

A laboratory study of host use by the cuckoo catfish *Synodontis multipunctatus*

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Abstract The only known non-avian vertebrate obligate brood parasite is the cuckoo catfish (*Synodontis multipunctatus*), a Lake Tanganyikan endemic. The cuckoo catfish parasitizes Tanganyikan mouthbrooding cichlids, and under captive conditions, will also parasitize cichlids from other Rift Valley lakes. Here we examine the frequency of parasitism by the cuckoo catfish of *Ctenochromis horei* from Lake Tanganyika and three species from Lake Malawi and the greater Lake Victorian system in a laboratory setting. *C. horei* was parasitized significantly less (17%) than the allopatric species *Haplochromis latifasciatus*, *Haplochromis nubilus*, and

Metriaclima estherae (combined parasitism rate of 28%). The lower rates of parasitism in *C. horei* may be due to differences in the mating ritual, oviposition (e.g., long periods of pseudo-spawning before actual oviposition), and behavioral adaptations (e.g., increased aggression towards the cuckoo catfish). The number of catfish eggs per parasitized brood was similar between *C. horei*, *H. latifasciatus*, *H. nubilus*, and *M. estherae*. Our results are comparable to findings from the field for *C. horei* parasitism frequency and number of cuckoo catfish per brood. We also analyzed the parasitism rate of the albino morph of *Metriaclima zebra*, a domestic strain. Parasitism rates and number of catfish per brood were the highest in the albino morphotype suggesting that the higher levels of parasitism may be related to lower aggressive behavior, lower visual acuity, or captive influence. Cuckoo catfish and mouthbrooding cichlids provide a model system for testing brood parasitism in a laboratory setting.

Alexander Cruz is deceased. This paper is dedicated to his memory.

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Introduction

The East African Rift Valley lakes contain an incredibly rich fish fauna. Cichlids (Perciformes: Cichlidae) in particular exhibit a diverse range of colors, morphology, and feeding methods. As many as 2000 species of cichlids have evolved within the last 10 million years, resulting in one of the most dramatic cases of vertebrate

speciation (Barlow 2000; Danley and Kocher 2001; Kocher 2004; Lande et al. 2001; Sturmbauer et al. 2011), and over 95% of the cichlids in the three major rift lakes (Tanganyika, Malawi, and Victoria) are endemic to an individual lake (Snoeks 2000). In Rift Valley cichlids, maternal mouthbrooding as a reproductive strategy is well represented. Mouthbrooding involves the female picking up recently oviposited eggs in her mouth, where they are brooded in the buccal (oral) cavity until free swimming (Keenleyside 1991; Barlow 2000). An obligate brood parasitic catfish (*Synodontis multipunctatus*, the cuckoo catfish, Siluriformes: Mochokidae) has been documented in Lake Tanganyika to use female mouthbrooding cichlids as hosts (Finley 1984; Sato 1986; Cruz et al. 2004).

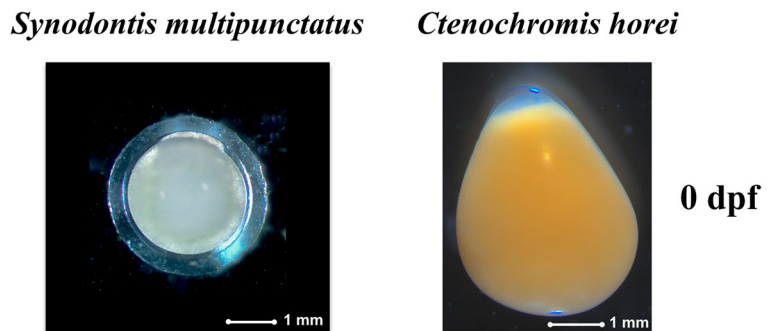
Brood parasitism has been studied extensively in insects and birds, with the majority of research focusing on avian obligate brood parasites (completely relying upon a host for successful breeding), as is the case for old world cuckoos and new world molothrine cowbirds (e.g., Davies 2000; Feeney et al. 2014; Friedmann 1929; Ortega 1998). Unlike the cuckoo catfish, other fish species are facultative brood parasites where they may resort to parasitic behavior, but do not rely on the host for successful breeding (Sato 1986; Wisenden 1999; Yom-Tov and Geffen 2006). The cuckoo catfish enters the cichlid spawning area and they breed in close synchrony with the cichlids, laying and fertilizing their eggs for the female mouthbrooder to pick up. The female cichlid picks up the catfish eggs, even though they are smaller in size and are different in appearance (Fig. 1). The catfish embryos are then brooded in the buccal cavity of the host together with the host embryos, but hatch earlier. The catfish grow and develop faster, and after they have exhausted their yolk sacs as a nutrition source, they begin to devour the host fry while still in the host's mouth. Thus, the catfish require their host for protection (suitable habitat for developing embryo) and to provide its first exogenous food source during the earliest stages of development (Sato 1986; Cruz et al. 2004).

There are approximately 120 species of *Synodontis* catfishes recognized (Poll 1971; Friel and Vigliotta 2006; Koblmuller et al. 2006; Wright and Page 2006), and while the non-parasitic congeners are all egg scatterers, the cuckoo catfish is the only species known to exhibit brood parasitic behavior. Furthermore, the cuckoo catfish is the only known non-avian obligate brood parasite among vertebrates (Sato 1986; Cruz et al. 2004). This is an important finding as it provides a system to study

brood parasitism under controlled laboratory conditions, where questions about parasitism dynamics can be addressed. Because selection is both spatially and temporally focused in the breeding area, factors affecting host-parasite interactions are easily discernible (Rothstein 1990). The cuckoo catfish is endemic to Lake Tanganyika, and in nature can only parasitize mouthbrooding cichlids found in that lake. However, under laboratory conditions, cuckoo catfish will parasitize mouthbrooding cichlids from other Rift Valley lakes and have even been observed parasitizing *Geophagus steindachneri*, a South American mouthbrooding cichlid species (Loiselle 1998; Wisenden 1999). Because of these close parasite-host interactions, questions about both ecology and coevolution of brood parasitism can be addressed, particularly how selection pressures and feedbacks influence reproductive behaviors. For example, brood parasitic birds (e.g., cowbirds or cuckoos) can reduce host fitness by egg removal or competition between host and parasite young, whereas hosts can reduce the parasite's fitness by recognizing and rejecting the eggs of the parasite or increased aggression towards the parasite (Rothstein 1975; Payne 1977; Rothstein 1990; Duckworth 1991; Peer and Rothstein 2010; Fossey et al. 2011; Thorogood and Davies 2013; Molina-Morales et al. 2014). This results in an evolutionary arms race between host and parasite (Dawkins and Krebs 1979; Davies et al. 1989; Rothstein 1990). Although studied extensively in insects (Cervo et al. 2004; Kilner and Langmore 2011) and birds (Rothstein 1990; Davies 2000), little is known about the subtleties of the host-parasite relationship in brood parasitic fishes. As is the case with avian cuckoo host nestlings (Davies 2000), the cuckoo catfish usually eliminates the entire host progeny (pers. obs), making it extremely costly from a fitness standpoint for parasitized cichlids. The cuckoo catfish uses both visual and pheromonal cues to synchronize its breeding with host species, and catfish females are able to lay eggs over a period of two to three days (Cruz et al. 2004). By laying eggs over several days, the cuckoo catfish adults are able to parasitize more broods and increase the chances of a successful parasitism event. Adaptations in sympatric hosts include extended displaying during mating behavior without oviposition, remote spawning site, and aggression.

The basic breeding mechanism of this host-parasite system has been documented through a series of observational studies. Brichard (1979) was the first to observe cuckoo catfish fry in the mouths of captured Tanganyikan cichlids, and

Fig. 1 The differences in appearance between the cuckoo catfish (*S. multipunctatus*) and *C. horei* cichlid eggs. These images are of embryos taken shortly after fertilization at zero days post-fertilization (0 dpf)



though they got there accidentally. There were also descriptions offered from aquarists (Ferguson 1983; Finley 1983), until a field study by Sato (1986) confirmed that the cuckoo catfish was an obligate brood parasite of Lake Tanganyikan cichlids. Sato (1986) examined differences between host species with regard to percentage of cichlid broods parasitized and number of catfish per brood. In addition, Wisenden (1999) mentioned parasitism rates observed in aquariums of cichlid species from Lake Victoria and Lake Malawi, while Cruz et al. (2004) described the breeding biology and early ontogeny of the host species and the catfish. Here we examine the frequency of parasitism by the cuckoo catfish in both sympatric (Lake Tanganyikan) and allopatric (Lake Malawian and the greater Lake Victorian system) host cichlid species in a laboratory setting.

Materials and methods

Sympatric study species (Fig. 2)

Synodontis multipunctatus (Boulenger 1898), the cuckoo catfish, endemic to Lake Tanganyika, is a generalist brood parasite on different species of mouthbrooding cichlids, and it can be distinguished from similar looking congeners by a humeral process that is narrow posteriorly (Eccles 1992). Wild-caught specimens were purchased from Old World Exotic Fish (<http://www.oldworldexoticfish.com>), and used for experimentation along with their F1 offspring that were bred in the lab.

Ctenochromis horei (Günther 1894) is a mouthbrooding cichlid endemic to Lake Tanganyika and surrounding river tributaries, and it is a naturally occurring host of the cuckoo catfish (Sato 1986). Wild-

caught specimens were purchased from Old World Exotic Fish (<http://www.oldworldexoticfish.com>) and used for experimentation along with their F1 and F2 offspring. Data were collected during 2006 and 2007.

Allopatric study species (Fig. 2)

Metriaclima estherae (Konings 1995), the red zebra cichlid, is a mouthbrooding cichlid endemic to Lake Malawi. Tank-raised specimens were purchased from Atlantis Tropical Fish Hatchery (<http://www.cichlids.net>), and used for experimentation along with their offspring. Data were collected from 2011 to 2013.

Haplochromis nubilus (Boulenger 1906) is a mouthbrooding cichlid endemic to Lake Victoria and surrounding smaller lakes and associated river tributaries in the greater Victoria system (Van Oijen et al. 1991). Tank-raised specimens were purchased locally from Golden Fish Aquarium (<http://www.goldenfishaquarium.com>), and used for experimentation along with their offspring. Data were collected from 2000 to 2002, and during 2006.

Haplochromis latifasciatus (Regan 1929) is a mouthbrooding cichlid endemic to Lake Kyoga and Lake Nawampasa (greater Victoria system), and little is known about the habitat and ecology of the species as it is endangered in the wild (Kaufman 1996). Although endangered in the wild, tank-raised specimens of this species are readily available for purchase through the aquarium trade. The tank-raised specimens were purchased from Old World Exotic Fish (<http://www.oldworldexoticfish.com>), and used for experimentation along with their offspring. Data were collected from 2011 to 2012.

Metriaclima zebra (Boulenger 1899), the zebra cichlid, is a mouthbrooding cichlid endemic to Lake Malawi. The albino morph was used to see whether this domestic strain differed from the

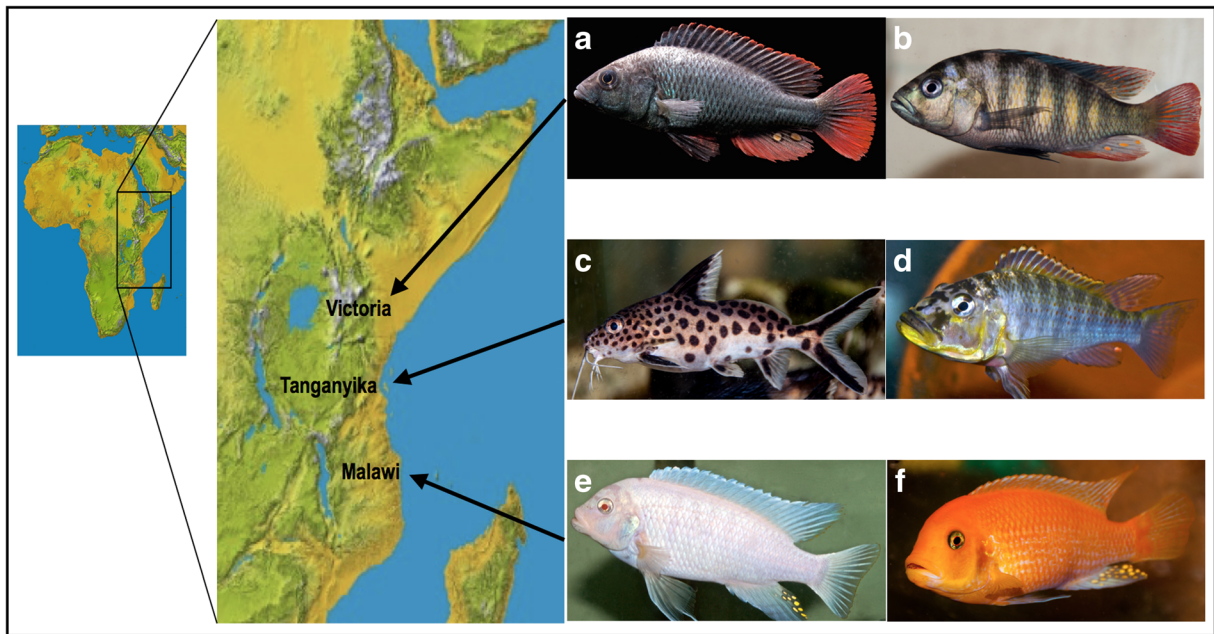


Fig. 2 Five African cichlid host species: (a) *H. nubilus*, (b) *H. latifasciatus*, (d) *C. horei*, (e) *M. zebra*, and (f) *M. estherae*. (c) The brood parasitic cuckoo catfish (*S. multipunctatus*). Black arrows indicate the Rift Valley lakes where the natural populations

of these host species are found and fish from the same area are organized by row (background map images source: NASA/JPL/NIMA)

above natural populations in frequency of parasitism. Aquarists have reported using them successfully to rear cuckoo catfish (pers. comm.). Specimens were purchased locally from PetSmart and used for experimentation along with their offspring. Data were collected during 2006.

Fish husbandry and experimental design

Cuckoo catfish were maintained separately with breeding populations of the above African cichlid species from Lake Tanganyika (*C. horei*), the greater Lake Victoria system (*H. nubilus* and *H. latifasciatus*), and Lake Malawi (*M. estherae*, and the aquarium strain of *M. zebra*). These populations were housed in 110 L (77 × 32 × 47 cm), 208 L (122 × 32 × 53 cm), 284 L (122 × 47 × 53 cm), and 473 L (184 × 47 × 59 cm) aquariums. Each species was distributed in multiple tank sizes, so tank size did not confound the effect of species. Because the host species are polygynous, the cichlids were maintained at 3:1 (female to male), while the catfish were 1:1 (female to male). However the ratio of host to parasite remained consistent at 2:1 (cichlids to catfish), as we found these ratios produce good breeding results.

The fish were maintained at 24–26 °C in a 14:10 light: dark cycle and were fed body size proportional amounts of food daily in midafternoon. Catfish were fed a combination of frozen chironomid larvae and *Artemia* shrimp pellets daily, while cichlids were fed Hikari® cichlid staple pellets or HBH® cichlid flake foods. Fifty percent water changes were conducted every other week. Sodium thiosulfate ($\text{Na}_2\text{S}_2\text{O}_3$) was added to the tap water to remove chlorine after the tap water was added to tanks. A pH of 8.0–9.0 was maintained by using crushed coral as the substrate and then buffering the pH and hardness up with a buffer mixture made from 1:1:1 sodium bicarbonate (NaHCO_3) to Epsom salt ($\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$) to Instant Ocean® sea salt after water changes. The buffer was added in small dosages to aquariums until a dKH of 10–14 was reached, and dKH levels were monitored using a KH carbonate hardness test kit from API®. Terracotta pots were placed in the aquariums and served as territorial display and spawning areas for cichlids.

Aquariums were monitored daily for female cichlids carrying eggs, which can be identified by their distended buccal (oral) cavity. Following identification, we carefully removed the carrying females from the tank. We

obtained eggs by gently holding the female's mouth open in a small volume of tank water and irrigating the oral cavity with a transfer pipette to dislodge the eggs from the mouth. The number of cichlid eggs and catfish eggs, if any, were then recorded. We obtained 100 broods from one cichlid species from Lake Tanganyika (*C. horei*), and 100 broods each from cichlid species from the greater Lake Victoria system (*H. nubilus* and *H. latifasciatus*) and Lake Malawi (*M. estherae* and the aquarium strain *M. zebra*). All experiments were approved by the university's Institutional Animal Care and Use Program and conducted under the guidelines they stipulated.

Statistical analyses

We analyzed our data using both binomial and Poisson models. To test for differences in the probability of parasitism among the species, we ran logistic regressions (generalized linear model with family = binomial and a logit link) with the presence or absence of a catfish egg in a brood as the response variable, and fish species as a fixed effect. For broods that were parasitized, we tested for differences in the number of catfish eggs among the five species using Poisson regressions (generalized linear model with family = poisson) with the number of catfish eggs per brood as the response variable, and fish species as a fixed effect. For both the logistic regressions and the Poisson regressions, we ran pairwise Tukey contrasts between each species pair using the `glht` and `mcp` functions in the R package 'multcomp' (Hothorn et al. 2008). For the logistic regressions, we also ran a model comparing parasitism in *C. horei* to the combined parasitism of the allopatric species *H. nubilus*, *H. latifasciatus*, and *M. estherae*. Confidence intervals (95%) were calculated using the `confint` function in R. All analyses were performed using the software R, version 3.4.4 (R Core Team 2018).

Results

Parasitism rates

We examined 100 broods from each of the four natural host species and the aquarium strain and found 17 *C. horei* broods were parasitized by the cuckoo catfish, as compared to 26 *H. nubilus*, 33 *H. latifasciatus*, 25 *M. estherae*, and 46 *M. zebra* broods (Fig. 3a).

C. horei was parasitized significantly less than the three natural allopatric species combined (Logistic regression, $p < 0.05$, Fig. 3b). Pairwise comparisons showed that *C. horei* was parasitized significantly less than *M. zebra*, and marginally significantly less than *H. latifasciatus* (Logistic regression, $p < 0.05$ and $p = 0.07$, respectively, Fig. 3a). *M. zebra* was parasitized at a significantly higher percentage than all other host species except for *H. latifasciatus* (Logistic regression, $p < 0.05$, Fig. 3a).

Number of catfish eggs

We found means of 7.5 catfish eggs per parasitized *C. horei* brood, 6.9 catfish per parasitized *H. nubilus* brood, 5.9 catfish per parasitized *H. latifasciatus* brood, 7.9 catfish per parasitized *M. estherae* brood, and 11.7 catfish per parasitized *M. zebra* brood (Fig. 4). The aquarium strain *M. zebra* had a significantly greater number of catfish eggs per parasitized brood than all of the other host species (Poisson regression, $p < 0.05$, Fig. 4). *M. estherae* also had a significantly greater number of catfish eggs per parasitized brood compared to *H. latifasciatus* (Poisson regression, $p < 0.05$, Fig. 4). The number of catfish eggs per parasitized brood of *C. horei* was not significantly different than any other fish species except for *M. zebra* (Poisson regression, $p < 0.05$, Fig. 4).

Discussion

Natural populations

C. horei was parasitized less (17%) than the three natural allopatric species combined (28%) and had a mean number of 7.5 catfish eggs per parasitized brood. Sato (1986) found comparable values of a 15% parasitism rate and average number of catfish eggs or fry per parasitized brood of 6.3 for *C. horei* in field studies in Lake Tanganyika. Subtle differences in the mating ritual and oviposition between species may help explain the disparity in parasitism frequencies we recorded. For example, Ochi (1993) described breeding behaviors of *C. horei* that are unique among mouthbrooders, noting that they spend up to 24 min before and after actual spawning engaging in displaying/mating behaviors without oviposition occurring. Furthermore, Ochi (1993) found that *C. horei* males defend females until leading them to a remote spawning site rather than waiting for females to enter a defended territory. These

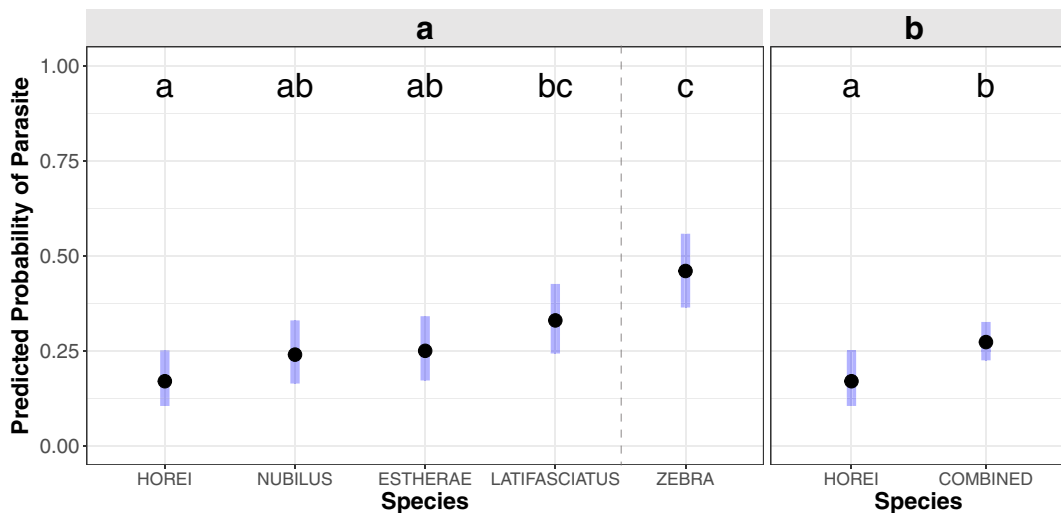


Fig. 3 Predicted probabilities and 95% confidence intervals of parasitism among the five species studied (panel a) and between the sympatric species *C. horei* and the combined allopatric species *H. nubilus*, *H. latifasciatus*, and *M. estherae* (panel b). Note that the dashed vertical line in panel A separates the natural

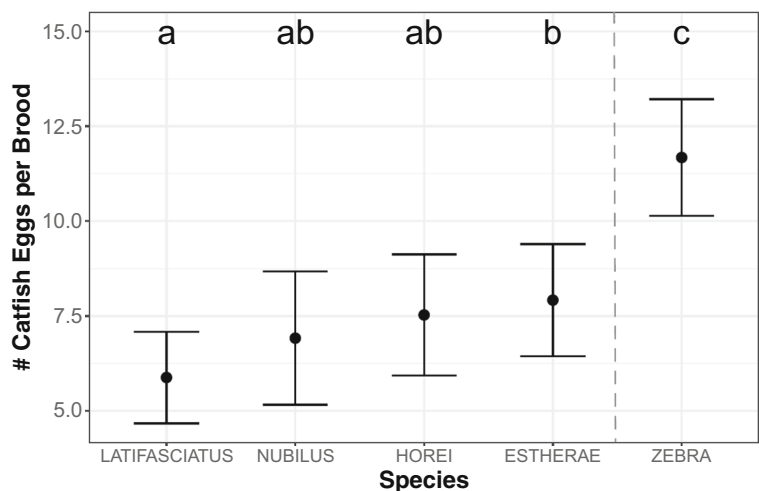
populations from *M. zebra*, an unnatural albino aquarium strain. Different letters within each panel represent significant ($p < 0.05$) or marginally significant ($p = 0.07$ *C. horei* – *H. latifasciatus*) pairwise differences from Tukey contrasts of logistic regression models

distinctive spawning activities of *C. horei* could present a moving target for the cuckoo catfish to locate and subsequently make it difficult for the catfish to then synchronize their parasitism with the timing of cichlid spawning. Interestingly, the parasitism rate and number of catfish per brood that Sato (1986) found for *C. horei* were the highest among the six Tanganyikan host species he surveyed. Other behavioral differences between host species, such as aggression, may help provide an explanation for the lower frequency of parasitism we detected in *C. horei*. Studies of cuckoos and cowbirds suggest that host aggression can be an effective behavior

to discourage brood parasites, and egg acceptor species appear more aggressive than their egg rejecting counterparts (Robertson and Norman 1976, 1977; Davies and Brooke 1989; Rothstein 1990).

It is unclear whether Tanganyikan host species, like *C. horei*, have coevolved aggression as a specific adaptation against brood parasitism from the cuckoo catfish, or if they are simply aggressive towards any perceived threat (e.g., predators). Barlow (2000) suggests that female cichlids evolving defenses specifically in response to brood parasitism might not be feasible, considering females cannot be selective in what they are picking up

Fig. 4 Mean (\pm standard error) number of catfish eggs in each parasitized brood for each of the five species. Species are sorted from left to right by the mean number of catfish eggs per brood. Note that the dashed vertical line separates the natural populations from *M. zebra*, an unnatural albino aquarium strain. Different letters represent significant ($p < 0.05$) pairwise differences from Tukey contrasts of Poisson regression models



and have to gather the eggs into their mouths so quickly (often before they are even fertilized) in order to prevent predation. It is unknown whether male cichlids are able to discriminate between a brood parasite and a potential predator or not, as they show aggression towards multiple threats to the spawning site. Furthermore, aggression in birds is also often a more universal response towards any nest invader, rather than a coevolved response to brood parasites, and being aggressive can at times be maladaptive for the host (Rothstein 1990). *C. horei* males are noticeably more aggressive than the other cichlid species we studied towards both the catfish and conspecifics, including both rival males and the females in their harem (pers. obs.). So, while useful for limiting parasitism, *C. horei* may just be a more aggressive cichlid species. The differences observed between the sympatric *C. horei* and the other host species (all allopatric) could be related to the fact that *C. horei* evolved with the cuckoo catfish and may have adaptations to minimize parasitism. Future studies will need to look at several Tanganyikan cichlids in comparison with cichlid species from other Rift Valley lakes to see if this is the case.

The sampling done by Sato (1986) in Lake Tanganyika and the results presented here represent only a glimpse of the possible variation in parasitism response by cichlid hosts. The distributions of the cuckoo catfish and mouthbrooding cichlid species in Lake Tanganyika are largely unknown, and could be important in determining what effects parasitism is having on localized cichlid populations. While endemic cichlid species represent the majority of the fish fauna, there are few species that are considered ubiquitous throughout Lake Tanganyika, which is primarily due to complex species interactions as well as the topography of the littoral zones where the cichlids are predominantly found (Fryer and Iles 1972; Sturmbauer et al. 2008). For cichlid species with limited distributions or small populations the consequences of parasitism could be severe. It is possible that the data provided by Sato (1986) may have been obtained in areas rich in the few species he sampled, and that the extent of the effect of cuckoo catfish parasitism could be very different in other regions of the lake. While many cichlid species in the Rift Valley lakes are stenotopic and philopatric (Ribbink 1990), the cuckoo catfish have been filmed traveling in large shoals among the rocky shores looking for cichlids to parasitize, and have been collected for the aquarium trade from multiple locations around the lake (Questar-Inc. 2000).

Albino zebra study

We found that the broods of the albino morph of *M. zebra* contained significantly more catfish eggs per brood (mean = 11.7 per brood) than the other host species. More importantly, we found that the parasitism rate of *M. zebra* (46% of broods) was nearly double the average rate of the other allopatric host species examined, and nearly three times (2.7) the rate of *C. horei*, the sympatric species. It is important to note that aquarists have selectively bred the albino morphotype for many generations. Thus, these fish are likely highly modified compared to wild caught specimens of the normal morphotype, possibly resulting in the loss of certain behaviors such as aggression.

Slavik et al. (2016), for example, observed agonistic behavior in albino and pigmented *Silurus glanis* catfish and found that the total number of aggressive interactions was lower in albinos than in pigmented catfish. Their results are also consistent with other findings showing that albinism has pleiotropic effects that are mediated through hormones that can affect both skin pigmentation and aggressive behaviour (Ducrest et al. 2008). Loss of pigmentation may not only be linked to aggression in albinos, but also have other pleiotropic effects such as impaired eyesight (Slavik et al. 2016).

The question of how vision affects the ability of hosts to avoid brood parasitism, if at all, is not understood, but albinism and the absence of eye pigmentation can be associated with poor vision in many species (Lashley 1930; Wahlsten 1972; Wilson et al. 1988; Abadi and Pascal 1991; Ren et al. 2002). If the albino *M. zebra* suffers from reduced visual acuity, then it is possible they cannot detect the catfish as well as the other cichlid species, possibly leading to the much higher level of parasitism we observed.

Concluding remarks

Although the exact underlying mechanisms driving the differential parasitism frequencies we observed (i.e. opportunity, quality of hosts, tempero-spatial aspects of parasitism, male to female ratio, aquarium size) are uncertain, it is clear that individual host species respond differently to the cuckoo catfish.

The cuckoo catfish has a very specialized system of brood parasitism, but they are generalists in regard to their selection of hosts to parasitize. This aspect of their behavior allows for them to parasitize mouthbrooders

from allopatric areas. Thus the cuckoo catfish-cichlid system provides a model for testing brood parasitism in a laboratory setting.

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Compliance with ethical standards

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

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