

# Size-dependent functional response of *Xenopus laevis* on mosquito larvae (#24758)

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# Size-dependent functional response of *Xenopus laevis* on mosquito larvae

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Predators can play an important role in regulating prey abundance and diversity, determining food web structure and function, and contributing to important ecosystem services, including the regulation of agricultural pests and disease vectors. Thus, the ability to predict predator impact on prey is an important goal in ecology. Often predators of the same species are assumed to be functionally equivalent, despite considerable individual variation in predator traits known to be important for shaping predator-prey interactions, like body size. This assumption may greatly oversimplify our understanding of within species functional diversity and undermine our ability to predict predator effects on prey. Here we examine the degree to which predator-prey interactions are functionally homogenous across a natural range of predator body size. Specifically, we quantify the size-dependence of the functional response of African clawed frogs (*Xenopus laevis*) preying on mosquito larvae (*Culex pipiens*). Three size classes of predators, small (15-30mm snout-vent length), medium (50-60mm) and large (105-120mm), were presented with five densities of prey to determine functional response type and to estimate search efficiency and handling time parameters generated from the models. The results of mesocosm experiments show that functional response of *X. laevis* changed with size: small predators exhibited a Type II response, while medium and large predators exhibited Type III responses. Both functional response and behavioural data showed an inversely proportional relationship between predator attack rate and predator size. Small and medium predators had highest and lowest handling time respectively. That the functional response changed with the size of predator suggests that predators with overlapping cohorts may have a dynamic impact on prey populations. Therefore, predicting the functional response of a single size-matched predator in an experiment may be a misrepresentation of the predator's potential impact on a prey population.

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# Abstract

Predators can play an important role in regulating prey abundance and diversity, determining food web structure and function, and contributing to important ecosystem services, including the regulation of agricultural pests and disease vectors. Thus, the ability to predict predator impact on prey is an important goal in ecology. Often predators of the same species are assumed to be functionally equivalent, despite considerable individual variation in predator traits known to be important for shaping predator-prey interactions, like body size. This assumption may greatly oversimplify our understanding of within species functional diversity and undermine our ability to predict predator effects on prey. Here we examine the degree to which predator-prey interactions are functionally homogenous across a natural range of predator body size. Specifically, we quantify the size-dependence of the functional response of African clawed frogs (*Xenopus laevis*) preying on mosquito larvae (*Culex pipiens*). Three size classes of predators, small (15-30mm snout-vent length), medium (50-60mm) and large (105-120mm), were presented with five densities of prey to determine functional response type and to estimate search efficiency and handling time parameters generated from the models. The results of mesocosm experiments show that functional response of *X. laevis* changed with size: small predators exhibited a Type II response, while medium and large predators exhibited Type III responses. Both functional response and behavioural data showed an inversely proportional relationship between predator attack rate and predator size. Small and medium predators had highest and lowest handling time respectively. That the functional response changed with the size of predator suggests that predators with overlapping cohorts may have a dynamic impact on prey populations. Therefore, predicting the functional response of a single size-matched predator in an experiment may be a misrepresentation of the predator's potential impact on a prey population.

Key words: attack rate, functional response, handling time, predator, size

# Introduction

Predator-prey interactions are important in regulating prey populations and determining the structure of aquatic communities (Brooks and Dodson, 1965; Carpenter *et al.* 1985). Predators directly impact prey populations by causing a decline in survival and recruitment, whereas prey quantity and quality directly affect feeding rate, growth, density, reproductive success and population dynamics of predators (Miller *et al.* 1988; Leucke *et al.* 1990; Beauchamp *et al.* 2007). Consequently, these interactions can affect the distribution, habitat choice, behaviour and foraging strategies of both predators and prey (Eggers, 1978; Sih, 1982; Walls *et al.* 1990). Classical predator-prey models typically assume that individual predators within a population are functionally equivalent (Lotka, 1924; Volterra, 1931; Rosenzweig and MacArthur, 1963). However, most species undergo considerable change in size during their ontogeny. Changing scaling relationships between predators and prey are known to produce nonlinear interactions, with intermediate size predators imposing the strongest *per capita* top-down interactions (Vucic-Pestic *et al.* 2010). Size differences of prey may have significant consequences for predator-prey interactions (Jansson *et al.* 2007, Rudolf 2008, McCoy *et al.* 2011). While few studies have quantified how predator size influences shapes of functional responses on the same prey, these highlights that predator handling time and attack rate can be size-dependent (e.g. Vucic-Pestic *et al.* 2010, Milonas *et al.* 2011, Anderson *et al.*, 2016) and that even the general form of the functional response may vary with predator size (Anderson *et al.*, 2016). These studies highlight that assuming predators of the same species are functionally equivalent may greatly oversimplify our understanding of within species functional diversity and undermine our ability to predict predator effects on prey.

The functional response is the key relationship linking predator and prey dynamics. Hollings (1963) described the three most common models of predator functional response. A Type I response is characterized as having a constant attack rate  $a$  with no handling time  $h$  (Holling, 1959; Hassell, 1978). A Type II response includes handling time and as a result, proportion of prey consumed is not constant, but instead declines with higher prey densities due to handling constraints. Predators that exhibit a Type II

75 response typically de-stabilise prey populations due to high consumption rates at low prey densities  
 76 (Rosenzweig and MacArthur, 1963; Oaten and Murdoch, 1975). A Type III response is characterised as  
 77 having low consumption rates at low prey densities. The proportion of prey consumed initially increases  
 78 with increasing prey availability then declines as in a Type II response (Holling, 1959; Hassell, 1978).  
 79 This can create a refuge for prey at low densities, facilitating the persistence of prey populations.  
 80 Therefore, the type of functional response a predator exhibits can result in quite different outcomes for  
 81 prey and by describing the response, the potential impact at a population level may be elucidated (e.g.,  
 82 Rosenzweig and MacArthur, 1963). Jeschke *et al.*, (2002) presented a mechanistic functional response  
 83 model that can be populated with observational data, enabling researchers to estimate the same set of  
 84 variables through independent observations. These provide insight into the mechanism that determines  
 85 how and why attack rate and handling time vary.  
 86  
 87 Several factors may influence the type of functional response exhibited for a specific predator-prey  
 88 interaction. This includes environmental conditions (e.g. Lavery *et al.* 2015, Englund *et al.* 2011) as well  
 89 as body size of participants (e.g. Brose *et al.* 2005, McCoy *et al.* 2011, Tucker *et al.* 2014, Anderson *et*  
 90 *al.*, 2016). Size variation is a common feature in animal populations and influences predator-prey  
 91 interactions, competition and individual life histories (Ebenman, 1988; Wilbur 1988; Samhouri *et al.*  
 92 2009; Asquith and Vonesh, 2012). However, preferred prey typically change with ontogeny for many  
 93 predators such that experiments are not able to present common prey across a range of predator sizes. For  
 94 example, Milonas *et al.* (2011) investigated the functional response of different instars of larval ladybirds  
 95 (*Nephus includens*) using increasing prey sizes; all exhibited the same functional response type (Type II),  
 96 but showed small differences in handling time and attack rate. For iteroparous amphibians with  
 97 indeterminate growth and overlapping cohorts, individual body size is especially important (Márquez *et*  
 98 *al.* 1997; Werner, 1994). Smaller predators in these populations may be limited by the range of prey size  
 99 they can consume (e.g., handling time may be greater for small predators; Anderson *et al.*, 2016) and  
 100 are often more efficient at assimilating consumed prey into their own biomass due to their high metabolic



rates (Werner, 1994; Asquith and Vonesh, 2012). In contrast, their larger conspecifics are generally less efficient in converting prey biomass into predator biomass but may have a much broader range of prey that they can consume (Schoener, 1969; Asquith and Vonesh, 2012; Cohen *et al.* 1993). In these populations, smaller predators may then have to deal with competition from larger predators that may result in a recruitment bottleneck that could potentially extend the period of time smaller predators remain at a vulnerable size (Schroder *et al.* 2009; Asquith and Vonesh, 2012). Therefore understanding the relationship between consumer size and their feeding rates can provide insights into intra-cohort interactions and population dynamics of structured predator populations.

To investigate the role of predator size on functional response, we conducted a comparative functional response study between African clawed frogs, *Xenopus laevis*, of different sizes on a single prey type mosquito larvae, *Culex pipiens*, in order to answer the following questions: 1) Do differences exist in functional response type between different sized predators of the same species for a standardised prey size? 2) Are there differences in the functional response parameters (attack rate, handling time, and maximum feeding rate) derived between these different sized predators? 3) Do attack rate and handling time obtained from observational studies agree with model-derived parameters?

## Materials and methods

### Study species

The focal predator species, the African clawed frog (*Xenopus laevis*, Daudin), has a wide distribution in southern Africa and inhabits permanent and temporary water bodies across its native range (Measey 2004). In *X. laevis*, individuals within a population can vary as much as 8-fold in body size, with metamorphs as small as 15 mm snout vent length (SVL), to large adults exceeding 120 mm SVL (de Villiers *et al.* 2016). *Xenopus laevis* is a voracious predator with a broad diet that includes a wide variety

of prey sizes and species, ranging from vertebrates, such as adult frogs, to very small prey, such as zooplankton (Vogt *et al.* 2017; Courant *et al.* 2017).

*Culex pipiens* (Bedford), the northern house mosquito, is among the most widely distributed species of mosquito in the world (Barr 1967). It is an important vector of St. Louis Encephalitis, West Nile Virus, Western Equine Encephalitis, Heartworm in dogs, and bird Malaria (Turell 2012). *Culex pipiens* breed in temporary surface-water habitats such as swamps, marshes, bogs, rice fields, and pastures, which can lack fish predators. Thus, *Xenopus laevis*, which also utilize these habitats and can readily disperse overland (Measey 2016; de Villiers & Measey 2017) to colonize newly formed aquatic habitats preferred by mosquitoes may play a role in mitigating environmental health risk posed by this species.

# **Specimen collection and maintenance**

Adult *X. laevis* were captured in the field using funnel traps baited with chicken liver at the Jonkershoek fish hatchery (-33.9631° S; 18.9252° E), Western Cape Province, South Africa. All captured *Xenopus* were marked with a Passive Integrated Transponder (PIT) tag. *Culex pipiens* were collected from naturally colonised populations using 50 l experimental tubs containing water and hay. Predators collected from Jonkershoek were transported to the Welgevallen Experimental Farm (-33.9426° S; 18.8664° E) where they were kept for a maximum of two weeks in  $\pm 500$  l holding tanks. Predators were maintained on a diet of chicken livers *ad libitum*. All applicable institutional and/or national guidelines for the care and use of animals were followed, with ethics clearance for experiments were granted by Stellenbosch University Research Ethics Committee: Animal Care & Use (SU-ACUD15-00011). Collection permits were granted by CapeNature (permit number AAA007-00159-0056).

# **Experimental procedure**

To quantify the dependence in the functional response of *Xenopus laevis* preying upon *Culex pipiens* mosquitoes on consumer body size, we conducted a 3 x 5 factorial experiment in which three size classes

of predator were crossed with 5 prey densities in independent trials. Predators were classified into three size classes according to their snout vent length (SVL, mm; mean  $\pm$  SD): small ( $21.0 \pm 3.9$ ), medium ( $54.6 \pm 2.6$ ) and large ( $113.3 \pm 4.6$ ). *Culex pipiens* larvae used were size-sorted (7-9 mm thorax length) using mesh screening and were all likely fourth instar. Prey density treatments were 20, 50, 100, 200 and 500 larvae per mesocosm. Treatments were randomly assigned and replicated four times.

Experiments were conducted between 15-Mar and 13-May-2016 in individual  $\pm 500$  l rectangular mesocosms placed outdoors in single block at the Welgevallen Experimental Farm, Stellenbosch. Predators were placed into the mesocosms 24h prior to experimental trials to acclimate. Hunger levels during were standardised by not feeding *Xenopus* for 48 h prior to the experiment. Experiments were initiated at 18:00 with the addition of mosquito larvae and were completed once the predators were removed after 14 h at 08:00 the following day. Remaining prey were counted in order to determine the predator's functional response. During the experiment, we maintained a mesocosm with the highest density of prey, but without predators, to assess short-term background mortality or biases in recovery. We observed no mortality and recaptured all larvae from these controls, thus we assume background mortality from causes other than *Xenopus* predation in experimental trials was negligible.

## Video analysis

Since feeding behaviour was not continuously observed in the mesocosm experiment, additional trials were conducted in the laboratory to observe attack rates and handling times of the different size classes of predator at a standardised prey density (50 larvae per aquarium), using the same experimental procedure. Individual predators were placed in aquaria ( $\pm 300 \times 240 \times 240$  mm) and recorded for 30 minutes using a video camera (GoPro Hero). Based on the footage collected, attack rate  $a$  and handling time  $h$  were calculated for comparison with data obtained from mesocosm experiments (Jeschke *et al.* 2002). Although experimental venue may influence predator-prey interactions (e.g., Skelly 2002), this approach allows us to see if general patterns observed are consistent across venues.

# Statistical analysis

All functional responses were modelled in R v3.3.1 (R Core Team, 2013) using the “friar” package (Pritchard, 2014) via a two-step process.

First, we used logistic regressions to distinguish between Type III and I & II functional response types (Trexler *et al.* 1998, Juliano, 2001). To accomplish this, we modelled proportion of prey killed as a function of prey density. If the first-order term of the analysis was significantly negative, the functional response was considered a Type II. If the first-order term was significantly positive, followed by a significantly negative second-order term, the functional response was considered a Type III (Juliano, 2001).

Second, once we determined the general form, functional responses were fit using a flexible model that includes a scaling exponent  $q$  to allow for a continuum of shapes between types I, II and III to be described (Barrios-O'Neill *et al.* 2015; Real, 1977):

$$N_e = N_0 (1 - \exp(-b N_0^q (h N_e - T))) \quad \text{Eq. 1}$$

where  $N_e$  is the number of prey eaten,  $N_0$  is the initial prey density,  $b$  is the search coefficient,  $h$  is the handling time,  $q$  is the scaling exponent and  $T$  is the total time available. Where Type II responses occur,  $q = 0$ , and functional responses become increasingly Type III in form when  $q > 0$ . In order to compare functional responses of different size classes, 95% confidence intervals were fitted around functional response curves by non-parametrically bootstrapping the data-sets (n = 2000).

Parameter values from observational experiments were calculated by video analysis using Quicktime v7.7.9 which allowed for frame-by-frame analysis of attack rate  $a$  and handling time  $h$ . In order to

measure these parameters, we used the approach developed by Jeschke *et al.* (2002), defining attack rate  $a$  as the product of encounter rate  $\beta$ , probability of prey detection by predator  $\gamma$ , probability of predator attacking detected prey  $\delta$ , and attack efficiency  $\epsilon$ . Encounter rate was defined as the total number of predator-prey encounters divided by the experimental time period. Probability of prey detection was calculated by dividing prey density by the volume of water in the aquaria. Probability of a predator attacking detected prey was calculated by dividing the total number of successful and unsuccessful attacks by the total amount of predator-prey encounters. Attack efficiency was calculated from the number of successful attacks divided by the total number of predation attempts. Jeschke *et al.* (2002) defined handling time as the eating time ( $t_{\text{eat}}$ ) added to the ratio of attacking time ( $t_{\text{att}}$ ) and attacking efficiency ( $\epsilon$ ). Eating time was calculated as the length of time it took from engulfing to ingestion of the prey; attacking time was defined as the length of time it took from the predator's initial lunge to when the prey was completely engulfed. Attack rate, handling time and attack efficiency calculated from video analyses were then compared between size classes using an ANOVA to determine whether there were significant differences. In the case of a significant difference, a Tukey HSD post-hoc analysis was used to determine the direction of the difference.

## Results

### *Functional response model*

Logistic regression indicated that of the three size classes of *X. laevis*, small frogs clearly exhibited a Type II functional response, as revealed by the significantly negative first-order term (Table 1, Fig. 1). The scaling exponent,  $q$ , was therefore fixed at 0. Logistic regression indicated Type III responses for medium and large size classes (Table 1, Fig. 1). For these size classes,  $q$  was unfixed for initial model fitting and then fixed at the generated maximum likelihood estimate. Bootstrapping was performed on the parameters  $b$  and  $h$  to provide an error estimate.

Table 2 provides estimates for the functional response parameters  $b$ ,  $h$  for all size classes studied and  $q$  in the case of medium and large *X. laevis*. The only differentiation occurring between functional response curves was at low prey densities (i.e. 0-100) where small frogs had higher predation rates compared to medium and large size classes (Fig. 1). This was further evidenced with the increased search coefficient for small size classes (Fig. 2a). Responses however converged at higher densities between medium and large size classes as well as small and large size classes, with confidence intervals associated with both functional response asymptotes (Fig. 1) and handling time coefficients (Fig. 2b) overlapping. Handling times were significantly different between small and medium frogs (Fig. 2b).





### Video analysis

Handling time from video analyses was significantly different between all size classes with medium predators having the lowest handling time and large predators having the highest ( $F_{2,42} = 125.67$ ,  $p < 0.05$ , Table 3). Attack efficiency was significantly higher in small predators compared to medium and large predators ( $F_{2,42} = 21.64$ ,  $p < 0.05$ ). Attack rate was significantly different between small predators and their larger cohorts with small predators showing the highest attack rate ( $F_{2,42} = 7.08$ ,  $p < 0.005$ ; Table 3). During a predation attempt, all predators exhibited inertial suction, preceded by a body lunge towards the prey. All predators exhibited scooping behaviour when searching for prey. Once a prey item was captured, small predators were the only size class to show sweeping behaviour which is defined as the handling of prey with their forelimbs to prevent prey escape (Avila and Frye, 1978).

### Discussion

Predators play an important role in ecosystems, including the regulation of agricultural pests and disease vectors. Often predators of the same species are assumed to be functionally equivalent, despite considerable individual variation in predator traits known to be important for shaping predator-prey interactions, like body size. This assumption may greatly oversimplify our understanding of within

species functional diversity and undermine our ability to predict predator effects on prey. Here we examine the degree to which predator-prey interactions are functionally homogenous across a natural range of predator body size. We show predator attack rates and handling times change with predator size. Search efficiency was found to be inversely proportional to predator body size whereas handling time exhibited a U-shaped function and maximum feeding rate was observed in medium sizes *X. laevis*. Attack rate and handling time from observational data shows a similar trend to that produced by the model, suggesting that a change in feeding mode and commensurate increase in handling efficiency was the mechanism responsible for the shift in functional response. Further, we show that changes in predator size can alter the basic form of the functional response. We found that the smallest predator size class exhibited a Type II response compared to Type III responses as exhibited in medium and large adults. This finding has important implications for understanding the how predator-prey dynamics change in systems where predators undergo large changes in body size relative to their prey through ontogeny.

Frequently, handling time initially decreases with increasing predator size, which can be attributed to an increased digestive capacity and gape size (Mittelbach, 1981; Persson, 1987). However, Persson *et al.* (1998) theorised that handling time will decrease until it reaches a minimum e, as found  in Mittelbach (1981), and at some point will begin to increase with predator size, as found  in Persson (1987). This is consistent with our findings where medium sized predators were found to have the lowest handling time, potentially representing the minimum amount of handling time across all size classes. A possible explanation is that large predators will have difficulty in handling very small prey and small predators may have  an increased handling time due to their digestive capacity or the prey being **too large to instantly consume** (Persson, 1987). Therefore, it might be expected that these larger predators will favour larger prey in order to increase their capture success rate. However, there are multiple examples in the literature that show *X. laevis* predators, independent of size, predominantly consume zoobenthos and zooplankton (Courant *et al.* 2017). This could be attributed to prey availability and density where the lower limit for prey size consumption depends on prey encounter rate and the cost of consumption (Elton,

1927; Owen-Smith and Mills, 2008). Very little movement is required to feed on zooplankton and zoobenthos which would reduce energy cost and predation risk. Low densities of small prey offer very little reward to large predators which may explain why both medium and large sized predators did not consume high proportions of prey when prey density was low (Griffiths, 1980).

The different feeding modes seen between size classes from observation data is likely due to the relationship between predator and prey size. The largest animals were able to use inertial suction to engulf prey entirely, while the smallest animals needed forearm scoops and jaw prehension in order to handle prey items. This resulted in a drastic increase in handling time from the largest to the smallest animals used. Members of the genus *Xenopus* all lack a tongue, a unique characteristic of the family Pipidae (Ridewood, 1897). They exhibit multiple feeding modes such as inertial suction, lunging, forearm scooping, jaw prehension and overhead kicks in order to capture and reduce a variety of prey (Avila and Frye, 1978; Measey 1998). Dean (2003) suggested that frogs of the genus *Hymenochirus* were the only pipids to use inertial suction, but Carreno and Nishikawa (2010) subsequently found that *X. laevis* (and other pipids) use multiple feeding modes, including inertial suction, when eating earthworms (see also Cundall *et al.* 2017). Our study suggests that while multiple feeding modes allow a wide variety of sizes of this principally aquatic frog to feed on the same prey, the impact on the prey population will likely drastically change depending on the level of predator ontogeny.

Attack rate, as a function of predator size, has been known to be dome shaped (Aljetlawi *et al.* 2004; Tripet and Perrin, 1994; Werner, 1988). In aquatic predators, the initial increase of attack rate with predator size is most likely due to an increase in burst swimming speeds, which will positively affect prey encounter rates (Keast & Webb 1966; Schoener, 1969). The eventual decline in attack rate with increasing predator size could be due to either prey being relatively too small to be detected or the inability of a predator to make fine-tuned movements, resulting in lower prey capture success rate (Hyatt, 1979). However, in our study, attack rate was not dome shaped with respect to prey size and instead



negatively correlated with size class (Table 1). One explanation is that the dome shape may only be observed if the experiment had additional size classes. Therefore, attack rate may yet hold a dome-shaped function of predator size, which may exist between the small and medium size classes measured in this study. Another explanation for the negative correlation could be that they prey are already at the optimal size for maximum attack rate in small sized predators.

Milonas *et al.* (2011) found different feeding modes in a predatory ladybird (*Nephus includens*) in which smaller instars (2nd instar, 2 mm) were found to partially consume prey of different sizes, whereas larger instars (4th instar, 3.3 mm) consumed prey whole. The differences in feeding mode between the large and small predators led to differences in handling time when prey size was increased. Smaller predators were able to maintain a constant handling time, whereas larger predator's handling time increased with prey size. However, in our study all predators completely consumed prey; thus the mosquito larvae were not too large for the smallest frogs to consume. The lower capture success rate found in medium and large predators was most likely due to their limited ability to hold relatively small prey (CJT pers. obs.), similar to observations made on fish (Persson, 1987). Observation data also showed a response from predators to movement from prey. Regardless of the predator's positioning in relation to the prey, detection was most likely when prey exhibited sudden movements. *Xenopus laevis* do not principally use visual or olfactory cues in order to detect aquatic prey, and instead rely on their sensitive lateral line systems (see Elepfandt, 1996).

Despite the potentially profound implications for predator-prey dynamics, few studies directly test whether the basic form of the functional response changes with consumer size. Recently, Anderson *et al.*, (2016) found that the form of the functional response changed with prey size, with smaller predators being more limited by handling times than large prey. In other words, smaller predator tended to exhibit a Type II functional response which larger predators exhibited a Type I functional response for the same prey. Type II functional responses as defined by Eq 1, collapse to a Type I functional response when

estimates of the handling time parameter overlap zero. None of their predators exhibited a Type III functional response. In this study we find that both medium and large sized *X. laevis* showing a Type III response and small predators exhibiting a Type II, smaller predators may be able to exploit prey at low densities. There is a trend towards a higher  $q$  values (or scaling exponent) and a more stabilising response (Alexander *et al.* 2012). Thus, the medium size class of *X. laevis* is most likely to destabilise a resource given fast handling times and a reduction in consumption suppression at low densities as indicated by a lower  $q$  than the large size class. Small frogs are likely to destabilise prey at low densities but over all they have a much lower handling time, and therefore feeding rate. When prey density is low, there is an increase in predation from small predators, and when prey density is high, there would be an increase in predation from larger predators (Rindone and Eggleston, 2011). Densities of *X. laevis* are known to reach very high levels, especially in invasive populations (e.g. Measey 2001; Loefer and Measey 2002; Faraone *et al* 2008), but also in natural assemblages (de Villiers *et al.* 2016). This work also has a conservation context as the smaller, but functionally similar, congener *X. gilli* is threatened by competition from *X. laevis* (see Vogt *et al.* 2017). Thus, having a population of predators of different sizes at the same time means that there is little relief for multiple prey species, and could lead to extirpation (Hassell, 1978). This could be advantageous, if the prey species is a potential disease vector, as in the case of *Culex pipiens*. Prey may experience a similar scenario with fish in aquatic ecosystems due to many fish species consisting of populations with overlapping cohorts (Werner, 1984). However, in populations where differences in predator size are less pronounced, prey may experience only one type of predator response (Milonas *et al.* 2011).

## Conclusion

Many studies compare functional responses of native and invasive predators and important inferences are made about the potential impacts of these invaders (Dick *et al.* 2013). However, little research focuses on the potential role predator size could play in determining these functional responses. Predators can change their foraging preference as they age and grow and selecting a single size class in functional response

experiments to represent an entire population may not be the best representation of populations with overlapping cohorts and large size ranges. It is important to consider whether the same pattern would be seen on different prey species. How would functional response curves be affected if prey size was increased (e.g., see McCoy *et al.* 2011) There may be a shift from a Type III to a Type II functional response in our medium and large-sized predators as prey size increases. It is therefore vital to answer these questions so that false representation of a predator population's functional response will not occur. This study has shown parameters such as attack rate, handling time and maximum feeding rate as well as functional response type are dependent on predator body size. Therefore when conducting a functional response experiment it is vital to consider factors such as the predator and prey size, foraging strategy and prey species.

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# **Table 1**(on next page)

Parameter estimates from logistic regression analyses of proportion of prey (*Culex pipiens*) consumed against initial prey density for small, medium and large size classes of *Xenopus laevis* predators.

Values for 1<sup>st</sup> order and 2<sup>nd</sup> order terms are presented with p values.

Table 1. Parameter estimates from logistic regression analyses of proportion of prey (*Culex pipiens*) consumed against initial prey density for small, medium and large size classes of *Xenopus laevis* predators. Values for 1<sup>st</sup> order and 2<sup>nd</sup> order terms are presented with p values.

| Size class | Intercept<br>(p-value) | 1 <sup>st</sup> order<br>(p-value) | 2 <sup>nd</sup> order<br>(p-value) | Functional<br>response type |
|------------|------------------------|------------------------------------|------------------------------------|-----------------------------|
| Small      | 2.541 (<0.001)         | -0.007 (<0.001)                    | -                                  | II                          |
| Medium     | -0.106 (<0.05)         | 0.0045 (<0.01)                     | -0.000006 (<0.01)                  | III                         |
| Large      | -1.494 (<0.001)        | 0.0098 (<0.001)                    | -0.000015 (<0.001)                 | III                         |



## Table 2 (on next page)

Results of the flexible functional response model to prey consumed by size classes of *Xenopus laevis*.

Parameter estimates of search coefficient ( $b$ ), handling time ( $h$ ) and scaling coefficient ( $q$ ) from fitting the flexible functional response model to prey (*Culex pipiens*) consumed against initial density for small, medium and large size classes of *Xenopus laevis*. Estimates presented with standard error.

Table 2. Parameter estimates of search coefficient ( $b$ ), handling time ( $h$ ) and scaling coefficient ( $q$ ) from fitting the flexible functional response model to prey (*Culex pipiens*) consumed against initial density for small, medium and large size classes of *Xenopus laevis*. Estimates presented with standard error.

| Parameter estimate | $b$               | $h$                | $q$               |
|--------------------|-------------------|--------------------|-------------------|
| Small              | $3.526 \pm 0.202$ | $0.005 \pm 0.0001$ | Fixed at 0        |
| Medium             | $0.212 \pm 0.064$ | $0.001 \pm 0.0003$ | $0.320 \pm 0.069$ |
| Large              | $0.117 \pm 0.080$ | $0.004 \pm 0.0003$ | $0.738 \pm 0.109$ |

# Table 3 (on next page)

Results of video analyses of *Xenopus laevis* consuming prey

Observational measurements of attack rate ( $a$ ) and handling time ( $h$ ) from video analysis of 50 prey (*Culex pipiens* at a density of 3 prey items per litre) eaten by *Xenopus laevis* of differing size classes in the laboratory experiment. Values are means presented with standard error.

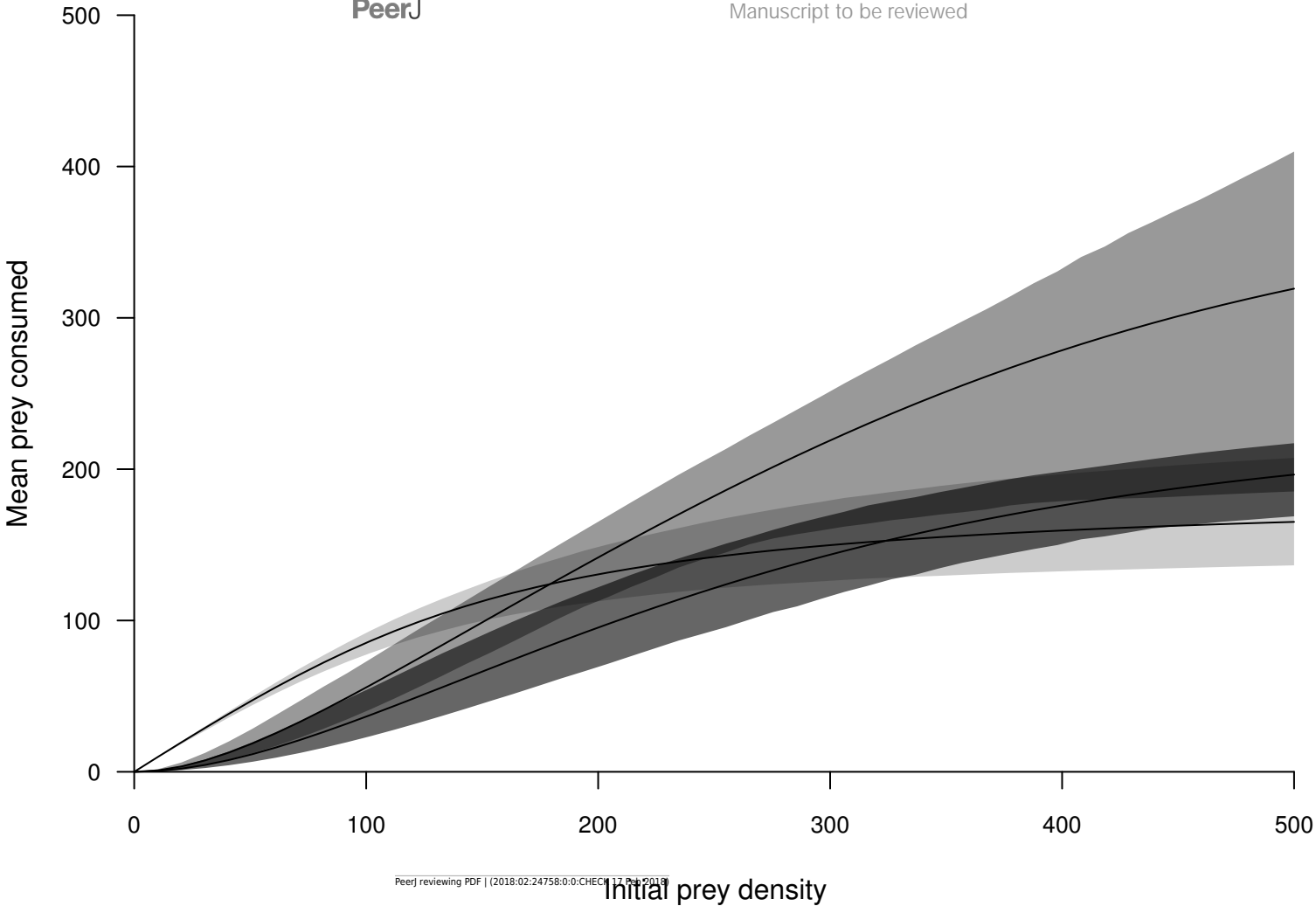
Table 3. Observational measurements of attack rate ( $a$ ) and handling time ( $h$ ) from video analysis of 50 prey (*Culex pipiens* at a density of 3 prey items per litre) eaten by *Xenopus laevis* of differing size classes in the laboratory experiment. Values are means presented with standard error.

| Size class | $a$             | $h$                 |
|------------|-----------------|---------------------|
| Small      | $4.34 \pm 0.67$ | $0.0016 \pm 0.0001$ |
| Medium     | $3.73 \pm 0.43$ | $0.0009 \pm 0.0002$ |
| Large      | $3.75 \pm 0.39$ | $0.0023 \pm 0.0002$ |

# **Figure 1**(on next page)

Functional responses of *Xenopus laevis* preying on mosquito larvae.

Functional responses of individual small (light grey), medium (grey) and large (dark grey) size classes of *Xenopus laevis*. Solid lines represent model curve and shaded areas represent 95% confidence intervals calculated by non-parametric bootstrapping.



## Figure 2 (on next page)

Search coefficient and handling time from functional response models.

a) Search coefficient and b) handling time parameters derived from flexible functional response models for small, medium and large size classes of *Xenopus laevis*. Points are original model values and error bars are bootstrapped 95% Confidence Intervals.

