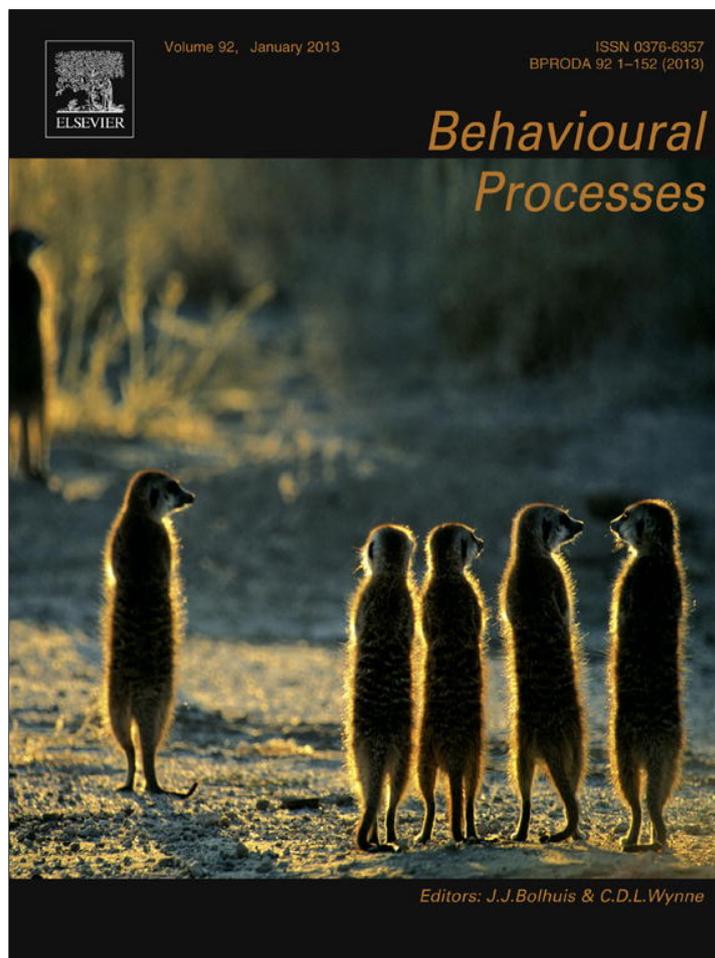


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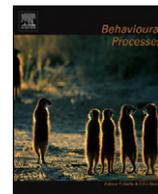
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# Probing aggressive motivation during territorial contests in a group-living cichlid fish

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## ABSTRACT

Many animals fight to win resources, repel competitors or establish dominance in a social group. Mutual-assessment of fighting ability, where competitors gather and compare information about their opponent's as well as their own fighting ability has been the dominant theoretical framework for understanding decision-making during fights. However, self-assessment, where each individual has a cost threshold and fights up until that point, may be more common than previously appreciated. In this study, we attempted to discriminate between these two potential assessment mechanisms in a group-living cichlid fish, *Neolamprologus pulcher* by probing aggressive motivation during a territorial contest. We measured aggressive motivation, and used this metric to investigate assessment rules during an ongoing contest. We predicted that if these social fish use self-assessment, we would observe a positive correlation between the fighting ability of the probed animal and its aggressive motivation. Alternatively, if mutual-assessment is used then we predicted we would find a negative effect of the opponent's fighting ability on the aggressive motivation of the probed fish because fish should be less motivated to fight against formidable opponents. Our results did not support either of these predictions. In contrast we found that small individuals were more aggressively motivated regardless of their opponent's size. We discuss this result in the context of theoretical models of aggression in individuals of small body size.

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## 1. Introduction

Aggressive contests are common when animals resolve conflict by direct interaction (Huntingford and Turner, 1987; Archer, 1988; Maynard-Smith and Harper, 2003; Briffa and Sneddon, 2010). Contests can be costly in terms energy (Briffa and Elwood, 2004; Castro et al., 2006), lost time for feeding and mating (Kemp and Wiklund, 2001), diverted attention from potential predators (Jakobsson et al., 1995), and the risk of injury or death (Enquist and Leimar, 1990). Consequently, contests typically include some form of assessment, which may reduce these costs to one or both competitors (Parker, 1974; Enquist and Leimar, 1983; Arnott and Elwood, 2009a).

Fighting ability (commonly referred to as resource holding potential or power, abbreviated 'RHP' in either case) is a key determinant of fight outcome and dynamics (Parker, 1974; Maynard-Smith, 1982). Models of fighting ability assessment can be broken up into two basic categories: 1) Self-assessment, where animals make the decision to persist or relent in a contest based on

a threshold for costs incurred and, 2) mutual-assessment, where each contestant gathers some information about the strength of its opponent and compares that information to its own fighting ability (Maynard-Smith and Parker, 1976; Parker and Rubenstein, 1981; Enquist and Leimar, 1983; Enquist et al., 1990; Mesterton-Gibbons et al., 1996; Payne and Pagel, 1996, 1997; Payne, 1998). Mutual-assessment is more complex, but carries with it the distinct advantage of reducing fight costs for the loser in asymmetric contests (Arnott and Elwood, 2009a).

Perhaps because mutual-assessment is intuitively satisfying, and mirrors the decision-making processes in our own species (Sell et al., 2009, 2010), mutual assessment has become the dominant paradigm in the study of aggression (Taylor and Elwood, 2003; Briffa and Elwood, 2009; Arnott and Elwood, 2009a). The most commonly reported evidence for mutual-assessment is a negative relationship between the degree of asymmetry in fighting ability between the two contestants and the duration of the contest (Taylor and Elwood, 2003). The logic being that closely matched contestants will have greater difficulty determining which one has an advantage, and therefore will need to fight longer before determining which is stronger (Enquist and Leimar, 1983). However, the relationship between fighting ability asymmetry and contest duration can be driven entirely by a positive relationship between the fighting ability of the loser and the duration of the contest

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(Taylor and Elwood, 2003). Therefore self-assessment can produce the same result as mutual-assessment.

Fortunately, Taylor and Elwood (2003) recommend a clever way to distinguish between these two forms of assessment by examining the effects of winner and loser fighting ability on contest duration separately. Under mutual assessment, opposite effects of winner and loser fighting ability on the duration of the contest is expected with stronger losers lengthening the contest and stronger winners shortening it. Under self-assessment, only the loser's fighting ability should be positively related to the duration of the contest (because the fight ends when the loser gives up) whereas the winner's fighting ability should be unimportant. The independent analysis of winner and loser fighting ability has been successfully applied in a number of empirical studies on a wide range of taxa (e.g., shore crabs, *Carcinus maenas*: Smallegange et al., 2007; jumping spiders, *Phidippus clarus*: Elias et al., 2008; house crickets, *Acheta domestica*: Briffa, 2008; sierra dome spiders, *Neriene litigiosa*: Keil and Watson, 2010; cichlid fish, *Neolamprologus pulcher*: Reddon et al., 2011; green anole lizards, *Anolis carolinensis*: Garcia et al., 2012; fallow deer, *Dama dama*: Jennings et al., 2012).

Recently, Arnott and Elwood (2009a) suggested that assaying aggressive motivation during an ongoing contest might be another way to discriminate between self- and mutual-assessment. The motivational probe technique involves interrupting one of two fighting animals with a simulated predator attack and measuring the latency for this disturbed animal to resume fighting its rival. The duration until resuming the fight can be taken as an inverse metric of aggressive motivation. This assay was initially developed for use during fights in the hermit crab (*Parurus bernhardus*; Elwood et al., 1998; Briffa and Elwood, 2001), but has been subsequently adapted for use during contests in a fish, the convict cichlid (*Amatitlania nigrofasciata*; Arnott and Elwood, 2009b, 2010). The motivational probe assay assumes that the interruption by a novel startle stimulus will activate antipredator responses in the startled animal, and that the motivation to continue fighting will be put in conflict with the motivation to avoid predators (Culshaw and Broom, 1980; Elwood et al., 1998). Presumably, animals that are more motivated to fight will show shorter latencies to resume aggression than those that are less motivated, and thus latency to resume aggression can be taken as an inverse measure of aggressive motivation (Elwood et al., 1998; Arnott and Elwood, 2009a,b, 2010). This method offers several potential advantages over the measures of contest cost taken at the end of a fight (e.g. fight duration, injury or energy expenditure). Namely, contest cost measures taken at the end of a contest can only provide insight into the final decision made by the loser (as the loser decides when the fight is over) while measuring aggressive motivation throughout a contest may provide information about the ongoing decision-making process in both winners and losers.

In this study, we applied the motivational probe technique for the first time to staged resource contests in the group-living cichlid fish, *N. pulcher*. *N. pulcher* are small cichlid fish endemic to Lake Tanganyika, Africa that form permanent social groups consisting of a single dominant breeding pair and 1–20 subordinate non-reproductive adults (Taborsky and Limberger, 1981; Taborsky, 1984, 1985; Balshine-Earn et al., 1998; Balshine et al., 2001; Wong and Balshine, 2011a). The subordinate helpers may be either related or unrelated to the breeding pair and to each other (Stiver et al., 2008). *N. pulcher* groups are organized as strict linear dominance hierarchies that are determined by body size and hence fighting ability (Taborsky, 1984, 1985; Balshine et al., 2001; Wong and Balshine, 2011a,b). Rank in the dominance hierarchy is strongly related to fitness outcomes of *N. pulcher*, and only a few fish ever attain a dominant breeding position (Stiver et al., 2004; Wong and Balshine, 2011a). Dominance relationships are formed and tested by direct aggressive interactions (Arnold and Taborsky, 2010; Riebli

et al., 2011), and therefore fighting behaviour in general and the assessment of fighting ability in particular is of paramount importance to the social structure of *N. pulcher* groups (Taborsky, 1984, 1985; Hamilton et al., 2005; Wong and Balshine, 2011b; Reddon et al., 2011).

A previous study on fighting behaviour in *N. pulcher* found that body size asymmetry between the competitors predicted contest duration and that a 5% advantage in body size was sufficient to determine which individual would win (Reddon et al., 2011). However, the results from Reddon et al. (2011) did not fit perfectly with any of the extant contest assessment models. Namely, opponent size was the primary determinant of fight dynamics and the fighting ability of the losing fish did not predict the duration or intensity of contests. In the present study, we aimed to further investigate the aggressive assessment abilities in this highly social fish using the motivational probe technique (Elwood et al., 1998). We predicted that if the latency to resume aggression correlates negatively with the probed individual's fighting ability and positively with its opponent's fighting ability then mutual-assessment likely underlies *N. pulcher* contests. In contrast, if the latency to resume aggression was uncorrelated with opponent fighting ability but negatively related to the probed individual's fighting ability then this would suggest that self-assessment is a better fit. We test these two competing predictions here.

## 2. Materials and methods

### 2.1. Animals

The fish used in this study were the laboratory-reared descendants of *N. pulcher* collected from Lake Tanganyika, Africa. The fish lived within naturalistic social groups, housed one group per 189 L glass aquarium (92 × 41 × 50 cm). Each group consisted of a dominant breeding pair and 2–10 adult subordinate helpers. Each group was housed in an aquarium that contained a pair of flow-erpot halves to serve as brood chambers, two large foam filters (10 × 10 × 30 cm), and 3 cm of crushed coral sand substrate. Aquaria were maintained at 26 ± 2 °C and exposed to a 14L:10D light cycle. Fish were fed commercial cichlid flake food (Hagen Nutrafin basix) once daily, 6 days per week.

We used 50 (26 males and 24 females) subordinate helper fish from these groups to form 25 experimental pairs. The fish ranged in size from 44.0 to 65.8 mm standard length (SL, measured from the tip of the snout to the caudal peduncle). We also weighed each fish and found that SL and mass were strongly correlated ( $r = 0.94$ ,  $N = 50$ ,  $p < 0.0001$ ), so we chose to use SL for all analyses to be consistent with previous research on contest behaviour in this species (Reddon et al., 2011, 2012). Fish were always paired with an unfamiliar, same sex, individual. Pairs were not size matched and the size asymmetry within each pair ranged from 0.7 to 26.9% different in SL. *N. pulcher* naturally fight with individuals from their own group and with potential group joiners over shelters and to establish dominance rank (Wong and Balshine, 2011a,b; Riebli et al., 2011, 2012; Reddon et al., 2011, 2012).

### 2.2. Procedure

Contests took place in a 38 L aquarium (50 × 26 × 30 cm). A permanent transparent barrier separated the contest aquarium into two equally sized compartments (25 × 26 × 30 cm) and a pair of fish from two randomly chosen social groups were placed into these two compartments. The pair of fish had no visual contact for a 3 h acclimation period because an opaque, removable barrier was inserted adjacent to the transparent barrier. We chose a 3 h acclimation time because prior work in our lab has suggested that a 3 h

residence time is sufficient to induce a robust aggressive response to perceived intruders in *N. pulcher* (Reddon et al., 2012). Following the acclimation period, the opaque barrier was removed (bar one 6 cm strip, that hid the motivational probe from the stimulus fish, see below), and the two fish could begin to interact across the transparent barrier. Fish were allowed to attack each other across the barrier for 2 min. We then probed aggressive motivation of one of the two fish, determined at random beforehand and henceforth referred to as the focal fish. The motivational probe consisted of a 22 g glass marble dropped through a plastic tube into the focal fish's compartment from a height of 26 cm. The marble was dropped with a remote trigger activated by an experimenter from 2.5 m away. The falling marble was visible to the focal but not the stimulus fish. The falling marble created a noticeable splash as it entered the water and sunk down to the substrate. However, the physical disturbance of the water caused by the falling marble did not penetrate the barrier separating the focal compartment from the stimulus fish compartment and appeared to be perceptible only to the focal fish. Following Arnott and Elwood (2009b, 2010), we assumed that this novel visual/tactile disturbance simulated a potential predator attack. The trials were video recorded for a period of 300 s following the marble drop at which point the opaque barrier was reinserted between the fish, terminating the trial. A trained observer, blind to the sex and the body size measurements of the fish, later scored the video recordings. We measured the time it took for the focal fish to resume attacking its opponent (biting at and/or ramming the barrier in the direction of the opponent). Fish that had not resumed aggression within 300 s were assigned a score of 300 s.

We considered the latency to resume physical attacks on the opponent fish as an inverse measure of the focal fish's aggressive motivation (Elwood et al., 1998; Arnott and Elwood, 2009b). Fish that were more motivated to attack their rival, presumably resumed aggression sooner than those that are less motivated to resume fighting. We also measured the time taken to begin attacking initially following the removal of the barrier as an index of aggressive motivation at the beginning of the fight and the time spent frozen motionless following the marble drop as an index of the fish's fear of the marble drop stimulus. We predicted that the motivation to resume fighting following the motivational probe would correlate with the focal fish's perception of its chances of winning and that fish that perceived themselves as having a high probability of winning a fight would be more motivated and would therefore resume fighting sooner.

Each pair was tested twice, 3 h apart with each fish in an experimental pair serving as both the focal fish and the stimulus fish in a randomly determined order. During the 3 h intertrial interval, the opaque barrier was reinserted between the fish preventing visual contact, and the marble dropping apparatus was shifted over to the other compartment of the contest aquarium.

### 2.3. Data analysis

We analyzed the time taken to attack from the beginning of the removal of the opaque barrier, the time spent frozen after the marble drop and the latency to resume fighting after the marble drop using generalized linear mixed models (GLMM) with an identity link function treating each pair as an experimental unit (following Briffa and Elwood, 2010). We included testing order as a within experimental units factor, sex as a between experimental units factor and both focal and opponent SL as continuous covariates. Analysis was conducted using SPSS 20.0 (SPSS Inc., Chicago, IL, USA).

### 2.4. Ethical note

Fish in this experiment did not suffer any injury nor did they exhibit any signs of undue stress. The methods for animal housing,

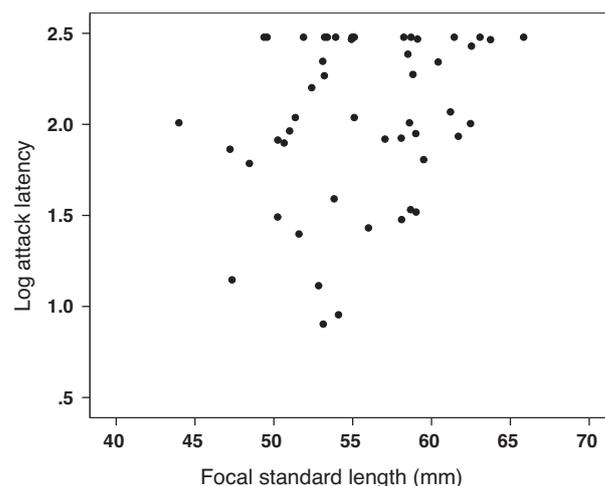


Fig. 1. Focal size (standard length in mm) plotted against the log of the latency to resume aggression following an experimental disturbance ( $p=0.001$ ).

handling and experimental protocols were assessed and approved by the Animal Research Ethics Board of McMaster University (Animal Utilization Protocol #10-11-71) and adhere to the guidelines of the Canadian Council for Animal Care and the Animal Behaviour Society.

## 3. Results

Fish took an average of  $63.6 \pm 13.0$  s to attack their rival across the transparent barrier following the removal of the opaque barrier. There was no difference between males and females in the time taken to attack rivals (GLMM effect of sex:  $F_{1,45} = 0.13$ ,  $p = 0.72$ ) or between fish in the first versus the second trial (effect of test order:  $F_{1,45} = 0.40$ ,  $p = 0.53$ ). There was no statistically significant relationship between the size of the focal fish or its opponent's size and the latency to attack after the barrier had been raised (effect of focal SL:  $F_{1,45} = 0.05$ ,  $p = 0.83$ ; effect of opponent SL:  $F_{1,45} = 2.00$ ,  $p = 0.16$ ).

Following the marble drop, on average, the focal fish remained frozen motionless for a period of  $21.7 \pm 5.3$  s. Males and females froze for a similar amount of time (GLMM effect of sex:  $F_{1,45} = 1.90$ ,  $p = 0.18$ ) and there was no effect of testing order on the duration that fish remained frozen (effect of testing order:  $F_{1,45} = 2.90$ ,  $p = 0.10$ ). The body size of the focal fish was not significantly related to its freezing duration (effect of focal SL:  $F_{1,45} = 0.06$ ,  $p = 0.81$ ) nor was the size of its opponent (effect of opponent SL:  $F_{1,45} = 0.85$ ,  $p = 0.36$ ).

Fish took an average of  $158.5 \pm 16.0$  s to resume attacking their opponent following the motivational probe. The size of the focal fish was positively related to its latency to resume attack (GLMM effect of focal SL:  $F_{1,45} = 11.45$ ,  $p = 0.001$ ; Fig. 1) such that smaller fish were faster to resume aggression than were larger fish. There was no relationship between opponent size and the latency of the focal fish to resume attacking (effect of opponent SL:  $F_{1,45} = 0.54$ ,  $p = 0.47$ ; Fig. 2). Also, there was no difference between males and females in terms of their latency to resume aggression (effect of sex:  $F_{1,45} = 0.86$ ,  $p = 0.36$ ) nor was there any effect of testing order (effect of test order:  $F_{1,45} = 2.30$ ,  $p = 0.14$ ). The latency to resume attacking following the probe stimulus was not significantly related to the latency to begin attacking initially following the removal of the opaque barrier ( $F_{1,46} = 0.28$ ,  $p = 0.60$ ) or the time spent frozen following the marble drop ( $F_{1,46} = 1.25$ ,  $p = 0.27$ ).

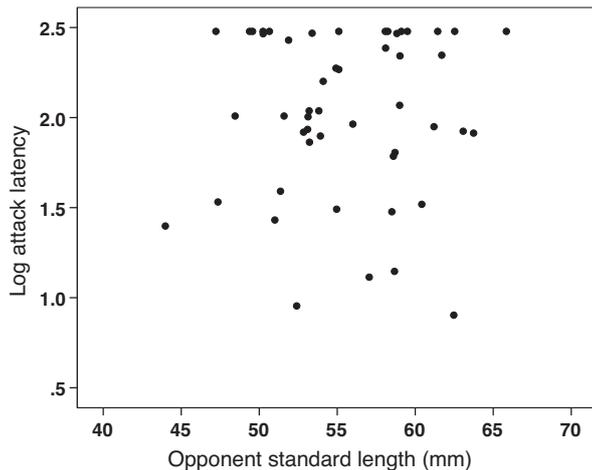


Fig. 2. Opponent size (standard length in mm) plotted against the log of the latency to resume aggression following an experimental disturbance ( $p = 0.47$ ).

#### 4. Discussion

Smaller individuals were more, not less, motivated to resume aggression and opponent size had no influence on the latency to resume aggression. Neither focal nor opponent size was significantly related to either the initial latency to begin aggression after the opaque barrier was raised or the time spent frozen following the marble drop. Therefore, our study does not provide clear evidence for either self- or mutual-assessment. Note that the only previous study to use a motivational probe to investigate assessment during resource contests, also did not find unambiguous support for either set of models (Arnott and Elwood, 2010). We did not find any effect of testing order on any of our measures, suggesting that there was not a priming or a habituation effect on aggression in *N. pulcher* with the intertrial interval used here. Males and females did not differ in their latency to attack initially or following the marble drop and spent equal time frozen after the marble drop.

Heightened aggressivity among small individuals has been observed in other species of fish and invertebrates (e.g. Dow et al., 1976; Enquist and Jakobsson, 1986; Ribowski and Franck, 1993; Smith et al., 1994; Morris et al., 1995; Moretz, 2003; Reddon and Hurd, 2009) and there have been several theories and models proposed to explain these seemingly illogical results (e.g. Grafen, 1987; Dugatkin and Ohlsen, 1990; Bradbury and Vehrencamp, 1998; Just and Morris, 2003; Morrell et al., 2005; Just et al., 2007). The best known of these ideas is the desperado hypothesis (Grafen, 1987) which postulates that weak or poor-quality individuals may have nothing to lose from escalating conflicts over resources they are not likely to secure otherwise. Furthermore, a low-value resource may be worth more to a weak individual than a strong one and hence a weak individual may be more motivated in a contest than is a strong one. The desperado effect is unlikely to explain our observations in *N. pulcher* because, like most fish species, this cichlid grows throughout its lifespan. So an individual with low current fighting ability may eventually become a strong competitor. In fact, the social system of *N. pulcher* is based on queuing within a social group to attain dominant status in the future (Taborsky and Limberger, 1981; Balshine-Earn et al., 1998; Wong and Balshine, 2011a,b). Furthermore, social rank and/or territory are likely to be valued even more by a large individual who might be close to capitalizing on its position and achieving breeding status (Wong and Balshine, 2011b). *N. pulcher* are more likely to play a wait-and-grow strategy as a social subordinate rather than recklessly challenging for dominance as expected by the desperado hypothesis.

An alternative explanation for the heightened aggression in smaller individuals is known as the Napoleon strategy (Morrell et al., 2005). Smaller individuals may be aggressive when the odds in the fight are only slightly against them, the value of the resource is high relative to the costs of fighting and fighting ability is not a perfect determinant of fight outcome (i.e., there are occasional upsets). The Napoleon strategy may be a reasonable explanation for why small *N. pulcher* are more aggressive because both territories and social rank are extremely valuable resources (Balshine et al., 2001; Wong and Balshine, 2011a,b), contests rarely result in severe injuries or death (Reddon et al., 2011) and smaller individuals occasionally win in closely matched contests (Reddon et al., 2011).

The increased aggressive motivation we observed among small *N. pulcher* may be unrelated to any form of fighting ability assessment, for example, small fish may have a higher resting metabolic rate which leads them to behave in a bolder and more aggressive manner (Biro and Stamps, 2010). However, the lack of correlation between the latency to begin the contest and to resume fighting following the startle stimulus suggests that boldness was not an important mediator of aggressive motivation in our study. Nevertheless, it is possible that factors unrelated to assessment may underlie some of the variation in aggression in *N. pulcher* and the precise reasons for the heightened aggressive motivation that we observed in smaller *N. pulcher* will need to be elucidated by future study.

The current experiment employed a motivational probe technique to study aggressive motivation in contesting *N. pulcher* in an attempt to clarify the processes underlying assessment and decision-making in this highly social vertebrate. We found that smaller *N. pulcher* appear to more motivated to resume aggression, but did not find support for any of the extant models of fighting ability assessment.

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