The biology and impacts of Oreochromis niloticus and Limnothrissa miodon introduced in Lake Kariba
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Comparative aggression and dominance of *Oreochromis niloticus* (Linnaeus, 1758) and *Oreochromis mortimeri* (Trewavas, 1966) from paired contest in aquaria

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**Abstract**

*Oreochromis niloticus* was introduced in Lake Kariba, and it displaced the endemic *Oreochromis mortimeri* from many areas of the lake. Studying the interaction between the two species sheds light on the nature of the displacement process. The levels of aggression within and between the two species and the effect of relative size were studied in the laboratory. *O. mortimeri* attacked *O. niloticus* first in most of the encounters whether it was the bigger or smaller of the pair. In encounters where *O. niloticus* was smaller, 2 (8.3%) *O. niloticus* made the first bite and 8 (40.0%) made the first bite when *O. niloticus* was the bigger of the pair. Over a 30-min encounter, *O. mortimeri* was dominant and delivered significantly more bites (7.79 ± 2.31 bites) than *O. niloticus* (4.53 ± 1.53 bites) ($p = 0.03, t = 2.18$). Unlike *O. mortimeri*, *O. niloticus* attacked first only when it was considerably bigger than the opponent. The association of large body size with higher aggression may mean that *O. niloticus*, which grows faster and larger than *O. mortimeri*, has size advantage. Therefore, interaction between the two species may be complex, and aggression may be just one of the factors that affect the interaction of these fish species.
Introduction

A cichlid endemic to the Zambezi system, *Oreochromis mortimeri* (Trewavas 1966) became abundant in Lake Kariba soon after its formation on the Zambezi River in 1957 for the purpose of generating hydroelectricity. In an unpublished report (1959), only 0.75% of the fish caught were *O. mortimeri*, and by 1962, the catch had risen to 35% of the total (Kenmuir 1984). In the 1980s, accidental introductions of *Oreochromis niloticus* (Linnaeus 1758) through escapees from fish ponds in Kariba resulted in the establishment of *O. niloticus* in the lake by 1993 (Chifamba 1998). With the introduction of *O. niloticus*, the once abundant *O. mortimeri* (Trewavas 1966) declined and disappeared in many parts of the Lake Kariba (Zengeya & Marshall 2008). Therefore, it was essential to investigate the attributes that may have imparted competitive advantage to the exotic species, enabling it to dominate over the native fish species.

Various studies suggest that the displacement of an indigenous species by an introduced species may be associated with similarities between the exotic and indigenous fish species. Similarity in diet and reproductive behaviour can stimulate aggressive behaviour. Both species feed on algae, organic detritus, plant material, insects and zooplankton, varying with availability (Chifamba 1998; Mhlanga 2000). In both species, males construct large nests in arenas which they defend (Marshall 2011). A female visits the arena and, after courtship that lasts a few minutes, lays eggs in the nest and after fertilization takes the eggs into her mouth for brooding. Fry are released by the mother into nursery areas, in the shallow inshore waters. Therefore, *O. niloticus* and *O. mortimeri* share food as well as nesting and nursery areas, which are contestable resources.

An introduced species can displace the native species through interspecific competition for space and food, intraguild predation and agonistic interaction (Taniguchi et al. 2002; Martin et al. 2010; Sanches et al. 2012; Kakareko et al. 2013). A native fish of the estuaries of the Gulf of Mexico, the redspotted sunfish, *Lepomis miniatus* (DS Jordan 1877), was displaced from the preferred structured habitats by the agonistic behaviour of the introduced *O. niloticus*, thus exposing it to higher predation. In Brazil, *O. niloticus* was also shown to be more aggressive than the native pearl cichlid, *Geophagus brasiliensis* (Quoy & Gaimard 1824), with which it has an overlapping ecological niche (Sanches et al. 2012). Relative aggressive tendencies of *O. niloticus* and *O. mortimeri* which were not known yet, might explain the competitive advantage of the former, and hence the need for the study.

Dominance status in fish is associated with growth rate (Abbott & Dill 1989; Tiira et al. 2009). Given the same amount of food, ten of twelve dominant steelhead trout, *Salmo gairdneri* (Richardson 1836), grew faster than their paired subordinates (Abbott & Dill 1989). Tiira et al. (2009) found that dominance status affected growth
in brown trout, *Salmo trutta* (Linnaeus 1758) populations, with individuals of the lowest ranks growing less compared to those of a higher rank. Further, Alvarenga & Volpato (1995) noted a significant association between some agonistic profiles and metabolism.

Reproductive success is also higher in dominant fish because they occupy the best nesting sites which attract mates (Philippart & Ruwet 1982; Seppänen *et al.* 2009). For example, breeding males in African cichlids make and fiercely defend nests in an arena. The best nests are suitably positioned for visits by females and are occupied by dominant males (Phillippart & Ruwet 1982). Compared to subordinate males, dominant male *O. niloticus* had the highest gonadosomatic index and higher levels of gonadotropins hormones that trigger spermatogenesis, whereas the subordinate had reduced gene expression of key factors for steroid production (Pfemmig *et al.* 2012), thus compromising the latter’s reproductive capacity. Aggression and dominance could have thus conferred a competitive advantage to the invader, *O. niloticus*, enabling it to displace *O. mortimeri*.

In their seminal paper on cichlid aggression behaviour, Baerends & Baerends-van Roon (1950) present ethograms for several species. The various acts of aggression generally include charging, chasing, biting and displaying. Aggression levels can be mild, consisting of threats or explicit, when the fish bite each other. In an established dominance relationship, the fish no longer participate in simultaneous or reciprocal threatening. Instead, the subordinate fish displays fleeing and escaping behaviour when approached by the dominant; the dominant chases and bites the subordinate (Miklosi *et al.* 1995; Oliveira & Almada 1996a).

We hypothesized that aggressive behaviour is one mechanism *O. niloticus* used to displace the native species *O. mortimeri* in Lake Kariba. The study investigated the aggression interaction of the two species in order to evaluate the role of aggression and dominance on the competitive advantage to *O. niloticus* over *O. mortimeri*.

**Materials and methods**

Live specimens of the two fish species, *O. niloticus* and *O. mortimeri*, were captured from Lake Kariba in 2005 and 2007 (more than 10 years after *O. niloticus* were known to have been established in the lake) and kept separately for more than a month in fish tanks, prior to the experiments. The water was aerated and maintained at temperature between 21.5 and 25.5 °C which was within the range of surface temperatures, between 21 and 28 °C, in Lake Kariba (Chifamba 2000). The fish were fed commercial pellets, to satiation, twice a day.

Fish used in the experiments were sub-adults: 6.9 – 14.9 and 9.3 – 14.3 cm long for *O. niloticus* and *O. mortimeri*, respectively. In Lake Kariba, *O. niloticus* grows to an asymptotic length of 44.6 cm and *O. mortimeri* 36.8 cm (Chapter 3 – Chifamba.
&Videler 2014). Only those fish without breeding colouration were used in the experiment because breeding behaviour would contribute to observed agonistic behaviour. Males, for example, become more aggressive when breeding and defending a breeding site (Marshall 2011). Three sets of experiments were conducted in a glass aquarium measuring 60 × 20 × 30 cm.

**Experiment 1: aggression assessment of O. mortimeri**

The objective was to assess the reaction of *O. mortimeri* to *O. niloticus* of different size and weight. The weight and total length were measured at the beginning of each trial, and pairs with matched size and weight were classified as same. The difference in weight and length of a pair was expressed as a proportion (%) of the length and weight of each fish of the pair. Four *O. mortimeri* were each exposed to twelve different *O. niloticus* of varying size and weight. *Oreochromis niloticus* used in the experiment weighed 28 – 107 g and were 7.9 – 14.2 cm long, whilst the four *O. mortimeri* were 36 – 66 g and 10.5 – 14.3 cm, respectively. These fish were scooped out of the holding aquarium, one at a time, to obtain *O. niloticus* smaller than, bigger than, or the same size as the *O. mortimeri* with whom they were confronted. As such, there were pairs where *O. niloticus* was bigger than, smaller than, or the same size as the *O. mortimeri*.

With each fish pair placed in the experimental tank at the same time, aggression was recorded for 10 min, starting from the time when the pair was placed in the aquarium. Acts of aggression used for scoring are similar to those identified by Baerends & Baerends-van Roon (1950). In this experiment, aggression was scored as the total number of attacks per fish, where a scored attack for each fish was any of the following: chasing, biting, mouth wrestling or side swiping. A bite was scored when the mouth of a fish touched that of the opponent irrespective of whether the fish was initiating or retaliating an offence.

**Experiment 2: intraspecific aggression (biting)**

The objective of the second experiment was to assess the level of aggression within a species. Sixteen pairs of unsexed *O. niloticus* from 17.4 to 60.2 g (6.9 – 13.9 cm length) and twelve of *O. mortimeri* from 22.9 to 77.0 g (9.3 – 16.0 cm standard length), respectively, were used. The same procedure of staging the confrontation was followed as in Experiment 1, except that each fish was confronted with another of the same species. During the experiment, each individual fish in a pair could be distinguished by size and colouration. Scoring was based on the number of bites made by each fish from the onset of the encounter. The bites were recorded for 30 min at 1-min intervals during the encounter.
Experiment 3: interspecific aggression biting and dominance

The aggression level between *O. niloticus* and *O. mortimeri* was compared using 64 pairs, each containing both species. The length (cm) of each fish was recorded, and the sex determined by examining the genital papilla. *Oreochromis niloticus* used in the experiment weighed 35.8 – 70.4 g and were 10.0 – 12.5 cm long, respectively. The ranges of *O. mortimeri* were 40.1 – 67.8 g and 10.5 – 14.0 cm. The level of aggression was scored as the number of bites made by each fish, at 1-min intervals during the encounter. Similar to intraspecific aggression, scoring was based on only the number of bites because these were easy to distinguish without ambiguity compared to attacks. The first bite was taken to signify the start of the aggressive encounter. The first bite, the time it was executed, and the fish that made it were noted and recorded for all pairs. At the end of the 30 min, the dominant fish was also noted. As in studies by Oliveira & Almada (1996a) and Corrêa et al. (2003), dominance was defined as
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when, within the pair, the fish no longer attacked or threatened each other, or when the ‘subordinate’ fled when approached by the ‘dominant’.

Statistical analysis
The mean number of attacks or bites, time of first bite and dominance of O. niloticus and O. mortimeri were tested for similarity using t-tests against a probability level of p = 0.05. The effect of species, sex and the difference in weight were statistically analysed simultaneously in a multivariable General Linear Model, using SPSS.

Results

Experiment 1: aggression assessment of O. mortimeri
Different trends in the number of attacks according to differences in relative weight and length were observed in the two species. Overall, O. mortimeri attacked significantly more times than O. niloticus (p = 0.035, t = 2.19, n = 52). Both species attacked more when one species was bigger than the other in a pair (Figure 5.1). Also, the number of attacks increased as the difference in size decreased to zero in O. mortimeri, especially when compared according to weight rather than to length (Figure 5.1a, b). However, there were almost no attacks when O. niloticus was the smaller of the pair, and the attacks were highest when it was bigger (Figure 5.1c, d).

Experiment 2: intraspecific aggression (biting)
The intraspecific aggression experiment revealed different levels of within-species aggression. The bites scored confirmed the higher aggression of O. mortimeri (Figure 5.2a, b). When statistical tests were conducted on results obtained from pairs of the same species, the mean number of bites of O. niloticus was again significantly lower than that of O. mortimeri (p = 0.025, t = -2.30, n = 56; Table 5.1).

Experiment 3: interspecific aggression (biting and dominance)
Different aggression trends according to size and species were recorded in this experiment. Body size determined the number of bites with the larger individuals mostly at an advantage (Figure 5.2c, d). There was a tendency for O. niloticus biting only when it was the larger in the pair (Table 5.1). On the other hand, whether larger or smaller in the pair, O. mortimeri bit the opponent almost the same amount of times, whereas for O. niloticus, relative size mattered more. When larger, O. mortimeri bit an average of 7.25 versus 7.32 times when smaller; yet, O. niloticus, when larger, bit 7.17 times and only 2.31 times when smaller (Table 5.1). The mean number of bites by O. mortimeri was higher than that of O. niloticus even when O. niloticus was the bigger of the pair (Figure 5.3a). Disregarding differences in size, O. mortimeri attacked significantly more times than O. niloticus (p = 0.03, t = 2.18, n = 128).
Table 5.1 Mean number of bites, number of pairs and 95% Confidence interval (CI) of bites from each species, in different pairing of species and size, in the intra- and interspecific experiments.

<table>
<thead>
<tr>
<th>Species</th>
<th>Species paired</th>
<th>Relative size</th>
<th>Mean bites</th>
<th>n</th>
<th>Lower CI</th>
<th>Upper CI</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>O. niloticus</em></td>
<td><em>O. niloticus</em> &amp; <em>O. niloticus</em></td>
<td>Larger</td>
<td>5.75</td>
<td>16</td>
<td>3.46</td>
<td>7.92</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Smaller</td>
<td>3.31</td>
<td>16</td>
<td>1.47</td>
<td>5.46</td>
</tr>
<tr>
<td></td>
<td></td>
<td>All</td>
<td>4.53</td>
<td>32</td>
<td>3.04</td>
<td>6.03</td>
</tr>
<tr>
<td><em>O. mortimeri</em></td>
<td><em>O. mortimeri</em> &amp; <em>O. mortimeri</em></td>
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<td>9.67</td>
<td>12</td>
<td>5.67</td>
<td>14.18</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Smaller</td>
<td>5.92</td>
<td>12</td>
<td>3.70</td>
<td>8.50</td>
</tr>
<tr>
<td></td>
<td></td>
<td>All</td>
<td>7.79</td>
<td>24</td>
<td>5.52</td>
<td>10.50</td>
</tr>
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<td><em>O. mortimeri</em></td>
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<td>7.43</td>
<td>28</td>
<td>5.23</td>
<td>9.60</td>
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<tr>
<td></td>
<td></td>
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<td>2.25</td>
<td>36</td>
<td>0.38</td>
<td>4.12</td>
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<tr>
<td></td>
<td></td>
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<td>4.52</td>
<td>64</td>
<td>3.99</td>
<td>6.04</td>
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<tr>
<td><em>O. mortimeri</em></td>
<td><em>O. mortimeri</em> &amp; <em>O. niloticus</em></td>
<td>Larger</td>
<td>7.25</td>
<td>36</td>
<td>5.14</td>
<td>9.36</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Smaller</td>
<td>7.32</td>
<td>28</td>
<td>4.46</td>
<td>10.80</td>
</tr>
<tr>
<td></td>
<td></td>
<td>All</td>
<td>7.28</td>
<td>64</td>
<td>5.61</td>
<td>8.96</td>
</tr>
</tbody>
</table>

Figure 5.2 Number of bites from *O. niloticus* and *O. mortimeri* against the relative difference in size, in experimental setup: a) *O. niloticus* alone, b) *O. mortimeri* alone, c) *O. niloticus* interspecific and d) *O. mortimeri* interspecific (Dashed lines denote % difference 10 units class means).
Figure 5.3 The mean number of attacks by *O. niloticus* (N) and *O. mortimeri* (M) in different sex combinations and where either *O. mortimeri* or *O. niloticus* was bigger: a) all data, b) *O. niloticus* is female and *O. mortimeri* is male, c) both are male and d) *O. niloticus* is male and *O. mortimeri* is female. Bars are standard error of means.

In mixed sex contests, female *O. niloticus* bit *O. mortimeri* more than those in other combinations (Figure 5.3b, d). No similar difference occurred when an *O. niloticus* male was paired with an *O. mortimeri* female. When both species were male, the smaller *O. niloticus* bit *O. mortimeri* the fewest times (0.5 times).

The mean time to first bite from *O. niloticus* was 13.1 min which was significantly higher than that of *O. mortimeri* at 9.6 min (*p* = 0.04; *t* = -2.12, *n* = 70). There was a delay in biting when the fish were about the same size compared to when the size difference was large (Figure 5.4). For *O. niloticus*, the time at first bite decreased exponentially with positive difference in fish weight (*R*² = 0.546; *p* = 0.000). The other trends in Figure 5.4 are not significant, even though for *O. mortimeri* there is a similar downward trend in the time at first bite with positive difference in weight.

Fewer *O. niloticus* than *O. mortimeri* made the first bite when paired with either a much smaller or much larger *O. mortimeri*. In encounters where *O. niloticus* was larger, eight (40%) made the first bite compared to two (8.3%) when *O. niloticus* was the smaller. In all the encounters, the worst injury was the loss of a few scales, which rarely occurred.
Attacks ended when the dominant fish chased the subordinate fish and swam round the whole aquarium tank, while the latter used a small section of the tank, hardly moving away from that position. Except in three cases, dominance was established by the end of the observation period. Figure 5.5 shows that most of the time *O. mortimeri* was dominant when it was bigger compared to *O. niloticus*. Eleven smaller *O. mortimeri* became dominant when compared to one smaller *O. niloticus*.

The species, more so difference in weight, significantly affected the number of bites and dominance status (Table 5.2). Judging on the *p*-values, these differences were more pronounced for dominance compared to the number of bites.
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Figure 5.5 The dominance status of a pair of *O. niloticus* and *O. mortimeri* of different weight for each encounter. The line represents similar weight below which *O. niloticus* is bigger and above smaller.

<table>
<thead>
<tr>
<th>Source</th>
<th>Type III sum of squares</th>
<th>df</th>
<th>Mean square</th>
<th>F</th>
<th>p (95%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Corrected model</td>
<td>Bites (30 min)</td>
<td>655.7</td>
<td>3</td>
<td>218.6</td>
<td>5.7</td>
</tr>
<tr>
<td></td>
<td>Dominance</td>
<td>15.1</td>
<td>3</td>
<td>5.0</td>
<td>10.1</td>
</tr>
<tr>
<td>Intercept</td>
<td>Bites (30 min)</td>
<td>492.7</td>
<td>1</td>
<td>492.7</td>
<td>12.7</td>
</tr>
<tr>
<td></td>
<td>Dominance</td>
<td>2.4</td>
<td>1</td>
<td>2.4</td>
<td>4.8</td>
</tr>
<tr>
<td>Weight difference (%)</td>
<td>Bites (30 min)</td>
<td>337.0</td>
<td>1</td>
<td>337.0</td>
<td>8.7</td>
</tr>
<tr>
<td></td>
<td>Dominance</td>
<td>9.5</td>
<td>1</td>
<td>9.5</td>
<td>19.1</td>
</tr>
<tr>
<td>Sex</td>
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<td>1</td>
<td>43.5</td>
<td>1.1</td>
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<td></td>
<td>Dominance</td>
<td>0.0</td>
<td>1</td>
<td>0.0</td>
<td>0.1</td>
</tr>
<tr>
<td>Species</td>
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<td>1</td>
<td>163.9</td>
<td>4.2</td>
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<tr>
<td></td>
<td>Dominance</td>
<td>3.1</td>
<td>1</td>
<td>3.1</td>
<td>6.3</td>
</tr>
</tbody>
</table>

Discussion

*Oreochromis niloticus* was found to be less aggressive than the native *O. mortimeri*, contrary to expectations based on that the former species displaced the latter from Lake Kariba. Taniguchi *et al.* (2002), Martin *et al.* (2010), Sanches *et al.* (2012) and Kakareko *et al.* (2013) explained how an introduced species can displace a native
species through interspecific competition for space and food, intraguild predation and agonistic interaction. For instance, a native fish of the estuaries of the Gulf of Mexico, redspotted sunfish (*Lepomis miniatus*), was displaced by the agonistic behaviour of the introduced *O. niloticus* from preferred structured habitats to exposed ones, where it might have suffered higher predation (Martin *et al.* 2010). The level of aggression displayed by *O. niloticus* may depend on the species it confronts or other factors such as size for advantage in an encounter.

The level of aggression and dominance can also be predicted from size, with larger fish exhibiting more aggression and often becoming dominant as shown in this and other studies (Turner & Huntingford 1986; Neat *et al.* 1998a; Cutts *et al.* 1999). Larger opponents won 35 of the 38 encounters of *Oreochromis mossambicus* (WKH Peters 1952) pairs in the study by Turner & Huntingford (1986). They also reported a weak and negative relationship between relative body size and the intensity of a fight. In our study, there was a tendency for the number of bites to increase with increase in size asymmetry. The time of the first attack by *O. niloticus* was shorter at high size asymmetry than at the lower end, demonstrating the tendency for large fish to be aggressive. Neat *et al.* (1998b) demonstrated that high size asymmetry is associated with greater cost because a large fish has more strength and ability to inflict more harm or cost to a smaller opponent through dislodging of scales and high accumulation of lactic acid in the muscles. This means that it is more costly for the smaller fish to contest against a larger fish when size asymmetry is high and domination of the smaller fish more possible. It also means that *O. niloticus* which grows faster and larger than *O. mortimeri* (Chapter 3 – Chifamba & Videler 2014) may have size advantage. Faster growth means that *O. niloticus* at any given age has a size advantage which we have shown to be significantly associated with number of bites and dominance. Being large, aggressive and dominant can determine growth and ability to acquire quality territories (Koebele 1985; Abbott & Dill 1989; Cutts *et al.* 1999). Baras & Lucas (2010) found a significant, positive relationship between individual growth and aggression or boldness in a study of individual growth trajectories of sibling *Brycon moorei*. (Steindachner 1878) raised in isolation since egg stage. Growth in aggressive fish can be a result of high food intake and growth efficiency (Carline & Hall 1973; Li & Brocksen 1977; Ejike & Schreck 1980). Dominant *O. niloticus* males had higher expression of factors important for steroid production, and gonadotropin that triggers spermatogenesis (Pfennig *et al.* 2012). Being aggressive and dominant must mean that *O. mortimeri* had an advantage over *O. niloticus* through better access to food and territories, which are important for nest building and mating. Although investment in a nest was related to female mate choice in *O. niloticus*, deprivation of nest, achieved by not providing gravel substrate, did not affect mating success (Mendonça & Gonçalves-de-Freitas 2008). Furthermore, aggression and confrontation are not always advantageous because it comes at an energetic cost for both winners and losers (Neat *et al.* 1998b). An
example of such cost was reported by Turner (1986) where dominant male *O. mossambicus* that held and defended territories in a tank, displayed less growth than the subordinate males. Therefore, high aggression may have an energetic cost for *O. mortimeri*.

Sex and the stage in the development of gonads affect the level of aggression in cichlids (Oliveira & Almada 1996b; Neat *et al.* 1998a). Smaller size *Tilapia zillii* (Gervais 1848) were more aggressive when gonads were at an advanced stage of development (Neat *et al.* 1998a). Sexual dimorphism in aggression occurs in a closely related cichlid, *O. mossambicus*, where the males display more agonistic behaviour than the females (Oliveira & Almada 1996b). In nature, there is a general preference for the own species as shown in mangrove killifish, *Kryptolebias marmoratus* (Poey 1880) — preferential association and reduced aggression towards members of their own genotype, compared to members of a different genotype (Edenbrow & Croft 2012). This may explain the sex difference observed in this study.

The laboratory techniques used in this study of aggression limit the application of the findings to nature, due to the unnatural conditions the fish were subjected to during the experiment. Experimental studies using different techniques either in the field or in the laboratory, are essential in the acquisition of knowledge of fish behaviour (Rowland 1999). Laboratory experiments enable the manipulation of the independent variables to test hypotheses and to elucidate the cause and effect relationships as done in this study. This manipulation of the environmental conditions in the laboratory might affect the results. Hence, the results in this behaviour study might not directly apply in the field, and this needs to be borne in mind when interpreting the results. Direct field observations ought to be done to increase our understanding of the interactions of *O. mortimeri* and *O. niloticus*. Almeida & Grossman (2012) reviewed studies where the direct methods were used and recommended them for studying the interaction between invasive and native species.

**Conclusion**

This research gives insight on the agonistic interaction between the introduced *O. niloticus* and the native *O. mortimeri*. Although *O. niloticus* is less aggressive, this seeming disadvantage may be compensated by being larger at a given age than *O. mortimeri*. Because *O. niloticus* was not dominant, aggression may not have been the most important factor in the displacement of *O. mortimeri* in Lake Kariba. The interaction between these two species is likely to be complex, involving a number of possible mechanisms that caused the disappearance of the native species that ought to be investigated. There is also need for research work on the effect of aggressive interaction on reproduction and feeding, hence fitness.
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Compliance with ethical standards

Ethical approval This research was approved by the Animal Research Ethics Committee in the Department of Livestock and Veterinary Services, Ministry of Agriculture, Mechanization and Irrigation Development. All procedures used in the research complied with the laws set out by the Animal Research Ethics Committee.
PART II

Biology and Impacts of *Limnothrissa miodon*