



# Simulated encounters with a novel competitor reveal the potential for maladaptive behavioural responses to invasive species

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**Abstract** During the early stage of biological invasions, interactions occur between native and non-native species that do not share an evolutionary history. This can result in ecological naïveté, causing native species to exhibit maladaptive behavioural responses to novel enemies, leading to negative consequences for individual fitness and ecosystem function. The behavioural response of native to non-native species during novel encounters can determine the impact of non-native species, and restrict or facilitate their establishment. In this study we simulated novel encounters between a widespread invasive fish species, the Nile tilapia (*Oreochromis niloticus*), and a threatened native Manyara tilapia (*Oreochromis amphimelas*). In the first experiment single adult *O. niloticus* were presented with a stimulus chamber (a transparent plastic cylinder) which was empty during control trials and contained a pair of juvenile *O. amphimelas* in stimulus trials. In the second experiment, the reciprocal set up was used, with pairs of juvenile *O. amphimelas* as the focal species and adult *O. niloticus* as the stimulus. Both species approached

the stimulus chamber more readily during stimulus trials, a behavioural response which would increase the prevalence of interspecific interactions in situ. This included physical aggression, observed from the competitively dominant *O. niloticus* towards *O. amphimelas*. Despite an initial lack of fear shown by *O. amphimelas*, close inspection of the stimulus chamber often resulted in an energetically costly dart response. Under field conditions we predict that naïve native individuals may readily approach *O. niloticus*, increasing the likelihood of interactions and exacerbating widely reported negative outcomes.

**Keywords** Naïveté · Invasion ecology · Interspecific competition · Alien species · *Oreochromis amphimelas* · *Oreochromis niloticus* · Nile tilapia

## Introduction

The establishment of species in areas outside of their native range can have wide ranging effects on ecosystems (Clavero and García-Berthou 2005). In some cases, non-native species have driven population declines and extinctions of native species following their establishment (Sax and Gaines 2008), while in others they have had limited impact or even provided desirable ecosystem functions (Richardson et al. 2000; Schlaepfer et al. 2011; Anton et al. 2019). This

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variation in impact is thought to be determined largely by the character and strength of interactions with native species (Carthey and Banks 2014). Studying interactions between native and non-native species can therefore be used to target mitigation strategies towards the most harmful invaders (Parker et al. 1999) and to inform policy decisions which may limit the spread of species with high potential for negative impact (Kulhanek et al. 2011).

During the early stage of invasion, novel interactions occur between native and non-native species (Schlaepfer et al. 2005). This can result in ecological naïveté, where native species are unable to respond appropriately to the level of threat posed by non-native species and exhibit maladaptive behavioural responses as a result (Carthey and Banks 2014). Naïveté can affect the outcome of any antagonistic interaction, but the majority of research to date has focused on predator–prey interactions (Carthey and Banks 2014). This work has highlighted how naïveté to both non-native predators and prey can result in increased mortality for native species, impacting ecosystem function (Llewelyn et al. 2009; Robbins et al. 2013; Papacostas and Freestone 2019; Anton et al. 2020). Alternatively, misidentification of non-predatory invasive species can result in unnecessary energy expenditure or missed opportunities to forage (Carthey and Blumstein 2018). While the selective forces relating to predator–prey interactions are particularly strong, naïveté can affect the outcome of any antagonistic interaction, resulting in consequences for individual and population fitness. For example, exploitative and interference competition shape community structure within ecosystems (Rowles and O’Dowd 2007), and naïveté to a novel competitor can influence the outcome of competitive interactions (Harrington et al. 2009; Heavener et al. 2014). Across all antagonistic interactions, maladaptive behavioural responses resulting from naïveté can lead to a number of harmful outcomes including predation (Salo et al. 2007), ingestion of toxic prey (Letnic et al. 2008), restricted access to resources (Heavener et al. 2014), increased disease and parasite transmission (Chalkowski et al. 2018), and hybridisation (Bleeker et al. 2007). These outcomes are closely linked to fitness and survival, and the need to explore how naïveté influences a wide range of antagonistic interactions has been highlighted in several publications (Carthey and Banks 2014; Heavener et al. 2014).

The initial stages of invasion are thought to play a particularly important role in determining the outcome of biological invasions (Chapple et al. 2012). This heightens the importance of early encounters, where an appropriate response to novel species may limit the establishment and impact of these non-native species, while maladaptive behavioural responses may lead to harmful outcomes for native species and facilitate the spread of the non-native species. Furthermore, naïveté is highest during early-encounters, limiting the available time for adaptive changes in response to non-native species (Phillips and Shine 2004). The majority of research on biological invasions has focused on well-established invasive populations, yet it is estimated that less than 10% of non-native species that are released will become established (Kolar and Lodge 2001). Research into interactions between native and non-native species during early encounters may therefore improve understanding of the mechanisms that govern success and failure at the establishment step of invasions. Investigating such interactions in the field is challenging because the precise timing of non-native species introductions is not typically known, and so interactions between native and non-native species have already occurred frequently before they can be investigated. Experimental approaches can therefore be used to investigate interspecific interactions which allows for control of prior experience.

In this study, we simulated novel interactions between a widespread invasive species (Nile tilapia *Oreochromis niloticus*) and a threatened tilapia native to Tanzania (Manyara tilapia *Oreochromis amphimelas*). *Oreochromis niloticus* has been introduced to several catchments containing *O. amphimelas*, and the two can be found in sympatry (Shechonge et al. 2019). Currently, little is known about the timing and history of this specific invasion, and limited research has been conducted on the natural history of *O. amphimelas*. However, both *O. niloticus* and *O. amphimelas* are mouthbrooders and are largely microphagous (Trewavas and Fryer 1965), suggesting strong resource overlap and the potential for competition over the limited resources of food and spawning areas. There is limited evidence for predation of native congeners by *O. niloticus*, yet the potential for harmful effects resulting from interactions with *O. niloticus* has been documented for many species (Martin et al. 2010; Sanches et al. 2012), including *O. amphimelas* (Champneys et al. 2020; Wing et al. 2020). For

example, *O. niloticus* and *O. amphimelas* have been shown to compete aggressively for shelter under experimental conditions, with *O. niloticus* dominating these interactions (Champneys et al. 2020). Thus, naïveté during early encounters with this novel competitor could lead to harmful outcomes for naïve *O. amphimelas* in situ.

In the first experiment, we presented an adult *O. niloticus* with a pair of juvenile *O. amphimelas* in a clear chamber, enabling us to determine how *O. niloticus* may first respond to native species when entering a novel habitat. Based on previous research we predicted *O. niloticus* to boldly approach the stimulus area and show aggression towards the chamber when it contained *O. amphimelas*. In the second experiment we presented pairs of juvenile *O. amphimelas* with an adult *O. niloticus* in a clear chamber, providing insight into the response of *O. amphimelas* as a naïve native species. Little is known about how native tilapia species respond to novel competitors and collectively the results of the two experiments allow discussion of the potential impact that different behavioural responses could have on the fitness and survival of the native species.

## Methods

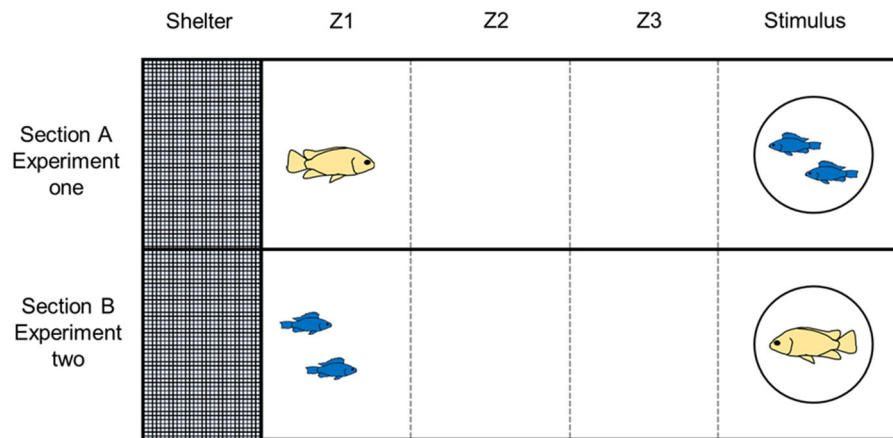
### Experimental subjects and housing

*Oreochromis niloticus* subjects were purchased from a commercial aquaculture supplier (Fish Farm UK, London) and *O. amphimelas* subjects were reared at the University of Bristol and were second generation from wild caught stock. Wild individuals were originally caught from Lake Manyara (3°36′29.5″S 35°49′01.2″E, precise coordinates unknown). *Oreochromis niloticus* are typically introduced via intentional stocking events, or through unintentional release from aquaculture (Canonico et al. 2005). Therefore, we used adult *O. niloticus* from aquaculture stock in this experiment which are likely to be the first individuals to interact with native species during the early stage of *O. niloticus* colonisation. Juvenile *O. amphimelas* from wild stock were used as this is when the size difference between the two species is largest allowing us to investigate a scenario where *O. amphimelas* may perceive *O. niloticus* as a predator. While little is known about the natural history of *O.*

*amphimelas*, juvenile tilapias are often found in groups and therefore a pair of *O. amphimelas* was used to measure their social response to *O. niloticus* which is likely to be an ecologically relevant response to threat in situ. Prior to this experiment, the *O. niloticus* subjects were used in one experiment where they interacted with sized matched *O. amphimelas* for a single 15-min trial (Champneys et al 2020), while the *O. amphimelas* had no prior experience interacting with *O. niloticus*. *Oreochromis niloticus* subjects had an average total length of  $83.13 \pm 7.21$  mm and *O. amphimelas* had an average total length of  $34.77 \pm 7.26$  mm. Fish were housed in a recirculating aquarium at the University of Bristol for at least three months prior to testing. *O. niloticus* were housed in 190L tanks with 30–40 individuals per tank and *O. amphimelas* were housed in 90L housing tanks with 100–110 individuals per tank. Housing tanks contained a variety of plastic plants and pipes to provide enrichment, reduce stereotypic behaviours and improve welfare (Favero Neto and Giaquinto 2020). Both species were fed daily with a mixed diet consisting of chopped prawn, brine shrimp, mysis shrimp and vegetable diet (Tropical Marine Centre, Chorley Wood, UK), ZM Large Premium Granular feed (Tecniplast, London, UK), TetraMin flake (Tetra, Melle, Germany), frozen bloodworm (CC Moore & Co, Templecome, UK) and Gamma TM Krill Pacifica. On trial days, fish were only fed after experiments finished to standardise hunger during trials. Housing tanks were maintained at a temperature of 26–28 °C. Lighting conditions were 12:12 h light: dark cycle to replicate conditions in the tropics. Trials took place during October and November 2019.

### Experimental set up and protocol

A single experimental tank (136 cm long × 72 cm wide × 40 cm high) was divided lengthways with a 136 cm long × 30 cm high opaque central divider into two identical experimental sections (Fig. 1). The divider was a fixed structure sealed to the tank to prevent water movement between the sections. Each section was filled daily with 49L of housing tank water to a depth of 10 cm. Each section of the tank had two distinct zones and three virtual zones which were added digitally for the purposes of analysis (Fig. 1). The shelter zone (21 cm x 36 cm) was situated at one of the long ends of the tank, covered by a 5 mm black



**Fig. 1** Overhead view of the experimental set up used in experiments one and two (not to scale). The tank was split lengthways using an opaque divider. Z1, Z2 and Z3 represent the three virtual zones in the centre of the tank which were used for

video analysis dashed grey lines represent digital divisions black circles represent the transparent cylinders which contained the stimulus subjects in stimulus trials and were empty in control trials

mesh plastic sheet 20 cm above the water level. At the opposite end was the stimulus zone (32 cm x 36 cm), which had a clear plastic cylinder in its centre (16 cm diameter x 25 high) which was filled with water to the same height as the rest of the tank. The section in between contained the three additional virtual zones (zone 1: 19 cm x 36 cm, zone 2: 26 cm x 36 cm and zone 3: 27 cm x 36 cm). A water heater and filter (Eheim 2213) were used to maintain water quality and temperature and were switched off during trials to avoid disturbance, with water temperature remaining at a constant 26 °C.

The experimental setup was used to run two separate experiments concurrently. In **experiment one**, a single *O. niloticus* was the focal subject, and the clear cylinder in the stimulus zone contained two size-matched *O. amphimelas* in stimulus trials and was empty in control trials. In **experiment two**, a size-matched pair of *O. amphimelas* were the focal species, with one randomly designated to be the focal subject and have its behaviour monitored. The clear cylinder contained a single *O. niloticus* in the stimulus trials and was empty in control trials. Experiment one took place in section A and experiment two in section B (Fig. 1). Stimulus individuals were always focal individuals from the previous trial so were partially acclimatised to the arena. Each trial day thus began with a control treatment in both experiments. From the first experiment of the day onwards, control or stimulus treatments were randomly selected before

each trial at a ratio of two stimulus trials to one control trial. This ratio was used to increase the sample size of stimulus trials, allowing separate analyses on this subset of the data to be run with sufficient statistical power, which included the size of the stimulus fish as a covariate.

At the start of each trial, focal individuals from the previous trial were either placed in the clear cylinder of the other section (for stimulus trials) or placed into dedicated housing tanks to avoid reusing individuals (for control trials). Focal individuals were then netted haphazardly from their housing tank using a hand net and transferred to the shelter zone of the experimental tank. Once all fish for both experiments had been transferred, the 12-min recording period began. After use as either focal or stimulus, all individuals had their total length measured using callipers and were transferred to the housing tanks for used fish.

#### Video recording and analysis

The 12-min trial was recorded by an overhead GoPro Hero 6 camera (linear field of view, 30 frames per second, 1280 x 720 resolution, GoPro Inc., San Mateo, CA, USA) situated 76 cm above the water surface. This filmed both experiments in a single video. Each video was analysed separately for each experiment using BORIS software v 9.7.4 by two observers (Friard and Gamba 2016). This software is used manually by the observer to record a previously

defined ethogram of behaviours as either single time point or state events. In [experiment two](#), one of the two *O. amphimelas* was randomly assigned as the test fish to be monitored and only the behaviour of this individual was recorded. The ethogram of behaviours was designed based on similar studies of fish behaviour and the full definition of each behaviour can be found in [Table 1](#). In [experiment one](#), the number of times the focal *O. niloticus* approached the stimulus, circled the stimulus, or showed aggression towards the stimulus was recorded. In [experiment two](#), the number of times the focal *O. amphimelas* approached the stimulus and showed a flight response (i.e. darted away) from the stimulus was recorded. The behaviours recorded differed between the species due to unique behaviours being exhibited by each species. Flight responses were not exhibited by *O. niloticus* and circle and aggression behaviours were not exhibited by *O. amphimelas*. The time taken for each of these behaviours to first occur in each trial was also recorded for both experiments. In both experiments, the location of the focal subject (shelter, zone 1, zone 2, zone 3 or stimulus zone) was recorded throughout the trial, and this provided the time taken to first leave the shelter and the time taken to first enter the stimulus zone. In [experiment two](#), the duration of time that the focal *O. amphimelas* spent in the same zone as the other *O. amphimelas* individual was recorded to provide a measure of sociability. The duration of time spent stationary by the focal individual was also recorded in both experiments to provide a measure of activity. The behaviours recorded are relevant in the context of ecological naivete and interactions between competitors because a willingness to approach a novel competitor would increase the frequency of interactions while avoidance behaviour would decrease the frequency of interactions. Thus, approach and dart

events along with the time taken to leave the shelter and enter the stimulus zone provided a measure of this willingness to approach the novel species. Additionally, circling and aggressive behaviours provided a measure of the likely outcome of interactions between the species, if the plastic chamber had not prevented physical contact. The final data set included 79 trials for experiment one (53 stimulus, 23 control), and 74 for experiment two (49 stimulus, 25 control), after one from experiment one and six from experiment two were discarded due to video recording failures.

### Statistical analysis

All analyses were conducted using R version 3.6.3 (R Core Team 2020). In both experiments, the time to response variables were analysed using Cox Proportional-Hazards Models using the ‘*coxph*’ function in the package ‘*survival*’ (Therneau 2020). This tests how the likelihood of an event is influenced by a set of risk factors at any given time over the measured duration. In [experiment one](#), the events were the time taken to first enter the stimulus zone, approach the stimulus, and circle the stimulus. In [experiment two](#), the events were the time taken for the focal subject to first leave the shelter, enter the stimulus zone, and approach the stimulus. In both experiments, the measured duration was the length of the experiment (720 s). The risk factors were the fixed effects which were treatment (control or stimulus) and test subject body size. In [experiment one](#), subject body size was the total length of the focal *O. niloticus*, in [experiment two](#) it was the mean total length of the *O. amphimelas* pair. The data were then subset to only include stimulus trials, and the same dependent variables were analysed using the same method, removing the treatment term but including stimulus body size as a

**Table 1** Definitions of behaviours recorded from the videos

Behaviour	Definition	Used in
Approach	The focal subject swims towards the stimulus until it is within less than one of its own body lengths (Frommen et al. 2009; Bevan et al. 2018)	Experiment one and experiment two
Circle	The focal subject circles around the entire circumference of the stimulus	Experiment one
Aggression	The focal subject swims rapidly towards the stimulus until it makes contact with the stimulus chamber (Ros et al. 2006; Champneys et al. 2018; Szopa-Comley et al. 2020)	Experiment one
Dart	The focal subject swims rapidly away from the stimulus (Kimbell and Morrell 2015)	Experiment two

model covariate to assess whether behavioural responses were influenced by the size of the stimulus fish.

The proportional hazards assumption is a central assumption of these models, and we tested it using the *cox.zph* function which revealed no violation for any of the models. The *'ggcoxdiagnostics'* command in the package *'survminer'* was used to test for influential observations (Kassambara et al. 2019) and this assumption was satisfied in all cases. To test for non-linearity, models were run with a smoothing parameter fitted to the linear covariate focal subject body size using a penalised spline method with the function *pspline* function in the package *'survival'*. This method smooths covariates which have non-linear effects on the dependent variable, improving the evaluation of the relationship between the predictor variable and the dependent variable. Models with and without spline terms were then compared using AICc (Akaike Information Criterion corrected (AICc) for small sample sizes) with the function *AICctab* in package *'bbmle'* (Bolker B, R Core Team, 2017; following methods in Roshani and Ghaderi 2016). In all cases, models without the spline term were more likely, confirming that fitting linear relationships was more appropriate. Packages *'survival'* and *'survminer'* were used to visualise the results.

In experiment one, the time spent stationary (a measure of activity) by the *O. niloticus* and the number of approach, circle and aggression events were analysed using Generalised Linear Models (GLMs). A Gaussian family was used for activity using the *glm* function with the default family, while a negative binomial family was used for approach, circle and aggression events using the *glm.nb* function in the package *'MASS'* (Venables and Ripley 2002). In experiment two, the time spent in the same zone by the two *O. amphimelas* (sociability), the time spent stationary by the focal *O. amphimelas* (activity), the number of approach events, and whether the trial contained at least one dart event, were also analysed using GLMs. A Gaussian family was used for sociability, a binomial family was used for dart events and a negative binomial family was used for activity and approaches. In both experiments, treatment (stimulus or control), focal body size (total length of the focal *O. niloticus* or mean total length of the *O. amphimelas* pair) and an interaction term between these two variables were included as covariates. In

order to assess the effect of stimulus body size within stimulus trials, the data were then subset to only include stimulus trials. With this dataset, the same four dependent variables per experiment were analysed using GLMs, and in both experiments, the body size of the stimulus fish, focal body size, and an interaction term including these two variables were included as covariates. For this analysis, negative binomial GLMs were used for all four dependent variables in experiment one. In experiment two, negative binomial GLMs were used for sociability, activity and number of approaches while GLMs with a binomial family were used for dart events.

The default link functions were used in each GLM. Plots of fitted values versus residuals and the distribution of residuals versus a normal distribution using a QQ plot were used to test the model assumptions in the Gaussian models. The overdispersion statistic was calculated for the negative binomial models to ensure it fell between 0.5 and 2, indicating that there was no overdispersion. Once these assumptions were satisfied, a set of models containing all combinations of the covariates and their interaction terms were run. These models were compared based on the Akaike information criterion corrected for small sample sizes (AICc) using the function *AICctab* to determine the models with most support. A difference in AICc between two models greater than two (i.e.  $\Delta\text{AICc} > 2$ ) indicates strong support for the model with lower AICc being the more likely model given the data (Burnham and Anderson 2004). Akaike weights were also calculated, these provide a conditional probability for each model further aiding interpretation of the level of support for each model (Wagenmakers and Farrell 2004). Therefore, by running a set of models with and without explanatory variables of interest, the variables which provide the best explanation of variation in the dependent variable can be inferred.

## Results

### Experiment one

#### *Time taken to enter the stimulus zone, approach the stimulus and circle the stimulus*

The likelihood of the focal *O. niloticus* entering the stimulus zone did not differ significantly between

trials with *O. amphimelas* as the stimulus and control trials without *O. amphimelas* (Cox Proportional-Hazards model,  $\text{coef} = 0.51$ ,  $\text{exp}(\text{coef}) = 1.66$ , lower 95% CI = 0.96, upper 95% CI = 2.86,  $P = 0.069$ ; Fig. 2a). However, *O. niloticus* were more likely to approach ( $\text{coef} = 0.7$ ,  $\text{exp}(\text{coef}) = 2.01$ , lower 95% CI = 1.11, upper 95% CI = 3.65,  $P = 0.021$ ; Fig. 2b) and circle ( $\text{coef} = 2.1$ ,  $\text{exp}(\text{coef}) = 8.14$ , lower 95% CI = 1.93, upper 95% CI = 34.4,  $P = 0.004$ ; Fig. 2c) the stimulus in trials with *O. amphimelas*. The size of the *O. niloticus* did not affect the likelihood of entering the stimulus zone ( $\text{coef} = 0.01$ ,  $\text{exp}(\text{coef}) = 1.01$ , lower 95% CI = 0.98, upper 95% CI = 1.05,  $P = 0.53$ ), approaching ( $\text{coef} = 0.006$ ,  $\text{exp}(\text{coef}) = 1.01$ , lower 95% CI = 0.97, upper 95% CI = 1.05,  $P = 0.76$ ) or circling the stimulus ( $\text{coef} = -0.03$ ,  $\text{exp}(\text{coef}) = 0.97$ , lower 95% CI = 0.92, upper 95% CI = 1.03,  $P = 0.31$ ). In the stimulus trials only, the likelihood of entering the stimulus zone ( $\text{coef} = 0.01$ ,  $\text{exp}(\text{coef}) = 1.01$ , lower 95% CI = 0.97, upper 95% CI = 1.06,  $P = 0.48$ ), approaching the stimulus ( $\text{coef} = 0.01$ ,  $\text{exp}(\text{coef}) = 1.01$ , lower 95% CI = 0.97, upper 95% CI = 1.06,  $P = 0.63$ ), and circling the stimulus ( $\text{coef} = -0.008$ ,  $\text{exp}(\text{coef}) = 0.99$ , lower 95% CI = 0.94, upper 95% CI = 1.05,  $P = 0.78$ ) was not significantly affected by the mean body size of the *O. amphimelas* pair used as the stimulus.

Activity

For the time spent stationary, AICc values and Akaike weights indicated strongest support for the model

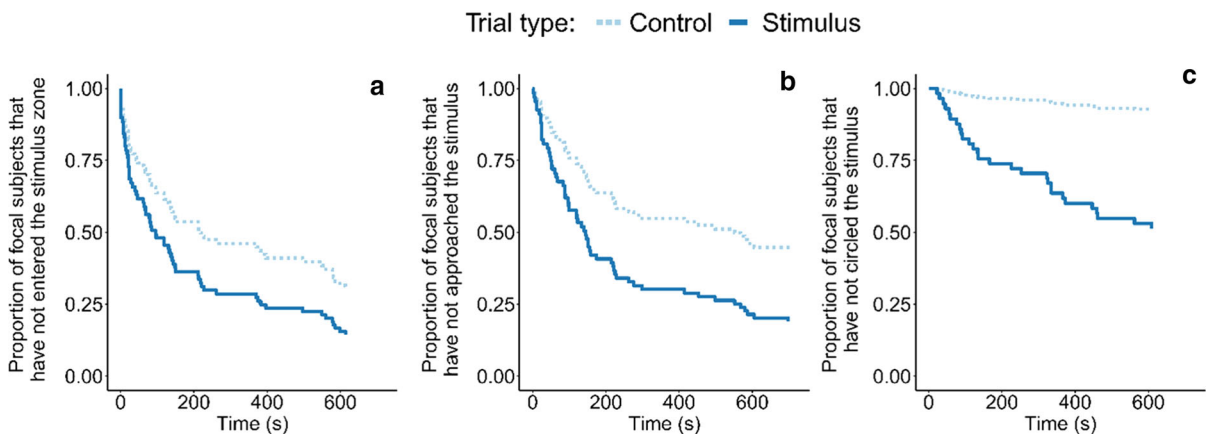
containing only focal body size as a covariate (Table 2), suggesting that activity levels were not significantly different between treatments (Fig. 3a). In the stimulus trials only, AICc values and Akaike weights also indicated strong support for the model containing only focal body size, suggesting no effect of stimulus body size on the time spent stationary by *O. niloticus* (Table 3). In both analyses, larger fish were shown to have lower activity than smaller fish.

Approach events

AICc values and Akaike weights indicated strongest support for the model containing only treatment as a fixed effect (Table 2), where approaches were more frequent toward the *O. amphimelas* than the empty cylinder in the control trials (Fig. 3b). In the stimulus trials only, AICc values and Akaike weights indicate support for the model containing the interaction term between stimulus body size and focal body size. Support for this model suggests that the effect of stimulus body size on the number of approaches may vary depending on focal body size. However, the model including only stimulus body size, also has strong support ( $\Delta\text{AICc} < 2$ ), where the number of approaches increased as stimulus body size increased (Table 3).

Circle events

AICc values and Akaike weights indicated strongest support for the model containing only treatment as a



**Fig. 2** The likelihood of *O. niloticus* **a** entering the stimulus zone, **b** approaching the stimulus, and **c** circling the stimulus in control and stimulus trials in experiment one

**Table 2** Model comparisons for GLMs used in experiment one to analyse how the dependent variables of *O. niloticus* activity, approach, circle, and aggression were affected by five different combinations of the fixed effects treatment and focal fish body size

Dependent variable	Model	Explanatory variables	AICc	$\Delta$ AICc	df	Akaike weight
Activity (Gaussian)	m4	Focal body size	1031.4	0	3	0.32
	m2	Treatment + Focal body size	1032	0.5	4	0.25
	m1	Treatment * Focal body size	1032.4	1	5	0.20
	m3	Treatment	1033.5	2	3	0.12
	m5	Null	1033.6	2.2	2	0.11
Approach events (Negative binomial)	m3	Treatment	403.1	0	3	0.48
	m2	Treatment + Focal body size	403.6	0.5	4	0.37
	m1	Treatment * Focal body size	405.4	2.3	5	0.15
	m4	Focal body size	420.3	17.2	3	< 0.001
	m5	Null	421.4	18.3	2	< 0.001
Circle events (Negative binomial)	m3	Treatment	193.2	0	3	0.53
	m2	Treatment + Focal body size	194.1	0.9	4	0.34
	m1	Treatment * Focal body size	195.9	2.7	5	0.13
	m4	Focal body size	206.4	13.3	3	< 0.001
	m5	Null	206.7	13.6	2	< 0.001
Aggression events (Negative binomial)	m2	Treatment + Focal body size	205.9	0	4	0.51
	m3	Treatment	206.8	0.9	3	0.33
	m1	Treatment * Focal body size	208.1	2.3	5	0.16
	m4	Focal body size	231	25.2	3	< 0.001
	m5	Null	232.7	26.8	2	< 0.001

fixed effect (Table 2), where the circle events were more frequent in stimulus than control trials (Fig. 3c). In the stimulus trials only, AICc values and Akaike weights indicated strong support for the null model (Table 3).

#### Aggression events

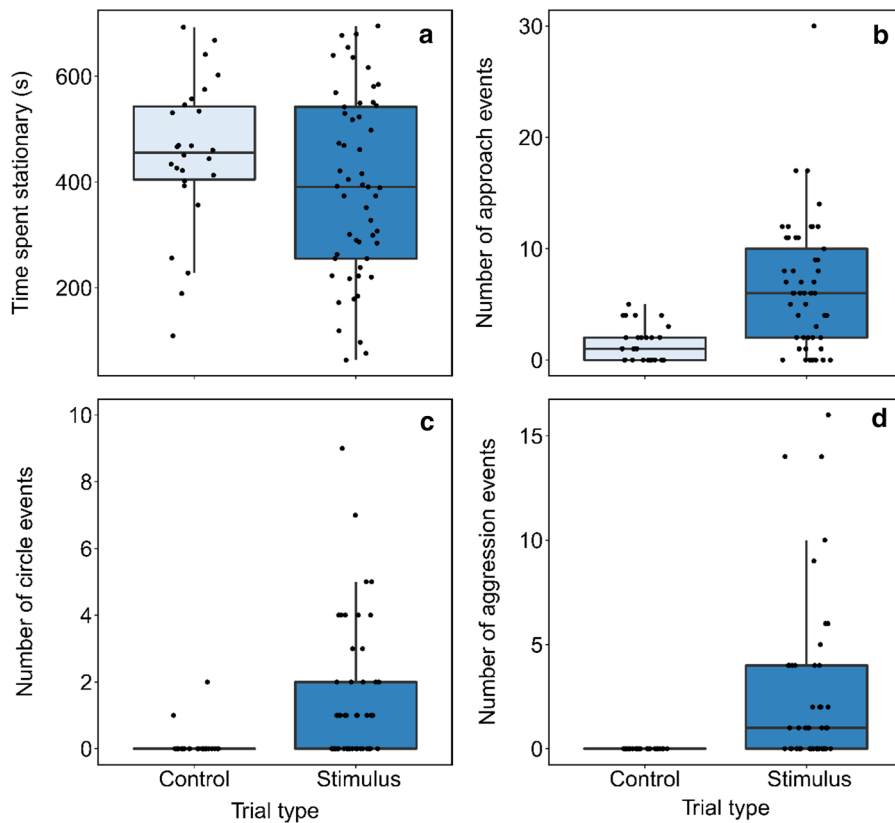
AICc values and Akaike weights indicated strongest support for the model containing treatment and focal body size as fixed effects (Table 2). Strong support is also given to the model containing only treatment ( $\Delta$ AICc < 2), with the aggression events being far more frequent in the stimulus than the control trials (Fig. 3d). In the stimulus trials only, AICc values and Akaike weights indicated strong support for the model containing focal body length as a covariate (Table 3), although there was also strong support for the null model ( $\Delta$ AICc < 2), suggesting that focal and stimulus body sizes had weak effects on the number of aggression events in the stimulus trials (Table 3).

#### Experiment two

##### *Time taken to leave the shelter, enter the stimulus zone, and approach the stimulus*

The likelihood of the focal *O. amphimelas* individual leaving the shelter did not differ significantly between stimulus and control trials (Cox Proportional-Hazards model, coef = 0.48, exp(coef) = 1.62, lower 95% CI = 0.98, upper 95% CI = 2.69,  $P = 0.058$ ; Fig. 4a). However, *O. amphimelas* were significantly more likely to enter the stimulus zone (coef = 0.55, exp(-coef) = 1.73, lower 95% CI = 1.01, upper 95% CI = 2.99,  $P = 0.045$ ; Fig. 4b) and approach the stimulus (coef = 1.41, exp(coef) = 4.11, lower 95% CI = 2.08, upper 95% CI = 8.11,  $P < 0.001$ ; Fig. 4c) in trials with *O. niloticus* as the stimulus. The mean body size of *O. amphimelas* pairs had no significant effect on the likelihood of leaving shelter (coef = 0.03, exp(-coef) = 1.03, lower 95% CI = 1, upper 95% CI = 1.07,  $P = 0.064$ ), entering the stimulus zone (coef = 0.02, exp(coef) = 1.02, lower 95% CI = 0.98, upper





**Fig. 3** Box plots showing **a** time spent stationary, **b** number of approach events, **c** number of circle events, and **d**) number of aggression events by the focal *O. niloticus* subject in experiment one. The distance between the top and bottom of each box represents interquartile range, whiskers extend to data points

95% CI = 1.05,  $P = 0.33$ ), or approaching the stimulus (coef = 0.02,  $\exp(\text{coef}) = 1.02$ , lower 95% CI = 0.99, upper 95% CI = 1.06,  $P = 0.21$ ). In the stimulus trials only, the body size of stimulus *O. niloticus* did not affect the likelihood of leaving shelter (coef = -0.0007,  $\exp(\text{coef}) = 0.99$ , lower 95% CI = 0.97, upper 95% CI = 1.03,  $P = 0.96$ ), entering the stimulus zone (coef = -0.0008,  $\exp(\text{coef}) = 0.99$ , lower 95% CI = 0.96, upper 95% CI = 1.04,  $P = 0.97$ ), or approaching the stimulus (coef = -0.006,  $\exp(\text{coef}) = 0.99$ , lower 95% CI = 0.96, upper 95% CI = 1.03,  $P = 0.77$ ).

**Sociability**

AICc values and Akaike weights indicated strong support for the null model (Table 4), suggesting no effect of treatment or focal body size on the time spent

within 1.5 times the interquartile range, and the line through the centre of each box represents the median. Individual data points are scattered over their corresponding treatment with added jitter for clarity and those above or below the whiskers represent outliers

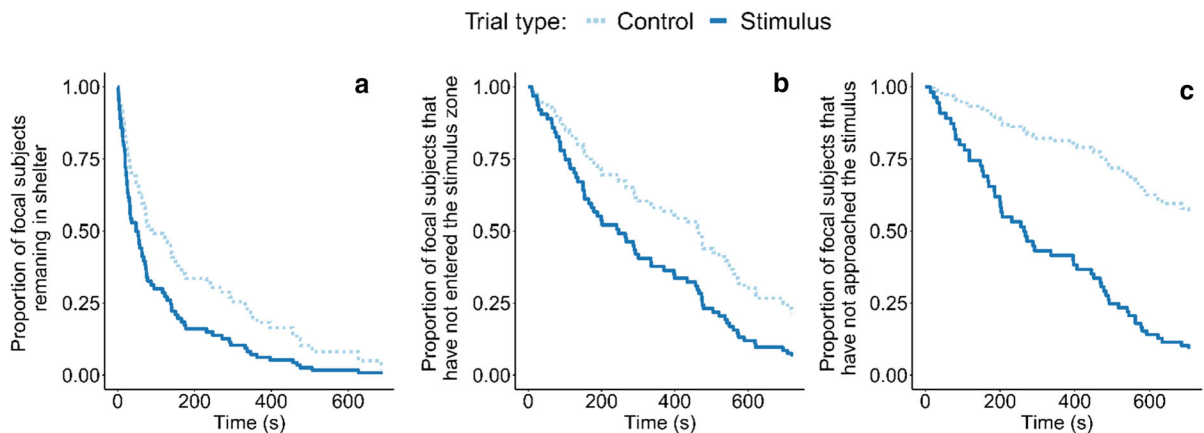
in the same zone by *O. amphimelas* subjects (Fig. 5a). In the stimulus trials only, AICc values and Akaike weights also indicated strong support for the null model, suggesting no effect of stimulus body size on the sociability of *O. amphimelas* pairs (Table 5).

**Activity**

For the time spent stationary, AICc values and Akaike weights indicated strongest support for the model containing only treatment as a fixed effect (Table 4), however, the AICc of the null model was within 1.2 units suggesting only weak evidence for the main effect of treatment (Fig. 5b). In the stimulus trials only, AICc values and Akaike weights indicated strongest support for the null model, suggesting no effect of stimulus body size on the time spent stationary by focal *O. amphimelas* pairs (Table 5).

**Table 3** Model comparisons for GLMs used in experiment one to analyse how the dependent variables of *O. niloticus* activity, approach, circle, and aggression events were affected by five different combinations of the covariates stimulus body size and focal body size in the stimulus trials only

Dependent variable	Model	Explanatory variables	AICc	$\Delta$ AICc	df	Akaike weight
Activity (Negative binomial)	m4	Focal body size	701.2	0	3	0.5
	m2	Stimulus body size + Focal body size	703.2	2	4	0.18
	m5	Null	703.3	2.1	2	0.17
	m3	Stimulus body size	704.7	3.6	3	0.08
	m1	Stimulus body size * Focal body size	705.3	4.1	5	0.06
Approach events (Negative binomial)	m1	Stimulus body size * Focal body size	311.5	0	5	0.37
	m3	Stimulus body size	312.9	1.4	3	0.19
	m2	Stimulus body size + Focal body size	312.9	1.4	4	0.19
	m5	Null	313.6	2	2	0.13
	m4	Focal body size	313.7	2.2	3	0.12
Circle events (Negative binomial)	m5	Null	172.2	0	2	0.39
	m4	Focal body size	172.7	0.5	3	0.31
	m3	Stimulus body size	174.3	2.1	3	0.14
	m2	Stimulus body size + Focal body size	174.6	2.4	4	0.11
	m1	Stimulus body size * Focal body size	176.6	4.4	5	0.04
Aggression events (Negative binomial)	m4	Focal body size	203.8	0	3	0.36
	m5	Null	204.7	0.9	2	0.23
	m2	Stimulus body size + Focal body size	205.1	1.3	4	0.18
	m3	Stimulus body size	206	2.2	3	0.12
	m1	Stimulus body size * Focal body size	206.2	2.3	5	0.11



**Fig. 4** The likelihood of *O. amphimelas* **a** leaving the shelter, **b** entering the stimulus zone, and **c** approaching the stimulus in control and stimulus trials in experiment two

### Approach events

The model with treatment and focal body size as fixed effects had the strongest support according to the AICc

(Table 4), where approach events were significantly more likely in stimulus trials (Fig. 5c), and the size of focal *O. amphimelas* significantly affected the number of approaches, with larger *O. amphimelas* making

**Table 4** Model comparisons for GLMs used to analyse how the dependent variables of *O. amphimelas* sociability, activity, dart events and approach events were affected by five different combinations of the fixed effects treatment and focal body size

Dependent variable	Model	Explanatory variables	AICc	$\Delta$ AICc	df	Akaike weight
Sociability (Gaussian)	m5	Null	965.1	0	2	0.52
	m4	Focal body size	967	1.9	3	0.2
	m3	Treatment	967.1	2	3	0.19
	m2	Treatment + Focal body size	669.1	4	4	0.07
	m1	Treatment * Focal body size	671.4	6.3	5	0.02
Activity (Negative binomial)	m3	Treatment	878.2	0	3	0.44
	m5	Null	879.3	1.2	2	0.24
	m2	Treatment + Focal body size	880.3	2.1	4	0.15
	m4	Focal body size	880.9	2.8	3	0.11
	m1	Treatment * Focal body size	882.1	3.9	5	0.06
Number of approaches (Negative binomial)	m2	Treatment + Focal body size	352.4	0	4	0.61
	m1	Treatment * Focal body size	353.3	0.9	5	0.39
	m3	Treatment	363.8	11.4	3	0.002
	m4	Focal body size	396.9	44.5	3	< 0.001
	m5	Null	405	52.6	2	< 0.001
Dart events (Binomial)	m3	Treatment	68.6	0	2	0.54
	m2	Treatment + Focal body size	69.5	0.9	3	0.35
	m1	Treatment * Focal body size	71.7	3.1	4	0.11
	m4	Focal body size	102.2	33.6	2	< 0.001
	m5	Null	102.7	34.1	1	< 0.001

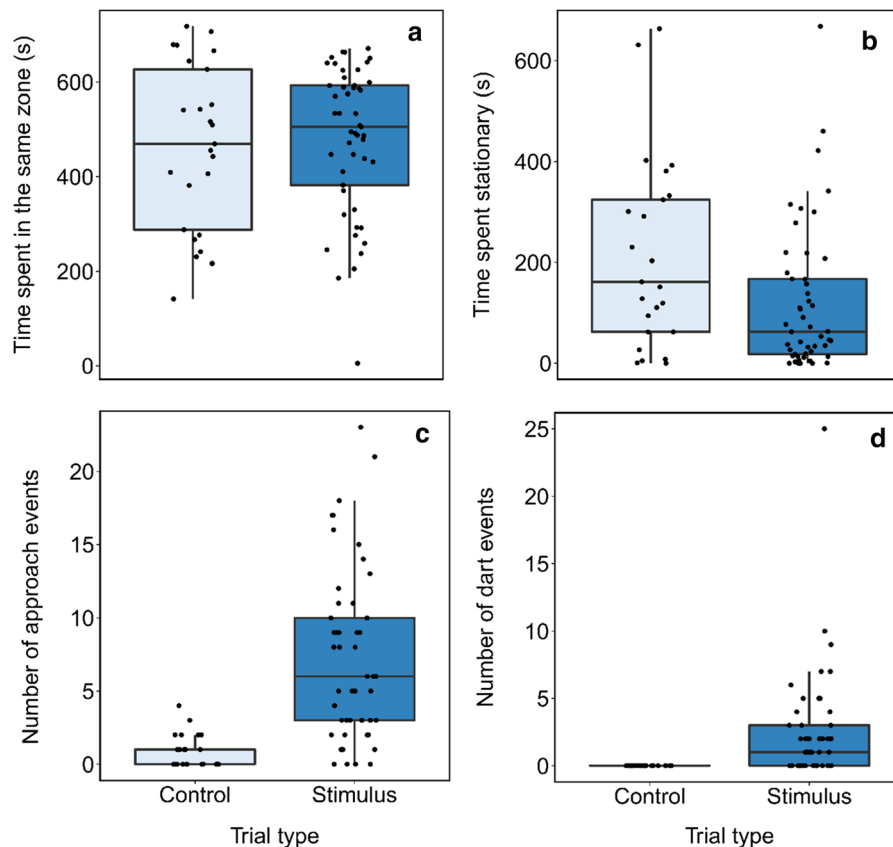
more approaches. In the stimulus trials only, AICc values and Akaike weights indicated strong support for the model containing only focal body size as a covariate. This further highlights the significant effect of focal subject body size on the number of approach events, while suggesting no effect of stimulus body size (Table 5).

#### Dart events

In the models for the likelihood of a dart event occurring during a trial, AICc values indicated strong support for the model containing only treatment as a fixed-effect (Table 4), where dart events were more likely to occur in stimulus trials than control trials (Fig. 5d). In stimulus trials, AICc values and Akaike weights indicated strongest support for the null model, suggesting no effect of stimulus body size on the likelihood of dart events occurring (Table 5).

#### Discussion

In experiment one, *O. niloticus* were more likely to approach and circle the stimulus when the stimulus chamber contained the *O. amphimelas* pair rather than when it was empty. A larger number of approach, circle and aggression events also occurred in these stimulus trials. Thus, despite limited experience interacting with *O. amphimelas*, *O. niloticus* were readily antagonistic towards them, suggesting that aggression towards juvenile *O. amphimelas* by adult *O. niloticus* is likely during novel encounters. In experiment two, the sociability of the *O. amphimelas* pair was unaffected by the presence of *O. niloticus*, and there was little evidence for a difference in activity between stimulus and control trials. Under the risk of potential predation, reduced activity (Sanches et al. 2015; Miyai et al. 2016; Ioannou et al. 2017) and increased sociability (Ioannou 2020; Romenskyy et al. 2020) are known behavioural responses, however neither were observed in this experiment when the stimulus chamber contained the *O. niloticus*. This



**Fig. 5** Box plots showing **a** time spent by *O. amphimelas* in the same zone with the conspecific, **b** time *O. amphimelas* spent stationary, **c** number of approach events by *O. amphimelas*, and **d** number of dart events by the focal *O. amphimelas* in experiment two. The distance between the top and bottom of each box represents interquartile range, whiskers extend to data

apparent lack of a response to the potential threat from *O. niloticus* is further highlighted by the fact that *O. amphimelas* entered the stimulus zone and approached the stimulus more readily when it contained an *O. niloticus*, suggesting that naïve individuals of native species may readily approach *O. niloticus*, a behavioural response which would increase the frequency of interactions. *O. amphimelas* also showed more frequent darting during stimulus trials but these were never observed in control trials. Darting is a rapid locomotory response which often occurs when fish are startled by a threat (McCormick et al. 2019). Thus, while *O. amphimelas* showed a lack of fear in approaching the stimulus chamber when it contained an *O. niloticus*, this often resulted in an energetically costly dart response.

points within 1.5 times the interquartile range, and the line through the centre of each box represents the median. Individual data points are scattered over their corresponding treatment with added jitter for clarity and those above or below the whiskers represent outliers

The response of *O. amphimelas* in this experiment demonstrates how naïveté to a novel competitor may result in maladaptive behavioural responses by non-native species. The aggression shown by *O. niloticus* in experiment one is in accordance with previous research demonstrating the tendency of *O. niloticus* to be aggressive to other species (Martin et al. 2010; Sanches et al. 2012), including *O. amphimelas* (Champneys et al. 2020). Such studies have demonstrated how interactions between *O. niloticus* and native species may lead to harmful outcomes including competition-induced restricted access to resources, increased predation, and parasite transfer (Jiménez-García et al. 2001; Martin et al. 2010). These are a consequence of direct antagonistic interactions, thus native species may reduce the impact of *O.*

**Table 5** Model comparisons for GLMs used to analyse how combinations of the covariates stimulus body size and focal body size in the stimulus trials only the dependent variables of *O. amphimelas* sociability, activity, dart events and approach events were affected by five different

Dependent variable	Model	Explanatory variables	AICc	ΔAICc	df	Akaike weight
Sociability (Negative binomial)	m5	Null	667	0	2	0.54
	m3	Stimulus body size	669.1	2.1	3	0.19
	m4	Focal body size	669.1	2.2	3	0.19
	m2	Stimulus body size + Focal body size	671.3	4.3	4	0.06
	m1	Stimulus body size * Focal body size	673.7	6.8	5	0.02
Activity (Negative binomial)	m5	Null	559.1	0	2	0.5
	m3	Stimulus body size	560.5	1.4	3	0.24
	m4	Focal body size	561.3	2.3	3	0.16
	m2	Stimulus body size + Focal body size	562.8	3.8	4	0.08
	m1	Stimulus body size * Focal body size	564.8	5.8	5	0.03
Number of approaches (Negative binomial)	m4	Focal body size	291.4	0	3	0.7
	m2	Stimulus body size + Focal body size	293.8	2.3	4	0.22
	m1	Stimulus body size * Focal body size	296.1	4.7	5	0.07
	m5	Null	299.9	8.4	2	0.01
	m3	Stimulus body size	302.1	10.7	3	0.003
Dart events (Binomial)	m5	Null	66.5	0	1	0.42
	m4	Focal body size	67.4	0.9	2	0.27
	m3	Stimulus body size	68.3	1.8	2	0.18
	m2	Stimulus body size + Focal body size	69.4	2.8	3	0.1
	m1	Stimulus body size * Focal body size	71.7	5.2	4	0.03

*niloticus* through avoidance behaviours. *Oreochromis amphimelas* showed a lack of threat perception in the presence of *O. niloticus* until they reached very close proximity with the stimulus chamber where they often showed darting responses (Kimbell and Morrell 2015). The stimulus chamber prevented physical aggression between the two species; however under natural conditions, such approaches would likely result in direct agonistic interactions, which could lead to injury or unnecessary energy expenditure from flight responses such as darting. Thus, the failure to detect the potential threat of *O. niloticus*, until within very close proximity, may drive harmful impacts for naïve native species.

In experiment one, larger *O. niloticus* were more active and were less aggressive towards the *O. amphimelas* pair. *Oreochromis niloticus* also approached more frequently when the *O. amphimelas* were larger. Similarly, in experiment two, larger *O. amphimelas* made more approaches in stimulus trials. Previous research has shown that *O. niloticus* are

highly aggressive towards *O. amphimelas* when they are similar sizes (Champneys et al. 2020). Given that the *O. niloticus* were considerably larger than the *O. amphimelas* in this experiment, increased aggression and approaches when the two species were more similarly sized (smaller *O. niloticus* and larger *O. amphimelas*) is in accordance with prior research. *O. niloticus* are much larger than the majority of native tilapia species in Tanzania (Shechonge et al. 2019), and the results of this experiment suggest that aggression may be reduced as body size differences increase. Conservation measures may therefore be targeted towards limiting the impact of *O. niloticus* on the largest-bodied native species.

Research suggests that naïveté is thought to be lower in response to congeneric or functionally similar species (Anton et al. 2020) because native species may recognise traits which are similar to those of species to which they have had eco-evolutionary exposure (Cox and Lima 2006). The experimental subjects used in this study are congeneric tilapia species and are both

maternal mouthbrooders and microphagous, suggesting functional similarity (Trewavas and Fryer 1965). This similarity may reduce naïveté and prevent maladaptive responses to invasive species. However, ecological similarity may also benefit the invasive species, by causing it to be well adapted to the novel ecosystem enabling it to exploit available resources and thrive as a result. The majority of research on this topic has focused on predator–prey naïveté, and future work could benefit understanding of how these principles may apply to naïveté of a native species towards a non-native competitor. Research has shown that *O. niloticus* can be conditioned to show an anti-predatory response to a novel predator stimulus under experimental conditions (Mesquita and Young 2007), suggesting that species within this genus may learn to recognise threats following sufficient exposure. Thus, studies assessing the cognitive abilities of native tilapia species would benefit our understanding of the impact of naïveté during invasions, given that rapid behavioural adaptation to novel enemies could greatly limit their negative impacts.

The results of this study highlight how naïveté during interactions with *O. niloticus* could drive harmful impacts for *O. amphimelas*, and other native fish species. Currently, very little is known about the timing or impacts of this specific invasion in situ, and this is the case for many *O. niloticus* invasions across its non-native range. Given that declines of native species following the introduction of *O. niloticus* have been reported in several areas including Tanzania (Canonica et al. 2005), future research focusing on how naïveté may impact early interactions with *O. niloticus* could help target conservation efforts towards vulnerable populations and aid policy decisions which may limit the further spread of this species.

**Author contributions** CCI, TC, KF, and ST conceived and designed the experiments. KF and ST performed the experiments. KF and ST reviewed video footage and recorded the behaviours. TC and CCI analysed the data. TC wrote the manuscript, with editorial advice from CCI and MG.

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**Data availability** The datasets generated during and/or analysed during the current study are available in the supplementary material, video files and code are available upon from the corresponding author on reasonable request.

#### Declarations

**Conflict of interest** The authors have no financial or proprietary interests in any material discussed in this article nor any other conflicts of interest to declare.

**Ethical approval** The experimental procedures and housing conditions used in this study were in accordance with the ethical standards of the University of Bristol and ethical approval was granted by the University's Animal Welfare and Ethical Review Body (UIN number: UB 18 067). All authors have given their permission for the submission of this manuscript.

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#### References

- Anton A, Geraldi NR, Lovelock CE et al (2019) Global ecological impacts of marine exotic species. *Nat Ecol Evol* 3:787–800. <https://doi.org/10.1038/s41559-019-0851-0>
- Anton A, Geraldi NR, Ricciardi A, Dick JTA (2020) Global determinants of prey naïveté to exotic predators. *Proc R Soc B Biol Sci* 287:20192978. <https://doi.org/10.1098/rspb.2019.2978>
- Bevan PA, Gosetto I, Jenkins ER et al (2018) Regulation between personality traits: individual social tendencies modulate whether boldness and leadership are correlated. *Proc R Soc B Biol Sci* 285:20180829. <https://doi.org/10.1098/rspb.2018.0829>
- Bleeker W, Schmitz U, Ristow M (2007) Interspecific hybridisation between alien and native plant species in Germany and its consequences for native biodiversity. *Biol Conserv* 137:248–253. <https://doi.org/10.1016/j.biocon.2007.02.004>
- Bolker B, R Core Team (2017) *bbmle: tools for general maximum likelihood estimation*

- Burnham KP, Anderson DR (2004) Multimodel inference: understanding AIC and BIC in model selection. *Sociol Methods Res* 33:261–304. <https://doi.org/10.1177/0049124104268644>
- Canonico GC, Arthington A, Mccrary JK, Thieme ML (2005) The effects of introduced tilapias on native biodiversity. *Aquat Conserv Mar Freshw Ecosyst* 15:463–483. <https://doi.org/10.1002/aqc.699>
- Carthey AJR, Banks PB (2014) Naïveté in novel ecological interactions: lessons from theory and experimental evidence. *Biol Rev* 89:932–949. <https://doi.org/10.1111/brv.12087>
- Carthey AJR, Blumstein DT (2018) Predicting predator recognition in a changing world. *Trends Ecol Evol* 33:106–115. <https://doi.org/10.1016/j.tree.2017.10.009>
- Chalkowski K, Lepczyk CA, Zohdy S (2018) Parasite ecology of invasive species: conceptual framework and new hypotheses. *Trends Parasitol* 34:655–663. <https://doi.org/10.1016/j.pt.2018.05.008>
- Champneys T, Castaldo G, Consuegra S, Garcia De Leaniz C (2018) Density-dependent changes in neophobia and stress-coping styles in the world’s oldest farmed fish. *R Soc Open Sci* 5:181473. <https://doi.org/10.1098/rsos.181473>
- Champneys T, Genner MG, Ioannou CC (2020) Invasive Nile tilapia dominates a threatened indigenous tilapia in competition over shelter. *Hydrobiologia* 8:1–16. <https://doi.org/10.1007/s10750-020-04341-8>
- Chapple DG, Simmonds SM, Wong BBM (2012) Can behavioural and personality traits influence the success of unintentional species introductions? *Trends Ecol Evol* 27:57–64. <https://doi.org/10.1016/j.tree.2011.09.010>
- Clavero M, Garcia-Berthou E (2005) Invasive species are a leading cause of animal extinctions. *Trends Ecol Evol* 20:110. <https://doi.org/10.1016/j.tree.2005.01.003>
- Cox JG, Lima SL (2006) Naïveté and an aquatic-terrestrial dichotomy in the effects of introduced predators. *Trends Ecol Evol* 21:674–680. <https://doi.org/10.1016/j.tree.2006.07.011>
- de Oliveira Mesquita F, Young RJ (2007) The behavioural responses of Nile tilapia (*Oreochromis niloticus*) to anti-predator training. *Appl Anim Behav Sci* 106:144–154. <https://doi.org/10.1016/j.applanim.2006.06.013>
- Favero Neto J, Giaquinto PC (2020) Environmental enrichment techniques and tryptophan supplementation used to improve the quality of life and animal welfare of Nile tilapia. *Aquac Reports* 17:100354. <https://doi.org/10.1016/j.aqrep.2020.100354>
- Friard O, Gamba M (2016) BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods Ecol Evol* 7:1325–1330. <https://doi.org/10.1111/2041-210X.12584>
- Frommen JG, Hiermes M, Bakker TCM (2009) Disentangling the effects of group size and density on shoaling decisions of three-spined sticklebacks (*Gasterosteus aculeatus*). *Behav Ecol Sociobiol* 63:1141–1148. <https://doi.org/10.1007/s00265-009-0767-9>
- Harrington LA, Harrington AL, Yamaguchi N et al (2009) The impact of native competitors on an alien invasive: Temporal niche shifts to avoid interspecific aggression? *Ecology* 90:1207–1216. <https://doi.org/10.1890/08-0302.1>
- Heavener SJ, Carthey AJR, Banks PB (2014) Competitive naïveté between a highly successful invader and a functionally similar native species. *Oecologia* 175:73–84. <https://doi.org/10.1007/s00442-013-2874-6>
- Ioannou CC (2020) Grouping and Predation. *Encycl Evol Psychol Sci*. <https://doi.org/10.1007/978-3-319-16999-6>
- Ioannou CC, Ramnarine IW, Torney CJ (2017) High-predation habitats affect the social dynamics of collective exploration in a shoaling fish. *Sci Adv*. <https://doi.org/10.1126/sciadv.1602682>
- Jiménez-García MI, Vidal-Martínez VM, López-Jiménez S (2001) Monogeneans in introduced and native cichlids in México: Evidence for transfer. *J Parasitol* 87:907–909. [https://doi.org/10.1645/0022-3395\(2001\)087\[0907:MIIANC\]2.0.CO;2](https://doi.org/10.1645/0022-3395(2001)087[0907:MIIANC]2.0.CO;2)
- Kassambara A, Kosinski M, Bieчек P (2019) survminer: drawing survival curves using “ggplot2”
- Kimbell HS, Morrell LJ (2015) Turbidity influences individual and group level responses to predation in guppies, *Poecilia reticulata*. *Anim Behav* 103:179–185. <https://doi.org/10.1016/j.anbehav.2015.02.027>
- Kolar CS, Lodge DM (2001) Progress in invasion biology: predicting invaders. *Trends Ecol Evol* 16:199–204. [https://doi.org/10.1016/S0169-5347\(01\)02101-2](https://doi.org/10.1016/S0169-5347(01)02101-2)
- Kulhanek SA, Ricciardi A, Leung B (2011) Is invasion history a useful tool for predicting the impacts of the world’s worst aquatic invasive species? *Ecol Appl* 21:189–202. <https://doi.org/10.1890/09-1452.1>
- Letnic M, Webb JK, Shine R (2008) Invasive cane toads (*Bufo marinus*) cause mass mortality of freshwater crocodiles (*Crocodylus johnstoni*) in tropical Australia. *Biol Conserv* 141:1773–1782. <https://doi.org/10.1016/j.biocon.2008.04.031>
- Llewelyn JS, Phillips BL, Shine R (2009) Sublethal costs associated with the consumption of toxic prey by snakes. *Austral Ecol* 34:179–184. <https://doi.org/10.1111/j.1442-9993.2008.01919.x>
- Martin CW, Valentine MM, Valentine JF (2010) Competitive interactions between invasive Nile tilapia and native fish: The potential for altered trophic exchange and modification of food webs. *PLoS ONE* 5:57–59. <https://doi.org/10.1371/journal.pone.0014395>
- McCormick MI, Fakan EP, Nedelec SL, Allan BJM (2019) Effects of boat noise on fish fast-start escape response depend on engine type. *Sci Rep* 9:1–10. <https://doi.org/10.1038/s41598-019-43099-5>
- Miyai CA, Sanches FHC, Pinho-Neto CF, Barreto RE (2016) Effects of predator odour on antipredator responses of Nile tilapia. *Physiol Behav* 165:22–27. <https://doi.org/10.1016/j.physbeh.2016.06.033>
- Papacostas KJ, Freestone AL (2019) Multi-trophic native and non-native prey naïveté shape marine invasion success. *PLoS ONE* 14:1–14. <https://doi.org/10.1371/journal.pone.0221969>
- Parker IM, Lonsdale WM, Goodell K et al (1999) Impact: toward a framework for understanding the ecological effects of invaders. *Biol Invasions* 1:3–19
- Phillips BL, Shine R (2004) Adapting to an invasive species: toxic cane toads induce morphological change in Australian snakes. *Proc Natl Acad Sci U S A*

- 101:17150–17155. <https://doi.org/10.1073/pnas.0406440101>
- R Core Team (2020) R: A language and environment for statistical computing
- Richardson DM, Pyšek P, Rejmánek M et al (2000) Naturalization and invasion of alien plants: concepts and definitions. *Divers Distrib* 6:93–107. <https://doi.org/10.1046/j.1472-4642.2000.00083.x>
- Robbins TR, Freidenfelds NA, Langkilde T (2013) Native predator eats invasive toxic prey: evidence for increased incidence of consumption rather than aversion-learning. *Biol Invasions* 15:407–415. <https://doi.org/10.1007/s10530-012-0295-9>
- Romensky M, Herbert-Read JE, Ioannou CC et al (2020) Quantifying the structure and dynamics of fish shoals under predation threat in three dimensions. *Behav Ecol* 31:311–321. <https://doi.org/10.1093/beheco/arz197>
- Ros AFH, Becker K, Oliveira RF (2006) Aggressive behaviour and energy metabolism in a cichlid fish, *Oreochromis mossambicus*. *Physiol Behav* 89:164–170. <https://doi.org/10.1016/j.physbeh.2006.05.043>
- Roshani D, Ghaderi E (2016) Comparing smoothing techniques for fitting the nonlinear effect of covariate in cox models. *Acta Inform Medica* 24:38–41. <https://doi.org/10.5455/aim.2016.24.38-41>
- Rowles AD, O'Dowd DJ (2007) Interference competition by Argentine ants displaces native ants: Implications for biotic resistance to invasion. *Biol Invasions* 9:73–85. <https://doi.org/10.1007/s10530-006-9009-5>
- Salo P, Korpimäki E, Banks PB et al (2007) Alien predators are more dangerous than native predators to prey populations. *Proc R Soc B Biol Sci* 274:1237–1243. <https://doi.org/10.1098/rspb.2006.0444>
- Sanches FHC, Miyai CA, CostaTâ TM et al (2012) Aggressiveness overcomes body-size effects in fights staged between invasive and native fish species with overlapping niches. *PLoS ONE* 7:e29746. <https://doi.org/10.1371/journal.pone.0029746>
- Sanches FHC, Miyai CA, Pinho-Neto CF, Barreto RE (2015) Stress responses to chemical alarm cues in Nile tilapia. *Physiol Behav* 149:8–13. <https://doi.org/10.1016/j.physbeh.2015.05.010>
- Sax DF, Gaines SD (2008) Species invasions and extinction: the future of native biodiversity on islands. *Proc Natl Acad Sci* 105:11490–11497. <https://doi.org/10.17226/12501>
- Schlaepfer MA, Sax DF, Olden JD (2011) The potential conservation value of non-native species. *Conserv Biol* 25:428–437. <https://doi.org/10.1111/j.1523-1739.2010.01646.x>
- Schlaepfer MA, Sherman PW, Blossey B, Runge MC (2005) Introduced species as evolutionary traps. *Ecol Lett* 8:241–246. <https://doi.org/10.1111/j.1461-0248.2005.00730.x>
- Shechonge A, Ngatunga BP, Bradbeer SJ et al (2019) Wide-spread colonisation of Tanzanian catchments by introduced *Oreochromis tilapia* fishes: the legacy from decades of deliberate introduction. *Hydrobiologia* 832:235–253. <https://doi.org/10.1007/s10750-018-3597-9>
- Szopa-Comley AW, Donald WG, Ioannou CC (2020) Predator personality and prey detection: inter-individual variation in responses to cryptic and conspicuous prey. *Behav Ecol Sociobiol*. <https://doi.org/10.1007/s00265-020-02854-9>
- Therneau TM (2020) A package for survival analysis in R
- Trewavas E, Fryer G (1965) Species of *Tilapia* (Pisces, Cichlidae) in Lake Kitangiri, Tanzania, East Africa. *Proc Zool Soc London* 147:108–118
- Venables B, Ripley B (2002) *Modern applied statistics with S*, 4th edn. Springer, New York
- Wagenmakers EJ, Farrell S (2004) AIC model selection using Akaike weights. *Psychon Bull Rev* 11:192–196. <https://doi.org/10.3758/BF03206482>
- Wing JDB, Champneys TS, Ioannou CC (2020) The impact of turbidity on foraging and risk taking in the invasive Nile tilapia (*Oreochromis niloticus*) and a threatened native cichlid (*Oreochromis amphimelas*). *bioRxiv* <https://doi.org/10.1101/2020.07.23.217513>

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