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Stag beetle *Cyclommatus mniszechi* employs both mutual- and self-assessment strategies in male-male combat

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ARTICLE INFO

ABSTRACT

Keywords: Fighting ability Mandible Mutual assessment Self-assessment Weaponry Animals may base contest decisions on their fighting ability alone (self-assessment) or also their opponents' (mutual assessment). Many male stag beetles develop disproportionately enlarged mandibles and use them as weapons. Information on their assessment strategy is limited. To investigate their assessment strategy and whether they adopt the same strategy at different stages of contests, we used food to encourage male *Cyclommatus mniszechi* of different (random pairings) or similar (ML-matched pairings) mandible length (ML) to interact. For the random pairings, losers had shorter mandibles than winners and were faster to feed. Overall contest duration and the tendency to escalate to tussles associated positively with winners' ML and average ML in the random and the ML-matched pairings, respectively, consistent with self-assessment. Non-tussle phase duration, however, positively associated with losers' ML in the random pairings and had no association with average ML in the ML-matched pairings, consistent with mutual assessment. These results show that (1) the males employ both assessment strategies, (2) winners have more control over contest intensity than losers, and (3) males with shorter mandibles are quicker to feed and also more likely to lose fights.

1. Introduction

Animals often fight each other to compete for limited resources (Armstrong, 1991; Chapman and Kramer, 1996; Riechert, 1986). Fighting can be costly, because by taking part in contests, animals expend energy and time, risk physical injuries and predation and forgo other opportunities (Austad, 1983; Brick, 1999; Neat et al., 1998). An asymmetry in fighting ability (or resource holding potential) between two competitors often has an important influence on their chances of winning and the costs of their participating in the fight (Arnott and Elwood, 2009). How the two competitors' fighting ability should influence their contest interactions depends on whether they base their decisions solely on their own fighting ability or also on their opponents' fighting ability (see Arnott and Elwood, 2009 for a review) (Table 1).

It could be advantageous for an individual to assess its fighting ability relative to that of its opponent (mutual assessment) and retreat immediately once it assesses itself to be a worse fighter than its opponent. This helps the individual to avoid incurring further unnecessary costs in contests that it cannot win. The larger the difference in their fighting abilities, the sooner the weaker contestant should be able to detect its inferiority and retreat; thus, contest duration and intensity should relate negatively with the difference in fighting ability (Enquist and Leimar, 1983). Many studies have, indeed, shown that contests between individuals with more similar fighting ability take longer to resolve (Austad, 1983; Hack, 1997; Rosenberg and Enquist, 1991). Taylor and Elwood (2003), however, used simulated data to demonstrate that negative associations between contest duration and the disparity in fighting ability can also occur even if individuals do not in fact assess their opponents' fighting ability (self-assessment). They further showed that, if individuals do employ mutual assessment in contests, the loser's persistence should relate positively with its own fighting ability but negatively with the winner's fighting ability (Table 1).

As mentioned above, some contestants make contest decisions based solely on their own fighting ability, without gathering information about their opponents' fighting ability (self-assessment) (Taylor and Elwood, 2003). For these contests, the loser's persistence should also relate positively with its own fighting abilities. How a loser's persistence in

https://doi.org/10.1016/j.beproc.2022.104750

Received 23 February 2022; Received in revised form 31 August 2022; Accepted 31 August 2022 Available online 5 September 2022 0376-6357/© 2022 Elsevier B.V. All rights reserved.

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Predicted relationships between contest duration/intensity and contestants' fighting ability (FA) from the three major assessment models: positive (+), negative (-) or no (N) relationship.

	Mutual Assessment	Pure self-assessment	Cumulative assessment
Decision making criterion	FA difference	Self FA	Self FA
Random pairings			
FA difference	-	N/-	_
Loser FA	+	+	+
Winner FA	_	N/+	_
FA-matched pairings			
Pair FA	Ν	+	+

these contests should relate with the winner's fighting ability, however, depends on whether the winner's actions inflict injuries on the losers (Table 1) (Arnott and Elwood, 2009; Taylor and Elwood, 2003). If the winner does not inflict injuries on the loser (pure self-assessment), the loser's persistence should have little or no relationship with the winner's fighting abilities (Arnott and Elwood, 2009; Taylor and Elwood, 2003). If the winner's actions inflict injuries on the loser (cumulative assessment), even if the loser does not acquire information about the winner's ability, the loser's performance will be compromised such that its persistence should relate negatively with the winner's fighting ability (Arnott and Elwood, 2009; Taylor and Elwood, 2003; Payne, 1998), which is the same relationship as expected for the mutual-assessment strategy.

Contests between rivals that are matched in fighting ability can be used to further distinguish between the mutual assessment and the two self-assessment (pure self-assessment and cumulative assessment) strategies (Table 1). With the mutual-assessment strategy, contest duration (or intensity) should not vary between pairs with better and worse fighting ability because the contestants' fighting ability remains matched (i.e., no difference) regardless. With the pure self-assessment strategy, contest duration/intensity should associate positively with the pair's fighting ability because individuals with better fighting ability are able to persist longer in contests. With the cumulative-assessment strategy, contest duration/intensity should also associate positively with the pair's fighting ability because endurance should relate positively with a contestant's own fighting ability but costs accruing due to the rival's action should vary only with the difference in fighting ability (i.e., relative fighting ability) (Arnott and Elwood, 2009).

The assessment strategies that individuals adopt in contests are rather diverse (Arnott and Elwood, 2009; Chapin et al., 2019; Pinto et al., 2019). Some individuals have been concluded to adopt mutual-assessment strategies (wasps: Kemp et al., 2006), some pure self-assessment strategies (amphipods: Prenter et al., 2006; Cape dwarf chameleons: Stuart-Fox, 2006) and some cumulative-assessment strategies (fiddler crabs: Morrell et al., 2005). Moreover, the contest interactions of many animals do not fit neatly into one of the three major assessment strategies (Arnott and Elwood, 2009; Chapin et al., 2019). Some individuals seem to assess the fighting ability of the opponents but not their own (cichlid fish: Reddon et al., 2011; crickets: Rillich et al., 2007). And, in some contests, only one of the contestants gathers information about the opponent (hermit crabs: Briffa and Elwood, 2001, 2004; swordtail fish, Prenter et al., 2008). Furthermore, some individuals use different assessment strategies at different stages of a contest (mangrove killifish: Hsu et al., 2008). So far, there seem to be no apparent rules for predicting what assessment strategy an individual would employ in contests. And, because individuals do not necessarily adopt the same assessment strategy throughout the entire contest, contest interactions should be measured and assessment strategy should be evaluated for different stages of a contest to gain a better understanding of the behavioural decisions over the progress of the contest.

Many animal species, including insects, develop disproportionately large, exaggerated weaponry traits (Emlen, 2008). Male stag beetles (Lucanidae), for instance, have enlarged mandibles which often serve as weapons in competition for limited resources (e.g., feeding sites, females) (Emlen, 2008). And males with longer mandibles are more likely to win fights (Goyens et al., 2015a; Songvorawit et al., 2018). In the stag beetle *Cyclommatus metallifer*, for instance, males with longer mandibles have larger bodies and mandible closer muscles and produce higher bite forces than males with smaller mandibles, showing mandible size to be an honest signal for fighting ability (Goyens et al., 2014; Mills et al., 2016).

It has been suggested that the display behavior of contesting male stag beetles, which face each other and stand up with their mandibles open wide, allows males to assess each other visually by comparing mandible opening width which correlates positively with body and mandible size (Okamoto and Hongo, 2013; Mills et al., 2016). The results that contests are more likely to escalate into mutual physical attacks between male stag beetles that are more matched in mandible and body size also lend support to the hypothesis that male stag beetles assess each other's fighting ability (Okamoto and Hongo, 2013). Furthermore, the mandibles of C. metallifer have high densities of mechanoreceptors and these sensors are distributed according to the distribution of the material stress imposed by biting (Govens et al., 2015b). In addition to providing feedback to regulate bite force and prevent jaw failure (Goyens et al., 2015b), these mechanoreceptors may also provide mechanosensory input to enable the males to assess opponents' size in contests as in the Japanese rhinoceros beetle (McCullough and Zinna, 2013). Overall, male stag beetles appear to have sensory structures and exhibit behaviors that allow them to assess each other's fighting ability in contests.

Despite their showy weaponry and noticeable combative tendencies, studies that have tested male stag beetles' assessment strategy are surprisingly scarce. For fights between male *C. metallifer*, contest duration associated positively with losers' mandible length but had no relationship with winners' mandible length and thus no clear assessment strategy could be concluded (Goyens et al., 2015a). For fights between male *Aegus chelifer*, although fight duration was negatively associated with the difference in head width (a good proxy of fighting ability), it did not have a significant association with either the winner's or the loser's head width, and thus, again, no clear assessment strategy could be concluded (Songvorawit et al., 2018). It therefore remains unclear whether stag beetles assess each other's fighting ability in combat.

This study aimed to investigate the assessment strategy of male *Cyclommatus mniszechi* stag beetles. Individuals of the stag beetle *C. mniszechi* are sexually dimorphic; females are smaller than males (Kuan, 2011) (Fig. 1a). Similar to many other stag beetles (Okamoto and Hongo, 2013), males and females of *C. mniszechi* aggregate on the surface of trees that exude sap, and males often encounter and fight each other around these sap spots (Fig. 1b; personal observation). The males' body and mandible sizes are highly variable.

We first staged contests between the males of different sizes to evaluate the importance of four morphological traits (mandible length, head width, elytra length and body weight) to the males' ability to win (fighting ability). With these contests, we also tested among the three major assessment strategies by examining the importance of winners' and losers' fighting ability to losers' decision to retreat. We then staged contests between males of similar fighting ability to further test among the three assessment strategies (Arnott and Elwood, 2009; Taylor and Elwood, 2003) by examining the relationship between pairs' fighting ability and losers' decision to retreat. Using these contests between beetles of different and similar fighting ability, we further investigated whether the male stag beetles use the same assessment strategies at different stages of a contest, as some animals have been shown to switch assessment strategies during contests (Hsu et al., 2008; Lobregat et al., 2019). Because the males aggregate and fight around feeding sites in their natural habitat, we placed a feeding station with insect jelly in the contest chamber for all contests to encourage the two contestants to encounter each other and interact. As resource ownership has been



Fig. 1. A male *C. mniszechi* guarding a female next to a sap site (a) on the trunk of a *Koelreuteria elegans* tree, and (b) against an intruding male on the trunk of a *Citrus* species.

known to affect an individual's aggressiveness and tendency to win (Arnott and Elwood, 2008), we took account of the potential influence of being the first to feed on the insect jelly when evaluating the importance of fighting ability to contest decisions.

2. Materials and methods

2.1. Study organism

Cyclommatus mniszechi inhabits lowland forests below approximately 750 m in southeast China, Vietnam and northern Taiwan (Li, 2004). The adult beetles are mostly seen in their natural habitats between May and August (personal observation). In the laboratory, it takes approximately 10 months for eggs to develop into adults (personal observation). The males can be divided into three morphs ($\alpha/\beta/\gamma$) based on mandible morphology (Kuan, 2011). The mandibles have (1) tusk-like projections (denticles) at their distal halves for the α males, (2) denticles at their proximal halves and close to their bases for the β males and (3) have with no apparent denticles for the γ males. Conversely, using the allometric relationship between mandible and body size, Chen et al. (2020) divided the males into two morphs, major and minor with mandibles longer and shorter than 14.01 mm, respectively. The allometric slopes were positive for both morphs but steeper for the minor morphs.

Contests between male *C. mniszechi* were staged in 2017 and 2018. Males from various sources (natural habitats, breeders, laboratory breeding) were used for the contests. We collected *C. mniszechi* from lowland forests of northern Taiwan between 2016 and 2018. Because it was difficult to find larvae or intact male beetles (no damaged or missing parts) in their natural habitats, we also acquired larvae from local breeders and reared them to adulthood in the laboratory. After being used for the contests, the males were bred with females and the male offspring were then used for the contests in the following year after they emerged as adults. Each male was used only once in this study.

Larvae were reared in 250 ml clear circular plastic containers (height = 4.5 cm; diameter = 7.5 cm for the bottom and 9.5 cm for the top) filled with fermented sawdust (good-quality microparticle fermented oak sawdust, Max Piggyfat Insect Feeding Facilities, Taiwan) under a 12 h:12 h (light:dark) cycle. The larvae of 2016 were kept at 25 °C. For the larvae of 2017, in an effort to synchronise males' emergence (Kojima, 2014; Kojima et al., 2014) for the contests in the following year, we adjusted the rearing temperature (15.8–25.3 °C) every two weeks to match the 2012–2016 mean monthly temperature at the Central Weather Bureau stations (Cyuchih and Shanjia) closest to the collection sites. All adult stag beetles were housed individually in translucent polypropylene maintenance containers (15 cm \times 10 cm \times 12 cm) containing moist moss at 25 °C under a 12 h:12 h (light:dark) cycle and fed insect jelly (PPS-801, Champ E Pets Corporation, Taipei, Taiwan) ad libitum.

2.2. Contests

Male beetles collected from the field were isolated for at least two weeks before being used for contests. Males reared in the laboratory were at least 21 days after eclosion when used for the contests. We paired up males randomly and staged contests between them in 2017 to examine which of the four morphological traits (mandible length, head width, elytra length and body weight) best predicted contest outcomes in C. mniszechi. This morphological trait was then used as a proxy for the fighting ability of the males and used to match them for the contests in 2018. We measured the mandible length (ML), head width (HW) and elytra length (EL) of the males to the nearest of 0.01 mm using a digital calliper (99MAD027M1, Mitutoyo, Kanagawa, Japan) on the day the beetles were collected from the field or the 21st day after the eclosion of the beetles reared in the laboratory. We measured the males' body weight (BW) to the nearest of 0.001 g using a digital scale (CT-50, HIRODA, Shenzhen, China) one day before the contests. Mandible length was the average linear distance between the distal tip of the mandible and the axis of the mandibular joint of the two mandibles (Goyens et al., 2016; Kuan, 2011; Songvorawit et al., 2018); HW was the linear distance between the tips of the protrusions anterior to the eyes; EL was the linear distance between the posterior ends of the scutellum and the elytra.

Sixty two males were divided into 31 pairs at random (random pairings) in 2017. Of these 62 males, 9 were wild-caught adults and 53 were larvae from various sources (lab bred: 28, local breeders: 25) reared to adulthood in the laboratory. Out of the four morphological traits (ML, HW, EL, BW), ML best predicted winners of the random pairings. We therefore matched for males' ML (ML-matched pairings) for the contests between males of similar fighting ability in 2018. The absolute difference in ML between the contestants was less than 1 mm (range: 0.01 – 0.81 mm, median = 0.16 mm, mean \pm SD = 0.21 \pm 0.19 mm). We matched a total of 57 pairs (ML of these 114 males: median = 13.66 mm, mean \pm SD = 13.67 \pm 3.13 mm). Of the 114 males in the 57 ML-matched pairings, 17 were wild-caught adults and 97 were larvae from various sources (lab bred: 71, local breeders: 9, field: 17) reared to adulthood in the laboratory.

All contests were staged in acrylic contest arenas ($32 \text{ cm} \times 18 \text{ cm} \times 30 \text{ cm}$) with 400 ml sawdust (1 cm height) at the bottom. An arena was divided into three zones with two acrylic dividers, one central zone (16 cm \times 18 cm) in-between two resting (8 cm \times 18 cm) zones (Fig. 2). We placed a piece of half-cut wood (16 cm \times 10 cm \times 5 cm) at the centre of the central zone to serve as a feeding station to facilitate interactions between the two males. We placed three to four dry oak leaves (*Quercus glauca*, Fagaceae) on the surface of the sawdust layer in each of the two resting zones for the beetles to hide under. The arenas were kept at 25 °C on a 12 L (6:00–18:00):12 D (18:00–6:00) photoperiod.

All contests were staged between 18:00 and 19:00 because *C. mniszechi* usually hide under cover during day time and become active



Fig. 2. The overhead view of a contest arena.

at dusk (personal observation). The day before the contest, the two males of a contest pair were individually marked on their elytra with nail polish. The two males were then placed in the two resting zones (one male per resting zone) of a contest arena at 18:00 to acclimatise in the arena for 1 d. The next day (the day of contest), at 18:00, we inserted a 2 ml tube filled with insect jelly at the centre of the feeding station and removed the two dividers. The males would emerge from under the dry leaves, move around the arena and walk towards the feeding station after the dividers were lifted. Agonistic interactions between males of C. mniszechi are described in detail in Chen et al. (2020). Briefly, a contest (Supplementary Video S1) starts with two contestants facing each other and one of the males challenging its opponent by standing up with its mandible widely open (defensive posture). The opponent responds with defensive postures or attacks. Attacks are brief bouts of physical interaction in which males use their mandibles to push, pinch or grasp their opponents. If both contestants persist, they escalate into tussles by interlocking their mandibles and pushing back and forth. One of the contesting males (i.e., the loser) could retreat at any of the stages described above by moving away (often backward) from its opponent (i. e., the winner). Once one of the contestants retreated, the contest was terminated. Contest duration was defined as the time period between the defensive posture and the time the loser retreated. A contest was divided into the non-tussle and the tussle phases to examine whether the male stag beetles adopt the same assessment strategies at different stages of a contest. Contests that did not escalate into tussles consisted of only the non-tussle phase and the duration of the non-tussle phase was the same as the contest duration. Contests that escalated into tussles consisted of both the non-tussle and the tussle phases. For these escalated contests, the duration of the non-tussle phase was the time period between the defensive posture and the time the two contestants first inter-locked their mandibles and the duration of the tussle phase was the time period between the first mandible inter-locking and the time the loser retreated. If the two males did not exhibit sufficient aggression towards each other to produce a clear winner and loser, the trials were terminated after 1 h. After the contest, the two males were removed from the arena and placed back in their maintenance containers. All contests were recorded using night-vision video monitors (DS-VR7160H, Der Shuenn, Taipei, Taiwan) positioned 65 cm above the arena. BORIS v. 7.4 (Behavior Observation Research Interactive Software) (Friard and Gamba, 2016) was used to transcribe the contest behaviours from the videos.

Supplementary material related to this article can be found online at doi:10.1016/j.beproc.2022.104750.

2.3. Statistical analyses

The two males in one of the random pairings did not interact with

each other and the contest trial was terminated after 1 h. This pair was excluded from subsequent data analyses. The final sample size was thus 30 for the random pairings and 57 for the ML-matched pairings. To identify the morphological traits that were important to the males' ability to win, we used paired t tests to examine whether winners and losers of the random pairings differed significantly in ML, HW, EL or BW. Cohen's *ds* were calculated for these paired t tests. In the contest arena, a feeding station with insect jelly was provided to encourage the two contestants to interact. To evaluate the potential influence of resource ownership on contest outcome, we used Fisher's exact tests to examine the association between feeding behavior and the tendency to win. We used two-sample t tests to examine the difference in ML between individuals that did and did not feed on the insect jelly before the contest started. Cohen's *ds* were calculated for these two-sample t tests.

To test among the three assessment strategies, we used multiple regression models to evaluate the importance of the winner's and the loser's ML (random pairings) or the average ML (ML-matched pairings) to overall contest duration (linear regression models), the likelihood of a contest escalating into the tussle phase (logistic regression models), the duration of the non-tussle phase (linear regression models) and the duration of the tussle phase (linear regression models), taking account the influence of whether the loser had arrived at the food station and fed on the insect jelly first. Because only a subset of the contests escalated to the tussle phase, for the duration of the non-tussle phase, we evaluated whether or not a contest escalating to the tussle phase affected the duration and the importance of contestants' ML to the duration. To do so, in the regression models of the non-tussle phase, we included a variable indicating if the contest escalated to the tussle phase as well as the interactions between this variable and the contestants' ML. Contest duration, the duration of the non-tussle phase and the duration of the tussle phase were natural log transformed for the residuals of the models to fit the normal distribution requirement (Shapiro-Wilk W test; $p \ge 0.219$). JMP 8 (SAS institute Inc., Cary, NC, USA) was used for the statistical analyses.

3. Results

3.1. Differences in morphological traits between winners and loser of the random pairings

The ML, HW, EL and BW of the 60 male stag beetles used for the random pairing were highly positively correlated ($r = 0.80 \sim 0.95$, p < 0.001 for all; α adjusted for multiple comparisons = 0.05/6 = 0.008) (Table 2). Despite the correlations, only some of these morphological traits differed significantly between the winners and losers. The difference between the winners and losers reached statistical significance in ML (p = 0.008), but not in HW (p = 0.026), EL (p = 0.215) or BW (p = 0.100) after adjusting α (= 0.05/4 = 0.013) for multiple comparisons (Table 3, Fig. 3). Because these results indicated that ML was a reasonable indicator for the fighting ability of the male beetles, ML was used in subsequent analyses to evaluate the relationships between fighting ability and contest decisions in the males.

Table 2

Pearson's pair-wise correlations (95 % CI) between the morphological traits of the males used for the random pairings (n = 60, p < 0.001 for all correlations; α adjusted for multiple comparisons = 0.05/6 = 0.008).

	Mandible length	Head width	Elytra length
Head width	0.95 (0.92, 0.97)	0.04 (0.01, 0.07)	
Body weight	0.92 (0.87, 0.95) 0.80 (0.69, 0.88)	0.94 (0.91, 0.97) 0.87 (0.79, 0.92)	0.86 (0.78, 0.91)

The differences in the morphological traits between the winners and losers (winner – loser; mean \pm SE) of the random pairings (paired t-test, n = 30, α adjusted for multiple comparisons = 0.05/4 = 0.013). Significant effects are in bold. d: Cohen's d.

Trait	Difference	df	t	р	d
Mandible length (mm)	1.16 ± 0.41	29	2.9	0.008	0.52
Head width (mm)	$\textbf{0.69} \pm \textbf{0.30}$	29	2.4	0.026	0.43
Elytra length (mm)	$\textbf{0.29} \pm \textbf{0.23}$	29	1.3	0.215	0.23
Body weight (g)	$\textbf{0.09} \pm \textbf{0.05}$	29	1.7	0.100	0.31



Fig. 3. The morphological traits (mean \pm SE) of the winners (\blacksquare) and the losers (\Box) of the random pairings (n = 30 for each of the bars).

3.2. Feeding behavior of the winners and losers

Out of the 30 winners and losers of the random pairs, a higher proportion of losers (21/30; 70 %) than winners (12/30; 40 %) (Fig. 4) arrived at the food station and fed on the insect jelly before the contest started (2-tailed Fisher's exact test, p = 0.037). For the winners, the mandibles of those that fed on the insect jelly before the contest started (mean \pm SE: 15.86 \pm 0.48 mm) were marginally shorter than the mandibles of those that did not (17.10 \pm 0.40 mm) ($t_{28} = 2.0$, p = 0.058, d = 0.74). Losers that did (15.50 \pm 0.57 mm) or did not (15.31 \pm 0.88 mm) feed on the insect jelly before the contest started did not differ significantly their mandible length ($t_{28} = 0.2$, p = 0.858, d = 0.07).

For the 57 ML-matched pairs, winners (31/57; 54 %) and losers (29/ 57; 51 %) (Fig. 4) did not differ in their likelihood of arriving at the food station and feeding on the insect jelly before the contest started (2-tailed Fisher's exact test, p = 0.851). Winners that did (13.22 \pm 0.56 mm) or did not (14.19 \pm 0.61 mm) feed on the insect jelly before the contest started did not differ significantly in their mandible length ($t_{55} = 1.2$, p = 0.250, d = 0.31). Similarly, losers that did (12.99 \pm 0.57 mm) or did not (14.36 \pm 0.58 mm) feed on the insect jelly before the contest started did not differ significantly in their mandible length ($t_{55} = 1.7$, p = 0.101, d = 0.44).





3.3. Assessment strategy

To account for the potential influence of resource ownership on contest strategy, we included whether or not the loser was the first to feed on the insect jelly before the contest started as a predictor variable in all regression models. A loser was deemed to be the first to feed on the insect jelly if it started feeding before the winner or if it was the only contestant to feed on the insect jelly before the contest started.

3.3.1. Overall contest duration

For the random pairings, the winner's (b = 0.38, p = 0.049) but not the loser's (b = 0.13, p = 0.296) ML was positively related with the overall contest duration (Table 4a) (Fig. 5a, b); the longer the winner's mandible, the longer the contest lasted. Whether or not the loser was the first to reach the food station and feed on the insect jelly did not have a significant effect on contest duration (b = 0.09, p = 0.876). For the MLmatched pairings (Table 4b), the average mandible length positively associated with contest duration (b = 0.15, p = 0.001) (Fig. 5c). The longer the contest pair's mandible, the longer the contest lasted. The influence of whether or not the loser was the first to reach the food station and feed on the insect jelly on the duration of ML-matched contests remained insignificant (b = -0.03, p = 0.931).

These relationships between overall contest duration and ML are mostly consistent with the pure self-assessment strategy and not the mutual- or the cumulative-assessment strategies.

3.3.2. Contest intensity - the likelihood of escalating into the tussle phase

Ten out of the 30 random pairings escalated into the tussle phase. The difference (larger - smaller) in ML did not differ significantly between the pairs in which the contest interactions did or did not escalate into the tussle phase (mean difference \pm SE: tussled 2.14 mm \pm 0.50 mm, did not tussle 1.82 mm \pm 0.36 mm; two sample t-test, t_{28} = 0.5, p = 0.609, d = 0.20). However, contestants with longer mandibles won more fights than those with shorter mandibles only in contests that escalated into the tussle phase (9:1; 2-tailed binomial test, p = 0.022) and not in those that did not escalate into the tussle phase (12:8; 2-tailed binomial test, p = 0.503). Fifteen out of the 57 ML-matched pairings escalated into the tussle phase. The difference in ML did not differ significantly between pairs in which the contest interactions did or did not escalate into the tussle phase (mean difference \pm SE: tussled 0.24 mm \pm 0.05 mm, did not tussle 0.20 mm \pm 0.03 mm; two sample ttest, $t_{55} = 0.5$, p = 0.592, d = 0.16). Contestants with longer and shorter mandibles did not win different numbers of fights, either those that escalated into the tussle phase (9:6; 2-tailed binomial test, p = 0.607) or those that did not (22:20; 2-tailed binomial test, p = 0.878), as expected because they were matched for ML.

For the random pairings (Table 5a), only the winner's ML (b = 1.15, p = 0.010) and not the loser's ML (b = -0.02, p = 0.940) significantly predicted the tendency to escalate into the tussle phase (Fig. 6a). The longer the winner's mandible, the more likely the interactions escalated

Table 4

Multiple linear regression models examining the importance of mandible length (ML) to the overall contest duration of the (a) random and (b) ML-matched pairings. Loser fed 1st: an indicator variable for losers that were the first or only contestant to feed on the insect jelly before the contests started; the baseline group comprised the losers that were not first. Significant effects are in bold.

	b	(95 % CI)	F	dfs	р	
(a) Random pairings (n $=$ 30):						
ML-winner	0.38	(0.00, 0.77)	4.2	1,26	0.049	
ML-loser	0.13	(-0.12, 0.37)	1.1	1,26	0.296	
Loser fed 1st	0.09	(-1.13, 1.32)	0.0	1,26	0.876	
(b) ML-matched pairings ($n = 57$):						
ML-average	0.15	(0.06, 0.25)	11.6	1,54	0.001	
Loser fed 1st	-0.03	(-0.61, 0.56)	0.0	1,54	0.931	



Fig. 5. The relationship between overall contest duration (ln transformed) and the mandible length of the (a) winners and the (b) losers of the random pairings, and the (c) average mandible length of the winners and losers of the ML-matched pairings.

Multiple logistic regression models examining the importance of mandible length (ML) to the likelihood of male *C. mniszechi* escalating contests into the tussle phase for the (a) random and (b) ML-matched pairings. Loser fed 1st: an indicator variable for losers that were the first or only contestant to feed on the insect jelly before the contests started; the baseline group comprised the losers that were not first. LR χ^2 : likelihood ratio χ^2 . Significant effects are in bold.

	b	(95 % CI)	$LR\chi^2$	df	р
(a) Random pairing	s (n = 30):				
ML-winner	1.15	(0.24, 2.46)	6.7	1	0.010
ML-loser	-0.02	(-0.55, 0.48)	0.0	1	0.940
Loser fed 1st	1.39	(-0.95, 4.54)	1.3	1	0.254
(b) ML-matched pa ML-average	irings (n = 5 0.23 0.98	57): (0.02, 0.48) ($-0.34, 2.39$)	4.6	1	0.033

into the tussle phase. Whether or not the loser fed first (b = 1.39, p = 0.254) did not predict the tendency to tussle. For the ML-matched pairings, the average ML contributed significantly to the tendency to tussle (b = 0.23, p = 0.033) (Table 5b); the longer the contest pair's mandibles, the more likely their interactions escalated into the tussle phase (Fig. 6b).

The relationships between the tendency to escalate to the tussle phase and ML are, again, mostly consistent with the pure self-assessment strategy and not the mutual- or the cumulative-assessment strategies.

3.3.3. Duration of the non-tussle phase

For the random pairings (Table 6a), whether or not the contests escalated to the tussle phase did not have a significant effect (b = 9.60, p = 0.201) or significant interaction effects with either the winner's ($b = -0.32 \ p = 0.509$) or the loser's (b = -0.24, p = 0.273) ML on the duration of the non-tussle phase. Furthermore, neither the winner's (b = 0.23, p = 0.170) nor the loser's (b = 0.12, p = 0.286) ML had significant association with the duration of the non-tussle phase (Fig. 7a, b). Whether or not the loser was the first to reach the food station and feed on the insect jelly also did not have a significant effect on the duration (b = -0.03, p = 0.953).

For the ML-matched pairings (Table 6b), whether or not the contests escalated to the tussle phase also did not have a significant effect (b = 1.68, p = 0.262) or interaction effect with the average ML (b = -0.11, p = 0.260) on the duration of the non-tussle phase. The average ML, however, associated positively with the duration of the non-tussle phase (b = 0.14, p = 0.004) (Fig. 7c). The longer the contest pair's mandibles, the longer the non-tussle phase lasted. The influence of whether or not the loser was the first to reach the food station and feed on the insect jelly on the duration remained insignificant (b = -0.18, p = 0.511).

The significant positive association between the duration and the average ML for the ML-matched pairings is consistent with both the pure self-assessment and the cumulative-assessment strategies. The lack of a negative association between the duration and the winner's ML for the random pairings, however, is consistent with the pure self-assessment but not the cumulative-assessment strategy.



Fig. 6. Mandible length of the winners and the losers of (a) the random pairings and (b) the ML-matched pairings that escalated (•) and did not escalate (•) into the tussle phase.

Multiple linear regression models examining the importance of mandible length (ML) to the duration of the non-tussle phase for the (a) random and (b) ML-matched pairings. For these models, we also evaluated whether a contest being escalated to the tussle phase (Tussled) affected the duration of the non-tussle phase and the importance of ML (ML×Tussled) to the duration. Tussled: an indicator variable for contests that were escalated to the tussle phase; the baseline comprised the contests that were not escalated to the tussle phase. Loser fed 1st: an indicator variable for losers that were the first or only contestant to feed on the insect jelly before the contests started; the baseline group comprised the losers that were not first. Significant effects are in bold.

	b	(95 % CI)	F	dfs	р
(a) Random pairings (n = 30):					
ML-winner	0.23	(-0.11, 0.58)	2.0	1,23	0.170
ML-loser	0.12	(-0.10, 0.33)	1.2	1,23	0.286
Loser fed 1 st	-0.03	(-1.01, 0.95)	0.0	1,23	0.953
Tussled	9.60	(-5.47, 24.67)	1.7	1,23	0.201
ML-winner×Tussled	-0.32	(-1.29, 0.66)	0.5	1,23	0.509
ML-loser×Tussled	-0.24	(-0.69, 0.21)	1.3	1,23	0.273
(b) ML-matched pairings ($n = 57$):					
ML-average	0.14	(0.05, 0.23)	8.9	1,52	0.004
Loser fed 1 st	-0.18	(-0.71, 0.36)	0.4	1,52	0.511
Tussled	1.68	(-1.30, 4.66)	1.3	1,52	0.262
ML-average×Tussled	-0.11	(-0.32, 0.09)	1.3	1,52	0.260



Fig. 7. The relationship between the duration of the non-tussle phase (In transformed) and the mandible length of the (a) winners and the (b) losers of the random pairings, and the (c) average mandible length of the winners and losers of the ML-matched pairings. •: contests that escalated into the tussle phase, o: contests that did not escalate into the tussle phase.

3.3.4. Duration of the tussle phases

For the 10 random pairings that escalated to the tussle phase, the loser's ML (b = 0.60, p = 0.046) but not the winner's ML (b = -0.59, p = 0.334) (Fig. 8a, b) or whether the loser fed first (b = -2.42, p = 0.164) had a significant relationship with the duration of the tussle phase (Table 7a-model 1). The longer the loser's ML the longer the tussle phase lasted. Because the regression coefficients of the winner's and the loser's ML had similar values with opposite signs, we constructed a new model and replaced the winner's ML and the loser's ML with the difference between their MLs (Table 7a-model 2). In the new model, the difference in ML (b = -0.60, p = 0.031) had a significant negative association with the duration; the larger the difference, the shorter the duration of the tussle phase (Fig. 8c).

For the 15 ML-matched pairings that escalated to the tussle phase, neither the pair's ML (b = -0.08, p = 0.572) (Fig. 8d) nor whether the loser was the first to feed on the insect jelly (b = -0.82, p = 0.274) had a significant relationship with the duration of the tussle phase (Table 7b).

Overall, the negative association between the duration of the tussle phase and ML difference is consistent with all three assessment models. The lack of a positive association between pair ML and the duration for the ML-matched pairings, however, lends support to the mutualassessment and not the pure self-assessment or the cumulativeassessment strategies.

4. Discussion

Our study shows that ML is a good predictor for fighting ability in male *C. mniszechi*. Both the overall duration of contests between males

and the likelihood of a contest escalating to the tussle phase related positively with the average ML for the ML-match pairings and the winner's ML for the random pairings. Furthermore, the duration of the non-tussle phase related positively with the average ML for the MLmatched pairings and did not have a negative association with the winner's ML for the random pairings. These results are mostly consistent with the pure self-assessment strategy and not the mutual- or the cumulative-assessment strategies. The expected strong positive influence of the loser's ML on the duration and intensity of the random-size pairings predicted by all three assessment strategies was not detected in our study. Once escalated into the tussle phase, the duration of the tussle phase (1) associated positively with the ML of the losers of the random pairings, (2) associated negatively with the ML-difference in the random pairings although it did not have a significant negative association with the ML of the winners and (3) did not have a positive association with the average ML of the ML-matched pairings. These results were consistent with the mutual-assessment strategy and not the pure self- or cumulative-assessment strategies. Male C. mniszechi thus appear to adopt different assessment strategies at different stages of a contest.

Moreover, losers of the random pairings were more likely to feed on the insect jelly before the contest started than the winners. And the winners that fed on the insect jelly before the contest started tended to have shorter mandibles than the winners that did not. The results that weaker males and males with shorter mandibles were quicker to locate and ingest food suggest that these males were more in need of stocking up or refilling their energy reserves. Stronger males and males with longer mandibles could afford to delay replenishing their energy reserves and still win fights.



Fig. 8. The relationship between the duration of the tussle phase (In transformed) and (a) the mandible length of the winners, (b) the mandible length of the loser and (c) the difference between the mandible length of the winner and the loser of the random pairings, and (d) the average mandible length of the winners and losers of the ML-matched pairings.

Multiple linear regression models examining the importance of mandible length (ML) to the duration of the tussle phase for the (a) random and (b) ML-matched pairings. Loser fed 1st: an indicator variable for losers that were the first or only contestant to feed on the insect jelly before the contests started; the baseline group comprised the losers that were not first. Significant effects are in bold.

	b	(95 % CI)	F	dfs	р
(a) Random pairing	gs (n = 10):				
(model 1)					
ML-winner	-0.59	(-1.97, 0.79)	1.1	1,6	0.334
ML-loser	0.60	(0.01, 1.20)	6.3	1,6	0.046
Loser fed 1st	-2.42	(-6.16, 1.31)	2.5	1,6	0.164
(model 2)					
ML-difference	-0.60	(-1.13, -0.08)	7.3	1,7	0.031
Loser fed 1st	-2.41	(-5.55, 0.73)	3.3	1,7	0.113
(b) ML-matched pairings ($n = 15$):					
ML-average	-0.08	(-0.37, 0.21)	0.3	1,12	0.572
Loser fed 1st	-0.82	(-2.38, 0.74)	1.3	1,12	0.274

4.1. Mandible length is important to contest outcomes in C. mniszechi

In our study, although ML, HW, EL and BW were all highly correlated with each other, ML was the only trait that differed significantly between contest winners and losers of the random pairings. Furthermore, out of the 10 random pairings that escalated into tussles, 9 were won by the contestants with the longer mandibles. ML is therefore a good indicator for body size, strength and the ability to win in male *C. mniszechi*. That males with larger weapons are bigger and win more fights has also been reported for the stag beetles *Cyclommatus metallifer* (Goyens et al., 2015a) and *Aegus chelifer chelifer* (Songvorawit et al., 2018). Longer mandibles can help male stag beetles to extend their reach towards their opponents and attack. In *C. metallifer*, for instance, long mandibles were observed to enable the males to reach forward to their opponents' legs to detach them (Goyens et al., 2015a). Longer mandibles in stag beetles can

also enable the males to bite more forcefully (Goyens et al., 2014, 2015a; Mills et al., 2016). Although it is possible that males of *C. mniszechi* with longer mandibles could reach and attack their opponent more easily, whether longer mandibles enable the males to attack with more force and cause their opponents to retreat remains to be investigated.

4.2. Male C. mniszechi utilized both self- and mutual-assessment strategies in contests

Mutual assessment is often considered to be more cognitively complex than self-assessment because, for mutual assessment, a contestant needs to evaluate not only its own but also its opponent's fighting ability (Elwood and Arnott, 2012; Reichert and Quinn, 2017; but see Fawcett and Mowles, 2013). A recent meta-analysis of animal contests concluded that, based on the relationships between contest duration and fighting ability, contestants of most species settle contests by following the rules predicted by the self- rather than the mutual-assessment strategy (Pinto et al., 2019). The study, however, also pointed out that the probability of escalation increases as the difference in fighting ability between the rivals decreases (after excluding one outlying study from the analysis), a trend that provides support for mutual assessment (Pinto et al., 2019). These findings point to the possibility that the contestants of most species do not adopt the same assessment strategy throughout the entire contest. Analyzing multiple measures of contest interactions, rather than just the overall contest duration, would help us to gain a better understanding of how individuals make decisions at different stages of a contest.

The results of our study suggest that male *C. mniszechi* use both selfand mutual-assessment strategies in contests. Contestants adopting different assessment strategies at different stages of a contest have been reported for other species. For instance, in the mangrove killifish (*Kryptolebias marmoratus*), contestants adopt mutual assessment at earlier stages (e.g., deciding whether or not to escalate a contest to physical fights) but switch to self-assessment once a contest is escalated into physical fights to decide how long to fight (Hsu et al., 2008). In the cricket *Melanotes ornata*, males were concluded to perform mutual assessment in the initial phase but switch to self-assessment when fights escalate (Lobregat et al., 2019). In the snapping shrimp *Alpheus angulosus*, contestants adopt the mutual-assessment strategy during the initiation and pre-snapping phases but switch to cumulative assessment during the snapping phase (Dinh et al., 2020).

Interestingly, in the studies other than ours, contestants often mutually assess each other at the initial stages of a conflict and switch to self-assessment in escalated phases (Chapin et al., 2019). In our study, male C. mniszechi, seemingly adopted self-assessment strategy initially but switched to mutual assessment once escalated into the tussle phase. Contestants' ability to use mutual-assessment strategy at earlier stages of a contest would depend on whether or not they have the means to assess their opponents at those stages. Male stag beetles facing each other and standing up with their mandibles widely open (defensive postures) at early stages of contest interactions have been suggested to facilitate visual assessment (Okamoto and Hongo, 2013; Mills et al., 2016). A male C. mniszechi's decision to escalate to tussles was primarily dependent on its own ability, which suggests that the male did not assess its opponent's relative mandible or body size through the defensive postures. The decision of how long to persist in the tussle phase, however, switched to mutual assessment, which suggests that the males were able to gather information about their relative strength through tussles. The vast majority (9 out of 10) of the tussles of the random-sized pairings were won by the contestants with longer mandibles, indicating that tussles provide the males with reliable information about their relative fighting ability. The mandibles of stag beetles (Goyens et al., 2015b) and rhinoceros beetles (McCullough and Zinna, 2013) have high densities of mechanoreceptors that could provide mechanosensory input to enable the males to assess their opponents' strengths. The mechanoreceptors on the mandibles probably also contribute to the ability of male C. mniszechi to assess their opponents in tussles.

C. mniszechi is a nocturnal species most active around midnight, so chemical and mechanical signals are more probable means of rival assessment than visual signals. Visual assessment was also concluded to be unimportant in the contest interactions of the male *C. metallifer* stag beetles which are active in the twilight (Goyens et al., 2015a). We are not aware of any studies that have presented evidence consistent with the display behavior (of males facing each other with their mandibles widely open) facilitating visual assessment in male stag beetles.

In our study, because only small subsets of the random pairings and the ML-matched pairings escalated into the tussle phase, the conclusions regarding the importance of ML to the duration of the phase were based on small samples (10 for the random pairings and 15 for the ML-matched pairings). Future studies with larger samples would help to further examine whether male *C. mniszechi* indeed switches to mutual assessment once a contest escalates into tussles.

4.3. Winners' ability more important than losers' ability to contest duration and intensity

If contestants follow a self-assessment strategy, contest duration and intensity are expected to have a strong positive association with the loser's fighting ability because as soon as the loser retreats, a contest is resolved. In our study, the overall contest duration, the likelihood of the contest escalating into the tussle phase and the duration of the nontussle phase of the ML-matched pairings were all significantly positively associated with the pair's average ML. However, the overall contest duration and the likelihood of the contests escalating into the tussle phase of the random pairings were significantly positively associated with the winner's, instead of the loser's, ML. One possible explanation for these trends is that larger males were more active than their smaller opponents in inter-locking their mandibles, which increased the likelihood of a contest entering the tussle phase and led the entire contest to last longer (contest duration of the random-sized pairs, In transformed, mean \pm SE: 4.9 \pm 0.4 for tussled pairs, 2.7 \pm 0.3 for non-tussled pairs; t₂₈ = 4.6, p < 0.001, d = 1.78). We could not reliably identify the 'initiator' of tussles when the males inter-locked their mandibles. In the random-pairings, the effect of the winner's ML was not significant for the duration of the non-tussle phase but reached significance for the overall contest duration (= the duration of the non-tussle phase + the duration of the tussle phase). These results show that winners of these contests had an important influence on the overall contest duration as a result of their influence on the likelihood of the contests escalating to the tussle phase.

An association between contest interactions and winners' rather than losers' fighting ability has also been reported in other studies. In contests between pairs of Tanganyikan cichlids (Neolamprologus pulcher), contest duration and contact aggression intensity related negatively with winners' body size but had no relationship with losers' body size (Reddon et al., 2011). Similarly, in male swordtail fish (Xiphophorus hellerii), contest duration related negatively with winners' sword length (body size adjusted) but had no relationship with losers' sword length (Prenter et al., 2008). In these studies, because contest duration/intensity associated negatively with winners' morphological traits, losers were concluded to assess their opponents but not themselves (opponent only assessment) (Reddon et al., 2011). In our study, the associations between winners' ML and contest duration/intensity were, however, positive (instead of negative), which cannot be explained by the 'opponent only assessment'. Overall, the results of our study and the studies of the Tanganyikan cichlids and the swordtail fish show that how long or how far a contest will progress is not always dictated by the loser's strength or condition. These results highlight a diversity in contest decisions and behaviors. Factors important to the relative influences of winners' versus losers' ability in determining contest interactions deserve further investigation.

4.4. Feeding and fighting

Resource ownership often increases an individual's aggressiveness and chance of winning fights over the resource (Arnott and Elwood, 2008; Sherratt and Mesterton-Gibbons, 2015). In the contests between male *C. mniszechi*, the losers of the random pairings were, however, more likely to arrive at the food station and feed on the insect jelly before the contests started than the winners. One explanation for these results is that individuals with lower energy reserves are more likely to lose fights and that the demand for energy supply drives the males' motivation to find food. Furthermore, being the first to arrive at the food station did not seem to provide much owner advantage to the hungry males as they still lost the fights.

Insects that carry disproportionally large weapons develop large weapon muscles which drive these insects to have disproportionately high resting metabolic rates (O'Brien et al., 2019). In the random-pairing contests of C. mniszechi males, winners with smaller mandibles and losers were more likely to feed on the insect jelly before the contests started. Because losers were often the contestants with shorter mandibles than their opponents, these results indicated that, in the stag beetle, males with shorter mandibles were more motivated to feed. Shorter mandibles should cost less energy to carry (O'Brien et al., 2019). In C. mniszechi, because mandible length is highly correlated with body size in males (Table 2), males with shorter mandibles tend to be smaller overall. Smaller males probably have smaller energy storage capacity, which causes them to feed as soon as they become active in the evening. Moreover, males with smaller mandibles are less able to compete for resources with those with larger mandibles. It could thus be adaptive for males with smaller mandibles to feed and store up energy reserves whenever possible.

5. Conclusions

Male C. mniszechi stag beetles appear to adopt both self- and mutual-

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assessment strategies in competition with conspecific males. There was no evidence to suggest that the males were able to assess their rivals visually. Interlocking mandibles in tussles, however, could provide the means for males to compare their relative strengths. The results that males with shorter mandibles and losers were more likely to arrive at the feeding station before the contest started suggest that these males were more in need of stocking up or replenishing their energy reserves. However, being the first to arrive at the feeding station did not seem to give the losers an advantage in deterring their competitors because they still lost the fights.

Funding

This research was supported in part by the Ministry of Science and Technology, Taiwan, R.O.C. (MOST 106-2621-B-003-001-MY3 to YH and MOST 106-2311-B-003-004-MY3 to C-P L).

Ethical approval

We made efforts to ensure adequate care and maintenance of all the stag beetles used for this study. No formal ethical approval from an institutional Animal Care and Use Committee is required for arthropods. Collection and research permits of *C. mniszechi* stag beetles were issued by New Taipei City and the Forestry Bureau, Council of Agriculture, Executive Yuan of Taiwan (No. 10606306500, 1062105547 and 1061152477).

CRediT authorship contribution statement

Zhen-Yi Chen: Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review & editing. **Chung-Ping Lin:** Conceptualization, Methodology, Resources, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Yuying Hsu:** Conceptualization, Methodology, Formal analysis, Resources, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Acknowledgments

We thank Alan Watson for help with comments and on the manuscript.

Competing interests

The authors declare that they have no competing interests.

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