

Temperature-dependent feeding interactions between two invasive fishes competing through interference and exploitation

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Abstract Context-dependent ecological interactions between invasive species are important in determining the outcomes of their introductions. The consequences of competitive interactions between the Nile tilapia *Oreochromis niloticus* (interference competitor) and common carp *Cyprinus carpio* (exploitative competitor) were investigated here across a temperature gradient (20–28°C). These highly invasive fish are now present in many regions where populations increasingly coexist, inducing trophic interactions and niche overlaps. Experimental feeding and growth trials revealed the feeding rate (items s⁻¹) and specific growth rate (% day⁻¹) of these fishes were not significantly different at 24°C, but were significantly higher for *C. carpio* at 20°C and significantly higher

for *O. niloticus* at 28°C. An additional experiment completed at 24°C revealed that *O. niloticus* rapidly form hierarchies, where dominant fish monopolise food resources through interference, resulting in their faster growth. Introductions of 1 and 3 *C. carpio* (an exploitative competitor) into the hierarchy had no effect on this food monopolisation as carp were excluded through aggression. The addition of 6 *C. carpio* did, however, significantly reduce the food intake of the dominant tilapia. This was due to increased exploitative competition rather than breaking of the hierarchy. The effect of adding 3 *O. niloticus* was similar to 6 *C. carpio*, suggesting inter- and intra-specific competitive strength was similar. These findings suggest when populations co-exist, temperature-dependent feeding interactions may result in the competitive exclusion of *C. carpio* through the aggressive interference by *O. niloticus*, potentially influencing invasion outcomes.

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Introduction

Competition is a major process structuring animal communities, with intra- and interspecific competition potentially impacting the fitness of individuals and, subsequently, population functioning (Kennedy and

Strange 1986; Canario et al. 1998). Increased interspecific competition may be triggered by introductions of alien species that compete with resident species in the recipient communities (Simon and Townsend 2003) and so may affect the outcome of the introduction and its ecological consequences (Crowl et al. 1992; Fausch 1998; Cucherousset and Olden 2011). Competition is most likely to occur and/or stronger in situations where species overlap in their trophic niches when food resources are limited (Bøhn et al. 2008). When competition is high, the weaker competitor may incur decreased feeding rates (Bøhn and Amundsen 2001) and reduced growth rates (Diehl and Eklov 1995), or even be displaced through competitive exclusion (Bøhn et al. 2008). The outcome of interspecific competition is, however, not just determined by the characteristics of available resources but also by the behavioural and physiological traits of the species concerned, and environmental variables such as temperature (Dick et al. 1993; Wijnhoven et al. 2003; Van der Velde et al. 2006).

Competition principally occurs through two modes; a direct mode of competition is interference, where a species interacts aggressively for resources, with more aggressive individuals excluding weaker ones leading to resource monopolisation and, potentially, competitive exclusion (Schoener 1983). By contrast, exploitative competition, in which species have similar feeding modes and/or are in the same trophic guild, all have access to the resource and exploit it non-aggressively, resulting in a general reduced resource availability and feeding rate for individuals (Connell 1983; Schoener 1983). In assessing the consequences of these competitive processes following an introduction, effects of interference competition have been measured through the displacement of coexisting species into inferior foraging sites (Baxter et al. 2007), reduced foraging behaviour of coexisting species (Lawler et al. 1999) and the disruption of existing dominance hierarchies in the coexisting species (Blanchet et al. 2007a). For exploitative species, competition generally increases as the population density of the invader increases, with effects of, for example, reduced growth rates (Britton et al. 2011).

The fishes Nile tilapia *Oreochromis niloticus* (interference competitor) and common carp *Cyprinus carpio* (exploitative competitor) have been introduced around the world, mainly for aquaculture purposes,

with escapees and intentional releases resulting in invasive populations in many regions (Lever 1996). Invasive populations are increasingly coexisting in the wild, despite *O. niloticus* preferring higher water temperatures compared to *C. carpio* (Zambrano et al. 2006; Wilson et al. 2009). For example, coexisting populations are present in Mexico, where trophic interactions and niche overlap between these invaders have been observed (Zambrano et al. 2010). Furthermore, determining the outcomes of competitive interactions between invasive interference and exploitative competitors remains challenging, as they are likely to be highly context-dependent. For instance, temperature has already been revealed to be a major determinant of competitive superiority among fish species. Indeed, Taniguchi et al. (1998) revealed in laboratory experiments involving brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) that the two species were equal competitors for food at cold temperatures, but that brown trout were superior competitors as temperature increased (Taniguchi et al. 1998).

Consequently, the aim of this study was to experimentally investigate the outcomes of competitive interactions for feeding, and their subsequent consequences on growth rates, between invasive interference and exploitative competitors across a temperature range and under varying levels of competitor density. Outputs should then provide insights into the interactions of these species that share resources when in sympatry (Zambrano et al. 2010). The specific objectives were to determine: (i) their foraging and growth rates across a temperature gradient to quantify the competitive interactions across different environmental contexts; and (ii) the outcome for the food intake and growth rates of competitive interactions between *O. niloticus* and *C. carpio* in relation to propagule pressure under limiting food resource conditions.

Materials and methods

Experimental set up

Completion of the two objectives required three complementary experiments to be conducted in tank aquaria. The tanks were 45 l in volume with a water surface area of 0.14 m². Tanks were set up in vertical

columns with three tanks per column that enabled the use of a pump-driven, flow-through recirculation system in each column. The experiments were conducted at 20, 24 and 28°C to represent a temperature gradient that both species experience across their range. The light:dark cycle was 14:10 h. All fish were juveniles measuring between 85 and 110 mm at the commencement of experiments and were sourced from aquaculture. Individual fish were recognisable in tanks through their scale patterns (*C. carpio*) and colouration and size (*O. niloticus*), enabling individual data to be collected during experiments without using individual tagging. At the start of each experiment, the fish were measured (*C. carpio*: fork length, *O. niloticus*: total length, nearest mm, L) and weighed (nearest 0.1 g; W). Following their introduction into the tanks, the fish acclimatised for 14 days before the experimental trials. The experiments involved filming the responses of the fish to released food items for a maximum of 5 min, where the food items were pelletized fish meal—pellets—of 2 mm diameter. These were used as the sole food item for four principal reasons: (i) the sharing of food resources between the species has been observed in the wild, although the consequences of niche overlap for the growth of the species have not been quantified (Zambrano et al. 2010); (ii) preliminary feeding trials revealed that pellets were taken rapidly by both species when introduced to the tank and in preference to maggots and daphnia; (iii) they provided a homogenous, highly visible and non-mobile food source, assisting filming and enabling their consumption to be observed and fish foraging rates to be determined accurately; and (iv) pellets are used to feed both species in captivity). At the conclusion of each experiment (40 days), the fish were re-measured and re-weighed, and were not used again experimentally to avoid pseudoreplication in subsequent trials.

Experiment 1: feeding and growth rates of *Oreochromis niloticus* and *Cyprinus carpio*

In preliminary feeding trials, the feeding behaviour of *C. carpio* was inhibited when they were placed individually in the tanks (no response to released food items), whereas when three fish per tank were used they immediately responded to released food. Thus, three fish were used per tank as there was no observation of aggression between individuals during

trials, with mean feeding rates calculated per tank on each experimental occasion. In contrast, when three *O. niloticus* were used per tank, this resulted in the rapid establishment of a feeding hierarchy where the dominant fish took the majority of the food. Consequently, to measure a comparable feeding rate to *C. carpio* required *O. niloticus* to be placed individually in tanks to avoid these antagonistic feeding behaviours.

Feeding rate was measured through introducing the pellets into the tanks at densities of 20, 30, 40, 50, 70, 100 and 150 items per tank (equivalent to 148, 222, 296, 370, 519, 740 and 1,111 items m^{-2} , respectively) and filming the foraging behaviour of the fish for five minutes. Each food density was used on each *C. carpio* tank ($n = 18$) and individual *O. niloticus* ($n = 30$), and at each temperature to provide a minimum of 70 individual data points per temperature and per species. At the end of each filming, any uneaten food was removed immediately. On the days when the fish were not used in the feeding experiments described above, they were fed on a ration of pellets at 2% mean initial body weight. In the video analysis, the data recorded was the time between the fish taking its first and fifth food item; feeding rate was then determined as the number of items per second.

To determine the somatic growth rates of both species, the fish were fed as described above during the experimental trials; outside of the trials, they were fed equal quantities of food that equated to a mean 2% initial body weight per day. The growth rate of the fish was determined through the specific growth rate (SGR ; $\% \cdot day^{-1}$), calculated by $[\ln W_{end} - \ln W_{start}] / t \times 100$, where W_{start} and W_{end} were the individual weights at the start and at the end of each thermal period respectively, and t was the duration of the experimental period (40 days).

Experiment 2: hierarchical feeding and growth rate of *Oreochromis niloticus*

For this experiment, 15 tanks were used, each at 24°C and holding 3 *O. niloticus*. The experiment involved introducing 30 pellets into the tank following a 24 h starvation period and filming foraging behaviour until all food items were consumed. Data recorded from the videos was the proportion (%) of food taken by each individual fish and the extent of their interfering behaviours during feeding (e.g. chasing and fighting).

If a particular fish in each tank was observed to consistently take a higher proportion of food and displayed consistent interfering behaviour against its conspecifics, then this individual was defined as the dominant fish in the established feeding hierarchy.

To determine the effect of the hierarchies (if present) on growth rates, then feeding was at 2% mean body weight per day outside of days when feeding trials were being performed. The experiment ran for 40 days and as the fish were measured and weighed at the beginning and conclusion of the experiment, specific growth rate was also calculated. Thus, for the 15 tanks, the data available were the proportion of food items taken on each experimental occasion per individual fish (and by rank if a hierarchy was apparent) and their overall specific growth rate of each individual across the experimental period to enable the mean SGR to be determined by rank.

Experiment 3: hierarchical feeding of *Oreochromis niloticus* in presence of *Cyprinus carpio*

Initially, we planned to conduct this experiment to also include effects on growth through using cohabitation experiments between *O. niloticus* and *C. carpio*. However, the antagonistic and aggressive behaviours of *O. niloticus* towards *C. carpio* over extended periods meant this was not feasible from a welfare perspective. Correspondingly, 15 tanks containing 3 *O. niloticus* were set up and run at 24°C. Following establishment of their hierarchies according to feeding and aggression, the effect on this hierarchy of introducing different propagule pressures of *C. carpio* (1, 3 and 6 individuals) was tested and compared to the effect of introducing 3 *O. niloticus*, and a control where no fish were introduced. On each occasion, the additional fish were introduced into the tanks and allowed to acclimatise for 30 min. The feeding trial then commenced as per the previous experiment (release of 30 pellets) and the response of the fish was filmed. Once all the pellets were consumed, the trial ended and the additional fish were removed and placed back into their holding tanks. During analysis of the videos, data recorded were the combined proportion of food items taken by *O. niloticus* compared to *C. carpio*, and the proportion of food items taken by each *O. niloticus* according to their original hierarchy.

Statistical analyses

In all experiments, data were tested for normality before parametric tests were used to test for differences between experimental treatments (groups) whilst blocking the effect of covariates such as fish length and food density (as appropriate and reported in the *Results* section). Models were only considered valid and used subsequently in analysis when the assumptions were met that variances were equal between the groups (Levene's test, $P > 0.05$), there was no interaction between the covariates and the groups (homogeneity of the regression slope; $P > 0.05$) and post-hoc power analysis indicated statistical power > 0.8 . Where error is provided around mean values, they represent 95% confidence limits. All statistical tests were completed in SPSS v. 16.0.

Results

Experiment 1: feeding and growth rates of *Oreochromis niloticus* and *Cyprinus carpio*

There were no significant differences in the feeding rate of *O. niloticus* and *C. carpio* at 20 and 24°C, although in both cases feeding rate increased as temperature increased ($P > 0.05$; Fig. 1). Between 24 and 28°C, there was a difference between the species, with the feeding rate of *O. niloticus* significantly higher than *C. carpio* [ANCOVA: mean difference between the temperatures (pairwise comparisons with Bonferroni adjustment for multiple comparisons): 0.43 ± 0.13 items s^{-1} ; $P = 0.001$; Fig. 1]. There was a significant difference in the specific growth rate according to temperature between the species, with the growth rate of *O. niloticus* significantly increasing as temperature increased up to 28°C ($F_{2,18} = 10.24$, $P = 0.001$; Fig. 1). For *C. carpio*, specific growth rate was not significantly different across the temperature range ($P = 0.32$; Fig. 1).

Experiment 2: hierarchical feeding and growth of *Oreochromis niloticus*

Following the introduction and acclimatisation of 3 *O. niloticus* into each tank, their behaviour revealed the rapid formation of a hierarchy and comprised an aggressive dominant fish and two sub-ordinate fish, of

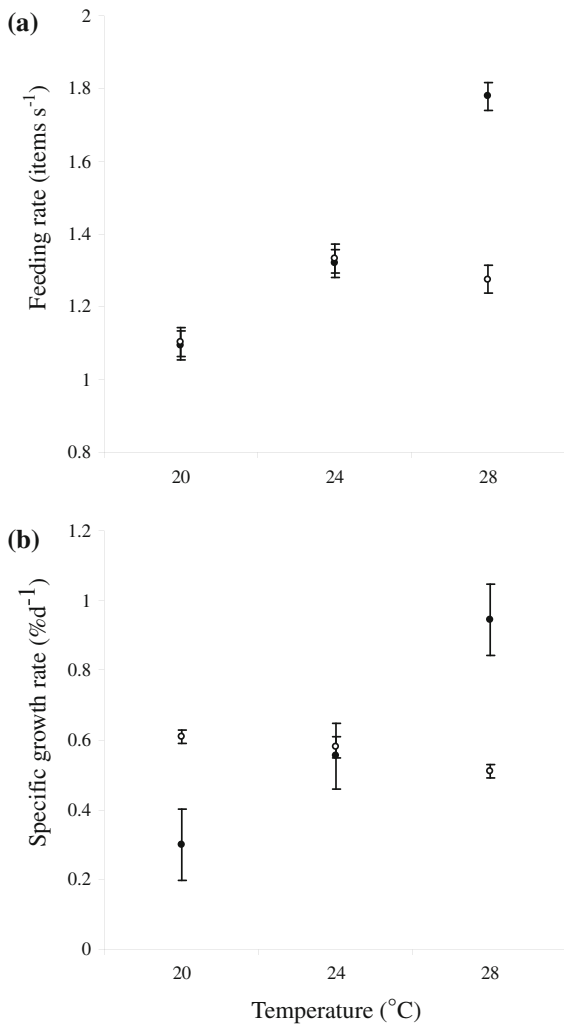


Fig. 1 Effect of temperature on feeding rates (a) and specific growth rates (b) of *Oreochromis niloticus* (Filled circle) and *Cyprinus carpio* (Circle). Error bars represent 95% confidence limits

which one was consistently more aggressive than the other. This occurred in all tanks. These fish were ranked as 1 (dominant), 2 and 3 (most sub-ordinate). In all tanks, the most aggressive, dominant individual (#1) that did most of the interfering during feeding took a higher proportion of the available food than the other two fish, with the more aggressive sub-dominant fish (#2) taking a higher mean proportion of food than the least aggressive fish (#3) (Fig. 2). This was also manifested in the specific growth rate of the fish, where the dominant individual grew at a significantly faster rate (Table 1; Fig. 2). There was no significant

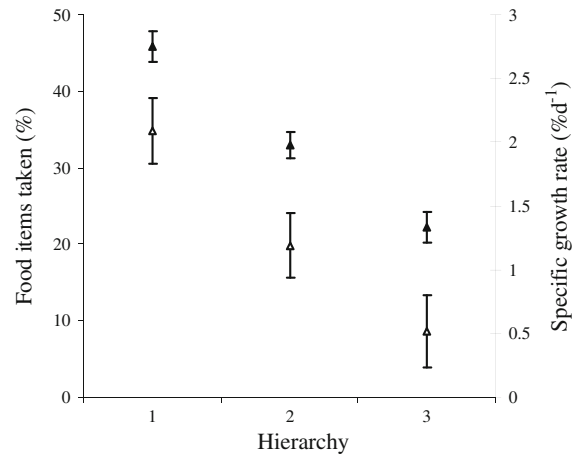


Fig. 2 Effects of hierarchical rank (1 dominant individual, 2 sub-ordinate individual, and 3 most sub-ordinate individual) on the percentage of food items taken (Filled triangle) and specific growth rate (Triangle) of *Oreochromis niloticus*. Error bars represent 95% confidence limits

difference, however, in the growth rate of the fish ranked at number 2 and 3 in the hierarchy (Table 1; Fig. 2). In 11 of 15 tanks, the fish of highest starting length was the dominant fish, although this length difference was as small as 3 mm. Starting body length thus had a significant influence on the formation of the hierarchical ranks (mean body lengths per hierarchical rank 1: 105.3 ± 3.6 mm; 2: 98.8 ± 3.6 ; 3: 90.2 ± 3.9 mm; $F_{2,42} = 15.30$, $P = 0.001$).

Experiment 3: hierarchical feeding of *Oreochromis niloticus* in presence of *Cyprinus carpio*

Compared against the control, the introduction of 1 and 3 *C. carpio* had no significant effect on the mean proportion of food taken by the individual *O. niloticus*, but when 6 *C. carpio* were added then there was a significant decrease in the food taken (Table 2; Fig. 3). The effect of adding 3 *O. niloticus* on the mean proportion of food taken by the 3 original fish was not significantly different to the addition of 3 and 6 *C. carpio*, but did represent a significant decrease compared to the control and the addition of 1 *C. carpio* (Table 2; Fig. 3).

Similarly, the effect of the treatments on the proportion of food taken per hierarchical rank also revealed that when compared against the control, there

Table 1 (a) Effects of hierarchical position and covariates on specific growth rate of *Oreochromis niloticus* (ANCOVA). (b) Corresponding differences between hierarchy positions are indicated by pairwise comparisons with Bonferroni adjustments for multiple comparisons

Effect	Specific growth rate (% day ⁻¹)	
(a)		
Hierarchical position	$F_{2,41} = 10.32, P < 0.01$	
Fish length	$F_{1,41} = 2.59, P > 0.05$	
(b) Difference between hierarchical positions (mean ± S.E.)		
1	2	0.90 ± 0.36*
	3	1.57 ± 0.41**
2	3	0.67 ± 0.40

* $P < 0.05$, ** $P < 0.01$

was no significant effect on the food taken by the dominant fish when 1 and 3 *C. carpio* were introduced (Table 3; Fig. 3). When 6 *C. carpio* and 3 *O. niloticus* were added, however, there was a significant decrease in the proportion of food that the dominant fish took. The sub-dominant *O. niloticus* did not take advantage of this by consuming more food as their proportions of food ingested did not change significantly over the treatments (Table 3; Fig. 3). Instead, the introduced *C. carpio* took the food items that were no longer being ingested by the dominant fish.

Table 2 (a) Effects of experimental treatments and covariates on the mean proportion of food taken by the *Oreochromis niloticus* (ANCOVA). (b) Corresponding differences between treatments are indicated by pairwise comparisons with Bonferroni adjustments for multiple comparisons

Effect	Mean proportion (%) of food taken by <i>O. niloticus</i>
(a)	
Treatment	$F_{4,199} = 4.82, P < 0.01$
Hierarchy	$F_{1,206} = 15.83, P < 0.01$
Starting length	$F_{1,206} = 4.91, P < 0.01$
(b) Difference between treatments (mean ± SE)	
Control	
+1 carp	-0.22 ± 3.40
+3 carp	6.73 ± 3.45
+6 carp	9.10 ± 2.30*
+3 tilapia	12.14 ± 3.34**
+3 tilapia	
Control	
+1 carp	-12.36 ± 3.34**
+3 carp	-12.14 ± 3.40**
+6 carp	-5.413 ± 4.01
+6 carp	-3.08 ± 3.92

* $P < 0.05$, ** $P < 0.01$

Discussion

The experiments were designed to determine the temperature-dependent feeding interactions between two globally invasive fishes that are increasingly occurring in sympatry in the wild and that compete through differing mechanisms. They revealed that the feeding and growth rates of *C. carpio* and *O. niloticus* differed according to temperature. Indeed, the growth rate of *C. carpio* was similar between 20 and 28°C while *O. niloticus* significantly increased with each incremental temperature increase. Similarly, whilst the feeding rate of *O. niloticus* also increased with each temperature increment, *C. carpio* was significantly lower at 28°C than 24°C. These thermal relationships mirror their invasion patterns observed in the wild, where *C. carpio* generally invade cooler temperate habitats and *O. niloticus* warmer tropical habitats (Zambrano et al. 2006, 2010). Locations where their invasive populations coexist tend to be subtropical (Mercado-Silva et al. 2008). This suggests that irrespective of any interfering behaviour during feeding, the consequences of resource competition in terms of food items taken and its subsequent influence on growth will be context-dependent, being influenced by a set of abiotic variables that includes temperature.

The influence of additional *C. carpio* on the growth of *O. niloticus* could not be determined here due to the

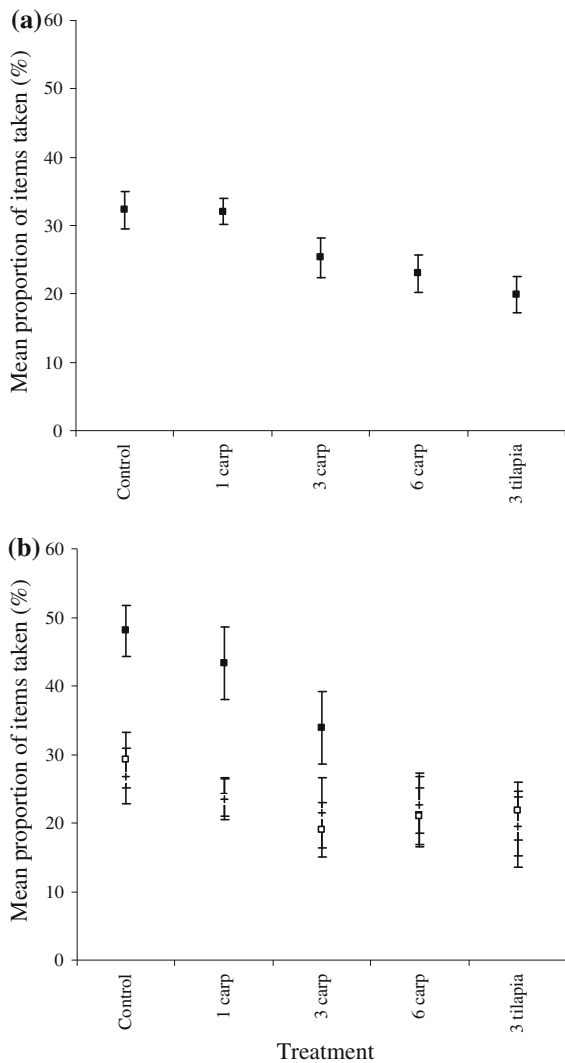


Fig. 3 a Mean proportion of food items taken (estimated marginal means from ANCOVA, cf. Table 3) (a) and (b) mean proportion taken by hierarchical rank (estimated marginal means from ANCOVA (cf. Table 3); rank 1 Filled square, 2 Square, 3 Plus symbol) by *Oreochromis niloticus* across the additive and substitutive treatments. Error bars represent 95% confidence limits

dominant tilapia aggressively competing for space with introduced *C. carpio* to the extent that prolonged exposure was likely to have resulted in the death of the *C. carpio*. This was despite their limited length range of between 85 and 110 mm and corresponding lack of sexual maturity. This suggests that in larger spatial areas, *O. niloticus* may have the potential to competitively exclude *C. carpio* of at least similar body sizes from their territorial areas, particularly when water

temperatures are relatively high. Indeed, species suffering from interspecific competition often develop ways to escape the consequent stress and injury arising from aggression, such as avoiding encounters by shifting their spatial niche (van Riel et al. 2009), an outcome that was not possible in the tank experiments due to their restricted size. Similar negative ecological outcomes have also been recorded in native fishes in other studies on the impacts of invasive *O. niloticus* (e.g. Weyl 2006; Martin et al. 2010).

The addition of 1 and 3 *C. carpio* during feeding trials had little influence on the proportion of food taken by *O. niloticus*, whereas the introduction of 6 *C. carpio* resulted in a significant decrease in the amount of food taken by the dominant tilapia. This was not through the introduced *C. carpio* breaking the hierarchy directly, as observed in studies on invasive salmonid fishes that disrupt established hierarchies (e.g. Blanchet et al. 2007a; Seiler and Keeley 2009). Rather, it was a consequence of the dominant fish continuing its interfering behaviours in a situation when there was increased exploitative competition from *C. carpio*. The increased number of *C. carpio* meant not all these fish could be chased at the same time, allowing some of them access to the food resources and so reducing the amount available to the tilapia. It has been discussed that secondary production, i.e. growth rates (Blanchet et al. 2007b), is an efficient way to identify and quantify the strength of interactions (Bohlin et al. 2002; Cross and Benke 2002). Whilst this could not be done directly here for reasons already outlined, given the positive relationship between hierarchical ranks, proportion of food ingested and growth rate for *O. niloticus* established in a previous experiment, then this decreased food intake may negatively influence the growth of the dominant tilapia. This, however, would be dependent on the number of introduced fish (i.e. propagule pressure) not decreasing in the spatial area as a consequence of the tilapia aggression.

Studies on competitive processes tend to be criticised for failing to consider the simultaneous effects of intra- and interspecific competition (Cross and Benke 2002; Blanchet et al. 2007b). Here, intra-specific competition was considered through a substitutive treatment in the final experiment that introduced 3 *O. niloticus* during feeding trials. This revealed that the consequence for the proportion of food taken by the dominant tilapia was a similar decrease to that

Table 3 (a) Effects of treatments and covariates on proportion of food taken by the dominant *Oreochromis niloticus* (ANCOVA); (b) effects on the second ranked *O. niloticus*; and (c) effects on the third ranked *O. niloticus*. Differences between treatments, indicated by pairwise comparisons with Bonferroni adjustments for multiple comparisons, are shown

Effect	Mean proportion (%) of food taken by ranked 1 <i>O. niloticus</i>
(a)	
Treatment	$F_{4,65} = 7.22, P < 0.01$
Starting length	$F_{1,70} = 1.20, P > 0.05$
Difference between treatments (mean \pm SE)	
<i>Control</i>	
+1 carp	-4.84 ± 6.40
+3 carp	9.29 ± 7.25
+6 carp	$21.32 \pm 5.20^*$
+3 tilapia	$24.12 \pm 6.11^*$
Effect	Mean proportion (%) of food taken by ranked 2 <i>O. niloticus</i>
(b)	
Treatment	$F_{4,65} = 0.58, P > 0.05$
Starting length	$F_{1,70} = 0.92, P > 0.05$
Difference between treatments (mean \pm SE)	
<i>Control</i>	
+1 carp	5.38 ± 4.90
+3 carp	10.20 ± 5.73
+6 carp	8.20 ± 5.70
+3 tilapia	7.44 ± 6.06
Effect	Mean proportion (%) of food taken by ranked 3 <i>O. niloticus</i>
(c)	
Treatment	$F_{4,65} = 0.04, P > 0.05$
Starting length	$F_{1,70} = 0.42, P > 0.05$
Difference between treatments (mean \pm SE)	
<i>Control</i>	
+1 carp	3.33 ± 5.07
+3 carp	5.34 ± 6.52
+6 carp	4.20 ± 5.78
+3 tilapia	7.3 ± 5.92

* $P < 0.05$, ** $P < 0.01$

elicited by the addition of 3 and 6 *C. carpio*. Consequently, the strength of intra-specific appeared as strong as the inter-specific competition at these propagule pressures. This finding is consistent with a number of other studies covering a variety of organisms and systems that indicate interspecific competition is rarely stronger than intraspecific competition. For example, Connell (1983) revealed that, in a review of experimental studies on interspecific competition, it was only stronger than intraspecific competition in less than 25% of cases.

An issue with many experimental studies on competition processes is that: (i) experimental data rarely match field observations due to the experimental spatial constraints causing unnaturally intense interactions that result in an over-extrapolation of laboratory data (e.g. Cross and Benke 2002); and (ii) issues relating to scaling up experimental data to represent more complex natural situations (e.g. Korsu et al. 2009). Thus, due caution must be given to any inferences made from the experiments conducted here for scaling up to the more complex systems.

Notwithstanding, given the trophic interactions and niche overlap observed in their coexisting populations in Mexico (Zambrano et al. 2010), then competition for resources between *C. carpio* and *O. niloticus* may be expected at some point during their lifecycles. The observations and experimental data presented here suggest that the aggression of *O. niloticus* towards *C. carpio* for both space and food may result in some spatial segregation of the species.

In summary, experimental tests revealed that the outcome of feeding interactions between two highly invasive fishes with different competition processes were likely to be context-dependent, determined by the abiotic conditions of their environment as well as their competitive processes and strengths. Where spaces and resources have to be shared, then the aggressive behaviour of *O. niloticus* may exclude *C. carpio*, although at high *C. carpio* densities, this may also result in reduced food intakes for the aggressive tilapia (and potentially decreased growth rates). The strength of this competition is, however, only as strong as that mediated by intraspecific competition, suggesting outcomes in the wild are likely to be complex and also dependent on biotic factors relating to population dynamics and the stage at which the species are in their invasion process. These findings thus highlight the complexity of predicting and assessing the outcomes of introductions of multiple alien species and their subsequent invasions when the species concerned may share resources but compete using contrasting feeding modes and behaviours.

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