Animal Behaviour 123 (2017) 249–257

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

# Accurate resource assessment requires experience in a territorial fish

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ARTICLE INFO

*Article history:*
Received 4 July 2016
Initial acceptance 19 July 2016
Final acceptance 26 August 2016
Available online 6 December 2016
MS. number: A16-00587R

*Keywords:*
aggression
information gathering
Laurentian Great Lakes
*Neogobius melanostomus*
resource value
RHP
round goby

Although the relationship between resource-holding potential and contest dynamics is well studied, how the value of a contested resource influences aggressive interactions has received far less attention. Questions about how animals assess a contested resource, and whether they can update their assessments of resource value during a contest require additional testing. To address this issue, we conducted a series of experiments using an invasive, territorial fish, the round goby, *Neogobius melanostomus*. We used this species to investigate the impact of resource quality on contest dynamics, and to test how animals gather information on resource value. First, we found that fish preferred an enclosed shelter ('high quality') to an open shelter ('low quality'). Despite this preference for high-quality shelter, fish fought equally hard for both high- and low-quality shelters in staged resource contests when they had no prior experience with the resource. However, when fish were given prior experience, contests over high-quality shelters began faster and had more aggressive acts than contests over low-quality shelters. Interestingly, when the value of the resource in the contest was switched from their prior experience, the fish seemed unable to fully update their appraisal of resource value, and contest dynamics were not strictly driven by the previous or current resource value. Round goby may therefore have a limited ability to update their appraisal of resource value when engaged in a contest. Together, our findings demonstrate that fish adjust their aggressive effort to reflect resource value, but previous experience with the resource is required to assess the resource efficiently.



Animals commonly fight over resources such as food, mates and territories, and such contests are more frequent when resources are limited in quantity or vary in quality (Enquist & Leimar, 1987; Hsu, Earley, & Wolf, 2011). A great deal of research has focused on what attributes an individual must possess to win a contest against a rival (see review Arnott & Elwood, 2009). These attributes include an individual's body size, weaponry and physiological scope for aggression (e.g. energy reserves). Larger individuals (Prenter, Taylor, & Elwood, 2008; Reddon et al., 2011; Wells, 1988), with more developed weaponry (Kelly, 2006; Sneddon, Huntingford, & Taylor, 1997), greater energy reserves and higher anaerobic capacity tend to prevail (reviewed in Briffa & Sneddon, 2007). For example, when sand gobies, *Pomatoschistus minutus*, fight over nesting burrows, the larger individuals are more likely to win (Lindström & Pampoulie, 2005). Collectively, the attributes of a competitor that contribute to the probability of winning a contest, or 'the absolute fighting ability of a given individual', are termed resource-holding potential ('RHP'; Parker, 1974).

Aggressive contests often occur because of resource discrepancies. Therefore, the characteristics of the resource being contested can also affect contest dynamics. How valuable a resource is to each contestant will depend on the resource quality, the scarcity and the value of the resource for survival and reproduction (Arnott & Elwood, 2008; Enquist & Leimar, 1987). Opponents should use information about the resource to decide whether and how to proceed with a fight. When the physical and physiological attributes of two contestants are similar, resource value can be a key determinant of contest dynamics (Enquist & Leimar, 1987). Moreover, resources that are strongly linked to reproductive success, such as high-quality shelters and territories, receptive mates or nutritious food, should provide a greater motivation for opponents to proceed with a contest. We would also expect that contests over high-quality resources would last longer and be more intense (Enquist & Leimar, 1987; Parker, 1974). It would therefore be advantageous for individuals to assess resource value before fighting, and optimize their aggressive behaviour accordingly in order to minimize the costs (e.g. wasted energy, potential injury) associated with aggressive interactions (Parker, 1974).

Prior experience 'owning' a resource will give animals time to evaluate resource quality and adjust their aggressive effort in an

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http://dx.doi.org/10.1016/j.anbehav.2016.10.032

ensuing contest. For example, Bridge, Elwood, and Dick (2000) found that resident male orb-weaving spiders (*Metellina mengei*) contesting with an intruder for access to a female mate had longer contests when the female was of higher value (i.e. they had larger body size and were more fecund). In resident–intruder experimental designs, resource ownership itself may also alter the internal state of the competitor rendering them a more motivated or physiologically capable competitor. For example, Johnsson and Forser (2002) found that brown trout, *Salmo trutta*, that were residents over a territory for 4 days were more likely to win contests against size-matched intruders than residents who occupied the same territory for only 2 days. In this scenario, the objective resource value (the physical characteristics of the territory) was identical, but ownership itself made the resource more valuable to the resident (subjective resource value).

To separate the effects of subjective resource value from objective resource value, it has been suggested that experimental designs where competing animals have symmetrical prior resource experience (sometimes termed 'owner–owner' contests) can offer another experimental approach to testing questions of resource value (Arnott & Elwood, 2008; Elwood & Arnott, 2012). Here, both opponents become resident over their own resources and are able to assess resource value before contesting, making the subjective resource value based on ownership approximately equal. This experimental design has been previously used to investigate RHP during contests (e.g. Groen et al., 2012; Koops & Grant, 1993; Reddon et al., 2011), but much less frequently to investigate the impact of resource value on contest dynamics. When this approach has been used, researchers have shown that animals tend to aggress longer and more intensely for high-quality resources (Arnott & Elwood, 2008). In parasitoid wasps (*Goniozus nephantidis*), females that owned larger, more valuable hosts on which to lay their eggs, fought longer and harder than females that owned a low-quality host resource (Humphries, Hebblethwaite, Batchelor, & Hardy, 2006).

While it is clear that animals may adjust their fighting effort to resource value when they have previous experience with the resource, less research has focused on whether animals are also able to assess resource value during the contest in real time. It is expected to be costly for an animal to simultaneously gather information about both their opponents and about resource value during a contest (Arnott & Elwood, 2008; Enquist & Leimar, 1987). Indeed, certain studies have found no evidence for resource assessment, indicating animals are unable to evaluate a resource during the contest, or that gathering information might constitute a cost that outweighs the potential gains (Jennings, Gammell, Carlin, & Hayden, 2004; Thornhill, 1984). Certain resources may also be easier to evaluate than others while engaged in an aggressive contest. For example, males may be able to rapidly evaluate the reproductive quality and resource value of a potential female mate using olfactory or visual cues (e.g. Prenter, Elwood, & Montgomery, 1994; Sneddon, Huntingford, Taylor, & Clare, 2003). Verrell (1986, red-spotted newts, *Notophthalmus viridescens*) and Dick and Elwood (1990, amphipods, *Gammarus pulex*) found that intruding males could quickly assess the reproductive value of a potential female mate being guarded by a resident male, and the intruders adjusted their aggressive effort according to female resource value. We would expect that evaluating the quality of a burrow, shelter or breeding territory would require individuals to interact with the resource to assess its structural or spatial features, meaning that animals would take longer to assess resource value. In some species of hermit crabs, individuals must use both visual and tactile cues to assess shell volume and fit (Doake & Elwood, 2011; Elwood & Briffa, 2001; Hazlett, 1996). It has been speculated that trade-offs must occur during the information-gathering process, especially if animals need to assess the opponents' ability along with the value of the resource at stake (Elwood & Arnott, 2012, 2013). However, investigations of resource assessment during contests in the literature are so far surprisingly limited, leaving much to be learned about this process.

To better understand how resource value can alter contest dynamics, and whether animals are able to update information about resources during contests, we conducted a series of experiments using the round goby, *Neogobius melanostomus*. This small, benthic fish species is native to the Ponto-Caspian region of Europe and is widely invasive in Western Europe and the Laurentian Great Lakes of North America (Kornis, Mercado-Silva, & Zanden, 2012). This species is a useful model for studies of contest dynamics because its invasion success has been strongly attributed to its aggressive nature (Charlebois et al., 1997; Corkum, Sapota, & Skora, 2004). Round goby use and defend shelter spaces in the rocky littoral zone to escape from predators, as sites for spawning and offspring care and they are known to outcompete similar-sized species for access to these limited shelters (Belanger & Corkum, 2003; Bergstrom & Mensinger, 2009; Corkum, MacInnis, & Wickett, 1998; Dubs & Corkum, 1996; Janssen & Jude, 2001). In the laboratory, round goby will readily display defensive behaviour over artificial shelters and are frequently aggressive to both conspecifics and heterospecifics (Balshine, Verma, Chant, & Theysmeyer, 2005; Groen et al., 2012; Sopinka, Marentette, & Balshine, 2010; Stammler & Corkum, 2005).

Based on the knowledge that shelter is a highly valuable resource for round goby, we posed three questions. First, we sought to establish whether round goby could differentiate between shelters of varying quality. To do this, we provided fish with a binary choice between a shelter that was enclosed and easy to protect (a 'high-quality' shelter), and a shelter that was open, making it both less safe and more difficult to defend (a 'low-quality' shelter; Fig. 1a). We predicted that round goby would prefer the more defendable shelter, because of shelter's importance for survival and reproduction in the wild (Bergstrom & Mensinger, 2009; Dubs & Corkum, 1996; Janssen & Jude, 2001). Second, we assessed whether resource value (high-quality versus low-quality shelters) influenced contest dynamics between individuals of similar RHP (body size) when fish had no previous experience with either shelter. To address this question, we conducted resource contests over high- and low-quality shelters, with resource-naïve fish. Here, opponents needed to gather information about resource value during the contest and appropriately adjust their fighting effort to reflect this information. We evaluated contest dynamics by measuring motivation to begin a contest as the time taken to start aggressing, contest duration and the total number of aggressive acts during the contest. We hypothesized that if round goby are able to evaluate resource value during a contest, and if they prefer high-quality shelters, then fish fighting over high-quality shelter would begin contests faster and have longer contests, and that the contests would be more intense than when fighting over low-quality shelters. Third, we evaluated the effect that prior resource experience had on contest dynamics and whether fish updated their evaluation of resource value during the aggressive contest. To do this, we housed fish for 24 h before the contest with either a high- or low-quality shelter. Using a $2 \times 2$ factorial design, we manipulated whether the resource present during the aggressive contest either matched or mismatched their prior housing experience. Thus, this third experiment created four contest scenarios (Fig. 2): (1) fish housed with a high-quality resource that fought over a high-quality resource; (2) fish housed with a low-quality resource that fought over a low-quality resource; (3) fish housed with a high-quality resource that fought over a low-quality resource; and (4) fish housed with a low-quality resource that

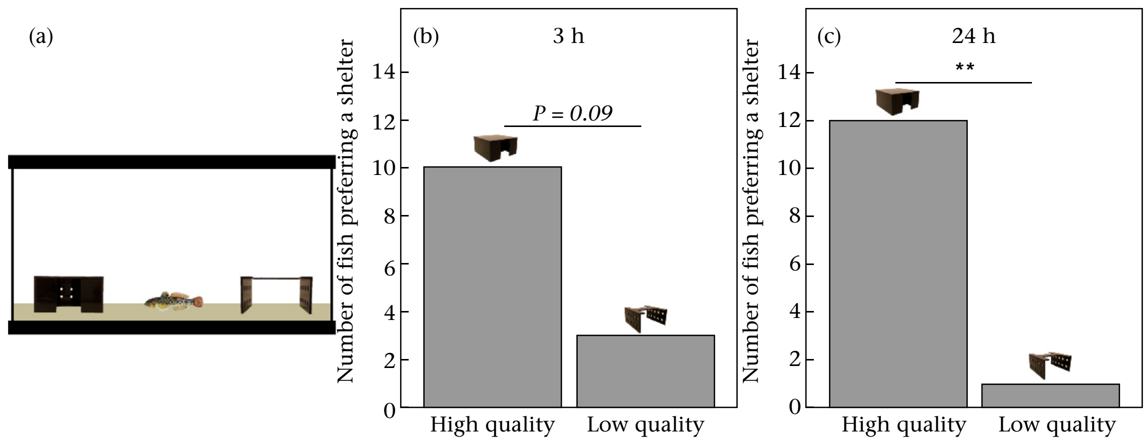


**Figure 1.** (a) Resource preference experimental tank set-up (experiment 1), depicting a choice between a high-quality and a low-quality shelter. (b) Resource preference after 3 h of the resource preference trial. (c) Resource preference after 24 h of the resource preference trial. $^{**}P < 0.01$.

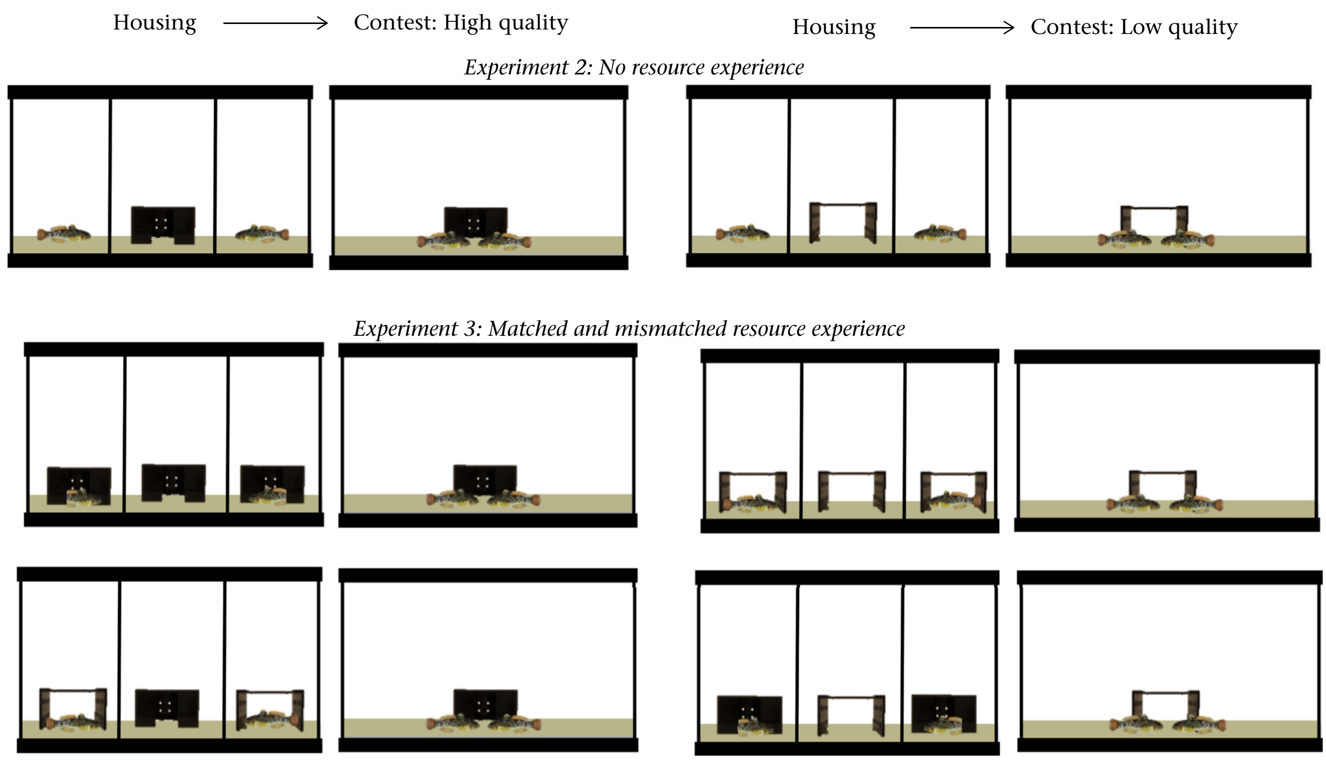


**Figure 2.** Example of resource contest experimental tank set-up. The 'housing' column shows precontest housing conditions: opponents were separated by opaque barriers and either housed with or without resources, depending on the experiment. The 'contest' column shows contest conditions over high- or low-quality resources: precontest shelters were removed (if present), barriers were lifted and opponents fought over a single remaining shelter resource.

fought over a high-quality resource. We hypothesized that if fish fight only based on previous resource experiences and are unable to update their evaluation of resource value during the contest, then contest dynamics would reflect prior housing conditions. Fish previously housed with high-quality resources would fight harder, regardless of resource value present in the actual contest. Contrarily, if fish were able to fully update their evaluation of resource value during the contest, we would expect contest dynamics to reflect the resource present during the contest itself and not the resources experienced during prior housing. In all contest experiments, we described how round goby gathered information about resource value during aggressive contests. To do this, we monitored when each fish first entered the shelter resource and the amount of time each fish spent inside the shelter resource during the contest.

## METHODS

### *Fish Collection and Housing*

We collected male round goby using baited minnow traps from LaSalle Park Marina (43°18′04″N, 79°50′43″W) in Hamilton Harbour, Lake Ontario, Canada (see McCallum et al., 2014; Young et al., 2010 for trapping and collection details). We transported the fish to the laboratory at McMaster University, and housed them in 75-litre (61.0 × 33.0 × 43.2 cm) holding tanks in groups of 6–10 fish. Housing tanks contained ~1 cm of natural gravel substrate, an airstone and a static renewal filter. We maintained these aquaria at 18–20 °C on a 16:8 h light:dark cycle. We fed fish flake food (Nutrafin Basix Staple, Rolf C. Hagen, Inc., Montreal, Quebec, Canada) daily.

### *Experiment 1: Shelter Preference*

Between 19 May and 12 June 2014, we conducted 14 shelter preference trials to ascertain whether round goby prefer an enclosed, defensible shelter to an open, less defensible shelter. We conducted these preference trials in 40-litre experimental tanks (50.8 × 27.9 × 33.0 cm) equipped with ~0.5 cm of natural gravel substrate and a static renewal filter. Each experimental tank contained one enclosed, defensible shelter and one open, less defensible shelter on opposite sides of the tank, with the sides counterbalanced between trials. The enclosed shelter was an enclosed black acrylic box (10.9 × 10.9 × 5.0 cm; Fig. 1a), with a single small entry/exit that would be easy to defend. The open shelter was identical in size and also built of black acrylic, but was open from the sides and from the top with only two intact sidewalls (Fig. 1a). This open shelter would be difficult to defend and would leave the fish more vulnerable to predation and challenges from rivals. We began each preference trail by releasing a focal fish into the centre of the experimental tank and then recorded its shelter preference after 3 h and 24 h. Fish were considered to prefer a particular shelter if they were inside the shelter or were within a half a body length from the shelter entrance(s). One trial was excluded from our analysis because the fish did not move during the trial and then died after 3 h in the test tank.

### *Experiment 2: Resource Contests with No Resource Experience*

After we determined that round goby prefer enclosed, defensible shelters ('high quality') to open, less defensible shelters ('low quality'; see Results), we staged 26 resource contests during 1–28 August 2015. Three contests were excluded from our final analyses because fish did not interact during the trial. We staged 12 contests over high-quality resources and 11 contests over low-quality resources. In all contests, we followed a 3-day protocol. On day 1, we selected two size-matched fish (based on body mass) from laboratory stock tanks. We uniquely tagged each fish to facilitate identification during the resource contests by injecting nontoxic acrylic paint along the dorsal fin (Wolfe & Marsden, 1998). These two fish were housed in isolation and separately from stock tank fish while recovering from tagging. On day 2, we transferred the marked pair to opposite ends of an experimental tank (40-litre aquaria, 50.8 × 27.9 × 33.0 cm) that was divided into three compartments by removable black opaque barriers (Fig. 2). A shelter (either high or low quality) was placed into the central chamber. We conducted the resource contests on day 3 between 0900 and 1100 hours. Contests began when the experimenter slowly and simultaneously removed the two barriers from behind an opaque blind. The ensuing resource contest was videorecorded for 30 min (Canon Vixia HF S100).

### *Experiment 3: Resource Contests with Matched and Mismatched Resource Experience*

Between 14 July and 28 August 2014, we conducted 66 resource contests to assess how prior resource experience affected contest dynamics. We excluded 13 contests from scoring because the fish did not interact during these trials. The contests were identical to those described in experiment 2, but on day 2 of our experimental protocol, we housed both opponents before a contest with either a high-quality resource or a low-quality resource for 24 h. Again, an additional shelter (either high or low quality) was placed into the central chamber that matched or mismatched the housing shelters. On day 3, the experimenter slowly removed the housing shelters and the opaque barriers to reveal the central shelter, allowing fish to interact with each other and the shelter (Fig. 2). This created four conditions: (1) fish housed with high-quality shelters that contested over a high-quality shelter ($N = 12$); (2) fish housed with low-quality shelters that contested over a low-quality shelter ($N = 15$); (3) fish housed with high-quality shelters that contested over a low-quality shelter ($N = 13$); and (4) fish housed with low-quality shelters that contested over a high-quality shelter ($N = 13$). We called the first two treatment groups matched experience groups and the second two treatment groups mismatched experience groups.

### *Postcontest Processing and Behavioural Scoring*

After each contest, we euthanized both opponents using an overdose of benzocaine (0.025%, Sigma Aldrich) and remeasured each fish for standard length using callipers accurate to 0.01 cm, and for body mass using a digital balance accurate to 0.001 g. We then measured gonad mass to confirm reproductive status using the gonadosomatic index (GSI: (gonad mass/(total mass − gonad mass)) × 100), where round goby males with a GSI over 1% are considered reproductive (Marentette & Corkum, 2008; Zeyl, Love, & Higgs, 2014). All fish used in this study were confirmed to be nonreproductive.

We scored the video recordings for aggressive motivation, contest intensity, contest duration, the time each fish spent inside the shelter and the winner of the contest. The behavioural scorer could not be truly blind to resource value treatment (as the quality of the shelter resource present in the tank was clearly visible); however, we corroborated their behavioural scores with another scorer blind to the motivations of the experiment ($N_{trials} = 15$, $R = 0.99$). We measured motivation to engage in aggression as the time taken for the fish to start an aggressive interaction following the barrier removal. Contest intensity was evaluated by summing the total aggressive acts during the contest. The total number of aggressive acts performed by each fish during the contest was scored following an ethogram for this species (see Supplementary Table S1, adapted from Sopinka et al., 2010). Contest duration was measured as the time from the first aggressive act to the time when one opponent ceased to retaliate with aggression and fled. The fleeing fish was termed the losing, subordinate fish, while the other fish was considered to be the winning, dominant fish. To track resource assessment throughout the entire trial, we recorded the time each fish entered the shelter and the total time spent in the shelter resource.

### *Statistical Analyses*

All statistical analyses were conducted in R (Version 3.2.3, R Core Team, 2015). We assessed shelter preference after 3 h and after 24 h using exact binomial tests. In our resource contest experiments, we size-matched pairs by body mass to control for RHP. For each pair, we calculated relative body mass difference as a percentage: ((mass 1 − mass 2)/(mass 1 + mass 2)/2) × 100; O'Connor et al., 2015; Reddon et al., 2011). More accurate size matching was achieved during experiment 2 (mean difference ± SE: 2.43 ± 0.44%, $N = 23$) than in experiment 3 (9.69 ± 1.04%, $N = 53$; Kruskal–Wallis test: $\chi^2_1 = 20.0$, $N = 76$, $P < 0.0001$), but size matching was not different between treatments within each experiment (Kruskal–Wallis test: experiment 2: $\chi^2_1 = 0.46$, $N = 23$, $P = 0.50$; experiment 3: $\chi^2_3 = 2.0$, $N = 53$, $P = 0.60$). To control for RHP in our subsequent analyses, we included the absolute percentage body mass asymmetry as a covariate in our models.

In our resource contests, we assessed (1) time to start a contest, (2) contest duration and (3) the number aggressive acts during the contest. Time to start a contest and contest duration were ln transformed to meet parametric assumptions before analysis. In experiment 2, we used a linear model to assess the effect of resource value on time to start a contest and contest duration. In experiment 3, we used a $2 \times 2$ ANOVA to analyse the effect of resource value and prior resource experience (matched or mismatched) on time to start a contest and contest duration. In both experiments, the number of aggressive acts performed during the contests were analysed using negative binomial regressions appropriate for count data.

To better understand the use and evaluation of resource quality between opponents, we evaluated whether contest winners spent more time in the shelter than contest losers using a linear mixed effects models, where contest ID was included as a random effect. We assessed whether resource value affected the time winners spent in the shelter using a linear model (experiment 2) or a $2 \times 2$ ANOVA (experiment 3), with a power transformation to meet parametric assumptions. To analyse the effect of information gathering across all resource contest experiments, we used linear models (with ln transformation) to examine whether contests were more likely to start faster or be longer when a fish entered the resource before the start of the aggressive contest, and we used a negative binomial regression to examine whether contests had more aggressive acts.

### Ethical Note

Our collection of round goby from Lake Ontario, Canada was approved by the Ontario Ministry of Natural Resources (Scientific Collection Licence No. 1076557 and Licence No. 1079371). The methods for handling, marking, behavioural trials and euthanasia were assessed and approved by the Animal Research Ethics Board of McMaster University (Animal Utilization Protocol No. 13-12-51), in accordance with the Canadian Council for Animal Care, and adhered to ASAB/ABS Guidelines for the use of animals in research. We monitored all trials carefully by checking the video camera regularly. Had we observed any visible injury, the trial would have been stopped immediately, but no such trials occurred and all fish were healthy. We visually inspected each fish for injury (tattered fins, missing scales) and observed no apparent damage. We followed the recommendation of Huntingford (1984), by minimally handling each fish and attempting to reduce stress by limiting the trials to a short duration (<30 min). Round goby are neither threatened nor endangered and are an invasive species in North America. Because they are invasive, round goby cannot legally be returned to the wild after collection and must be euthanized as detailed in our Scientific Collection Licences and Animal Utilization Protocols.

## RESULTS

### Experiment 1: Shelter Preference

Can fish differentiate between resources? Yes. When we provided round goby a choice between an enclosed, defensible shelter and an open, less defensible shelter, the fish tended to prefer the enclosed, defensible shelter. This effect was marginally nonsignificant after 3 h (exact binomial test: $N = 13$, $P = 0.09$; Fig. 1b), but after 24 h, fish clearly preferred the enclosed, defensible shelter (exact binomial test: $N = 13$, $P = 0.003$; Fig. 1c).

### Experiment 2: Resource Contests Without Prior Experience

Without prior resource experience, does resource value influence contest dynamics? No. Contests over enclosed, defensible ('high-quality') shelters and open, less defensible ('low-quality') shelters did not differ when fish had no prior experience with the resource. Regardless of whether the shelters were of high or low quality, contests began after a mean $\pm$ SE of $366 \pm 91$ s (linear model: $t_{20} = -0.02$, $N = 23$, $P = 0.98$; Fig. 3a), contained a similar number of aggressive acts ($22 \pm 3$; negative binomial regression: $Z = -0.34$, $N = 23$, $P = 0.74$; Fig. 3b) and were of similar durations, lasting on average $46 \pm 8$ s (linear model: $t_{20} = 0.93$, $N = 23$, $P = 0.36$; Fig. 3c). Together, these results suggest that fish did not fight according to the value of the resource present during the contest. All contests, regardless of resource type, ended with a clear winner and loser. After the contest, winners always spent more time in the shelter than losers (linear mixed effects model: $t = 4.24$, $N = 46$, $P < 0.001$). Winners that fought over a high-quality shelter tended to spend more time in shelter than winners that fought over a low-quality shelter, although this effect was marginally nonsignificant (linear model: $t_{20} = 2.08$, $N = 23$, $P = 0.065$; Fig. 3d).

### Experiment 3: Resource Contests with Matched or Mismatched Prior Experience

Does experience with the resource influence contest dynamics? Yes. Can fish update their assessment of resource value during a contest? Somewhat. We found that fish with matched resource experience aggressed faster and more intensely over high-quality resources than over low-quality resources; however, fish showed limited ability to update their appraisal of resource value in the mismatched experience condition. Contests began faster over high-quality resources when compared to low-quality resources in the matched condition, but this was not apparent in the mismatched resource condition (resource value*experience interaction: ANOVA: $F_{1, 48} = 5.86$, $P = 0.019$; Fig. 4a). Similarly, contests over high-quality resources contained more aggressive acts, but this was only true when fish had matched prior resource experience and this difference was not apparent when the fish had mismatched prior resource experience (resource value*experience interaction: negative binomial regression: $Z = 2.17$, $N = 53$, $P = 0.030$; Fig. 4b). However, contests over high-quality resources were longer, and this was true in both matched and mismatched housing experiences (main effect of resource value: ANOVA: $F_{1, 48} = 7.75$, $P = 0.0076$; Fig. 4c). After the contest, winners always spent more time in the shelter than losers (linear mixed effects model: $t = 7.81$, $N = 106$, $P < 0.001$). Winners spent more time in high-quality resources than in low-quality resources in both the matched and mismatched housing experiences (main effect of resource value: ANOVA: $F_{1, 48} = 9.38$, $P = 0.0036$). Winners spent longer investigating resources of either quality in the mismatched prior experience condition than winners from the matched prior experience condition (main effect of experience: ANOVA: $F_{1, 48} = 7.30$, $P = 0.0095$; Fig. 4d).

### Information Gathering Across Resource Contest Experiments

Did fish physically evaluate the resource during the contest? Mostly no. After the contest trial started, but before engaging in aggression, only 25% of the fish used in both experiment 2 and experiment 3 actually entered the shelter (38 of 152). A similar number of fish entered the shelter before fighting across experiments (experiment 2: $N_{\text{high quality}} = 4$, $N_{\text{low quality}} = 6$; experiment 3: $N_{\text{high quality}} = 10$, $N_{\text{low quality}} = 18$). Both opponents had entered the shelter before starting a contest in only two trials. Whether or

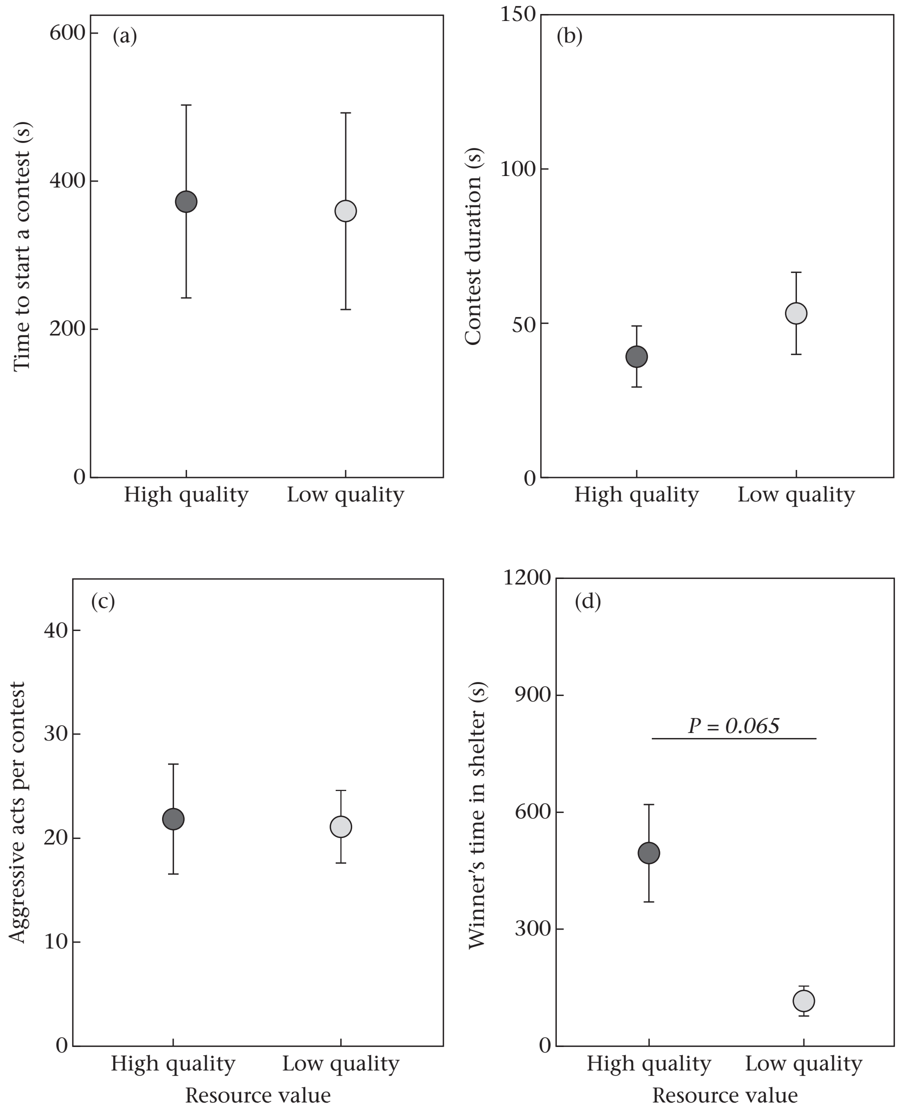


**Figure 3.** Results of contests without prior resource experience (experiment 2) showing (a) time to start a contest, (b) number of aggressive acts per contest, (c) contest duration and (d) winner's time in the shelter in relation to resource value. In all panels, error bars represent ± 1 SE.

not a fish had entered the shelter resource before beginning to aggress did not affect contest dynamics. For example, contests lasted for similar durations (linear model: $t_{74} = 0.25$, $N = 76$, $P = 0.80$) and had a similar number of aggressive acts (negative binomial regression: $Z = -0.46$, $N = 76$, $P = 0.64$) in contests where at least one opponent entered the shelter before fighting and in contests where neither fish entered the shelter before fighting. However, the majority of fish (91%, 138 out of 152) entered the shelter at some time point during the 30 min trial.

*Contest Outcome and RHP Covariates*

Although contest outcome and the physical differences between contestants were not focal variables in this study, we tracked this information. Larger fish won more contests in experiment 3 (binomial logistic regression: $Z = 2.94$, $N = 53$, $P = 0.0033$) but not in experiment 2 (binomial logistic regression: $Z = 0.079$, $N = 23$, $P = 0.94$). Body size asymmetry between contestants (our measure of RHP) did not predict how fast the contest would start or its duration in either experiment (all analyses, effect of RHP: $P > 0.10$). However, contests where the contestants had larger body size asymmetries contained fewer aggressive acts per contest, but this was apparent only in experiment 3 (negative binomial regression: $Z = -2.56$, $N = 53$, $P = 0.010$), not in experiment 2, where the contestants were more closely matched in size (see Methods; negative binomial regression: $Z = -1.00$, $N = 23$, $P = 0.31$).

## DISCUSSION

In this study, we investigated resource assessment abilities and how resource value affected contest dynamics in the round goby fish. We first established that fish strongly preferred an enclosed ('high-quality') shelter resource to an open ('low-quality') shelter resource during our resource preference experiment. This preference for enclosed, well-protected shelter was expected given that round goby prefer rocky, sheltered habitats in the wild (Bergstrom & Mensinger, 2009; Dubs & Corkum, 1996; Janssen & Jude, 2001; Young et al., 2010). The high-quality shelter in our experiment would be more defendable from both rival conspecifics and heterospecifics, and would provide better protection from predators

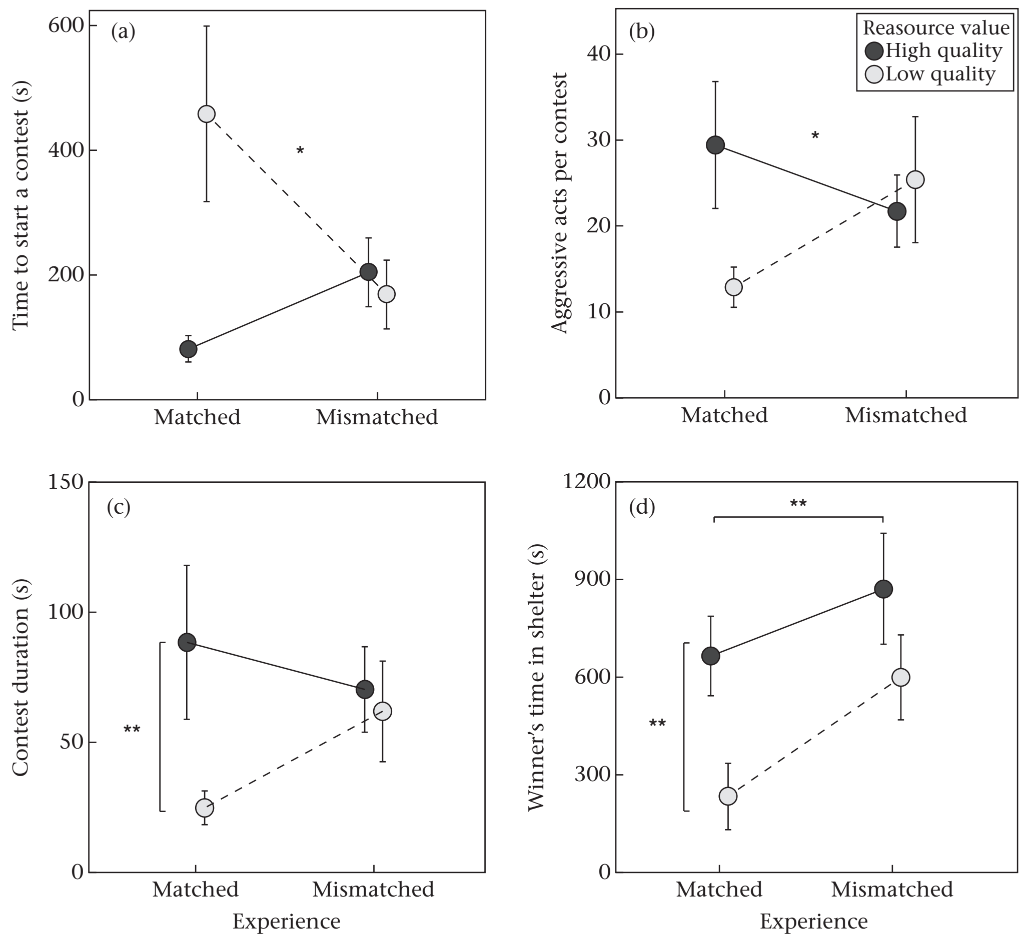


**Figure 4.** Results of contests with matched or mismatched prior resource experience (experiment 3) showing (a) time to start a contest, depicting an interaction between resource value and experience, (b) number of aggressive acts per contest, depicting an interaction between resource value and experience, (c) contest duration, depicting a main effect of resource quality, and (d) winner's time in the shelter, depicting a main effect of resource quality and a main effect of experience. In all panels, error bars represent ± 1 SE. $^{*}P < 0.05$; $^{**}P < 0.01$.

than the open, low-quality shelter. Moreover, the high-quality shelter could offer a positional advantage during a fight, making fish more prepared to defend the resource. Round goby monopolize sheltered spaces in the rocky littoral zone, and such habitat provides protection from predation by larger fish species (Crane & Einhouse, 2016; Reyjol, Brodeur, Mailhot, Mingelbier, & Dumont, 2010), water snakes (King, Ray, & Stanford, 2006) and avian predators (Hebert & Morrison, 2003; Somers, Lozer, Kjoss, & Quinn, 2003). These rocky shelters are doubly valuable as they also create areas for round goby to reproduce and care for offspring during the breeding season (Corkum et al., 1998; MacInnis & Corkum, 2000).

Given that round goby prefer high-quality shelter resources, we then conducted two experiments to understand how fish assess resource value and use this information in aggressive contests. In experiment 2, we asked whether round goby could assess the value of a resource without any opportunity to evaluate the resource before the contest had started. We found that when fish had no prior experience with the shelter, resource value did not influence contest dynamics, indicating that round goby may need to interact with the shelter to assess its value. Our findings are similar to those of Jennings et al. (2004; fallow deer, *Dama dama*) and Thornhill (1984; scorpionflies, *Harpobittacus nigriceps*), where animals appear to be unable to assess a resource during a contest, or are unable to modify their behaviour based on any gathered information. Likewise, our findings are also similar to those of Bridge et al. (2000), who found that intruding male orb-weaving spiders (*M. mengei*) were unable to evaluate the resource value of a potential female mate during aggressive contests with resident, rival males. Our results from experiment 2 are further supported by our resource preference experiment, where we found that individual fish only showed a clear preference for high-quality shelters after 24 h. Our results suggest that round goby need time to gather information about a shelter resource before being able to use this information to adjust their effort in an aggressive contest.

In experiment 3, we tested whether round goby would fight harder for a high-quality shelter if they were given prior experience with the resource before beginning an aggressive contest (the 'matched' experience condition). We further asked whether fish were able to update their appraisal of resource value during the contest by creating a mismatch in the value of the shelter present during the prior experience phase and the value of the shelter present during the contest phase (the 'mismatched' experience condition). Here, we found that fish with matched prior experiences fought according to resource value: they started contests faster and had contests with more aggressive acts when fighting over high-quality compared to low-quality shelters. However, fish appeared to be limited in their ability to fully update their appraisal of resource value during contests where the resource present in the contest did not match the resource they had previously experienced. Other studies have similarly shown that when animals are given experience with a resource, they will evaluate its value and use this information to adjust their aggressive effort. For example, Humphries et al. (2006) demonstrated that parasitoid wasps (*G. nephantidis*) with prior resource experience fought harder for high-quality hosts than for low-quality hosts. Additionally, Ewald (1985) found that black-chinned hummingbirds, *Archilochus alexandri*, with high- or low-quality food territories fought harder when they had previously experienced a high-quality territory.

Interestingly, our findings also suggest that round goby may be partially updating their evaluation of the shelter resource present during the contest. Although competing fish were clearly unable to fully assess and update their evaluation of the new resource during the contest, they appeared to recognize that the resource present in the contest was dissimilar to the resource from their prior experience. In support of this notion, contest winners spent more time evaluating the contested resource after the contest had ended in the mismatched experience condition than in the matched experience condition. Fish may therefore be 'updating' their prior appraisal of the resource. Across both resource contest experiments (no prior experience and matched/mismatched prior experience), we found that information gathering about the resource mainly occurred after the aggressive contest was resolved, and not before aggressive interactions began. Fish were unlikely to enter the shelter before the contest started, but almost all fish entered the shelter at some point after the contest was decided. Lindström (1992) found that sand goby appeared to be unable to assess resource value without physically entering the burrow, but were also unlikely to enter a burrow before resolving an aggressive contest. It is likely that the fish in our study were assessing their opponent at the start of each trial more than the resource present. More work will be needed to clarify what cues round goby are using to assess resource quality before entering the shelter. It is possible that round goby may be using visual cues of overall shelter size, size of the shelter entrance opening, or general illumination within the shelter to evaluate the shelter's structural features when observed at a distance before entering the shelter.

In summary, our novel investigation of resource assessment and information-gathering abilities of round goby allowed us to explore the effect that resource value has on contest dynamics. We showed that high-quality resources are preferred to low-quality resources. We also showed that fish needed prior experience with a resource to alter their aggressive effort in a contest to accurately reflect resource value. The fish appeared to be limited in their ability to update their appraisal of resource value during a contest. We have clearly shown that the characteristics of a contested resource can affect contest dynamics, but we cannot definitively show that fish are willing to pay a higher cost (e.g. energy expenditure, injury) in order to win a high-quality shelter, as would be predicted by traditional game-theory models of aggressive contests (Enquist & Leimar, 1987; Parker, 1974). It would be fruitful to follow our work with measures of the physiological costs of fighting to determine whether longer contests are more energetically costly in this system (Briffa & Sneddon, 2007). We recommend the further use of resource contests where competitors have symmetrical prior resource experience for understanding the impact of resource valuation on contest dynamics. Our findings contribute to a growing body of literature investigating how resource value affects animal contests, and our work helps to elucidate how animals gather information and assess resource value during contests.

## Acknowledgments

We thank T. Warriner and K. Goodick for field assistance with fish collections, and A. Bose, C. O'Connor and A. Reddon for their helpful comments on this manuscript. This research was supported by a Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant (RGPIN-2016-05772) and the Canada Research Chair Program to S. Balshine, and an NSERC Postgraduate Scholarships-Doctoral Program to E. McCallum.

## Supplementary Material

Supplementary material associated with this article is available, in the online version, at http://dx.doi.org/10.1016/j.anbehav.2016.10.032.

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