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

Erin S. McCallum*, Sarah T. Gulas, Sigal Balshine

Aquatic Behavioural Ecology Laboratory, Department of Psychology, Neuroscience & Behaviour, McMaster University, Hamilton, ON, Canada

ARTICLE INFO

Article history:
Received 4 July 2016
Initial acceptance 19 July 2016
Final acceptance 26 August 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

* Correspondence: E. S. McCallum, Aquatic Behavioural Ecology Laboratory, Department of Psychology, Neuroscience & Behaviour, McMaster University, 1280 Main Street West, Hamilton, ON L8S 4K1, Canada.
E-mail address: mccalles@mcmaster.ca (E. S. McCallum).

http://dx.doi.org/10.1016/j.anbehav.2016.10.032
0003-3472/

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 2×2 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