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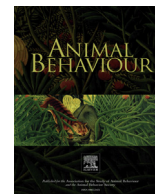
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The angle of attack: rapping technique predicts skill in hermit crab contests

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Skill, the ability to perform a challenging behaviour well, has been shown to be an important determinant of success in a variety of contexts, including human sports, animal courtship and, most recently, animal contests. Because skilful movement requires precise motor control, skill is assumed to be underpinned by traits that determine these abilities. However, while these traits determine an individual's potential to perform effective movements (known as technique), this potential may not translate into skilful fighting due to interference from the opponent. Here, we investigated the relationship between technique and skill using the European hermit crab, *Pagurus bernhardus*. By examining the spatial distribution of shell raps, we found that, on average, technique exhibited during a 'training' fight predicted the level of skill displayed in a real contest. However, our results also demonstrated substantial among-individual variation in the direction of change across the two fights, with some individuals exhibiting better technique than skill and others showing the opposite pattern. Finally, we found that winners, but not losers, progressively adapted their targeting of strikes when faced with a fully functional opponent. Our results indicate that skill is a combination of innate technique and the ability to adapt to an opponent's behaviour.

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Identifying sources of variation in fighting success remains a central and enduring question within the field of animal contest research. Fighting ability or resource-holding potential (RHP) has largely been considered the product of fixed morphological traits such as body size and weapon size, but the relative importance of these traits under laboratory and natural conditions has recently come into question (see Briffa & Sneddon, 2007; Morrell et al., 2005; O'Connor et al., 2015). Mounting evidence demonstrates that victory is dependent not just on static morphological traits but also on the performance of agonistic behaviours. Fights are dynamic interactions and the majority of contests involve behaviours that are repeated multiple times, often in quick succession. The repetitive nature of these performances is assumed to provide the opponent with information on the performer's stamina, and thus RHP (see Mowles & Ord, 2012 for a review on repetitive signals). Indeed, studies have shown that the rate at which repeated agonistic behaviours are performed (known as vigour) is a key determinant of contest success in some species (e.g. mantis shrimp, *Neogonodactylus bredini*, Green & Patek, 2015; European hermit crab, *Pagurus bernhardus*, Briffa et al., 1998). These repeated

behaviours may also provide individuals with information on a less well-studied aspect of RHP, skill. Skill is broadly defined as how well a behaviour is performed (Byers et al., 2010), but more specifically, skill incorporates the efficiency, accuracy, precision and appropriateness with which a behaviour is performed (see Briffa & Lane, 2017 for a review). Precision may be particularly key for the performance of repeated behaviours as this component captures the consistency of spatial performance (e.g. targeting specific areas) over time. Consistency may be important if success is dependent on the cumulative effects of repeatedly striking the same region of an opponent, for example.

Unlike morphological RHP traits which generally remain constant across fights (unless damaged, e.g. antler damage in deer, Jennings et al., 2017; also see Lane & Briffa, 2017 for a review), an individual's performance is dependent on both intrinsic traits and extrinsic factors and can thus vary within and between fights. For instance, an individual will have an innate potential to perform, known as technique, which is underpinned by their musculoskeletal, nervous and sensory systems (Byers et al., 2010). However, the extent to which technique translates into skilful fighting may be influenced by interference from the contestant's opponent. This is perhaps best understood using a sports analogy. Training for many athletes consists of practising motor patterns against an opponent offering reduced resistance. For instance, combat athletes will

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practise throwing various combinations of punches and kicks against punchbags or pads held by a training partner, a potential competitor who is not fighting back. Competitive tournaments, on the other hand, will be fought against opponents who are rapidly moving while performing their own offensive and defensive behaviours. The performance of the fighter during training would provide a measure of technique, while the ability to perform the same motor patterns just as well against a real opponent is an example of skill. Thus, evidence from human sport indicates a clear distinction between an individual's potential to fight skilfully (technique) and what they are actually able to achieve in a real contest (skill). In nonhuman animals, however, the disparity between technique and skill has yet to be examined.

Here, using *P. bernhardus*, we investigated the relationship between technique and skill, and their contributions to successful fighting, during agonistic shell rapping. *Pagurus bernhardus* is a well-established model for studying agonistic behaviour and has been the focus of most contest skill research (Briffa & Fortescue, 2017; Lane & Briffa, 2020). This species relies on empty gastropod shells for protection, and crabs in suboptimal shells (attackers) will readily initiate fights with conspecifics in more suitably sized shells (defenders). During a fight, the attacker grabs the defender and raps its shell against the defender's shell in an attempt to evict it. The attacker performs these raps repeatedly in bouts, interspersed by pauses, during which it tries to pull the defender out of its shell. Both the vigour and skill with which rapping is performed have been shown to influence the likelihood of an eviction. An attacker can increase its chances of eliciting an eviction by rapping more vigorously (Briffa et al., 1998, 2003; Elwood et al., 1998), more efficiently (Briffa & Fortescue, 2017) and more accurately (Lane & Briffa, 2020).

As the defender is withdrawn into its shell for the duration of the fight, it is not clear exactly how rapping affects the defender. However, the defender clearly resists the attacker's behaviour throughout the fight by holding onto its shell internally and performing intermittent interference through displays such as 'cheliped flicking' (Dowds & Elwood, 1983). Thus, it appears that attackers experience substantial resistance and interference from the defender during shell fights, but how this affects their ability to rap skilfully remains unknown. Here, we aimed to disentangle the contributions of technique and skill to this agonistic behaviour, and hence fighting success, of attacking hermit crabs. We utilized an experimental design in which attackers fought the same defender twice. In the first of these two fights the defender's RHP was experimentally reduced, while in the second fight it remained unaltered, mirroring the training and competition contexts experienced by athletes. Using this design, we first asked whether shell-rapping technique can be distinguished from realized skill. If they can be distinguished, we would expect to see differences in the accuracy (a spatial component of skill) of raps between fights where the defender's RHP has been reduced ('training') and fights where it has not (contests). If technique is distinct from skill, accuracy should be greater in training compared with contests against unaltered defenders. We then confirmed whether the accuracy of rapping during training and real contests is correlated, which should be the case if skill is underpinned by good technique.

METHODS

Crab Collection and Staging Fights

Pagurus bernhardus were collected from Hannafore Point, Looe (Cornwall, U.K.; Grid reference: SX 255523) between August and November 2020. Crabs were taken to the laboratory within 2 h of collection and kept in groups of 70–100 in 80-litre tanks containing

aerated sea water. The crabs were maintained at 15 °C on a 12:12 h light:dark cycle and fed ad libitum on frozen white fish once a week.

After an acclimation period of at least 24 h, crabs were carefully removed from their gastropod shells using a bench vice. This method allowed us to quickly remove the crab from its original shell without causing any damage to the crab itself. Crabs were weighed (weight range 0.18–1.61 g, $N = 150$) and allocated to pairs consisting of a larger crab (the attacker) and a smaller crab (the defender). Only male crabs without missing appendages or visible parasites were used. All other crabs were provided with a new shell and returned to the field site. Within pairs, the attacker was given a shell that was 60% of its optimal shell weight, while the defender received a shell 100% of the optimal shell weight for the attacker. Preferred shell weight was calculated using regression equations derived from a previous shell selection experiment (Briffa & Elwood, 2007). Crabs were then placed individually in plastic dishes (12 cm diameter) containing aerated sea water and left to acclimatize for 15–20 h.

To measure technique and skill, we presented attackers with the same opponent twice. In the first 'training' fight the defender's RHP was experimentally reduced, allowing us to quantify technique, whereas for the second 'contest' fight (conducted 24 h later), the defender had been allowed to recover, allowing us to measure skill. Fights were conducted in this order to minimize the amount of information carried over into the second fight, both in terms of the attacker gaining information about its opponent's defensive behaviour and in terms of potential winner/loser effects experienced by either opponent. To reduce the potential for winner/loser effects, in fight 1, attackers were only allowed to perform four bouts of rapping before the pair were separated. If an eviction occurred before the end of the four bouts ($N = 15$), the observer quickly intervened to allow the defender to re-enter its original shell. For fight 1, the defender's fighting ability was reduced through exposure to 30% hypoxia (a level that has previously been shown to reduce fighting ability in *P. bernhardus*, Briffa & Elwood, 2000) for 30 min prior to the fight. Hypoxic conditions were produced by mixing nitrogen and air (70% nitrogen, 30% air) using a precision gas mixing pump (Wösthoff Messtechnik GmbH, Bochum, Germany). Pairs were then introduced into a glass crystallizing dish (14 cm diameter) containing aerated sea water and observed for 20 min or until a fight occurred. As mentioned above, if a fight occurred during this time attackers were allowed to rap for four bouts before the pair were separated. After the fight, crabs were returned to their original plastic dishes and left to recover for 24 h.

After 24 h, the original crab pairs were reintroduced into the glass crystallizing dish and observed for 20 min (fight 2). If a fight occurred during this time, it was allowed to run until an outcome, either an eviction or a noneviction (i.e. the attacker gave up), occurred ($N = 68$; evictions = 56, nonevictions = 12). Each crab fought against the same opponent twice, never multiple opponents.

Measuring Fighting Performance

During both fights, the temporal pattern of rapping (total number of raps and bouts, mean number of raps per bout) was recorded by the observer using JWatcher V.1.0 (Blumstein & Daniel, 2007) along with the outcome of the fight (For fight 1, outcomes were categorized as eviction (where the defender was evicted within four or fewer bouts; $N = 15$), noneviction (where the attacker gave up within four or fewer bouts; $N = 6$) or no outcome (where the defender was not evicted and the attacker did not give up within four bouts; $N = 47$)). We have previously demonstrated that attackers are more likely to elicit an eviction when landing a

higher proportion of raps on the body whorl adjacent to the defender's aperture (Lane & Briffa, 2020). The ability to land raps in this 'sweet spot' appears to depend largely on the angle at which the attacker holds the defender's shell relative to itself. If the apertures of both shells are parallel to one another, raps will land on this 'sweet spot', but as the angle between apertures increases, the point of impact moves away from this zone (see Lane & Briffa, 2020 for a visual representation of this). Thus, a lower average angle will equate to more accurate rapping. To quantify technique (fight 1) and skill (fight 2), we measured the angle between the defender's aperture and the attacker's aperture (Fig. 1) for each rap performed in the first four bouts of the fights. To do so, the crystallizing dish in which the crabs fought was placed on top of a turntable, enabling us to turn the fighting arena to record each bout of rapping side on. Individual frames were then extracted from the fight videos for each rap using Batch Video to Image Extractor V0.1.7 (<http://www.audane.com/>). The angle between the shell's aperture and 90° to the horizontal was measured separately for both the attacker and defender using ImageJ (V1.53e, Schneider et al., 2012). Total aperture angle was then calculated as the sum of these two angles (Fig. 1).

Ethical Note

The research described in this study adheres to the ASAB Guidelines for the Use of Animals in Research. After use in this study all hermit crabs were supplied with an adequate shell and returned to the collection site at Hannafore Point. No licences or permits were required for this study.

Statistical Analyses

If pretreating defenders with hypoxic sea water reduces their ability to interfere with the agonistic behaviour of attackers, we should see an elevated vigour of rapping by attackers fighting hypoxic defenders in fight 1 compared to normoxic defenders in fight 2. Thus to compare the vigour of the attacker's shell rapping in fight 1 and fight 2 we ran two linear mixed-effects models (LMM) using the R package lme4 (Bates et al., 2015), with total number of raps and average raps per bout as response variables, respectively. Fight number (1 or 2) was included as a fixed effect and attacker ID as a random effect.

To assess the impact of technique and skill on the eventual fighting success of individual attackers, we performed an LMM

which consisted of total aperture angle as the response variable, outcome (fight 2; eviction or noneviction), fight number (fight 1 or 2), bout number (1–4) and their interaction as fixed effects. Including this three-way interaction allowed us to examine the effect of changes in technique/skill across the four bouts of each fight on the likelihood of winning fight 2. To avoid any possible winner/loser effects from fight 1, we only included attackers that neither won nor lost fight 1 in this analysis ($N = 46$; fight 2 outcomes: evictions = 38, nonevictions = 8). Attacker ID was included as a random effect. Relative weight difference between attackers and defenders ((attacker weight-defender weight)/mean of attacker and defender weight) was included as a covariate in all models. Statistical significance of each variable and their interactions was determined by stepwise model comparison.

In addition, a multivariate, character state, mixed-effects model was used to estimate adjusted repeatability of total aperture angle in fight 1 (F1, technique) and fight 2 (F2, skill) and among-individual correlations between these traits (i.e. the proportion of phenotypic variation in aperture angle across fights that is due to differences between individuals). Total aperture angle was divided into discrete character states for each of the two fighting contexts (F1_{angle} and F2_{angle}). Response variables were then centred and standardized to a mean of 0 and a variance of 1 (z-transformed), to facilitate convergence (Schielzeth, 2010). To each character state, bout number and relative weight difference were fitted as fixed effects (the addition of F2_outcome led to convergence issues and was thus not included as a fixed effect). To facilitate the interpretation of the main effects, bout number (effect of time within a fight) and relative weight difference were centred and standardized to a mean of 0 and a variance of 1 (Housley & Wilson, 2017). To test for individual differences in mean level aperture angle, as well as individual differences in angle across bouts, individual identity (ID) and bout number were additionally specified as random effects. The random slope effect of ID accounts for multiple responses from each individual and allows for estimation of individual responsiveness (changes in aperture angle) across contexts (fight 1 and fight 2), and bout number quantifies individual differences in responsiveness across bouts.

Parameters were estimated using the Markov chain Monte Carlo (MCMC) method with the 'MCMCglmm' package (Hadfield, 2010), in RStudio (R Studio Team, 2015). The posterior distributions and autocorrelation plots of five independent chains were compared to ensure convergence and adequate chain mixing from 850 000 iterations, 80 000 burn-ins and 400 thinnings. An 'uninformative',

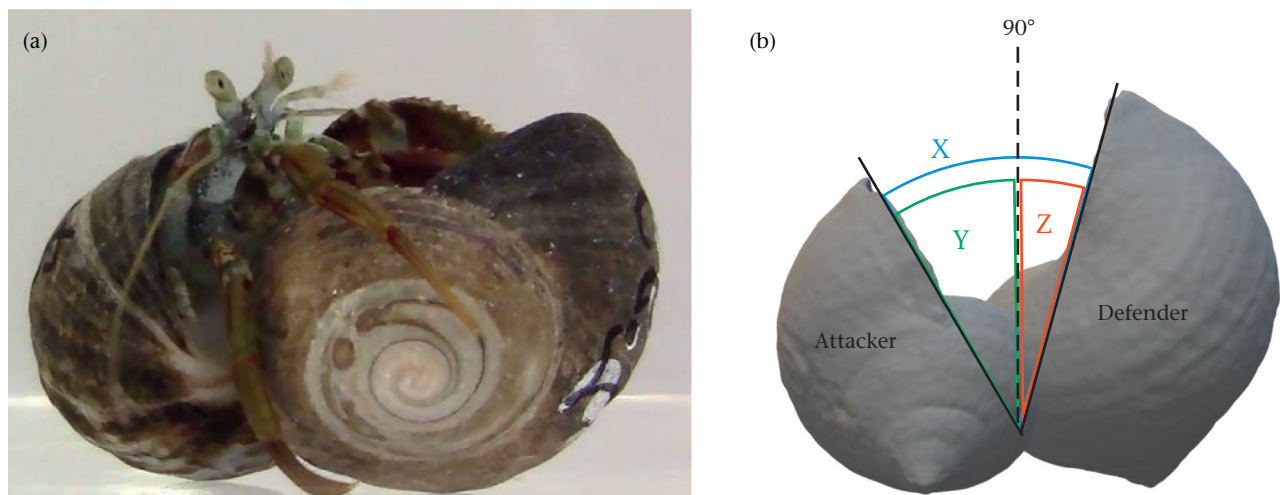


Figure 1. (a) An example of rapping position in hermit crab shell fights. (b) Calculation of total aperture angle (X) for each rap as the sum of the angle of the attacker's aperture relative to 90° (Y) and the angle of the defender's aperture relative to 90° (Z). Photo credit: Sarah Lane.

parameter-expanded, model prior was used for among-individual (co)variances, and an 'unstructured' variance–covariance matrix was specified to account for the random effects of individual 'ID' and 'bout number', estimating the among-individual variance of $F1_{\text{angle}}$ and $F2_{\text{angle}}$ (VAR_{ind}) and the covariances between them (COV_{ind}).

Model (co)variances were used to estimate among-individual correlations (r_{ind}) between traits by dividing the corresponding covariance between variables by the product of the square root of their variances:

$$(r_{\text{ind}} = \text{COV}_{\text{ind}} / (\text{sqrt}(\text{VAR}_{\text{ind}}) \times \text{sqrt}(\text{VAR}_{\text{ind}})))$$

Among-individual (co)variances were also used to detect behavioural plasticity across fight contexts, by calculating the among-individual correlations (as above) between environment-specific character states ($F1_{\text{angle}}$ and $F2_{\text{angle}}$), which, in the absence of cross-context plasticity, will be $r = +1$ (Mitchell & Houslay, 2021). Therefore, where confidence intervals (CIs) for correlations between environment-specific character states exclude $+1$, it was inferred that among-individual plasticity was present across contexts.

Finally, context-specific adjusted repeatability (R_j) for aperture angle (i.e. conditioned on the fixed effects) were estimated by dividing their respective among-individual variance estimates by the sum of their among-individual and residual variances:

$$(R_j = \text{VAR}_{\text{ind}} / (\text{VAR}_{\text{ind}} + \text{VAR}_r))$$

The posterior modes of the random effects were then used to create graphical representations of r_{ind} to illustrate associations between aperture angle in fight 1 and fight 2, and to plot individual reaction norms (RNs) for aperture angle across fight contexts and across bouts.

RESULTS

Mean Level Results

Comparison of performance across fights

Both the average number of raps per bout (estimate = -0.084 , $\chi^2_{1,4} = 9.872$, $P = 0.002$) and the total number of raps (estimate = -0.087 , $\chi^2_{1,4} = 9.69$, $P = 0.002$) performed were significantly higher for fight 1 than for fight 2 indicating reduced defender resistance and interference as a result of our hypoxia treatment in fight 1.

On average, there was no difference between aperture angles in fight 1 (estimate = 1.308 , CI [-0.279 ; 2.088]) and fight 2 (estimate = 1.172 , CI [0.172 ; 2.372]; Fig. 2). There was no significant effect of bout number on aperture angle, on average; however, average aperture angle was significantly influenced by the relative weight difference, with angles decreasing with higher relative weight difference in both fight 1 (estimate = -1.853 , CI [-3.335 ; -0.270], $\text{pMCMC} < 0.05$) and fight 2 (estimate = -2.129 , CI [-3.925 ; -0.521], $\text{pMCMC} < 0.05$). There was no significant interaction between bout number and relative weight difference (for full fixed-effects output see Supplementary Material Table S1).

Impact of technique and skill on fighting success

We found a significant three-way interaction between fight number (1 or 2), bout number (1–4) and outcome (eviction or noneviction) on total aperture angle ($\chi^2_{3,17} = 39.4$, $P < 0.001$; for full model output see Supplementary Material, Table S2). Visualization of this interaction indicates that all attackers maintained consistent rapping angles across bouts in fight 1, and furthermore attackers that went on to successfully evict the defender in fight 2

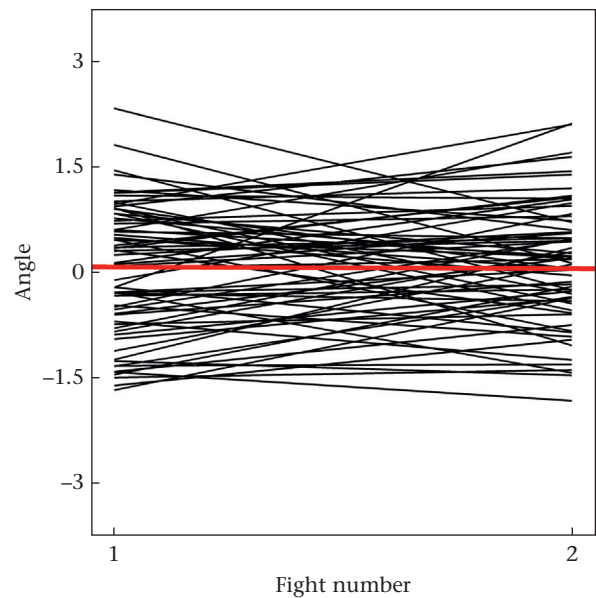


Figure 2. Individual reaction norms representing variation in aperture angle across fights. Black lines represent individual reaction norms and the red line represents the mean level trend for the population ($N = 67$). Trait values are expressed in units of standard deviation (see Methods).

exhibited lower angles than those that failed to elicit an eviction, suggesting that successful attackers rapped more accurately during fight 1. In fight 2 the difference in angle between successful and unsuccessful attackers appeared to diverge over the four bouts, with the raps of successful attackers becoming more accurate (decreasing angle) over time, and those of unsuccessful attackers becoming less accurate (increasing angle; Fig. 3). There was also a significant effect of relative weight difference on total aperture angle ($\chi^2_{1,19} = 9.92$, $P = 0.002$), with total aperture angle decreasing as relative weight difference increased.

Individual Level Results

Repeatability and plasticity across fights

After accounting for the fixed effects of bout number and relative weight difference, aperture angles were highly repeatable in both fight 1 ($R_j = 0.92$, CI [0.876 ; 0.941]) and fight 2 ($R_j = 0.93$, CI [0.908 ; 0.956]). The consistency of individual aperture angle means that among-individual covariance was possible between fight 1 and fight 2. Indeed, results revealed significant positive covariance between aperture angle across fights 1 and 2, at the among-individual level ($\text{COV}_{\text{ind}} = 0.352$, CI [0.106 ; 0.620]). This estimate provided a moderate positive correlation between aperture angle in fight 1 and fight 2, at the among-individual level ($r_{\text{ind}} = 0.43$, [0.096 ; 0.624]; Fig. 4).

The significant among-individual correlation between fight-specific aperture angle also revealed clear among-individual plasticity across fight contexts, where 95% credible intervals excluded $+1$ (0.096 ; 0.624), wherein individuals differed in their responses to fight context. For example, some individuals exhibited substantially higher aperture angle in fight 1 compared to fight 2, whereas others showed the opposite trend, with aperture angle being substantially higher in fight 2 than in fight 1 (Fig. 2).

Performance across bouts

Individuals did not differ in their trends of aperture angle across bout number during either fight 1 or fight 2. The random effect of bout number, which captures any changes in aperture angle over time (during a given fight), was estimated to be zero where

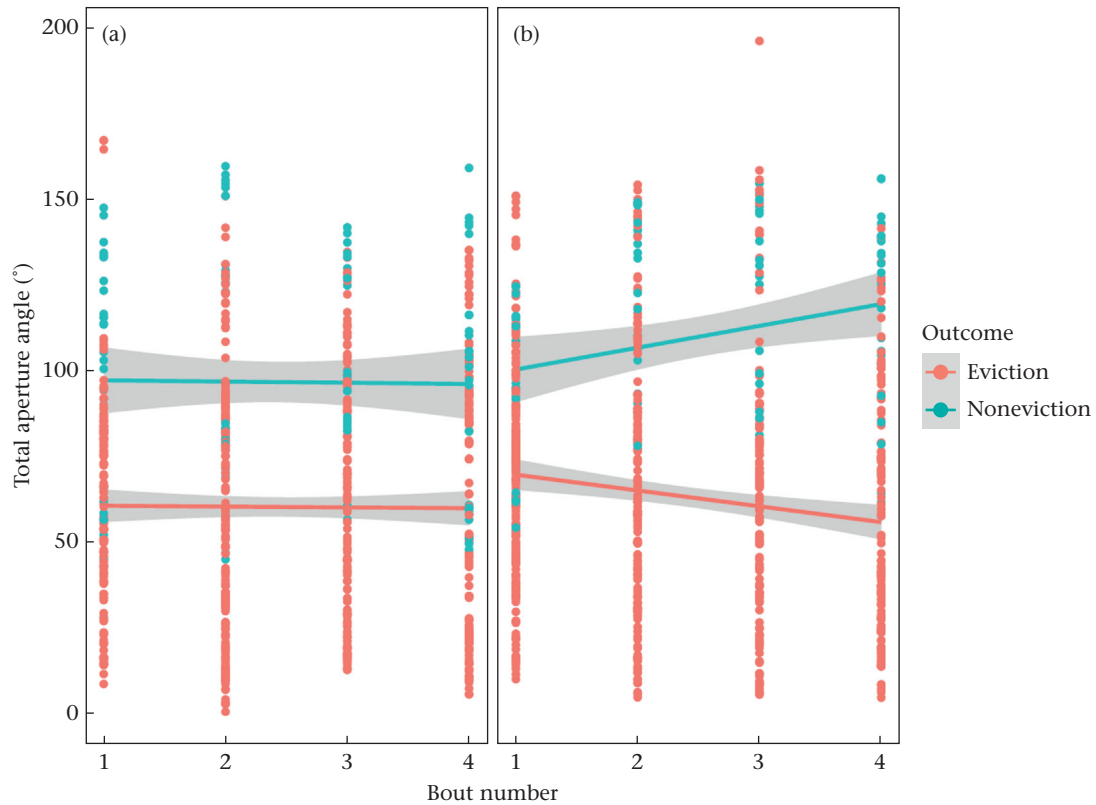


Figure 3. Three-way interaction between fight number ((a) fight 1; (b) fight 2), bout number (1–4) and outcome (of fight 2) on total aperture angle. Dots represent the raw data, lines show predictions from linear models and grey error bands illustrate 95% confidence intervals for these predictions.

individual predicted mean values were maintained relative to one another, and where the posterior distributions for variance components relating to bout number included zero for both $F1_{\text{angle}}$ (intercept–slope correlation: $r = 0.005$, $[-0.231; 0.308]$) and $F2_{\text{angle}}$ ($r = 0.180$, $[-0.054; 0.442]$; Fig. 5).

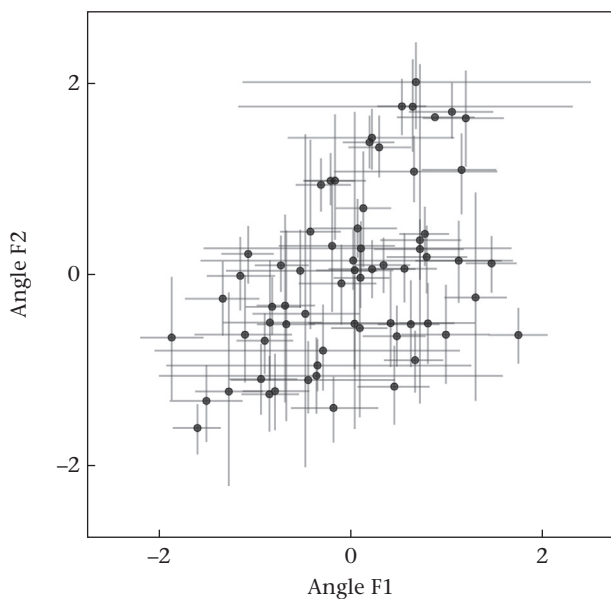


Figure 4. Representation of the among-individual correlation (r_{ind}) between aperture angle in fight 1 and fight 2. Data are based on the posterior modes of the random effects (equivalent to best linear unbiased predictions) from the multivariate linear mixed model. Error bars denote 95% credible intervals.

DISCUSSION

As expected, we found that, on average, rapping technique exhibited during training against an opponent with experimentally reduced RHP directly predicted the level of skill displayed during the subsequent fight after the opponent's RHP had been allowed to recover. However, underlying this mean level pattern was substantial variation in how individual rapping accuracy changed across the two fights; while many attackers showed an increase in accuracy in fight 2 compared to fight 1, others showed the opposite pattern. Furthermore, attackers that successfully evicted their opponent in fight 2 increased the accuracy of their raps as the fight progressed, while unsuccessful attackers did not.

The level of technique exhibited in the training fight (fight 1) was positively correlated with the level of skill exhibited during the real contest (fight 2). This suggests that, on average, good technique translates directly into skilful fighting. Theory predicts that the level of matching between technique and skill should be inversely proportional to the amount of resistance and interference exhibited by the fighter's opponent (Briffa & Lane, 2017). Thus, this result implies that, on average, the resistance offered by defenders in *P. bernhardus* is not sufficient to break the link between technique and skill. In *P. bernhardus*, defenders remain tightly withdrawn into their shells for the duration of the fight and thus the level of resistance they display is difficult to quantify. While defenders will occasionally perform defensive displays (e.g. cheliped flicking, see Mowles & Briffa, 2012), their main mechanism of resistance appears to be the strength of their abdominal musculature and uropods with which they hold on to their shell while the attacker raps. While this resistance is unlikely to affect the attacker's ability to rap skilfully per se, it could provide the attacker with information about the defender's stamina which may be utilized to make strategic decisions.

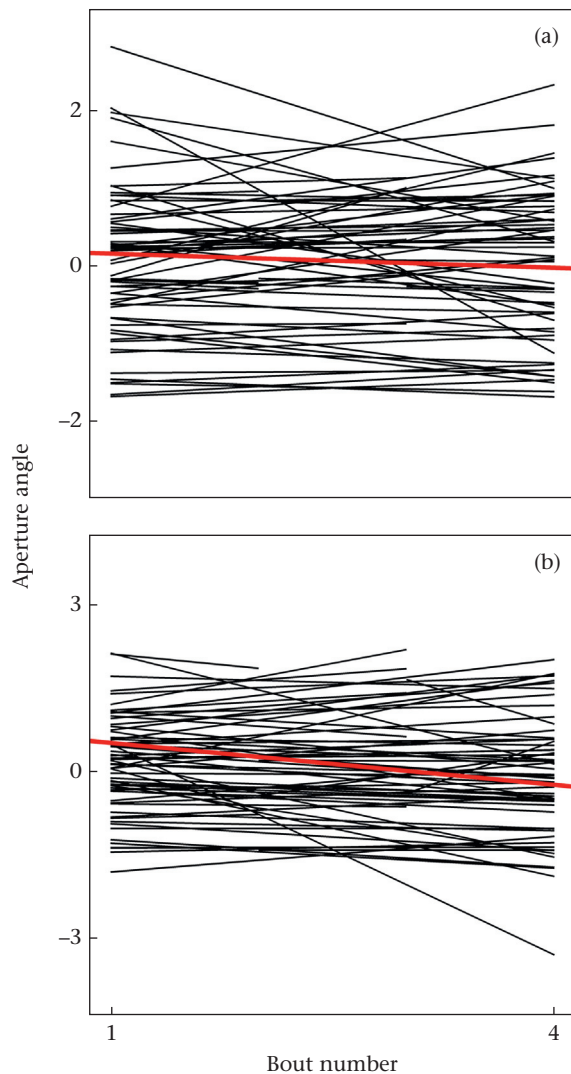


Figure 5. Individual reaction norms representing variation across bout number for aperture angle in (a) fight 1 and (b) fight 2. Black lines represent individual reaction norms and red lines represent the mean level trends for the population ($N = 67$). Incomplete lines indicate missing values. Trait values are expressed in units of standard deviation (see [Methods](#)).

Successful attackers demonstrated a significantly lower aperture angle in fight 2 compared to unsuccessful attackers. A lower, more acute, angle between the attacker and defender's shell is known to result in a higher proportion of raps landing in the 'sweet spot' associated with successful eviction (Lane & Briffa, 2020), and thus this indicates that successful attackers rapped more accurately than unsuccessful attackers on average. Furthermore, the accuracy of raps increased over the four bouts for successful attackers but decreased for unsuccessful attackers (Fig. 3). These findings suggest that successful attackers were able to adapt their fighting performance when faced with a fully functional opponent, while unsuccessful attackers were not. Similar patterns of change have been shown for vigour, a trait known to be energetically expensive, with successful attackers increasing vigour over the final bouts of a fight and unsuccessful attackers reducing vigour (Briffa et al., 1998). Thus, the differences in aperture angle between outcomes indicate that skill may also be constrained by fatigue, a result that is also seen in competitive combat sports in humans (Ashker, 2011). Alternatively, differences in cognitive ability may be responsible for the difference in how aperture angles change as fights progress.

Successful attackers might be better able to process information gathered from their opponent and adapt their performance accordingly (Reichert & Quinn, 2017). Note, however, that these two possibilities are not mutually exclusive.

We found evidence of substantial among-individual variation in the direction of change in accuracy between the two fights. While some attackers demonstrated a decrease in average aperture angle, and thus an increase in accuracy, in fight 2 compared to fight 1, other attackers showed the opposite trend, their raps becoming less accurate in fight 2. This indicates that although there is an overall positive correlation between technique and skill, the relationship between these performance traits is highly variable at an individual level and, moreover, that there is variation in the ability to translate technique into skill. Interestingly, relative weight difference had a significant effect on aperture angle in both fight 1 and fight 2, with rapping accuracy decreasing as opponents became more similar in size. This effect indicates that, regardless of specific defensive behaviours expressed, defender RHP can significantly affect the ability of attackers to rap accurately. Opponent RHP has been shown to affect the level of matching between agonistic behaviours expressed during standardized behavioural assays and real contests. For example, by measuring components of aggressiveness in male green swordtails, *Xiphophorus helleri*, in repeated mirror trials and dyadic interactions, Wilson et al. (2011) found that, despite being repeatable within contexts, display duration and tendency to attack were only weakly correlated within individuals between contexts. Larger individuals were much more likely to attack the live opponent than they were to attack the mirror, owing to changes in relative size difference. As the crabs in our study fought the same opponents twice, relative weight difference was held constant between the two fights experienced. However, other physiological components of RHP will have changed between fights as defenders recovered from their exposure to hypoxia, and thus it could be that these changes in RHP affected the translation of technique into skill. With this in mind it is clear that the opponent can be a key determinant of an individual's agonistic behaviour, and as such could affect the validity of RHP measures. Aside from play fighting (analogous to training in humans) technique is less likely to be a product of experience than skill and, moreover, it is not influenced by the behaviour of an opponent. Thus, technique is more likely to represent an individual's innate RHP, providing a more direct insight into selection for fighting compared with skill. However, our results indicate that technique alone is not enough to win a fight, but rather it is the ability to translate technique into skill in the face of an opponent that ultimately determines success.

Conclusions

This is the first study to our knowledge to examine the relationship between technique and skill in animal contests. We have demonstrated that while technique predicts skill on average, there is substantial among-individual variation in the ability to translate technique into skill. A priority for future research will be to determine what drives this variation, individual differences (e.g. personality, cognition), opponent effects or both. An additional challenge will be to incorporate measures of technique or skill into studies of strategic decision making, specifically in contests with symmetric roles, as opposed to the asymmetric fights analysed here.

Author Contributions

Sarah M Lane: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – Original draft, Writing – Review & editing, Visualization, Project administration, Funding acquisition. **Tomas O Cornwell:** Formal analysis, Writing – Review

& editing, Visualization. **Mark Briffa**: Conceptualization, Methodology, Formal analysis, Writing – Original draft, Writing – Review & editing, Supervision, Project administration, Funding acquisition.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at <https://doi.org/10.1016/j.anbehav.2022.02.017>.

References

- Ashker, S. E. (2011). Technical and tactical aspects that differentiate winning and losing performances in boxing. *International Journal of Performance Analysis in Sport*, 11, 356–364. <https://doi.org/10.1080/24748668.2011.11868555>
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Blumstein, D. T., & Daniel, J. C. (2007). *Quantifying behaviour the JWatcher way*. Sinauer Associates.
- Briffa, M., & Elwood, R. W. (2000). Cumulative or sequential assessment during hermit crab shell fights: Effects of oxygen on decision rules. *Proceedings of the Royal Society B: Biological Sciences*, 267, 2445–2452. <https://doi.org/10.1098/rspb.2000.1304>
- Briffa, M., & Elwood, R. W. (2007). Monoamines and decision making during contests in the hermit crab *Pagurus bernhardus*. *Animal Behaviour*, 73, 605–612. <https://doi.org/10.1016/j.anbehav.2006.06.008>
- Briffa, M., Elwood, R. W., & Dick, J. T. A. (1998). Analysis of repeated signals during shell fights in the hermit crab *Pagurus bernhardus*. *Proceedings of the Royal Society B: Biological Sciences*, 265, 1467–1474.
- Briffa, M., Elwood, R. W., & Russ, J. M. (2003). Analysis of multiple aspects of a repeated signal: Power and rate of rapping during shell fights in hermit crabs. *Behavioral Ecology*, 14, 74–79. <https://doi.org/10.1093/behec/14.1.74>
- Briffa, M., & Fortescue, K. J. (2017). Motor pattern during fights in the hermit crab *Pagurus bernhardus*: Evidence for the role of skill in animal contests. *Animal Behaviour*, 128, 13–20. <https://doi.org/10.1016/j.anbehav.2017.03.031>
- Briffa, M., & Lane, S. M. (2017). The role of skill in animal contests: A neglected component of fighting ability. *Proceedings of the Royal Society B: Biological Sciences*, 284, 20171596. <https://doi.org/10.1098/rspb.2017.1596>
- Briffa, M., & Sneddon, L. U. (2007). Physiological constraints on contest behaviour. *Functional Ecology*, 21, 627–637. <https://doi.org/10.1111/j.1365-2435.2006.01188.x>
- Byers, J. A., Hebets, E., & Podos, J. (2010). Female choice based upon male motor performance. *Animal Behaviour*, 79, 771–778. <https://doi.org/10.1016/j.anbehav.2010.01.009>
- Dowds, B. M., & Elwood, R. W. (1983). Shell wars: Assessment strategies and the timing of decisions in hermit crab shell fights. *Behaviour*, 85, 1–24.
- Elwood, R. W., Wood, K. E., Gallagher, M. B., & Dick, J. T. A. (1998). Probing motivational state during agonistic encounters in animals. *Nature*, 393, 66–68.
- Green, P. A., & Patek, S. N. (2015). Contests with deadly weapons: Telson sparring in mantis shrimp (Stomatopoda). *Biology Letters*, 11, Article 20150558. <https://doi.org/10.1098/rsbl.2015.0558>
- Hadfield, J. D. (2010). MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R package. *Journal of Statistical Software*, 33, 1–22. <http://www.jstatsoft.org/v33/i02/>
- Houslay, T. M., & Wilson, A. J. (2017). Avoiding the misuse of BLUP in behavioural ecology. *Behavioral Ecology*, 28, 948–952. <https://doi.org/10.1093/beheco/axx023>
- Jennings, D. J., Boys, R. J., & Gammell, M. P. (2017). Weapon damage is associated with contest dynamics but not mating success in fall deer (*Dama dama*). *Biology Letters*, 13, 20170565. <https://doi.org/10.1098/rsbl.2017.0565>
- Lane, S. M., & Briffa, M. (2017). The price of attack: Rethinking damage costs in animal contests. *Animal Behaviour*, 126, 23–29. <https://doi.org/10.1016/j.anbehav.2017.01.015>
- Lane, S. M., & Briffa, M. (2020). The role of spatial accuracy and precision in hermit crab contests. *Animal Behaviour*, 167, 111–118. <https://doi.org/10.1016/j.anbehav.2020.07.013>
- Mitchell, D. J., & Houslay, T. M. (2021). Context-dependent trait covariances: How plasticity shapes behavioral syndromes. *Behavioral Ecology*, 32, 25–29. <https://doi.org/10.1093/beheco/araal115>
- Morrell, L. J., Backwell, P. R. Y., & Metcalfe, N. B. (2005). Fighting in fiddler crabs *Uca mjoebergi*: What determines duration? *Animal Behaviour*, 84, 295–304. <https://doi.org/10.1016/j.anbehav.2012.05.015>
- Mowles, S. L., & Briffa, M. (2012). Forewarned is forearmed: Early signals of RHP predict opponent fatigue in hermit crab shell fights. *Behavioral Ecology*, 23, 1324–1329. <https://doi.org/10.1093/beheco/ars124>
- Mowles, S. L., & Ord, T. J. (2012). Repetitive signals and mate choice: Insights from contest theory. *Animal Behaviour*, 84, 295–304. <https://doi.org/10.1016/j.anbehav.2012.05.015>
- O'Connor, C. M., Reddon, A. R., Ligocki, I. Y., Hellmann, J. K., Garvy, K. A., Marsh-Rollo, S. E., Hamilton, I. M., & Balshine, S. (2015). Motivation but not body size influences territorial contest dynamics in a wild cichlid fish. *Animal Behaviour*, 107, 19–29. <https://doi.org/10.1016/j.anbehav.2015.06.001>
- R Studio Team. (2015). *RStudio. Integrated development for R*. RStudio Inc.. <http://www.rstudio.com>
- Reichert, M. S., & Quinn, J. L. (2017). Cognition in contests: Mechanisms, ecology and evolution. *Trends in Ecology & Evolution*, 32, 773–785. <https://doi.org/10.1016/j.tree.2017.07.003>
- Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, 1, 103–113. <https://doi.org/10.1111/j.2041-210X.2010.00012.x>
- Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, 9, 671–675. <https://doi.org/10.1038/nmeth.2089>
- Wilson, A. J., de Boer, M., Arnott, G., & Grimmer, A. (2011). Integrating personality research and animal contest theory in the green swordtail *Xiphophorus helleri*. *PLoS One*, 6(11), Article e28024. <https://doi.org/10.1371/journal.pone.0028024>