



Subordinate Fish Mediate Aggressiveness Using Recent Contest Information

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Memorizing dominance relationships can help animals avoid unwinnable subsequent contests. However, when competitive ability changes over time—for example, as a function of condition—it may be adaptive to “forget” these dominance relationships and for subordinates to once again enter contests with previously dominant individuals. Here, we examined the behavior of pairs of male cichlid fish, *Julidochromis transcriptus*, in repeated contests separated by different time intervals. We found that the time taken to reach resolution of dominance relationships influenced subsequent aggressive behavior of the subordinate toward the dominant, with longer initial contests leading to higher subsequent aggression. Longer time intervals between contests also increased aggression from the subordinate toward the dominant. These results are consistent with increasing uncertainty due to ambiguous contest outcomes and increasing time intervals. Our results also show that a longer time was necessary to resolve contests between larger pairs, suggesting a self-assessment strategy, but not a mutual assessment strategy. Taken together, larger individuals appear to adaptively lose or ignore previously gathered social information because they have a higher fighting ability and better body condition. Therefore, we conclude that losing or ignoring unreliable information may be an adaptive strategy in the context of dominance relationships.

Keywords: adaptive forgetting theory, cichlid, contest duration, *Julidochromis transcriptus*, memory, self-assessment

INTRODUCTION

Engaging in physical contests can be costly; contestants often expend energy and time, risk injuring themselves (Briffa and Sneddon, 2007), and in many cases, the cost is higher for individuals who lose contests (Neat et al., 1998). As such, memorizing dominance relationships may prove beneficial if it allows subordinates to avoid unwinnable contests (Barnard and Burk, 1979), and empirical evidence demonstrates that subordinates can recognize dominant social partners and avoid repeated contests (Tibbetts and Dale, 2007). This memory of dominance relationships may be transient; however, several studies have shown that in chicks, lizards, fish, and invertebrates, subordinates exhibit aggression toward previously dominant individuals after approximately a week of isolation (Peeke et al., 1979; Miklósi et al., 1992; Karavanich and Atema, 1998; Forster et al., 2005; Gherardi and Atema, 2005; Hotta et al., 2014).

A lack of behavioral change or response to a stimulus may lead to the conclusion that the subject has lost the information, and that this represents a failure to retain or retrieve information owing to the physiological costs of maintaining the memory (Kraemer and Golding, 1997; Dukas, 1999). It is therefore possible that in these cases of contest resumption, subordinates simply forget dominance relationships over time. However, memories lasting several weeks have been reported even in taxa assumed to have poor memory; for instance, male paradise fish (*Macropodus opercularis*) can remember goldfish (*Carassius auratus*) after 3 months (Csányi et al., 1989), although memory of dominance relationships lasts only up to 6 days (Miklósi et al., 1992). This difference suggests the possibility that re-testing dominance relationships after a certain period is not simply representative of a limitation on social memory but may be an adaptive re-sampling and re-evaluation of changing information (Ferrari et al., 2010). In the context of foraging, patch use, and predator recognition, theoretical models propose that the retention of acquired information is flexible depending on the recency or accuracy of the information; for example, recent information should contribute to optimal decision-making (Hirvonen et al., 1999). In other words, losing or ignoring information may be an adaptive function if information is no longer reliable, which is also known as adaptive forgetting theory (Kraemer and Golding, 1997; Dunlap et al., 2009; Ferrari et al., 2010, 2012). For instance, tadpoles repeatedly exposed to salamander odor associated with conspecific alarm cues exhibit anti-predator responses for a long period (Ferrari et al., 2012). The authors argue that this repeated conditioning increases the reliability of using odor to inform the presence of a predator (Ferrari et al., 2012).

Adaptive forgetting may also be prudent in contest behavior; however, to the best of our knowledge, this has not yet been tested. Relying on recent information and eschewing previous dominance relationship information may be beneficial for subordinates, as preserving unreliable information can be costly because it deprives subordinates of access to resources (Hotta et al., 2014; Thompson et al., 2014). Thus, losing or ignoring dominance relationship information based on previous contests is also adaptive when the information becomes unreliable, and the adaptive forgetting theory predicts that subordinates adjust their decision to participate in a contest depending on information acquired from recent contests. For example, when the difference in the competitive ability of rivals is greater, subordinates may utilize information on previous dominant individuals for a longer period, as the probability of winning against them would be low for a longer time (Hotta et al., 2014). However, to date, researchers have examined only how the outcome, but not the dynamics of previous contests, influences the fighting behavior of subordinates in subsequent contests with familiar or unfamiliar opponents (Hsu et al., 2006).

In this study, we assessed whether the Tanganyika cichlid, *Julidochromis transcriptus*, adjusted its aggression level against familiar dominants based on information acquired from initial contests. Our previous study showed that male *J. transcriptus* can recall dominance relationships for up to 5 days but resumed attacks on dominants after 7 days

(Hotta et al., 2014). Aggressive behaviors against unknown individuals did not change over this interval, suggesting that *J. transcriptus* memorizes dominance relationships rather than being influenced by winner/loser effects (Hsu et al., 2006; Hotta et al., 2014). These fish did not avoid the winners in observed contests (i.e., social eavesdropping), but they avoided unfamiliar fish that defeated their previous dominants (i.e., transitive inference; Hotta et al., 2015). This suggests that *J. transcriptus* utilize various elements of social information to avoid unwinnable contests. Based on the adaptive forgetting theory, we predicted that subordinates would quickly abandon past information and increase aggression against previous dominant individuals when the probability of winning subsequent contests increases with time.

To test our prediction, we examined whether the aggressiveness of subordinates in subsequent contests changed depending on the duration necessary to resolve the initial contest (i.e., contest duration) as an index of the reliability of social information on dominance relationships. There are two major models depicting the method by which subordinates decide to withdraw from a contest: self-assessment and mutual assessment strategy models (for review, Arnott and Elwood, 2009). The self-assessment strategy model suggests that each contestant has only information about its own fighting ability or state, and weaker individuals tend to reach their limits and give up the contest faster. In contrast, the mutual assessment strategy model proposes that both contestants assess the fighting ability of opponents relative to their own. Because a longer contest duration means that differences in fighting abilities between dominants and subordinates are small, or that subordinates have a high fighting ability or a good body condition (Arnott and Elwood, 2009), subordinates would behave aggressively against previous dominants in subsequent contests when the contest duration in the initial contest was longer. However, contest duration may simply reflect the aggressiveness of subordinates, but not social information on dominance relationships (Rudin and Briffa, 2012). Therefore, more aggressive subordinates may persist in the initial contest and engage in more aggression against their previous dominants after social intervals. If this is the case, we predicted that subordinates with a longer initial contest duration would also behave more aggressively against unfamiliar individuals. To test this, we examined the relationship between contest duration and the responses of subordinates toward unfamiliar conspecifics (Hotta et al., 2014). Finally, we examined whether subordinates decided to withdraw from the initial contests based on a self-assessment or mutual assessment strategy. In contests between size-matched contestants, two assessment strategy models are discriminated by examining the relationship between contest duration and mean size of contestants (Taylor and Elwood, 2003; Arnott and Elwood, 2009). If subordinates decided based only on their fighting ability or state, contests between large individuals would persist for a longer duration. However, if they assessed the contestant's fighting ability relative to themselves, the mean size of the contestants would not determine the contest duration.

MATERIALS AND METHODS

Test Fish

The genus *Julidochromis* consists of five species, all of which breed in rock crevices and may compete over limited resources (Awata and Kohda, 2004; Awata et al., 2005, 2006). The *J. transcriptus* individuals used in this study were obtained from commercial breeders. The experiments were conducted in a laboratory at Osaka City University, Osaka, Japan. We used 68 sexually mature males [total length (TL), 66.90–81.55 mm] that had been kept with females either in 60 cm × 30 cm × 40 cm or in 180 cm × 45 cm × 40 cm glass tanks. The subjects were measured for TL 3 days prior to being placed individually in 30 cm × 17 cm × 15 cm glass tanks (home tank) that contained 2 cm of coral substrate and were aerated. To prevent visual interactions, all tank sides were covered with opaque sheets. This isolation lasted 14 days to neutralize the effects of previous experience (Hsu et al., 2006). The tanks were kept at 24–26°C under a 12:12-h light/dark cycle. Fish were fed commercial food (Tetramin; Tetrawerke, Melle, Germany) twice daily.

Experimental Procedure

Two males from the home tanks were simultaneously placed into an open contest tank (30 cm × 17 cm × 15 cm). They were size-matched (mean TL difference ± SD = 0.90 ± 0.73 mm, $N = 34$ pairs) and this body size difference has not been observed to affect contest outcomes in this species (Hotta et al., 2014, 2015). Immediately after being introduced to the contest tank, the two males displayed aggressive behaviors, such as frontal display, mouth fighting, bites, mutual wrestling, and chasing each other (Hotta et al., 2014, 2015). We declared a fish to be the subordinate of the contest when it retreated or fled from another male's attack on two consecutive occasions (Hotta et al., 2014, 2015). The contests were videotaped using a video camera (HDR-CX370; Sony Corp., Tokyo, Japan) for approximately 30 min (32.1 ± 5.2 min, mean ± SD), after which the contests were terminated and males were placed into their respective house tanks and isolated. However, in one case, two contestants were together in a contest tank for 62.7 min (**Supplementary Table 1**). The contest duration was calculated by the recorded videos as the time elapsed between the initial aggressive behaviors performed by either fish and the second submissive act from the losing fish.

After being socially isolated for either 3 ($N = 12$ pairs), 5 ($N = 12$ pairs), or 7 days ($N = 10$ pairs), the same pair was placed again into the contest tank, in which an opaque sheet was inserted to prevent visual interactions (**Figure 1**). Each pair was randomly assigned to one of the three interval treatments, and there was no size difference among the groups [one-way analysis of variance (ANOVA), $F_{2,31} = 0.32$, $P = 0.73$]. The sheet was removed after 10 min, and visual interactions across a glass divide between the two males were recorded for 10 min using a video camera (HDR-CX370; Sony Corp., Tokyo, Japan). To examine whether contest duration may simply reflect the aggressiveness of subordinates, but not social information on dominance relationships (Rudin and Briffa, 2012), we also examined their aggressive response toward unfamiliar conspecifics. To account for this, when the

contest against the previous dominant had finished, the sheet was replaced and the previous dominant was removed and replaced with a novel stimulus fish (i.e., an unfamiliar fish). Unfamiliar fish were kept in other stock tanks and did not differ in size from the dominant fish (paired t -test, $t = -0.87$, $P = 0.39$). After 10 min of habituation, the sheet was removed, and the interactions between the focal fish and the stimulus fish were videotaped (**Figure 1**). The size difference between subordinates and unfamiliar opponents did not differ among the 3-, 5-, and 7-days interval groups (one-way ANOVA, $F_{2,31} = 0.89$, $P = 0.42$). We followed a fixed order to prevent interference from the memory of dominance relationships (Hotta et al., 2014). For both sequential contests with dominants and unfamiliar opponents, we measured the aggression duration during which subordinates attacked the glass divider with their mouths open, using video recordings of the first 30 s of the interaction (Hotta et al., 2014, 2015). We chose only the first 30 s to exclude the possibility that dominant behavior influenced subordinates' behavior (Earley and Dugatkin, 2002).

Statistical Analysis

Statistical analyses were performed using R. 3.3.3 (R Core Team, 2017). Data normality was checked using the Shapiro-Wilk test. Non-normally distributed data were square-root-transformed before the parametric analyses. All statistical tests were two-sided at a significance level of $\alpha = 0.05$. First, we assessed whether the contest duration of the initial contest and the social separation intervals influenced the aggressive behavior of subordinates in the subsequent contest with previous dominants. We compared the aggression duration of subordinates against previous dominants (square-root transformed) among social intervals (3, 5, or 7 days) with an analysis of covariance (ANCOVA), which was also evaluated for the effects of the covariate contest duration. A two-way interaction term was included in the full model and, if no significant effect of the term was detected, we presented the results from reduced models in which the interaction term was removed. We predicted that subordinates would behave aggressively against previous dominants when the contest duration was longer, either because the difference between their competitive ability was small or because the former had high fighting ability or good condition. We used a *post hoc* Tukey's HSD test to compare aggression duration against previous winners among social intervals. Second, we assessed whether the contest duration simply reflects the aggressiveness of subordinates but not social information on dominance relationships (Rudin and Briffa, 2012). To test this, we examined the relationship between contest duration and the aggressive response of subordinates toward unfamiliar conspecifics (Hotta et al., 2014). Therefore, similar to the first analysis, we constructed ANCOVA models with the aggression duration of subordinates against unfamiliar conspecifics (square-root-transformed) as the dependent variable, social intervals (3, 5, or 7 days) as an independent variable, and the contest duration of the initial contest as a covariate, including a two-way interaction (full model). A reduced model was also constructed if the interaction term was not statistically significant. Finally, we tested whether subordinates decided to withdraw from the initial contests

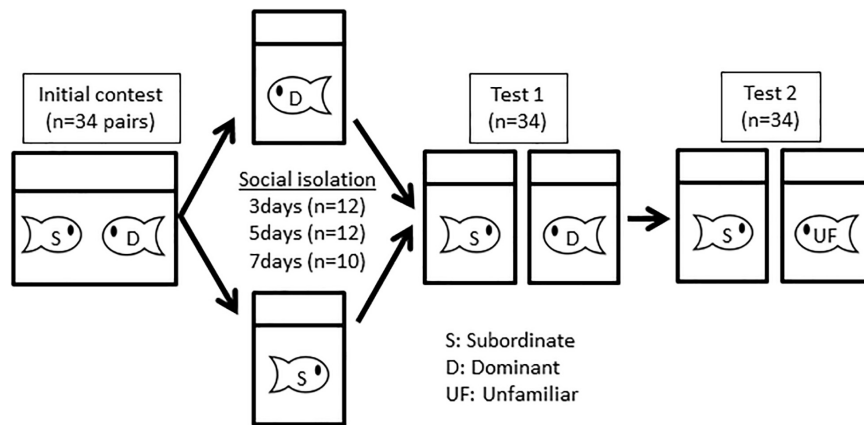


FIGURE 1 | The sequence of the experiment. After the initial contest, two fish were removed and isolated for either 3 ($N = 12$ pairs), 5 ($N = 12$ pairs), or 7 days ($N = 10$ pairs). Then, the subordinates encountered their previous dominants again. S and D indicate subordinate fish and dominant fish, respectively.

based on a self-assessment or mutual assessment strategy. We examined the relationship between contest duration (square-root-transformed) and mean body size (TL) of the contestants using a simple regression analysis (Taylor and Elwood, 2003). If subordinates perform a process of self-assessment, and larger subordinates can persist for a longer duration, the contest duration will increase as the mean body size of contestants increases (Hsu et al., 2008; Arnott and Elwood, 2009). However, if the mutual assessment strategy model is applied, the body size will not affect the contest duration.

Ethical Note

All experiments adhered to the Association for the Study of Animal Behaviors guidelines for the Use of Animals in Research and were conducted in compliance with the Regulations on Animal Experiments at Osaka City University. The Japanese government did not require a permit for experiments involving *J. transcriptus*.

We did not injure fish during our experiments. We provided food once a day and maintained the tanks in good conditions. In the escalated contests, fish engaged in mouth wrestling. All contests were videotaped and carefully monitored by an observer. The observer was instructed to intervene and terminate contests if either fish appeared to suffer visible physical injury (e.g., scale loss, wounds, and abnormal behavior) or intensive biting. However, no interventions were required because most escalations were brief. All fish were returned to their home tank after contests, fed with flake food, and visually inspected. No fish appeared to suffer physical damage from the contests.

RESULTS

The average contest duration was 626.1 ± 580.5 s (mean \pm SD, $N = 34$). First, we examined whether the aggression of subordinates against previous dominants was influenced by the initial contest duration and social interval. There was no significant effect of the previous interaction between them on

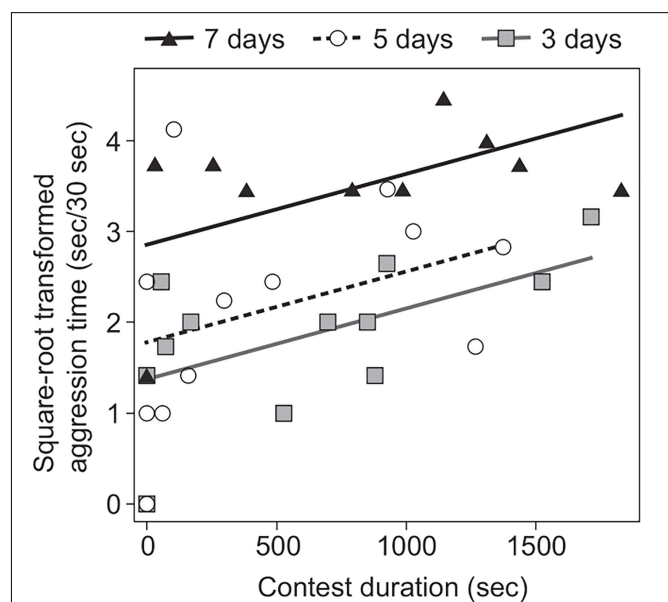


FIGURE 2 | The relationship between the contest duration and the attack duration of the subordinates. Regression lines for different separation time intervals are obtained from the reduced ANCOVA model. The aggression duration in 7-day period of separation was significantly longer than that in 5- and 3-day periods (see "Results").

subordinate aggression (ANCOVA, full model, $F_{2,28} = 0.13$, $P = 0.87$). When the interaction was removed as a variable, the reduced model revealed that the aggression duration increased with the contest duration ($F_{1,30} = 8.51$, $P < 0.01$, **Figure 2**). We also detected a significant effect of the social separation interval on aggression by subordinates (reduced model, $F_{2,30} = 8.32$, $P < 0.01$, **Figure 2**). Multiple comparisons revealed that the aggression duration after a 7-day period of separation was significantly longer than that recorded after a 3-day period (Tukey's HSD test, $t = 4.01$, $P < 0.001$) and 5-day period ($t = 2.88$, $P < 0.05$). No difference in

aggression duration was detected between the 3- and 5-day periods of separation ($t = 1.12$, $P = 0.51$). Second, we examined whether the contest duration simply reflects the aggressiveness of subordinates, but not social information on dominance relationships. However, we did not observe any significant effects of the contest duration and the social interval period on aggression against unfamiliar fish (ANCOVA, contest duration \times social interval: full model, $F_{2,28} = 0.10$, $P = 0.90$; contest duration: reduced model, $F_{1,30} = 0.72$, $P = 0.40$; social interval: reduced model, $F_{2,30} = 2.37$, $P = 0.11$). Finally, we examined whether the mean body size of the contestants affected the initial contest duration. A simple regression analysis revealed that the contest duration increased with the mean body size of contestants ($r = 0.38$, $F_{1,32} = 5.30$, $P < 0.05$).

DISCUSSION

Memorizing dominance relationships can be beneficial for subordinates to avoid the risk of injury and energy expenditure in unwinnable repeated contests (Briffa and Sneddon, 2007). However, without the ability to update the information they have on their social rivals, subordinate fish would have no chance of raising their rank in social interactions and of getting an opportunity for mating (Hotta et al., 2014). The adaptive forgetting theory suggests that subordinates forget or ignore past information on previous dominants because adherence to past dominance relationships can become maladaptive (Ferrari et al., 2010; Thompson et al., 2014). Subordinate *J. transcriptus* individuals showed higher levels of aggression against their dominant rivals when the initial contest was prolonged, irrespective of the interval. Additionally, no significant correlations were observed between contest duration and aggression duration against unfamiliar fish. These suggest that subordinates decide whether or not to enter a contest with their dominants depending on the dynamics of previous contests (Hirvonen et al., 1999; Dunlap et al., 2009; Ferrari et al., 2010, 2012).

Our results also indicated that the contest duration increased as the mean size of the contestants increased. This result is consistent with a self-assessment strategy model, in which subjects make contest decisions depending on their own fighting ability or state rather than integrating information about their opponents (Hsu et al., 2008; Arnott and Elwood, 2009). Self-assessment strategy models propose that larger subordinates can endure more energetic and/or physical costs (Hsu et al., 2008; Arnott and Elwood, 2009), suggesting that larger subordinates can better tolerate the costs of contests, increasing the probability of winning. A mathematical model that investigates the influence of memory retrieval on reproductive success predicted that memory length depends on an individual's physical state, such as their energy reserves or stress level (Dunlap et al., 2009). In other words, organisms in a poor state should be able to recall information for a longer period of time than those in a good state. This model contrasts classic theories that memory loss is caused by the physiological cost to maintain memory, such as synaptic

decay, and claims that memory loss can be adaptive (Dunlap et al., 2009; Ferrari et al., 2010).

Some claim that it is difficult to identify the single "best" assessment strategy for contest decisions (e.g., Taylor et al., 2001; Kelly, 2006; Prenter et al., 2006; Hsu et al., 2008; Arnott and Elwood, 2009). Indeed, some species change their assessment strategy as the contest escalates; mangrove killifish and fiddler crabs adopt a mutual assessment strategy in the early stages of the contest, but once the contest escalates, they use a self-assessment strategy to make decisions for retreating from the contests (Morrell et al., 2005; Hsu et al., 2008). Our experimental design of fighting against individuals of matched size may have simply made it impossible for the subjects to adopt a mutual assessment strategy, and our results only showed that they decided when to retreat from the contest with a size-matched opponent based on self-assessment strategy on the escalated contests. One claims that this study cannot identify the "best" assessment strategy in *J. transcriptus*. However, since the purpose of examining the assessment strategy was to find out what kind of information was reflected by the length of the contest duration, it would not affect the results that the retention time of information is changed depending on own fighting ability and state.

Although we showed that subordinates used contest duration as social information, it has been proposed that subordinates associate a negative experience (being chased or bitten) with post-contest cohabitation with dominants (McDonald et al., 1968). Experiences involving high emotional arousal, such as threatening experiences, are likely to form strong and long-lasting memories (Brown, 2015; Silveira et al., 2019). Therefore, this suggests that a longer cohabitation after forming a dominance relationship (i.e., a Dominant-Subordinate phase; D-S phase) leads to a longer duration of avoiding previous dominants (Miklósi et al., 1997). In this study, we cannot exclude this possibility because the contestants were placed together for a fixed duration (approximately 30 min), and the contest duration correlated negatively with the D-S phase. However, in one case of a 3-day interval treatment, two contestants were together in a contest tank for 62.7 min, meaning that both the contest duration and the D-S phase were longer (contest duration was 27.5 min and D-S phase was 28.6 min). In the 3-day treatment, the attack of the subordinate fish lasted longer (10 s) compared with the attacks of other fish (mean = 4 s), suggesting that post-contest cohabitation did not influence the contest decision against previous dominants. It has also been demonstrated (Miklósi et al., 1997) that the duration of the D-S phase does not affect the memory of subordinates in male paradise fish; the authors of this study suggested that subordinates do not generally prepare to experience a negative situation as in nature they can escape.

It has been proposed that both intrinsic (e.g., body size and growth rate) and extrinsic (e.g., predator predictability) factors may influence the retention period of information by prey species (Ferrari et al., 2010). In the context of dominance relationships, previous contest experiences influence the retention period of information regarding recent contests. *Julidochromis transcriptus* does not exhibit a winner/loser effect (Hotta et al., 2014); however, this does not necessarily mean that they do not change their perception of their own fighting ability. Rather, they do

not utilize their past fighting experience when the dominance relationship with unfamiliar individuals is unclear (Hotta et al., 2015). If the information on past contests accumulates and mediates subordinates' perception of their fighting ability, subordinates with more winning experiences do not retain the information on dominance relationships for a longer period. Additionally, researchers have considered that the frequency of encountering conspecifics affects the information retention period (Miklósi et al., 1992; Dreiss et al., 2015). *Julidochromis ornatus*, which is closely related to *J. transcriptus*, frequently encounters both familiar and unfamiliar conspecifics (Awata and Kohda, 2004; Awata et al., 2005). Thus, subordinates do not rely on information about dominants because the information is updated rapidly and becomes inefficient (Hotta et al., 2014). Both cichlid density and the frequency of attacking interactions with conspecifics differ among populations in Lake Tanganyika (Matsumoto and Kohda, 1998; Sturmbauer et al., 2008). In the memory about foraging strategy, sticklebacks from marine keep the information up to 8 days, but those from residential freshwater can keep for over 25 days (Hughes and Mackney, 1995). The authors suggest that sticklebacks from marine environment encounter a wide variety of prey, so they do not have to remember one foraging strategy for a long time. In contrast, great tits do not show any differences in spatial memory by environmental harshness (Hermer et al., 2021). A comparison of the information retention period among these different populations within species could reveal the influence and frequency of encounters for memory retention about dominance relationships. Taken together, both intrinsic and extrinsic factors could affect the retention period of information on dominance relationships in a similar manner as they affect the information retention of predator threats (Ferrari et al., 2010).

In conclusion, we found that *J. transcriptus* subordinates mediated their aggressiveness against their dominants, depending on the dynamics of recent contests. When subordinates had a high fighting ability or good condition, they tended not to rely on information relating to recent contests. In other words, losing or ignoring information could be an adaptive function if information is no longer reliable in the context of dominance relationships (Ferrari et al., 2010). More empirical evidence on the factors that affect the retention period of information on dominants is necessary to develop our understanding of contest decisions in animals.

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DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because the Japanese government did not require a permit for experiments involving *Julidochromis transcriptus*.

AUTHOR CONTRIBUTIONS

TH, LJ, and MK developed the study concept and contributed to the study design. TH collected the data. TH and SA performed the statistical analyses. TH and LJ drafted the manuscript. SA and MK provided critical revisions. All authors have read and approved the final version of the manuscript for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2021.685907/full#supplementary-material>

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