strepitans*: Size, mating and seasonal effects. Oikos (1990): 153-160.