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ORIGINAL PAPER

Contest experience and body size affect different types of contest decisions

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Abstract This study examined the relative importance of contest experience and size differences to behavioral decisions over the course of contests. Using a mangrove rivulus fish, *Kryptolebias marmoratus*, we showed that although contest experience and size differences jointly determined contest outcomes, they affected contestants' interactions at different stages of contests. Contest experience affected behavioral decisions at earlier stages of contests, including the tendency and latency to launch attacks, the tendency to escalate contests into mutual attacks and the outcome of non-escalated contests. Once contests were escalated into mutual attacks, the degree of size difference affected the fish's persistence in escalation and chance of winning, but contest experience did not. These results support the hypothesis that contest experience modifies individuals' estimation of their fighting ability rather than their actual strength. Furthermore, (1) in contests between two naïve contestants, more than 60 % of fish that were 2–3 mm smaller than their opponent escalated the contest to physical fights, even though their larger opponents eventually won 92 % of escalated fights and (2) fish with a losing experience were very likely to retreat in the face of an opponent 2–3 mm smaller than them without escalating. The result that a 2–3 mm size advantage could not offset the influence of a losing experience on the tendency to escalate suggests that, as well as depending on body size, the fish's physical strength is influenced by other factors which require further investigation.

Keywords Animal contest · Behavioral decisions · Winner–loser effect · Size difference · *Kryptolebias marmoratus*

Introduction

Fighting for access to limited resources can be costly because of the expenditure of time and energy and the risk of physical injuries and predation (Neat et al. 1998; Brick 1999). A more able contestant has a better chance of winning, resolving a contest quickly and avoiding injury. An individual's potential contest costs should therefore decrease with its fighting ability and increase with its opponent's (Enquist et al. 1990). It would be beneficial for an individual to adjust its contest decisions based on its and its opponent's fighting ability. Body size is, in many species, a good surrogate measurement for physical strength and the ability to win fights (see Hsu et al. 2006 for a review); larger individuals tend to persist longer in contests, are more likely to advance contests into more intensive interactions (Taylor et al. 2001; Morrell et al. 2005) and more likely to win than their smaller rivals.

Because a more able contestant has a better chance of winning, the outcomes of previous fights could provide an individual with sampling information about how its ability to fight compares with those of others in the population; winning experiences raise while losing experiences lower its estimated fighting ability (Dugatkin 1997; Whitehouse 1997; Mesterton-Gibbons 1999; Mesterton-Gibbons et al. 2016). These changes in an individual's estimate of its own

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fighting ability modify its anticipated fighting costs and consequently its contest decisions: after wins individuals behave more aggressively and enjoy a higher chance of winning (winner effect); after defeats they behave more submissively and suffer a higher chance of losing again (loser effect). Individuals of a wide array of taxa (insects, arachnids, crustaceans, fish, reptiles, birds, mammals) display winner and/or loser effects (Hsu et al. 2006). In *Kryptolebias marmoratus*, an individual's previous winning and losing experiences have been found to modify only its and not its opponent's contest decisions (Hsu et al. 2009).

In the field, it is likely that the two contestants in a contest have fought and experienced wins and/or losses previously and differ in both their body size and their fighting experience. The information about their likely fighting costs from these two sources should ideally be integrated to guide the fish's contest decisions. If winning–losing experiences modify an individual's *assessment* of its fighting ability, whereas the difference in body size is positively associated with the difference in *actual* fighting ability, the relative importance of these two factors to an individual's contest decisions might change over the course of a contest. At earlier stages of a contest, when reliable information about each other's relative fighting ability is not yet available, previous winning and losing experiences should have more influence on contest decisions than size difference. As a contest progresses to later stages (i.e., with physical interactions) and more reliable information about relative fighting ability becomes available, the information from previous contest experience is no longer useful, and size difference should have more influence on contest decisions than previous contest experience. Moreover, the information from previous contest experience should be more useful to contestants when their relative fighting ability is highly uncertain. So the importance of winning–losing experience to contest decisions should be negatively associated with the difference between the relative sizes of the two contestants.

Some previous studies have examined the relative importance of size asymmetry and past contest experience to contest outcomes (Beacham 1988; Beaugrand et al. 1991, 1996; Martin et al. 1997a, b; Schuett 1997; Kasumovic et al. 2009; Reaney et al. 2011). Some of the studies showed the influence of previous experience on contest outcome to be negatively associated with the degree of size asymmetry (Beacham 1988; Beaugrand et al. 1991, 1996), some showed previous experiences to overpower the influence of size asymmetry (Martin et al. 1997a, b; Schuett 1997), while some concluded size asymmetry to be more important than previous experiences (Reaney et al. 2011). In most of these studies, the effect of experience per se was not completely isolated from the intrinsic ability to win: contestants with winning experiences were probably also better fighters than those with losing experiences. And most of the studies measured the effects of these factors on contest outcome but not on interactions at earlier stages of the contests (but see Martin et al. 1997b, in which the importance of hens' body weight on both the interactions in and the outcome of their contests were examined although no significant influences were detected). Whether the relative importance of size difference and contest experience to behavioral decisions changes over the progress of a contest, and if so how, remains largely untested.

In this study, we investigated the effect of contest experience and size difference on decisions over the course of a contest, using individuals of *Kryptolebias marmoratus* (Cyprinodontiformes, Rivulidae), a mangrove killifish, as the study animal (Fig. S1). *K. marmoratus* is an internally self-fertilizing hermaphroditic fish living in mangrove swamps in all of North, Central and South America (Taylor 2012). It is usually found in crab burrows and ephemeral pools, hiding under leaf litter and inside decaying logs (Taylor 2012). The fish does not exhibit schooling behavior but behaves aggressively in both the field and the laboratory (Kristensen 1970; Huehner et al. 1985; Taylor 1990). The fish exhibits significant winner and loser effects, behaving more and less aggressively after experiencing recent wins and losses, respectively (Hsu and Wolf 1999; Hsu et al. 2009). The fish's contest behavior is affected by its previous contest experience but not its opponent's (Hsu et al. 2009). Furthermore, the fish's contest decisions are dependent on both its and its opponent's size: individuals that are larger and/or fighting against smaller opponents have a higher tendency to escalate contests into physical interactions (Hsu et al. 2008). Building on these findings, this study tested the hypotheses that (1) contest experience has a greater influence on behaviors at earlier stages of a contest (i.e., before physical interactions), (2) size difference has a greater influence on behaviors at later stages of a contest (i.e., after progressing into physical interactions), and (3) the importance of contest experience is negatively associated with the relative difference between the size of the two contestants.

Materials and methods

Study organism

Natural populations of *K. marmoratus* consist mainly of isogenic homozygous hermaphrodites with <1 % males (Mackiewicz et al. 2006). The fish is capable of producing fertilized eggs all year round and does not have obvious oviposition cycles (Taylor 2012). Laboratory fish usually start to lay fertilized eggs 3–6 months after hatching

(Harrington 1975; Grageda et al. 2005). This study used the hermaphroditic descendants of five isogenic lineages of *K. marmoratus* originally collected by Dr. D. Scott Taylor from various locations (DAN2K: Dangriga, Belize, collected in 2000; HON9: Utila, Honduras, collected in 1996; RHL: San Salvador, Bahamas, collected in 1997; SLC8E: St. Lucie County, FL, USA, collected in 1995; VOL: Volusia County, Florida, USA, collected in 1995). Fish were placed in individual translucent polypropylene maintenance containers (13 × 13 × 9 cm) filled with 550 ml 25 ppt synthetic sea water (Instant Ocean^{TM} powder) and given a unique identification code within a month of hatching. Fish were kept at 25 ± 2 °C on a 14:10-h photoperiod and fed newly hatched brine shrimp (*Artemia*) nauplii daily. Maintenance containers were cleaned and water replaced every 2 weeks. All fish used in this study had been re-isolated for at least 1 month after use in previous studies as a precaution to avoid over-using them and minimize the potential influence of previous interactions with other fish (Hsu and Wolf 1999, 2001; Huang et al. 2011).

Experimental design and procedures

We used a 3 × 3 factorial design to examine the importance of contest experience and size difference to contest behaviors and outcomes. There were three experience treatments, namely no contest experience vs. no contest experience, winning experience vs. no contest experience and no contest experience vs. losing, experience and three size-difference treatments, namely 0–1, 1–2 or 2–3 mm difference in standard length (SL, measured from the tip of the snout to the caudal peduncle). Sixty pairs of fish were used for each of the nine treatment combinations making a total of 540 pairs, which were formed of 1080 unique fish.

Previous studies of the fish (Hsu et al. 2008) showed that there is no observable difference in the probabilities of the fish winning when difference in SL is less than 1 mm. Once the size difference exceeds 2 mm, the larger contestant has close to a 90 % chance of beating the smaller contestant. We therefore set up three size asymmetries for this study: 0–1, 1–2 and 2–3 mm. The SL of the experimental fish was measured to the nearest 0.01 mm with a digital caliper approximately 1 week before the experiments. The SL of the smaller contestants did not differ significantly between various size-difference treatments (mean ± SE for 0–1, 1–2 and 2–3 mm size difference: 27.3 ± 0.3, 26.7 ± 0.3 and 26.7 ± 0.3 mm, respectively; $F_{2,537} = 1.3$, $P = 0.282$). The SL of the larger contestants was, however, larger in the larger-difference treatments (mean ± SE for 0–1, 1–2 and 2–3 size difference: 27.6 ± 0.3, 28.2 ± 0.3 and 29.2 ± 0.3 mm, respectively; $F_{2,537} = 6.8$, $P = 0.001$). The smaller and the larger contestant of a contest pair were matched for their lineage and the outcome of their last contest prior to this study (both previous winners or both previous losers).

For each size-difference treatment, pairs of fish were randomly divided into three groups and assigned to one of the three experience treatments: (1) both the smaller and larger contestants received a no-contest experience (N–N pair), (2) the smaller contestant received a winning experience, while the larger contestant received a no-contest experience (W–N pair), and (3) the smaller contestant received a no-contest experience, while the larger contestant received a losing experience (N–L pair). The purpose of giving the larger contestants a more negative experience and the smaller contestants a more positive experience was to test the relative importance of the differences in size and experience.

On Day 0, we marked the two fish of a contest pair by breaking the non-vascular thin membrane between the two soft rays in the upper or lower margins of the caudal fin (randomly assigned) with a needle. Immediately after marking, fish were replaced in their maintenance containers and fed small amounts of newly hatched brine shrimp.

On Day 1, the two individuals of a contest pair received their pre-designated winning, losing or no-contest experience. To ensure that fish received their pre-designated losing (or winning) experience, we fought them against much larger (smaller) fish (difference in SL > 2 mm) that had won (lost) several fights against similar-sized opponents. All experience training took place in standard aquaria (12 × 8 × 20 cm) containing 2 cm of gravel filled with water 12 cm deep. The sides and the back panels of the aquaria were covered with black plastic boards. The front panels of the aquaria were left uncovered to allow observation. The experience training was staged by placing an experimental fish in one of the two similar-sized compartments (randomly assigned) of a standard aquarium divided by a black partition and the larger (smaller) trainer fish in the other compartment. After 15-min acclimatization, the partition was removed to allow the fish to interact. A losing experience was completed when the experimental fish retreated from a display/attack by the larger trainer fish and quickly swam away. A winning experience was completed when the smaller trainer fish retreated from the experimental individual's display/attack and quickly swam away. Upon the completion of the experience training, the partition was re-inserted to separate the two fish. Fish assigned to receive a no contest experience were treated exactly as above, with procedures synchronized with those assigned losing or winning experiences, except that there was no opponent in the other compartment. Upon completion of the experience training, the fish were replaced in their maintenance containers and fed newly hatched brine shrimp. Two hours after being fed, the two individuals of a

contest pair were placed one in each of the two similar-sized compartments (randomly assigned) of a standard aquarium separated by a black partition and left to acclimatize overnight (for approximately 20 h).

On Day 2, a contest was started by removing the black partition between the two compartments. Please refer to previous studies of *K. marmoratus* for detailed descriptions of its contest behavior (Hsu and Wolf 2001; Hsu et al. 2008). After the partition was removed, one of the contestants usually initiates interactions by orienting and swimming toward its opponent. This behavior is considered a threat display. After a few bouts of mutual displays, if neither contestant has retreated, one of them usually launches a first attack by swimming rapidly toward and pushing against or biting its opponent. The fish that has received the first attack either retreats or responds with attacks. The individual that first retreated from its opponent's displays/attacks for 5 min without retaliating was the loser and its opponent the winner. A contest is considered to be '*non-escalated*' if resolved with mutual displays or one initial attack. A contest is '*escalated*' if resolved after mutual attacks. If the two individuals of a contest pair did not engage in sufficient interactions to result in a clear winner/loser in 1 h, the contest was terminated and classified as '*unresolved*'. The partition was replaced to separate the two contestants after the contest was resolved with a clear winner/loser or terminated. All contests were recorded with camcorders for behavioral analysis. The behavioral data were later transcribed from the recordings. To evaluate inter-rater reliabilities of the behavioral data, we randomly selected a subset of 60 contests to be transcribed by a graduate student who had not participated in the study and had no knowledge of the treatments to which the experimental fish had been assigned. The two transcriptions of the contest behaviors were in good agreement: display initiators (percent agreement: 54/60 = 90 %), attack initiators (56/60 = 93.3 %), whether or not escalated (60/60 = 100 %), contest winners (60/60 = 100 %), latency to initiation of displays (Pearson's correlation coefficient, $r = 0.958$), latency to launching attacks ($r = 0.996$), duration of contest escalation ($r = 0.997$).

Statistical analyses

We analyzed the fish's behavioral decisions at various stages of the contest to investigate the relative importance of contest experience and size difference to these decisions. We first analyzed decisions relating to contest initiation, namely the tendency of an individual to initiate interactions and its latency to do so. We then analyzed decisions relating to physical interactions, namely the tendency of an individual to launch the first attack and its latency to do so, the tendency of a contest to escalate into mutual attacks and the duration of any such escalation. We also examined the tendency of an individual to win non-escalated, escalated and all contests. We predicted (1) previous experience to have more influence than size difference on the decision to initiate contests and to launch attacks, (2) size difference to have more influence than previous experience on the tendency of a contest progressing to escalation and on the duration of escalation, (3) previous experience to have more influence on the outcome of non-escalated contests and size difference to have more influence on the outcome of escalated contests, and (4) the influence of experience to be negatively correlated with size difference.

We used generalized linear models (binomial distribution with a logit link function) to examine the importance of contest experience and size difference to the contestants' tendencies to initiate displays and attacks, escalate contests and win non-escalated, escalated and all contests. We used general linear models to examine the importance of contest experience and size difference to the latency (ln-transformed) to the first display, the latency (ln-transformed) to the first attack (the time period between the first display and the first attack) and the duration of escalation (ln-transformed). As described earlier, in W–N pairs, the smaller contestant was given a winning experience, while the larger contestant had a no-experience treatment; for N–L pairs, the smaller contestant was given a no-experience treatment, while its larger opponent was given the losing experience. We therefore tested the effect of a winning experience by comparing the behaviors of the smaller W contestants in the W–N pairs with those of the smaller contestants in the N–N pairs. Similarly, we tested the effect of a losing experience by comparing the behaviors of the larger L contestant in the N–L pairs with those of the larger contestant in the N–N pairs. We included experience × size difference interactions in the models to test the dependence of experience effects on size difference. For these linear models, we used contrast analyses to evaluate the differences between different levels of treatment (when significant) and interaction effects. The contestant's SL, the outcome of the contest pair's last fight and lineage were included in all the models to account for their influence.

We used SAS Enterprise Guide 7.1 (SAS Institute Inc., Cary, NC, USA) for the statistical analyses.

Results

Contest initiation

Of the 540 contests, all but one was initiated with threat displays (without physical contact); i.e., only one was initiated with an attack. None of experience treatment (the

winning experience of the smaller contestant in the W–N pairs and the losing experience of the larger contestant in the N-L pairs) (W–N vs. N–N, $P = 0.673$; N–L vs. N–N, $P = 0.932$), size difference (W–N vs. N–N, $P = 0.640$; N–L vs. N–N, $P = 0.820$) or the interaction between them (W–N vs. N–N, $P = 0.658$; N–L vs. N–N, $P = 0.069$) had a significant influence on the tendency of an individual to initiate contest interactions (Table S1).

Neither did any of experience treatment (W–N vs. N–N, $P = 0.203$; N–L vs. N–N, $P = 0.058$), size difference (W–N vs. N–N, $P = 0.900$; N–L vs. N–N, $P = 0.849$), the interaction between them (W–N vs. N–N, $P = 0.812$; N–L vs. N–N, $P = 0.754$) or whether or not the W (in the W–N pairs; $P = 0.995$) or the L individual (in the N–L pairs; $P = 0.761$) initiated the interactions have a significant effect on how fast the contest pairs started to interact with each other (Table S2). Contest pairs of different lineages differed significantly in the latency to initiation of interactions ($P < 0.001$ for both W–N vs. N–N and N–L vs. N–N); contest pairs of the VOL and HON9 lineages had the shortest and longest latencies, respectively (Fig. S2). The size of the contestants also had a significant influence on how fast contest pairs started to interact (W–N vs. N–N, $P = 0.006$; N–L vs. N–N, $P = 0.003$); larger contestants took longer to initiate interactions.

Physical interactions

Physical interactions occurred in 488 out of the 540 contests. The smaller contestant's winning experience did not significantly influence the likelihood that it would initiate attacks (W–N vs. N–N, $P = 0.933$; Table S3). The larger contestant's losing experience, however, reduced the likelihood of it doing so (N–L vs. N–N, $P = 0.017$) (Table S3, Fig. 1). Size difference did not have a significant influence on the tendency of the smaller W individuals in the W–N pairs ($P = 0.752$) or the larger L individuals in the N-L pairs to initiate attacks ($P = 0.982$).

A winning experience significantly shortened the latency to launch the first attack (W–N vs. N–N, $P = 0.002$) (Table S4, Fig. 2). A losing experience did not have a significant effect on this (N–L vs. N–N, $P = 0.121$). None of size difference (W–N vs. N–N, $P = 0.083$; N–L vs. N–N, $P = 0.430$), the interaction between experience and size difference (W–N vs. N–N, $P = 0.408$; N–L vs. N–N, $P = 0.917$) and which of the contestants (W or N individual of the W–N pairs: $P = 0.773$; N or L individuals of the N–L pairs: $P = 0.117$) initiated attacks significantly influenced the latency to launch the first attack. The size of the contestants, however, did have a significant influence on how fast contest pairs launched attacks (W–N vs. N–N, $P < 0.001$; N–L vs. N–N, $P < 0.001$); larger contestants took longer to do so.

Escalation

Out of the 540 contests, 283 (52.4 %) escalated into mutual attacks. The effect of the smaller contestant's winning experience on the W–N pair's tendency to escalate into mutual attacks was weakly dependent on the size difference treatment (W–N vs. N–N, Experience × Size, $P = 0.044$; Table S5). The W–N pairs had a higher tendency to escalate than the N–N pairs only for the 0–1 ($P = 0.014$) but not the 1–2 ($P = 0.857$) or 2–3 ($P = 0.334$) mm size difference treatments (Fig. 3). The larger contestant's losing experience, however, significantly lowered the likelihood of the N–L pairs to escalate contests (N–L vs. N–N, $P < 0.001$) independent of the size difference treatment (Experience × Size, $P = 0.915$) (Table S5). Size difference had no significant influence on the likelihood to escalate (W–N vs. N–N, $P = 0.069$; N–L vs. N–N, $P = 0.754$).

Escalation duration was not affected by winning (W–N vs. N–N, $P = 0.347$) or losing (N–L vs. N–N, $P = 0.302$) experience (Table S6). Escalation duration was, however,

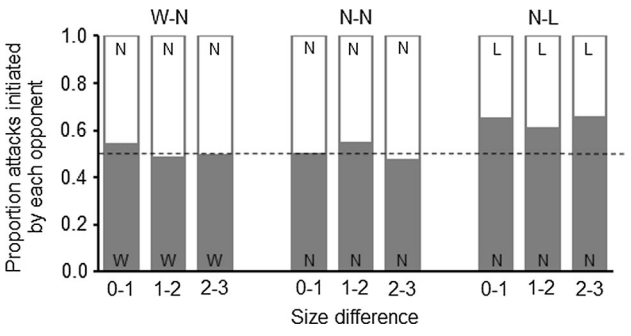

Fig. 1 Proportion of attacks initiated by the smaller (*shaded*) and the larger (*clear*) contestants in the contest pairs by contest experience × size difference treatments. The *letters* in the *shaded* and *clear portions* of the *bars* label the experience treatments. The *central dashed line* indicates an equal proportion between the two contestants

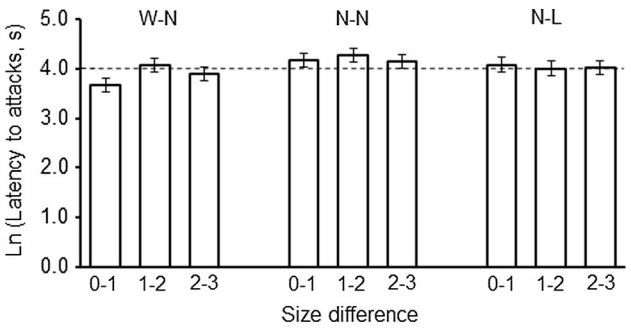

Fig. 2 Latency to attacks (s, ln-transformed, mean ± SE) in contests by contest experience × size difference treatments. The *dashed line* indicates the grand mean

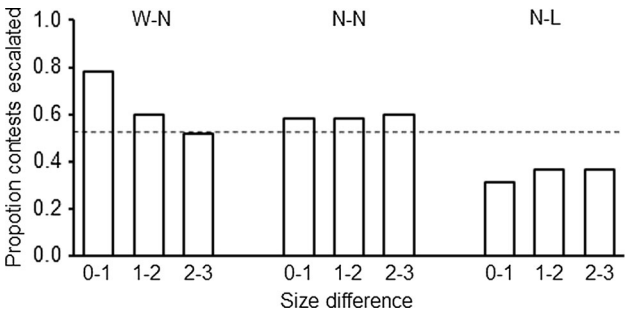

Fig. 3 Proportion of contests escalated into mutual attacks by contest experience × size difference treatments. The *dashed line* shows the overall proportion of contests escalated

affected by the size difference treatment (N–L vs. N–N, $P = 0.006$): contest pairs with smaller size differences tended to escalate for longer (Fig. 4).

Contest pairs' last outcome and lineage also had important relationships with their escalation decisions. Contest pairs formed of contestants that had won the last fight one month previously were more likely to escalate than those formed of contestants that had lost (W–N vs. N–N, $P < 0.001$; N–L vs. N–N, $P < 0.001$; Table S5). Contest pairs of different lineages differed in both the tendency to escalate (W–N vs. N–N, $P < 0.001$; N–L vs. N–N, $P < 0.001$; Table S5) and escalation duration (W–N vs. N–N, $P = 0.004$; N–L vs. N–N, $P < 0.001$; Table S6). Contest pairs of the VOL lineage were more likely to escalate into mutual attacks (Fig. S3) than those of the other lineages and escalated for longer (Fig. S4).

Outcomes of non-escalated, escalated and all contests

Thirteen out of the total 540 contests did not resolve in an hour with a clear winner and loser. The probability of a contest being unresolved did not depend on experience ($\chi^2 = 0.63$, $df = 2$, $P = 0.730$) or size difference

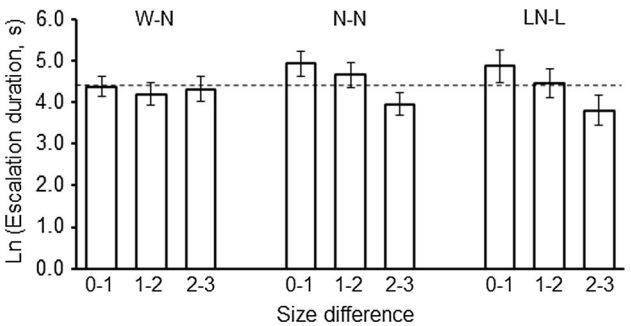

Fig. 4 Duration of escalation (s, ln-transformed, mean ± SE) in contests by contest experience × size difference treatments. The *dashed line* indicates the grand mean

($\chi^2 = 0.63$, $df = 2$, $P = 0.730$) treatments. These contests were excluded from the analyses in this section.

The smaller contestant's winning experience did not increase its likelihood of winning non-escalated W–N contests (W–N vs. N–N, $P = 0.559$; Table S7a). The larger contestant's losing experience, however, significantly lowered its chance of winning non-escalated N–L contests (N–L vs. N–N, $P < 0.001$; Table S7a) (Fig. 5a). These trends were not dependent on the size-difference treatment (Experience × Size: W–N vs. N–N, $P = 0.242$; N–L vs. N–N, $P = 0.475$). Nor did size-difference treatment significantly affect the probability of an individual winning non-escalated contests (W–N vs. N–N, $P = 0.574$; N–L vs. N–N, $P = 0.543$).

The outcomes of the escalated contests, conversely, were affected by the size-difference treatments ($P < 0.001$ for both W–N vs. N–N and N–L vs. N–N, Table S7b) but not by winning (W–N vs. N–N, $P = 0.460$) or losing (N–L vs. N–N, $P = 0.408$) experiences (Fig. 5b). As the size difference increased, the smaller contestant's likelihood of winning escalated fights decreased (W–N vs. N–N), while the larger contestant's likelihood increased (N–L vs. N–N).

When non-escalated and escalated contests were analyzed together, the influence of losing experience (N–L vs. N–N, $P < 0.001$) and size-difference treatments ($P < 0.001$ for both W–N vs. N–N and N–L vs. N–N) on the likelihood of winning remained significant (Table S7c). The effect of the smaller contestant's winning experience on its tendency to win was weakly dependent on the size difference treatment (W–N vs. N–N, Experience × Size, $P = 0.042$), caused by the smaller contestant's chance of winning falling less in the W–N than in the N–N treatment as size difference increased (Fig. 5c).

Discussion

Individuals can use information from various sources to fine-tune their estimate of the cost to them of participating in a contest (see Hsu et al. 2011 for a discussion). The results of this study, as predicted, showed that both previous contest experience and size difference affected the fish's fighting behavior and that their influences appeared at different stages of contests. Previous winning and losing experience affected the fish's behaviors at earlier stages of contests (i.e., whether or not and how fast to initiate attacks and whether or not to escalate contests into mutual attacks) and, consequently, their chance of winning contests that were not escalated into mutual attacks. Once contests were escalated, the degree of difference in size affected the fish's persistence in escalation and chance of winning, but experience treatment did not. These results are consistent with the hypothesis that the fish utilized the information

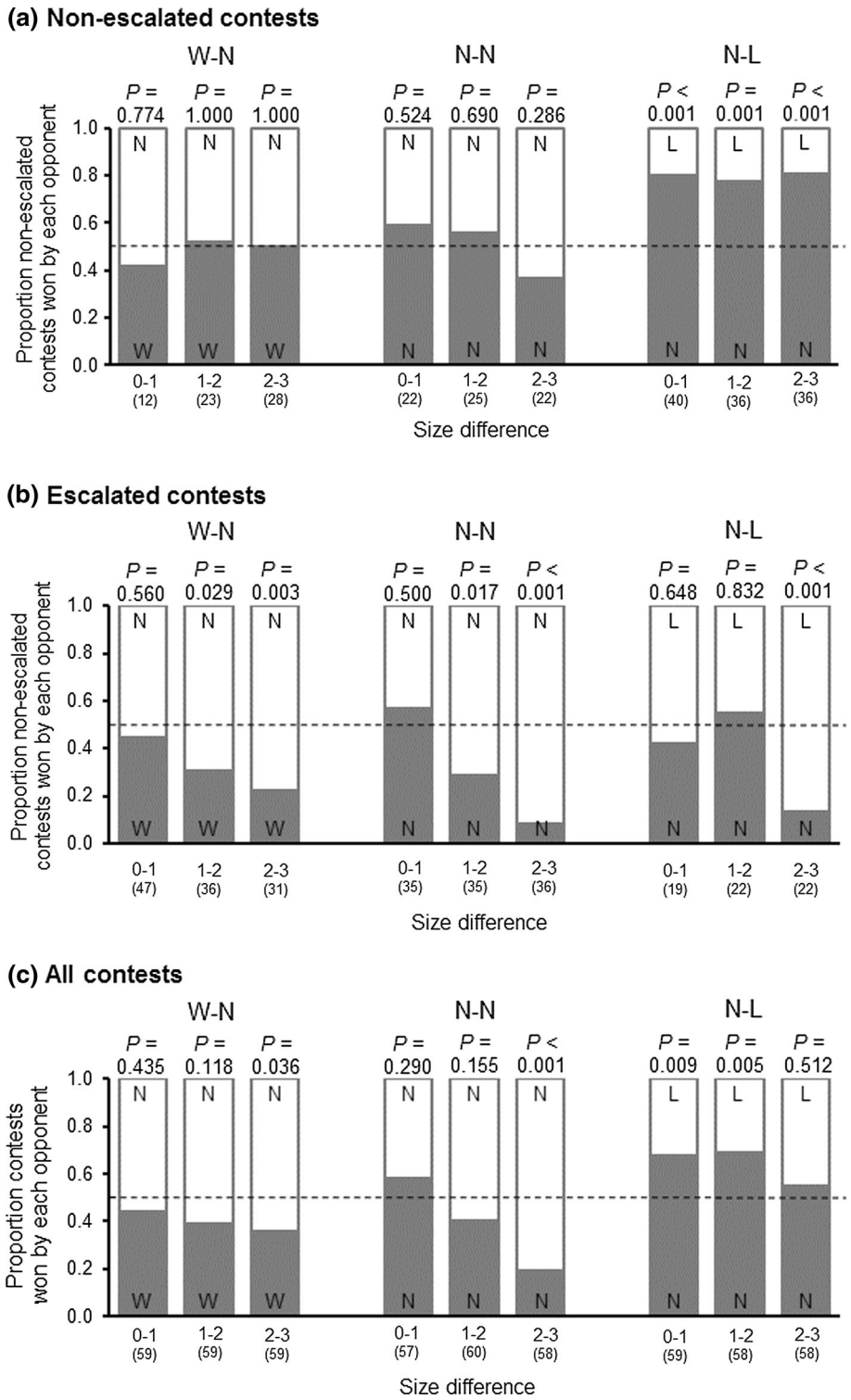

Fig. 5 Proportion of **a** non-escalated, **b** escalated and **c** all contests won by the smaller (*shaded*) and the larger (*clear*) contestant of the contest pairs by contest experience × size difference treatments. The *letters* in the *shaded* and *clear portions* of the *bars* label the experience treatments. The *central dashed line* indicates an equal proportion between the two contestants. The *P* values *above* the *bars* show whether the proportion of contests won by each contestant deviated significantly from the equal proportion of 0.5 (2-tailed binomial tests). The sample size for each bar is presented in parentheses on the *bottom* of the *bar*

from the outcomes of previous fights to assess fighting ability and make fighting decisions when reliable fighting-ability-related information was not available. Once the contestants had the opportunity to evaluate each other's actual strength/ability through direct physical interactions, the information from previous contest experiences was no longer valuable, and contest interactions were primarily dependent on the asymmetry in strength. These observations are consistent with the hypothesis that the outcomes of previous contests modify an individual's assessment of its fighting ability but do not alter its physical strength. That previous contest experience is useful in predicting the

outcomes of non-escalated contests but not those of contests with physical interactions has also been observed previously in other lineages of this fish (Hsu and Wolf 2001) as well as in some other species (male copperhead snakes, *Agkistrodon contortrix*, Schuett 1997; black field cricket, *Teleogryllus commodus*, Reaney et al. 2011). The current study adds a new analysis of how size difference and contest experience influence the individual behaviors that determine the outcomes of these different types of contests.

The importance of contest experience to the fish's contest behaviors, for the most part, was independent of the degree of size difference, contrary to our expectations. The only size-difference-dependent experience effect was the influence of a winning experience on the fish's tendency to escalate contests, which was detected only when the two contestants were similar in size (0–1 mm difference). None of the influences that a losing experience exerted on the larger contestant's behaviors depended on size difference. Together with the observations from previous studies of the fish that loser effects are always readily detectable but winner effects less so (Hsu and Wolf 1999; Huang et al. 2011; Earley et al. 2013; Hsu et al. 2014), these results showed that individuals of *K. marmoratus* were more cautious when utilizing the information from a winning than from a losing experience to modify contest decisions. Stronger and longer lasting responses to losing than winning experiences appear to be the pattern commonly observed in studies that evaluated winner and loser effects separately (e.g., Stickleback fish, *Gasterosteus aculeatus*, Bakker et al. 1989; Copperhead snake, *Agkistrodon contortrix*, Schuett 1997; Blue-footed booby, *Sula nebouxii*, Drummond and Canales 1998; see Hsu et al. 2006 for a review). In contests, animals expend energy and time and risk physical injuries and predation (Neat et al. 1998; Brick 1999); furthermore, individuals engaging in more intensive interactions with rivals risk incurring higher retaliation costs if they lose (Li et al. 2014). These costs could contribute to individuals adopting more conservative approaches to increasing aggressiveness after recent victories. Even though most of the species examined exhibit stronger loser than winner effects, in a parasitoid wasp, *Eupelmus vuilleti*, a winning experience increased the probability that a female would win a subsequent, non-escalated contest, but a losing experience did not affect it (Goubault and Decuignière 2012). To the best of our knowledge, this is the only species that has been documented to exhibit winner effects in absence of loser effects. In this species, the ability of a female to win is positively associated with its egg load: females that received a winning experience had a slightly higher egg load than females assigned to the other experience treatments, and the winner of a contest is the contestant to first parasitize and feed from the host provided. The authors therefore suggest that the winner effect in this species acted by modifying an individual's evaluation of the value of the resource. This example shows that the influences of previous wins and losses on subsequent contest decisions vary with the biology and ecology of an organism.

Body size has been shown to correlate positively with an individual's ability to fight in a wide range of taxa (e.g., spiders, fish, frogs, lizards, snakes; Hsu et al. 2006 for a brief review). The ability of body size to predict contest outcomes, however, still varies among species. For instance, egg load but not body weight predicts contest outcome in the female parasitoid wasp, *Eupelmus vuilleti* (Goubault and Decuignière 2012), differences in testis weight but not differences in body weight determine the outcome of pairwise fights in the male African cichlid *Tilapia zillii* (Neat 1998) and relative standard length (difference in SL $\leq$ 18 %) does not predict the outcome of territory disputes between owners and intruders in the wild cichlid fish *Neolamprologus pulcher* (O'Connor et al. 2015). The results of the present study showed that the standard length in *K. marmoratus* provides an appropriate proxy for the physical strength in the fish because the larger contestants have a higher chance of winning than their smaller opponents, and the difference in their chance of winning increases with the difference in their SL. Given that the smaller contestants in the N–N contests won only 8 % of escalated fights against opponents that were 2–3 mm larger, it is intriguing that 60 % of the smaller contestants in N–N contests elected to escalate. The contest decisions of the fish in the N-L contests and the contests' outcomes could perhaps provide some insights. This fish's decision to escalate a contest was greatly affected by a recent losing experience. A high percentage of individuals that were given a losing experience retreated without escalating the contest, despite their size advantage. As a result, the N individuals with a severe size disadvantage (2–3 mm smaller) in the N-L contests claimed victory of 81 % of the non-escalated contests (55 % of escalated and non-escalated contests combined). In addition to previous contest experience, this fish's contest decisions are also influenced by the familiarity of its opponents (Li et al. 2014) and any asymmetry in resource ownership (Huang and Hsu 2015). Because the fish's contest decisions are highly sensitive to environmental factors (and not solely dependent on differences in physical strength), it pays for size disadvantaged individuals to probe and challenge larger opponents. Furthermore, the result that 60 % of the smaller contestants in N–N contests elected to escalate with opponents that were 2–3 mm larger in SL may suggest that the fish's physical strength could be sensitive to factors that were not manipulated in the study, for instance parasite load

(Ellison et al. 2011) or the quantity and quality of the food eaten shortly before the contest, which has yet to be explored. Although, in the present study, the escalation rate only decreased with the increase in size difference for the W–N and not for N–N and N–L contests (Fig. 3), previous studies of the fish showed that contests involving small individuals (<21.5 mm in SL) fighting against much larger opponents (difference in SL > 4 mm) tend to resolve without escalating into mutual attacks (Hsu et al. 2011). The size disadvantaged individual's decision to challenge its larger opponent is therefore still influenced by (relative) physical strengths of the two contestants. The proportion of contests escalated in the present study did not show a strong tendency to decrease as size difference increased, as it did in previous studies. This could be because the smaller contestants were larger (more than 90 % of the smaller contestants >21.5 mm) than those used in previous studies, because the size difference was not large enough (differences ≤3 mm) or a combination of both.

In addition to the difference in the contestants' size, the absolute body size of a contest pair had a complicated relationship with the pair's contest behaviors. Absolute size had a positive relationship with the latency to initiate threat displays and launch attacks; i.e., contest pairs composed of individuals with larger absolute sizes took longer to initiate aggressive acts. The absolute size of the contestants, however, did not significantly affect the likelihood of contests escalating to mutual attacks. Fish in contests between larger individuals were slower to initiate aggressive interactions but just as likely to escalate into physical fights. As shown in this study, body size is a good indicator for physical strength in this fish. Large fish could be allowing time for their rivals to assess their size and retreat voluntarily, which could cause larger individuals to have longer display and attack latencies without compromising their willingness to escalate contests. That larger individuals took long to initiate aggressive interactions has also been reported in earlier studies of the fish. For contests between size-matched pairs, larger pairs took longer to initiate threat displays and to launch the first attack (Lan and Hsu 2011). When exposed to their own mirror images, larger individuals took longer to launch the first attack (Chang et al. 2012). These trends, however, should be interpreted with caution. In all these studies, the size of the two contestants in a pair (or of an individual and its own mirror image) was either similar or highly positively correlated, with a larger contestant facing a larger opponent. The size of the contestants and their opponents are therefore confounded; it is not clear whether the delay in the behavioral responses was caused by the size of the contestant, the size of its opponent or the combination of the two.

Although not the focus of this study, different lineages of *K. marmoratus* differed in their aggressiveness; individuals of the VOL lineage were more ready to engage in physical fights and persisted longer in physical fights than those of the other lineages. A previous study, using a different set of 5 lineages (BP11, LK15, LK2, LK6 and NNKN1) of *K. marmoratus* also detected significant lineage effects on aggressiveness (Edenbrow and Croft 2013). Moreover, the fish's aggressiveness is positively correlated with the pre-contest levels of testosterone and cortisol (Chang et al. 2012) and individuals of the VOL lineage had higher pre-contest levels of cortisol than the HON9, RHL and SLC8E lineages and higher pre-contest testosterone levels than the RHL and SLC8E lineages (Earley and Hsu 2008). These results together with its recently published genome sequence (Kelley et al. 2016) make this self-fertilizing hermaphroditic fish an excellent candidate for investigating the genetic background of aggressiveness and the physiological mechanisms closely associated with aggression.

In summary, the results of the present study show that, although previous contest experience and the difference in body size jointly determined contest outcomes in *K. marmoratus*, they affected different types of behavioral decisions. Contest experience affected behaviors at earlier stages of contests, and its influence was largely independent of size difference (0–3 mm). Once contests were escalated into mutual attacks, persistence and the chance of winning were affected only by size difference. These results are consistent with the hypothesis that contest experiences modify an individual's assessment of its own fighting ability and fighting costs, but do not alter its actual strength or fighting ability. The results (1) that in contests between two naïve fish, 60 % of those 2–3 mm smaller than their larger opponent opted to escalate, despite the fact that the larger opponent eventually won 92 % of escalated fights and (2) that a significant proportion of fish that had received a losing experience opted to retreat from opponents 2–3 mm smaller than them without escalating suggest that, in addition to body size, the fish's physical strength is dependent on other factors which requires further investigation.

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Compliance with ethical standards

Conflict of interest The authors assert that they have no conflicts of interest.

Ethics statement The Animal Care and Use Committee of National Taiwan Normal University approved *K. marmoratus* as the study organism and the procedures for the use of the fish (permit #99034). To measure a fish's SL, we moved the fish from its maintenance container to a clear plastic bag where it could be measured and kept moist with a hand net. We measured the fish through the bag with a digital caliper and then returned the fish to its maintenance container. To mark the fish, we netted the fish and placed it inside folded plastic wrap to keep it moist. We exposed the tail and dragged a needle over the non-vascularized thin membrane between two of the caudal fin rays to break it. All fish resumed regular feeding behavior within 5 s of marking, which did not cause bleeding or observable adverse effects upon the fishes' health or behavior (Hsu et al. 2008). The membrane usually grows back completely in 3 d. All contests were videotaped and monitored by an observer sitting behind the camcorder. Contests were terminated 5 min after one of the contestants retreated from its opponent's displays/attacks. This time period was used to confirm the winner–loser status of a contest pair. During this period, the loser was able to flip out of water and stick to the side of the aquarium to avoid post-contest harassment from the winner. All fish were visually inspected, returned to their maintenance containers and fed brine shrimp (*Artemia*) nauplii after the contests. None of the fish suffered visible physical injury (e.g., scale loss, wounds, bleeding, abnormal swimming behavior) from the contests.

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