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The effect of performance capacity and decision-making speed on skilful fighting

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Skilful fighting encompasses an individual’s ability not only to perform agonistic behaviours accurately and efficiently, but also to choose the most appropriate behaviour or tactic from its repertoire based on the information available. The efficacy of different tactics may depend both on the behaviour of the opponent and on the individual’s internal state, for example a specific behaviour may become less effective over time as fatigue sets in. Furthermore, because fights are dynamic interactions, the ability to choose the appropriate tactic will require rapid information processing and may thus be constrained by an individual’s cognitive ability. Here, we conducted a three-phase experiment to investigate the effects of reduced performance capacity induced by exposure to hypoxia and decision-making speed on skilful fighting in the European hermit crab, Pagurus bernhardus. During fights attackers attempt to elicit an eviction either by rapping on the defender’s shell or by rocking the defender’s shell back and forth. By analysing the effect of exposure to hypoxia and decision-making speed on the relative use of these tactics, we show that contrary to our prediction, neither performance capacity nor decision-making speed alone predicted the type of behaviour performed. Rather, these two traits interacted to determine the amount of effort (raps and rocks) attackers needed to exert to elicit an eviction. Furthermore, we show that while neither performance capacity nor decision-making speed predicted skill when fights were analysed as a whole, the effects of these variables became apparent when analysing the change in accuracy as fights progressed, likely due to the accumulating effects of fatigue.

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(Briffa & Lane, 2017). Manica et al. (2017) suggested a variety of physiological mechanisms relating to neuromuscular coordination and whole-body performance capacities which might contribute to skill as well as vigour, due to the demands of maintaining specific postures that allow for the expression of the spatial aspects of skill (i.e. efficiency, accuracy, precision). Indeed, evidence from bearded manakins, *Manacus manacus*, demonstrates how constraints in muscle performance capacity has influenced the divergent evolution of courtship display between species (Miles et al., 2018). At an individual level, evidence from human sports indicates that the ability to accurately target punches decreases over the course of a single fight (Ashker, 2011), presumably due to a reduction in performance capacity over time as a result of accumulating energetic costs (referred to hereafter as fatigue) on the maintenance of neuromuscular coordination. Similarly, in shell fights in the hermit crab *Pagurus bernhardus* the ability of an attacker to strike specific regions of its opponent’s shell changes as the fight progresses, with successful attackers better able to maintain (and even increase) accuracy over time compared to unsuccessful attackers (Lane et al., 2022).

However, successful fighting is dependent not simply on executing a predetermined set of behaviours, but also on the ability to continuously adapt one’s behaviour in the face of both the opponent’s behaviour (Briffa et al., 2015) and the cumulative costs of engagement (e.g. Briffa & Snodden, 2007). This ability is encapsulated by the fourth and final aspect of skill, appropriateness, which describes an individual’s capacity to choose the optimum behaviour to perform from a range of options, based on the current situation (Briffa & Lane, 2017). Therefore, as well as being reliant on whole-body performance capacities, an individual’s ability to perform agonistic behaviours skilfully may depend on its ability to rapidly process and utilize information. Indeed, much of animal contest theory centres on the sources of information opponents use to make strategic decisions (e.g. self-versus mutual assessment; Parker, 1974; Maynard Smith & Parker, 1976; Parker & Rubenstein, 1981; Arnott & Elwood, 2009), but whether variation in the ability to utilize this information rapidly and accurately influences fighting success has yet to be examined empirically (see Reichert & Quinn, 2017 for a review of the role of cognition in contests).

*Pagurus bernhardus* provides a highly appropriate model system for investigating links between information processing and fighting skill because capacities for rapid decision making can be assessed through shell selection behaviour independently of the fight and the within-fight variables (e.g. actions of the opponent) that might affect it. Like other hermit crabs, *P. bernhardus* occupy empty gastropod shells, which act as portable shelters affording protection to their weakly calcified abdomen. Owing to the importance of gastropod shells, hermit crabs conduct an array of shell investigation behaviours that allow them to gather information about the quality of unoccupied shells they encounter, and to compare this to the quality of their current shell (Elwood & Neil, 1992). This allows hermit crabs to make optimal decisions about whether to abandon their current shell in favour of a new one (Elwood et al., 1979). In addition, because unoccupied shells are often in short supply, crabs in inadequate shells will readily initiate agonistic encounters against an individual that possesses a more suitable shell, attempting to evict them. During the initial phase of a fight, the attacker gathers information about the quality of the defender’s shell via tactile investigation, using this information to decide whether to escalate the fight to a shell rapping phase. After this, the attacker inserts its chelipeds through the aperture of the defender’s shell, and strikes its shell against that of the defender, with the strikes or ‘raps’ occurring in a series of bouts separated by pauses (Dowds & Elwood, 1983). Numerous analyses have shown that defenders are more likely to release their abdominal grip on the shell when the vigour of rapping is high (see Briffa, 2013 for a review). Recent studies have also shown that the attacker’s chance of effecting an eviction varies with rapping skill. First, attackers that rap more efficiently in terms of displacement distance are more likely to win the fight than those that displace too far (Briffa & Fortescue, 2017). Second, attackers that consistently target a specific region of the defender’s shell are more likely to win (Lane & Briffa, 2020a). However, rapping is not the only tactic used by attackers in their attempt to evict the defender. During pauses between bouts of rapping, attackers may exhibit an additional agonistic behaviour known as shell rocking, whereby they gently rock the defender’s shell back and forth. While this behaviour is never performed in place of shell rapping, it does appear to augment the effects of rapping. During an experiment in which the impact of shell rapping was mechanically reduced, attackers were found to increase the number of shell rocks they performed (Edmonds & Briffa, 2015). These findings indicate that attackers (1) are able to assess the effectiveness of their own agonistic behaviour and (2) adapt their tactics depending on this assessment. These results also suggest that shell rocking becomes a more appropriate tactic when the effectiveness of rapping is reduced.

Here, using *P. bernhardus*, we investigated the role of energetic and cognitive constraints on skillful fighting. We utilized a three-phase experiment comprising (1) an initial assessment of the attacker’s decision-making speed via a shell selection task, (2) a prefight manipulation of the attacker’s performance capacity via exposure to hypoxic versus saturated normoxic sea water (Briffa & Elwood, 2000) and (3) staged agonistic encounters held under normoxic conditions, from which skill was quantified in terms of appropriateness (rock or rap) and accuracy (targeting of raps). We expected exposure to hypoxic water to reduce the effectiveness of rapping due to directly reducing performance capacity by accelerating the onset of fatigue. As such, if information-processing ability (assayed using decision-making speed) influenced the ability of attackers to choose appropriate agonistic tactics, we expected those exhibiting faster decision times to increase the number of shell rocks when subject to hypoxia but to use fewer rocks when exposed to normoxia. In contrast, attackers that take longer to swap shells might deploy shell rocking when it is less appropriate (i.e. when not subject to prefight hypoxia). Furthermore, if accuracy is influenced by performance capacity, we expected to see less accurate targeting of raps in attackers pretreated with hypoxic than with normoxic sea water. Additionally, if accuracy is also influenced by decision-making speed, we expected to see a negative relationship between the accuracy of raps and time taken to swap shells. Moreover, if decision-making speed can offset any limitations of fatigue on accuracy, we expected to see another interaction between these variables whereby the accuracy of rapping was eroded to a greater extent by hypoxic pretreatment in attackers with long shell selection times compared with attackers that chose the better shell more quickly. Finally, we expected all of these patterns to become more obvious as fights progressed due to the cumulative effects of fatigue.

**METHODS**

**Crab Collection and Husbandry**

*Pagurus bernhardus* were collected by hand from tide-pools at Hannafore Point, Looe (Cornwall, U.K.; Grid reference: SX 25630 52273) between March and June 2021. Crabs were returned to the laboratory within 1–2 h of collection and kept in groups of 80–100 individuals in 80-litre tanks containing aerated sea water. They were fed ad libitum on frozen white fish once a week and maintained at 15 °C on a 12:12 light:dark cycle. Crabs were allowed to
acclimate for 24 h before being carefully removed from their gastropod shells using a bench vice. This method allows for speedy removal of the crab from its shell without causing any damage to the crab itself. Crabs were then sexed, weighed (weight range 0.18–1.61 g) and allocated to pairs containing a larger crab (the potential attacker) and a smaller crab (the potential defender); relative weight difference between pairs (calculated as 1−(defender weight/attacker weight)) ranged from 0.35 to 0.94 g. Within their pairs, crabs assigned as attackers were given a shell that was 40% of their optimal shell weight while defenders were given a shell of 100% optimal shell weight for the attacker. Preferred shell weight was calculated using regression equations derived from a previous shell selection experiment (Briffa & Elwood, 2007). Only male crabs with intact appendages and no visible parasites were used in this experiment. All other crabs were provided with a new shell and returned to the collection site. Crabs were then placed individually into plastic dishes (12 cm diameter) containing aerated sea water as above. Defenders were left to acclimate for 15–20 h whereas attackers were given 2 h to change into their new shell.

Phase 1: Decision-making Speed

Attackers were subjected to a shell choice trial 24 h before fighting to gain a measure of decision-making speed outside of the context of aggression. Two hours after the attacker received the 40% optimum shell, a new shell of 60% optimum shell weight was placed in its dish (ca. 6 cm from the crab). The attackers were then observed for 20 min. During this time, the latency to enter the 60% shell was recorded. Entrance latency (referred to hereafter as decision time) was calculated from the beginning of the trial to the time the crab entered the 60% shell. When the attacker entered the new shell, the 40% shell was immediately removed from the dish to prevent the crab from switching back to its old shell. At the end of the trial, the attackers were left to recover for 15–20 h. If the attacker failed to enter the 60% shell within 30 min it was removed from the experiment. Thus, in the next phase of the experiment the potential gain in resource value (i.e. an increase from 60% to 100% of optimal shell mass) was standardized across all attackers.

Phase 2: Manipulating Performance Capacity

Attackers were randomly assigned to two prefight fatigue treatments: normoxic or hypoxic. Attackers assigned to the hypoxic treatment were individually exposed to hypoxia of 30% oxygen saturation for 30 min prior to the fight, within a sealed container containing sea water of equivalent volume to the holding dishes described above. This treatment was chosen because it has previously been shown to be sufficient to reduce fighting ability in terms of vigour in P. bernhardus and thus is likely to simulate fatigue (Briffa & Elwood, 2000). Hypoxic conditions were produced by bubbling a nitrogen–air mix (70% nitrogen, 30% air) using a precision gas-mixing pump (Wösthoff Messtechnik GmbH, Bochum, Germany) through the sea water using an air stone. For the normoxic treatment 100% oxygen saturation was chosen (Briffa & Elwood, 2000). Dissolved O2 levels were monitored using an oxygen probe (YSI Pro2030, YSI Inc., Yellow Springs, OH, U.S.A.).

Phase 3: Staging Fights

Within their assigned pairs, attackers and defenders 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. All fights were recorded using a Canon LEGRIA HF R706 High-Definition Camcorder (Canon, Tokyo, Japan). A total of 86 interactions were observed, resulting in 74 fights (eviction = 68; noneviction = 6). Interactions not resulting in a fight were excluded from the analysis. Similarly, as the number of fights ending in nonevictions was particularly low in this instance, these fights were also excluded from the analyses.

Quantifying Fight Performance

The temporal pattern of shell rapping (raps per bouts, total number of raps) was recorded by the observer using JWWatcher V.1.0 (Blumstein & Daniel, 2007) along with the time taken to attack (attack latency) and the outcome of the fight (eviction or non-eviction). We quantified two aspects of fighting skill: accuracy and appropriateness. Accuracy was quantified as in Lane et al. (2022), by measuring the angle between the defender’s aperture and the attacker’s aperture (referred to as total aperture angle, lower angles being more accurate and higher angles being less accurate) for each rap performed in the first bouts of the fights. To do so, individual frames were extracted from the fight videos for each rap using Batch Video to Image Extractor V.0.1.7 (www.audane.com). The angle between both fighter’s shell aperture and 90° to the horizontal was measured in each of the frames using Imagej 1.53e (Schneider et al., 2012). Total aperture angle was then calculated as the sum of these two angles (see Lane et al., 2022 for a visual representation). Appropriateness was quantified by recording the temporal pattern of shell rapping as described above (rocks per bout, total number of rocks). Using these data we then calculated the ratio of rocks to raps (referred to hereafter as rock:rap ratio) performed across the entirety of the fight by dividing the total number of rocks performed by the total number of raps performed.

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 Harnaføre Point. No licences or permits were required for this study.

Statistical Methods

Despite attackers being allocated to prefight fatigue treatments prior to the shell choice assays, upon inspection of the entrance latency data we discovered that there were a disproportionate number of ‘slow’ crabs (latency > 1000 s) in the hypoxia treatment. While this skew did not appear to have any significant effect on the results of our statistical analysis, in pursuit of transparency, we report the results of the analysis on crabs with a latency of <1000 s (N = 57, hypoxic = 26; normoxic = 31) here, and also report the analysis of the full data set in the Appendix.

Decision-making speed across contexts

To assess the relationship between decision making during shell choice trials and decision making during contests, we conducted a general linear model (GLM) with a Poisson error family containing attack latency as the response variable, treatment (hypoxia or normoxia), latency to enter the new shell and their interaction as fixed effects and relative weight difference as a covariate.

Effect of hypoxia and decision-making speed on fight performance

We conducted GLMs containing treatment, decision time and their interaction as fixed effects. This fixed-effects structure was used with total number of shell rocks, average aperture angle, rock:rap ratio, average number of raps per bout (log10 transformed to normalize the distribution) and total number of raps as response variables, respectively. For shell rocks and total number of raps, a
Poisson error family was used due to the right-skewed nature of these count data, while a quasibinomial error family was used in the model containing rock:rap ratio as the response variable. Relative weight difference was included as a covariate in all analyses to account for effects of difference in body size between the two roles.

**Effect of hypoxia and decision-making speed across bouts**

To assess the effect of fatigue and decision-making speed on fight performance over time (i.e. across bouts as the fights progressed), we conducted linear mixed-effects models (LMMs) using R package lme4 (Bates et al., 2015). These models were run using performance data from the first four bouts of the fights and contained treatment, decision time, bout number and their interactions as fixed effects. This fixed-effects structure was then used with number of rocks, number of raps, rock:rap ratio (calculated for each bout as number of rocks/number of raps), and total aperture angle, respectively. Relative weight difference was included as a covariate and fight ID was included as a random intercept in all models to account for taking multiple measures from a single fight. To aid convergence, decision time was scaled in these models. All statistical analyses were conducted in R Studio (R Studio Team., 2015).

**RESULTS**

**Decision-making Speed Across Contexts**

There was a significant interaction between fatigue treatment and the time taken to swap shells on attack latency ($\chi^2_{1,50} = 574.31, P < 0.001$). This interaction indicated that under normoxic conditions, there was a positive relationship between decision-making speed in both contexts, with attackers that took less time to enter the more optimal shell attacking the defender faster and vice versa. However, under hypoxic conditions, this relationship was absent (Fig. 1).

**Effect of Hypoxia and Decision-making Speed on Fight Performance**

We found a significant interaction between prefight treatment (hypoxic or normoxic) and decision time on the total number of shell rocks performed in a fight ($\chi^2_{1,52} = 14.32, P < 0.001$). For normoxic attackers, there was a negative relationship between decision time and number of shell rocks, whereas attackers pretreated with hypoxia demonstrated a slight positive relationship between these two variables (Fig. 2a). There was also a significant effect of relative weight difference on the number of shell rocks performed ($\chi^2_{1,52} = 77.33, P < 0.001$), indicating that attackers performed more rocks as relative weight difference between opponents increased. We also found a significant interaction between treatment and decision time on total number of raps performed ($\chi^2_{1,52} = 85.45, P < 0.001$). Similar to that seen for shell rocks, there was a negative relationship between number of raps and decision time for normoxic attackers but a positive relationship between these variables for attackers pre-treated with hypoxia (Fig. 2b). There was also a significant positive effect of relative weight difference on total number of raps performed ($\chi^2_{1,52} = 23.01, P = 0.01$), indicating that the number of raps performed by attackers increased with relative weight difference. There was no effect of treatment, decision time or their interaction on the average number of raps performed per bout, average aperture angle or rock:rap ratio. There was, however, a significant effect of relative weight difference on rock:rap ratio ($F_{1.53} = 9.98, P = 0.003$), indicating that as relative weight difference between opponents increased, attackers performed a higher overall proportion of rocks to raps (Fig. 3).

**Effect of Hypoxia and Decision-making Speed on Fight Performance Across Bouts**

There was a significant three-way interaction between prefight treatment, decision time and bout number (1–4) on the number of shell rocks performed ($\chi^2_{1,15} = 17.184, P < 0.001$). For attackers exposed to hypoxia, there was no relationship between these variables across any of the bouts (Fig. 4a). For normoxic attackers on the other hand, the relationship between these variables was negative in bout 1 and then either neutral or positive in the remaining three bouts (Fig. 4b). We also found a significant three-way interaction between treatment, decision time and bout number on total aperture angle ($\chi^2_{1,16} = 39.18, P < 0.001$). For hypoxic attackers, there was a negative relationship between decision time and aperture angle in bout 1, but a positive relationship between these variables in subsequent bouts. This indicates that the aperture angle of attackers that exhibited faster decision times became more accurate (lower angle) over time compared to those that took longer to switch shells (Fig. 5a). For normoxic attackers, decision time appeared to affect the variation in aperture angle seen across fights, with faster decision times resulting in lower variation in angle between bouts (Fig. 5b).

**DISCUSSION**

Contrary to our predictions, when considering fights as a whole, we found no evidence that decision-making speed or hypoxia influenced fighting skill in terms of either accuracy or appropriateness. Rather, we found that these factors combined to determine the overall amount of effort (in terms of raps and rocks) that successful attackers had to allocate to the fight in order to win. However, we did find an influence of hypoxia and decision-making speed on the accuracy of raps as the fights progressed.

Under normal oxygen conditions, there was a positive relationship between the time taken to enter the more optimal shell and the time taken to inflict an attack. This suggests that decision-making speed is correlated across contexts within individuals, and moreover that the shell choice trials provided an accurate estimation of decision-making speed. However, contrary to our predictions, we found no evidence to indicate that decision-making speed or hypoxia had any influence on an individual’s overall fighting skill. Neither factor had any significant influence on
rapping accuracy or appropriateness (ratio of rocks to raps) when fights were analysed as a whole. Rather, choice of tactic was driven by relative weight difference between opponents. As relative weight difference increased, so did the ratio of rocks to raps performed, suggesting that as size difference between opponents increases, the effectiveness of rapping decreases leading attackers to switch to performing more shell rocks. Surprisingly little is known about how shell rapping affects defenders, but there is some suggestion that it may trigger reflex contractions in the defender’s abdominal muscles (Chapple, 1993), potentially causing them to lose their internal grasp on their shell. Indeed, recent evidence that successful attackers targeted raps on a particular area of the defender’s shell, located approximately above the abdomen (Lane & Briffa, 2020a), appears to support this suggestion. During staged fights, the size of the defender’s shell is determined by the size of its attacker (60% optimal based on the attacker’s weight) and thus smaller defenders will be able to retract further into the shell during a fight (Briffa & Elwood, 2001b). This may mean that it is harder for attackers facing smaller opponents to target their raps effectively and thus they switch to rocking. However, whether this switch in tactics increases the likelihood of eviction between opponents of greater relative weight difference remains to be tested.

Under normoxic conditions, we found a negative relationship between entrance latency and both total number of rocks and total number of raps performed. This indicates that attackers that took less time to enter the better (more optimal) shell had to exert more effort to convince the defender to give up. However, this effect disappeared when attackers were pretreated with hypoxia, even reversing for the number of raps performed, with attackers that were faster to enter the better shell eliciting an eviction after fewer raps than those that took longer to change shells. Thus, under normoxic conditions, attackers that made faster decisions were less effective fighters than those that took more time. At first this appears to be counterintuitive, especially considering the rapid information processing required to make decisions during agonistic contests (Reichert & Quinn, 2017). However, decision speed has been shown to trade-off with the accuracy of that decision (see Chittka et al., 2009 for a review), which is especially pertinent in situations of high risk. Here, we have assumed that faster decision times during shell assessment equate to higher cognitive ability in P. bernhardus; however the decision to change shells brings with it the risk of predation as hermit crabs must expose their vulnerable bodies during the switch. Therefore, attackers that take longer to change shells may actually benefit from gaining more information about the risk of predation, and indeed about the resource they are assessing, before committing to a decision. Perhaps then, these slower attackers are better able to gather accurate information during contests, allowing them to tailor their behaviour in order to evict defenders faster than crabs that make more hasty decisions. Previous evidence has shown a negative relationship between

Figure 2. Interaction between prefight fatigue treatment and latency to enter new shell on (a) total number of shell rocks and (b) total number of raps performed across the fight. Dots represent the data, lines show predictions from linear models and error bands illustrate 95% confidence intervals for these predictions. \( N = 26 \) hypoxic; \( N = 31 \) normoxic.

Figure 3. Effect of relative weight difference on total rock:rap ratio for entire fight. Dots represent data (\( N = 57 \)).
Figure 4. Interaction between prefight fatigue treatment, decision time and bout number on number of shell rocks performed for (a) hypoxic \((N = 26)\) and (b) normoxic attackers \((N = 31)\). Dots represent the data, lines show predictions from linear models and error bands illustrate 95% confidence intervals for these predictions.

Figure 5. Interaction between prefight fatigue treatment, decision time and bout number on total aperture angle for (a) hypoxic \((N = 26)\) and (b) normoxic attackers \((N = 31)\). Dots represent the data, lines show predictions from linear models and error bands illustrate 95% confidence intervals for these predictions.
latency to initiate investigation of a new shell and boldness, a personality trait that equates to risk-taking behaviour (Mowles et al., 2012), suggesting that personality differences may be reflected in decision making speed. However, whether decision speed is (1) repeatable and (2) forms part of a wider behavioural syndrome along with boldness remains to be tested. Despite there being no effect of hypoxia or decision-making speed on rapping accuracy (total aperture angle) when averaged over fights, we found a significant interaction between these variables when analysing how rapping accuracy changed over consecutive bouts. For attackers pretreated with hypoxia, there was a negative relationship between entrance latency and aperture angle in bout 1, indicating that attackers that took longer to switch shells initially landed more accurate raps (lower aperture angle). However, this relationship reversed in subsequent bouts with attackers that took less time to switch shells landing more accurate raps in bouts 2–4. This disparity across bouts could be due to the effects of hypoxia wearing off after the first bout of the fight, but interestingly the relationship seen across bouts 2–4 is not the same as that seen for normoxic attackers. Rather, for attackers pretreated with normoxia, while the direction of the relationship between entrance latency and aperture angle varied across bouts, overall it appeared that attackers that switched shells faster exhibited less variation in aperture angle between bouts compared to those that took longer. We have previously shown that successful attackers are better able to maintain rapping accuracy (i.e. are more precise) over the course of a fight (Lane et al., 2022), and while our results here do not suggest that decision-making speed directly influences accuracy per se, they do indicate that decision-making speed varies with the precision of raps as the fight progresses, that is, there is a latent correlation that is only revealed as the fight progresses. Perhaps then accuracy (the ability to hit the target once) and precision (the ability to hit the target repeatedly) are underpinned by different traits. This possibility is supported somewhat by the fact that decision-making speed affects accuracy when attackers are pretreated with hypoxia yet affects precision (but not accuracy) under normal oxygen levels.

Numerous studies on animal contests have highlighted the role of energetic demands, and variation in the capacity to meet these, in driving contest dynamics and outcomes (reviewed in Briffa & Sneddon, 2007). Here we have demonstrated that fight performance is also affected by decision-making speed. Importantly, the links between decision-making speed and spatial skill only became apparent as the fights progressed, potentially due to the accumulating effects of fatigue. The potential importance of both information processing ability (Reichert & Quinn, 2017) and skill (Briffa & Lane, 2017) for fighting have recently been highlighted and here we have shown that the former might underpin the latter. Further understanding of the roles of these traits, which are understudied in relation to animal contests and sexually selected displays, could provide new insights into any dyadic interaction where there is a clear conflict of interests.

Author Contributions

Sarah M. Lane: Conceptualization, Methodology, Investigation, Formal analysis, Visualization, Writing — original draft, Writing — review and editing. Mark Briffa: Conceptualization, Methodology, Writing — review and editing, Supervision, Project administration, Funding acquisition.

Data Availability

Data are available via Mendeley Data Repository at http://doi.org/10.17632/2n5f8hccvh.1.

Declaration of Interest

The authors have no conflicts of interest to report.

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References


Appendix

Here we give the results for the full data set including crabs that took >1000 s to enter the new shell.

Decision-making speed across contexts

There was a significant interaction between fatigue treatment and the time taken to swap shells on attack latency ($\chi^2_{1,59} = 124.87, P < 0.001$). This interaction indicated that under normoxic conditions, there was a positive relationship between decision-making speed in both contexts, with attackers that took less time to enter the new shell also attacking quicker and vice versa. However, under hypoxic conditions, the direction of this relationship was reversed.

Effect of fatigue and decision-making speed on fight performance

We found a significant interaction between treatment (hypoxic or normoxic) and decision time on the total number of shell rocks performed in a fight ($\chi^2_{1,59} = 12.237, P < 0.001$). For normoxic attackers, there was a negative relationship between decision time and number of shell rocks, whereas attackers pretreated with hypoxia demonstrated a slight positive relationship between these two variables. There was also a significant effect of relative weight difference on the number of shell rocks performed ($\chi^2_{1,59} = 64.501, P < 0.001$), indicating that attackers performed more rocks as relative weight difference increased. We also found a significant interaction between treatment and decision time on total number of raps performed ($\chi^2_{1,59} = 192.86, P < 0.001$). Similar to that seen for shell rocks, there was a negative relationship between number of raps and decision time for normoxic attackers and a positive relationship between these variables for attackers pretreated with hypoxia. There was no effect of treatment ($F_{1,65} = 1.24, P = 0.27$), decision time ($F_{1,64} = 0.96, P = 0.33$) or their interaction ($F_{1,63} = 2.63, P = 0.11$) on the average number of raps performed per bout. We also found no effect of treatment ($F_{1,62} = 0.75, P = 0.39$), decision time ($F_{1,60} = 0.21, P = 0.65$) or their interaction ($F_{1,59} = 0.02, P = 0.89$) on average total aperture angle. There was no effect of treatment ($F_{1,64} = 0.003, P = 0.96$), decision time ($F_{1,65} = 0.19, P = 0.67$) or their interaction ($F_{1,63} = 1.38, P = 0.24$) on rock:rap ratio. There was, however, a significant effect of relative weight difference on rock:rap ratio ($F_{1,62} = 12.261, P < 0.001$), indicating that as relative weight difference between opponents increased attackers performed a higher overall proportion of rocks to raps.

Effect of fatigue on fight performance over time

There was a significant three-way interaction between prefight treatment, decision time and bout number (1–4) on the number of shell rocks performed ($\chi^2_{3,15} = 31.038, P < 0.001$). For attackers exposed to hypoxia, we found a positive relationship between decision time and number of shell rocks performed in bout 1, but no relationship between these variables in subsequent bouts. For normoxic attackers on the other hand, the relationship between these variables was negative in bout 1 and then either neutral or positive in the remaining three bouts. We also found a significant three-way interaction between treatment, decision time and bout number on total aperture angle ($\chi^2_{3,8} = 39.211, P < 0.001$). While the relationship between decision time and aperture angle was negative for both treatments in bout 1, the direction of this relationship diverged between treatments over the subsequent bouts. Moreover, in the hypoxic treatment, the aperture angle of attackers that exhibited faster decision times became more accurate over time compared to those that took longer to switch shells. For normoxic attackers, decision time appeared to affect the variation in aperture angle seen across fights, with faster decision time resulting in lower variation in angle between bouts. There were no significant effects of the three fixed effects on either rock:rap ratio or the number of raps performed. However, both rock:rap ratio ($\chi^2_{3,9} = 8.673, P = 0.03$) and number of raps ($\chi^2_{3,8} = 22.94, P < 0.001$) were significantly affected by bout number. Post hoc analysis indicated a significant reduction in the number of raps between bout 1 and all subsequent bouts.