



Original Article

The functional role of sibling aggression and “best of a bad job” strategies in cichlid juveniles

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Siblings often compete for limited resources, such as food provided by their parents. However, although several functions of nonlethal sibling (nonsiblicidal) aggression have been proposed, there is currently little empirical evidence for these, apart from food monopolization. Here, we investigated the functions of nonlethal sibling aggression in the biparental-caring territorial herbivorous cichlid *Varibilichromis moorii*. We found that the juveniles of this species are highly aggressive and that larger juveniles are more aggressive toward their smaller siblings. Larger juveniles feed on algae more frequently than smaller siblings, thereby indicating a dominance hierarchy. Sibling aggression decreased when algae in the nest was experimentally removed. Furthermore, the removal of smaller juveniles decreased sibling aggression among the remaining larger juveniles, whereas the removal of larger juveniles increased aggression among smaller juveniles. The algal feeding rate of juveniles only increased when larger individuals were removed from the nest. Moreover, larger juveniles attained higher growth rates and remained in natal nests longer than smaller individuals. Our results indicate that sibling aggression may facilitate the monopolization of resources by larger juveniles and extend the parental care period. Interestingly, a small subset of juveniles was observed to migrate to other nests. These juveniles were larger than those of the host brood, and their growth rate increased within the new nests. We suggest that subordinate juveniles may disperse from natal nests and sneak into new nests to enhance their rank, which may represent a novel example of a “best of a bad job” strategy associated with sibling competition.

Key words: dispersal, dominance hierarchy, food monopolization, Lake Tanganyika, parental care, *Varibilichromis moorii*

INTRODUCTION

In species with parental care, siblings often compete for limited resources (Hamilton 1963; Trivers 1974; Mock and Parker 1997; Roulin and Dreiss 2012). Various forms of sibling competition have been documented, including begging, scramble competition, and jockeying for position within nests (Mock and Parker 1997; Drummond 2001; Roulin and Dreiss 2012) and generally take the form as nonaggressive competition. In some species, however, it can involve overt aggression between siblings, such as pecking or biting (Mock and Parker 1997; Drummond 2001; Roulin and Dreiss 2012). In birds, such aggressive competition between siblings often has lethal consequences for subordinates (e.g., Brown et al. 1977;

Evans, 1996; Machmer and Ydenberg, 1998; Viñuela 1999). It is generally the monopolization of food resources by dominant chicks (often by directing aggression toward subordinates) that leads to siblicide (Cash and Evans 1986; Drummond and Chavelas 1989; Clifford and Anderdon 2001; Trillmich and Wolf 2008). For example, in great egrets, dominant chicks will peck at a subordinate chick until it stops competing for food when a parent arrives. In such instances, subordinates often succumb to starvation or fall out of nests in an attempt to evade the aggressive behavior by dominant chicks (Mock et al. 1987). However, although prevalent, sibling aggression does not invariably result in siblicide (Leonard et al. 1988; Hodge et al. 2007; Satoh et al. 2019), and more detailed studies of such cases are necessary to gain a more complete understanding of the diverse functions of nonlethal sibling aggression in animals.

In common with lethal sibling aggression, nonlethal aggressive interactions among siblings often involve competition for food

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provided by parents (Mock and Parker 1997; Drummond 2001; Roulin and Dreiss 2012). Dominant offspring can aggressively obstruct begging and/or feeding by subordinates in order to gain a larger share of the available food, thereby enabling them to grow to a larger size than subordinates at the time of fledging (Leonard et al. 1988; Mock and Parker 1997; Ploger and Medeiros 2004). In addition to food monopolization, several other functions of nonlethal sibling aggression have been proposed, although there is currently little empirical evidence to indicate the potential functional significance of this type of behavior (Hodge et al. 2007; Satoh et al. 2019). In family-living Siberian jays (*Perisoreus infaustus*), only dominant fledglings can prolong the period in which they remain in the natal territory, whereas subordinates are forced to disperse by aggressive competition with dominants (Ekman et al. 2002). Furthermore, several other functions of nonlethal sibling aggression have been proposed in birds and mammals, including the establishment of a future dominance hierarchy (Drummond 2006; but see Hodge et al. 2009), elimination of competitors for future reproduction (Frank et al. 1990; White 2005; but see Wahaj and Holekamp 2006), acquisition of priority for territory inheritance, and prolongation of the duration of parental care (Kokko and Johnstone 1999).

Although aggression among juveniles under parental care has been reported in some teleost fish species that show brood care behavior (Fraser et al. 1993; Kim et al. 2004; Satoh et al. 2019), quantitative studies on sibling competition are surprisingly limited in teleosts compared with other taxonomic groups (Roulin and Dreiss 2012). Here, we report clear evidence for the direct benefits of nonlethal sibling aggression in a substrate-brooding cichlid fish, *Variabilichromis moorii*, in Lake Tanganyika, Africa. *Variabilichromis moorii* is a territorial herbivorous cichlid inhabiting the rocky areas of Lake Tanganyika (Sturmbauer et al. 2008a). Individual fish of this species feed primarily on algae growing on the substrate and defend this resource from other vertebrate and invertebrate herbivores (Rossiter 1991; Karino 1997). Although both parents guard their juveniles against predators within their territory until dispersal, they do not directly provide food for their offspring (Rossiter 1991; Karino 1997). Furthermore, despite the fact that both sexes care for their offspring, multiple paternity often occurs within a brood (Sefc et al. 2008; Bose et al. 2018, 2019). Given that multiple paternity is an important factor promoting the evolution of severe sibling competition (Royle et al. 1999), this species is ostensibly a promising candidate for studies on sibling competition. Preliminary observations revealed that the juveniles of this species feed on algae and/or plankton within the parental territory and frequently display aggression toward their siblings (Satoh S, personal observation). Accordingly, in this study, we evaluated predictions pertaining to sibling aggression theory by focusing on the potential benefits of this form of aggressive behavior among *V. moorii* juveniles.

We initially examined whether sibling aggression in *V. moorii* functions to enhance the monopolization of food resources in a nest (the “food monopolization hypothesis”). We predicted that the larger dominant juveniles would acquire more algae and grow at a faster rate than smaller subordinates. If dominant juveniles gain priority access to food, they can prolong the duration of parental care (the “care prolongation hypothesis”) and, thus, we investigated whether the dominance hierarchy influences the timing of dispersal from the nest. Additionally, we attempted to monitor juvenile dispersal from natal nests using individually marked juveniles to assess whether a dominance hierarchy influences the distance of dispersal. Finally, we investigated whether subordinate juveniles would adopt a “best of a bad job” strategy. Despite the fact that the aggressive

behavior of dominants generally does not lead to direct subordinate mortality, reduced food intake in early life will impair certain fitness-related traits, such as growth rate (Stamps and Tanaka 1981), body size (Emlen et al. 1991), and immunocompetence (Saino et al. 1997). Therefore, subordinates should behave strategically in a way that enhances their fitness and/or reduces costs in detrimental situations. In this study, we provide evidence of a novel example of the “best of a bad job” strategy in subordinate *V. moorii* juveniles that experience sibling competition.

MATERIAL AND METHODS

Study species and general fieldwork methods

Variabilichromis moorii is a territorial herbivorous cichlid endemic to rocky shores located at the southern end of Lake Tanganyika in Africa (Karino 1998; Sturmbauer et al. 2008a). In contrast to the adults of this species, which are characterized by a black or dark body coloration, the juveniles are typically bright yellow (Kohda et al. 1996; Ochi and Awata 2009). After juveniles disperse from the parental nest, they tend to individually occupy small areas near the adult territories and retain their yellow body coloration until reaching approximately 50 mm in total length (Ochi and Awata 2009). The territories occupied by breeding pairs, which range in size from 1 to 4 m² (Sturmbauer et al. 2008b), tend to be characterized by an abundance of unicellular and filamentous algae and are defended by breeders against other herbivorous fishes (Karino 1998; Sturmbauer et al. 2008b).

Underwater SCUBA observations and experiments were conducted from September to November 2018 at Wonzye Point (8°4330'S, 31°0757'E) near Mpulungu in Zambia. The study site is located on a rocky reef at a depth of between 3.9 and 6.0 m, where breeding pairs of *V. moorii* are abundant. The areas defended by both parents were readily distinguished from other areas on account of the presence of a thick growth of algae (Ochi et al. 2017). We defined these algal-rich areas as “nests,” and for the purposes of the present study, selected 32 such nests, wherein juveniles of approximately 10 weeks of age were guarded by both parents, to facilitate observations of sibling competitions and perform experiments. We estimated the age of juveniles based on body size and the lunar cycle (Rossiter 1991). Among the 32 nests investigated, 10 were used for behavioral observations, growth analysis, and monitoring of juvenile dispersal, 8 were used for algal removal experiments, and in the remaining 14, we performed juvenile removal experiments. Of the 10 nests used for behavioral observations, 5 were haphazardly selected to examine the spatial distribution of juveniles.

Observations of juvenile behavior and analyses of growth and dispersal

To examine whether dominance hierarchies affect sibling aggression and feeding activities, we performed behavioral observations for 10 nests. Before conducting observations, all juveniles in the broods were caught using fine mesh hand nets and retained in small plastic bags perforated with fine holes. The mean number of juveniles in each nest (brood size) examined in this study was 13.5 (± 2.5 standard deviation, $n = 10$ nests). To minimize the effects of manipulation on the focal juveniles, body size measurements and elastomer tagging were performed underwater. Body size (standard length [SL]) was measured to the nearest 0.1 mm. The fish were individually identified by visual implant elastomer tagging (VIE tagging). We used fluorescent

red, blue, pink, orange, and green elastomer (giving 47 different color combinations), which was injected behind the dorsal and caudal fins of the left and right body flanks using a small syringe. Generally, the coloration of VIE tagging does not influence the sociality or survival rate of focal juveniles (Jungwirth et al. 2019). The marked juveniles were released back into the nest of origin and, on average, the time between capturing a given individual and subsequently releasing it was 3–5 min. On the basis of body size within broods, juveniles were classified into three categories. The largest 33% of juveniles were classed as large-sized juveniles (22.1–31.6 mm SL, $n = 42$ individuals from 10 nests), whereas the smallest 33% were classed as small-sized juveniles (18.1–24.2 mm SL, $n = 42$), and the remainder were designated medium-sized juveniles (20.1–27.4 mm SL, $n = 48$; [Supplementary Table S1](#)). These categories were used as a proxy for the dominance hierarchy index. Behavioral observations were performed on the following day and repeated 6 days after the measurement of body size. Thus, almost all juveniles were observed twice on two different days, the exceptions being five juveniles that were observed only a single time, owing to their disappearance between the first and second observations. During each 5-min behavioral observation, we recorded the number of occasions on which a focal juvenile acted as an aggressor toward siblings or was a recipient of sibling aggression ($n = 132$ juveniles from 10 nests). Aggressive behaviors were defined as physical contact, which involved collisions between two individuals. In this aggressive display, the aggressor approached the recipient at a high speed before collision, and this interaction sometimes included bites and rams. Although such aggressive behavior can include physical contact multiple times, the outcome is generally settled immediately. Thus, we considered successive aggressive events as a single aggressive behavior. Juveniles often show certain characteristic behaviors, such as operculum spreading, parallel swimming, and tail bending, which have been identified as submissive behavior in other Tanganyika cichlids (e.g., [Tanaka et al. 2015](#)). However, for the purposes of the present study, we did not specifically focus on these behaviors during observations. We also recorded the identity of the opponent with which the focal juvenile interacted. Juveniles of this species showed two types of foraging behavior; namely, either pecking at the rock surface to feed on algae or feeding on plankton in the water column several centimeters above the rock surface. To minimize potential disturbance during behavioral observations, the observer maintained a distance of approximately 2.0 m from the focal breeding nest.

Five of the nests used for behavioral observations were also used to investigate the home range of juveniles to determine whether dominance hierarchies within broods influenced their spatial distribution. Before conducting observations, using an underwater digital camera (OM-D EM1 Mark I; Olympus, Tokyo, Japan), we photographed the nest areas (including a ruler for scale) from an overhead view to create topographic maps for each nest. The digitized maps were printed on water-proof paper, and, using these maps, we traced the swimming tracks of individual juveniles for 5 min. The focal juvenile often moved rapidly to evade predators or sibling aggression. In such events, we temporarily discontinued tracing their home range and resumed tracing when the fish had returned to its original position. In the laboratory, we measured the home-range area of the focal juveniles using the digitized swimming routes plotted on the topographic maps (cm^2 , $n = 62$ juveniles from five nests in total). We also calculated the proportion of overlapping area (%) between the home ranges of juveniles and the nest area of their parents, as well as the distance (cm) between the centroid of the juvenile home range and that of the nest area occupied by its

parents. These measurements were performed using ImageJ 1.52q software ([Rasband 2018](#)).

Ten days after the first body size measurements were taken, we succeeded in recapturing 51.5% of the marked juveniles ($n = 68$ juveniles from six nests) from their nest and took further SL measurements to gain an estimate of growth rate. The juveniles were subsequently returned to their natal nests and, thereafter, we monitored the released marked juveniles at 2-day intervals to examine their dispersal (18–32 days from the first day of observation). Brood size was also recorded in these nests. We predicted that status in the dominance hierarchy should affect the dispersal patterns of siblings. Under circumstances in which marked juveniles in their natal nests could not be detected during a 5-min observation, we assumed that these individuals had dispersed from the nest or have been predated upon. If all juveniles had disappeared from the nest, this was taken to be indicative that the parents had finished parental care. In order to verify these assumptions, we undertook exhaustive searches for marked juveniles in the study area for 1 h or more each day. When we found marked juveniles at a site other than their natal nest, we assumed that these juveniles had dispersed and recorded movements in their new home range for 5 min and also measured the linear distance between its location and the center point of the original nest to the nearest 0.1 m. In total, we obtained dispersal data for 28% of the marked juveniles ($n = 38$ juveniles from six nests). Two nests were removed from subsequent analyses of growth rate and dispersal as all juveniles disappeared from these nests at the same time, whereas we were unable to obtain data from further two nests, owing to the fact that the observer (S.S.) was suffering from malaria during the designated period of observation.

We found that four juveniles from four different nests had migrated to another nest containing offspring cared for by different parents. These four juveniles were recaptured for body size measurement and subsequently released into the host nest. To compare the body size and growth of resident juveniles in these host nests with those of the four immigrants, we haphazardly selected five juveniles in each host nest, which were captured, tagged using elastomer, measured for SL, and then released into their nests ($n = 20$ juveniles from four nests). Ten days after taking measurements, the four invading juveniles were recaptured and SL measurements were taken to enable estimates of the growth rates of these juveniles in host nests.

Experimental removal of algae from nests

To establish whether juveniles aggressively compete for algae as a food resource, we conducted an alga removal experiment in eight nests and observed sibling aggression. Before algal removal, we videotaped several juveniles in each nest for 30 min using underwater video cameras (HERO5 or HERO6; GoPro, CA). Having made the video recordings, we removed algae from four of the eight nests using a scrubbing brush for approximately 5 min (algal removal experiment group). In the other four nests, we simulated algal removal from the nest area for 5 min using the same brush (control group). On the following day, we videotaped the aggressive interactions of juveniles in the eight nests for 30 min.

Five juveniles per recording were haphazardly selected to determine the number of aggressive interactions with siblings. Given that the juveniles were not individually identified in this experiment and that larger juveniles more frequently showed attacking behaviors than smaller individuals in the same nest, the total number of aggressive interactions recorded over 5 min in which juveniles were aggressors and/or recipients were used for analyses. In total,

we analyzed data obtained for 80 juveniles (five juveniles from each of the four experimental and four control groups before and after treatment).

Experimental removal of dominant and subordinate juveniles

To determine whether larger dominant juveniles aggressively monopolize algal resources and whether the foraging of smaller subordinate juveniles is restricted as a consequence of sibling aggression, we removed dominant or subordinate juveniles from their nests. For the purpose of this experiment, all *V. moorii* juveniles in 14 nests were captured, measured for SL, and tagged using elastomer. In seven nests, we removed subordinate juveniles, whereas in the other seven nests, dominant juveniles were removed. For both sets of nests, individuals removed from three nests were subsequently returned to the nests as control treatments. In the subordinate juvenile removal experiment, we observed the aggressive behavior against siblings and algal feeding of large-sized juveniles for 5 min in each of the seven nests. Following observations, we removed half of the juveniles (six–eight individuals) per nest using a hand net in ascending order of body size. In the four subordinate juvenile removal groups, captured juveniles were maintained in fine mesh plastic bags for 1 day until the end of the experiments. In the three control groups, captured juveniles were released soon after capture. On the day after the removal, we again recorded the behaviors of focal juveniles for 5 min. The juveniles retained in bags were carefully released back into their nests after the experiments. In the dominant juvenile removal experiment, we removed half of the juveniles (4–7 individuals) per nest in descending order of body size, after observing the behaviors of small-sized juveniles. The methods used for the dominant juvenile removal experiment were the same as those used for the subordinate removal experiment. In total, we observed 58 large-sized juveniles from seven nests for the subordinate removal experiment ($n = 36$ juveniles from four nests for the experimental group and $n = 22$ juveniles from three nests for the control group) and 54 small-sized juveniles from seven nests for the dominant removal experiment ($n = 30$ juveniles from four nests for the experiment group and $n = 24$ juveniles from three nests for control group).

Statistical analyses

Statistical analyses were performed using R version 3.6.3 (R Core Team 2020). All data were analyzed using generalized linear mixed models (GLMMs) to account for the repeated design of the study. For GLMMs with two or more random factors and small sample sizes, it is often difficult to precisely calculate the model parameters (Bolker et al. 2009) and, therefore, we used the Markov chain Monte Carlo (MCMC) method to calculate the parameters using the rstan package. For each model, three model chains were run for 500 000 iterations with a burn-in of 200 000 iterations and thinning intervals of 100 iterations. To evaluate the convergence of the model parameters, we assessed the mixing of chains visually and computed an index of convergence, the Gelman–Rubin statistical index (Gelman and Rubin 1992). If the index value was <1.01 , the model convergence was considered appropriate. We evaluated the significance of each model parameter by determining whether 0 was included in the 95% confidence intervals (CIs) for the intercepts between the three groups of large-, medium-, and small-sized

juveniles of the posterior distributions of coefficients of each explanatory variable.

We initially examined whether the rank of juveniles in the nest affected their spatial distribution. We constructed gamma GLMMs, in which nest ID was fitted as a random factor. Home range areas (cm^2), distance between the centroids of the home ranges and nests of parents (cm), and the proportion of overlapping areas between the home ranges of focal juveniles and their nests (%) were compared among large-, medium-, and small-sized juveniles.

To determine whether the rank of juveniles affected their aggressiveness and feeding behaviors, we constructed negative binomial GLMMs with the number of aggressive interactions in which a focal juvenile was an aggressor or recipient, or the number of feedings on algae on the rock surface, or the number of feedings on plankton in the water column, as response variables; the rank of juveniles (large, medium, or small sized) as a fixed variable; and juvenile and nest IDs as random variables (note that juvenile ID was nested by nest ID).

We also examined whether size rank affects the growth rate of juveniles and their dispersal. We constructed gamma GLMMs with growth rate per day (millimeters) and dispersal distance from a natal nest, and Weibull GLMM with duration of parental care period (days) as the response variables; the rank of juveniles (large, medium, or small) as a fixed variable; and nest ID as a random variable.

We observed the migration of four juveniles to another nest containing offspring cared for by different parents, and to determine whether immigrants attained a superior rank within a host nest, we compared the SL of immigrants and resident juveniles in the host nests. We constructed gamma GLMMs, which included juvenile ID as a random factor, the SL of juveniles as a response variable, and the type of juveniles (immigrant or resident) as a fixed variable. Additionally, to determine whether intruding juveniles gained benefits from a change of nest, we compared their growth rate in the periods before and after immigration to a new nest.

Furthermore, to investigate whether the amount of algae in nests affects the aggressiveness of juveniles, we compared the frequency of their aggressive behaviors in the periods before and after the removal of algae. We constructed a negative binomial GLMM, with the number of aggressive interactions (5 min per juvenile) as a response variable, treatment (removal or control group) and before/after treatment, including their interactions, as fixed variables, and the nest ID as a random variable.

Finally, to establish whether the experimental removal of subordinate and dominant juveniles from the nests affected the sibling aggression and algal feeding of juveniles, we constructed negative binomial GLMMs, in which juvenile and nest IDs were included as random variables. We fitted the frequency of aggressions or algal feeding by larger dominant or smaller subordinate juveniles as a response variable, and treatment (removal or control group), before/after treatment, and their interactions as fixed variables.

Ethical statement

No fish were killed during our observations or experiments. All experimental protocols were approved by the Animal Care and Use Committees at Osaka City University for Advanced Studies and adhered to the ASAB/ABS guidelines for the treatment of animals in behavioral research. Our field research in Lake Tanganyika was conducted with permission from the Zambian Ministry of

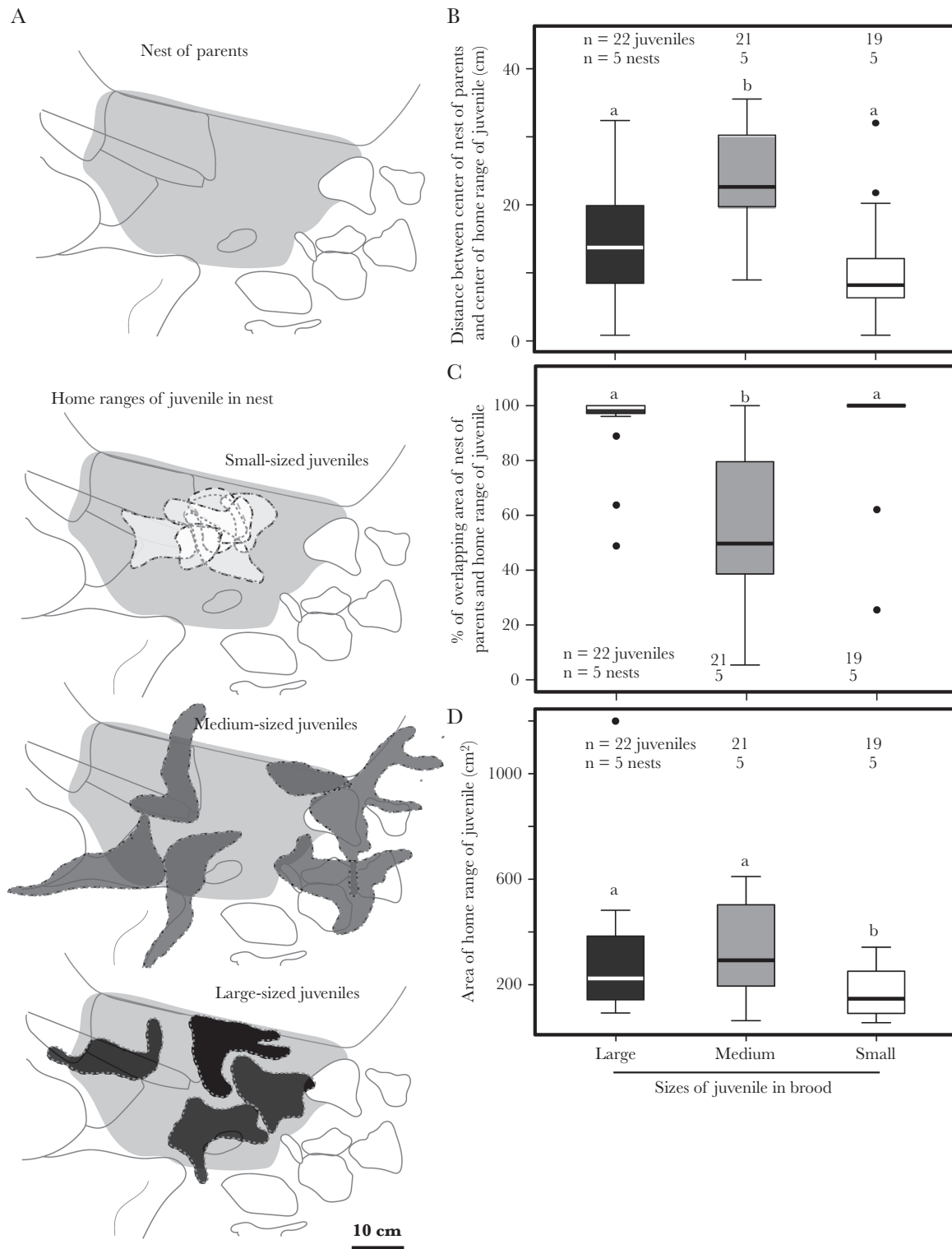


Figure 1

(a) A typical example of a *Variabilichromis moorii* parental nest and the home range of juveniles. The effect of size rank among siblings on (b) home range area, (c) distance between the center of the parental nest and home range of juveniles, and (d) percentage of overlapping area between the home range of juveniles with the parental nest. Boxes extend from the lower to the upper quartiles, the horizontal lines represent median values, and the whiskers extend to the maximum and minimum values. The sample sizes are shown above the error bars. Different letters indicate significant differences between size ranks, in which upper and lower 95% CIs did not include zero (see Table 1 for statistics).

Table 1

Summary of the results of statistical analyses using MCMC GLMMs. L, M, and S denote large-, medium-, and small-sized juveniles, respectively. Upper and lower values of 95% CIs that do not include zero are highlighted in bold

Response terms	Distribution	Lower and upper 95% CIs			Comparison
		L vs. M	L vs. S	M vs. S	
Distance between center of nest and home range	Gamma	0.091, 0.849	−0.733, 0.020	−1.207, −0.464	M > L = S
Percentage of overlapping area of nest and home range	Gamma	−0.777, −0.261	−0.265, 0.255	0.203, 0.847	M < L = S
Area of home range	Gamma	−0.018, 0.419	−0.592, −0.138	−0.809, −0.379	L = M < S
The number of sibling aggression	Negative binomial	−0.851, −0.232	−1.733, −0.978	−1.347, −0.390	L < M < S
The number of aggression received	Negative binomial	0.203, 0.180	0.935, 1.690	0.433, 1.008	L > M > S
The number of algae feeding	Negative binomial	−0.884, −0.447	−2.060, −1.542	−1.478, −0.883	L > M > S
The number of plankton feeding	Negative binomial	0.465, 0.760	0.625, 0.939	0.054, 0.278	L < M < S
Growth rate	Gamma	−0.635, −0.216	−1.259, −0.813	−0.851, −0.364	L > M > S
Parental care period	Weibull	0.288, 4.423	1.033, 5.577	−0.485, 1.553	L > M = S
Dispersal distance	Gamma	−1.048, 0.482	−0.565, 0.978	−0.223, 1.314	L = M = S

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RESULTS

Brood size, body size, and spatial distribution of juveniles in nests

In this study, we investigated 10 breeding nests of *V. moorii* (Supplementary Table S1), in which brood size ranged from 8 to 17 and the body size (SL in mm) of juveniles ranged from 18.4 to 32.5 mm. These juveniles were classified into three categories based on size: large-sized (22.1–31.6 mm SL, $n = 42$ individuals from 10 nests), medium-sized (20.1–27.4 mm SL, $n = 48$), and small-sized (18.1–24.2 mm SL, $n = 42$) juveniles (Supplementary Table S1).

Home range locations differed depending on the size rank of juveniles, with large- and small-sized juveniles generally being located in the central area of their parents' nests, whereas medium-sized juveniles were found at the outer edges (Figure 1a). The distance from the center of the juvenile home range to the center of the parents' nest (i.e., area centroid) differed depending on juvenile size rank, with distances being larger for medium-sized juveniles than those of the other two size classes (Figure 1b; Table 1). Similarly, the percentage of overlap between the juvenile home range and the parents' nest differed according to size rank, with the overlapping area being found to be larger for large- and small-sized juveniles than that for medium-sized juveniles (Figure 1c). Moreover, we found that the home range sizes of large- and medium-sized juveniles were larger than those of smaller juveniles (Figure 1d; Table 1).

Aggressiveness, feeding behavior, and growth of juveniles

We detected significant differences in the aggressiveness of juveniles toward siblings according to size rank, with large-sized juveniles being more aggressive and small-sized juveniles less aggressive than their medium-sized siblings (Figure 2a; Table 1). Consequently, large-sized juveniles were less likely to be attacked by their siblings, whereas small-sized juveniles were the most likely to be attacked (Figure 2b; Table 1). All juveniles foraged on benthic algae and/or plankton in the water column, although feeding patterns tended to differ according to size rank (Figure 2c,d), with the rate of algal feeding rate of large-sized juveniles being significantly higher than that of the other individuals, and medium-sized juveniles foraged

more frequently on algae than small-sized juveniles (Figure 2c; Table 1). The opposite trend was observed for feeding on plankton (Figure 2d; Table 1). During the period of parental care, we found that the body size of juveniles increased by 0.11 ± 0.05 mm per day ($n = 68$ juveniles from 10 nests) and that the growth rate of large-sized juveniles was greater than that of medium- and small-sized juveniles, although no significant difference was detected in the growth rates of medium- and small-sized juveniles (Figure 2e; Table 1).

Patterns of juvenile dispersal

The timing of juvenile dispersal from the natal nests was found to differ among the different size ranks (Figure 3). Small-sized juveniles dispersed from their natal nests significantly earlier than either medium- and large-sized juveniles, whereas large-sized juveniles tended to remain within these nests considerably longer than medium- and small-sized juveniles. With respect to the dispersal of large-, medium-, and small-sized juveniles, the median number of days before the end of parental care was 1, 7, and 13 days, respectively (Figure 3; Table 1). We also detected a high variability in the distance dispersed by the juveniles of different size rank, ranging from 1.0 to 52.8 m, although differences among the different size ranks were all nonsignificant ($n = 10$ large-sized, 14 medium-sized, 14 small-sized juveniles, respectively, from six nests; Table 1).

Similarly, for the four juveniles that migrated from their natal nest to another nest, the distance between the nests was found to be highly variable, ranging from 4.0 to 52.8 m (Table 2). All of these juveniles were of the small-sized category in their natal nest but were larger than the resident juveniles of the host nest (MCMC GLMM, 95% CIs = [3.38, 3.80], $n = 4$ nests; Table 2). Moreover, we observed that the growth rates of immigrant juveniles in host nests were significantly greater than they had been in their natal nests (95% CIs = [0.02, 0.13], $n = 3$ juveniles; Table 2).

Experimental manipulation of algal availability

The frequency of aggressive interactions among juveniles significantly decreased following the experimental removal of algae from nest, a trend not seen in the control nests (Figure 4; MCMC negative binomial GLMM, 95% CIs of experimental manipulation \times before and after treatment = [3.665 to 17.521]).

Removal of subordinate and dominant juveniles

In response to the removal of half of the juveniles in broods based on ascending order of body size, we observed a significant

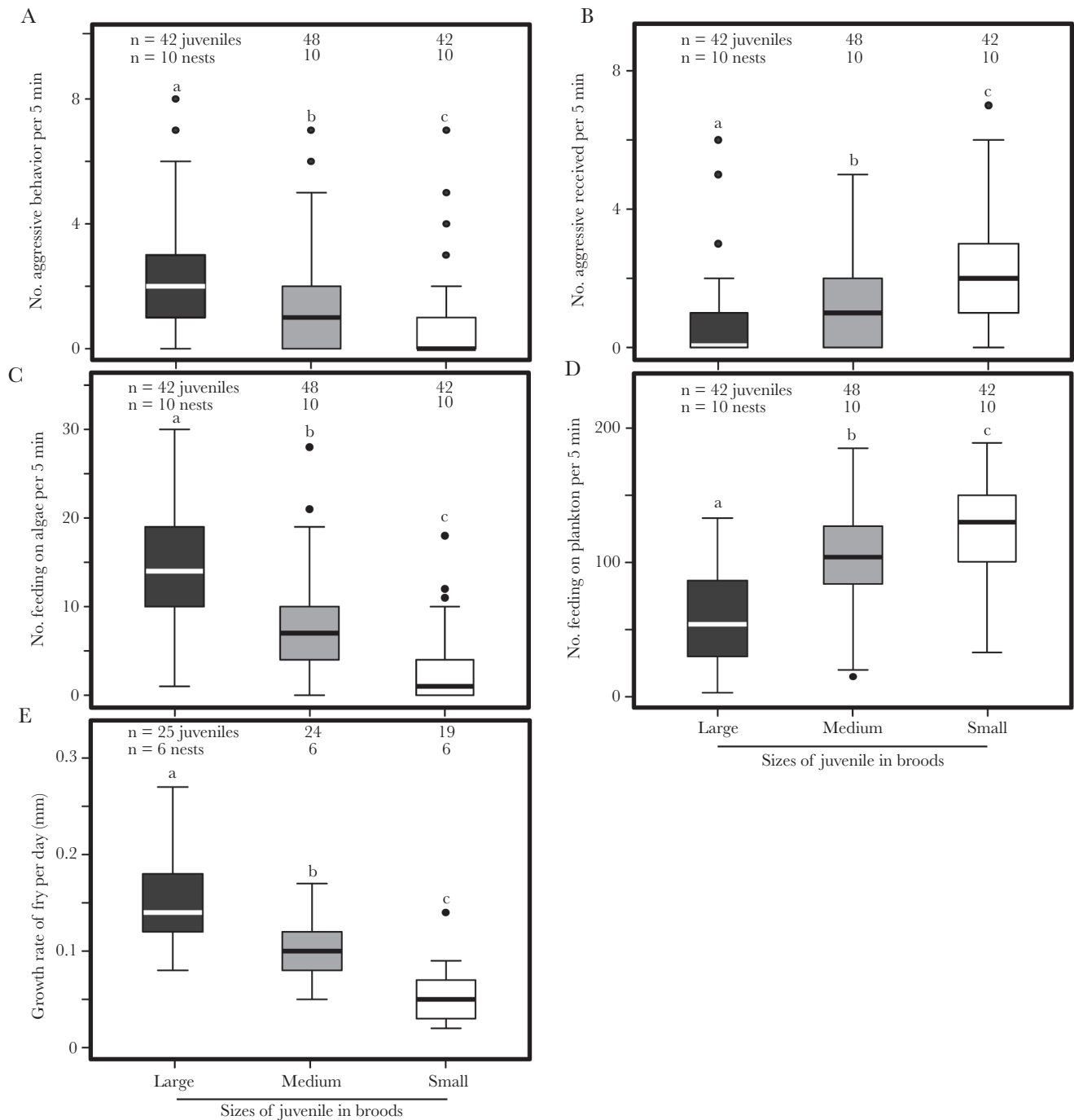


Figure 2

The influence of size dominance rank of *Variabilichromis moorii* juveniles on (a) the number of aggressive behaviors against siblings, (b) aggression received, (c) frequency of algal feeding, and (d) frequency of plankton feeding (e) per 5 min. The influence of size dominance rank among siblings on the growth rate of juveniles. Boxes extend from the lower to the upper quartiles, the horizontal lines represent the median values, and the whiskers extend to the maximum and minimum values. Sample sizes are shown above the error bars. Different letters indicate significant differences between size rank, in which upper and lower 95% CIs did not include zero (see Table 1 for statistics).

reduction in the frequency of aggressive behavior in the remaining larger juveniles, whereas the frequency remained unchanged in the control groups (Figure 5a; MCMC negative binomial GLMM, 95% CIs of experimental manipulation \times before and after treatment = [0.584 to 2.532]). However, experimental removal of smaller juveniles did not affect the rate of algal feeding by larger juveniles (Figure 5b; 95% CIs of interaction, experimental manipulation,

and before and after treatment = [−0.501 to 0.634], [−0.473 to 0.513], [−0.435 to 0.265], respectively).

In contrast to the results obtained for larger juveniles following the removal of smaller juveniles, the aggressive behavior of the remaining smaller juveniles remained unchanged, regardless of experimental manipulation (Figure 5c; MCMC negative binomial GLMM, 95% CIs of interaction and experimental manipulation

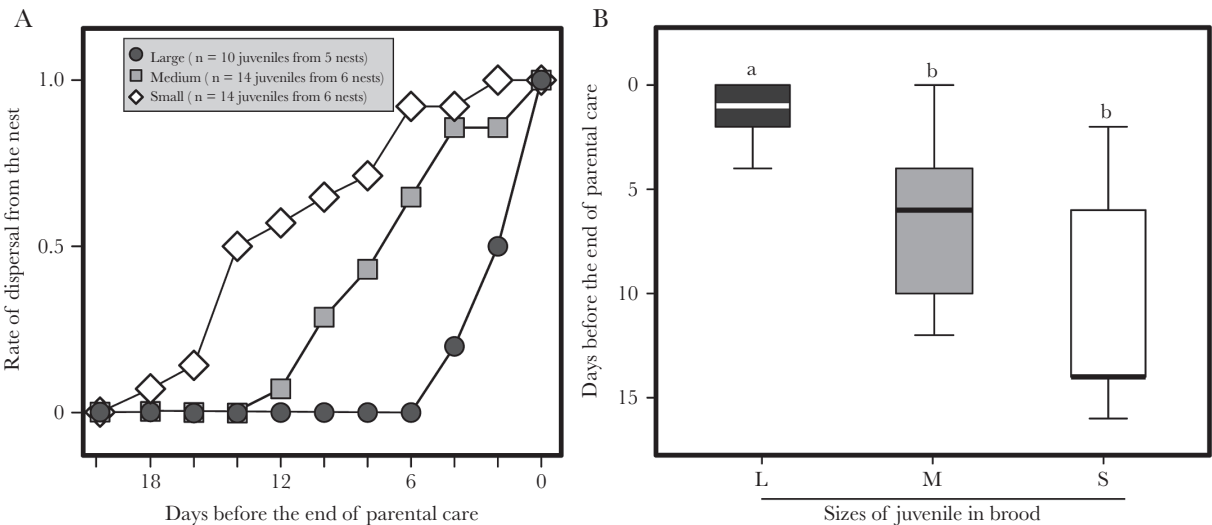


Figure 3 (a) Relationship between the rate of dispersal from the nest and days before the end of parental care. (b) The influence of size dominance rank among siblings on days before the end of parental care of *Variabilichromis moorii* juveniles. Boxes extend from the lower to the upper quartiles, the horizontal lines represent the median values, and the whiskers extend to the maximum and minimum values. Sample sizes are shown above the error bars. Different letters indicate significant differences between size rank, in which upper and lower 95% CIs did not include zero (see Table 1 for statistics).

Table 2
Data on *Variabilichromis moorii* juveniles that migrated from the natal nest and took up residence in a host nest. SL, standard length

Juvenile ID	Natal nest ID	Host nest ID	Growth rate in natal nest	Growth rate in host nest	SL of focal fry	SL of original fry in host nest	Distance between natal and host nest
2-19	2	α	0.03 mm	0.21 mm	22.2 mm	18.7 \pm 0.3 mm ($n = 5$)	30.6 m
4-5	4	β	0.03 mm	0.24 mm	22.1 mm	18.5 \pm 0.7 mm ($n = 5$)	4.0 m
5-1	5	γ	0.06 mm	0.19 mm	21.8 mm	18.2 \pm 1.0 mm ($n = 5$)	52.8 m
7-2	7	δ	No data	0.28 mm	21.1 mm	17.4 \pm 0.6 mm ($n = 5$)	5.5 m

= [−3.989 to 1.085], [−0.957 to 5.073], respectively). However, in response to the removal of larger juveniles, we found that the aggressive behavior of smaller juveniles increased after treatment in both experimental and control groups (Figure 5c; CIs = [0.065 to 4.130]), although the reason for this remains unclear. Furthermore, the frequency of algal feeding by smaller juveniles was observed to increase in response to the experimental removal of larger juveniles (Figure 5d; 95% CIs of experimental manipulation \times before and after treatment = [−4.194 to −1514]).

DISCUSSION

Although previous studies that have investigated the diversity of siblicidal species have identified the function and proximate and ultimate triggers of sibling aggression (Mock and Parker 1997; Cook et al. 2000; Gonzalez-Voyer et al. 2007), there have been few studies that have attempted to identify the function and ultimate cause of such aggressive behaviors in nonlethal species (Hodge et al. 2009; Satoh et al. 2019). In the present study, we performed field observations and experiments to examine the functional role of sibling aggression in juveniles of the territorial herbivorous cichlid *V. moorii* whilst still under parental care. Overall, our findings provide evidence in support of the two hypotheses that nonlethal sibling aggression in this species plays important roles in the monopolization food resources

and in extending the period of parental care. Additionally, by investigating the spatial distribution and dispersal patterns of juveniles, we identified a novel example of the “best of a bad job” strategy.

Food monopolization hypothesis

We observed that large-sized juveniles behave more aggressively toward their siblings than either medium- and small-sized juveniles, indicating that the juveniles of this species establish a dominance hierarchy among siblings. Additionally, it was found that large-sized juveniles forage more frequently on algae than do medium- and small-sized juveniles. Energy intake gained by juveniles when foraging on plankton would predictably depend on both the physical environment, including factors such as current direction and velocity, weather, and season, and the social environment, such as the number and status juveniles, which can affect the degree of sibling aggressiveness (Satoh et al. 2019). In contrast, once siblings have monopolized a certain area by defending it from the other juveniles, they can exploit the daily fresh growth of algae in defended patches, which presumably represents a beneficial foraging strategy for dominant juveniles in a brood. Indeed, in the early stages of development, during which plankton feeding is most important, *V. moorii* juveniles tend to be more tolerant toward their siblings (Satoh et al., in preparation). Our observations that the

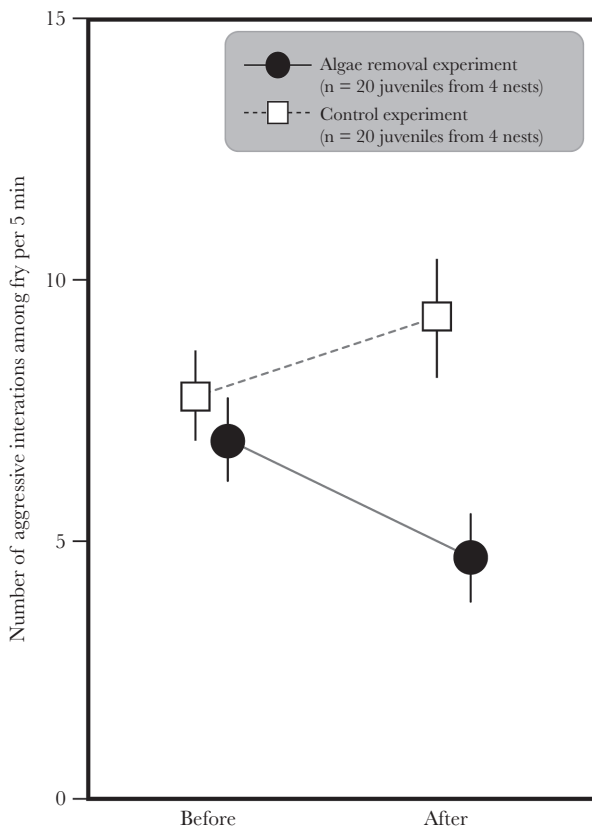


Figure 4

The effects of the experimental removal of algae on the number of aggressive interactions among *Variabilichromis moorii* juveniles in the field. Black and white plots show experimental ($n = 20$ juveniles from four nests) and control ($n = 20$ juveniles from four nests) groups, respectively. Plots with bars show the mean \pm SE.

dominant juveniles of *V. moorii* may aggressively defend algae in their own home range against siblings, which is akin to territorial defense, thus provides evidence in support of the food monopolization hypothesis.

In response to an experimental removal of algae in cichlid nests, we noted a significant reduction in sibling aggression. Ostensibly, this finding is contrary to expectations, given that food limitation is assumed to be the primary ecological factor driving the evolution of sibling competition in many mammals and birds (Mock and Parker 1997). This disparity could, however, be explained in terms of differences in the feeding ecology of juvenile fish. In the case of many birds, the chicks are highly dependent on food provided by their parents, and thus lack the option of switching food sources, even if availability is low (Mock and Parker 1997; Cook et al. 2000). However, unlike birds, the juveniles of *V. moorii* often have the opportunity to switch from algae to plankton when unable to gain access to the former. Similarly, in the Tanganyika cichlid *Neolamprologus furcifer*, the juvenile siblings of which compete for shrimps that gather in the female parent's nests, sibling aggression has been observed to become less pronounced when shrimps in the nest are experimentally removed (Satoh et al. 2019).

The findings of our juvenile removal experiments provide further evidence in support of the food monopolization hypothesis. We found that the experimental removal of smaller subordinates from their nests resulted in a significant reduction in aggression

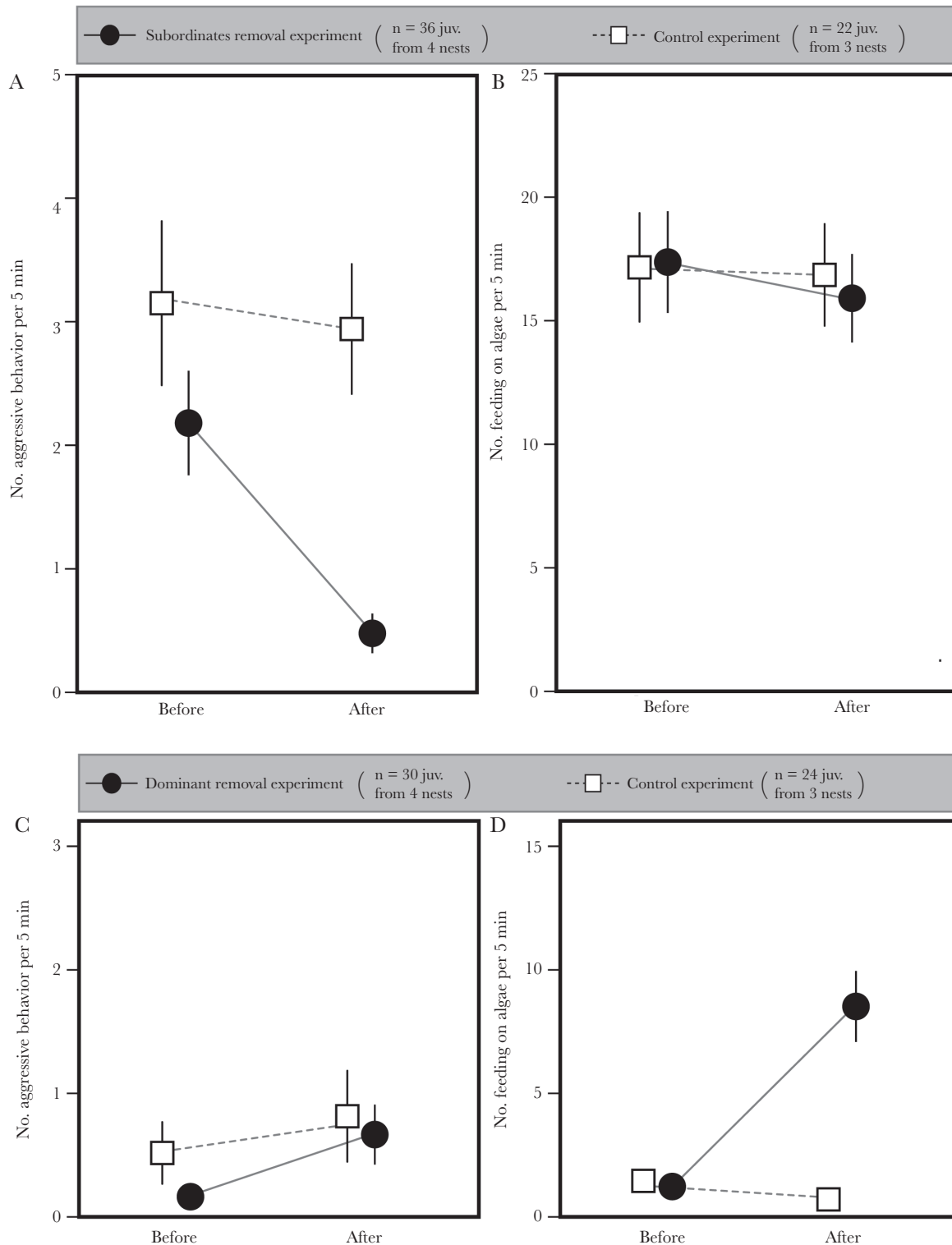
between larger dominants, although it did not have an appreciable effect on the rate at which these juveniles fed on algae. In contrast, the frequency of algal consumption, although not the extent of aggressive interactions, among subordinate juveniles increased when dominant juveniles were removed from the nest. These findings are consistent with the assumption that dominant juveniles drive away subordinates to monopolize algae, whereas subordinates cease feeding on algae as a consequence of the aggressive behavior of dominant juveniles. This also tends to be consistent with our observation that the growth rate of dominant juveniles was greater than that of subordinate juveniles. The monopolization of algae can contribute to accelerating the growth of juveniles and, in turn, increased growth can promote dominance. Consequently, sibling aggression in this species may serve as a means of monopolizing the algal resources in a nest.

Care prolongation hypothesis

We found that dominant *V. moorii* juveniles remained within the natal nest for a longer period of time than their subordinates. Given that algal resources tend to be more abundant in the nests of these fish than in the immediate surroundings (Karino 1998; Sturmbauer et al. 2008b), our observations indicate that juveniles may maintain a greater access to algae as a food resource if they can postpone dispersal from their natal nest. Moreover, juveniles would potentially be exposed to higher predation risks after dispersal (Hori 1983; Hori et al. 1993; Groenewoud et al. 2016; Tanaka et al. 2016). It is thus conceivable that dominant juveniles might aggressively evict subordinates from their natal territory, although we did not find any evidence of such behavior in the present study. There are, however, plausible alternative explanations for our findings, including the possibility that size-dependent dispersal of juveniles is determined by the behavior of parents rather than by sibling aggression. Although further verification is necessary in this regard, we speculate that, given that we obtained no evidence of parent–offspring aggression directed specifically toward small-sized juveniles, subordinate individuals may be evicted from natal nests as a consequence of their interaction with aggressive dominant juveniles (Satoh S, personal observation). In general, it is believed that dispersal in fish with brood care is determined by parental behavior (e.g., Yanagisawa 1987); however, our findings indicate that dispersal may not only be determined by parents but also by the dominance hierarchy among siblings.

“Best of a bad job” strategy in subordinate juveniles

The spatial distribution of juveniles in their natal nests was found to differ depending on their rank in the dominance hierarchy. Large-sized (dominant) juveniles generally occupied the central area of nests and fed on algae. Similarly, small-sized (subordinate) juveniles were also observed to congregate in these central areas, although they mainly foraged on plankton in the water column. We suspect that these feeding patterns may represent an example of a “best of a bad job” foraging strategy in subordinate juveniles, given that, if small juveniles enter into competition with larger dominant juveniles for algal resource, there is a high likelihood that they will be driven to the less optimal outer edges of the nest. In general, the risk of predation tends to be lower in the center of a school than on the periphery (Bumann et al. 1997) and, thus, juveniles foraging on algae at the outer edge of the nest are potentially at a greater risk of predation. Although swimming up in the water column to

**Figure 5**

The effects of experimental removal of smaller juveniles on the number of (a) aggressive behaviors against siblings and (b) frequency of algal feeding in *Variabilichromis moorii* dominant (large-sized) juveniles. The effects of experimental removal of dominant juveniles on the number of (c) aggressive behaviors against siblings and (d) frequency of algal feeding in subordinate (small-sized) juveniles. Black and white plots show the experiment and control groups, respectively. Plots with bars show the mean \pm SE.

feed on plankton may also heighten the risk of predation (Nagoshi and Yanagisawa 1997), foraging on plankton in the central area of the nest may represent a safer feeding strategy for subordinate juveniles than feeding on algae at the nest's periphery.

Interestingly, we also found that four small subordinate juveniles migrated from their natal nests to other nests. Although similar results have been reported in previous studies on *V. moorii* (Rossiter 1991; Bose et al. 2018) and *Neolamprologus caudopunctatus*

(Scheadelin et al. 2013), the reason why juveniles take up residence in another nest has yet to be determined. Alloparental care commonly occurs in mouth-brooding cichlids in Lake Tanganyika, where donor parents transfer their young to other brood-caring parents (known as brood mixing; e.g., Ochi et al. 1995). However, we only found single individuals dispersing to other groups and noted that dispersal distances tended to be large. Therefore, it appears unlikely that the dispersal of these four individuals was in some way mediated by parental behavior. However, we observed that the body size of the intruding juveniles was invariably larger than that of the resident juveniles in the invaded host nests, thereby indicating that this immigration may be a life-history strategy whereby subordinates in the natal nest assume the status of dominant juveniles in a host nest. Although this strategic dispersal between nests may incur potential costs for small juveniles, such as a heightened risk of predation during migration (Hori 1983; Hori et al. 1993) and the potential failure of intrusion and/or harassment by the host parents (Jordan et al. 2013), there may be greater benefits for subordinate juveniles in migrating than in remaining in the natal nest. Indeed, we found that the growth rate of intruding juveniles was higher in the host nests than in their natal nests in which they held a subordinate status. Having successfully dispersed, intruding juveniles may be able to exploit the resources of the host nest. At present, however, we have no data to indicate how many juveniles perish (e.g., through predation) when they vacate their natal nests. Consequently, we are currently unable to evaluate the strategic value of emigration and, accordingly, should exercise caution in interpreting our observations, given the very small sample size. Nevertheless, migration to another nest, as well as their specific foraging modes, may represent “best of a bad job” strategies for *V. moorii* juveniles when they rank low in the hierarchy of sibling rivalry.

CONCLUSIONS

In this study, we examined the functional role of nonlethal sibling aggression in the territorial herbivorous cichlid *V. moorii*. We established that dominant juveniles can gain benefits by monopolizing food and extending the period of parental care via aggressive behavior toward their siblings, whereas subordinate juveniles can strategically sneak into nests under the care of unrelated parents to increase their status in the dominance hierarchy. However, with regards to spatial distribution and the care prolongation hypothesis, we were unable to provide empirical evidence to indicate whether sibling aggression is associated with these phenomena. Additionally, the influence of the level of relatedness and sex of juveniles on the intensity of sibling aggression is an interesting factor warranting further study. *Variabilichromis moorii* is characterized by low breeding-male paternity despite both sexes caring for their offspring (Sefc et al. 2008; Bose et al. 2018, 2019). It is likely that the high frequency of extra-paternity promotes strong aggressive competition among juveniles in this species. Although several previous studies have examined the sex-dependent dispersal (Clarke et al. 1997; van Dongen et al. 2014) and territorial inheritance (Dierkes et al. 2005; Stiver et al. 2006) of cichlids, we were unable to determine the sexes of focal juveniles, owing to the difficulty of sexing in the field (Tanaka et al. 2015) and, accordingly, future studies should focus on whether the sex of juveniles affects sibling aggression in this species. The authors thank the members of the Maneno Tanganyika Research team and the Laboratory of Animal Sociology, Osaka City University, for

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SUPPLEMENTARY MATERIAL

Supplementary material can be available at *Behavioral Ecology* online.

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