ethology international journal of behavioural biology

Ethology

Fine- and Broad-Scale Approaches to Understanding the Evolution of Aggression in Crickets

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Received: June 15, 2011
Initital acceptance: August 5, 2011
Final acceptance: September 3, 2011
(S. Foster)

doi: 10.1111/j.1439-0310.2011.01970.x

Abstract

Male field crickets frequently engage in agonistic contests to establish dominance in social interactions and gain access to mate attraction territories. Crickets (Orthoptera: Gryllidae) are often used as a model taxon to study aggression, but limited documentation of aggression in some cricket species hinders our understanding of its evolutionary costs and benefits. Our study investigated cricket aggression at two scales: the within-species scale for two cricket species, *Gryllus assimilis* and *G. veletis*, whose aggression had not been adequately documented and the among-species scale to detect evolutionary patterns in species' levels of aggression. In both *G. veletis* and *G. assimilis*, winners spent more time being aggressive than losers, but they were not larger or heavier. Collectively, our results reveal that *G. veletis* males are more aggressive than *G. assimilis*. Male *G. veletis* had higher aggression scores that male *G. assimilis*. The majority of *G. veletis* contests escalated to grappling (a highly aggressive behavior), while less than one quarter of *G. assimilis* contests escalated to grappling. Further, *G. veletis* males transitioned between two of the most aggressive behaviors most often while *G. assimilis* transitioned between two of the least aggressive behaviors most often. We integrate this new information on aggression for *G. assimilis* and *G. veletis* with previously documented aggression data for many cricket species to investigate aggression in a broader evolutionary context than previously possible. Within a phylogenetic context, we test the hypothesis that species whose males use burrows from which to call and attract females are more aggressive than species with non-burrowing males. We found evidence consistent with this hypothesis; species with burrowing males tended to be more aggressive than species with non-burrowing males. Together, our study provides fine-scale understanding of aggression in two cricket species and broad-scale evolutionary context for aggression across cricket species.

Introduction

Agonistic contests are adaptive when the benefits of winning the contest (access to food, territory, or mates) outweigh the costs (energetic expenses, risk of injury, and loss of territory; Tachon et al. 1999). Darwin (1871) proposed that costs of aggression might be compensated by the benefits gained through subsequent reproduction. Supporting this idea, many researchers have found that females prefer to mate with contest winners (fish: Berglund & Rosenqvist 2001; reptiles: López et al. 2002; birds: Double & Cockburn 2003). For example, in male copperhead snakes contest winners are first to locate, court and guard females that observed the contest (Schuett 1997). Fighting potential can, therefore, directly influence subsequent reproductive success. Females can benefit from mating with contest winners by gaining protection or access to superior resources (Cordero & Eberhard 2003). When males offer females nothing more than their ejaculate, females may still gain genetic benefits for their offspring if sons who inherit their fathers' genes are more likely to win fights and gain access to limited resources (Shackleton et al. 2005). Given the potential impacts aggressive interactions can have on subsequent mate choice and fitness, it is important to understand the factors influencing aggression and contest outcome within and across species.

Given that aggressive behavior is costly, males in good condition should have more energy to sustain agonistic displays, allowing them to win more contests than males in poor condition (Shackleton et al. 2005; Brown et al. 2006). Likewise, larger males should be stronger and thus more able to defend themselves against smaller males, ultimately outcompeting them (Schuett 1997; Brown et al. 2006). These ideas have been supported by studies in diverse taxa (spiders: Kotiaho et al. 1997; birds: Hagelin 2002; lizards: López et al. 2002).

Here, we investigate factors influencing aggression and contest outcome in field crickets (Orthoptera: Gryllidae). Male field crickets frequently engage in agonistic contests to establish dominance in social interactions and gain access to mate attraction territories (Alexander 1961). Cricket agonistic contests are composed of a series of discrete, stereotypical and easily scored behaviors that increase in aggression and energy expenditure as the fight progresses (Alexander 1961; Hack 1997b). Fights typically escalate in a fixed sequence of mutual behaviors; however, any aggressive behavior can be performed at any time (Hofmann & Schildberger 2001; Bertram et al. 2010). Winners and losers can be clearly identified (Hofmann & Schildberger 2001).

Jang et al. (2008) published a comparative study of aggression and factors influencing contest outcome in four field cricket species (*G. fultoni, G. vernalis, G. pennsylvanicus*, and *G. rubens*). *Gryllus pennsylvanicus* and *G. rubens* were highly aggressive; there was always a clear winner, and the majority of contests escalated to grappling (83% in *G. pennsylvanicus* and 63% in *G. rubens*; Jang et al. 2008). A logistic regression revealed that contest outcome was influenced by male size and age, with larger and older males winning more contests than smaller and younger males (Jang et al. 2008). In contrast, *G. fultoni* and *G. vernalis* were much less aggressive; there was a clear winner in only 80% of the contests, and none of the contests escalated to grappling (Jang et al. 2008). Further, male size and age did not influence contest outcome. Together Jang et al.'s (2008) findings suggest that when a cricket species is highly aggressive, age and size influence fight outcome. Jang et al. (2008) did not quantify condition, so it is unknown how condition affected fight outcome. Other studies suggest that condition is important in determining the outcome of aggressive contests. For example, studies on the European house cricket *Acheta domesticus* have found contest winners are generally heavier (Hack 1997b) or heavier for their size (i.e., in better condition; Brown et al. 2006) than losers.

Here, we explore the factors influencing aggression and contest outcome in two field cricket species, field-captured and laboratory-reared spring field crickets (*G. veletis*) and laboratory-reared Jamaican field crickets (*G. assimilis*). We chose these two species because (1) there were no published data on aggression in *G. assimilis* (Jang et al. 2008) and (2) while there were some published data on aggression in *G. veletis*, the most comprehensive description of their aggression came from a study of five males reared together in a terrarium (Alexander 1961). Bertram et al. (2010) recently quantified aggression in naïve *G. veletis* (crickets that had never fought as adults), but their study focused on post-conflict displays rather than understanding the behavioral dynamics of the agonistic contest and quantifying the factors influencing contest outcome. Our research explores whether male size and condition explain any of the variation in fighting behavior, aggression, and contest outcome.

Using the aggression results for *G. assimilis* and *G. veletis* from our study, we compare aggression among cricket species in an evolutionary context, building upon the work of Jang et al. (2008). Jang et al. (2008) hypothesized that cricket species whose males use burrows from which they call to attract females would be more aggressive than species with non-burrowing males because burrows are fitness-related investments that should be defended aggressively from other males. Jang et al. (2008) also hypothesized that non-aggressive cricket species are closely related phylogenetically. We quantify the phylogenetic signal (i.e., how similar traits are among closely related species) for both aggression and burrowing behavior. We then test the hypothesis that species whose males use burrows are more aggressive than species whose males do not use burrows. Altogether, our study provides fine-scale understanding of aggression in two cricket species and broad-scale evolutionary context for aggression across many cricket species.

Methods

Collections and Cricket Care

We captured adult *G. veletis* in Ottawa, Ontario, Canada, in June 2008 and transported them back to our laboratory. Because captured males were of unknown age, mating status, and fighting status, they were held individually for 3 d prior to fighting to minimize effects of previous experience. We also fought the first generation laboratory-reared offspring of *G. veletis* we captured in June 2008. We captured adult *G. assimilis* in Austin, Texas, USA, in Sept. 2008 and transported them back to our laboratory. We were unable to fight these field-captured individuals because of time constraints, so we fought third generation laboratory-reared *G. assimilis*.

We set up communal containers, so we could create laboratory populations for each species. These containers were checked daily for males that had undergone final (imaginal) molt and reached adulthood. Upon reaching imaginal molt, each male was housed individually until day 14 of adulthood to (1) control social experiences, (2) ensure they were naïve virgins, and (3) allow them to mature well beyond the age at which they typically begin to produce acoustic mate attraction signals. Crickets were housed individually in clear plastic containers (11 cm diameter, 7 cm height) in a communal rearing room (controlled temperature = 25 ± 2°C; lighting = 12 h light:12 h dark cycle). Males were likely able to detect each other through acoustic and olfactory sensory modalities. Crickets were provided with *ad libitum* food (powdered Harlan Teklad Rodent diet #8604M) and water. Food and water were checked daily and replaced as required.

Agonistic Contests

Agonistic trials were conducted in a small, sand-covered Plexiglas arena (15 cm L × 15 cm W × 21 cm H) with two compartments separated by a removable divider. All trials were filmed from above using a color video camera (Canon Vixia HG10) mounted on a tripod. We covered the outside of the arena with white paper so that our presence did not disturb the crickets. We conducted trials between 10:00 and 12:00 h (3–5 h after the lights came on). We ran trials in the morning for two main reasons. First, we were limited in the timing of our trials with the field-caught crickets, because our nights were spent catching crickets in the field. Second, calling and mating activity has been shown to peak at and after dawn in several species of cricket, including *G. veletis* (French & Cade 1987), and thus, the morning likely represents an important time of day for males when motivation to fight is expected to be high.

Males were weighed using a Denver Instruments analytical balance (Pinnacle Series model PI-314). We placed a male in a small container to limit movement and then placed the container into the calibrated balance. Field-captured *G. veletis* were weighed the morning after we captured them; laboratory-reared *G. assimilis* and *G. veletis* were weighed on day seven post-imaginal molt. Immediately after weighing, *G. veletis* and *G. assimilis* opponents were weight-matched so that there was no more than a 25% difference in body mass between opponents. Opponents were weight-matched to increase the probability that they would fight because several studies have shown that opponent size difference can critically influence aggression and fight outcome in crickets (Hack 1997a; Jang et al. 2008). Males were not matched for differences in overall body size or head size, although both body size and head size correlate positively with body mass. Immediately following weighing, we painted each male's pronotum with a distinct color of nail polish to allow for easy identification during trials. Males were paired in agonistic trials beginning the day after they were weighed and marked. For field-captured and lab-reared *G. veletis*, we were limited in the number of trials we could run each day, so males were weighed 2 d before trials on average (range: 1–3 d; average age = day nine of adulthood for lab-reared *G. veletis*). We recorded trials with *G. assimilis* males on day 14 of adulthood (7 d after weighing) because we recorded the acoustic signaling behavior of these males continuously between days 7 and 14 as part of a separate experiment. All lab-reared males (*G. veletis* and *G. assimilis*) participated in an agonistic trial with a male of the same age.

Forty field-captured male *G. veletis* were paired in 20 experimental trials, 22 laboratory-reared males *G. veletis* were paired in 11 trials, and 124 laboratory-reared male *G. assimilis* were paired in 62 trials. Crickets were used in only one trial. We define a 'trial' as the time from when males were placed in the arena until the time males were removed. One male was placed on each side of the divider and given 2 min to acclimatize to the arena. The divider was then removed allowing the males to come into contact. Because agonistic behaviors are initiated after body contact (Jang et al. 2008), we define a 'contest' as the period of time from when males first came into body contact through to the establishment of clear dominance. Winners are easily identified because they typically chase the loser and often perform post-conflict victory displays (judder/body jerks, aggressive stridulation; Bertram et al. 2010; Logue et al. 2010), while losers retreat upon further contact (Alexander 1961; Hofmann & Schildberger 2001; Judge & Bonanno 2008; Bertram et al. 2010). We defined the end of the contest operationally as when one individual retreated in two consecutive encounters because we observed instances of dominance reversals in successive encounters in several contests. Cricket contests are typically comprised of short bursts of combat (termed 'encounters' in the present study) followed by longer periods of relative inactivity (Hack 1997b). Thus, a trial was the entire observation period, a contest was the period within a trial that the crickets were interacting and performing agonistic behaviors, and most contests were comprised of several agonistic encounters before clear dominance was established. Trials were terminated after the conclusion of the contest; once clear dominance was established between males, the fighting had ceased and all post-conflict displays had been completed. Individuals were identified as having won or lost their agonistic contest. Once a trial was completed, the walls of the arena were wiped with 95% ethyl alcohol, and the sand raked to minimize the chance of pheromones affecting future fights (Judge & Bonanno 2008).

The timing, duration, and frequency of all agonistic behaviors were scored for each individual by replaying the video in slow motion on a monitor. We quantified agonistic behavior of the contest participants following Adamo & Hoy (1995) and Jang et al. (2008). Our scale of aggressive behaviors ranged from zero to four: withdraw = zero; antennal fencing = one; kick = two; mandible spread, chase, mandible engagement, or bite = three; and grapple = four. We also noted when males performed aggressive stridulation and juddering (body jerks), behaviors thought to function as victory displays (Bertram et al. 2010; Logue et al. 2010), but these behaviors were not given an aggression score.

We quantified contest aggressiveness following Bertram et al. (2010). For each individual male, we quantified three values of aggressiveness (maximum aggression score, average aggression score, and aggression intensity score). 'Maximum aggression score' refers to the aggression score of the most aggressive behavior performed in a contest (zero to four). For each male, we then tallied the aggression scores for all behaviors performed during its contest and then calculated an 'average aggression score' (average aggression score = summed value of aggressive behaviors/total number of behaviors performed). Because many contests reach the most aggressive level (grappling) in *G. veletis*, variation in how much time individuals spend being aggressive can be masked if we only examine maximum aggression scores (Bertram et al. 2010). Given this, we also calculated weighted aggression scores to allow us to better tease apart individual differences in aggressive behavior. We multiplied each behavior's aggression score by the total number of seconds it was performed, resulting in weighted aggression scores for each agonistic act (Bertram et al. 2010). These weighted aggression scores were summed across all of the behaviors each individual performed in a contest. That sum was then divided by the contest duration to account for variable contest duration; this product was termed the 'aggression intensity score'. Refer to Bertram et al. (2010) for further details.

Measuring Condition and Size

Upon the conclusion of the experiments, males were euthanized (frozen), and their body size quantified using a Zeiss Discovery V12 inverted dissecting microscope and highly magnified photographs (AxioVision v4.8, Carl Zeiss; magnification: approx. 8.5×, resolution: approx. 1.60 μm). Size measurements included measures of head width and pronotum width, length, and area. These measures were incorporated into principal component (PC) analyses by population. The first principal component (PC1) was a good measure of overall size explaining 80–94% of variation, with larger individuals having higher PC1 size scores than smaller individuals (Table 1). Condition was quantified using the residuals from an allometric regression of body mass on body size (PC1), and residual head size was quantified from a regression of head size on body size. Residual mass and head size were used because this method standardizes mean residual condition and head size within each group to zero (Gray & Eckhardt 2001).

Agonistic Contest Statistical Analyses

We performed all statistical analyses for agonistic contests in JMP v8.0.2 (SAS, Cary, NC, USA). Values

Table 1: Results of principal component analyses for body size measurements in *Gryllus veletis* and *G. assimilis*. PC1 was a good measure of overall body size in all three populations; large males had high PC1 scores

Measure	*G. veletis* field	*G. veletis* lab	*G. assimilis* lab
Sample size (no. of individuals)	40	22	124
PC1 Eigenvalue	3.76	3.69	3.21
Variance explained by PC1 (%)	94.13	92.22	80.17
PC1 loadings			
Pronotum area	0.51	0.51	0.52
Pronotum length	0.50	0.50	0.51
Pronotum width	0.50	0.49	0.51
Head width	0.49	0.49	0.45

PC, principal component.

are given as mean ± standard error. Of the 93 contests recorded, 13 contests (4 *G. veletis* and 9 *G. assimilis*) had no clear winner and were therefore excluded from analyses. We used paired *t*-tests to determine whether winners were more likely to perform aggressive displays at higher rates or for longer durations than losers. We also used paired *t*-tests to determine whether winners were more aggressive, were larger (higher PC1 body size scores), had larger heads for their body size, or were in better condition than losers. Paired *t*-tests allowed us to block our data by fight, such that each pair consisted of the winner and the loser of one fight. We used a false discovery rate B-Y adjustment ($\alpha < 0.013$) to account for the 24 paired *t*-tests we performed to compare winners and losers within populations. We used the FDR_{BY} adjustment instead of the Bonferroni adjustment because the Bonferroni adjustment ($\alpha < 0.002$ for the 24 paired *t*-tests) has repeatedly been shown to be overly conservative (e.g., Benjamini et al. 2001; Nakagawa 2004; Narum 2006).

We compared aggressiveness among field-captured *G. veletis*, lab-reared *G. veletis*, and lab-reared *G. assimilis* using Analyses of Variance (ANOVA). We compared five metrics of aggression: maximum aggression score, average aggression score, the sum of weighted aggression scores, aggression intensity score (controlling for variable contest duration), and the amount of time males spent engaged in agonistic behaviors during contests. Each male represents a datum point in each of the five analyses. We used an FDR_{BY} adjustment ($\alpha < 0.022$) to account for the five ANOVA we performed to compare aggression among populations.

We performed Markov chain analysis to examine whether agonistic behaviors were performed in non-random sequences. We included eight behaviors in our analyses: antennal fencing, kick, mandible spread, chase, mandible engagement, grapple, aggressive song, and judder. We constructed transition matrices for winners and losers of *G. assimilis* and *G. veletis* fights, separated by laboratory-reared and field-captured males for *G. veletis* (six matrices total). The values for the matrix cells were the total number of transitions between one behavior and the following behavior (Chen et al. 2002; Jang et al. 2008). We performed a contingency analysis on each matrix to test whether the transition frequencies in the matrix differed from what we would expect by chance. For the matrices that were significantly different from expected, we examined each cell to determine which cells contributed to the overall significance (i.e., which behavioral transitions occurred more or less often than expected by chance).

Evolutionary Comparisons – Data Sources

Burrowing data were obtained from the literature when available and from experts who have observed crickets' habitat use in nature (*G. veletis*: Alexander & Bigelow 1960 and L. P. Fitzsimmons. pers. obs.; *G. bimaculatus*: Simmons 1986; *Teleogryllus oceanicus*: L. W. Simmons pers. comm.; *A. domesticus*: Hack 1997a; *G. assimilis*: D. B. Weissman pers. comm.; *G. integer*: Hedrick et al. 2002; *G. vernalis*: Jang & Gerhardt 2006; *G. campestris*: Hissmann 1990; Ritz & Köhler 2007; *G. texensis*: S. A. Adamo and W. H. Cade pers. comm., S. M. Bertram pers. obs.; *G. rubens*: Jang et al. 2008; *G. firmus*: Mitra et al. 2011). We asked experts to describe burrow and crack use in the species with which they were familiar, and we asked them to categorize burrowing behavior as rare, opportunistic, or frequent. For 10 cricket species, we were able to find information in the primary literature about burrow use, and for the remaining three species, we had to rely on expert opinion alone. Eliciting experts' opinions is a method of ecological research that is growing in popularity (Brook & McLachlan 2008), and studies have found general consistency among experts' opinions on ecological subjects (e.g., butterfly species' mobility, Burke et al. 2011). Reliability of the experts' opinions used in our research is suggested by the consensus between their opinions and the published literature for the cricket species for which both sources of burrowing information were available. We obtained species' aggression data from Jang et al. (2008) and references therein, except for *G. assimilis* and *G. veletis*, which we obtained from the results of our agonistic contests. We adopt the definition of Jang et al. (2008) in classifying species as aggressive if contests contained antennal fencing, mandible spreading, and grappling.

To compare levels of aggression across cricket species, we used a phylogenetic tree slightly modified from the one constructed by Huang et al. (2000) from two mitochondrial DNA loci. Previous evolutionary comparisons using this tree have ignored branch length data (e.g., Jang et al. 2008). We reconstructed the tree from Huang et al. (2000) by measuring branch lengths on their Fig. 3 with a ruler and replicating this tree using Mesquite version 2.74 (Maddison & Maddison 2010). *Gryllus vernalis* was not included in Huang et al.'s (2000) tree. We followed Jang et al.'s (2008) precedent in adding *G. vernalis* branching off from *G. veletis*. Jang et al.'s (2008) tree did not include branch lengths, so we added the node splitting *G. vernalis* and *G. veletis* halfway down the *G. veletis* branch obtained from Huang et al. (2000). We used this phylogenetic tree for analyses of phylogenetic signal and phylogenetically explicit analyses of the relationship between species' burrowing behavior and aggression. The phylogenetic tree is available as a supporting file in Newick format (Supp Data. S1), or in Nexus format from the authors.

Evolutionary Comparisons – Statistical Analyses

We used the phylogenetic tree described previously to test whether there is a phylogenetic signal for either aggression or burrowing behavior among the 13 cricket species in the tree for which we have behavioral data. Variance–covariance matrices of phylogenetic distances were generated with PDAP (Midford et al. 2010) within Mesquite. Species' aggression was coded as a zero/one binary variable, with zero representing non-aggressive and one representing aggressive. We used the program PLogReg (Ives & Garland 2010) within Matlab version 7.0.4.365 to test for phylogenetic signal of aggression with default settings (i.e., 2000 randomizations, Firth correction, and $\alpha = 0.05$). PLogReg randomizations preserve the structure of trees while swapping species' values to determine whether closely related species are more likely to have the same level of aggression than distantly related species, following an Ornstein–Uhlenbeck model of evolution (Ives & Garland 2010). Burrowing behavior was coded as zero, one, or two corresponding to rare or no burrow and crack use, opportunistic burrow and crack use, and frequent burrowing behavior. We are not aware of any method to quantify phylogenetic signal in an ordinal variable, so we considered burrowing a continuous variable and estimated its phylogenetic signal with Regressionv2 (Lavin et al. 2008) in Matlab. Regressionv2 allows comparison of the fit of phylogenetic trees to the burrowing data set corresponding to a star-shaped phylogeny (i.e., no phylogenetic signal) and trees constructed according to each of five different models of evolution. Each evolutionary model makes different assumptions (for details on the models see Garland et al. 2005; Lavin et al. 2008).

We determined whether comparison of species' burrowing behavior and aggression violated assumptions of phylogenetic non-independence. Because we analyzed the relationship between two traits among species, we accounted for phylogenetic autocorrelation to reduce Type I error rates (Rohlf 2006). This is necessary even if neither trait exhibits a phylogenetic signal, because it is phylogenetic non-independence of model residuals, rather than phylogenetic non-independence of the traits, that violates assumptions made in traditional ordinary least squares analyses (Ives & Zhu 2006). We thus determined whether the residuals in our comparison of species' aggression (binary response variable) and burrowing behavior (three-class categorical predictor variable) had a phylogenetic signal using PLogReg with default settings. This analysis revealed no phylogenetic signal among residuals ($\alpha = -2.46$; confidence interval = −4–0.53; null hypothesis of $\alpha = -4$ corresponding to no signal; $p = 0.45$), allowing us to analyze the relationship between burrowing behavior and aggression with traditional methods that give easily interpretable results. We repeated this analysis with burrowing behavior coded as a binary variable, and it produced similar results (not shown), suggesting the assumption of phylogenetic independence of residuals was robust to variable classification methods.

Given the phylogenetic independence of residuals, we analyzed the relationship between species' burrowing behavior and aggression in a traditional 2×3 contingency table (aggression scored using two states and burrowing scored using three states) to determine whether the traits were independent of each other. Our small sample size prohibited the use of a χ^2 test, so we instead used the Freeman–Halton extension (used for contingency tables larger than 2×2) of Fisher's exact probability test using VassarStats (http://faculty.vassar.edu/lowry/VassarStats.html). Our analysis considered burrowing behavior categories to be independent, while in reality, one

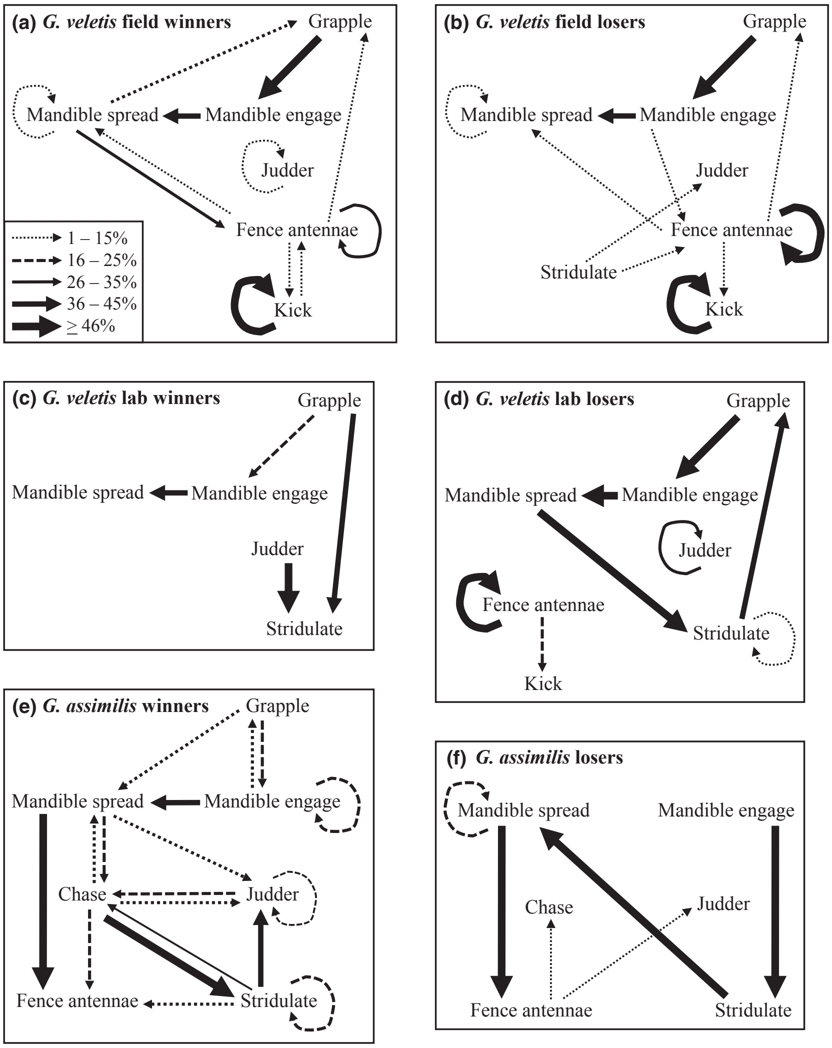

Fig. 1: Markov chain diagrams for agonistic contests in field crickets. (a) *Gryllus veletis* field-caught winners (N = 579 total transitions), (b) *G. veletis* field-caught losers (N = 344), (c) *G. veletis* lab-reared winners (N = 79), (d) *G. veletis* lab-reared losers (N = 69), (e) *G. assimilis* winners (N = 888), (f) *G. assimilis* losers (N = 192). Arrows represent transitions from one behavior (start of arrow) to the following behavior (pointed end), with the probability of that transition indicated by the thickness of the line. Curved arrows that start and end at the same behavior signify that behavior was repeated consecutively. Transitions that were not significantly different than expected by chance are not included in the diagrams.

category (opportunistic burrowers) is intermediate between the other two. To determine the sensitivity of results to our classification of opportunistic burrowing behavior, we repeated Fisher's exact probability tests with burrowing behavior classified as a binary variable in three different 2 × 2 contingency tables with opportunistic burrowers omitted, binned with burrowers, or binned with non-burrowers. Fisher's exact probability tests provide results on statistical significance, but do not provide effect sizes that are integral to understanding the nature of biological relationships (Nakagawa & Cuthill 2007). We thus calculated the relative risk (risk ratio) of how much more probable a species is to be aggressive if it is a burrower than if it is a non-burrower. For this analysis, opportunistic burrowers were omitted.

Results

Fight Descriptions

For *G. veletis* field-captured males, 19 of 20 trials (95%) had a clear winner and loser. Of the 19 contests with a clear winner, 11 (58%) escalated to grappling, the most aggressive behavior in our scoring scheme. The other eight contests escalated to mandible spreading, chases, and mandible engagements. In comparison, eight of 11 trials (73%) had a clear winner and loser for *G. veletis* F1 lab-reared males. Of these eight contests with a clear winner, 5 (63%) escalated to grappling; the other three contests escalated to mandible spreading, chases, and biting. Thus, a similar proportion of contests escalated to grappling in both field-captured and lab-reared

G. veletis. Most of the *G. assimilis* trials had clear winners (53 of 62 or 85%), but only 12 of 53 (23%) of the contests escalated to grappling; the other 41 contests escalated to mandible spreading and engagement, chasing, and biting.

Most males performed aggressive behaviors in a particular order, moving from least aggressive interactions (e.g., antennation and antennal fencing) to most aggressive interactions (e.g., mandible engagement and grappling/wrestling). At any point, males could disengage from physical contact, either to chase their opponent, perform aggressive stridulation, and/or perform body jerk displays. In field-captured *G. veletis*, the aggressive behaviors observed most often (in rank order) were antennation, stridulation, mandible spreading, mandible engagement, grappling, and chasing (Table 2). The order was similar for laboratory-reared *G. veletis* crickets except they spent more time spreading their mandibles and juddering but grappled less often. For *G. assimilis*, crickets spent most time stridulating and spreading their mandibles, less time juddering, antennating, and chasing, and little to no time grappling and kicking.

Our comparisons of aggression between species revealed that male *G. veletis* were more aggressive than *G. assimilis* (Table 3). For four of the five aggression metrics we compared, both field-caught and lab-reared *G. veletis* scores were higher than *G. assimilis* scores (Table 3). For the fifth metric, lab-reared *G. veletis* had lower aggression intensity scores than *G. assimilis* and field-captured *G. veletis* (Table 3). For two of the aggression scores (maximum aggression and weighted aggression), field-captured *G. veletis* males had higher scores than *G. assimilis* males, but lab-reared *G. veletis* were not statistically different than either *G. assimilis* or field-captured *G. veletis* (Table 3). This may be the result of a relatively small sample size for lab-reared *G. veletis* reducing the power of significance testing. Overall, our results indicated that *G. veletis* males were more aggressive than *G. assimilis*, and within *G. veletis*, the field-captured males tended to be more aggressive than lab-reared males.

Table 2: Each population's proportion of time spent engaged in the different agonistic behaviors

Behavior	*Gryllus veletis* field	*G. veletis* lab	*G. assimilis* lab
Antennation	38.68	31.91	12.64
Stridulation	33.26	26.88	33.47
Mandible spread	10.03	28.06	22.35
Mandible engagement	6.85	2.61	5.45
Grapple	5.83	1.80	0.62
Chase	3.51	3.54	10.91
Judder	1.55	4.90	14.57
Kick	0.29	0.31	0.00

Winners vs. Losers

Gryllus assimilis winners tended to be more aggressive than losers (Table 4). Winners had higher average aggression scores than losers. There were also non-significant trends for winners to have higher aggression intensity scores and higher maximum aggression scores ($p = 0.08$, $p = 0.06$ respectively; Table 4). Further, winners spent more time being aggressive than losers. Laboratory-reared *G. veletis* winners tended to spend more time being aggressive than losers ($p = 0.03$; not significant after correction for multiple hypothesis testing), but field-captured *G. veletis* did not differ. *Gryllus veletis* winners did not differ from losers in their scores for average aggression, aggression intensity, and maximum aggression (Table 4). Winners were not larger, heavier, or in better condition than losers in either of the species examined (Table 4).

Markov Chain Analysis

For both winners and losers of *G. assimilis* and *G. veletis* agonistic contests, first-order Markov chain analysis identified non-random associations between

Table 3: Comparison of aggression metrics among populations using ANOVA. See text for descriptions of aggression scores

Parameter	*Gryllus veletis* field	*G. veletis* lab	*G. assimilis* lab	$F_{2,157}$	p
Maximum aggression score	3.53 ± 0.09^{A}	3.50 ± 0.14^{AB}	3.17 ± 0.06^{B}	6.53	0.0019
Average aggression score	2.51 ± 0.07^{A}	2.79 ± 0.11^{A}	2.30 ± 0.04^{B}	10.48	<0.0001
Sum of weighted aggression scores	309.24 ± 29.80^{A}	238.81 ± 45.93^{AB}	135.20 ± 17.84^{B}	13.26	<0.0001
Aggression intensity score	2.45 ± 0.08^{A}	1.84 ± 0.12^{B}	2.34 ± 0.05^{A}	9.62	<0.0001
Duration of aggressive behavior (s)	134.53 ± 15.82^{A}	146.44 ± 24.38^{A}	54.92 ± 9.47^{B}	13.08	<0.0001

Populations with different superscript letters are statistically different using *post hoc* Tukey–Kramer tests. All ANOVA are significant after correction for multiple tests (FDR_{BY} adjusted $\alpha < 0.022$).

Table 4: Differences between contest winners and losers for the Jamaican field cricket (*Gryllus assimilis*) and the spring field cricket (*G. veletis*)

Species	Parameter	Winners	Losers	*t*	p	df
G. assimilis lab-reared	Average aggression score	**2.41 ± 0.03**	**2.19 ± 0.06**	3.71	0.0005	52
	Aggression intensity score	2.40 ± 0.04	2.27 ± 0.07	1.79	0.0788	52
	Maximum aggression score	3.23 ± 0.06	3.11 ± 0.08	1.95	0.0570	52
	Aggression time (s)	**83.10 ± 8.59**	**26.73 ± 4.98**	8.97	<0.0001	52
	Body size (PC1)	0.11 ± 0.25	−0.11 ± 0.24	1.28	0.2075	51
	Body weight (mg)	475.04 ± 8.92	468.87 ± 8.89	1.76	0.0848	52
	Condition (residual mass)	−1.41 ± 6.34	1.38 ± 6.20	−0.77	0.4478	51
	Head width (residual)	0.02 ± 0.09	−0.02 ± 0.09	0.82	0.4147	51
G. veletis field-caught	Average aggression score	2.51 ± 0.09	2.51 ± 0.12	0.03	0.9797	18
	Aggression intensity score	2.48 ± 0.08	2.42 ± 0.12	0.86	0.3998	18
	Maximum aggression score	3.58 ± 0.12	3.47 ± 0.18	1.00	0.3306	18
	Aggression time (s)	141.00 ± 21.90	128.05 ± 43.07	0.45	0.6548	18
	Body size (PC1)	0.14 ± 0.49	−0.14 ± 0.48	0.89	0.3873	14
	Body weight (mg)	350.70 ± 12.16	358.05 ± 13.47	−0.78	0.4458	18
	Condition (residual mass)	−5.76 ± 3.06	2.22 ± 6.35	−0.86	0.4021	14
	Head width (residual)	−0.42 ± 0.09	−0.62 ± 0.09	0.55	0.5877	14
G. veletis lab-reared	Average aggression score	2.79 ± 0.18	2.79 ± 0.30	−0.03	0.9779	7
	Aggression intensity score	1.65 ± 0.23	2.03 ± 0.31	−0.98	0.3591	7
	Maximum aggression score	3.63 ± 0.18	3.38 ± 0.38	1.00	0.3506	7
	Aggression time (s)	178.63 ± 58.29	114.25 ± 55.90	2.71	0.0303	7
	Body size (PC1)	0.13 ± 0.89	−0.13 ± 0.42	0.44	0.6729	7
	Body weight (mg)	374.53 ± 27.87	371.25 ± 19.11	0.22	0.8338	7
	Condition (residual mass)	4.11 ± 7.80	2.98 ± 10.03	0.10	0.9212	7
	Head width (residual)	1.31 ± 0.09	0.38 ± 0.09	0.88	0.4082	7

PC, principal component.

Significant differences between winners and losers are bolded. We accounted for multiple tests using $\mathrm{FDR}_{\mathrm{BY}}$ adjusted $\alpha < 0.013$.

behavioral transitions (Fig. 1; likelihood ratio test: $\chi^2 = 404$, df = 36, $p < 0.001$ for *G. assimilis* winners; $\chi^2 = 110$, df = 30, $p < 0.001$ for *G. assimilis* losers; $\chi^2 = 92$, df = 49, $p < 0.001$ for *G. veletis* laboratory-reared winners; $\chi^2 = 89$, df = 36, $p < 0.001$ for *G. veletis* laboratory-reared losers; $\chi^2 = 261$, df = 49, $p < 0.001$ for *G. veletis* field-caught winners; $\chi^2 = 239$, df = 42, $p < 0.001$ for *G. veletis* field-caught losers). The highest probability of the first-order transition was different in each group we analyzed, but species differences were evident when comparing the two most frequently performed transitions. Among *G. assimilis* winners, the highest probability of the first-order transition was from mandible spreading to antennal fencing (65.3%), and this transition had the second highest probability for *G. assimilis* losers (57.5%). In *G. veletis*, the transition from grappling to mandible engagement was the transition with either the first or second highest probability for both winners and losers in the laboratory-reared and field-caught males (range: 49.0–88.9%). Thus, *G. assimilis* performed mandible spreading and antennal fencing, which are low to moderately aggressive behaviors, more often than expected by chance, whereas *G. veletis* performed the highly aggressive grappling and mandible engagement more often than expected by chance. Other transitions with high-level probabilities differed between species (see Fig. 1), but often ended with aggressive stridulation.

Phylogenetic Signal

Aggression did not have a phylogenetic signal ($\alpha = -3.06$; confidence interval = −4.00 to −0.67; null hypothesis of $\alpha = -4$ corresponding to no signal; p = 0.52). Likewise, burrowing behavior did not have a phylogenetic signal; the star-shaped phylogeny corresponding to no phylogenetic signal had AIC values 2.0 lower than any phylogenetic model (i.e., it was a better fit). This corresponds to an evidence ratio of 2.72, which can be interpreted as no phylogenetic signal being 2.72 times more likely than phylogenetic signal for burrowing. Thus, neither aggression nor burrowing behavior was more similar among closely- than distantly-related species (Fig. 2). These results should be interpreted with caution because we could only analyze 13 species; analyses with such small sample sizes can fail to detect phylogenetic signal (Blomberg et al. 2003).

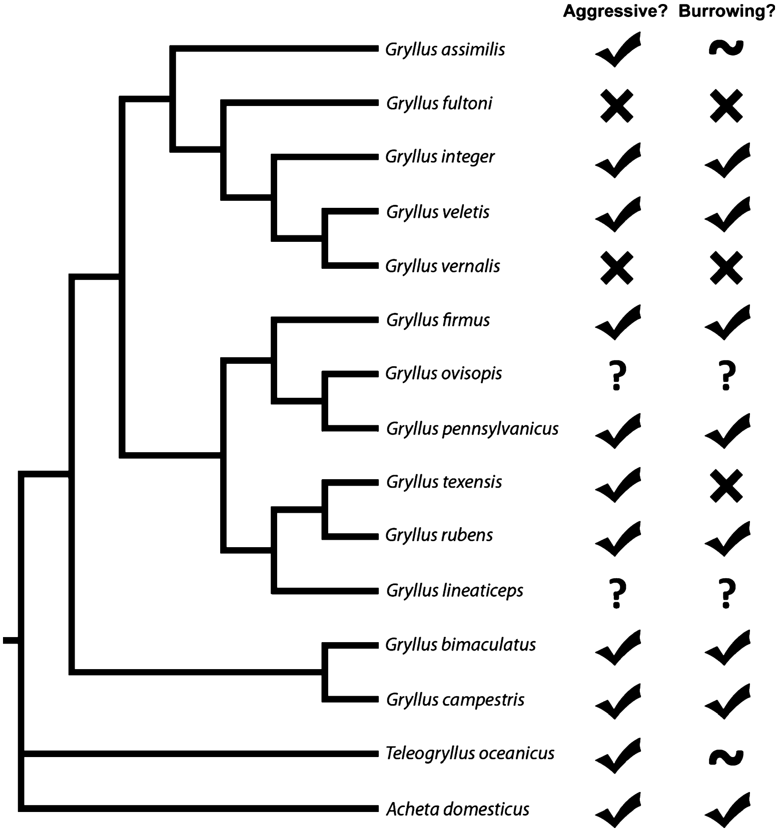

Fig. 2: Phylogenetic tree of the 15 cricket species used in our analyses, showing each species' aggression and burrowing behavior. A checkmark represents yes, X represents no, question mark represents no data, and ∼ represents opportunistic, occasional burrow or crack use. Note that this tree has been ultrametricized (i.e., branch length data removed) to have all species' tips flush for the purpose of this figure, but our analyses used this tree with accurate branch lengths.

Relationship Between Aggression and Burrowing

Cricket species that burrow tended to be more aggressive than those that do not, but whether this relationship was significant depended on how we coded opportunistic burrow and crack use. The relationship was significant when the two opportunistic burrowing species were binned with burrowers ($p = 0.0385$), but not when binned with non-burrowers ($p = 0.1282$), omitted from analyses ($p = 0.0545$), or considered a distinct category ($p = 0.0513$). Omitting opportunistic burrowers, we calculated a relative risk of aggression for burrowing species as 3.0, indicating burrowing species were three times more likely to be aggressive than were non-burrowing species.

Discussion

Spring field crickets, *G. veletis*, were more aggressive than Jamaican field crickets, *G. assimilis.* We observed grappling in the majority of *G. veletis'* contests (58% of field-captured and 63% of laboratory-reared contests), but grappling was detected in less than one quarter of *G. assimilis'* contests (23% of contests). Overall, *G. veletis* males had higher aggression scores than *G. assimilis*, and within *G. veletis*, the field-captured males tended to be more aggressive than the lab-reared males. *Gryllus veletis* males transitioned most often from grappling to mandible engagement, which are two of the most aggressive behaviors, while the most frequent transition in *G. assimilis* was from mandible spreading to antennal fencing, two of the less-aggressive behaviors.

Winners vs. Losers

Theoretically, body condition should predict contest outcome because males in better condition should be able to allocate more energy to aggressive behaviors and therefore last longer in a contest because they have a higher resource-holding potential (Moretz 2003; Shackleton et al. 2005). Several cricket species provide support for this hypothesis, as larger or heavier males are more likely to win contests against smaller or lighter males (Jang et al. 2008). However, mass and size differences do not always affect contest outcome, as they do not predict who will win contests in *G. fultoni, G. vernalis,* and *G. rubens* (Jang et al. 2008). Our *G. assimilis* and *G. veletis* results did not provide direct support for the hypothesis that body condition is predictive of contest outcome, as winners were neither significantly heavier (mass), larger (body size), nor in better condition (residual mass) than losers. This result may be an artifact of our study having weight-matched opponents. We weight-matched opponents to increase the odds that a fight would occur, as aggressive encounters with large size/mass differences often result in immediate dominance (Robertson 1986; Olsson 1992; Brown et al. 2006). A formal test of the hypothesis that individuals in better condition win more fights may require a more precise measure of condition than residual mass. One such measure would involve performing fat extraction on males following contests, which would likely provide a better indication of energetic reserves than mass alone.

The size of males' weaponry can also influence contest outcome. Field cricket head size, mandible size, and maxillae size are sexually dimorphic in crickets (Judge & Bonanno 2008). Heads, mandibles, and maxillae are thought to act as weapons during agonistic contests because most escalated contests include mouthpart grappling. Further, contest outcome is influenced by bite force in several non-cricket species (Sneddon et al. 2000; Husak et al. 2006), which is in turn influenced by weapon size (Sneddon et al. 2000; Lappin & Husak 2005). These findings suggest that weapon size may be an important indicator of contest outcome (Judge & Bonanno 2008). In support of this idea, Judge & Bonanno (2008) revealed that male head width was the best predictor of contest outcome. Using weight-matched fall field crickets, *G. pennsylvanicus*, Judge & Bonanno (2008) found that males with larger weapons won more aggressive contests than males with smaller weapons. Further, the probability that a male with larger weapons would win the aggressive contest increased as the magnitude of the difference in weapon size increased (Judge & Bonanno 2008). Because head size may be an important indicator of fight outcome, we quantified male head size relative to body size (residual head size) and then determined whether winners had relatively larger heads than losers. Winners and losers did not differ significantly in their relative head size. Together, our head, condition, and body size findings provide no clear indication of why some males win fights and others lose them.

Our results do, however, indirectly support the hypothesis that winners allocate more energy to aggressive behaviors than losers. Laboratory-reared *G. veletis* and *G. assimilis* winners were aggressive for longer periods of time during contests than losers. Further, *G. assimilis* winners reached higher levels of aggression than losers. Given aggressive behaviors are energetically costly to maintain and costs escalate with increasing aggressiveness (Hack 1997b), our findings suggest that winners may have higher resource-holding potential than losers.

Comparing Aggression Across Species

Gryllus veletis' aggression levels appear similar to those of fall field crickets, *G. pennsylvanicus*, and southeastern field crickets, *G. rubens*, as most of their agonistic contests also escalated to grappling (76% and 62%, respectively; Jang et al. 2008). The agonistic contests of *G. assimilis* did not quite reach the level of aggression of *G. pennsylvanicus*, *G. rubens*, or *G. veletis*, as only 23% of their fights escalated to grappling. Agonistic contests of *G. assimilis* appear to be intermediate between the more aggressive species mentioned previously and relatively less-aggressive southern and northern wood crickets, *G. fultoni* and *G. vernalis*. While these wood crickets will engage in agonistic contests, they have not been observed to grapple (Jang et al. 2008).

Most biological traits are more similar among closely- than distantly-related species, but behavioral traits tend to have weaker phylogenetic signal than do physiological or other traits (Blomberg et al. 2003). Because of these general trends, our *a priori* expectation was that aggression would show a weak phylogenetic signal. Jang et al.'s (2008) qualitative observations suggested that the few non-aggressive *Gryllus* species are somewhat closely related; visual inspection of our phylogenetic tree reveals this apparent pattern (Fig. 2). However, our phylogenetic signal results suggest closely-related species are no more similar with respect to aggression than are distantly-related species. This finding should be treated with caution, however, because we were only able to include 13 species in our analyses. Overall, the question of whether aggression has a phylogenetic pattern among cricket species requires more species' data for a conclusive answer.

We tested Jang et al.'s (2008) hypothesis that species whose males compete for limited signaling sites (i.e., burrows) should be more aggressive than non-burrowing species. We found some evidence consistent with this hypothesis. Burrowing species tend to be aggressive, but whether this trend was significant or not depended on how we classified species that only burrow opportunistically. Both of the opportunistically burrowing species (*G. assimilis* and *T. oceanicus*) are aggressive, resulting in a significant relationship between burrowing and aggression when these two species were classified as burrowers. However, when opportunistically burrowing species were classified as non-burrowers or excluded from the analysis, the relationships between burrowing and aggression were not quite significant.

Jang et al. (2008) noted that both of the non-aggressive species in their (and our) analyses (*G. fultoni* and *G. vernalis*) are non-burrowers and speculated that species with burrows may have greater incentive than species with roaming (non-burrowing) males to be aggressive to defend their territory from other males. Thus, selection may act in favor of aggression in species in which burrowing site defense influences mating success and against aggression in species without burrow sites if the costs of aggression outweigh its benefits. Jang et al. (2008) did not include *G. texensis* in their analysis. *Gryllus texensis* appears to contradict Jang et al.'s (2008) prediction because it is an aggressive species that only rarely signals from cracks or burrows (W. H. Cade and S. Adamo pers. comm.; S. M. Bertram. pers obs.). We classified it as a non-burrower because of the rarity of its burrow use but it could also be considered an occasional burrow and crack user. Classifying continuous complex behaviors as discrete categories is imprecise but necessary when data are limited. For example, our study reveals that *G. veletis* is more aggressive than *G. assimilis*, but both species were categorized simply as 'aggressive' for phylogenetic analyses, along with several other species that vary in the intensity of aggressive behavior. When possible, researchers should classify and analyze continuous behaviors as such to retain the fine-scale variation that exists between individuals and species, which may allow a more refined understanding of the relationships between behaviors. Given the limited data available, our analyses suggest there may be a relationship between burrowing and aggression. Future research could investigate the relationship between burrowing and aggression with more precise (i.e., continuous) data. Natural history research on additional cricket species' aggression and burrowing behaviors may further clarify the relationship between burrowing and aggression, thus revealing potential costs and benefits to aggression.

Acknowledgements

This work was supported by a Natural Science and Engineering Research Council of Canada (NSERC) Canada Graduate Scholarship to LPF, a NSERC Discovery Grant to SMB, a Carleton University start up Grant to SMB, a Canadian Foundation of Innovation Grant to SMB, and an Ontario Research Fund Grant to SMB. Special thanks to A. Agarwal, A. Rouble, and H. Bocz for their help with video analysis.

Literature Cited

Adamo, S. A. & Hoy, R. R. 1995: Agonistic behaviour in male and female crickets, *Gryllus bimaculatus*, and how behavioural context influences its expression. Anim. Behav. **49**, 1491—1501.

Alexander, R. D. 1961: Aggressiveness, territoriality, and sexual behavior in field crickets (Orthoptera: Gryllidae). Behaviour **17**, 130—223.

Alexander, R. D. & Bigelow, R. S. 1960: Allochronic speciation in field crickets, and a new species, *Acheta veletis*. Evolution **14**, 334—346.

Benjamini, Y., Drai, D., Elmer, G., Kafkadi, N. & Golani, I. 2001: Controlling the false discovery rate in behavior genetics research. Behav. Brain Res. **125**, 279—284.

Berglund, A. & Rosenqvist, G. 2001: Male pipefish prefer dominant over attractive females. Behav. Ecol. **12**, 402—406.

Bertram, S. M., Rook, V. L. M. & Fitzsimmons, L. P. 2010: Strutting their stuff: victory displays in the spring field cricket, *Gryllus veletis*. Behaviour **147**, 1249—1266.

Blomberg, S. P., Garland, T. J. & Ives, A. R. 2003: Testing for phylogenetic signal in comparative data: behavioral traits are more labile. Evolution **57**, 717—745.

Brook, R. K. & McLachlan, S. M. 2008: Trends and prospects for local knowledge in ecological and conservation research and monitoring. Biodivers. Conserv. **17**, 3501—3512.

Brown, W. D., Smith, A. T., Moskalik, B. & Gabriel, J. 2006: Aggressive contests in house crickets: size, motivation and the information content of aggressive songs. Anim. Behav. **72**, 225—233.

Burke, R. J., Fitzsimmons, J. M. & Kerr, J. T. 2011: A mobility index for Canadian butterfly species based on naturalists' knowledge. Biodivers. Conserv. **20**, 2273—2295.

Chen, S., Lee, A. Y., Bowens, N. M., Huber, R. & Kravitz, E. A. 2002: Fighting fruit flies: a model system for the study of aggression. Proc. Natl Acad. Sci. U.S.A. **99**, 5664—5668.

Cordero, C. & Eberhard, W. G. 2003: Female choice of sexually antagonistic male adaptations: a critical review of some current research. J. Evol. Biol. **16**, 1—6.

Darwin, C. R. 1871: The Descent of Man and Selection in Relation to Sex. John Murray, London.

Double, M. C. & Cockburn, A. 2003: Subordinate superb fairy-wrens (*Malurus cyaneus)* parasitize the reproductive success of attractive dominant males. Proc. Roy. Soc. Lond. B **270**, 379—384.

French, B. W. & Cade, W. H. 1987: The timing of calling, movement, and mating in the field crickets *Gryllus veletis*, *G. pennsylvanicus*, and *G. integer*. Behav. Ecol. Sociobiol. **21**, 157—162.

Garland, T. J., Bennett, A. F. & Rezende, E. L. 2005: Phylogenetic approaches in comparative physiology. J. Exp. Biol. **208**, 3015—3035.

Gray, D. A. & Eckhardt, G. 2001: Is cricket courtship song condition dependent? Anim. Behav. **62**, 871—877.

Hack, M. A. 1997a: Assessment strategies in the contests of male crickets, *Acheta domesticus* (L.). Anim. Behav. **53**, 733—747.

Hack, M. A. 1997b: The energetic costs of fighting in the house cricket, *Acheta domesticus* L. Behav. Ecol. **8**, 28—36.

Hagelin, J. C. 2002: The kinds of traits involved in male-male competition: a comparison of plumage, behavior, and body size in quail. Behav. Ecol. **13**, 32—41.

Hedrick, A. V., Perez, D., Lichti, N. & Yew, J. 2002: Temperature preferences of male field crickets (*Gryllus integer*) alter their mating calls. J. Comp. Physiol. A. **188**, 799—805.

Hissmann, K. 1990: Strategies of mate finding in the European field cricket *Gryllus campestris* at different population densities a field study. Ecol. Entomol. **15**, 281—292.

Hofmann, H. A. & Schildberger, K. 2001: Assessment of strength and willingness to fight during aggressive encounters in crickets. Anim. Behav. **62**, 337—348.

Huang, Y., Ortí, G., Sutherlin, M., Duhachek, A. & Zera, A. 2000: Phylogenetic relationships of North American field crickets inferred from mitochondrial DNA data. Mol. Phylogenet. Evol. **17**, 48—57.

Husak, J. F., Lappin, A. K., Fox, S. F. & Lemos-Espinal, J. A. 2006: Bite-force performance predicts dominance in male venerable collared lizards (*Crotaphytus antiquus*). Copeia **2006**, 301—306.

Ives, A. R. & Garland, T. J. 2010: Phylogenetic logistic regression for binary dependent variables. Syst. Biol. **59**, 9—26.

Ives, A. R. & Zhu, J. 2006: Statistics for correlated data: phylogenies, space, and time. Ecol. Appl. **16**, 20—32.

Jang, Y. & Gerhardt, H. C. 2006: Divergence in the calling songs between sympatric and allopatric populations of the southern wood cricket *Gryllus fultoni* (Orthoptera: Gryllidae). J. Evol. Biol. **19**, 459—472.

Jang, Y., Gerhardt, H. C. & Choe, J. C. 2008: A comparative study of aggressiveness in eastern North American field cricket species (genus *Gryllus*). Behav. Ecol. Sociobiol. **62**, 1397—1407.

Judge, K. A. & Bonanno, V. L. 2008: Male weaponry in a fighting cricket. PLoS One **3**, e3980.

Kotiaho, J., Alatalo, R. V., Mappes, J. & Parri, S. 1997: Fighting success in relation to body mass and drumming activity in the male wolf spider *Hygrolycosa rubrofasciata*. Can. J. Zool. **75**, 1532—1535.

Lappin, A. K. & Husak, J. F. 2005: Weapon performance, not size, determines mating success and potential reproductive output in the collared lizard (*Crotaphytus collaris*). Am. Nat. **166**, 426—436.

Lavin, S. R., Karasov, W. H., Ives, A. R., Middleton, K. M. & Garland, T. J. 2008: Morphometrics of the avian small intestine compared with that of nonflying mammals: a phylogenetic approach. Physiol. Biochem. Zool. **81**, 526—550.

Logue, D. M., Abiola, I. O., Rains, D., Bailey, N. W., Zuk, M. & Cade, W. H. 2010: Does signalling mitigate the cost of agonistic interactions? A test in a cricket that has lost its song. Proc. Roy. Soc. Lond. B **277**, 2571—2575.

López, P., Muñoz, A. & Martín, J. 2002: Symmetry, male dominance, and female mate preferences in the Iberian rock lizard, *Lacerta monticola*. Behav. Ecol. Sociobiol. **52**, 342—347.

Maddison, W. P. & Maddison, D. R. 2010: Mesquite: a modular system for evolutionary analysis. http://mesquiteproject.org Version 2.74.

Midford, P. E., Garland, T. J. & Maddison, W. P. 2010: PDAP package. http://mesquiteproject.org/pdap_mesquite/ Version 1.15.

Mitra, C., Wagner, W. E., Zera, A. J. & Tolle, A. E. 2011: Variation in singing behaviour among morphs of the sand field cricket, *Gryllus firmus*. Ecol. Entomol. **36**, 152—160.

Moretz, J. A. 2003: Aggression and RHP in the Northern swordtail fish, *Xiphophorus cortezi*: the relationship between size and contest dynamics in male–male competition. Ethology **109**, 995—1008.

Nakagawa, S. 2004: A farewell to Bonferroni: the problems of low statistical power and publication bias. Behav. Ecol. **15**, 1044—1045.

Nakagawa, S. & Cuthill, I. C. 2007: Effect size, confidence interval and statistical significance: a practical guide for biologists. Biol. Rev. **82**, 591—605.

Narum, S. R. 2006: Beyond Bonferroni: less conservative analyses for conservation genetics. Conserv. Genet. **7**, 783—787.

Olsson, M. 1992: Contest success in relation to size and residency in male sand lizards, *Lacerta agilis*. Anim. Behav. **44**, 386—388.

Ritz, M. S. & Köhler, G. 2007: Male behaviour over the season in a wild population of the field cricket *Gryllus campestris* L. Ecol. Entomol. **32**, 384—392.

Robertson, J. G. M. 1986: Male territoriality, fighting and assessment of fighting ability in the Australian frog *Uperoleia rugosa*. Anim. Behav. **34**, 763—772.

Rohlf, F. J. 2006: A comment on phylogenetic correction. Evolution **60**, 1509—1515.

Schuett, G. W. 1997: Body size and agonistic experience affect dominance and mating success in male copperheads. Anim. Behav. **54**, 213—224.

Shackleton, M. A., Jennions, M. D. & Hunt, J. 2005: Fighting success and attractiveness as predictors of male mating success in the black field cricket, *Teleogryllus commodus*: the effectiveness of no-choice tests. Behav. Ecol. Sociobiol. **58**, 1—8.

Simmons, L. W. 1986: Inter-male competition and mating success in the field cricket, *Gryllus bimaculatus* (de Geer). Anim. Behav. **34**, 567—579.

Sneddon, L. U., Huntingford, F. A., Taylor, A. C. & Orr, J. F. 2000: Weapon strength and competitive success in the fights of shore crabs (*Carcinus maenas*). J. Zool. **250**, 397—403.

Tachon, G., Murray, A.-M., Gray, D. A. & Cade, W. H. 1999: Agonistic displays and the benefits of fighting in the field cricket, *Gryllus bimaculatus*. J. Insect Behav. **12**, 533—543.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1: Phylogenetic tree used in analyses, in Newick format.