When to fight? Disentangling temperature and circadian effects on aggression and agonistic contests

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Agonistic behaviour is an important component of intraspecific competition because outcomes of agonistic contests can serve as indicators of fitness, helping the victors secure critical resources. Although several factors affecting aggression, including age and body size, have been well documented, few studies have examined the effects of abiotic factors on aggression and outcomes of agonistic contests. Abiotic factors affect a broad range of behaviours and can naturally covary, but some factors are becoming increasingly uncoupled. For example, ongoing climate change continues to shift temperature, but not light:dark, cycles. Thus, we employed a 2×2 factorial design in sand field crickets, *Gryllus firmus*, to disentangle the naturally covarying effects of temperature and circadian rhythms. During early adulthood, virgin males were maintained in either a typical or inverted diel temperature cycle (i.e. cool in the morning and warm in the afternoon, or warm in the morning and cool in the afternoon, respectively) reflecting field conditions (20.5−32 °C). Agonistic contests occurred at either cool (22 °C) or warm (31 °C) periods in the temperature cycle. Morphological traits, such as head width, femur length and testes mass, positively covaried and influenced the outcome of contests where relatively large crickets won most contests. However, temperature and time of day had additive, interactive effects on the level of aggression and the duration of contests. Contests occurring in cool, morning conditions were relatively long and aggressive. Although crickets appeared to use a mutual assessment strategy (contests between males of mismatched body size took longer to initiate), there may have been a context-dependent shift to a self-assessment strategy during warm evenings. Thus, plasticity in agonistic behaviour occurred due to the interactive, additive effects of temperature and circadian dynamics. We encourage continued investigation into studies that disentangle the effects of temperature and circadian effects on other fitness-related behaviours, such as mate choice or foraging.

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Agonistic behaviour is an important component of intraspecific competition for many animals (Alexander, 1961; Choe & Crespi, 1997). Often, outcomes of agonistic contests serve as indicators of individual fitness, helping the victors secure essential resources (e.g. territory, food and/or mates: Huntingford, 2013; Zeng, Zhu, & Kang, 2016). However, 'winning' an agonistic contest via aggressive behaviour incurs metabolic and physiological costs, increased risks of injury and predation, and loss of time available for other activities (Briffa & Sneddon, 2007). Thus, contestants may evaluate one another's relative fighting abilities (resource-holding potential, RHP) and motivation prior to aggressive escalation to minimize these potential costs (Hofmann & Schildberger, 2001; Jenssen, Decourcy, & Congdon, 2005; Maynard Smith & Parker, 1976).

Morphological features (i.e. body size and specialized weaponry) of males strongly influence the outcomes of agonistic contests within many species (DiMarco & Hanlon, 1997; Huyghe, Vanhooydonck, Scheers, Molina-Borja, & Van Damme, 2005; Jenssen et al., 2005; Murai & Blackwell, 2005; reviewed in ; Arnott & Elwood, 2009). Intercontestant variation in RHP can mediate agonistic contests via self-assessment where each contestant only has information about its own RHP (e.g. when quickly initiated, prolonged and/or aggressive contests are associated with larger losers) (Arnott & Elwood, 2009; Prenter, Elwood, & Taylor, 2006). Alternatively, morphological variation can be mutually assessed where each contestant assesses its own RHP relative to that of its opponent (e.g. when briefer and/or less aggressive contests are associated with larger winners) (Arnott & Elwood, 2009; Prenter et al., 2006). Across taxa, other factors also affect aggression, such as variation in age (Humphries, Hebblethwaite, Batchelor, & Hardy, 2006), sex (Draud, Macias-Ordonez, Verga, & Itzkowiz, 2004; Elias, Botero, Andrade, Mason, & Kasumovic, 2010), perceived resource

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value (Tobias, 1997) and agonistic experience (Hsu, Earley, & Wolf, 2006; Kasumovic, Elias, Sivalinghem, Mason, & Andrade, 2010; Stevenson, Dyakonova, Rillich, & Schildberger, 2005). Yet, the role of abiotic factors in behavioural aggression and contest dynamics is less understood (Lane & Briffa, 2018) even though the abiotic environment influences many common biological processes. For example, temperature exhibits spatiotemporal variation and influences most physiological processes in many animals, including locomotion (Huey & Berrigan, 2001) and standard metabolic rate (Nespolo, Lardies, & Bozinovic, 2003). Moreover, ambient temperature affects animal behaviours, including sexually selected behaviours in insects (Doherty, 1985; Martin, Gray, & Cade, 2000; Pires & Hoy, 1992; Ritchie, Saarikettu, Livingstone, & Hoikkala, 2001), frogs (Gerhardt, 1978; Gerhardt & Doherty, 1988; Navas, 1996; Navas & Beveir, 2001) and lizards (Brattstrom, 1974). For example, in male crickets, temperature influences song structure (Martin et al., 2000), which contains information about the caller's RHP and ability to win a fight — body size affects song structure and predicts the winners of agonistic contests (Brown, Smith, Moskalik, & Gabriel, 2006). Thus, temperature may be an important factor in modulating the dynamics of agonistic contests (Stutt & Wilmer, 1998).

In the natural environment, daily temperature cycles typically covary with the photophase: it is cooler early in the photophase and warmer later in the photophase. Consequently, temperature effects on animal behaviour and physiology are often closely intertwined with light-driven effects. For example, the natural coupling of temperature and light cycles produces covarying effects on the circadian timing system, a nearly ubiquitous biological system responsible for coordinating physiological processes and daily rhythms of behaviour (Stanewsky, 2003; Van Someren, 2003). While circadian clocks may exhibit both thermal sensitivity and photosensitivity, the entrainment of the circadian clocks of many animals is facilitated primarily through animals' visual systems (Barlow, Chamberlain, & Lehman, 1989; Berson, Dunn, & Takao, 2002; Helfrich-Förster, Stengl, & Homberg, 1998). Thus, the sensitivity of temperature- and circadian-driven sensory systems may affect males' abilities to efficiently evaluate the RHP of themselves and/or their competitors. In addition, temperature and/or time-of-day effects may limit the expression of RHP by each competitor. For example, during a cool morning, a large male may not fully express its high RHP but quickly win a contest with a smaller male given the strong effect of temperature on muscle function and locomotor capacity (reviewed in Bennett, 1985, 1990; James, 2013). In summary, temperature or time of day may influence the dynamics of agonistic contests by influencing either the perception or the expression of RHP.

Although difficult, it is important to disentangle the effects of temperature and time of day on behavioural dynamics. Animal behaviour influences population and community ecology, as well as conservation biology (Sih, Bell, Johnson, & Ziemba, 2004), and most behaviours exhibit significant plasticity in response to environmental or temporal factors (Bell, Hankison, & Laskowski, 2009). Ongoing climate change continues to shift temperatures (IPCC, 2014), but not light:dark cycles, and this uncoupling leads to global changes in phenology that often result in ecosystem disruption (Burrows et al., 2011; Parmesan, 2006; Parmesan & Yohe, 2003). To understand the relative importance of temperature and time of day in behavioural dynamics, careful independent manipulation of the thermal and light environments is required.

Thus, we used such a factorial experimental approach in male sand field crickets, *Gryllus firmus*, to evaluate and disentangle the modulating potential of temperature and time of day. *Gryllus* crickets offer a well-documented system of agonistic behaviour exhibiting context dependency or plasticity (Adamo, Gomez-Juliano, LeDue, Little, & Sullivan, 2015; Adamo & Hoy, 1995; Alexander, 1961; Rillich, Schildberger, & Stevenson, 2007; Stevenson et al., 2005), and other crickets (house cricket, *Acheta domesticus*) have been shown to exhibit mutual assessment strategies related to agonistic contests (Briffa, 2008; Hack, 1997a). We tested two hypotheses. First, morphological traits affect the outcome of male–male agonistic contests. Here, we predicted larger, heavier males with larger mandibles (specialized weaponry for fighting: Alexander, 1961) would be more likely to win contests relative to smaller males. Second, contest dynamics depend on the interaction of time of day and temperature. Here, we specifically predicted additive effects of time of day and temperature where males' assessment or expression of RHP would be relatively less precise early in the day and at cooler temperatures. In the field, the early photophase is associated with reduced movement by some *Gryllus* cricket males (French & Cade, 1987) — thus, we predicted that these conditions would result in less efficient contest strategies and, therefore, lead to more aggressive or longer contests. By experimentally uncoupling two inescapable and covarying factors, this study aims to clarify the complexity of the effects of the natural environment on the plasticity of a fitness-related behaviour. Although our study focuses on agonistic behaviour, the experimental approach we use can be similarly applied to other behavioural dynamics, such as mating or foraging decisions.

METHODS

Study Animals

Gryllus firmus is an omnivorous field cricket native to the southeastern United States (Capinera, Scott, & Walker, 2004). Crickets used in the study had been raised in outbred populations that were artificially selected to produce either long-winged (typically, flight-capable) or flightless short-winged morphs for several decades as previously described (Zera, 2005; Zera & Larsen, 2001). In particular, short-winged *G. firmus* from three selected blocks were used in our study because the short-winged morph is the more aggressive morph in other *Gryllus* crickets (Guerra & Pollack, 2010). Crickets were reared in standard conditions (16:8 h light:dark cycle and 28 ± 1 °C with ad libitum access to water and commercial dry cat food) until adulthood. To ensure virginity, male crickets were removed from group housing at approx. 1 day postadult moult.

Crickets were then individually housed for 6 days prior to the experiment to limit agonistic behaviour, which can influence subsequent contest outcomes (Adamo & Hoy, 1995; Hofmann & Stevenson, 2000). Isolated males were individually housed in round, translucent plastic containers (0.5 litre; height: 7.5 cm; mean width: 10 cm) with a small shelter, as well as ad libitum food and water. During this pre-experiment isolation period, males were placed in an incubator (model I-36, Percival Scientific, Inc., Perry, IA, U.S.A.) with a 16:8 h light:dark cycle at a diel temperature cycle reflecting field conditions (20.5–32 °C, which is the average daily temperature range in Gainesville, Florida, U.S.A. (location where the founders of the stock were collected) during the crickets' active season (May–September): National Weather Service, Silver Spring, MD, U.S.A.). Half of the crickets were randomly assigned to an incubator mimicking a 'typical' diel temperature cycle — that is, cooler in the morning (early in the photophase) and warmer in the evening (later in the photophase). To disentangle thermal and circadian effects, we randomly assigned the other half of the crickets to an 'inverted' diel temperature cycle — that is, warmer in the morning and cooler in the evening. All crickets experienced the same light:dark cycle (lights on from 0600 to 2200 hours) throughout ontogeny and the duration of the experiment

(described below). Isolated crickets received no tactile stimuli from conspecifics, but they could potentially hear or smell other individually housed males within the incubator as they each acclimated to one of two temperature treatments (i.e. typical versus inverted diel temperature cycle). At 7 days of adulthood, virgin male crickets were weighed and marked with nontoxic paint on the pronotum for identification in preparation for agonistic trials (see below). Field observations of behaviour in *G. firmus* is scant, but male–male agonistic behaviour in captivity is frequently observed throughout the day and night in these blocks (Z. R. Stahlschmidt, personal observation) and in other *Gryllus* crickets (Dixon & Cade, 1986).

Experimental Design

A 2×2 factorial design was implemented to determine the effects of temperature and time of day on agonistic behaviour in *G. firmus*. Males ($N = 280$) were randomly assigned to agonistic trials occurring in either cool (21.7 °C) or warm (31.3 °C) conditions, and either early or late into the photophase (6% (<1 h) into the photophase versus 75% (12 h) into the photophase, respectively). For example, a male acclimated to the typical temperature cycle (see above) could only be assigned to a cool morning or a warm evening trial whereas a male acclimated to the inverted temperature cycle could only be assigned to a warm morning or a cool evening trial. After weighing and marking at 5–7 days of adulthood (see above), each cricket was paired with another male from the same temperature treatment group (i.e. typical versus inverted diel temperature cycle experienced during first 6 days of adulthood). Results from a linear mixed model (block as a random effect) indicated that the body mass of contestants was not influenced by temperature treatment ($F_{1,284} = 0.15$, $P = 0.70$), time of day ($F_{1,284} = 0.18$, $P = 0.67$) or a temperature*time interaction ($F_{1,284} = 0.003$, $P = 0.96$).

Each cricket in a pair was placed on opposite ends of a rectangular, translucent plastic arena (1.9 litre; height 10 cm; mean width: 11.5 cm; mean length: 17.5 cm) filled with 3 cm of sand. Each cricket pair was separated by a removable opaque plastic barrier that limited tactile and visual cues between opponents prior to the initiation of a given trial. Crickets were provided food and water, and were allowed to acclimate to the arena in the incubator overnight. The following day, food and water were removed 10 min prior to the start of each trial to improve behavioural observations. Each trial ($N = 140$) began when the opaque barrier was removed, and each trial ended by either the determination of a clear victor or after 10 min. All trials were videorecorded and later analysed (see below), with the exception of the data for four trials that were not analysed because no victor was determined in these trials within 10 min. Each cricket only underwent a single trial. After trials, crickets were frozen at -20 °C and later measured for the several traits. Femur length and head width were measured as a proxies for body size (Roff & DeRose, 2001; Simmons, 1986), and in other *Gryllus* crickets, head width strongly correlates with the size of mandibles, which are sexually dimorphic and can be used during agonistic contests (Adamo & Hoy, 1995; Alexander, 1961; Judge & Bonanno, 2008). Dry testes mass was also determined as a proxy for postcopulatory investment or sperm competition (Simmons & Fitzpatrick, 2012).

Analyses of Agonistic Contests

Gryllus crickets follow stereotyped patterns of escalation in agonistic contests among males (Adamo & Hoy, 1995; Rillich et al., 2007). Thus, agonistic contests were analysed to determine the following: the latency to initiate a contest (time from removal of barrier until the onset of antennal fencing, which is the initial stage

of agonistic behaviour in *Gryllus* crickets: Adamo & Hoy, 1995; Rillich et al., 2007), the duration of a contest (time from antennal fencing until an outcome was determined) and the outcome of a contest (i.e. who won and lost). Contests were also analysed for the level of aggression (scored on a 0–6 scale): zero (mutual avoidance), 1 (pre-established dominance), 2 (antennal fencing), 3 (unilateral mandible spreading, where only one of the contestants exhibits aggressive mandible spreading), 4 (bilateral mandible spreading, where both contests spread mandibles), 5 (mandible engagement) and 6 (grappling) (sensu Rillich et al., 2007; Stevenson et al., 2005). Winners and losers can be distinguished unambiguously by the submission and retreat of the loser, often coupled with an aggressive song from the victor (Adamo & Hoy, 1995; Alexander, 1961; Bertram, Rook, & Fitzsimmons, 2010).

Statistical Analyses

To create a comprehensive index of body size, morphological measurements (femur length, head width, body mass and dry testes mass) were entered into a principal components analysis (PCA). This PCA produced a principal component (PC) that explained over 80% of the variance among initial morphological variables. That is, a cricket with a high PC value was relatively large and heavy, and had a wide head and large testes. This PC (herein, 'morphological index') was used in subsequent analyses.

Several linear mixed models were performed in SPSS (v.22 IBM Corp., Armonk, NY, U.S.A.), data were log transformed when necessary, and two-tailed significance was determined at $\alpha = 0.05$. Linear models were used on data from each contest to determine the main (independent) and interactive effects of temperature (cool versus warm) and time of day (morning versus evening) on the latency to initiate contests, the contest durations and the level of aggression during contests. For these models, morphological differential (absolute difference in morphological index between each pair of contestants) was also included as a covariate and block was included as a random effect. Pairwise, post hoc comparisons were adjusted using sequential Bonferroni corrections. A binary logistic generalized linear model was used on data from each cricket to determine the main and interactive effects of temperature, time of day and morphological index (covariate) on agonistic contest outcome (0: loss; 1: win). To examine whether the relative roles of self-assessment and mutual assessment in contest dynamics (sensu Prenter et al., 2006; Taylor & Elwood, 2003) changed due to treatments, correlations between morphological metrics (i.e. morphological index of loser, morphological index of winner and morphological differential) and contest metrics (i.e. latency to initiate, duration and level of aggression of contests) were examined in each of the four treatment combinations (e.g. cool morning, cool evening, etc.). To examine the general dynamics of agonistic contests, correlations between latency to initiate contests, contest duration and level of aggression during contests were examined by pooling data across all four treatment combinations.

RESULTS

The level of aggression during contests was influenced by the interactive effect of temperature and time of day ($F_{1,135} = 4.6$, $P = 0.033$) where contests were less aggressive during warm evenings (Fig. 1a). Due to this interaction, time of day also influenced aggression level ($F_{1,135} = 4.4$, $P = 0.038$; evening contests were less aggressive) (Fig. 1a). Aggression level was not affected by temperature ($F_{1,135} = 3.3$, $P = 0.073$) or morphological differential ($F_{1,135} = 0.032$, $P = 0.86$).

The duration of contests was driven by the interactive effect of temperature and time of day ($F_{1,135} = 9.1$, $P = 0.0036$; Fig. 1b).
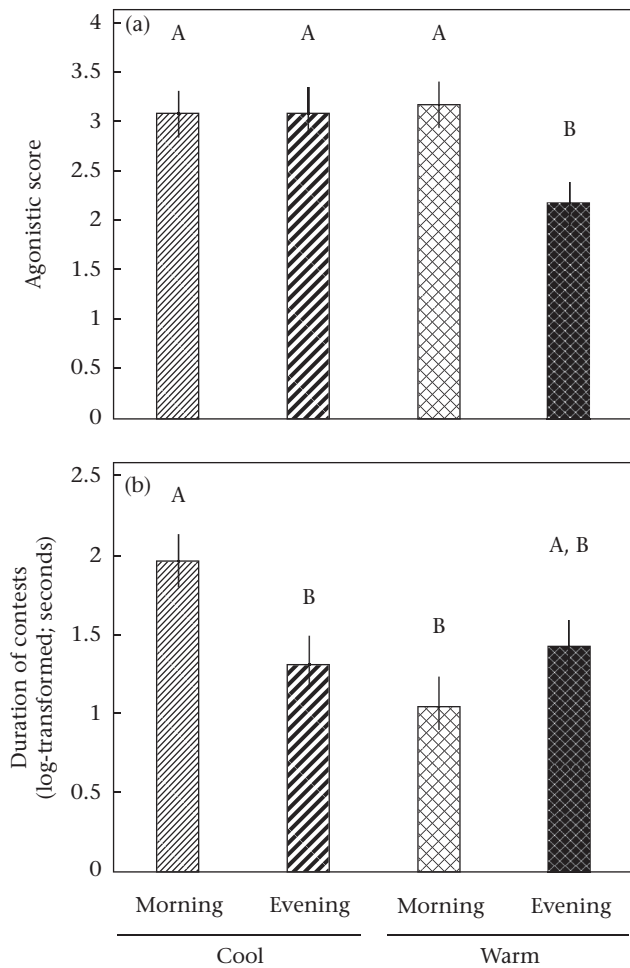
Figure 1. Effects of temperature and time of day on (a) agonistic score (0—6 scale) and (b) duration of contests between male *Gryllus firmus* ($N = 140$ contests). Values are means ± SEM, and significant differences are denoted by different uppercase letters above each column.

Morphological index influenced the outcome of contests ($\chi^2_1 = 19$, $P < 0.001$). A relatively large cricket was more likely to win a contest than a relatively small cricket (Fig. 2). Contest outcome was not affected by temperature ($\chi^2_1 = 0.038$, $P = 0.85$), time of day ($\chi^2_1 = 0.005$, $P = 0.94$) or a temperature∗time interaction ($\chi^2_1 = 0.23$, $P = 0.64$).

There was only one significant relationship between variables of agonistic contests. The duration of contests was positively correlated with the level of aggression of contests (Spearman correlation: $r_S = 0.48$, $N = 140$, $P < 0.001$).

DISCUSSION

Our results demonstrate that agonistic contests between males can be influenced by interactions between widespread, covarying cues experienced during adulthood. The dynamics of male—male agonistic contests (i.e. level of aggression and contest duration) in *G. firmus* shifted with the combined effects of temperature and time of day (Fig. 1). That is, we found support for additive (but not independent) effects of temperature and time of day on several metrics of agonistic contests. Body size or RHP played a role in one metric of contest dynamics (latency to initiate), and it also influenced the outcomes of contests. Crickets with a larger body mass, body size, mandible width and testes size (all strongly correlated) tended to win more frequently against smaller conspecifics (Fig. 2). In summary, although final outcomes of male—male contests appeared solely the result of biotic (body size or RHP) effects, dynamics of agonistic contests exhibited plasticity in response to thermal and circadian effects.

In male—male competition, morphological advantages, such as larger body size or more lethal specialized weaponry, can translate into a greater ability to secure resources (Huntingford, 2013). Indeed, *G. firmus* males with a significant size advantage over their opponents were more likely to win their contests in our study. This result is consistent with agonistic studies conducted with other crickets (Adamo & Hoy, 1995; Alexander, 1961; Hack, 1997a; Judge & Bonanno, 2008; but see ; Bertram, Rook, Fitzsimmons, & Fitzsimmons, 2011) and invertebrates (DiMarco & Hanlon, 1997; Elias, Kasumovic, Punzalan, Andrade, & Mason, 2008; Murai &
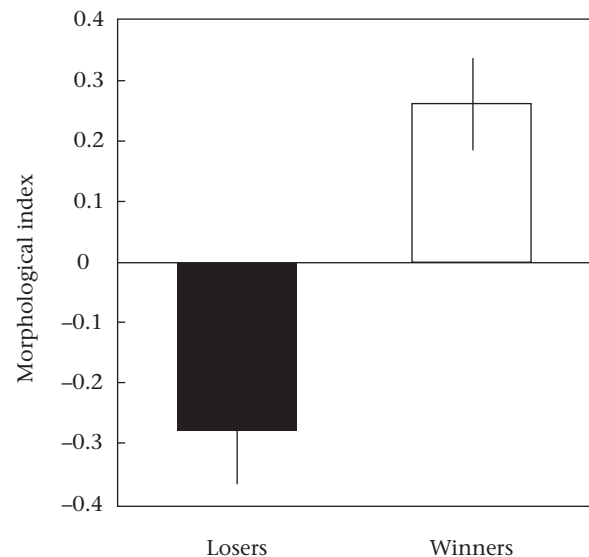
Morning fights, in particular, were nearly twice as long when they occurred in cool conditions compared to warm conditions (Fig. 1b). Due to this interactive effect, temperature also influenced contest duration ($F_{1,134} = 5.2$, $P = 0.024$; contests were longer in cooler conditions). Contest duration was not affected by time of day ($F_{1,135} = 0.69$, $P = 0.41$) or morphological differential ($F_{1,135} = 0.20$, $P = 0.66$).

Morphological differential (a proxy for opponents' differences in RHP) influenced the latency to initiate aggressive behaviour ($F_{1,135} = 5.5$, $P = 0.021$). Contests with a greater mismatch in opponent size led to a longer latency (Pearson correlation: $r_{138} = 0.21$). The latency to initiate aggression was not affected by temperature ($F_{1,135} = 2.2$, $P = 0.14$), time of day ($F_{1,135} = 2.5$, $P = 0.11$) or a temperature∗time interaction ($F_{1,135} = 0.73$, $P = 0.40$). In three of the four treatment combinations — cool morning, cool evening and warm morning — there were no significant correlations between morphological metrics (i.e. morphological index of loser, morphological index of winner, morphological differential) and contest metrics (i.e. latency to initiate, contest duration, level of aggression during contests). However, on warm evenings, the latency to initiate contests negatively covaried with the morphological index of the loser ($r_{35} = -0.46$, $P = 0.004$). There were no other significant correlations between morphological and contest metrics on warm evenings.

Figure 2. Difference in morphological index (a principal component explaining >80% of the variance in femur length, head width, body mass and testes mass) between losers and winners of contests. Values are means ± SEM for male *Gryllus firmus* ($N = 280$ individuals).

Blackwell, 2005; Prenter et al., 2006), as well as across vertebrate taxa — from swordtail fish (Moretz, 2003) to lizards (Huyghe et al., 2005; Jensson et al., 2005) to elephant seals (Le Boeuf, 1974). However, the development and maintenance of morphological advantages are not without costs. In dung beetles, for instance, the development of horns limits the resources allocated towards growth of nearby body parts (e.g. eyes, antennae or wings). Thus, selective pressure for weaponry balances the function of a given weapon in a specific habitat with the energetic costs of developing and maintaining this morphological character (Emlen, 2001, 2005; McCullough, Miller, & Emlen, 2016). Our data further indicate that taxa without specialized weaponry may similarly exhibit positive covariation among fitness-related traits. Males in our study with large morphological indices exhibited both high pre- and post-copulatory investment (i.e. larger external anatomy indicating high RHP and larger testes, respectively). Yet, the direction (i.e. positive or negative) of covariation between traits under pre- and post-copulatory selection varies across taxa (reviewed in Kahrl, Cox, & Cox, 2016).

Intraspecific aggression can improve the acquisition or protection of resources, but it is also associated with increased metabolic expenditure (e.g. Ros, Becker, & Oliveira, 2006; Xu, Chi, Cao, & Zhao, 2018). In contests between male crickets, displays of higher levels of aggression (e.g. grappling) are associated with higher rates of oxygen consumption than less aggressive displays (e.g. antennal fencing; Hack, 1997b), and male—male agonism may lead to damaged mandibles (Judge & Bonanno, 2008). *Acheta* crickets rely largely on mutual assessment of size-indicated RHP to decide when and for how long to engage in an aggressive interaction (Briffa, 2008; Hack, 1997a). For example, when faced with a large size asymmetry between opponents, the smaller cricket typically displays less aggression towards the perceivably larger cricket, thereby avoiding the higher metabolic costs of engaging in a disadvantageous (likely unwinnable) contest, while size-matched crickets tend to engage in more aggressive contests at higher energetic expenses (Hack, 1997a). Our results provide some support for mutual assessment in *Gryllus* crickets. Across all treatment combinations, contests between *G. firmus* males of mismatched body size (large difference in morphological index) took longer to initiate contests, potentially due to smaller males avoiding their larger opponents. Yet, this correlation (and most others comparing morphological and contest metrics) was not significant within any specific treatment combination. Rather, our results indicate a self-assessment (rather than a mutual assessment) strategy during warm evenings whereby contests with larger losers were quickly initiated (Prenter et al., 2006; Taylor & Elwood, 2003). Other species similarly rely on self-assessment or individual persistence, which occurs when disadvantaged (smaller) males do not adopt risk-abating strategies when engaged in a disadvantageous contest. For example, small male *Anolis* lizards display risky behaviour by invading the territories of larger males and engaging in highly aggressive, physical contests, despite losing most fights due to their morphological disadvantages (Jensson et al., 2005). Differences in strategies among taxa and across contexts suggest that modes of assessment and factors affecting assessment play a significant role in determining contest dynamics, although, ultimately, the victor is typically the individual with greater RHP or body size (reviewed in Arnott & Elwood, 2008, 2009).

Across animal taxa, the regulation of important behavioural patterns (e.g. agonistic contests) is a multifactorial process that adaptively integrates sensory systems (e.g. sensing and responding to RHP differential) with changes in the environment and circadian rhythms. For instance, male frogs express a circadian pattern of peak vocalization (for both attracting females and defending against competing males) that is regulated by variation in the microenvironment, such as increased temperature or humidity, two abiotic factors closely tied to reproductive success (Cui et al., 2011; Navas & Bevier, 2001). Many fish consistently display behavioural sleep, and circadian clocks programme sleep behaviour during the time of day in which fishes' sensory systems are less effective (e.g. diurnal fish that depend on visual foraging sleep at night when visibility is low; reviewed by Reebs, 2002). Salmonid fish can shift from diurnal to nocturnal foraging in response to lower environmental temperatures, as physiological changes in retinal pigments make the fish more dark-adapted (Fraser, Metcalfe, & Thorpe, 1993). Changes in temperature at certain times of day lead to a significant shift in refuge use in European minnows — individuals leave their refuges more frequently in the daytime under warm conditions whereas refuge use in the night remains low irrespective of temperature, reflecting the role of temperature and time of day on shifting predator avoidance behaviour (Greenwood & Metcalfe, 1998). Thus, although many studies have demonstrated the effects of time of day or temperature on fitness-related behaviours in isolation, our study is an important step in determining how these widespread factors combine to interact and affect important animal behaviours.

We show that the dynamics of male—male agonistic contests can be influenced by a combination of temperature and time of day (Fig. 1). Warm evening conditions elicited significantly lower levels of aggression compared to other time—temperature combinations (Fig. 1a). In addition, temperature influenced the duration of contests in the mornings. Cool conditions resulted in significantly longer fights than those in warm conditions (Fig. 1b), but this temperature effect was largely driven by morning (not evening) dynamics (Fig. 1b), suggesting the combined or additive roles of time of day and temperature. The observed change in contest strategy may be adaptive in relation to demand for accurate opponent assessment and/or to agonistic contest performance during certain times of the day in the field. In their natural environment, males in some species of *Gryllus* exhibit decreased movement during the cooler hours early in the photophase (French & Cade, 1987); thus, this may naturally be a time of day when there is a lower demand for effective agonistic contest strategies. Yet, future work in field-caught individuals is necessary to better understand the ecological and physiological costs and benefits of agonistic contests and whether plasticity in agonistic behaviour is evident in different environmental or temporal contexts.

We offer three proximate explanations for our results of longer, more aggressive contests (i.e. less efficient contest strategy) in cool morning conditions (Fig. 1). First, the sensory system may be influenced or constrained by the additive effects of temperature and time of day. The sensitivity of visual systems of many species is controlled, in part, by circadian rhythms (Barlow et al., 1989), which in turn, may be entrained by both light and temperature (Van Someren, 2003). These environmental cues may affect males' abilities to efficiently evaluate the RHP of their competitors. Maintaining accurate vision may be temperature dependent because temperature directly modulates synaptic transmission in invertebrates and mammals where an increase in temperature is accompanied by an increased effectiveness of synaptic transmission and a higher frequency of neuron firing (Fujii, Sasaki, Ito, Kaneko, & Kato, 2002; Kullmann & Asztely, 1998; Reig, Mattia, Compte, Belmonte, & Sanchez-Vives, 2009; Thompson, Masukawa, & Prince, 1985; Volgushev, Vidyasagar, Chistiakova, & Eysel, 2000). As temperature and light fluctuate, animals can compensate physiologically and/or behaviourally. Physiologically, light detection in the eyes at low illuminance is improved by spatial and temporal summation of photoreceptor signals in vertebrates and insects, but this improvement is offset by reduced temporal and

spatial resolution (Barlow, 1958; Pick & Buchner, 1979; Warrant, 1999; Warrant, Porombka, & Kirchner, 1996). Hornets decrease flight speed at low illuminance to behaviourally compensate for lower-quality visual processing and avoid potential in-flight collisions, and they also alter flight speed with changes in temperature (Spiewok & Schmolz, 2005). Vision is also important in agonistic behaviour. Blinded male crickets fight more aggressively than nonblinded males, even when disadvantaged with smaller body size or losing a previous agonistic contest (Hofmann & Schildberger, 2001; Rillich et al., 2007). Our results indicate that more subtle and widespread factors (i.e. temperature or time of day, rather than blinding) may influence fitness-related behaviours that are linked to visual acuity.

Second, longer, more aggressive contests may occur on cool mornings (Fig. 1) due to the influence of temperature and time of day on performance or the expression of RHP. Temperature strongly influences muscle function and locomotor capacity (reviewed in Bennett, 1985, 1990; James, 2013). Thus, cooler conditions may limit a male's fighting ability whereby a cooler male's RHP would not be fully expressed. Furthermore, across many animal taxa, time of day affects variation in hormone levels, which are responsible for a range of behaviours — from reproduction to dispersal to agonistic behaviour (Juarez-Tapia & Miranda-Anaya, 2017; Kou et al., 2008, 2009; Pilorz, Helfrich-Förster, & Oster, 2018; Schoeller et al., 2016; Zera, 2016). For example, juvenile hormone (JH) levels fluctuate daily in crickets and other insects (Bloch, Hazan, & Rafaeli, 2013; Zera, 2016), and shifts in JH levels are also associated with agonistic contest success in cockroaches (Kou et al., 2008, 2009). Future work is necessary to determine whether the additive effects of temperature or time of day on agonistic contests is due to these factors' influence on either the perception or expression of RHP.

Third, longer, more aggressive contests (i.e. less efficient contest strategy) on cool morning conditions (Fig. 1) may be due to motivational differences driven by the combined effects of temperature and time of day. Across many taxa, contestants compete longer or more intensely if they are competing for a resource of greater value (reviewed in Briffa & Sneddon, 2007). Gryllus crickets have a strong preference for refuges (Hedrick & Kortet, 2006), which are an important resource across taxa (Berryman & Hawkins, 2006), and male–male contests likely serve to mediate refuge use in crickets (e.g. Adamo & Hoy, 1995). If refuges are less valuable or females less receptive in the morning, then male crickets would be less likely to engage in male–male contests in the field during (presumably cooler) mornings. Thus, staging contests in cool morning conditions results in less efficient contests, and it further highlights the need to better characterize agonistic behavioural dynamics in nature for our study system. Related, aggressive motivation in Gryllus crickets is mediated by the neurotransmitter, octopamine (Rillich & Stevenson, 2011), and octopamine levels in other insects are modulated by light:dark regimes (Linn, Campbell, Poole, Wu, & Roelofs, 1996; Linn & Roelofs, 1992) and temperature (Armstrong & Robertson, 2006). Thus, aggressive motivation may vary with temperature and time of day due to ultimate and/or proximate causation (i.e. variation in resource value and/or octopamine levels, respectively).

In summary, our results reaffirm the importance of morphological features in determining contest outcome, but they also demonstrate that environmental cues have complex effects on the dynamics of agonistic contests. Most notably, interactions between temperature and time of day can modulate the duration and aggression level of contests (Fig. 1), as well as contest assessment strategy. Future work should continue to examine whether the sensitivity of temperature and circadian-driven sensory or locomotor systems may affect males' abilities to efficiently evaluate or express RHP because this may hinder males' abilities to adopt the most cost-efficient contest strategies in some conditions. We thus encourage investigations into the energetic consequences of inefficient decision making related to male–male contests. For example, how much energy is wasted on longer, more aggressive contests during cool mornings relative to the amount of energy conserved by forgoing energetic investment into the maintenance of contest-related processes (e.g. sensory and locomotor systems)? Furthermore, despite the strong correlation between level of aggressive escalation and contest duration, each contest metric responded differently to temperature and time of day (Fig. 1), lending support for the need to examine important animal behaviours in a range of environmental conditions to better understand the interdependence and plasticity of behaviours.

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