

Aggression in closely related Malawi cichlids varies inversely with habitat complexity

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Abstract Within the past 2 million years, the cichlids of Lake Malawi have diversified into well over 500 species resulting in one of the worlds largest lacustrine fish radiations. As a result, many of the habitats within the lake support a high diversity of species. In these highly species rich communities, male cichlids must acquire and defend a territory to successfully reproduce. Within the rock-dwelling cichlids of Lake Malawi (mbuna), this has resulted in the formation of poly-specific leks on the heterogeneous rocky benthos. Aggression is fairly common in these leks and has been tied not only to individual reproduction but to the larger phenomenon of community assembly and the maintenance of biological diversity. In this study, I examined the patterns of aggressive acts of four species within the mbuna genus *Maylandia* at two locations in the southern Lake Malawi. The number of aggressive acts of two sympatric species was examined at each location. At each site, one species defends territories over bedrock and the other over cobble. The number of aggressive acts across the four species was compared. The influence of habitat type on male aggression was examined and the targets of male aggression were identified to evaluate several hypotheses concerning the evolution of male aggression. The results show that aggression quantitatively varied among species, was largely directed towards heterospecifics, and was

strongly influenced by habitat type. The aggressive behavior of one sympatric species pair, *Maylandia benetos* and *Maylandia zebra*, was observed under controlled laboratory conditions. Laboratory results support field observations: the bedrock associated species performed more aggressive acts and aggressive acts were directed equally at con- and heterospecifics. The results of this study suggest that habitat complexity plays a larger role in shaping aggressive behavior than other suggested factors such as competition for resources.

Keywords Mbuna · Aggressive behavior · Speciation · Habitat utilization · Lake Malawi · Metriaclima · Pseudotropheus

Abbreviations

Mc-cobble *Maylandia callainos*
Ma-bedrock *Maylandia aurora*
Mz-cobble *Maylandia zebra*
Mb-bedrock *Maylandia benetos*

Introduction

The cichlid fishes of Lake Malawi have undergone an extraordinary radiation since the formation of the lake 1–2 million years ago (Meyer 1993; Albertson et al. 1999). Adaptations to the different macrohabitats (Fryer and Iles 1972) and different diets (Liem 1991) have played an important role in the early

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diversification of Lake Malawi cichlid fishes, while the evolution of reproductive characters, specifically female mate preferences, male color pattern, and male reproductive behavior, are thought to have played a primary role in the diversification of the most closely related extant species (Danley and Kocher 2001).

Male aggression is one aspect of cichlid reproductive behavior that is gaining greater attention. Aggression is necessary for males to acquire and retain breeding territories (Holzberg 1978). Within the rocky habitats, this results in the establishment of year long poly-specific leks. Over and within the heterogeneous rocky benthos, males from as many as 40 species compete with each other to establish a territory from which they may approach and display to passing females. In most species of mbuna, if the male successfully attracts a female, she will follow him back to a breeding area typically located in the center of the male's territory. While there appears to be some species specificity to type of substrate males of different species utilize (Danley 2001), the highly heterogeneous environment of the benthos dictates that heterospecific males utilizing different rock types may occur in close proximity to one another. This may lead to potentially high levels of interspecific competition and aggression.

While male aggressive behavior may have arisen from the need to establish a platform from which males can court and mate, male aggression may serve several additional functions. Male aggression may be used to reduce the number of potential competitors for females by discouraging the presence of similarly colored males (Seehausen and Schluter 2004). Heavily defended territories develop 'algal gardens' which might provide trophic resources for females (Genner et al. 1999) thereby increasing the male appeal. Alternatively, male aggression may be a secondary consequence of selection on male vigor (Borgia and Coleman 2000) or may evolve in response to physical complexity of the habitat (Jensen et al. 2005). Physically simple habitats provide little cover for breeding and may expose a breeding pair to higher rates of predation, egg predation, or disruption from interlopers. Males in such habitats may need to increase their aggressive behavior to successfully secure their breeding territory relative to males breeding over more complex habitat.

Understanding the evolution and diversification of aggressive behavior of the mbuna will facilitate our understanding of the creation and maintenance of biological diversity while informing us of the role that

aggressive behavior may play in structuring species rich communities (Mikami et al. 2004). To this end, this study examines the aggressive behavior of four closely related species of Lake Malawi's rock-dwelling cichlids. Through an analysis of their behavior, I address several hypotheses concerning the evolution of aggressive behavior in the mbuna. These include several competition for resources hypotheses (mates, space, food). I find that the most comprehensive hypothesis takes into account the complexity of the habitat in which males establish territories.

Methods

Lake Malawi mbuna

Mbuna communities tend to be highly diverse; at this study's sites, territorial males could potentially interact with at least 10 other mbuna species. In these highly diverse communities, males must acquire a territory to successfully breed (Holzberg 1978). Within any given territory, the physical features of the substrate define multiple breeding areas and, generally, the male will choose one such area as the focus of his territory. In doing so, the male prevents both con- and heterospecific males from utilizing many of the remaining, unoccupied breeding areas within his territory. The necessity of male territory acquisition, the high diversity of these communities, and the presence of multiple potential breeding sites per territory provide conditions that may generate interspecific aggression.

Field analysis

Study species

This study focused on the behavioral ecology of two species at each of two separate communities (Fig. 1): Thumbi West Island (14° 01'27.58" S 34°49' 25.55" E) and Mazinzi Reef (14° 7'55.98" S 34° 56'38.87"E). These sites are located in the southwest and southeast basins of the lake, respectively. Mbuna communities at each location are extremely diverse. Ribbink et al. (1983) identified 43 species of mbuna at Thumbi West Island and at least 10 mbuna species occur at Mazinzi Reef (Danley, pers. obs.). At each location, a number of different habitat types can be identified (fields of boulders >2 m in diameter, areas of rock-sand interface,

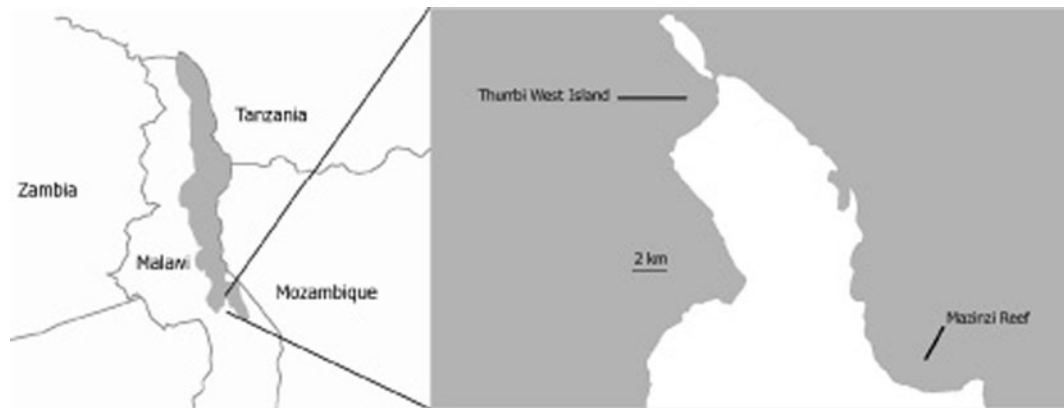


Fig. 1 Map of Malawi and inset of study area

etc.) Of these habitat types, the study species typically occupied habitats dominated by either a bedrock or cobble. Bedrock habitat consisted of flat stretches of continuous bedrock occasionally pocked by dislodged strata. Cobble habitat contained areas of rocks 20–100 cm in size. Bedrock is a relatively simple habitat; it is generally uniform save for the closed ended caves created by the dislodged strata. Cobble, in contrast, is topographically complex and possesses ample interstitial areas beneath and between individual rocks. Behavioral observations at Thumbi West Island focused on *Maylandia callainos* ($N=20$, designated *Mc-cobble*), which occupy territories over cobble, and *Maylandia aurora* ($N=18$, *Ma-bedrock*), which tend to mate in cracks in the bedrock. At Mazinzi Reef, behavioral observations focused on one cobble dwelling species, *Maylanida zebra* ($N=15$, *Mz-cobble*), and one bedrock inhabiting species, *Maylandia benetos* ($N=15$, *Mb-bedrock*). At each location, each focal male defended a territory within 2 m of a heterospecific focal male to control for encounter rates.

Data collection

Aggression data was collected by four observers familiar with mbuna reproductive behavior (PDD, T. D. Kocher, M. Kidd, R. C. Albertson). No measure of inter-observer error was made. A focal male was observed for 10 min. During this period all aggressive acts were scored. An aggressive act consisted of the focal male rapidly pursuing a target individual until that individual fled the focal male's territory. In addition to the number of aggressive acts performed, the gender, genus, and species (when possible) of the target were noted.

Data analysis

Counts of aggressive acts were \log_{10} transformed to achieve a normal distribution. Bartlett's and Levene's Tests were used throughout to confirm normality and homoscedacity of the data (data not shown). Non-parametric test were used when the data was not normally distributed after transformation. An analysis of variance (ANOVA) was performed to determine if significant differences existed in the number of aggressive acts performed by each species. A Tukey's post hoc test was used to identify significant differences between individual species. Wilcoxon tests were used to compare the number of aggressive acts directed towards conspecifics versus heterospecifics as these data were not normally distributed after transformation. Similarly, Wilcoxon tests were used to compare the number of aggressive acts directed towards mbuna versus non-mbuna species. An analysis of covariance (ANCOVA) was used to examine the hypothesis that bedrock species performed more aggressive acts towards non-mbuna species while controlling for overall frequency of aggressive acts; the total number of observed aggressive acts was used as a covariate in this analysis. Bonferroni corrections for multiple comparisons were used when appropriate.

Laboratory analysis

The aggressive behavior of two species, *Mb-bedrock* and *Mz-cobble*, was studied under controlled laboratory conditions. A male of a given species was introduced into a 37.85 l (50.8 cm × 25.4 cm × 30.48 cm) aquarium. Within this aquarium, a 10.16 cm (diameter) terracotta

pot was placed in the male's tank to serve as a territorial focus. This pot was inverted and had a hole cut into its side to allow the focal male access to the interior of the pot. Along one side of this aquarium, a separate but clearly visible 37.85 l aquarium containing 4 conspecific females was placed. The focal male was allowed to acclimate with visual access to the female tank for at least 24 h. During testing, an opaque divider was inserted between the male and the female tanks.

To assess male aggressive behavior, a stimulus male was introduced into the focal male's tank. The stimulus male was housed in a 20 cm×20 cm×20 cm clear plastic cube with a mesh lid. This allowed the stimulus and focal males to interact visually, chemically, and acoustically, but prevented physical interaction and the resulting bodily injury. The stimulus male enclosure was placed within 30 cm of the center of the focal male's aquarium. The focal male's aggression was assessed during two 30 min trials. During one 30 min trial, the focal male was exposed to a conspecific male. During the alternative 30 min trial, the focal male was exposed to a heterospecific male. The order of exposure of stimulus males (con- versus heterospecific) was randomized. Both 30 min trials were run within 15 min of each other.

All stimulus males were either *Mb-bedrock* or *Mz-cobble*. All males for the lab study were of approximately equal size (mean standard length ±SD: *Mb-bedrock*=103 mm ±9.5; *Mz-cobble* 102.5 mm ±8.35). The standard lengths of focal and stimulus male never differed more than 3 cm in any given trial. Both stimulus and focal males were at least the 5th generation of laboratory reared *M. benetos* and *M. zebra* offspring of wild caught individuals collected from Mazinzi Reef.

Ten males of each species were observed and the frequency of two aggressive behaviors, bite and quiver, were recorded during a 30 min observation period. The 'bite' behavior consisted of the focal male trying to bite that target male through the enclosure wall. During the 'quiver' behavior, the focal male positions himself parallel to the target male's enclosure, erects his dorsal, pectoral, and anal fins, and rapidly quivered his rigid body while remaining stationary in the water column. Both bite and quiver displays have been observed in the aggressive interactions of both species in the field. A Kruskal-Wallis test was used to test the hypothesis that the species differ in the frequency of their aggressive acts. Wilcoxon Signed Ranks tests were used to test the

hypotheses that within each species conspecific aggression was equivalent to heterospecific aggression.

Results

Field analysis

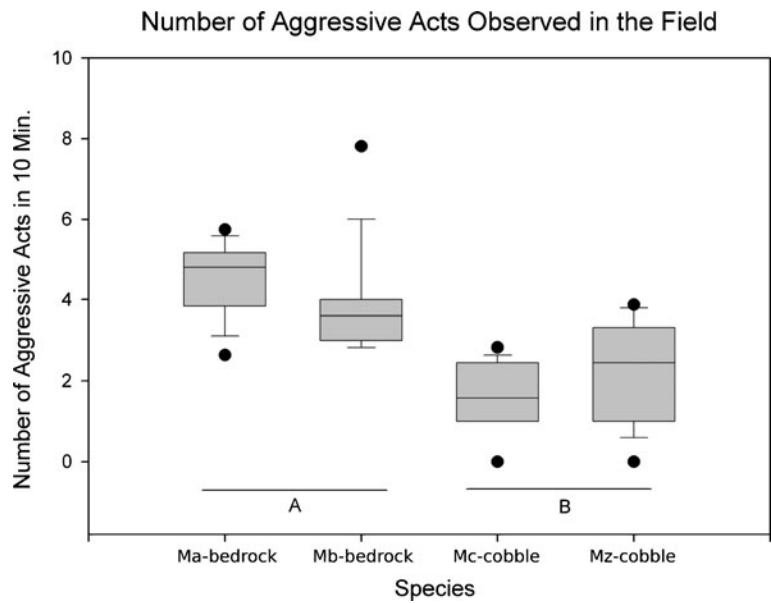
Species varied in the number of aggressive acts performed during the 10 min focal watches (Fig. 2; $F=31.41$, $df=3$, $p<0.001$). *Ma-bedrock* exhibited the greatest number of aggressive acts per 10 min observation (21.27 ± 7.44 (mean±standard deviation)). *Mb-bedrock* was also highly aggressive (15.93 ± 13.13). *Mz-cobble* (6.07 ± 5.33) and *Mc-cobble* (3.35 ± 2.50) exhibited the fewest average number of aggressive acts per focal observation. Post hoc analysis revealed that $(Mc-cobble\sim Mz-cobble)<(Ma-bedrock\sim Mb-bedrock)$ (Table 1).

Both *Ma-bedrock* and *Mb-bedrock* directed a greater number of aggressive acts towards heterospecifics than conspecifics (Fig. 3; *Ma-bedrock* Wilcoxon $V=0$, $p=0.0002$, *Mb-bedrock* paired Wilcoxon $V=0$, $p<0.001$). *Mz-cobble* also performed a greater number of aggressive acts towards heterospecifics (Fig. 3; paired Wilcoxon $V=8$, $p=0.009$). *Mc-cobble* was the only species to show a greater number of aggressive acts directed towards conspecifics. However this difference was not statistically significant (Fig. 3; Wilcoxon $V=73.5$, $p=0.61$). The numerical abundance of heterospecifics has likely contributed to the elevated number of aggressive acts directed towards heterospecifics during the focal observations.

Because interspecific competition for space is likely to be high within the mbuna, the number of aggressive acts directed towards all mbuna species, the broadest category of likely competitors for space, was compared to the frequency of aggressive acts towards non-mbuna. Both *Mz-cobble* and *Mc-cobble* performed significantly more aggressive acts towards mbuna versus non-mbuna species (Fig. 4; *Mz-cobble* paired Wilcoxon $V=9.5$, $p=0.0125$; *Mc-cobble* Wilcoxon $V=7$, $p=0.0006$). The number of aggressive acts directed towards mbuna and non-mbuna species was not statistically different in *Ma-bedrock* (Fig. 4; Wilcoxon $V=75$, $p=0.66$) or *Mb-bedrock* (Fig. 4; Wilcoxon $V=82$, $p=0.068$).

Species preferred habitat has a significant effect on the number of aggressive acts that were performed. *Ma-bedrock* and *Mb-bedrock*, which perform the

Fig. 2 Box plot of the number of aggressive acts observed during 10 min observations in the field for each of the study species. Horizontal lines indicate species whose number of aggressive acts were statistically indistinguishable. Letters identify species pairs with significantly different numbers of aggressive acts at $p < 0.0001$



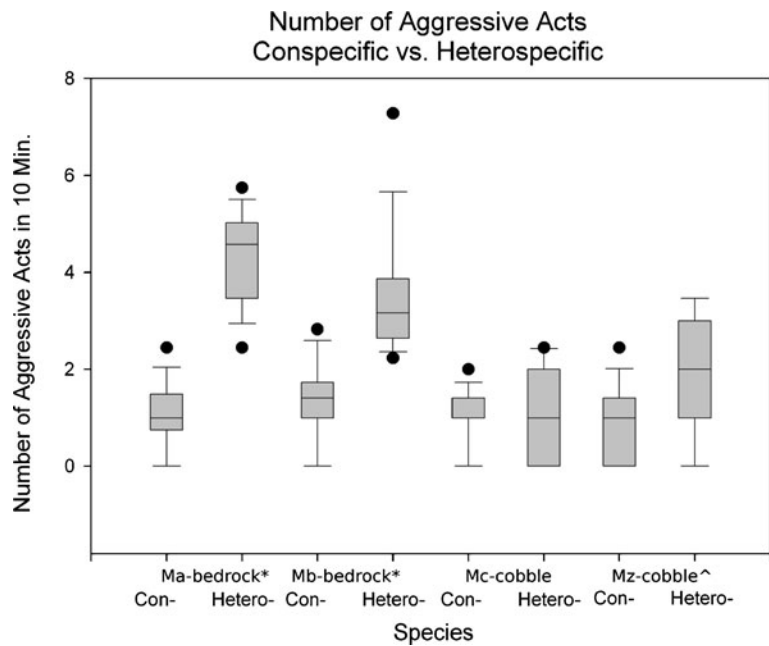
greatest number of aggressive acts, predominantly inhabit territories over cracked bedrock. In contrast, *Mz-cobble* and *Mc-cobble*, perform fewer aggressive acts and predominantly inhabit territories in cobble. Not only do the bedrock inhabiting species perform more aggressive acts in general, but their aggressive behavior appears to be preferentially directed towards non-mbuna. To decouple the influence of overall frequency of aggressive acts from the number of aggressive acts directed towards non-mbuna, an analysis of covariance (ANCOVA) was performed using the total number of aggressive acts as a covariate. Using ANCOVA, I found that bedrock inhabiting species perform more aggressive acts towards non-mbuna than cobble inhabiting species ($F=138.7$, $df=2$, $p < 10^{-16}$).

Table 1 P values of pairwise comparisons of mean aggressive levels of all four species using a Tukey’s post hoc test. The significance levels, after performing a Bonferroni correction for multiple comparisons, equaled $p_{0.05/6}=0.0083$ and $p_{0.01/6}=0.0016$. Significant comparisons are in bold

	Ma-bedrock	Mb-bedrock	Mc-cobble	Mz-cobble
Ma-bedrock	1.0000			
Mb-bedrock	0.3669	1.0000		
Mc-cobble	< 0.0001	< 0.0001	1.0000	
Mz-cobble	< 0.0001	< 0.0001	0.4891	1.0000

I compiled the five most frequent targets of aggressive acts for the four species included in this study (Table 2). *Ma-bedrock* and *Mb-bedrock* directed most of their aggressive acts towards unrecognized non-mbuna or *Protomelas teanolatus*, a herbivorous cichlid belonging to Lake Malawi’s sand-dwelling clade that often feed on the algae covering the rocks. The remaining targets for both species consisted of non-territorial mbuna (a class that consists of both females and males potentially attempting to acquire a territory) or conspecific males. Unidentified non-mbuna species were, as a single group, the most frequent target of *Mz-cobble* male aggression (22%), though 51% of aggressive acts were directed towards mbuna species: *Pseudotropheus tropheops* spp. (non-territorial) (15%), *Mb-bedrock* (non-territorial) (14%), *Mz-cobble* (non-territorial) (13%), and *Mz-cobble* (male) (9%). The majority of *Mc-cobble* aggressive behavior was directed towards male (27%) and non-territorial (18%) conspecifics. 19% of *Mc-cobble* aggressive acts were directed toward other rock-dwellers: *Mz-cobble* (male) (12%) and *P. tropheops* spp. (non-territorial) (7%). 16% of *Mc-cobble* aggressive acts were directed towards unidentified non-mbuna. It is worthwhile to note that aggression towards predators was an extremely rare event. Of the 780 aggressive acts observed in this study, only 3 aggressive acts were directed towards known predators or egg predators.

Fig. 3 Box plot of the number of observed aggressive acts directed towards con- and heterospecific individuals for each of the four species over a 10 min observation period. (*) indicates a statistically significant difference in con-versus heterospecific aggressive acts at the $p < 0.001$. (^) indicates a statistically significant difference in con-versus heterospecific aggressive acts at the $p < 0.0125$



Laboratory analysis

In the laboratory, as in the field, *Mb-bedrock* was more aggressive than *Mz-cobble*. *Mb-bedrock* performed a greater number of quivers than *Mz-cobble* (Fig. 5; *Mb-bedrock* 77.5 ± 51.95 ; *Mz-cobble* 6.6 ± 9.01 ; Mann–Whitney $U = 97.00$, $p = 0.0004$). *Mb-bedrock* also

performed a greater number of bites than *Mz-cobble*, though this difference was not statistically significant (Fig. 5; *Mb-bedrock* 121.30 ± 79.52 ; *Mz-cobble* 103.2 ± 113.07 ; Mann–Whitney $U = 60.00$, $p = 0.45$).

In the lab, as in the field, *Mb-bedrock* performed more aggressive acts towards heterospecifics than conspecifics. Heterospecifics were more frequently

Fig. 4 Box plot of the number of observed aggressive acts directed towards mbuna and non-mbuna individuals for each of the four species over a 10 min observation period. * indicates a statistically significant difference in mbuna versus non-mbuna aggressive acts at the $p < 0.001$. ^ indicates a statistically significant difference in mbuna versus non-mbuna aggressive acts at $p = 0.0125$

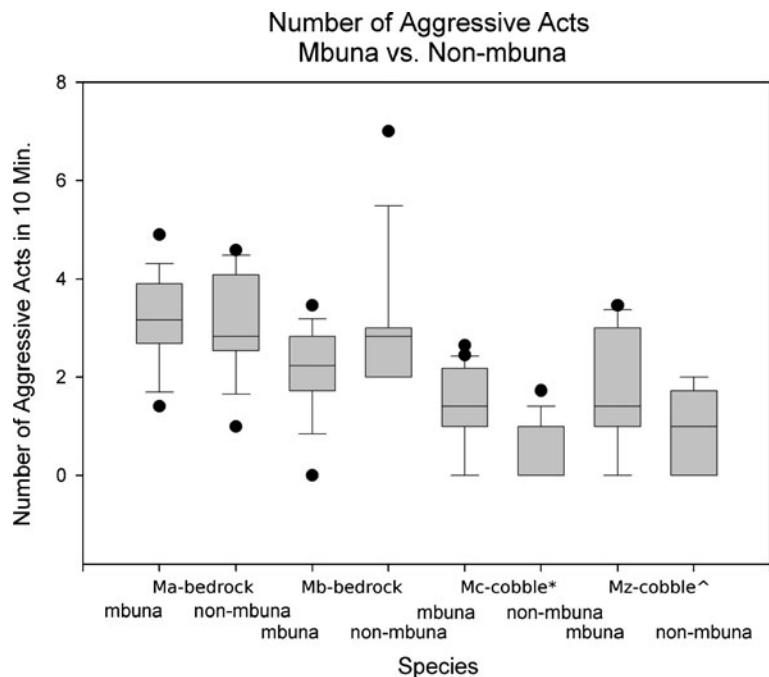


Table 2 The five most frequent targets of aggression for each of the study species. The observed aggression directed towards known predators is also presented. The numbers following each group indicates the total numbers of aggressive acts directed

toward members of the group during all focal observations. The number in parentheses is the percentage of the total number of targets that belong to each group

Ma-bedrock		Mb-bedrock		Mz-cobble		Mc-cobble	
<i>P. taenolatus</i> (non-mbuna)	95 (25%)	Other	126 (52%)	Other	20 (22%)	<i>M. callainos</i> —male	18 (27%)
Other	86 (23%)	<i>P. taenolatus</i> (non-mbuna)	31 (13%)	<i>P. tropheops</i> spp.—non male	14 (15%)	<i>M. callainos</i> —non male	12 (18%)
<i>M. zebra</i> —non male	59 (15%)	<i>Mb-bedrock</i> —non male	26 (11%)	<i>M. benetos</i> —non male	13 (14%)	Other	11 (16%)
<i>P. tropheops</i> spp.—non male	44 (12%)	<i>P. tropheops</i> spp.—non male	18 (8%)	<i>M. zebra</i> —non male	12 (13%)	<i>M. zebra</i> —male	8 (12%)
<i>M. aurora</i> —males	20 (5%)	<i>M. benetos</i> males	14 (6%)	<i>M. zebra</i> —male	8 (9%)	<i>P. tropheops</i> spp.—non male	5 (7%)
Predator	2	Predator	0	Predator	0	Predator	1

the target of bites (Fig. 6; heterospecific 79.9 ± 55.87 ; conspecific 41.40 ± 35.26 ; $Z=2.19$, $p=0.02$). *Mb-bedrock* also directed the majority of their quivers towards heterospecifics but difference was not statistically significant (Fig. 7; heterospecific 45.4 ± 30.72 ; conspecific 32.10 ± 37.58 ; $Z=1.007$, $p=0.31$). *Mz-cobble* directed its bites (Fig. 6; heterospecific 46.7 ± 56.71 ; conspecific 56.50 ± 70.85 ; $Z=0.65$, $p=0.51$) and quivers (Fig. 7; heterospecific 2.0 ± 2.94 ; conspecific 4.6 ± 7.5 ; $Z=0.89$, $p=0.37$) equally towards conspecifics and heterospecifics.

Discussion

In the species-rich, density-high cichlid communities found in Lake Malawi’s rocky habitats, male aggressive behavior could serve a variety of functions. Competition for conspecific females (Seehausen and Schluter 2004), access to breeding territories (Dubois and Giraldeau 2005), and/or competition for trophic resources (Genner et al. 1999) may lead to aggressive behavior. Aggressive behavior may be a result of sexual selection on male vigor (Borgia and Coleman

Fig. 5 Box plot of the number of aggressive acts observed during 30 min laboratory observations of *Mb-bedrock* and *Mz-cobble*. Two behaviors were scored, bite and quiver. *Mb-bedrock* performed more quivers than *Mz-cobble*. * indicates a statistically significant difference between *Mb-bedrock* and *Mz-cobble* at $p=0.001$

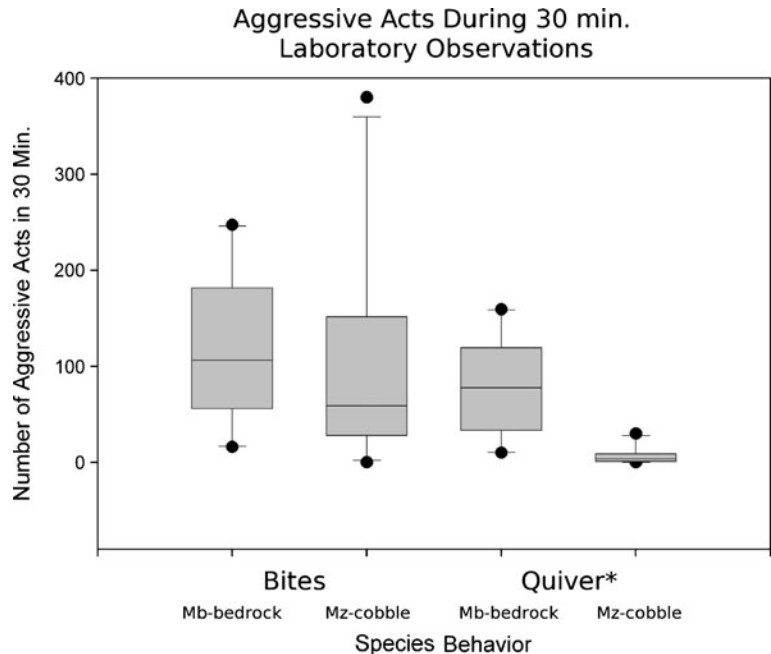
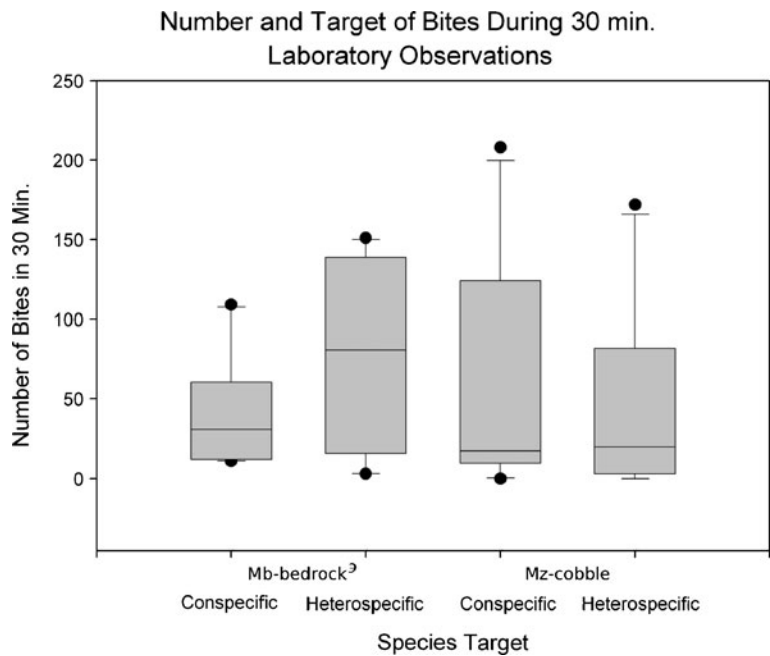


Fig. 6 Box plots of the number and targets (conspecific or heterospecific) of *Mb-bedrock* and *Mz-cobble* bites. *Mb-bedrock* performed more bites towards heterospecifics than conspecifics. \ominus indicates a statistically significant difference in the number of bites at $p < 0.02$

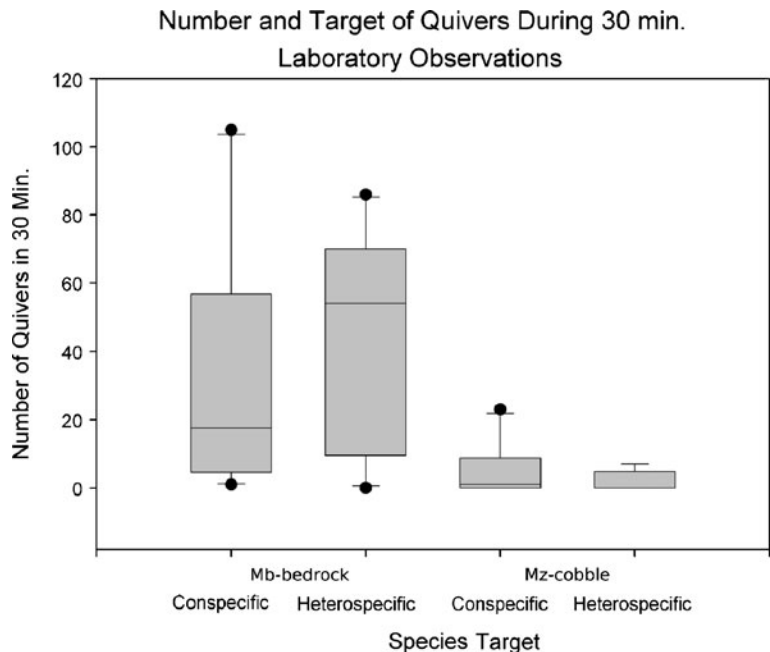


2000), or may evolve in response to habitat complexity and the increased/decreased exposure to predation or interference (Jensen et al. 2005). Below, I discuss how the results of this study provide limited support for many of these hypotheses.

The least aggressive species in this study, *Mc-cobble*, directed the majority of its aggressive behavior towards

conspecifics particularly conspecific males. This observation supports the competition for mates hypothesis. However, *Mc-cobble* was the only species observed to direct its aggressive behavior towards conspecifics. This finding suggests that competition for mates does not drive the majority of aggressive behavior within the rock-dwelling cichlids of Lake Malawi.

Fig. 7 Box plots of the number and targets (conspecific or heterospecific) of *Mb-bedrock* and *Mz-cobble* quivers. No statistical difference was detected in the number of con- versus heterospecific quivers in either species



In contrast, *Mz-cobble* directed the majority of its aggressive acts towards other mbuna. This observation supports the hypothesis that competition for territories in these species-rich communities is high. It remains unclear why *Mc-cobble* does not exhibit similar levels of mbuna-specific aggression. The hypothesis that competition for territories as a primary driver of male aggression, while supported by *Mz-cobble*, is not supported by the remainder of the species, suggesting that competition for space does not drive the majority of aggressive behavior in the mbuna.

The two most aggressive species, *Ma-bedrock* and *Mb-bedrock*, directed the majority of their aggressive acts toward non-mbuna species. This behavior contradicts expectations based on the competition for mates or competition for space hypotheses. This behavior may be consistent with competition for trophic resources hypothesis, though it is unclear why *Mz-cobble* and *Mc-cobble* species are not competing for resources with these non-mbuna species as well.

These ‘competition for resources’ hypotheses fail to provide a comprehensive explanation for the patterns of aggressive behavior exhibited by these closely related species. An examination of the microhabitat in which these species are found provides more complete explanation of their behavior.

These species can be grouped into two sympatric species pairs. Within each pair one species inhabits exposed bedrock and is more aggressive, the other lives in cobble and is less aggressive. These observations are consistent with aggressive behavior evolving in response to habitat complexity. In less complex habitats, territorial borders lack geographic markers, such as the edges of rocks, and may be less well defined. As a result, these less well defined territories may require a higher frequency of aggressive acts to enforce territorial boundaries.

Territories in less complex areas also provide less cover for reproduction. All of the studied species are maternal mouthbrooders. Females transfer eggs from their urogenital opening to their mouth by first depositing the eggs briefly on the substrate during reproduction. During this time, the eggs may be highly vulnerable to predation. The rocks in the territories of the cobble breeding species likely provide protection for the female’s eggs. Species that breed on bedrock may compensate for the lack of protection offered by their territories through an increased aggressive level. Greater aggressive activity by individuals inhabiting less com-

plex habitat has been observed in Neotropicals cichlids (Barley and Coleman 2010; Kadry and Barreto 2010). The observations presented here suggest that habitat complexity and aggressive behavior may be correlated across cichlids in general.

Sexual selection, via female choice, may have exaggerated male aggressive behavior in the bedrock dwelling species beyond the aggressive level that is established through natural selection alone (Humphries and Ruxton 2001). The role of sexual selection in the divergence of male aggressive behavior has yet to be examined. I propose that male aggressive behavior may provide both direct benefits through egg protection and indirect benefits through transmitting genes that confer highly vigorous offspring. Additional studies are needed to evaluate this hypothesis.

The differences in aggressive behavior between two of the species, *Mz-cobble* and *Mb-bedrock*, were observed in progeny of individuals reared in a common lab environment for several generations. The results of the lab work supports the observations made in the field: bedrock species are more aggressive, and their aggressive behavior is often directed toward heterospecifics. Confirmation of these observations in the lab were important since the lab environment allows for the control of several factors that are difficult to control in the field: encounter rates, size discrepancy, and developmental environment. In the lab experiments, males of both species had equal opportunity to interact with con- and heterospecific males thereby removing any effect of encounter rate that may have influenced the observations in the field. Likewise, in the lab focal males and target males were matched for standard length which removed the effect of body size on aggressive acts that could not be controlled in the field. Finally, the fish used in the lab studies had been raised in a ‘common garden’ and derived from stocks raised in a ‘common garden’ for several generations. This indicates that male aggression is under genetic control and may be a heritable target of natural and/or sexual selection.

The results of this study suggest many conclusions. Competition for limiting resources such as mates or food may account for some species aggressive behavior as suggested by previous studies. However, habitat complexity may play a larger role in dictating aggressive behavior in the rock-dwelling species than has been previously thought. In addition, aggressive behavior appears to be a heritable character that may

have evolved in response to both natural and sexual selection.

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