Aggression and conflict management in social cichlid fish, *Julidochromis regani*

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SOKENDAI (The Graduate University for Advanced Studies)

Doctoral Thesis

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Acknowledgements

Abstract

Compared to individuals living solitarily, the ones living in a group are believed to have high fitness benefits. On the other hand, group living also incurs costs to its members. For example, conflict is inevitable among group members because of competition for limited resources. Conflict occasionally develops into aggression with physical and energetic costs for its participants. Since aggression threatens maintenance of group living, it is predicted that group members have behavioral tactics, so called conflict management, to reduce costs of conflict caused by group living.

Studies of social fish have been demonstrating that species-specific features of sociality determine patterns and function of aggression and conflict management. In this sense, social cichlid fish *Julidochromis regani* provides a nice opportunity to investigate a link between species-specific features and those social behaviors. *J. regani* exhibits intraspecific variation in mating systems, ranging from monogamy to polyandry with sex-role reversal. In addition, *J. regani* is a facultative cooperative breeder in which nonparent group members contribute to care of immature individuals. Using this unique system, my thesis aimed to reveal patterns and function of aggression and conflict management. This thesis contains two studies.

In the first study, I reported intrasexual aggression in *J. regani*. In sex-role-reversed species, females compete for resources (e.g., mates) more intensively than males do. In cooperatively breeding species in which nonparents help to rear offspring, the reproductive skew can be higher among females than among males, which can lead to selection for female aggressiveness with respect to monopolizing

reproduction. However, it remains unclear whether these species exhibit sex differences in the intensity of aggressive behavior in the context of within-sex contests. In this study, I observed aggressive interactions among three same-sex individuals in *J. regani* in the laboratory and tested whether inter-female aggression was more intense than inter-male aggression. Although difference in body size strongly determined the direction of aggression in fish, aggression by a smaller-sized individual toward larger ones was occasionally observed in this species. This type of aggression was common between individuals of a similar body size (≤5 mm) and occurred more frequently among females than males. In contrast, differences in body size and sex did not affect the frequency of aggression by larger-sized individuals against smaller ones. Bidirectional aggression (i.e., mouth fighting) occurred frequently when two individuals had similar body size, and there was no difference in its frequency between sexes. However, temporal analysis showed that females performed bidirectional aggression more persistently than males. These sex differences in the intensity of intrasexual aggression could be the behavioral mechanisms underpinning cooperative polyandry.

In the second study, I focused on a complex pattern of polyadic aggression, redirected aggression. Redirected aggression – aggression by an attacked individual towards a third-party individual immediately after an original aggression – has been considered as one of the conflict management by a victim because it could reduce a probability of receiving further aggression. The occurrence of redirected aggression has been reported in many vertebrates, but few quantitative studies have been conducted in fish. I examined the function of redirected aggression in *J. regani*. Behavioral

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experiments showed that redirection aggression functioned to divert original aggressor's target toward a third-party individual and to prevent from being attacked by the third-party individual preemptively. In contrast, redirected aggression did not delay a timing of the aggression reoccurrence by an original aggressor. These results suggest that a primary function of redirected aggression is to maintain the dominance of its actor against a subordinate occupying the adjacent rank. This study provides the first evidence that the redirected aggression has functions of managing conflict in social fish.

Overall, this doctoral thesis shed light on how species characteristics would affect patterns and functions of social interactions such as aggressiveness and conflict management. At the same time, however, I also found results that do not match to this bidirectional relationship. This could have been caused either by the fact that my studies were conducted in laboratory settings or by lack of our knowledge on behavior of this species in the wild. This thesis suggests that studies of social behavior in different mating and/or social systems are required to fully understand complex systems in social fish. This thesis also suggests importance of analyzing cognitive abilities linked to social behavior, as complicated social contexts can be a background for the evolution of sophisticated cognitive abilities.

Chapter I. General introduction

Compared to solitary living, group living provides its members benefits such as improves access to resources, decreases risk of being preyed, and increases opportunities of mating or finding social partners (Krause & Ruxton 2002). However, group living incurs costs to its members. For example, conflict is inevitable among group members because of competition for limited resources such as mates or foods (Krause & Ruxton 2002). Also, group living individuals suffer a high risk of infection compared to solitary living ones (Côté & Poulinb 1995). From a perspective of evolution, group living is predicted to be stable when its benefits exceed its costs for each group member.

Intense conflict among group members occasionally develops into aggression with physical and energetic costs for its participants. The distribution, direction, and intensity of aggression reflect the degree of conflict, therefore can be a good behavioral way to understand social structure in animals (Hemelrijk 2000). For instance, occurrence of bidirectional aggression or counter-attack would be rare once dominance relationships are formed among group members.

Since aggression threatens maintenance of group living, it is predicted that group members have behavioral tactics to reduce costs of conflict caused by group living. This behavior is called conflict management (Aureli & de Waal 2000). In the case that behavioral tactic resolves a cause of conflict, it is called conflict resolution (Aureli & de Waal 2000). Many studies of conflict management and resolution were conduced in mammals (reconciliation, consolation, and redirection: Aureli & van Schaik 1991; Aureli et al. 1993; Aureli & de Waal 2000) and birds (re-hiding food

caches: Clayton & Emery 2007; allopreening: Radford 2008).

As such, studies of aggression and conflict management are important for understanding how animals maintain group living. However, it is true that previous studies on this topic have been concentrated on mammals and birds, and it is required that studies will be done in other taxa. Also, it is necessary to conduct experimental studies, which are hard to do for mammals and birds. From these points, "social fish" is an ideal species to address these questions.

A group structure of social fish can be summarized as follows. First, social fish form a group in which the number of matured individuals is countable, often less than 10 (Buston 2003; Wong 2011). Second, group membership is relatively stable and reproduction as well as social interactions usually occurs among members. Third, group members have stable dominance relationships that were determined by their relative body size (Buston 2003; Ang & Manica 2010). Fourth, group members sometimes compete for limited resources such as mates, foods, and spatial resources such as shelters or nests. Aggression and conflict management have been studied in social fish. Below, I explain two cases of aggression and conflict management in social fish (note that I do not explain interspecific social interactions although series of studies in a cleaner-client mutualistic system demonstrated conflict management; Bshary & Grutter 2005).

Clownfish *Amphiprion percula*: clownfish forms a group inside a sea anemone. For the clownfish, it is hard to disperse from their home sea anemone to others because of high predation risk. The clownfish is a sex changer in which the

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largest individual is female while others male or sexually not matured. Within a group that is composed of unrelated individuals, individuals form a linear dominance hierarchy that is determined by individuals' sizes. A relatively dominant individual attacks and evicts subordinates whose size is close to itself (Buston 2003). Subordinates adaptively do growth modification so as not to be a similar size to its adjacent dominant individual, and consequently prevent eviction from a group. As a result, body size ratio between two individuals whose dominance rank is adjacent becomes about 1.3 times (Buston 2003).

Cichlid fish *Neolamprologus pulcher*: *N. pulcher* is a cooperatively breeding species in which non-parent helpers (usually offspring of a dominant pair) participate to offspring care (Wong & Balshine 2010). In this species, dominant males or females were more aggressive toward the same sex subordinates (Mitchell et al. 2009). Helpers that help less frequently were attacked and evicted from a group by dominant individuals. Those idle helpers increase the frequency of helping behavior after experimental removal for a short duration, possibly for increasing likelihood that helpers are tolerated by the dominants in the territory (Bergmüller & Taborsky 2005; Fischer et al. 2014).

As such, previous studies in social fish suggested not only the presence of aggression and conflict management, but also that species-specific features determine its pattern and within-group distribution. Accordingly, different species equip different patterns. Studies of both aggression and conflict management in various species will facilitate our understanding of sociality in fish.

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In this thesis, I studied aggression and conflict management in *Julidochromis regani*, social cichlid living in Lake Tanganyika. This species can be a unique model for studying aggression and conflict management because of unique social characteristics stated in Chapter II. In the first study (Chapter III), I report sex differences in intrasexual aggression. In the second study (Chapter IV), I report that redirected aggression has function of conflict management. In Chapter V, I will summarize my findings and discuss future research direction. A broad aim of this thesis is to expand our knowledge of how species-specific characteristics determine social traits such as aggressiveness and conflict management. Accordingly, my studies will help our understanding of social complexity in fish.

Chapter II. Study Species

This study was conducted on *J. regani*, a species belonging to Lamprologine cichlids. Lamprologines are endemic to Lake Tanganyika in East Africa. Species of genus *Julidochromis* are substrate brooding species and use narrow rocky crevices as nests around which individuals form a territory. Individuals that share or overlap territories form a mating group and have social interactions therein (Yamagishi & Kohda 1996; Sunobe 2000; Awata et al. 2005).

Species of genus *Julidochromis* has been traditionally subdivided into five species based on color patterns. Phylogenetic studies using molecular analyses have shown that three species of *Julidochromis* (*J. transcriptus, J. ornatus and J. dicfeldi*) forms a monophyletic group that is close to species in the genus *Chalinochromis* (Dey et al. 2017). On the other hand, *J. regani* and *J. marlieri* are sister species that are separated from the other three species (Dey et al. 2017). One study suggested the presence of a hybrid between these two species and further mentioned *J. marlieri* as *J. regani* affinis (Sturmbauer et al. 2017). Anatomical study suggests that *J. regani* and *J. marlieri* are the same species (Tashiro 2011). Based on those studies, it is hard to distinguish *J. marlieri* and *J. regani* completely and it is further suggested that these are the same species. Therefore, I assumed that the behavioral patterns of *J. marlieri* were equivalent to those of *J. regani*, although I use the conventional names of *J. regani* and *J. marlieri*. Note that the phylogenetic relationship between two sub-groups of *Julidochromis* should be considered as tentative because of difficulties of estimating phylogenetic relationships in cichlids in Lake Tanganyika. Although future studies will elucidate whether knowledge of other species in genus *Julidochromis* can be applied to

J. regani, I explain characteristics of *Julidochromis* species revealed by previous studies below.

Previous studies of *Julidochromis* species have been concentrated on two species, *J. ornatus* and *J. transcriptus*. Those studies showed that those *Julidochromis* species exhibit an intraspecific variation in mating systems (monogamy, polygyny, and polyandry) and are facultative cooperative breeders in which nonparent group members contribute to the care of immature individuals (*J. ornatus*: Awata et al. 2006a; Heg & Bachar 2006; Bruintjes et al. 2013).

In *J. ornatus,* field observations suggested that 70% of group is monogamous, 30% monogamous with helpers. In monogamous pairs with large difference in body size, smaller individual mainly takes care of juveniles (Awata & Kohda 2004). Sex ratio of helpers was biased to males, and most helpers are nonrelated with breeders. These helpers stay in nest and attack different species frequently (Heg & Bachar 2006). Male helpers occasionally participate in reproduction, attaining to 41% of the paternity (Awata et al. 2005). Testis weight of a breeder male with helpers was heavier than the one without helper, indicating that male adjusts investment to testis according to a degree of sperm competition (Awata et al. 2006a). Awata et al. (2010) found that group size (i.e., a number of helper) is positively related to the group reproductive output, and particularly that the presence of two male breeders increased the reproductive success of a breeding female (but see Heg & Bachar 2006; Bruintjes et al. 2013 for the absence of this effect).

J. transcriptus have been studied under laboratory settings. Experimental

formation of a mating group suggested flexibility of mating system, with a monogamous mating system being formed when a male and a female are similar in their body size. In contrast, a larger sexed-individual mated small individuals of the opposite sex when there is an asymmetry in body size by sexes, resulting in either polyandrous or polygynous mating system. In monogamous pairs, both parents engaged in parental care almost equally. In the polygamous settings, however, a larger individual of pairs did parental care less frequently than smaller ones (Awata et al. 2006b). In polyandrous mating system in which a risk of sperm competition is high, males increase their testis size but decrease their growth rate (Awata et al. 2008). Female could control paternity of eggs by changing multiple spawning sites where only a small (beta) male could access to and fertilize eggs (Kohda et al. 2009; Li et al. 2015). When paternity of a brood is mixed, a beta male performs parental care more frequently than a large one (Kohda et al. 2009).

Compared to these two species, *J. marlieri* and *J. regani* have been less studied. The mating system in *J. marlieri* and *J. regani* has been reported to be monogamous or cooperative polyandrous (*J. marlieri*: Yamagishi & Kohda 1996; Sunobe 2000; *J. regani*: Awata, pers. comm.). In *J. marlieri* and *J. regani*, females are larger than males in the wild (*J. marlieri*: Yamagishi & Kohda 1996; *J. regani*: Gonzalez-Voyer et al. 2008), and this sex difference was also observed in the same age cohort (laboratory *J. marlieri*: Wood et al. 2014). Barlow and Lee (2005) suggested that *J. marlieri* is a sex-role-reversed species based on sex differences in the aggressiveness and a mating system in the wild (Yamagishi & Kohda 1996).

As such, studies of *J. regani* will not only compensate our knowledge of genus *Julidochromis* but also give an opportunity to examine an effect of a unique social and mating system on aggression and conflict management.

Chapter III. Sex differences in intrasexual aggression

(This chapter slightly modified Ito et al. 2017 in *Journal of Ethology*)

Introduction

The standard sexual selection theory predicts that males compete for access to females, whereas females choose mating partners (Andersson 1994; Shuster & Wade 2003). This sex difference is attributed to a fundamental difference in gametic investments between males and females, which leads to a faster potential reproductive rate in males compared with females (Trivers 1972; Kokko & Jennions 2008). Moreover, intense intrasexual competition selects for a large body size, the evolution of sexual ornaments, and specialized weapons for males (Andersson 1994).

Although such a "typical" pattern has been confirmed in many species, females in some species with particular mating/social systems were found to experience more intense competition compared with males. Those mating/social systems include sex-role reversal and cooperative breeding/polyandry. In a sex-role-reversed species, the availability of caregiving males limits the reproductive opportunities of females, leading to intense intrasexual competition and interference among females [e.g., female Wilson's phalaropes (*Phalaropus tricolor*) destroy eggs laid by other females to increase their own reproductive opportunities; Emlen et al. 1989]. In cooperatively breeding species in which nonparents help to rear offspring, the reproductive skew can be higher among females than among males (Clutton-Brock et al. 2006), which can select for female aggressiveness with respect to monopolizing reproduction (e.g., the eviction of subordinate females or the killing of the pups of subordinate females in meerkats *Suricata suricatta*; Clutton-Brock et al. 2006; Kutsukake & Clutton-Brock 2006; Young et al. 2006) or the evolution of ornament plumage for females (e.g.,

African starlings; Rubenstein & Lovette 2009). In cooperative polyandry, one female has multiple mating partners and, consequently, nonparental males take care of offspring (Faaborg & Patterson 1981; Davies 1992). In some species with these systems, females are larger than males (e.g., cichlid fish *Julidochromis marlieri*: Yamagishi & Kohda 1996, and *J. regani*: Awata, pers. comm.).

Previous studies have provided ample evidence that females can compete more intensively or frequently than males, leading to a renewed attention to female-female competition (Clutton-Brock 2007; Tobias et al. 2012). Morphological traits, such as size dimorphism, ornamentation, and weaponry, are measurable and can be easily compared between sexes (Owens & Hartley 1998; Tobias et al. 2012). In contrast, behavioral traits are relatively difficult to measure because intrasexual competition is not always reflected in the occurrence of contests or aggression. If same-sex individuals seldom encounter or avoid one another because of intense competition under specific mating systems (e.g., harem or cooperative polyandry), the observed frequency of contests or aggression will be low. In addition, males and females may compete for different purposes and in different contexts. Thus, a comparison of the frequency or intensity of aggression based on naturalistic observations may lead to an overly simplified view of aggressiveness. Although previous research has investigated intrasexual aggression as well as sex differences, with some studies detecting no sex differences (sex-role-reversed species: Owens et al. 1994; Emlen & Wrege 2004) and others observing female aggressiveness over males (cooperative breeders: Clutton-Brock et al. 2006), it is necessary to compare aggressive

behavior under an experimental condition in which the effects of various factors are controlled.

In this study, I compared the intensity of intrasexual aggression between males and females in the social cichlid *J. regani*, the rock-dwelling, biparental substrate-breeding cichlid fish endemic to Lake Tanganyika, Africa (Axelrod 1996). Species of the genus *Julidochromis* exhibit unique characteristics of sex-role reversal and cooperative breeding/polyandry (see Materials and methods for details). I tested an idea that females are more aggressive than males in intrasexual competitions in *J. regani* by examining the effects of differences in body size, sex, and the direction of aggression on aggression frequency. Based on a general pattern that difference in body size determines the outcome of contests in fish (e.g., Draud & Lynch 2002; Werner et al. 2003; Reddon et al. 2011; Dey et al. 2013), I predicted that aggression between individuals would be more frequent when the difference between their body sizes were small. Regarding sex differences, I predicted that females would show aggression more frequently than males and, particularly, that smaller-sized females would attack larger-sized ones more frequently than smaller-sized males attack larger-sized males (see Barlow & Lee 2005 for females having a higher probability of winning in intersexual conflicts than males). In addition to unidirectional aggression, *J. regani* occasionally perform bidirectional aggression (mouth fighting) to assess an opponent's strength. For the aforementioned reasons regarding the body size, I predicted that this bidirectional aggression would occur more often when two individuals' body sizes were similar. I also predicted that females would perform mouth fighting more frequently

than males. Furthermore, I analyzed the temporal distribution of mouth fighting relative to that of unidirectional aggression to determine whether the occurrence of bidirectional aggression was more frequent in the early stages of an encounter and whether females performed bidirectional aggression more persistently than males.

Methods

Study species

This study was conducted on *J. regani*. Traditionally, the genus *Julidochromis* has been subdivided into five species based on color patterns, but *J. regani* and *J. marlieri* are now believed to be the same species (Tashiro 2011; see also Sturmbauer et al. 1994, 2010). Therefore, I assumed that the behavioral patterns of *J. marlieri* were equivalent to those of *J. regani*, although I use the conventional names of *J. regani* and *J. marlieri* in my study. *Julidochromis* species exhibit an intraspecific variation in mating systems (monogamy, polygyny, and polyandry) and are facultative cooperative breeders in which nonparent group members contribute to the care of immature individuals (Awata et al. 2006b; Heg & Bachar 2006; Bruintjes et al. 2013). The mating system in *J. marlieri* and *J. regani* has been reported to be monogamous or cooperative polyandrous (*J. marlieri*, Yamagishi & Kohda 1996; Sunobe 2000; *J. regani*, S. Awata, personal communication). In *J. marlieri* and *J. regani*, females are larger than males in the wild (*J. marlieri*, Yamagishi and Kohda 1996; *J. regani*, S. Awata, personal communication), and this sex difference was also observed in the same age cohort (laboratory *J. marlieri*, Wood et al. 2014). Regarding sex differences in the

aggressiveness of the different species of this genus, Barlow and Lee (2005) experimentally investigated an effect of differences in body size between male and female *J. marlieri* on the outcomes of intersexual contests. Their results suggested a higher aggressiveness in females than in males and also taking into account previous data on a mating system in the wild (Yamagishi & Kohda 1996), these authors suggested that this species is a sex-role-reversed species. This intersexual aggression may be a behavior for deciding or reflecting within-pair dominance, which determines the parental role (wild *J. ornatus*, Awata & Kohda 2004). The aggressiveness of females is also supported by a molecular study showing that female *J. marlieri* share most of the neural gene expression with *J. transcriptus* males, known to be an aggressive sex (Schumer et al. 2011).

Study animals

Wild *J. regani*, originally caught around Sumbu, Zambia, were purchased from an aquarium shop. The experimental fish (17 males and 11 females based on the shape of genital papilla; Tashiro 2011) were kept in a laboratory at SOKENDAI (Hayama, Japan). Prior to the experiments, each fish was kept in a separate aquarium (600 × 275 × 450 mm), with each aquarium visually separated from all others. Each aquarium contained a plastic case (90 × 60 × 100 mm) filled with coral sand, which provided hiding places; the pH value of the coral sand was high to simulate conditions in Lake Tanganyika (Awata et al. 2006b). The water was filtered through an outside sponge filter, and the water temperature and pH value were maintained at between 26

and 28 °C and 7.2–7.8, respectively. The photoperiod was set to 12:12 hours light:dark with light provided by fluorescent lighting. Fish were fed commercial flake food (TetraMin; Tetra Werke, Melle, Germany), which were provided for a few minutes once per day, 5 days per week. One-third to one-half of the water was changed once weekly.

Experimental setting

In each experimental session, I selected three females or three males (females: 8 sessions; males: 11 sessions). Each individual was used for one to four experimental sessions (mean 2 sessions). For each experimental session, the standard length (SL) of the experimental fish was measured to the nearest 0.1 mm with a digital vernier caliper. I chose three individuals to allow for various combinations of body size [mean SL of males 74.8 mm, range 61.7–86.0 mm, standard deviation (SD) 7.31 mm; mean SL of females 86.2 mm, range 69.3–99.1 mm, SD 8.37 mm]. I labeled the three individuals large, medium, or small according to their SL. One reason for using three rather than two individuals was that I also sought to study polyadic interactions or sequences of social interactions occurring among different dyads (Ito et al. 2017). In nature, a situation in which three males coexist in the same group can occur when male offspring have not yet dispersed from a nest with a male breeder and male helper(s). Although helpers are typically male, the presence of a female helper has also been confirmed (Yamagishi & Kohda 1996). Therefore, three females (a breeding female, female helper, and female offspring) can coexist in the same nest, albeit more rarely than three males. The interval between each experiment for individuals was at least 10 (mean 88.14) days.

It is unknown how long the effect of contest experience (e.g., winner effect or loser effect) persists in *J. regani*. In other species (*J. transcriptus*), however, Hotta et al. (2014) reported that the memory of dominance relationships persists for less than 7 days and that no winner-loser effect exists. All experiments were conducted from 1000 to 1700 hours, 30 minutes after providing the flake food to each aquarium. During the first day of the experimental session, I put three individuals together in the experimental aquarium (750 × 500 × 500 mm), which was continuously aerated and its bottom was covered with a 2 cm layer of coral sand. The water depth was 40 cm. With the exception of the front side, the sides of the experimental aquarium were covered with black plastic plates to prevent reflections of the fish body. During the first day of the experimental session, I put three individuals together in the experimental aquarium to allow them to acclimate to the experimental setting. The three individuals were immediately separated from each other by two transparent partitions, dividing the aquarium into three equal compartments (250 × 500 × 500 mm for each individual). After 1 hour of acclimation to the experimental settings, the transparent partitions were removed, allowing the three individuals to interact and to form dominance relationships. One hour later, the transparent partitions were put back in place. It should be noted that interactions during this acclimation period were not analyzed because both of these experimental settings were unfamiliar to each fish, making the observation of social interactions difficult or impossible. Observation of social interactions was particularly problematic in my study as I was interested in observing how patterns of aggression (i.e., unidirectional vs. bidirectional aggression; see Introduction) changed after the start of such interactions.

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The three individuals were kept in separate compartments of the experimental aquarium until the end of the experimental session. I conducted two observational sessions for each experimental session (hereafter called the ''first'' and ''second'' observational session). At the start of the observational sessions, the transparent partitions were removed to allow the three individuals to interact. At the end of the first observational session, I used the partitions to once again separate the three fish. At the end of the second observational session (i.e., the end of one experimental session), each of the three fish was returned to its separate aquarium. The first observational session was conducted 2 or 3 days after acclimation, and the second observational session was conducted 4 or 5 days after acclimation. I stopped the observational session when a smaller-sized fish was severely attacked. In addition, when a pattern of social interactions was judged to be fixed (e.g., a large fish repeatedly attacked a medium- or small-sized fish), the observational session ended 10 min after that time point (mean duration of the observational sessions 20.5 minutes, SD = 7.8 minutes, range 12.9–38.0 minutes).

Behavioral observation and coding.

I recorded social interactions using a video camera (placed 30 cm in front of the experimental aquarium; model iVIS HF R32; Canon, Tokyo, Japan) that covered all areas of the experimental aquarium. I then exported the video data to a computer (MacBook Pro; Apple, Cupertino, CA) to perform behavioral coding. I recorded all cases of unidirectional aggressive behavior (chasing, rushing, and bumping) and

bidirectional conduct (mouth fighting) as well as the timing of occurrence and the identities of aggressor and recipient. Multiple bouts of aggression often occurred successively in the same dyad. If a subsequent aggressive behavior occurred within 10 seconds of the end of the former aggressive behavior, I also defined each event as a bout of aggression. In total, I observed 2738 cases of unidirectional aggression (mean ± SD: 72.05 ± 30.02 cases per one observational session) and 159 cases of mouth fighting (4.18 ± 10.17 cases per one observational session).

Data analyses

Generalized linear mixed models (GLMMs; lme4 package) in R (version 3.0.2) were used for all data analyses. In the GLMMs, I included interactions among the independent variables. The results of the interactions were not presented if they were not significant. The alpha level was set at 0.05.

Frequencies of aggression

In the analyses of unidirectional aggression, I used GLMMs with a Poisson error structure and log link function. The response variable was the frequency of aggression bout for each dyad during an observational session, which means that one observational session included six data units (large, medium, or small individual for an aggressor; one of the other two for its recipient). The independent variables included the difference in body size between two individuals (e.g., large individual's SL − medium individual's SL), sex (male or female), and the direction of aggression (whether a

smaller-sized individual attacked a larger-sized individual or a larger-sized individual attacked a smaller-sized individual). The observation time was set as an offset function to control for the difference in the observation duration among observational sessions. The identity of aggressor and experimental session were used as random factors.

Frequency of mouth fighting

In the analysis of mouth fighting, I used GLMMs with a Poisson error structure and log link function. The response variable was the frequency of mouth fighting. Independent variables were type of dyad (large vs. medium or medium vs. small; mouth fighting between large and small individuals was not observed), difference in body size, and sex. The observation time was set as an offset, and the identities of two individuals performing mouth fighting were set as random factors.

Timing of aggression

To examine the temporal distributions of mouth fighting, I used GLMMs with a binomial error structure and logit link function. I first calculated the timing of each aggression bout starting from the initiation of each observational session. The response variable was the type of aggression (mouth fighting or other unidirectional aggression), and timing and sex comprised the independent variables. The experimental session was set as a random factor.

Results

Frequency of unidirectional aggression

I found a significant three-way interaction among sex, difference in body size, and direction of aggression (Table 3.1a). This might indicate that the effect of difference in body size on frequency of aggression varied between the sexes and that this pattern also differed according to the direction of aggression. Because interpreting the results of such complicated interactions is not easy, I divided the data into two sub-data units according to the direction of aggression dependent on body size differences and reran the GLMMs.

The analysis of aggression by smaller-sized individuals against larger-sized individuals reflected a significant two-way interaction between difference in body size and sex, with a significant main effect of the difference in body size (Table 3.1b; Figure 3.1a). This means that size-reversed aggression occurred frequently in a dyad with a small difference in body size, and the effect of size difference varied between sexes. When I reran the GLMM after separating the data into subunits of small size difference (≤ 5 mm) and large size difference (>5 mm), smaller-sized individuals were more likely to attack larger-sized ones among females than males in both datasets (small size difference: $b = -2.296 + 0.849$, $z = -2.703$, $p = 0.0069$; large size difference: $b = -2.008 + 0.461$, $z = -4.359$, $p < 0.0001$). These results indicate that size-reversed aggression was more common among females than males.

The analysis of aggression by larger-sized individuals toward smaller-sized individuals revealed that no independent terms affected frequency (Table 3.1c; Figure

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3.1b).

Frequency and timing of bidirectional aggression

A significant effect of difference in body size suggested that individuals with a similar body size (≤5 mm, see Figure 3.2) performed mouth fighting frequently. The frequency of mouth fighting was higher among females than males, although this difference was not significant (Table 3.2; Figure 3.2). The type of dyad (large vs. medium or medium vs. small) did not affect the frequency of mouth fighting (Table 3.2).

Bidirectional aggression (i.e. mouth fighting) occurred more immediately after the start of the experiments than unidirectional aggression (Table 3.3; Figure 3.3). This result was confirmed after controlling for the significant effect of sex (females > males; Table 3.3).

Discussion

In this study, I observed aggressive interactions among three same-sex members of a sex-role-reversed, cooperative breeding fish species, *J. regani*. As expected, inter-female aggression was more intense than inter-male aggression in two contexts. The first was that the frequency of aggression by smaller-sized individuals against larger-sized ones was higher among females than males when the size difference was small (≤5 mm; Table 3.1b; Figure 3.1a). The second finding was that females performed bidirectional aggression (i.e., mouth fighting) more persistently than males

(Table 3.3; Figure 3.3). Mouth fighting was observed mainly between individuals whose size difference was small (≤ 5 mm; Table 3.2; Figure 3.2) and at an early stage of the experiments, indicating that mouth fighting has the function of assessing the opponent's relative strength (Neat et al. 1998).

Frequent aggression between two individuals with similar body size, particularly among females, indicates that these two individuals have intense conflict (Figure 3.1a). My results were consistent with the general pattern of body size being a strong predictor of contests (Arnott & Elwood, 2009) and dominance in animals (Clutton-Brock & Parker, 1995), including among fish (e.g., Draud & Lynch 2002; Werner et al. 2003; Reddon et al. 2011; Dey et al. 2013). Why did aggression frequently occur between individuals with similar body sizes? One possibility involves the difficulty of forming stable dominance relationships among individuals. Under such conditions, small individuals would not accept a relatively subordinate position to larger-sized individuals. Another possibility is that the dominance relationship was established but that smaller-sized individuals assessed the strength of a dominant one via aggression. Such "dominance testing" has been observed in other social animals with a stable dominance hierarchy (e.g., Reeve & Ratnieks 1993; Cant & Johnstone 2000). However, the frequent occurrence of bidirectional aggression, particularly among females, suggests that clear dominance relationships were not established between these individuals.

Although these overall results reflected intense aggression among females, some analyses showed that, inconsistent with my expectation, aggression among males

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was of a similar intensity to that among females. First, I found no sex difference in aggression frequency by larger-sized individuals against smaller-sized ones. In this analysis, the difference in body size did not affect the frequency of aggression by larger-sized individuals against smaller-sized ones (Table 3.1c; Figure 3.1b). If the difference in body size were a strong determinant of contests and aggression, larger-sized individuals may not need to attack the smaller-sized ones because of the obvious physical superiority of the former. However, larger-sized individuals incur little cost for attacking smaller-sized ones because of the unlikelihood of counter-attack and bidirectional aggression when the size difference is large. If so, consistent aggression by the large individual may be a behavioral tactic to reinforce and stabilize dominance with marginal costs. This explanation fits a situation in which mature individuals attack the co-living helpers within their home range. Alternately, this aggression might be to enable larger-sized individuals to exclude smaller-sized ones from the home range of the former. The home ranges of same-sex individuals are adjacent (for males) and occasionally overlap (for females), which renders aggressive inter-home-range encounters likely to occur.

Thus, my data showed sex differences in intrasexual aggression in *J. regani*. Intense aggression among females in this species may be linked to sex-role reversal and cooperative breeding/polyandry. In species with these characteristics, females commonly compete for reproductive opportunities in the context of limited resources (see Introduction). This intrasexual competition is possibly linked to the larger-sized female body size (see Introduction) and the facultative polyandry in which female

coexistence is rare. The mating system in *J. marlieri* and *J. regani* is monogamous or cooperatively polyandrous, consisting of one adult female, males, and helpers (*J. marlieri*: Yamagishi & Kohda 1996; Sunobe 2000; *J. regani*: Awata, pers. comm.). Helpers are more likely to be male than female, and three males (including male helpers) have been described coexisting in the same group (Yamagishi & Kohda 1996; Sunobe, 2000). It has been reported that a subordinate (beta) male can have high siring success (41% of young in total; Awata et al. 2005) in *J. ornatus*, although it remains unstudied whether males of my study species, *J. regani*, have a similar moderate reproductive skew. In contrast to males, females do not tolerate other females within their territories, and three mature females have not been reported as coexisting in *J. marlieri* (Yamagishi & Kohda 1996). These observations suggest that females might not form stable social relationships such as dominance, which could explain intense aggression among females.
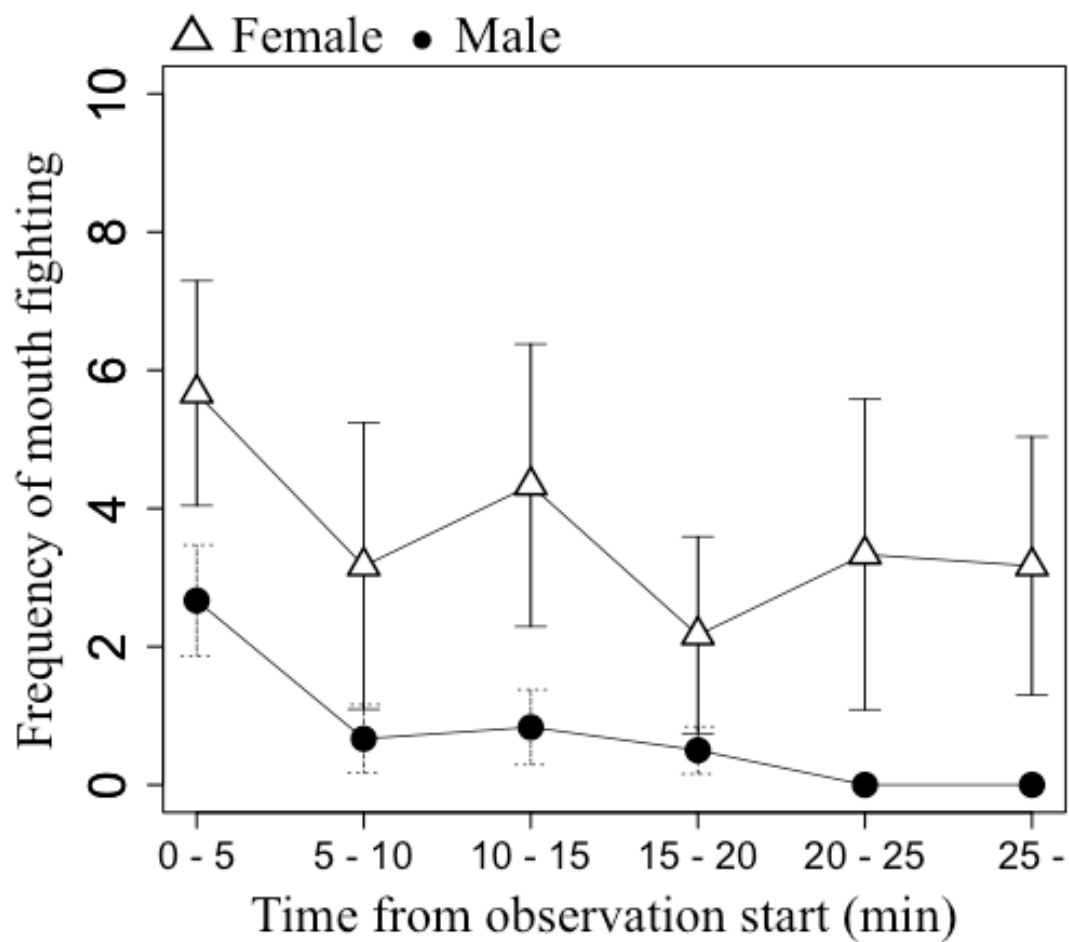
Figure 3.1. Sex differences in the effects of differences in body size on aggression frequency (a) by smaller-sized to larger-sized individuals; (b) and by larger-sized to smaller-sized individuals.

(a)   (b)
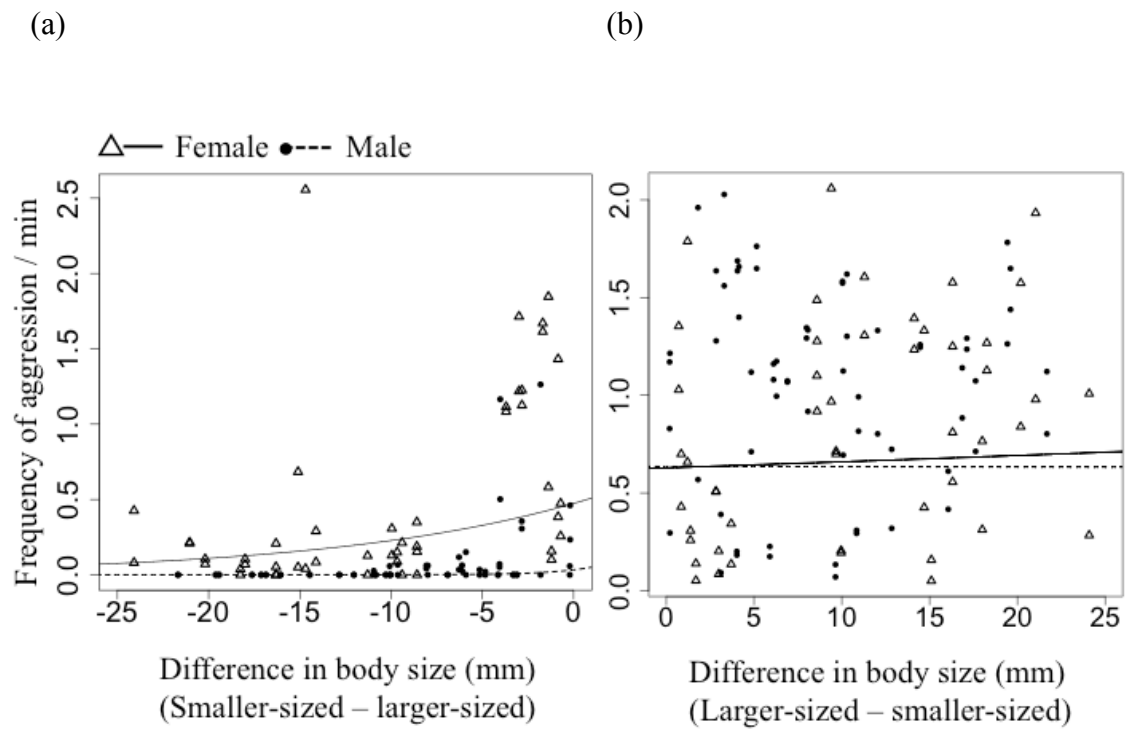
Figure 3.2. Sex differences in the effects of differences in body size on the frequency of mouth fighting.
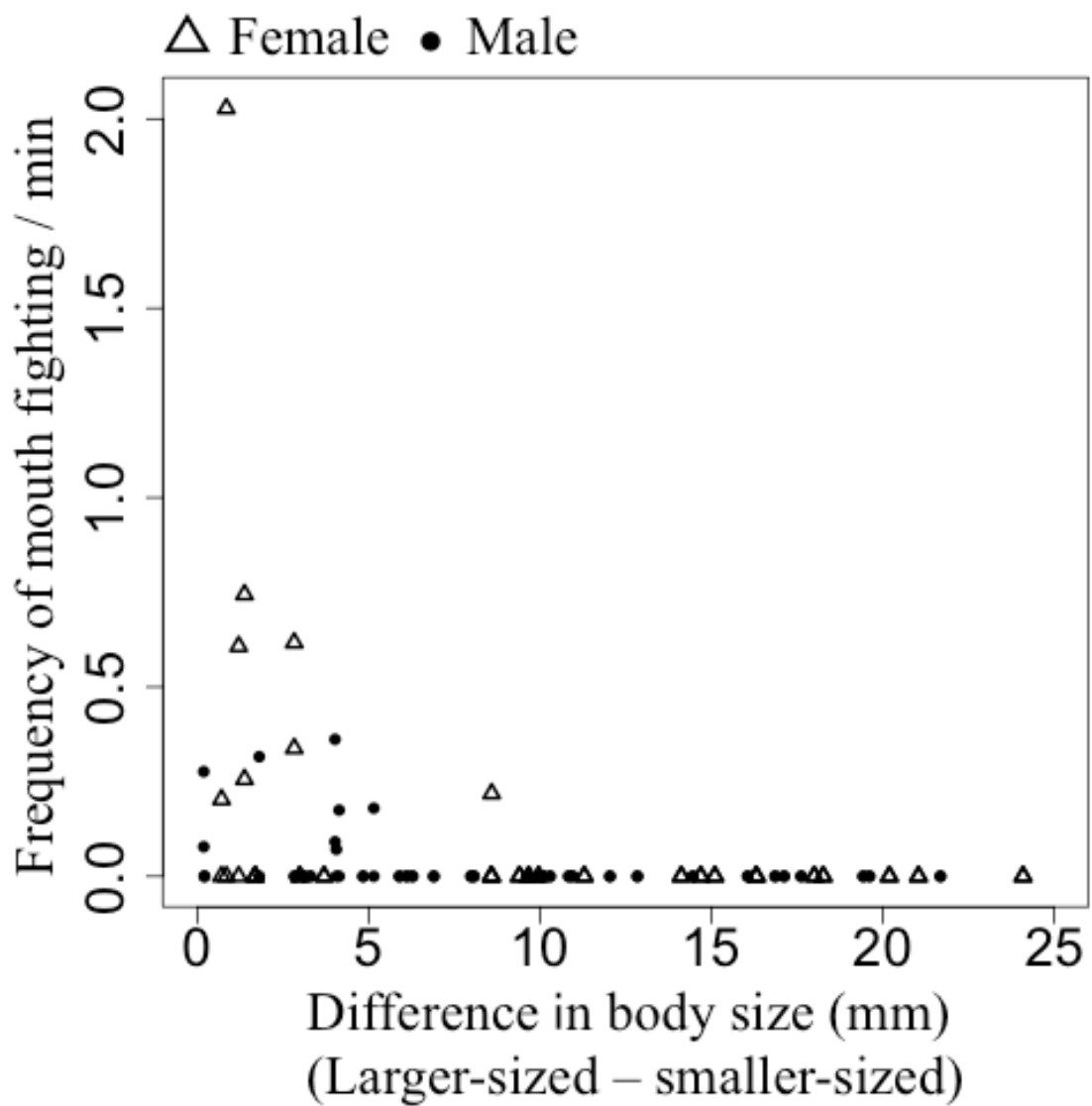
Figure 3.3. Temporal changes in the frequency of mouth fighting. The frequency of mouth fighting indicated an individual mean and 1 standard error for each time period. It should be noted that mouth fighting was not observed in all experimental sessions (males: 6 bouts of mouth fighting in 11 sessions; females: 6 bouts of mouth fighting in 8 sessions).

Table 3.1. Predictors of the frequency of unidirectional aggression. (a) All data. (b) Aggression by smaller-sized to larger-sized individuals. (c) Aggression by larger-sized to smaller-sized individuals.

Independent variable	b	SE	Z	p
(a) All aggression (N = 2738)				
Difference in body size × sex × direction of aggression	0.295	0.057	5.179	<0.001
Difference in body size × direction of aggression	0.123	0.015	7.971	<0.001
Difference in body size × sex	−0.288	0.056	−5.173	<0.001
Direction of aggression × sex	1.087	0.275	3.950	<0.001
Difference in body size	−0.134	0.013	−10.695	<0.001
Direction of aggression	−0.092	0.131	−0.706	0.480
Sex	−0.799	0.440	−1.816	0.069
(b) Aggression by smaller-sized to larger-sized individuals (N = 465)				
Difference in body size × sex	−0.275	0.067	−4.117	<0.001
Difference in body size	−0.092	0.015	−6.105	<0.001
Sex	−0.506	0.674	−0.751	0.453
(c) Aggression by larger-sized to smaller-sized individuals (N = 2273)				
Difference in body size	0.002	0.006	0.342	0.732
Sex	0.023	0.346	0.065	0.948

Table 3.2. Predictors of the frequency of bidirectional aggression (N = 159).

Independent variable	b	SE	Z	p
Sex	−1.878	1.034	−1.816	0.069
Difference in body size	−0.591	0.087	−6.790	<0.001
Dyad	0.624	0.802	0.778	0.436

Table 3.3. Predictors of the occurrence of mouth fighting (total aggression: N = 2738, total mouth fighting: N = 159).

Independent variable	b	SE	Z	p
Sex (Female > Male)	−1.663	0.812	−2.049	0.041
Time from observation start	−0.0005	0.0002	−2.461	0.014

Chapter IV. Redirected aggression as a conflict management tactic

Introduction

Group living, as compared to solitary living, provides benefits such as improved access to resources, decreases predation risk, and increases opportunities to find mates and/or social partners (Krause & Ruxton 2002). However, conflict is inevitable among group members because of competition for limited resources such as mates or foods (Krause & Ruxton 2002). Group living is predicts to be stable when its benefits exceed its cost for each group member. Behavioral tactics that reduce social costs of group living for individuals, i.e., conflict management (Aureli & de Waal 2000), are likely to evolve in these group living animals (Aureli & de Waal 2000; Flack & de Waal 2004). Conflict management has been reported in various mammals (Aureli & van Schaik 1991; Aureli et al. 1993; Aureli & de Waal 2000), birds (Clayton & Emery 2007; Radford 2008), and also in social fishes (Bshary et al. 2002; Buston 2003; Ang & Manica 2010). For instance, subordinate fish suppressed own growth to prevent eviction from a group (anemonefish *Amphiprion ocellaris*; Buston 2003, marine angelfish *Centropyge bicolor*; Ang & Manica 2010). Male cichlid fish intervene in female-female aggression (*Lamprologus ocellatus*: Walter & Trillmich 1994; *Neolamprologus multifasciatus*: Schradin & Lamprecht 2000).

Redirected aggression – an aggression by an attacked individual towards a third party following the initial attack – is thought to be a conflict management. One of its functions is to divert the first aggressor's attention, thus preventing further attacks on the individual that was initially targeted (reviewed in Kazem & Aureli 2005, which also discusses other possible functions). Redirected aggression has been reported in many

species of mammals (e.g., reviewed in Kazem & Aureli 2005; Japanese macaques *Macaca fuscata* Aureli et al. 1992; long-tailed macaques *Macaca fascicularis* Aureli & van Schaik 1991; Aureli 1992; vervet monkeys *Cercopithecus aethiops* Cheney & Seyfarth 1986, 1989; mountain gorillas *Gorilla gorilla beringei* Watts 1995a, 1995b; mandrills *Mandrillus sphinx* Schino & Marini 2014; wolves *Canis lupus* Palagi & Cordoni 2009; spotted hyenas *Crocuta crocuta* Engh et al. 2005). Although redirected aggression is believed to occur in many fishes, Kazem & Aureli (2005) listed fish species in which redirected aggression was observed (Atlantic salmon *Salmo salar*, bluegill sunfish *Lepomis macrochirus*, amarillo fish *Gtrardinichthys multiradiatus*). To the best of my knowledge, however, there is only one study that investigated redirected aggression quantitatively (Øverli et al. 2004). Øverli et al. (2004) showed that a medium-sized individual attacked a smaller one after being attacked by a larger-sized one in rainbow trout *Oncorhynchus mykiss*. Its frequency was higher than that of the control condition in which a medium-sized individual did not interact to a large individual. Although this study showed that the increased frequency of aggression by a defeated individual after the initial aggression, it did not investigate successive redirected aggression – i.e., the second aggression did not occur immediately after the first aggression because the experiments were conducted by excluding the large one or by putting the small one into the experimental aquarium. This behavioral definition is somewhat different from that in other animals (e.g., mammals) in which the original aggression and redirected aggression occurs successively. In addition, Øverli et al. (2004) did not investigate a function of redirected aggression such as whether it

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decreases a risk of further aggression and functions as conflict management. So, it remains unclear how common redirected aggression is in a social fish, and for what its actor perform redirected aggression.

In this study, I showed that occurrence of redirected aggression and investigated its function in a social cichlid *J. regani*, a rock-dwelling, biparental substrate-breeding cichlid fish endemic to Lake Tanganyika (Axelrod 1996). This species has including sex role reversal, cooperative breeding, and cooperative polyandry (Ito et al. 2017). In this experiment, I observed aggressive interactions among group of three males or three females. In descending order of relative body size, I labeled three individuals in each group as large (L), medium (M), and small (S). I first statistically demonstrated the occurrence of redirected aggression (M attacks S after being attacked by L). Next, I addressed the following questions to test a functional hypothesis that redirected aggression serves to prevent an individual (M) from receiving further, both by the original aggressor (L) and by other, uninvolved individuals (S). First, does redirected aggression by M divert aggression from an original aggressor (L) to the uninvolved individual (S)? Second, does redirected aggression by M delay timing of further aggression by the original aggressor (L)? Third, does redirected aggression by M reduce the probability of aggression by the uninvolved individual (S)? Finally, I analyzed predictors of redirected aggression, and asked whether redirected aggression was more likely to occur when conflict between two individuals (L and M or M and S) was intense

Dominance relationships in fish are usually determined by relative body sizes.

Individuals with similar body sizes (hence adjacent or unclear dominance ranks) show frequent aggression and thus are believed to have intense inter-individual conflict in several fish species (e.g., Draud & Lynch 2002; Werner et al. 2003; Wong et al 2007; Reddon et al. 2011; Dey et al. 2013; Ang & Manica 2010), including *J. regani* (Ito et al. 2017). Thus, I used the difference in body size between two individuals as a proxy for inter-individual conflict. I predicted that M would perform redirected aggression more frequently when M and L were of similar sizes because in such a case, M would have a higher incentive to divert aggression by L to S. I further predicted that M might perform redirected aggression to avoid being the object of aggression by S, a behavior that would be particularly important when the difference in body size between M and S was small. I also analyzed sex difference in redirected aggression. In *J. regani*, females are more aggressive than males in intra-sexual contests; both bidirectional and aggressions by smaller individuals toward larger occur more frequently between females than males (Ito et al. 2017). Based on this sex difference, I predicted that females would perform redirected aggression more frequently than males.

Methods

Study Animals and Experimental Setting

In this chapter, I used the data used in the study of intrasexual aggression (see Chapter III, pp. 17–38).

Data coding

In total, I observed instances of aggression (total N = 4472, mean and SD of cases per one observational session, 117.68 and 43.0). Several instances of aggression often occurred successively with short intervals. If aggressive behavior occurred between the same individuals within 10 seconds of a previous act of aggression, I defined these as a single bout of aggression (Ito et al. 2017). Accordingly, bouts as defined in this study could be classified into two types based on duration. "Continuous" aggression indicated a bout of aggression with a substantial duration (range: 1−866 seconds, mean: 6.68). By contrast, "brief" aggression consist of a single instance of aggression with a short duration; for example, a rush and bump. As duration was different, it is likely that continuous and brief aggression have different effects on the occurrence and function of redirected aggression. My dataset included in total 2800 bouts of aggression (mean and SD of cases per one observational session, 73.68 and 32.0).

Hereafter, I have abbreviated bouts of aggression by indicating an aggressor and a recipient; for example, LM, MS, and LS respectively indicate aggression by L to M, by M to S, and by L to S.

Data analyses

All analyses were done in R (version 3.0.2). The level of significance was set to 0.05.

Occurrence of redirected aggression

I operationally defined redirected aggression as aggression of MS occurring within 5 seconds after LM. I used 5 seconds because the distribution of the time interval between bouts of LM and MS suggested that in more than half of MS cases (Figure 4.1a; 53.3%, 136/255) occurred within 5 seconds after LM (see Figure 4.1b and see also Results). Using this criterion, I counted 136 cases of redirected aggression in my experimental data.

This operational definition, using 5-seconds window after LM, is conservative and even works against the detection of redirected aggression. Based on this standard, bouts of MS that occurred more than 5 seconds after LM were not counted as redirected aggression, even though they may have served the same function as bouts that occurred within the allotted 5 seconds.

I needed to verify whether the observed number of cases of redirected aggression actually represented behavioral tactics by M individual, or merely reflected the typical occurrence of aggression among three individuals. I thus conducted a randomization test as follow (see Ikkatai et al. 2016 for a similar approach).

1. I measured the frequencies of LM and MS (both continuous and brief aggression) and timing of the occurrence of MS relative to LM for each ith observation session (i: 1 ~ 38).

2. Based on the results of the above observation, I generated artificial data. The timings of bouts of aggression within each dyad were decided randomly within a simulated experimental session of a

duration equals to that of the *i*th session. If there was temporal overlap between these randomly generated bouts of aggression, I re-simulated one of the bouts until there was no overlap. In cases of continuous aggression, the length of each bout was generated from a positive random value derived from a normal distribution whose mean and SD were obtained from the real data of the corresponding dyad (e.g., mean = 12.78 and SD = 10.44 seconds).

3. In the dataset thus generated, I counted the number of cases in which MS occurred after LM or during a continuous LM.

4. I repeated the above processes for all *i* sessions in one simulation round. After one round was over, the frequency of redirected aggression and the timing of redirected aggression relative to LM were calculated.

5. I obtained a null distribution of the frequency and the timing by repeating the simulation (steps 1 through 4) for 500 rounds. I then tested whether the observed pattern of redirected aggression deviated from the simulated null distribution.

Does redirected aggression divert aggression by the original aggressor to the uninvolved individual?

I tested whether redirected aggression (MS) functions to divert aggression by L to the uninvolved S. MS may occur either during a continuous LM bout or

immediately after a brief LM. Accordingly, I classified LM based on two variables: the aggression type (brief or continuous) and the occurrence of redirected aggression. I analyzed how these variables predicted the probability of LS within a given time window. I chose to use 5 seconds as a time window, the same length of time used in our definition of redirected aggression (see above). When redirected aggression occurred, I focused on a time window of 5 seconds immediately after the instance of redirected aggression. In the case where was not followed by redirected aggression, I observed a 5-second period beginning 5 seconds after the end of LM; this allowed us to observe comparable time periods between cases with and without redirected aggression.

I constructed generalized linear mixed models (GLMMs; lme4 package) with a binomial error structure and logit link function. The response variable was the occurrence of LS within the 5-seconds window. Independent variables were the type of aggression (brief or continuous), whether M performed redirected aggression (yes or no), and the sex (male or female). I also included interactions among the independent variables, but the results of the interactions were not presented if they were not significant. The experimental session was set as a random term.

Does redirected aggression delay timing of further aggression by an original aggressor?

Similar to the preceding analysis, I tested whether redirected aggression (MS) delays the timing of further occurrence of LM. I measured the time interval between two bouts of LM in four aggression categories (brief or continuous, with or without redirected aggression). The category of LM was set as a response term in a (general)

linear mixed model (LMM). The independent terms and the random term were the same to the preceding analysis.

It also considered the possibility that LM was only delayed when redirected aggression succeeded in diverting L's aggression toward S, and was not affected in instances where L did not attack S after redirected aggression. I tested this possibility by running a separate LMM and compared the timing of the subsequent LMs between the two scenarios.

Does redirected aggression prevent aggression by an uninvolved individual?

In *J. regani*, body size determines the direction of aggression; smaller individuals will attack larger ones only when the difference in body size between the two individuals is <5 mm (Ito et al. 2017). I thus used data from 18 observational sessions in which the body size difference between M and S was <5 mm. I counted the number bouts of SM, following the same procedure used to analyze diversion the L's aggression towards S (see above). I excluded data from one observational session in which redirected aggression did not occur. In the remaining 17 sessions, many produced zero data (i.e., SM did not occur) and only one case of SM was observed after redirected aggression (see Results); I was thus unable to implement a GLMM. Instead, I conducted Fisher's exact probability test for comparing whether occurrence of SM associated to occurrence of redirected aggression, and further non-parametric Wilcoxon signed-rank tests for comparing proportions of aggression after which SM occurred.

Is redirected aggression more likely to occur after the recipient of aggression is involved in an intense conflict?

I used GLMMs with a Poisson error structure and log link function. The response variable was the frequency of redirected aggression in each observational session. Independent variables were sex and difference in body size between L and M or that between M and S. Experimental session was set as random variables. The observation time was set as an offset function to control for the difference in the observation duration among observational sessions.

Results

Occurrence of redirected aggression

The observed cases of redirected aggression (N = 136) accounted for, on average, 13.70% of the total MS in each observational session. The randomization test suggests that the observed number of cases of redirected aggression was less than the predicted by the null distribution generated under an assumption of random occurrence of aggression (Figure 4.1a). This indicates that the occurrence of redirected aggression was *less* frequent than random occurrence of aggression. However, the observed temporal distribution of all types of MS (including redirected aggression that occurred within 5 seconds) was also different from that of randomized data, with MS occurring earlier than predicted by the null distribution (Figure 4.1b). The difference in cumulative distribution between the observed and simulated data showed a blunt peak at around 5 to 10 seconds (Figure 4.1b).

Does redirected aggression divert aggression by the original aggressor to the uninvolved

individual?

Redirected aggression had an effect of diverting aggression by L to S, but this

effect varied according to the type of aggression. I found a significant two-way

interaction between the occurrence of redirected aggression and the type of aggression

(Figure 4.2; binomial GLMM; $b + SE = -1.413 + 0.632$, $Z = -2.238$, $p = 0.025$; main

effect of redirected aggression: $b + SE = 1.347 + 0.458$, $Z = 2.942$, $p = 0.003$; main

effect of aggression type: $b + SE = -0.032 + 0.246$, $Z = -0.131$, $p = 0.896$). This

indicates that the occurrence of redirected aggression increased the probability of LS,

and this effect was particularly evident when the LM was brief as opposed to

continuous (Figure 4.2). Sex did not affect the likelihood that redirected aggression

would divert aggression ($b + SE = 0.092 + 0.229$, $Z = 0.399$, $p = 0.690$).

Does redirected aggression delay timing of further aggression by an original aggressor?

The occurrence of redirected aggression did not affect the timing of further

aggression by the original aggressor (Figure 4.3; $b + SE = -3.748 + 4.507$, $t = -0.832$, p

$= 0.411$) after controlling for a marginally significant effect of aggression type on the

timing of further aggression by an original aggressor (brief > continuous aggression; $b +$

$SE = -5.929 + 3.073$, $t = -1.929$, $p = 0.052$). The sex did not affect to the timing of

further aggression by an original aggressor ($b + SE = -1.602 + 8.790$, $t = -0.182$, $p =$

0.859). The effect of delaying aggression may only have been present when M

succeeded in diverting L's aggression to S (see Methods). However, my analysis

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suggests that the occurrence of LS after redirected aggression did not delay the subsequent LM (b = –11.490, SE = 7.911, p = 0.144).

Does redirected aggression prevent aggression by an uninvolved individual?

Overall, SM occurred rarely. Only one case of SM was observed after redirected aggression. By contrast, 33 instances (in 8 observational sessions) of SM were observed in cases when M did not perform redirected aggression. There was a significant difference in the occurrence of SM after redirected aggression (Fisher's exact probability test, p = 0.017). However, the proportions of SM that occurred after redirected aggression did not differ from those in cases without redirected aggression (Figure 4.4; Wilcoxon signed-rank test; V = 8, p = 0.195). This result should be treated with caution because the single instance of SM after redirected aggression seems to have caused the results to be non-significant (Figure 4.4).

Is redirected aggression more likely to occur after the recipient of aggression is involved in an intense conflict?

Differences in body size between L and M (Poisson GLMMs; b + SE = 0.004 + 0.027, Z = 0.148, p = 0.882) or between M and S (b + SE = 0.003 + 0.0370, Z = 0.067, p = 0.946) did not affect the frequency of redirected aggression; nor did sex (Poisson GLMMs; b + SE = 0.392 + 0.304, Z = 1.287, p = 0.198).

Discussion

To the best my knowledge, this is the first quantitative study of redirected aggression in fish. I confirmed the occurrence of redirected aggression, but its detection was not straightforward and our observations differed from those of other taxa published in previous study (Watts et al. 2000). The results of my randomization test suggest that the observed frequency of redirected aggression was not higher but lower than the value predicted if aggression occurred randomly (Figure 4.1a). At first glance, this result appears to suggest that redirected aggression is not in the behavioral repertoire of this species, since previous studies on redirected aggression have shown it to increase in frequency after an initial aggression when compared to control conditions (Watts et al. 2000; cf. Øverli et al. 2004). However, the decrease of aggression by M is understandable given that aggression in social fish is known to be suppressed by the presence of a dominant individual (e.g., Desjardins et al. 2012). An experimental setting in which three individuals interacted in a limited space might have reinforced this behavioral suppression. An alternative possibility is that M was damaged or exhausted after being the object of and thus its physical condition might not have allowed it to attack S. This idea is unlikely, however, because as the temporal distribution of the observed data showed, M was able to attack S immediately after LM (Figure 4.1b). The observed timing of redirected aggression was earlier than that of the data generated by randomization procedures (Figure 4.1b), which suggests that M tactically decided the timing for performing redirected aggression.

Testing three potential functions of redirected aggression for conflict management, I found evidence to support two of them. First, redirection aggression functioned to divert the original aggressor's attention to a third party. This pattern was effective particularly when the original aggression was brief as opposed to continuous (Figure 4.2). The reason for this difference is unknown, but L could have different aggressive tactics for continuous aggression with persistent chasing compared to brief aggression. This experiment was conducted in a limited space in which subordinates cannot avoid the aggressor. During the durable LM in which L's attention was fixed to M, it might be difficult for L to shift the target of ongoing aggression.

The second function of redirection aggression was preventing the occurrence of SM (Figure 4.4). I analyzed data only from groupings in which the size difference between M and S was small (5 mm or less) because size-reversed aggression in this species is quite rare when the difference in body size is large (Ito et al. 2017). SM would occur immediately after LM if S takes advantage of the opportunity to attack M, either to assess the strength of a dominant individual or seeking a chance for dominance reversal (dominance testing: Reeve and Ratnieks 1993; Cant and Johnstone 2000).

Challenging M immediately after LM might increase S's chance of success, as M would be less able to cope with further aggression when already fatigued. From M's perspective, then, redirected aggression could be a pre-emptive behavioral tactic to prevent such an attempt by S, transferring L's attention to S and signaling M's own superiority to S. Such signaling may also communicate to other subordinate individuals uninvolved in the original aggression (i.e. audience effect; Matos & McGregor 2002),

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although my experiments with three individuals were not designed to test this idea.

These two effects suggest that redirected aggression by M could reduce the negative consequences of aggression by L, indicating that it functions as a conflict management tactic. Contrary to my expectation, redirected aggression did not delay the timing of further aggression by L (Figure 4.3). This suggests that redirected aggression is a behavioral tactic that is primarily directed at S, rather than at L. Still, I believe that redirected aggression may serve other functions that have not been revealed by this study. In support of this idea, redirected aggression was observed in experimental sessions in which S was much smaller than M (>5 mm difference in size), such that size difference between S and M had no effect on the frequency of redirected aggression. This suggests that social threat by S is not a sole factor determining the M's redirected aggression. This suggests that the degree of social threat presented by S is not the sole factor determining whether M performs redirected aggression.

Both sexes performed redirected aggression at the same frequency. These results disagree with my prediction that redirected aggression was more likely to occur in females, who engage in more intense inter-individual conflict (Ito et al. 2017). The absence of an effect of sex suggests that redirected aggression is a common behavioral tactics for both sexes. Furthermore, no significant effects of sex were found in our functional analyses, suggesting that the function of redirected aggression was similar for both sexes.

In summary, this study provides the first experimental data demonstrating the occurrence and function of redirected aggression in social fish. Various conflict

management strategies have been reported in social fishes (e.g., Buston 2003; Schradin & Lamprecht 2000; Ang & Manica 2010), but redirected aggression has largely been overlooked. Anecdotal reports indicate that several species of social fish in addition to *J. regani* may perform redirected aggression (see Introduction). I predict that redirected aggression occurs and plays an important role in conflict management in other species of social fish that engage in dominance competitions between individuals of adjacent rank.

Figure 4.1a. There were fewer observed cases of redirected aggression (N = 136; indicated by arrow) than predicted by the null distribution generated by a randomization test (500 rounds, shown by histogram).
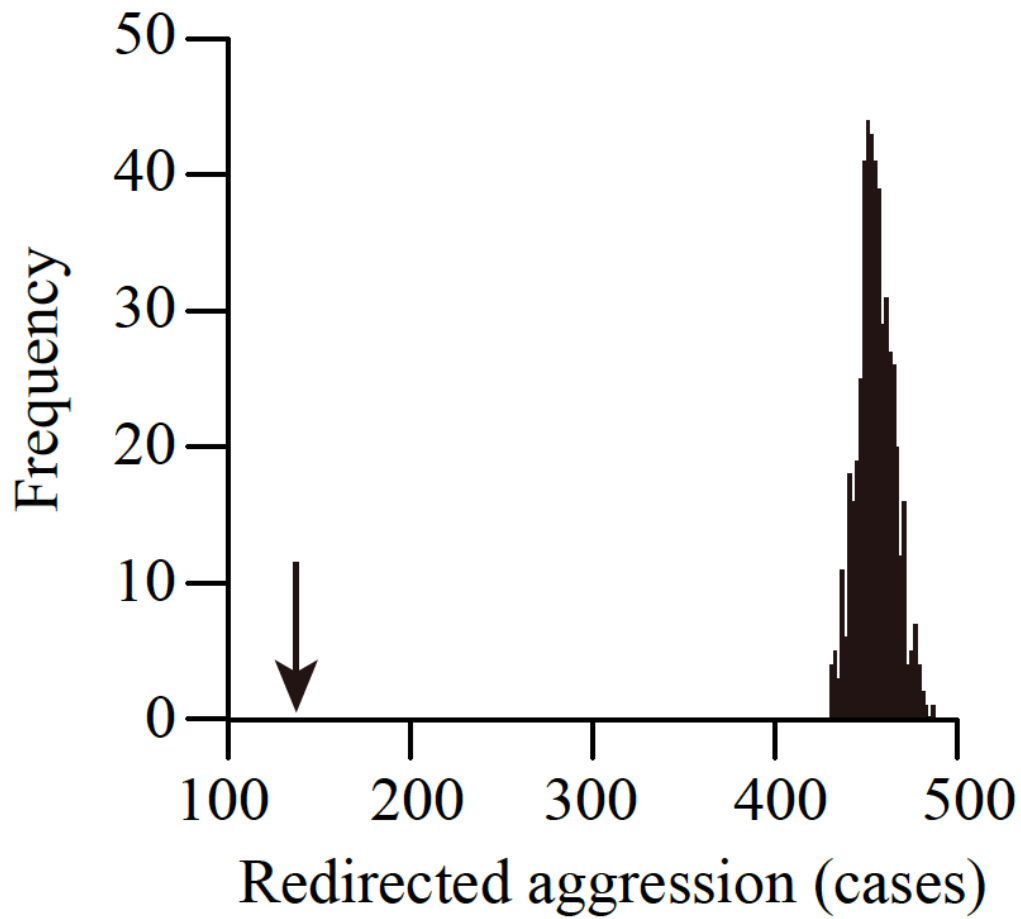
Figure 4.1b. Cumulative percentage of the timing of redirected aggression (observed: black line; simulated: grey line). The differences between predicted and observed values (observed − generated) are indicated by the red line. Inset shows the time window immediately after LM (0 to 10 seconds) to illustrate the lack of overlap between the observed and generated graph.
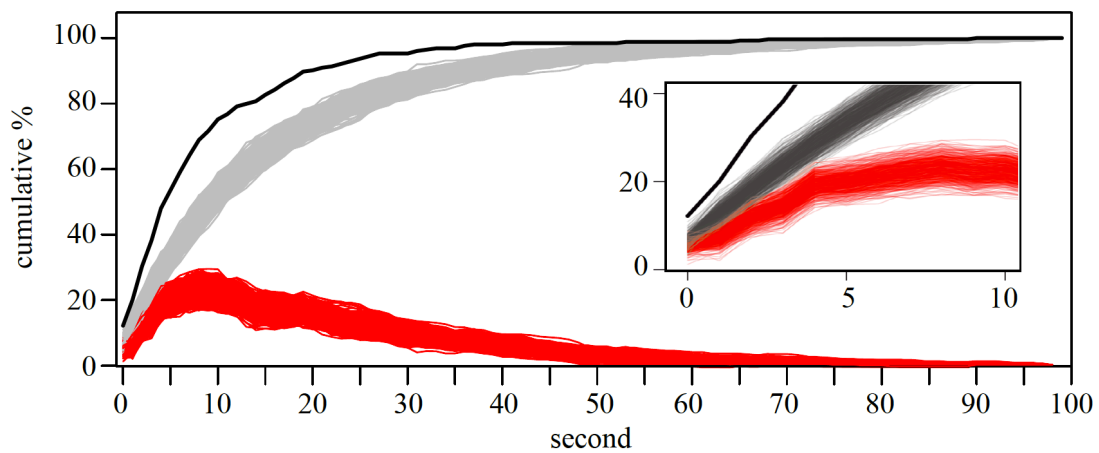
Figure 4.2. Mean proportions of data in which LS occurred. Data was classified into four types according to the aggression type and the occurrence of redirected aggression (RA).
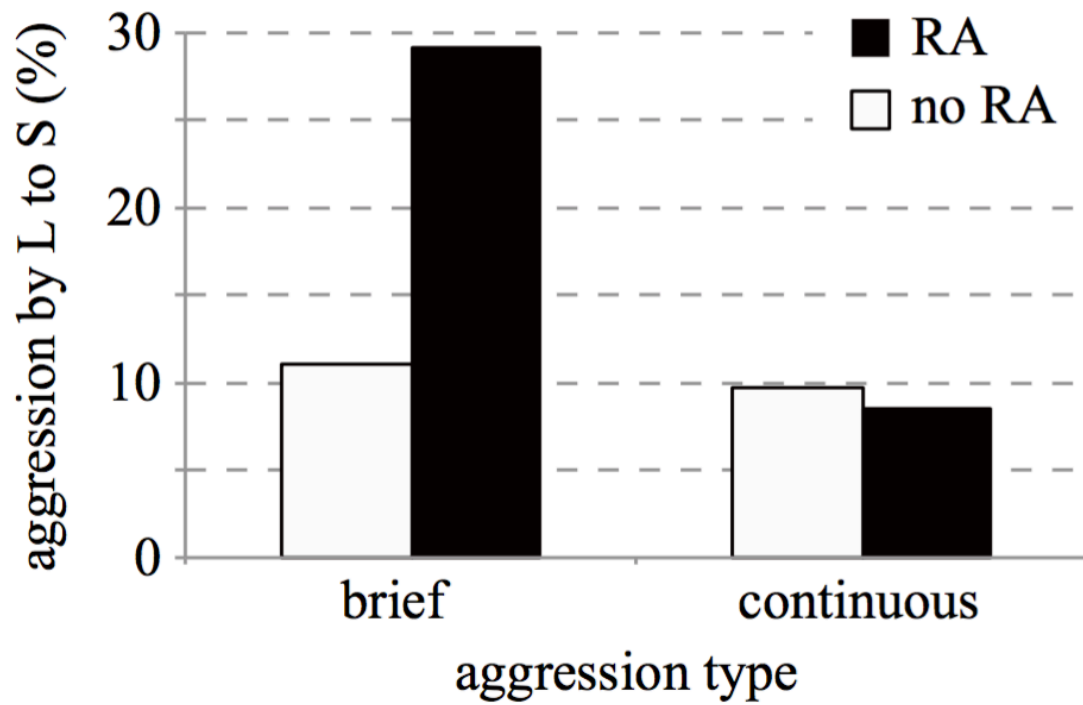
Figure 4.3. Timing of further aggression by an original aggressor (L) towards M in cases with and without redirected aggression (RA). Mean ± 1 SE was shown for two type of LM (i.e., continuous and brief aggression).
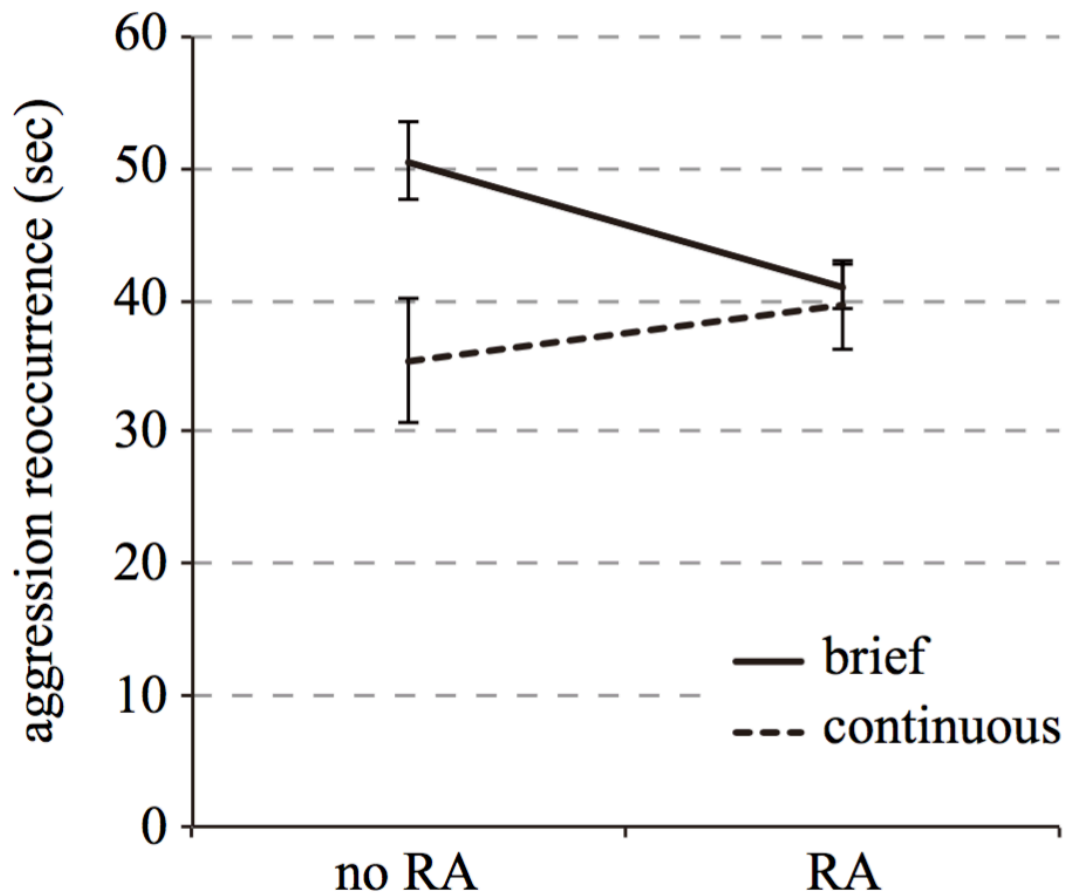
Figure 4.4. Proportion of S that attacked M. Each line indicates data from one experimental session. RA, redirected aggression.
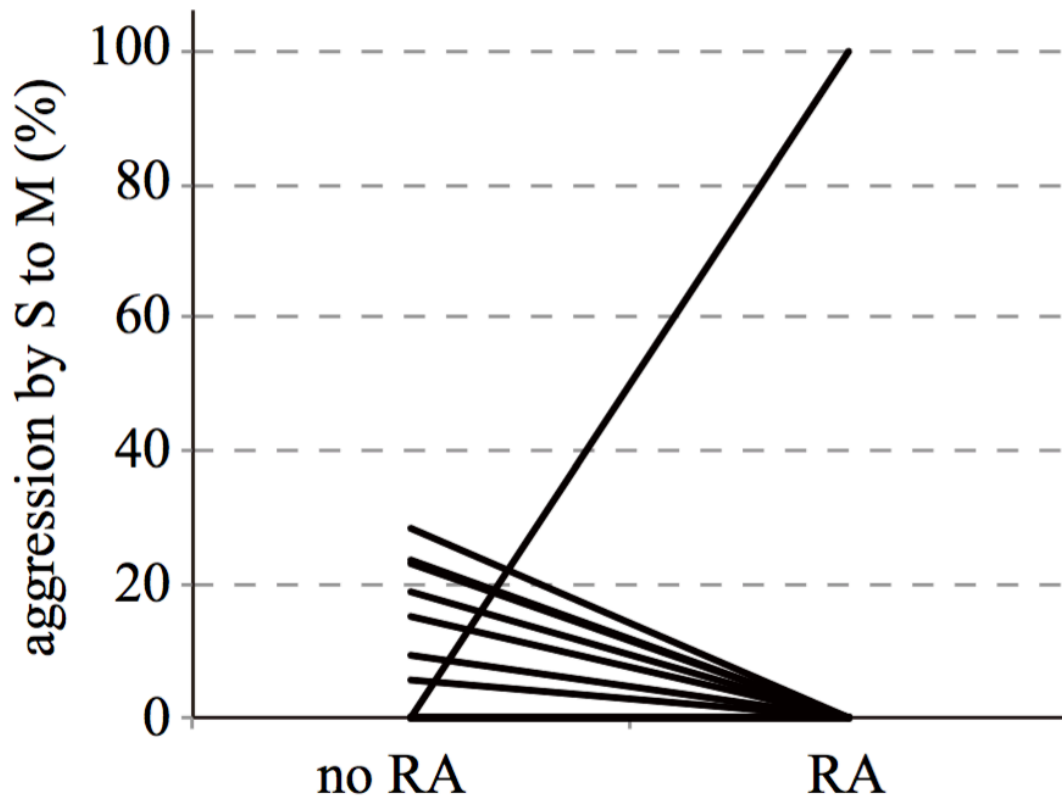
Chapter V. General discussion

This thesis investigated aggression and conflict management in social cichlid, *J. regani*, and found that those patterns reflected social characteristic of this species. This first study (Chapter III) provided detailed experimental data demonstrating that intrasexual aggression was more frequent and intense among females than males. This sex difference is possibly linked to the larger-sized female body size (Gonzalez-Voyer et al. 2008) and their mating system – i.e., facultative polyandry in which female coexistence is rare and helpers are more likely to be male than female in the same group (Yamagishi & Kohda 1996; Sunobe 2000). Female aggression might be a behavioral underpinning of cooperative polyandry and a behavioral consequence of intense intrasexual competitions and sex-role reversal.

In the second study (Chapter IV), I found that redirection aggression functioned to divert original aggressor's target toward a third-party individual and to prevent from being attacked by the third-party individual preemptively. These results augmented the concept of conflict management because redirected aggression has function of reducing costs of conflict among individuals. To the best of my knowledge, conflict management by redirected aggression has never reported in social fish. These findings are also supposed to relate to their social lives, i.e., group members repeatedly interact in a narrow crevice and form dominance relationships according to the body size. To alleviate costs of group living among individuals, social behavior such as redirected aggression must be beneficial for its actor. Note that not all individuals have benefits by redirected aggression as the recipient of redirected aggression (S) incurs costs of being attacked by the actor of redirected aggression (M) and further loses an

opportunity to attack the actor of redirected aggression (M). Therefore, this redirected aggression should be considered as selfish behavior even though it may stabilize dominance relationships and function to maintain group stability.

At the same time, however, not all of the results fit to the idea that species-specific characteristics shape aggression and conflict management. In the Chapter III of intrasexual aggression, the predicted sex difference was not consistently found in all analyses. In the Chapter IV, the occurrence of redirected aggression was affected neither by sex nor size difference (a proxy of conflict), which suggests that redirected aggression is a common behavioral repertoire in this species. There are two possibilities underlying these discrepancies. First, this study was conducted in a laboratory condition with spatial limitation and experimental settings of individuals' social encounters. These might have hindered or overemphasized their natural behavioral patterns. Second, the discrepancies might be caused by lack of our knowledge on this species in the wild. As discussed in Chapter II, only two studies were conducted in wild population of *J. marlieri*. Further studies may reveal factors that could explain the results of this thesis that seemingly disagrees with current knowledge of this species.

Overall, I conclude that the findings of this thesis add evidence of complex nature in fish societies. Social behavior can be a background for the evolution of cognition, and vice versa. Social intelligence hypothesis states that sophisticated cognitive ability and large brain size are an adaptation to a complex social context (Bshary et al. 2002, 2014; Holekamp 2007). Although studies of social intelligence

hypothesis have been mainly conducted in primates and corvids (Reader & Laland 2002; Emery 2006), recent studies began to reveal sophisticated cognitive abilities in social fish (transitive inference: Grosenick et al. 2007; Hotta et al. 2015; reconciliation: Bshary & Würth 2001; Soares et al. 2011; intervention: Schradin & Lamprecht 2000; facial recognition: Kohda et al. 2015; Hotta et al. 2017; reviewed in Bshary et al. 2002, 2014; Brown 2015). An interesting direction for further study would be an investigation of whether fish use redirected aggression as a more complex social maneuver, as has been observed in other taxa (kin-oriented revenge system; primates: Aureli et al. 1992; Watts et al. 2000; Tiddi et al. 2017; spotted hyenas: Engh et al. 2005). Although far less studied, investigation of redirected aggression will be fruitful for studying the presence of socially complex behavior in fish.

Based on my studies, two directions of future studies can be proposed. First, it is interesting to investigate proximate mechanisms (cf: Øverli et al. 2004) and cognitive abilities exhibited during complex social interactions such as redirected aggression in social fish. Second, studies of social behavior in different mating and/or social systems are required to fully understand the behavioral diversity in social fish. These studies will shed light on bidirectional relationship of (i) how species characteristics would affect the distribution and function social interactions and (ii) how social relationships with different quality would shape their social systems.

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Ethics Statement

This study was conducted according to Japanese laws and the animal research guideline of SOKENDAI (The Graduate University for Advanced Studies). The SOKENDAI Ethics Committee for Animal Research approved all research protocols (#2014A003). As mentioned, I paid special attention to the risk of severe aggression during the experiments. No fish were injured in this study.

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