

Density-dependence of comparative functional responses in two globally invasive fish species

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Abstract

Characterising the trophic interactions of invasive species is critical to understanding and predicting their ecological impacts. The comparative functional response metric, which quantifies predator-prey interaction strength, is increasingly used as a tool to predict impacts and prioritize the management of high-impact invasive species. However, functional responses are not consistent across populations nor individuals of a species and, like other physiological metrics, functional responses exhibit intra-individual variation (e.g., plasticity), in response to external conditions. Here, we experimentally examine the potential for plasticity in functional responses in response to conspecific population density, an environmental variable that exerts effects on both individual-level physiology and population-level numeric processes. Using wild populations of two high-impact globally invasive freshwater fish species (Goldfish, *Carassius auratus*, and Common Carp, *Cyprinus carpio*), we experimentally applied a 10-week long acclimation to low vs. high conspecific density, then examined comparative functional responses. We found that both species had significantly lower maximum feeding rates after acclimation to high density, although species-level variation persisted, with Goldfish consistently outperforming Carp in feeding trials. Our results suggest that variation in conspecific density can cause considerable variation in per-capita functional responses, consequently affecting impact predictions across gradients of invasion intensity.

Introduction

Trophic interactions are key determinants of invasive species establishment and the magnitude of their ecological impacts (David et al. 2017). High-impact invasive species are often characterized by their ability to rapidly and efficiently exploit resources in novel environments, and subsequent impacts can be linked directly to the strength of trophic interactions between invasive species and native prey (Johnson et al. 2008; Morrison and Hay 2011; Alexander et al. 2014; Faria et al. 2025). Indirectly, through feeding-linked mechanisms, invasive species can also drive habitat modifications that serve to benefit their proliferation, often to the disadvantage of native communities (Cuddington and Hastings 2004; Fei et al. 2014).

These observations linking trophic processes to invasion biology have culminated in the widespread use of comparative functional responses, which describe the relationship between consumption and resource availability in an environment, to quantify and predict the impact of invasive species in the wild (Holling 1965; Dick et al. 2013, 2014, 2017a). In invasion biology, comparative functional responses offer a generalized solution to the notoriously difficult problem of defining invader impacts (Dick et al. 2013, 2014, 2017a). Invasive species with higher functional responses have been empirically demonstrated to impose greater relative ecological impacts (Faria et al. 2025), and these comparisons can ultimately be used to prioritize the context-specific management of invasive species (Byers et al. 2002; Simberloff et al. 2013).

However, functional responses are unlikely to be consistent across all individuals within a species, nor over time, which affects our ability to accurately predict ecological impacts (Howard et al. 2018). Intraspecific variation in factors such as body size (Franta et al. 2023), sex and gravidity (Dalal et al. 2021; Sheppard et al. 2024; Ventura et al. 2024), metabolic aerobic scope (Auer et al. 2015), and even parasitic infection (Lavery et al. 2017), have been linked to variation in feeding rates. Organisms also exhibit considerable plasticity in functional responses in response to changes in external environmental conditions. In fishes, short-term acclimation to different temperature (South and Dick 2017; Mofu et al. 2019; Tarkan et al. 2024; Ventura et al. 2024; Claus et al. 2025; Benjamin et al. 2026) and salinity (Claus et al. 2025) regimes drive changes in maximum functional responses, suggesting there are environmental optima for feeding performance that vary based on current or previous environments (Iacarella et al. 2015; Tarkan et al. 2024; Benjamin et al. 2026).

In ecology, the abundance and, therefore, density, of populations is a biotic context that ubiquitously modulates broader population processes, including rates of growth, recruitment, and survival (Post et al. 1999; Myers 2001; Hixon and Jones 2005; Sibly et al. 2005; Minto et al. 2008; Andersen et al. 2017). Density-dependence is particularly relevant to invasion ecology, given that the density of invasive populations can vary substantially across their introduced range (Hansen et al. 2013), including scenarios in which populations grow or decline, temporally during seasonal aggregations (Johnsen and Hasler 1977) and along gradients of the invasion pathway (Paton et al. 2019). Such variation in density exerts influence on the total ecological impacts of an invasive population and, consequently, understanding the density-dependence of invasive populations is critical to informing management efforts that mediate these impacts (Kornis et al. 2014). Although ecological impacts are often assumed to be positively (and often, linearly, e.g., (Yokomizo et al. 2009; Dick et al. 2017b)) related to invader density, empirical data suggest that variation in invader density can lead to unexpected and nonlinear responses in prey communities and habitats (Kornis et al. 2014; Jackson et al. 2015). These effects are often attributed direct interference or facilitation between conspecifics during foraging, which ultimately impact per-capita feeding efficiency (Kornis et al. 2014; DeRoy et al. 2020).

It is also possible that indirect effects of density on organismal performance occurring alongside conspecific interactions can lead to variation in invader impacts. For example, population density has been shown to influence organismal-level performance traits linked to foraging and energetics, including metabolism (DeLong et al. 2014), movement (McKenzie et al. 2012), and growth (Newman et al. 2015). If the physiological processes underlying energetic uptake show plasticity in response to conspecific density, it follows that the functional responses of invaders will also be labile, even in the absence of direct intraspecific interference or facilitation (DeLong et al. 2014).

In this study, we explore this prediction by examining comparative density-dependent plasticity of functional responses in two high-impact global invaders, Goldfish (*Carassius auratus*) and Common Carp (*Cyprinus carpio*). In Lake Ontario of the Laurentian Great Lakes, populations of both species occupy and cause severe habitat modifications in ecologically significant wetlands (Weber and Brown 2009; Massey et al. 2025). Both populations are also contemporarily undergoing shifts in abundance. In Coote's

Paradise, one of the largest river-mouth wetlands of Lake Ontario, the historically dominant Common Carp is contemporarily declining – in large part, due to ‘The Fishway’, a spawning-barrier management initiative (Boston et al. 2024). Concomitantly, Goldfish is increasing in abundance here and elsewhere in Canada, even where it does not coexist with Common Carp, likely as the result of increased habitat suitability under climate change (Massey et al. 2025). Although both Common Carp and Goldfish have centuries-long invasion histories in Lake Ontario (Boston et al. 2024), little information is available on the fundamental biology and ecology of Goldfish, which remains largely unmanaged relative to Common Carp in the Laurentian Great Lakes (Massey et al. 2025). If invader densities exert influence on functional responses, the relative shifts in Common Carp and Goldfish population abundances have the potential to alter invasion dynamics and impacts, and forecasting these changes will be critical to ongoing management as Goldfish abundance increases (Hubbard et al. 2023; Massey et al. 2025).

Methods

Natural history of study species and site

Our study focused on coexisting populations of invasive Goldfish (*Carassius auratus*) and Common Carp (*Cyprinus carpio*) from Lake Ontario, Canada, sourced from an ecologically significant wetland (Cootes Paradise, Hamilton Harbour). Although both populations have been established in Lake Ontario for over a century (Scott and Crossman 1973), long-term monitoring projects in Lake Ontario indicate that, while the population of Common Carp has declined in the past decade, the local abundance of Goldfish is increasing at an alarming rate (Boston et al. 2024). Notably, increasing mean temperatures in northern climates may be facilitating northward establishment of Goldfish (Hubbard et al. 2023; Massey et al. 2025). In Cootes Paradise, over the past decade, surface water temperatures have increased to exceed 20°C during the late-spring to early-summer breeding season, which is predicted to increase habitat suitability for this species (Hubbard et al. 2023; Massey et al. 2025). Both Common Carp and Goldfish share a common diet and primarily benthic feeding behaviours, suggesting they are appropriate comparators with similar ecological impacts, including the destruction of aquatic vegetation and generation of turbidity (Richardson et al. 1990, 1995).

Collection and husbandry

In September 2025, size-matched Goldfish and Common Carp (mean masses $\pm$ standard deviation: 9.13 $\pm$ 1.92 g, 9.45 $\pm$ 3.25 g, respectively) were collected from Hamilton Harbour, Ontario, Canada, by seine netting. Fishes were transported to the University of Toronto Scarborough Aquatics Facility in aerated 50 L coolers half-filled with source water. Individuals were then randomly allocated to species-specific 57 L static treatment tanks at high (8 fish per tank; two replicates) or low (4 fish per tank; four replicates) densities. Five additional Goldfish were kept separately for pilot functional-response experiments.

Treatment tanks were kept at a static temperature of 22.5°C throughout the experiment, reflecting summer daytime temperature in Cootes Paradise. To develop a nitrifying bacterial filter, all static tanks were cycled for one month prior to introduction of fish. Each treatment tank was equipped with an aquarium filter containing a sponge, a heater set to 22.5°C, and enrichment (two granite rocks, four plastic plants, and a 10 cm section of trimmed PVC pipe forming a small tunnel). Water temperature was measured daily and additional water parameters (pH, hardness, ammonia, nitrite, nitrate) were monitored biweekly. All parameters were kept consistent between tanks; 20% water changes were done as needed based on parameters, ensuring ammonia and nitrites were consistently absent, and nitrates were kept below 30–40 ppm. Fishes were fed *ad libitum* with 2 mm sinking Goldfish pellets (API) daily and 5–6 mm frozen chironomid larvae (Hikari) twice weekly; we provided a small excess of food during feedings and siphoned uneaten food items when fish appeared satiated.

Fishes were allowed to acclimate to captive conditions for 2 w in their respective treatment groups. After this observation period, to track individual-level responses, we tagged each fish using 8 mm PIT tags (Mini HPT8 Pit Tag, Biomark). Each fish was anesthetized in 60 mg/L eugenol until they lacked a caudal-pinch reaction. We then injected PIT tags ventrally (~ 2 mm postero-laterally from the pelvic fin) into the abdominal cavity, measured and weighed fishes to establish individual baseline measurements, then placed them in an aerated recovery chamber under observation for ~ 30 min, before returning them to their respective tanks. We continued to acclimate fishes in their respective density treatments for a further 8 w, totalling 10 w of acclimation.

Pilot trials

Due to uncertainty regarding the feeding behaviours of wild-caught fishes under lab conditions, pilot trials with a separate group of 5 Goldfish were conducted to determine appropriate experimental conditions, food items, and quantity of food, for functional-response experiments. Our pilot trials indicated fish would only consume prey if feeding arenas were covered (darkened) and that acclimation periods of 1, 2, and 6 h to experimental arenas resulted in a high proportion of trials with no prey consumption. When fish were acclimated individually overnight (~ 16 h) to arenas, 100% of fish consumed prey. We also found that small, frozen chironomid larvae were not logistically feasible to use as prey items, due to difficulty associated with counting and recovering larvae after the trial (Goldfish of mass ~ 9 g were able to consume > 200 5–6 mm larvae in 1 h, but were unable to consume whole 30–50 mm “Jumbo” larvae). However, fish readily consumed reasonable quantities of 1–2 mm sinking pellets and maximum consumption over 1 h did not increase when the number of pellets was increased to 80–100 pellets. In pilot trials using fishless, aerated arenas filled with dechlorinated system water, all pellets remained intact and were counted accurately after periods of 1 and 2 h. We therefore chose to use sinking pellets, due to the willingness of Goldfish to consume them, their standardized size, logistic feasibility with respect to counting initial and remaining food items, and to enable comparisons with other comparative functional response studies (Claus et al. 2025) in these species.

Functional response experiments

Following the 10 w density acclimation period, we began functional-response trials. Individual fish of known identity were tested every 5–6 days, and each fish was assigned a randomized order of prey densities across the experiment. Trials were conducted with eight fish simultaneously, in eight separate arenas, with two fish per species×density treatment group tested during each trial day. Fish were starved for 24 h before each trial to standardize hunger levels and reduce output of wastes into arenas, which consisted of 11.3 L opaque lidded plastic tubs, $\frac{3}{4}$ filled with continuously aerated system water set to 22.5°C. Fishes were left undisturbed for 16 h overnight to recover from handling and acclimate to experimental conditions, before initiating trials at the typical feeding time (09:00 h). Prey items (pellets) were then offered at densities of 8, 16, 32, 64, and 84, introduced to the arena by gently lifting the opaque cover and scattering pellets evenly throughout the arena, ensuring minimal light exposure. Fish were then left to feed, uninterrupted, over a 1 h period. Each fish was subsequently removed and returned to its tank of origin, before remaining food items were counted in each arena. We ultimately collected consumption data for individual fish in our experiment at each of five prey densities (total N = 160 trials).

Statistical analyses

We conducted functional-response analyses using the *frair* package (Pritchard et al., 2025) workflow in the R Statistical Computing Environment. To estimate FR parameters, we applied a maximum likelihood estimation method, fitting data from each species×density group (Goldfish High Density, Goldfish Low Density, Common Carp High Density, Common Carp Low Density) to Rogers' Random Predator function using the *frair_fit* function (Pritchard et al., 2025). We selected this equation because it assumes prey are depleted throughout the trial, and it models the Type II functional response, which was confirmed in our data both visually and *via* generalized linear models demonstrating a single, increasing initial slope of prey consumption vs. density (*frair_test* function (Pritchard et al. 2017); see Supplementary Materials). Rogers' Random Predator function took the form:

$$\text{Equation 1: } N_e = N_0(1 - e^{a(N_e h - T)})$$

Where N_e is the number of prey consumed, N_0 is the number of prey offered, a is the attack rate, h is the handling time, and T is the duration of the experiment (set to 1 h).

We made statistical comparisons of parameter (a and h) estimates between species×density groups by modelling the differences between curves through maximum likelihood estimation, using the same fitting procedure described above, then determining if parameter estimates from the resultant 'difference model' were significantly different from zero (Juliano 2001); details are in Supplementary Materials. These comparisons were facilitated through the *frair_compare* function (Pritchard et al. 2017). For visual purposes, we estimated 95% confidence intervals (CIs) for each species×density group by non-parametrically bootstrapping ($n = 999$) functional-response models for each species×density group. We

also examined two additional parameters based on estimates from our functional-response models, including maximum feeding rate ($1/h$) and functional-response ratios (FRR; a/h ; (Cuthbert et al. 2019)).

Results

Metadata reporting

There were no mortalities as a result of the tagging procedure, and all fish resumed normal feeding and behaviours the following day. Two individuals in different tanks (one Low Density Common Carp and one High Density Goldfish) rejected their tags after 1–2 weeks; we ultimately did not replace these tags to prevent additional stress to the animals but were able to maintain unique identification of these individuals as they were the only fish without tags in their respective tanks.

Functional responses

Both species and density treatment impacted functional-response curves (Fig. 1, Table 1). Regardless of density treatment, Goldfish had shorter handling times and higher maximum functional responses than Common Carp (Fig. 1; Table 1). Acclimation to High Density led to significantly lower attack rates for Goldfish (2.08 vs. 3.79, SE = 0.48, $z = -3.57$, $p = 0.00036$; Table 1), but not Common Carp (2.22 vs. 2.52, SE = 0.54, $z = -0.57$, $p = 0.57$; Table 1). However, acclimation to High Density led to significantly higher handling times for both species (Goldfish: 0.03 vs. 0.02, SE = 0.01, $z = 2.52$, $p = 0.01$; Common Carp: 0.06 vs. 0.04, SE = 0.01, $z = 5.08$, $p < 2 \times 10^{-16}$; Table 1).

Table 1

Functional-response parameters of wild-caught, invasive Goldfish and Common Carp from High Density and Low Density 10-week acclimation treatments, including attack rate (a) and handling time (h), and the respective bootstrapped 95% confidence intervals of a and h , maximum feeding rate ($1/hT$, where $T = 1$ h), and functional response ratio (a/h) fitted to Rogers' random predator equation using maximum likelihood estimation. Pairwise comparisons between species×density groups for estimates of a and h were made; estimates that do not significantly differ share the same number of asterisks.

Goldfish High Density	Attack rate (a) and 95% CIs	Handling time (h) and 95% CIs	Maximum feeding rate ($1/h$)	Functional response ratio (a/h)	Comparison attack rate (a)	Comparison handling time (h)
	2.08 [1.16, 3.50]	0.03 [0.02, 0.04]	37.04	77.11	*	*
Common Carp High Density	2.22 [0.89, 5.11]	0.06 [0.05, 0.09]	15.87	35.24	*	**
Goldfish Low Density	3.79 [2.02, 6.45]	0.02 [0.01, 0.03]	47.62	180.38	**	***
Common Carp Low Density	2.52 [1.37, 4.07]	0.04 [0.03, 0.05]	27.03	68.21	*	****

With respect to maximum feeding rates ($1/h$) and functional response ratios (a/h), differences in handling times resulted in higher maximum feeding rates ($1/h$) for both species in the Low Density treatment group (Goldfish: 48 vs. 37; Common Carp: 27 vs. 16; Table 1). Within density treatments, Goldfish had higher FRRs than Common Carp in both High Density (35.2 vs. 77.1) and Low Density (180.4 vs. 68.2) treatments.

Discussion

Conspecific density can exert a powerful influence on both population dynamics and the physiology of individuals (Post et al. 1999; Myers 2001; Hixon and Jones 2005; Sibly et al. 2005; Minto et al. 2008). The functional-response metric, which measures the strength of interaction between predator and prey, is a tool used to conceptually bridge these population- and individual-level processes through foraging performance (Holling 1959). However, in the context of invasion biology, despite the increasing use of comparative functional responses to predict invader impacts, density-dependence is infrequently explored as an environmental variable that influences feeding rates (Faria et al. 2025).

Here, we found that 10 weeks of acclimation to low vs. high conspecific density led to changes in functional responses in two destructive invasive fish species, Common Carp and Goldfish. These plasticity-facilitated changes were evident in both species through increased maximum feeding rates, and, equivalently, reduced prey handling times, after acclimation to low conspecific density. We also found that Goldfish consistently outperformed Common Carp in terms of maximum feeding rates at both

high and low densities, with low-density Goldfish displaying significantly higher attack rates. Integrating both maximum feeding rates and attack rates, we find that Goldfish have a two-to-threefold increase in functional-response ratios relative to Common Carp, suggesting Goldfish populations could have comparatively substantial ecological impacts when numeric population responses are taken into consideration (Cuthbert et al. 2019).

Density-dependence of functional responses

The density-dependence of functional responses is often examined in the context of multiple predator effects, in which per-capita feeding rates are estimated in trials testing varying group sizes of predators (Beddington 1975; Sih et al. 1998). Using this approach, when per-capita functional responses of multiple predators diverge from additive predictions based on single predators, it is assumed that conspecific interference (e.g., intimidation) or facilitation (e.g., group foraging enhances identification of prey) are responsible (Beddington 1975; Sih et al. 1998; Kornis et al. 2014; Grimm et al. 2020).

In invasion biology, there is indirect evidence from single-predator comparative functional-response experiments along invasion gradients (*i.e.*, where density is low at invasion fronts, but high in established sites) to suggest that density-dependent mechanisms cause variation in per-capita consumption outside of direct predator-predator interactions (Iacarella et al. 2015; Paton et al. 2019). For example, Paton et al. (Paton et al. 2019) found that the attack rates of individually tested Round Goby (*Neogobius melanostomus*) from high-density established sites were greater than those from the low-density invasion front, despite equivalent maximum feeding rates along the invasion gradient. By contrast, in a reciprocal transplant experiment controlling for the confounding effect of variation in environmental quality along the invasion gradient, Iacarella et al. (Iacarella et al. 2015) found higher functional responses in low-density invasion-front populations of the crustacean *Hemimysis anomala*. In these experiments, density-dependent behavioural differences affecting attack rates along the invasion gradient were the primary explanation for changes in functional responses, although there was uncertainty regarding whether these differences were genetic or plastic in origin (Iacarella et al. 2015; Paton et al. 2019).

Our study adds to this growing body of work, suggesting that there is a considerable effect of within-lifetime plasticity that accounts for variation in functional responses. In the absence of local adaptation, we found that a relatively short 10-week acclimation to high or low conspecific density was sufficient to induce significant changes in the functional responses of both Common Carp and Goldfish. Unlike previous studies that found density-dependent differences in attack rates (Iacarella et al. 2015; Paton et al. 2019), we found that low-density acclimation led to increases in maximum feeding rates for both species, whereas there was species-specific density-dependence in attack rates for Goldfish only.

It is possible that these changes were mediated through physiological plasticity occurring at the level of the individual. Aquaculture studies have found that rearing fishes at high densities reduces individual-level efficiency of food conversion and lipid metabolism (Procarione et al. 1999; Stone et al. 2003). At

high stocking densities, the routine metabolic rates of fishes also increase, suggesting that higher conspecific density may plastically reduce energetic efficiency at rest (Ruer et al. 1987; Sloman et al. 2000; Larsen et al. 2012). Density-dependent plastic changes to the metabolic phenotype of our study fishes may ultimately explain why feeding performance was reduced after high-density acclimation, despite the lack of direct conspecific interference during trials. Because physiological traits, such as metabolism and behaviour, mechanistically underlie foraging performance (Auer et al. 2015; Taylor and Dunn 2018; Linzmaier and Jeschke 2020; McGlade et al. 2022) and are highly environmentally responsive (Seebacher and Little 2026), they warrant consideration in impact prediction frameworks going forward.

Functional responses, the rise of Goldfish, and the fall of Common Carp

Over the past two decades, the invasive range and population abundances of Goldfish have rapidly increased across northern latitudes (Massey et al. 2025). One explanation for these increases is that global warming has enhanced the suitability of freshwater habitats for Goldfish (Hubbard et al. 2023), whose thermal optimum is relatively high, peaking at 20–29°C, depending on prior acclimation temperature (Ferreira et al. 2014). This explanation may also contextualize contemporary population shifts in Cootes Paradise, where the previously dominant Common Carp is now facing population decline (Boston et al. 2024). Although decreases in abundance of Common Carp are likely, in part, explained by significant and ongoing management efforts occurring in the wetland (Lougheed et al. 2004), Common Carp management alone cannot explain the rapid spread of Goldfish in other sites across North America (Massey et al. 2025).

Instead, local habitat suitability may also be decreasing under warming conditions for Common Carp. Our results support this explanation, given the context of the thermal biology of these two species. Using the current-day summer temperatures experienced in the study area (~ 22.5°C), we found that Goldfish had higher maximum feeding rates and functional-response ratios than Common Carp, regardless of density. Yet, prior work using aquaculture strains found the opposite pattern at cooler temperatures (18°C), suggesting the thermal optimum for foraging occurs at a higher temperature for Goldfish than Common Carp (Tarkan et al. 2024). Common Carp further demonstrate declines in growth rates at temperatures above 20°C (Oyugi et al. 2012). When the high physiological thermal optimum (> 20°C (Ferreira et al. 2014)) of Goldfish is taken into account, it is likely that the foraging rates of Goldfish, and, consequently, the rates of energetic uptake that contribute to recruitment and population growth, are increasing in step with rising temperatures in our study area, and elsewhere in North America (Piczak et al. 2025).

Conclusions

Here, we show that the density at which conspecific invaders live is a critical context-dependency that plastically affects functional responses. This plasticity in functional responses occurs outside of direct

conspecific interactions, suggesting alternative underlying mechanisms, such as metabolic plasticity, can contribute to variation in invader impacts. In the context of ongoing invasions in our study area, our results predict that the per-capita ecological impacts of both Common Carp and Goldfish individuals will decline if population densities locally increase, even if the sum total of all per-capita effects amplifies alongside abundance. Given the remarkably high comparative functional responses of Goldfish, our results also suggest that urgent management efforts will be required to minimize the ecological impacts of growing Goldfish populations in the Laurentian Great Lakes and elsewhere.

Declarations

Competing Interests

All authors declare they have no competing interests.

Animal ethics statement

This study was approved by the University of Toronto Scarborough Animal Care Committee under Protocol #20013252.

Use of Artificial Intelligence (AI) and AI-assisted technologies

No artificial intelligence/language learning models were used at any stage of this study.

Competing interests

The authors declare no competing interests.

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Author Contributions

M.D.M. and N. E. M. contributed to study conceptualization and design. N. E. M. was responsible for supervision. M. D. M. collected field specimens with assistance from our partner organization. M. D. M. and S. H. collected data and performed animal husbandry. M. D. M. conducted statistical analyses. M. D. M. wrote the first manuscript draft and all authors contributed to editing. All authors approved of the final manuscript.

Data availability

Data are included in the electronic Supplementary Material.

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Figures

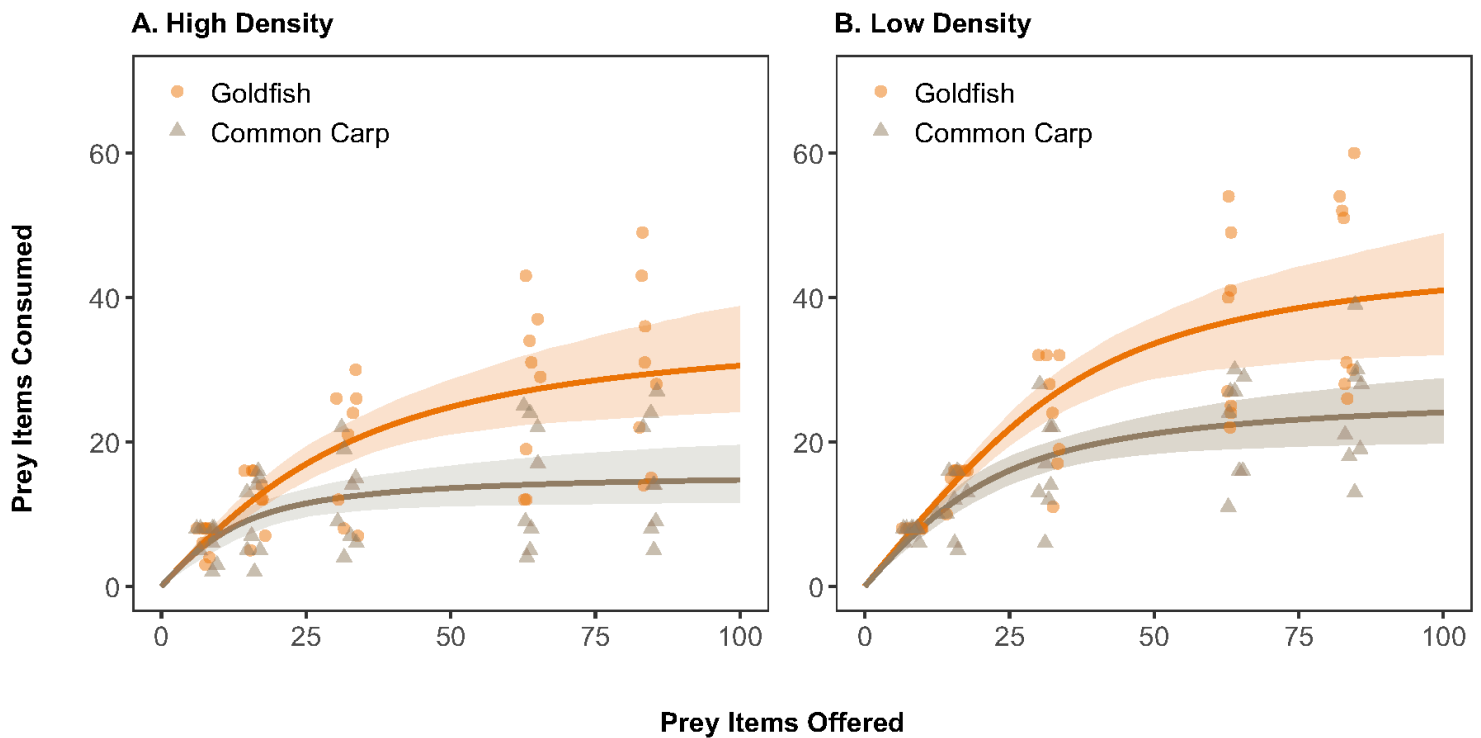


Figure 1

Functional responses of wild-caught, invasive Goldfish (orange circles) and Common Carp (brown triangles) from High Density (A) and Low Density (B) 10-week acclimation treatments. Functional-response trials lasted 1 hour and tagged individuals (N=32) were tested repeatedly every 5-6 days in a randomized order with respect to prey density. Points denote individual prey consumption, lines denote maximum likelihood-estimated functional response relationships modelled using Rogers' random predator equation, and shaded areas represent predicted 95% confidence intervals estimated from bootstrapped (n=999) model fits.

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