Asymmetric interspecific territorial competition over food resources amongst Lake Malawi cichlid fishes

Atsushi Maruyama^{1*}, Bosco Rusuwa² & Masahide Yuma¹

¹Faculty of Science and Technology, Ryukoku University, Yokotani 1–5, Seta-Oe, Otsu, Shiga 520-2194, Japan ²Department of Biology, Chancellor College, University of Malawi, Zomba, Malawi Received 18 March 2009. Accepted 8 October 2009

The rock-dwelling cichlids in Lake Malawi comprise the most diverse freshwater fish community in the world. Individuals frequently interact with heterospecifics through feeding territoriality. Underwater observations and experiments were conducted to examine interspecific variation in the frequencies of territorial behaviour and its influence on the feeding habits of heterospecifics. Frequencies of chasing and fleeing associated with interspecific territoriality were remarkably different amongst 10 cichlid species. In addition, individual fish that attacked heterospecifics more frequently were attacked less often by them, suggesting that interspecific interactions amongst cichlid species are asymmetric. The experimental removal of territory owners belonging to the most aggressive species resulted in almost fivefold increase in feeding within territories, suggesting that territorial aggression preserves food resources for the territory holder and influences the feeding habits of other species, including those with some dietary dissimilarities. Additional information regarding asymmetric interspecific interactions would improve understanding about how diverse cichlids within trophic groups manage to coexist.

Key words: interspecific aggression, feeding territoriality, Lake Malawi, cichlid fish.

INTRODUCTION

Over the last few million years, Lake Malawi cichlids have evolved into the most diverse community of endemic fishes in the world (Reinthal 1993). The rocky littoral zones of this lake contain densities of up to 22 species of cichlid and more than 500 individuals in a 50 m² area (Ribbink et al. 1983a). Most of these cichlids feed on algal mats composed of attached algae and microbes. It has been hypothesized that the diversity of these cichlids is maintained by fine niche partitioning in feeding strategies and microhabitats (e.g. Marsh & Ribbink 1985; Reinthal 1990). On the other hand, niche overlaps amongst cichlids have been reported from the field (e.g. Genner et al. 1999a). Fryer (1959) proposed that interspecific resource competition had little impact on cichlid populations that are limited by predation. Genner et al. (1999b) referred to a possibility that speciation is happening at such a rapid rate in Malawian cichlid community that individuals of some species are acting as ecological equals and competitive exclusion has not had sufficient time to operate between closely related cichlids that diverged rapidly (after Hubbell 2001).

The feeding habits of these cichlids appear to be organized by social ranks within the community, which are associated with interspecific territoriality (Ribbink & Eccles 1988). Therefore, territoriality in these cichlids has attracted ecologists, who have investigated how diverse cichlids within trophic groups manage to coexist given interspecific competition (Ribbink et al. 1983a; Kohda 1995; Genner et al. 1999b). Males of most cichlids are territorial, possessing three types of territories for different purposes (Kohda 1995; Genner & Turner 2005). First, the mating territory is guarded against conspecific males to facilitate mating with conspecific females. Heterospecifics are allowed to intrude and forage in these territories. Second, the feeding territory tends to be guarded against conspecifics and heterospecifics that feed on similar foods. These territories are usually smaller than the mating territory, and sometimes overlap with feeding territories of heterospecifics with different diets. The spawning territory (nest) is usually the smallest of the three territories. Territory owners chase all fish away from spawning territories probably to protect current and future spawning.

^{*}Author for correspondence. Present address: School of Biological Sciences, University of Queensland, St Lucia, Brisbane, 4072 Queensland, Australia. E-mail: maruyama@rins.ryukoku.ac.jp

Amongst the three territory types, feeding territories are considered most likely to promote or reduce interspecific competition and resource control amongst cichlids (Genner *et al.* 1999b).

Based on qualitative observations, Ribbink et al. (1983) reported that the levels of interspecific aggression associated with feeding territories in Malawian cichlids varied amongst species. One would expect from this report that the influence from a neighbouring territory owner on the feeding habits of a focal territory owner is variable according to the relative aggressiveness of the neighbour and the focal owner. In other words, the importance of interspecific interactions may be spatially heterogeneous, even in a community, reflecting the local distributions of each species. Thus, quantitative investigations of interspecific variation in the aggressiveness associated with feeding territoriality will further our understanding of the structure of cichlid communities.

The objective of this study was to quantitatively describe feeding territoriality amongst cichlids in the rocky littoral zones of Lake Malawi. Underwater observations were used to investigate species differences in the frequencies of interspecific aggressive interactions. The effect of feeding territoriality on feeding by other cichlids was also examined through the experimental removal of territory owners that belonged to the most aggressive species.

MATERIALS & METHODS

Study sites and cichlid communities

Lake Malawi is located at the southernmost end of the Great Rift Valley in Africa. The lake has a surface area of approximately 30 800 km² and a maximum depth of approximately 700 m. Quantitative observations of territorial behaviours were conducted in the rocky littoral area (locally called 'Ketche', 14°02' S, 34°81' E) of Thumbi West Island in Lake Malawi National Park. Experimental removals of territory owners were carried out in the rocky littoral area (11°60'S, 34°30'E) near Mayoka village in Nkhata Bay. Observations and experiments were both performed using scuba in areas that were approximately 10×10 m. The depth of both areas was targeted at 3–7 m, where cichlid diversity is highest (Ribbink et al. 1983; Genner et al. 2004). Rocks that were 50–100 cm in diameter dominated the substrates.

The rock-dwelling cichlids of Lake Malawi (locally called 'mbuna') comprise more than 200 putative species (Ribbink *et al.* 1983).

Forty-four and 34 of them occur at Thumbi West Island and Nkhata Bay, respectively. Species compositions of both areas are given in Ribbink *et al.* (1983).

Interspecific interactions

Frequencies of chasing and fleeing territorial behaviours were observed on five occasions classified into three seasons, the beginning (July 2006 and June 2007), middle (November 1999), and end (February and April 2007) of the reproductive season in Malawian cichlids. This classification was done to examine species differences in frequencies of territorial behaviours independently of effects of seasonal change, on the basis of a previous study, in which reproductive activity of rock-dwelling cichlids declined in May (Marsh et al. 1986). In 2006/2007, observations were conducted on the seven species that occurred most frequently, namely *Pseudotropheus* (Tropheops) sp. 'red cheek', Ps. (Maylandia) zebra Günther, Ps. (Maylandia) callainos Stauffer & Hert, Protomelas fenestratus Trewavasae, Labeotropheus fuelleborni Ahl, L. trewavasae Fryer, and Melanochromis auratus Boulenger. In 1999, three further species, Ps. (Tropheops) 'black', Ps. (Maylandia) heteropictus Staeck, and Cynotilapia afra Günther were also observed. The taxonomic status of some of these species is unresolved, but some are known to be reproductively isolated (Stauffer et al. 1997; van Oppen et al. 1998). In the present study, formal names were used for described species and the informal species names provided by Konings (1991a) were assigned to any species lacking a formal description.

During each observation, interspecific attacks and evasion were counted during 10 min periods for each individual. The frequencies of interspecific attacks and evasion were expressed as incidence of these behaviours per minute, since observation periods were occasionally shorter than 10 min when the diver lost sight of the target individual. Interspecific attacks and evasion were defined as chasing heterospecifics away and rushing away after being attacked by heterospecifics, respectively. Observations were replicated with 7-12 mature males in each season for each species that was observed in 2006/2007, and with 4-14 mature males for each species observed in 1999. Mature males were selected because their underwater colouration makes species identification easy. Total lengths were roughly measured for each observed individual (except those observed in

26

African Zoology Vol. 45, No. 1, April 2010

Cichlid groups	Main food (after Konings 1991a)	Intrusion (times/min)§		Feeding (bites/min)§	
		Before (% fleeing)	After	Before	After
Territory owner	Attached algae			6.80 ± 3.98	
Territory intruders					
(1) Conspecific male [†]	Attached algae	0.02 ± 0.04 (100)	0.06 ± 0.09	0.00 ± 0.00	0.84 ± 1.47
(2) Conspecific female [†]	Attached algae	0.14 ± 0.14 (100)	0.02 ± 0.04	0.00 ± 0.00	1.10 ± 2.46
(3) Ps. (T) others [†]	Attached algae	1.42 ± 0.38 (77)	1.54 ± 0.32	1.60 ± 1.62	27.26 ± 22.22
(4) Ps. (M.) zebra [†]	Algae & zooplankton	0.50 ± 0.32 (72)	0.62 ± 0.27	1.20 ± 2.04	8.16 ± 4.69*
(5) Ps. (M.) callainos [†]	Algae & zooplankton	0.52 ± 0.30 (50)	0.42 ± 0.24	0.48 ± 0.87	2.78 ± 2.68
(6) Petrotilapia ⁺	Attached algae	0.12 ± 0.22 (0)	0.02 ± 0.04	0.18 ± 0.25	0.00 ± 0.00
(7) Mylochromis [†]	Benthos	0.24 ± 0.22 (83)	0.20 ± 0.12	0.64 ± 0.40	3.00 ± 3.99
(8) Other benthos feeders [†]	Benthos	0.20 ± 0.28 (90)	0.12 ± 0.04	0.20 ± 0.31	0.04 ± 0.09
(9) Cynotilapia afra†	Zooplankton	1.18 ± 1.61 (49)	0.20 ± 0.29	0.00 ± 0.00	0.26 ± 0.58
Total [‡]	-	3.16 ± 1.50 (57)	3.66 ± 1.04	2.82 ± 2.13	51.52 ± 23.82*

 Table 1. Frequencies of intrusion (fleeing) and feeding by owners and intruders (classified into nine groups) in the territories of *Pseudotropheus (Tropheops)* 'black' before and after the removal of the territory owner.

 $\ensuremath{^\$}\xspace{Mean \pm S.D.s.}$ Experiments were replicated with five owners.

[†]Cichlid groups 1–9 are defined in the text. [‡]Total indicates the sum of intruders of groups 1–9 and other cichlids.

*Significant according to paired *t*-tests (*P* < 0.05).

1999; measurements were estimated to the nearest 1 cm by eye) to examine body size effects on the frequencies of territorial behaviours.

Experimental removals of the most aggressive territory owners

Behavioural changes by some species in response to the removal of the most aggressive territorial species were examined by a field experiment conducted in November 1999. Prior to the experiment, 2 m-interval grids were set with measuring tapes and all substrates were mapped, so that the positions of individual fish could be recorded with errors less than 10 cm (\approx fish total length).

During a first observation period of each trial (replicated with 5 territory owners), interspecific feeding territory of a Ps. (T.) 'black' male was determined on a map by recording feeding positions of the territory owner and the positions of heterospecifics when the owner first displayed interspecific aggression toward them (after Kohda 1995). Territories were defined by the outermost of these positions. Pecks on the rock surface were taken as feeding. Intraspecific male-male interference was sometimes observed but not recorded since intrasexual aggression is known to occur within the boundaries of mating territories, which tend to be larger than feeding territories (Kohda 1995; Matsumoto & Kohda 2004). The first observation period lasted >15 min, since a preliminary 60 min observation indicated that 15 min is sufficient to determine the territory boundaries.

During a subsequent 15 min observation period,

the number of individuals that crossed the territory boundaries (hereafter, intruders) was counted. The number of pecks (bites) on the rock surface was also recorded to determine frequencies of feeding by owners and intruders. The frequencies of intrusion and feeding were expressed as times of these behaviours per minute. The ratio of intruders that fled after attacks by the territory owner was also recorded. During observations of intrusion and feeding, intruding cichlids were classified into nine groups based on their similarity to the owner with regard to taxonomic relationships and feeding strategies (Konings 1991a,b):

- (1) conspecific males,
- (2) conspecific females,
- (3) heterospecifics belonging to the same subgenus, *Pseudotropheus* (*Tropheops*), with closely packed teeth specialized for plucking attached algae, included *Ps*. (*T*.) 'rust', 'band', and 'olive',
- (4, 5) common congeneric species, *Ps.* (*M.*) zebra and *Ps.* (*M.*) callainos,
- (6) algal feeders of the genus, *Petrotilapia*, which have large bodies (15–18 cm in total length) compared to the territory owners (≈ 12 cm; Konings 1991a),
- (7) *Mylochromis*, abundant, feed on benthic invertebrates from among sediment,
- (8) other benthic sediment feeders, including individuals of the genera *Melanochromis*, *Mchenga* and *Otopharynx*,
- (9) plankton-feeding mbuna *Cynotilapia afra* (Table 1).
- When observed intruders did not belong to any

of groups 1–9, or when the group identification of an individual fish was uncertain, the count data were only used to calculate the sum of intruders (groups 1–9 and the other cichlids).

After the observations, territorial males were captured using small-mesh gill nets and scoop nets, which enabled catching fish without damage. After 30 min, intrusions and feeding were again counted during another 15 min period as above. The captured territory owners were released near their respective territories upon the completion of observations.

Statistics

Before examining species difference in frequencies of territorial behaviours, the relationships of fish size to frequencies of interspecific attack and evasion were respectively tested by Spearman's correlation coefficient analyses. Separate analyses were done for each of seven species observed in 2006/2007. Further analyses were carried out using pooled data from individuals of seven different species. The relationships between the frequencies of interspecific attacks and evasion were also examined using both separate data for each species and pooled data from 10 different species observed in all observation occasions.

Analyses of variances (ANOVA) was conducted to examine species difference in the frequency (per minute) of interspecific attacks and evasion, with factors of fish species, seasonality, and an interaction term (fish species \times seasonality), using data from 10 species, replicated with 4-14 males in each season. These ANOVAs involved seasonality as a factor, because preliminary simple ANOVAs detected apparently significant seasonal effects on the frequency of attacks in one species (L. trewa*vasae*: $F_{2,12} = 9.0$, P = 0.004; the other six species that were observed in more than two survey periods: P > 0.05) and on the frequency of evasion in one species (*Pr. fenestratus*: $F_{2,12} = 4.51$, *P* = 0.035; others: P > 0.05). They did not involve fish size (total length) as a factor, because size effect was not detected in any species by Spearman's correlation analyses mentioned above.

Using data from the field experiment, the frequencies (per minute) of intrusions and feeding were compared before and after the removal of territory owners (n = 5) by paired *t*-tests in each of nine cichlid groups described in the section on the experimental removals. The frequencies of intrusions and feeding by all intruders (including individuals of groups 1–9 and others cichlids)

were also compared in the same manner.

The frequencies of attacks and evasion were transformed by log 10 (x + 1) before ANOVAs to satisfy the assumptions of the parametric tests. All statistical tests were two-tailed and used alpha values of 0.05 for statistical significance, except for separate analyses of Spearman's correlation coefficient for each species, alpha values that were divided by the number of tests (species). They were conducted using the software package, Stata (version 9.2; Stata Corp, College Station, TX, U.S.A.).

RESULTS

Variation in frequencies of interspecific attacks and evasion

The relationships of fish size (total length, ranked) to the frequency (ranked) of interspecific attacks were not significant in any species (Spearman's correlation, n = 9-23, P > 0.05; Fig. 1a), or when 126 individuals from all of the species examined were pooled together ($r_s =$ 0.003, P = 0.97). The relationships of fish size (total length, ranked) to the frequency (ranked) of interspecific evasion were not significant in any species, while a slightly positive correlation was observed in Pr. fenestratus ($n = 9, r_s = 0.689, P =$ 0.04; Fig. 1b). When 126 individuals were pooled, larger fish tended to flee less often from heterospecifics ($r_s = -0.256$, P = 0.004). Among the 10 species, frequencies of interspecific attacks and evasion were significantly correlated only in *Ps.* (*T*) 'red cheek' ($r_s = -0.593$, n = 28, P < 0.001) but not in the other species (P > 0.05). When 175 individuals from different species were combined in a single analysis, rates of attacking and fleeing from heterospecifics were negatively correlated $(r_{\rm s} = -0.347, P < 0.001).$

The first ANOVA model accounted for a significant component of the variance in the frequency of interspecific attacks ($F_{22,156} = 4.22$, P < 0.001; Fig. 2). Fish species differed significantly in their frequencies of attacking heterospecifics ($F_{9,156} =$ 8.16, P < 0.001), whilst seasonality and the interaction were not significant (seasonality: $F_{2,156} = 0.51$, P = 0.60, interaction: $F_{11,156} = 1.75$, P = 0.067). The second ANOVA model accounted for a significant component of the variance in the frequency of interspecific evasion ($F_{22,156} = 4.49$, P < 0.001). Fish species differed significantly in their frequencies of attacking heterospecifics ($F_{9,156} = 8.42$, P <0.001), whilst seasonality and the interaction were

African Zoology Vol. 45, No. 1, April 2010



Fig. 1. Frequencies of interspecific attacks (a) and evasion (b) by Lake Malawi cichlids as a function of the total length of the individual fish.

not significant (seasonality: $F_{2,156} = 2.30$, P = 0.103, interaction: $F_{11,156} = 1.59$, P = 0.105).

Changes in the frequencies of intrusion and feeding after territory owner removal

At least half of the intruders from eight cichlid groups (all except *Petrotilapia* spp.) fled from territories because they were attacked by the owners (Table 1). By contrast, *Petrotilapia* (group 6) individuals were never observed to be attacked by territory owners.

In response to the experimental removal of territory owning *Ps. (Tropheops)* 'black', conspecific females (group 2) slightly decreased the frequency with which they intruded into territories, while this change was not statistically significant (paired *t*-tests, P = 0.061). Neither the intrusion frequencies of the other eight cichlid groups nor of the total number of intrusions changed after territory owners were removed (P > 0.200).

The increase in feeding frequencies was significant for a congeneric cichlid group that feed mainly on attached algae (group 4, P = 0.009). The other two congeneric groups also showed apparent increases, while these changes were not statistically significant (group 3: P = 0.063, group 5: P = 0.092). Conspecifics (groups 1–2), the large algal feeder (group 6) and three cichlid groups that mainly feed on benthic invertebrates and zooplankton (groups 7-9) did not change their feeding frequencies. When the frequency of feeding by all intruders (comprising individuals of groups 1-9 and the other cichlids) was compared, it increased by more than 18-fold in response to the removal of the territory owner (P = 0.013). Even when the feeding by the territory owners before the removal was included into the comparison, the increase was fivefold, from 9.62 bites/min to 51.52 bites/min.

Maruyama et al.: Competition over food resources amongst Lake Malawi cichlid fishes



Fig. 2. Seasonal and interspecific variation in the frequencies of interspecific attacks (right) and evasion (left) by 10 cichlid species observed at the beginning, middle, and end of their reproductive season in Lake Malawi. Columns, bars, figures, and 'x' indicate means, S.D.s, sample sizes and lack of data, respectively.

DISCUSSION

Territorial behaviours are often body size-dependent in fish because body size is related to prey type and feeding site preferences (Werner & Gilliam 1984; Kohda et al. 2008). Similar-sized individuals tend to compete frequently with each other for feeding site. In addition, body size is often responsible for social rank within schools, which would make large individuals more aggressive than small ones (Keeley & McPhail 1998). However, size effects on the frequencies of interspecific attacks or evasion were not obviously found except with Pr. fenestratus, in which, unexpectedly, larger individuals tended to flee more frequently (Fig. 1). This may have resulted from the limited intraspecific variation in body size in the present study, which focussed on interspecific comparisons between mature males that held territories. In addition, Lake Malawi cichlid communities are diverse and hence individuals may often interact more frequently with heterospecifics than conspecifics. Interspecific social ranks associated with interspecific body size variation may have more influence on territorial interactions than intraspecific social rank. This was consistent with the statistical trend for smaller individuals to flee more frequently when data were pooled across species (Fig. 1b).

Seasonality in the frequency of territorial behaviours was not detected in the present study (Fig. 2). This may have resulted from large individual vari-

ation. Seasonal patterns in territorial behaviours might be identified in future studies, which should be designed to account for individual variation in some factors (e.g. daily periodicity) and have greater replication. Otherwise, small seasonal variations in territorial behaviours might be associated with the water temperature stability in Lake Malawi. Since the annual range in surface water temperature is no greater than 6°C (between 22°C and 28°C, Konings 1991b), the thermal condition required for spawning is always available for most rocky shore cichlid species. They show continuous reproductive activity throughout the year (Marsh *et al.* 1986), and hence, the importance of holding territories may not vary too much throughout the seasonal cycle.

Seasonality and size effects thus had relatively minor influence on frequencies of interspecific attacks and evasion. In comparison, there was substantial influence of species identity in the present study (Fig. 2). These quantitative results support previous reports that were based on qualitative observations (Ribbink *et al.* 1983). In addition, we found that fish that attacked heterospecifics more frequently were attacked and chased less frequently. It can be concluded that interspecific interactions amongst cichlid species are asymmetric: some species may affect others more than the reverse.

Observations of the most aggressive territory owners provided supporting evidence for such asymmetric interactions (Table 1). More than half of the intruders left a territory because the owner attacked them. A previous field study, in which 70×70 cm quadrats were set in each territory to define territory space without prior observation, revealed that territorial males of four species belonging to subgenus *Pseudotropheus* (*Tropheops*) preferentially excluded conspecific intruders and heterospecifics that had the most similar diets to their own, but tolerated intruders with different diets (Genner et al. 1999b). This is consistent with our finding that the percentage of chased individuals was high in conspecifics and heterospecifics within the same subgenus (Ps. (T.)) compared to those from *Pseudotropheus* (Maylandia). Amongst algae-feeding cichlids, only Petrotilapia was seldom attacked by territory owners. This is probably because they were larger than the owners, making attack risky for the owners through possible counterattacks (Fig. 1). In addition, fish of very different sizes might have lower resource-use overlaps, which implies that territorial aggression against them bring relatively lower benefits to the owners. Recently, Kohda et al. (2008) reported size-dependent feeding territoriality within a benthic-feeding Tanganyikan cichlid, whereby individuals defended against similar-sized conspecifics but did not exclude individuals of markedly different sizes. It can be assumed that attacks on Petrotilapia would bring higher risks but lower benefits to the owners compared to attacks on smaller algae-feeding cichlids.

In response to removal of territory owners, only conspecific females slightly decreased their intrusion frequency (Table 1). This seems to be associated with their courtship behaviour, in which a female follows a territorial male into his territory and stays until spawning or until she is attacked by the male. The low feeding frequencies recorded before the removal of territory owners and the low intrusion frequencies observed after removal both support the speculation that conspecific females were not primarily intruding to feed. The other eight cichlid groups showed no change in intrusion frequencies. This result can be explained by the territoriality of Malawian cichlids. Most species have their own networks of abutting feeding territories (Genner & Turner 2005), maintain by intraspecific and interspecific territorial behaviour (Genner et al. 1999b). As a result, it is likely that individuals could rarely move long distances to the newly vacant territorial area within the short time available. Thus the majority of intruders might have been restricted to resident individuals from surrounding territories.

Before a territory owner was removed, the frequency with which intruders fed in the territory (2.8 times/min) was approximately 40% of the feeding rate of the territory owner (Table 1). After the territory owner was removed, the frequency of feeding in the territory increased more than fivefold. These results imply that aggression preserved food resources for the territory owners. Algaefeeding cichlids that were often chased off by the territory owner seems to have contributed to the increase in intruders' feeding frequencies. In addition to heterospecific Pseudotropheus (Tropheops), with similar teeth adapted for plucking attached algae, Pseudotropheus (Maylandia) also showed increased feeding frequencies. These results suggest that aggression influences feeding habits of other species, including those with some dietary dissimilarities. In contrast, species that had very different diets (benthic invertebrates, zooplankton) only slightly contributed to the change in intruders' feeding frequencies in spite of the high percentage of intrusions ending with their being chased off by the territorial male (49–90%). The frequent attacks directed toward them could probably be attributed to other purposes, such as reducing egg predation.

In conclusion, the present study showed that interspecific interactions amongst cichlid species are asymmetric, with some species having far stronger influences through territorial behaviours on other species than the reverse. Territorial aggression influences the feeding habits of some other species, including those with some dietary dissimilarity. If interspecific interactions are asymmetric amongst cichlid species with respect to competition, we must again consider how they manage to coexist. One would expect that community-level responses to environmental fluctuations might involve such asymmetric interactions, with 'keystone' species having a strong influence on the feeding opportunities and hence fitness of other species while themselves being little impacted by heterospecifics. One possible answer might be found in the relationship between territorial aggressiveness shown in the present study and feeding microhabitat reported by Genner et al. (1999a). More aggressive species tend to feed at the upper side of the rock, where the algal production may be high, whereas less aggressive species seem to avoid competition by feeding from the underside of the rock. If the choice of feeding

positions is highly associated with the time allocation to the feeding and territorial behaviours, niche difference, which has been generally considered to stabilize coexistence by causing species to limit themselves more than they limit their competitors (Chesson 2000), might have been underestimated amongst cichlid species. Future studies are required that examine whether such influences on heterospecific individuals differ amongst species with different aggressiveness, which would improve our understanding about how diverse cichlids within trophic groups manage to coexist given interspecific competition.

ACKNOWLEDGEMENTS

We thank R. Zatha, Y. Kazembe, A. Mangawa, B. Matundu, A. Nyoni, Y. Nonomatsu and the late A. Mwale for supporting our fieldwork. We are deeply grateful to G.F. Turner, K. Magellan and O.L.F. Weyl for constructive comments on the manuscript. This study was conducted in accordance with the prevailing laws of the Republic of Malawi. Financial support was provided by the Research Fellowship and the Joint Research Centre for Science and Technology of Ryukoku University.

REFERENCES

- CHESSON, P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics 31: 343–366.
- FRYER, G. 1959. The trophic interrelationships and ecology of some of the littoral communities of Lake Nyasa with especial reference to the fishes, and a discussion of a group of rock frequenting *Cichlidae*. *Proceedings of the Zoological Society of London* 132: 153–281.
- GENNER, M.J., TAYLOR, M.I., CLEARY, D.F.R., HAWKINS, S.J., KNIGHT, M.E. & TURNER, G.F. 2004. Beta diversity of rock-restricted cichlid fishes in Lake Malawi: importance of environmental and spatial factors. *Ecography* 27: 601–610.
- GENNER, M.J. & TURNER, G.F. 2005. The mbuna cichlids of Lake Malawi: a model for rapid speciation and adaptive radiation. *Fish and Fisheries* 6: 1–34.
- GENNER, M.J., TURNER, G.F. & HAWKINS, S.J. 1999a. Foraging of rocky habitat cichlid fishes in Lake Malawi: coexistence through niche partitioning? *Oecologia* **121**: 283–292.
- GENNER, M.J., TURNER, G.F. & HAWKINS, S.J. 1999b. Resource control by territorial male cichlid fish in Lake Malawi. Journal of Animal Ecology 68: 522–529.
- HUBBELL, S.P. 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press, City, U.S.A.

- KEELEY, E.R. & MCPHAIL, J.D. 1998. Food abundance, intruder pressure, and body size as determinants of territory size in juvenile steelhead trout (Oncorhynchus mykiss). Behaviour 135: 65–82.
- KOHDA, M. 1995. Territoriality of male cichlid fishes in Lake Tanganyika. Ecology of Freshwater Fish 4: 180–184.
- KOHDA, M., SHIBATA, J., AWATA, S., GOMAGANO, D., TAKEYAMA, T., HORI, M. & HEG, D. 2008. Niche differentiation depends on body size in a cichlid fish: a model system of a community structured according to size regularities. *Journal of Animal Ecology* 77: 859–868.
- KONINGS, A. 1991a. Ad Konings's Book of Cichlids and all the other Fishes of Lake Malawi. T. F.H. Publishers, New Jersey.
- KONINGS, A. 1991b. *Lake Malawi Cichlids in their Natural Habitat*, 2nd edn. Cichlid Press, Germany.
- MARSH, B.A., MARSH, A.C. & RIBBINK, A.J. 1986. Reproductive seasonality in a group of rockfrequenting cichlid fishes in Lake Malawi. *Journal of Zoology* 209: 9–20.
- MARSH, A.C. & RIBBINK, A.J. 1985. Feeding site utilization in three sympatric species of *Petrotilapia* (Pisces: Cichlidae) from Lake Malawi. *Biological Journal of Linnean Society* 25: 331–338.
- MATSUMOTO, K. & KOHDA, M. 2004. Territorial defense against various food competitors in the Tanganyikan benthophagous cichlid *Neolamprologus tetracanthus*. *Ichthyological Research* **51**: 354–359.
- REINTHAL, P.N. 1990. The feeding habits of a group of herbivorous rock-dwelling fishes (Cichlidae: Perciformes) from Lake Malawi. *Environmental Biology of Fishes* 27: 215–233.
- REINTHAL, P.N. 1993. Evaluating biodiversity and conserving Lake Malawi's cichlid fish fauna. *Conservation Biology* 7: 712–718.
- RIBBINK, A.J. & ECCLES, D.H. 1988. Fish communities in the east African Great Lakes. In: *Biology and Ecology* of African Freshwater Fishes, vol. 216, (eds) C. Leveque, M.N. Bruton & G.W. Ssentongo, pp. 277–301. ORSTOM, Paris.
- RIBBINK, A.J., MARSH, B.A., MARSH, A.C., RIBBINK, A.C. & SHARP, B.J. 1983. A preliminary survey of the cichlid fishes of rocky habitats in Lake Malawi. *South African Journal of Zoology* 18: 149–310.
- STAUFFER, J.R., BOWERS, N.J., KELLOGG, K.A. & McKAYE, K.R. 1997. A revision of the blue-black *Pseudotropheus zebra* (Teleostei: Cichlidae) complex from Lake Malawi, Africa, with a description of a new genus and ten new species. *Proceedings of the Academy* of Natural Sciences of Philadelphia 148: 189–230.
- VAN OPPEN, M.J.H., TURNER, G.F., RICO, C., ROBINSON, R.L., DEUTSCH, J.C., GENNER, M.J. & HEWITT, G.M. 1998. Assortative mating among rock-dwelling cichlid fishes supports high estimates of species richness from Lake Malawi. *Molecular Ecology* 7: 991–1001.
- WERNER, E.E. & GILLIAM, J.F. 1984. The ontogenetic niche and species interactions in size structured populations. *Annual Review of Ecology and Systematics* 15: 393–425.

Responsible Editor: O. Weyl