The energetic costs of fighting in the house cricket, *Acheta domesticus* L.

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The cost of performing an agonistic behavior, or tactic, will have consequences for an individual’s rate of cost accrual, the tactic’s evolutionary stability if used as an assessment signal, and its pattern of use in the behavioral choreography of a contest. Few studies have attempted to quantify the costs of fighting, particularly with regard to energy expenditure. However, conflicts of interest between thesender and receiver of a signal, inherent to contests, will favor manipulative or unreliable signaling (Krebs and Dawkins, 1984). Unless an aspect of the signal and RHP are obligately correlated (e.g., call fundamental frequency and body size: Davies and Halliday, 1978), reliable signals of RHP will remain evolutionarily stable only if the signaler incurs a cost (Enquist, 1985; Grafen, 1990; Maynard Smith, 1991; Zahavi, 1977a, 1977b). Description of the costs associated with a signal can indicate both a tactic’s relative reliability as a signal and the type of information it communicates (Grafen, 1990).

Finally, a tactic’s relative cost is predicted to affect its pattern of use in the choreography of acts during a single contest (Enquist et al., 1990; Enquist et al., 1985; Parker and Rubenstein, 1981). Observations of fighting behavior from a variety of species concur that there are general rules determining the temporal sequence and relative frequencies of tactics during contests (Clutton-Brock and Albon, 1979; Enquist et al., 1990; Hack, 1994; Keeley and Grant, 1993; Riechert, 1978; Rubenstein and Hack, 1992), often suggesting an escalation sequence from low cost to progressively more costly tactics. However, a significant impediment to testing the effect of economics on these observed patterns of tactic use is the lack of quantitative data on tactic costs.

Two cost currencies are likely to vary among alternative agonistic tactics: injury risk and energy expense. Tactics involving physical contact presumably pose a greater risk of injury to opponents than displays, or those without contact (Berzins and Caldwell, 1983; Clutton-Brock et al., 1979; Riechert, 1978). Alternative tactics may be further differentiated by their energetic costs, although direct measurements of energy expenditure during contests are rarely made (but see Bennett and Houck, 1983; Smith and Taylor, 1998). Variance in tactic "intensity," used to estimate fighting costs and test contest models (Catterall, 1989; Riechert, 1988), implies variance in energetic cost among tactics, yet the subjectively determined intensity ranks of tactics may have little basis in reality. Nevertheless, some indirect evidence indicates the importance of...
energy costs to contest behavior, including increased feeding rates as a result of more intense resource defense (Ewald and Rohwer, 1980), lower fat reserves among the losers of contests (Marden and Waage, 1990), and the apparent physical exhaustion of contest losers (Clutton-Brock et al., 1979; Rand and Rand, 1976; Wells, 1988). Clearly, more direct measurements of energy expenditure while fighting are needed.

In this study, I quantify the energetic costs of fighting for male house crickets (A. a. domesti c o) by continuously monitoring their instantaneous rates of oxygen consumption. Field crickets, or members of the family Gryllidae, are particularly well-suited to the study of contest energetics. Male crickets do not have specialized weapons, nor is body size always a strong determinant of fighting success (Burk, 1983; Hack, 1994). Indeed, dominance relationships are temporally unstable in most species that have been studied (Alexander, 1961; Burk, 1988; Dixon and Cade, 1986; Hack, 1994; Sandford, 1987; Simmons, 1986), implying the importance of transient characters, such as physical condition, in the determination of fighting success. In addition, an individual’s behavior varies considerably during a single contest (Adamo and Hoy, 1995; Alexander, 1961; Hack, 1994; Simmons, 1986), from low-intensity displays to highly escalated, intense physical contact, so that fighting costs in addition to time are likely to influence contest behavior. Injuries to the antennae, cerci, and legs resulting from fighting have been reported anecdotally for some species (Alexander, 1961; Burk, 1979; Sandford, 1987; Simmons, 1986), but their rarity suggests that energy costs may have a more general and important influence on contest strategy in gryllids.

METHODS

Flow-through respirometry

The male crickets used in this study came from a laboratory population maintained at 23-26°C on a 12.5:11.5 light:dark schedule. Temperature and light conditions during the collection of respirometry data were identical to those under which the crickets were raised.

I measured the oxygen consumption rates of crickets in an open, flow-through system using a dual-sensor oxygen analyzer (5-SA Applied Electrochemistry Inc.). Differences in the fractional concentration of oxygen between an empty control chamber and an identical chamber containing the test animals were sampled three times per second, at a resolution of 0.001% oxygen, and averaged to produce a single datum per second. Control and metabolic chambers consisted of hard plastic tubes, each with a total volume of 35 mL. Chamber temperature varied less than 0.1°C during any single trial (Bai ley Instruments BAT-12 digital thermocouple thermometer), indicating that the test animals’ own activity did not significantly raise chamber air temperature. The range in chamber temperature across the entire study did not exceed 0.5°C (24.5-25.1°C). An R-2 pump and flow-control unit (Applied Electrochemistry Inc.) maintained a fixed flow rate of 40 mL/min through the experimental chambers. I independently verified the flow rate with a Gilmont flow meter before and after each experimental trial.

I corrected all samples of excretory O2 differences to respirometry instantaneous rates of oxygen consumption (VO2; Bartholomew et al., 1981). The use of tubular chambers and the relatively small air volume between chamber and sensor (<10% of the chamber’s volume) ensured appropriate mixing characteristics for applying the instantaneous correction (Frappell et al., 1989). Baseline correction for sensor drift, curve smoothing to remove random noise in sensor readings, calculation of effective volume, and the instantaneous correction were all performed with custom software for the Macintosh. All reported rates of oxygen consumption have been standardized to STPD (0°C, 760 torr, dry) conditions.

More detailed descriptions of the experimental apparatus and the methodology of data collection are given in Hack (1994).

Staged contests

To elicit the full repertoire of agonistic behaviors observed in natural interactions, I simultaneously placed two males into the same metabolic chamber. Some tactics can only be observed and measured under these conditions since they require the coordinated actions of both opponents. To control the timing of male interaction, I installed a screen baffle midway down the metabolic chamber’s length. When closed, the baffle prevented a cricket from moving between the halves of the chamber without impeding air flow. Separating males within the chamber allowed them to settle to a stable resting rate of VO2 consumption before the initiation of fighting.

I conducted a total of nine two-male trials, ranging in duration from 20 to 50 min. No male was used in more than one trial. Male body mass ranged from 0.293 to 0.481 g (± SD = 0.572 ± 0.057) and adult age (i.e., days since eclosion) varied from 14 to 30 days (± SD = 19.3 ± 6.3). Opponents were matched for mass to within ±6% and were identical in adult age (except for one pair differing by three days). Mass and age matching minimized variance in resting VO2 between opponents and simplified the data analysis.

Behavioral analysis

I filmed male behavior during each trial using a Canon VC-30 color video recorder. A Hoya +1 dropper lens provided close-range magnification and a small condenser microphone (Realistic Back Electret), placed inside the chamber, recorded male sounds. Slow-motion analysis of the videotapes allowed me to quantify the frequencies of 13 agonistic tactics used by males (Appendix). Two additional behaviors, courtship display (Alexander, 1962) and walking, were also quantified. I defined a “step” as the basic unit of walking and measured its frequency by arbitrarily choosing a hind leg and counting only its cycles of movement.

Step, kick, head butt, head charge, fore leg punch, and mandible lunge occurred in discrete acts; one act of these behaviors counted as a single repetition in the analysis. Stridulation, shake, antennae lash, and stridulation lash each consisted of a small number of acts too rapid to distinguish individually, yet all three tactics generally occurred in discrete bouts of ≤1 s; one bout of these behaviors was treated as a single repetition. Cerci raise, courtship display, mandible flash, mandible snap, and wrestle constitute behavioral states; one second of these behaviors counted as a single repetition.

Video and VO2 records were temporally aligned by correcting for the time an air sample required to travel from the metabolic chamber to the sensor. I determined this time lag using three independent methods: (1) the time elapsed between injection at the influx port of an O2-deficient sample until peak deflection at the sensor; (2) division of the total volume of the metabolic chamber and its downstream plumbing to the sensor by the known flow rate; (3) inspection of the video record to find short (<5 s), isolated bursts of activity and matching of these actions to the oxygen consumption record. Estimates of the lag time from all three methods agreed to within ±5 s and was determined to be 30 s.

Cricket fights tended to occur in short bursts of combat followed by longer periods of relative inactivity. To account for any oxygen debt incurred by opponents, and because of
the several-second error in temporally matching the activity and VO\textsubscript{\text{O}} records, I divided complete trials into contiguous time intervals of 60 s for the multiple regression analysis.

**Regression analysis**

I used multiple regression to estimate the independent contribution of each tactic's performance to the total oxygen consumed by fighting males. This involved simultaneously regressing the oxygen consumed by both males combined, per sample interval, against the cumulative frequency of each tactic performed during the same interval. (I calculated combined oxygen consumption per sample interval by integrating the observed VO\textsubscript{\text{O}} versus time plot.) Since data were pooled across pairs (see below), I first removed variance among pairs in resting oxygen consumption rates by subtracting the oxygen consumed at rest by both males from their total combined oxygen consumption. This resulted in a measure of net combined oxygen consumption, or that attributable solely to the activity of one or both males. Multiple regression through the origin of net consumption values resulted in a set of slopes (partial regression coefficients), each representing the incremental or net oxygen consumed per single repetition of a particular tactic. By assuming males of equal mass and age consumed equivalent amounts of oxygen when performing the same behavior, I was able to sum the frequency of each behavior across opponents, and thereby reduce by a factor of two the number of independent variables entered into the model. This essentially attributed all net oxygen consumption to a single hypothetical male and was valid provided intermale variance in VO\textsubscript{\text{O}} per tactic did not exceed variance in mean VO\textsubscript{\text{O}} among alternative tactics.

I calculated mass-specific estimates of tactic cost by dividing net combined oxygen consumption by the mean mass of opponents. (Mean mass closely approximated the actual mass of each male since opponents were weight-matched to within ±6%.) I used mean mass, rather than the sum of opponent masses, because males did not perform the same behaviors at equal frequencies per sample interval; their contributions to net combined oxygen consumption were not equivalent. If one male rested during the sample interval while the other performed several agonistic acts, the division of net combined oxygen consumption by their summed mass would underestimate the oxygen consumed per act repetition, per male. In this case, the net oxygen consumed would be attributed to a male twice the actual size of the actor, and the energy cost per unit mass would be half the actual cost to the actor.

Ideally, intrapair and interpair variance in the energy cost per tactic could be distinguished with a separate multiple regression analysis for each pair. However, the division of trials into 60-s sampling intervals meant that 60 measurements of VO\textsubscript{\text{O}} were summed in this interval to produce a single datum for the multiple regression. This substantially reduced intrapair variance in tactic frequency for some tactics. For example, some steps in other contexts to create a single measure for locomotion during fights termed "charge." Each second of mandible sparring added to the duration of mandible flaring accounted for the mandible and head movements involved in this tactic. Stridulation was decomposed into stridulate and antennal lashing.

The full regression model of 11 behaviors explained 90.4% of the variance in the net oxygen consumed by fighting cric-
wrestling, the most costly. In general, the tactical repertoire
nae lash, and wrestle, raised active VO_{2} by 6-8 times resting levels
second, of mandible flare (r = 2.01, df = 165, p < .0001). One chirp of stridulation consumed less oxygen than one
rapid locomotion and physical contact, such as charge, antennae lash, and wrestle, raised active VO_{2} 6-8 times resting levels.

One nonagonistic behavior, courtship display, showed no statistically significant difference from zero (Figure 2). Two additional displays, shake and cerci raise, fell within the group of higher cost tactics. Shake consumed significantly more oxygen than stridulate (t = 5.81, df = 165, p < .0001) and mandible flare (t = 6.15, df = 165, p < .0001), presumably because it involved the rapid movement of the whole body rather than just the tegmina or mandibles and head. Cerci raise also involved lifting the entire body; its estimated energetic cost did not statistically differ from those of the other displays.

Examination of each tactic's pattern of use suggests an important influence of energetic cost on fighting strategy. Across all 12 observed fights, opponents used tactics of high energetic cost significantly less often than tactics of lower energetic cost (Figure 5). In addition, the proportion of fights in which house cricket males performed a particular tactic decreased with increasing tactic energy cost (r = -0.811, p < 0.05, n = 7).

Total energy expended per opponent

Measures of tactic energetic cost provide a means of calculating the cumulative net energy expended per opponent. I calculated a male's net oxygen consumption per fight by tallying the frequencies with which it performed each tactic, multiplying by each tactic's cost per repetition, and summing across tactics. The accuracies of calculated totals are likely to be high since the seven tactics measured account for 90% of the variance in net male oxygen consumption.

Cumulative net oxygen consumption per opponent averaged 41.81 µg g^{-1}·fight^{-1} (SD = 38.66, range = 1.22-160.38). In nine of 12 fights the winner's cumulative net consumption exceeded the loser's, although the average magnitude of this difference was not large (2 ± SE = 11.92 ± 5.37, paired t =...
for any species, few data from other studies are available for behaviors, including walking, grooming, calling for mates, and more energetically costly than other common cricket behaviors. Several agonistic tactics raise rates of oxygen consumption six to eight times above resting levels, making them more energetically costly than other common cricket behaviors, including walking, grooming, calling for mates, and courtship (Hack, 1994). Since this is one of the first studies to quantify the energetic costs of alternative agonistic tactics for any species, few data from other studies are available for direct comparison. However, the accuracy of the metabolic measurements can be evaluated by comparing oxygen consumption measured for mechanically similar behaviors in other orthopterans: (1) the cost per pulse of aggressive stridulation falls within the range of costs per pulse for mate-attracting stridulation (reviewed by Bailey et al., 1993).

The influence of energy expenditure on the evolution of fighting strategy will ultimately depend upon its consequences for an individual's survival and reproduction. It is difficult to determine these consequences under laboratory conditions, but some proximate measures are available. The proportion of an individual's daily energy budget spent fighting represents energy not spent more directly on survival or reproduction. The daily energy expenditures measured under semi-natural conditions in this study cannot substitute for actual field measurements, but if they are accurate, they are likely to be more representative of males occupying burrows or other calling sites. Male gryllids adopting this strategy are relatively sedentary and primarily call to attract mates (Cade and Cade, 1992; Evans, 1983; Hissmann, 1990; Zuk et al., 1993) — a daily pattern of behavior similar to that observed among the experimental males.

A single escalated fight constitutes, on average, less than 1% of the average daily energy budget measured in the absence of fighting. However, paired male A. domestica may fight several times before clearly determining control of a resource (e.g., burrow, female) or establishing a consistent dominance relationship (Hack, 1994). High interaction rates have been observed under laboratory and field conditions for other gryllids (52 fights/h: Alexander, 1961; six escalated fights/h: Simmons, 1986) and the generally short (few days) tenure of males occupying burrows in field populations further suggests frequent, intense competition (Campbell and Shipp, 1979; Evans, 1983; Hissmann, 1990; Rost and Honegger, 1987).

Figure 3
The relationship between the oxygen consumed per repetition of each tactic and its cumulative frequency (log-transformed) over 12 fights (nine male pairs). More energetically costly tactics are used less frequently by opponents: \( r^2 = 0.667, F_{1,10} = 10.00, p < .05, Y = 8.06 - 4.46X \). Tact \( \text{tactic key: SD (stridulate), MF (mandible flare), SK (shake), CH (charge), AL (antennae lash), CR (ceri raise), WR (wrestle).} \)

2.14, \( df = 11, p < .06 \). Cumulative net consumption for both winners and losers increased linearly with fight duration (Figure 4). The net consumption of winners also tended to increase at a greater rate with fight duration (i.e., the difference between the net consumptions of winners and losers grew larger as fight duration increased \( r^2 = 0.566, F_{1,10} = 13.04, p < .01 \)). Differences in the frequencies of two tactics, stridulate and shake, largely accounted for the disparity between the energy expenditures of winners and losers.

Daily energy expenditure
The total oxygen consumed per male at 24-26°C averaged 4.594 ml/day (SD = 1.085, \( n = 14 \), range = 2.552-9.916), or, in mass-specific units, 16.240 ml·g\(^{-1}\)·day\(^{-1}\) (SD = 3.808, range = 9.350-22.326). Daily oxygen consumptions during the subsequent 48 hour period were very similar (mean difference = 0.481 ml·g\(^{-1}\)·day\(^{-1}\), paired \( t = 0.595, DF = 13, NS \)), suggesting the lack of variance in daily energy expenditures for the three-day period. Using the mean daily energy expenditure of isolated males to gauge the relative energetic cost of winning the energy expenditures of winners and losers. The total oxygen consumed per male at 24-26°C averaged 32.140 ml·g\(^{-1}\)·day\(^{-1}\) (SD = 3.808, range = 9.350-22.326). Daily oxygen consumptions during the subsequent 48 hour period were very similar (mean difference = 0.481 ml·g\(^{-1}\)·day\(^{-1}\), paired \( t = 0.595, DF = 13, NS \)) suggesting the lack of variance in daily energy expenditures for the three-day period. Using the mean daily energy expenditure of isolated males to gauge the relative energetic cost of winning the energy expenditures of winners and losers.

Relation of energetic cost to fitness
The influence of energy expenditure on the evolution of fighting strategy will ultimately depend upon its consequences for an individual's survival and reproduction. It is difficult to determine these consequences under laboratory conditions, but some proximate measures are available. The proportion of an individual's daily energy budget spent fighting represents energy not spent more directly on survival or reproduction. The daily energy expenditures measured under semi-natural conditions in this study cannot substitute for actual field measurements, but if they are accurate, they are likely to be more representative of males occupying burrows or other calling sites. Male gryllids adopting this strategy are relatively sedentary and primarily call to attract mates (Cade and Cade, 1992; Evans, 1983; Hissmann, 1990; Zuk et al., 1993) — a daily pattern of behavior similar to that observed among the experimental males.

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Thus, frequent fighting may result in a cumulative energetic cost that constitutes a significant proportion of an individual's daily energy budget. Daily energy expenditures on fighting may be even greater in other gryllids, since *A. domesticus* appears to be less aggressive than other field cricket species.

Energy expended while fighting must either be replenished through foraging or cause a permanent reduction in reserves. Foraging presumably involves increased predation risk, and the costs of performing it may represent a significant loss of mating opportunities in species with short adult life-spans, such as crickets and insects in general. Depleted energy reserves reduce an individual's ability to secure a mating territory in the damselfly *Calopteryx maculata* (Marden and Waage, 1990) and to attract mates through signaling in the bushcricket *Requena verticalis* (Simmons et al., 1992). The physiological cost to a female *Gryllus rubens* of simply maintaining operative flight muscles is substantial enough to reduce her fecundity by more than 20% (Mole and Zera, 1993). A similar trade-off may apply to male gamete production in crickets, since mating success often depends on a male's ability to mate multiply and rapidly with the same female (Sakaluk and Cade, 1983; Simmons, 1988b; Simmons, 1988c; Zuk, 1987). Assuming an average spermatophore mass in *A. domesticus* of 0.9 mg of protein and a net cost of an escalated fight equal to 0.05 ml O₂ for a 0.5 g cricket, the energy required to produce a single spermatophore is equivalent to approximately 19 escalated fights (efficiency equations from Woodring et al., 1979).

For *A. domesticus*, a moderate number of fights per day potentially incurs enough of an energetic cost to reduce a male's mating success by limiting spermatophore production. Indeed, energetic costs imposed by gregarine parasites have similarly been shown to reduce spermatophore production in two gryllid species (Zuk, 1987).

**Tactic cost and function**

Wrestling incurs the greatest energetic cost among *A. domesticus* tactics and presumably also entails the greatest risk of injury. Contests that escalate to wrestling typically end with the loser getting thrown or flipped by its opponent and rapidly retreating. Thus, wrestling represents all-out combat and preceding tactics potentially allow the assessment of likely success in a wrestling bout. For a tactic to signal RHP or motivation reliably, it must either be obligately correlated in some aspect of performance with a quality contributing to fighting success (Maynard Smith, 1982; Maynard Smith and Harper, 1988) or incur a cost to produce (Enquist, 1985; Grafen, 1990; Maynard Smith, 1991; Zahavi, 1977a; Zahavi, 1977b). Signaling costs include prior investment in costly structures (Alvarez, 1990; Ferrie, 1988), a commitment to performing costly behavior (Enquist, 1985; Enquist et al., 1985), retaliation by an opponent that inflicts costs if the signal is false (Müller, 1987), and the immediate performance costs focused on in this study.

Measurements of energetic performance cost provide a basis for evaluating the communicative function of alternative agonistic tactics in the repertoire of *A. domesticus*. Among tactics with negligible risks of injury, shake and antennae lash incur relatively large energetic performance costs per repetition. The relatively small signal a male's ability to incite the greater energetic cost of all-out combat (Grafen, 1996; Zahavi, 1977a; Zahavi, 1977b). Both tactics are frequently performed before escalation to wrestling and in the intervals between bouts of wrestling. In contrast, stridulate and mandible flare expend relatively little energy and consequently should be evolutionarily unstable as signals of fighting ability. Nevertheless, house cricket contests, and those of other gryllids, often do not escalate beyond stridulation and mandible flaring (*Adamo* and Hoy, 1995; Alexander, 1961; Burk, 1983; Hack, 1994; Simmons, 1986), suggesting that both tactics still function as effective signals in the resolution of contests. The performance of mandible flare may commit an individual to more costly subsequent behavior and thereby reliably signal motivation (Enquist, 1985); it often directly precedes the more costly tactics of mandible spar and wrestle.

Stridulation does not consistently appear to precede costly behavior by either opponent, although it is more often performed by the winner directly after its opponent's retreat in *A. domesticus* (Hack, 1994) and other gryllids (*Adamo* and Hoy, 1995; Alexander, 1961; Burk, 1983; Simmons, 1986). This observation suggests that stridulation constitutes a conventional signal (senso: Maynard Smith and Harper, 1988) of fighting ability or prior fighting success. Its relatively low cost implies a low reliability as well. However, it may be informative in some contexts since a receiver pays little cost to perceive it accurately (Dawkins and Guilford, 1991); a signaler will stridulate without requiring reciprocally costly action from the receiver and, as an acoustic signal, it can be detected from a distance without exposing the receiver to attack. The costs of probing the signal's reliability through physical contact or more energetically costly behavior may not always be justified if resource value is low or the likelihood of success is small. Aggressive stridulation may alternatively function as an obligate indicator of body size since acoustic parameters of the similar advertisement call correlate with body size in *Gryllus bimaculatus* (Simmons, 1988a). However, such correlations may not be general to gryllid signals (Souroukis et al., 1992).

Furthermore, it is unclear why the signaling of relative body size should occur as frequently after a contest has been resolved as during it, when assessment of RHP would have the most utility.

Charge (including head charge and mandible lunge) and cerd raise have relatively high energetic costs, but probably do not function as signals in the process of assessment. Charges often displace an opponent and resemble all-out combat. Cerd raise is typically given by a retreating individual and appears to protect these sensory organs from charges and potential damage. It may also signal retreat, or submission, and discourage further attack from the contest winner.

**Do energy costs influence tactic use?**

The lower frequency of more energetically costly tactics implies an escalating tactical convention (Enquist et al., 1990; Parker and Rubenstein, 1981) whereby opponents begin contests with relatively low-cost tactics and escalate to progressively more costly tactics as the contest proceeds. If low-cost contests are more common than high-cost contests, as predicted if opponents are usually asymmetric in fighting ability or motivation (Enquist and Leimar, 1985; Hammerstein and Parker, 1982; Maynard Smith and Parker, 1976), tactics used to begin contests will be much more frequently observed than more costly tactics employed only during the final stages of highly escalated contests. Indeed, tactics such as stridulate and mandible flare generally preceded more energetically costly tactics during fights, although small sample sizes preclude statistical verification of these patterns. (The influence of energy cost on contest choreography is currently being analyzed with a larger dataset (Hack, in preparation)) Although escalating tactical conventions appear general to gryllids (*Adamo* and Hoy, 1995; Alexander, 1961; Simmons, 1986), and may be a common aspect of animal contest behavior (Clutton-Brock and Albon, 1979; Keeley and Grant, 1993; Riechert, 1978; Rubenstein and Hack, 1992), this is one of the few demonstrations of an escalating convention based on actual measurements of tactic cost.
The argument that energetic costs influence the use of particular tactics by *A. domestica* males is subject to an important caveat: Gollinarity among the possible types of cost incurred during a contest can confound the clear identification of one cost type as the primary determinant of contest strategy. In perhaps the best study to date of contest strategy economics, estimated energy costs of fighting for the spider *Agelenopsis aperta* closely followed theoretical predictions of total contest fitness costs, yet the injury risks incurred during contests reduced the evolutionary importance of energy expenditures to negligible levels (Hammerstein and Riechert, 1988; Riechert, 1988). However, this conclusion is unlikely to apply to house cricket contests since they never result in lethal or debilitating injury (n > 3000), whereas 56% of *A. aperta* contests end in severe injury in some contests. House cricket contests occasionally result in minor injuries, suggesting some influence of injury risk on fight strategy, though not one strong enough to account for either differences in the use of tactics unlikely to cause injury or the observed patterns of total cost in contests without tactics of high injury risk.

**Implications of cost measures for contest theory**

Contest models (Enquist and Leimar, 1983; Enquist et al., 1990; Hammerstein and Parker, 1982; Parker and Rubenstein, 1981) make several assumptions about opponents' relative rates of cost accrual: (1) costs accrue as linear functions of time, or as nonlinear functions provided those for two opponents do not intersect; (2) cost accrual rate is a primary asymmetry distinguishing opponents; and (3) the poorer fighter, as defined, accrues costs more quickly than its opponent. In this study, the cumulative net energy expenditures of both contest winners and losers fit linear functions with time, supporting the first assumption. It is more difficult to verify the second and third assumptions. Opponents have different rates of injury cost accrual if one is more likely to be damaged in combat (Austad, 1985). In contrast, asymmetry in accrual rates for energy or time costs are likely to result from opponent differences in their abilities to recover from the same absolute energy expenditure or duration of lost opportunity (Grafen, 1996; Parker and Thompson, 1980). Similar net energy expenditures per contest by *A. domestica* opponents suggest that good fighters start with greater energy reserves (Marden and Rollins, 1994) or perhaps forage more efficiently (Vehrencamp et al., 1989). If poor fighters accrued energy costs more quickly, because of for example wasteful activity, the net energy expended per fight for losers should have consistently exceeded that of winners, yet the opposite result was obtained.

Activity differences presumably account for the greater net energy expended per fight by winners relative to losers. The artificially confined space of the metabolic chamber partially explains this observation since it prevented the full retreat of the loser in some cases and prolonged the winner's aggressive behavior. However, greater activity (stridulation, shaking) by a contest winner immediately after the retreat of its opponent typifies the fighting behavior of gryllids (Adamo and Hoy, 1995; Alexander, 1961; Bailey and Stoddart, 1982; Burk, 1983; Simmons, 1986) and impairs a functional importance to the greater energy expenditures of winners. Perhaps by advertising their recent victory, winners reinforce a dominance relationship and strengthen the effect of prior experience in subsequent contests with the same opponent (Adamo and Hoy, 1995; Alexander, 1961; Burk, 1979; Hack, 1994; Simmons, 1986). As this study demonstrates, significant energetic costs incurred by both contest winners and losers can have important effects on the choreography of tactics by each opponent and thereby shape their overall strategies in the resolution of conflict.

**APPENDIX**

Description of tactics observed in the contests of male house crickets, categorized by the degree of physical contact each entails (modified from Alexander, 1961).

**Display (no physical contact):**

Cerci raise: a high lifting of the abdomen's tip and cerci
Mandible flare: a presentation of open mandibles to an opponent
Stridulation: a chirp of sound produced by rubbing the wings together
Shake: a quick rocking of the whole body forward and back several times

**Light physical contact:**

Head butt: a slow push of the head into an opponent
Fore leg punch: a batting of an opponent with one of the fore legs
Antennae lash: a whipping of an opponent's dorsum and head with both antennae, often accompanied by a rapid fanning of the fore legs without physical contact
Stridulation lash: an antennae lash and stridulation performed simultaneously
Mandible spar: both males rapidly maneuver around each other, barely apart or briefly touching, with flared mandibles

**Hard physical contact:**

Head charge: a rapid ram of the head into an opponent
Kick: an outward thrust of the hind leg, capable of throwing an opponent
Mandible lunge: a head charge with flared mandibles, resulting in a bite
Wrestle: a grasping and locking together of mandibles with an opponent, followed by a twisting of the head in an attempt to overturn or throw it

I would like to thank S. Vehrencamp for the equipment and advice she provided in collecting the respirometry data. M. Chappell's custom software and respirometry expertise were also critical to the success of this study. J. Bradbury, J. Kohn, K. Williams, S. Vehrencamp, M. Chappell, L. Simmona, W. Gade, and an anonymous reviewer provided many helpful comments in the preparation of this manuscript. This research was partially funded by a Predoctoral Fellowship from the National Science Foundation.

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Hack - Energetics of fighting

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