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Published in:
PeerJ

DOI:
[10.7717/peerj.5813](https://doi.org/10.7717/peerj.5813)

Published: 26/10/2018

Document Version
Peer reviewed version

[Link to publication on the UWS Academic Portal](#)

Citation for published version (APA):

Thorp, C. J., Alexander, M. E., Vonesh, J. R., & Measey, J. (2018). Size-dependent functional response of *Xenopus laevis* on mosquito larvae. *PeerJ*, 6, [5813]. <https://doi.org/10.7717/peerj.5813>

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

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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 sizes. 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 (15-30 mm snout-vent length), medium (50-60 mm) and large (105-120 mm), 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 showed that type of functional response of *X. laevis* changed with size: small predators exhibited a Type II response, while medium and large predators exhibited Type III responses. Functional response data showed an inversely proportional relationship between predator attack rate and predator size. Small and medium predators had highest and lowest handling time, respectively. The change in functional response 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 misrepresent 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). The few studies that have quantified how predator size influences shapes of functional responses on the same prey have highlighted size-dependence of predator handling time and attack rate (e.g. Eveleigh and Chant 1981, Vucic-Pestic *et al.* 2010, Milonas *et al.*, 2011, Anderson *et al.*, 2016), and even the general form of the functional response (Anderson *et al.*, 2016). These studies show that assuming that 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 and describes a predator's uptake of prey as a function of the prey density. Holling (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, the rate of prey consumption by a predator divided by prey abundance

declines with prey abundance. Handling time is the period predators are occupied with processing (e.g., ingesting, digesting) captured prey and are not able to engage new prey items. This constraint can produce nonlinearity to the relationship between prey availability and prey eaten. Predators that exhibit a Type II response typically de-stabilise prey populations is due to the positive feedback on prey population growth caused by decreased predator consumption rates as a prey population increases, as predators are unable to regulate prey populations at densities beyond predator satiation (Rosenzweig and MacArthur, 1963; Oaten and Murdoch, 1975). A Type III response is defined by an accelerating increase in prey capture with increasing prey density for a range of low prey densities. The proportion of prey consumed initially increases with increasing prey availability then declines as in a Type II response (Holling, 1959; Hassell, 1978). This can create a refuge for prey at low densities, facilitating the persistence of prey populations, and a physical refuge in limited supply can create a Type III response. Therefore, the type of functional response a predator exhibits can result in quite different outcomes for prey. By describing the response, the potential impact at a population level may be elucidated (e.g., Rosenzweig and MacArthur, 1963).

Several factors may influence the type of functional response exhibited for a specific predator-prey interaction. This includes environmental conditions (e.g. Lavery *et al.* 2015, Englund *et al.* 2011) as well as body size of participants (e.g. Brose *et al.* 2005, McCoy *et al.* 2011, Tucker *et al.* 2014, Anderson *et al.*, 2016). Size variation is a common feature in animal populations and influences predator-prey interactions, competition and individual life histories (Ebenman, 1988; Wilbur 1988; Samhouri *et al.* 2009; Asquith and Vonesh, 2012). However, preferred prey typically change with ontogeny for many predators such that experiments are not able to present common prey across a range of predator sizes. For example, Milonas *et al.* (2011) investigated the functional response of different instars of larval ladybirds (*Nephus includens*) using increasing prey sizes; all exhibited the same functional response type (Type II), but showed small differences in handling time and attack rate. For iteroparous amphibians with indeterminate growth and overlapping cohorts, individual body size is especially important (Márquez *et al.* 1997; Werner, 1994). Smaller predators in these populations may be limited by the range of prey size

they can consume (e.g., handling time may be greater for smaller predators; Anderson *et al.*, 2016) and are often more efficient at assimilating consumed prey 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 sizes 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) of different sized predators?

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 temporary surface-water 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 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 functional response of *Xenopus laevis* preying upon *Culex pipiens* mosquitoes dependent on consumer body size, we conducted a 3 x 5 factorial experiment in which three size classes of predator were crossed with five 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 ± 3.9), medium (54.6 ± 2.6) and large (113.3 ± 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 ± 500 l rectangular mesocosm, giving densities of 0.04, 0.1, 0.2, 0.4 and 1 mosquitoes per litre, respectively. Treatments with single predators were randomly assigned and replicated four times.

Experiments were conducted between 15-Mar and 13-May-2016 in individual ± 500 l rectangular mesocosms placed outdoors in single block at the Welgevallen Experimental Farm, Stellenbosch. Mesocosms were rectangular plastic bins with a capacity of 1000 l, half-filled with water to 50 cm depth (volume of approximately 500 l), and covered with mesh screening to prevent any disturbance. These frogs are active between evening and midnight of each day (Ringeis et al 2017), while the mosquito larvae are suspended at the surface at all times. Predators were placed into the mesocosms 24 h prior to experimental trials to acclimate. Hunger levels 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.

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 attack rate, 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 datasets ($n = 2000$).

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 and 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 supported by the higher attack rate for small size classes (Fig. 2a). Responses converged at higher densities between medium and large size classes as well as small and large size classes, with overlapping confidence intervals for the asymptotes (Fig. 1). and handling time coefficients (Fig. 2b) overlapping. Handling time coefficient was highest in the smallest predator size class, and lowest in the medium size class, with a significant difference (Table 2; Fig. 2b). Handling time for frogs in the largest size class was intermediate, and not significantly different between medium and small frogs (Fig. 2b).

Discussion

We found changes in the basic form of the functional response type between different sized predators of the same species for a standardised prey size. 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 how predator-prey dynamics change in systems where predators undergo large changes in body size relative to their prey through ontogeny. Moreover, 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 of *X. laevis*. Predators of the same species are often assumed to be functionally equivalent, despite individual variation in predator traits known to be important for shaping predator-prey interactions, like body size (McCoy et al 2011, but see Gonzalez-Suarez et al. 2011). 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.

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 value, as found by Mittelbach (1981), and at some point will begin to increase with predator size (e.g., 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 large to ingest by inertial suction (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 both 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).

254

255 There are a number of examples that exist showing unimodal ('dome shaped') relationships between
256 attack rate and predator size (Aljetlawi *et al.* 2004; Tripet and Perrin, 1994; Werner, 1988). In aquatic
257 predators, the initial increase of attack rate with predator size is most likely due to an increase in predator
258 search speed, which will positively affect prey encounter rates (Keast & Webb 1966; Schoener, 1969).
259 The eventual decline in attack rate with increasing predator size could be due to either prey being
260 relatively too small to be detected or the inability of a predator to make fine-tuned movements, resulting
261 in lower prey capture success rate (Hyatt, 1979). However, in our study, attack rate was not dome shaped
262 with respect to prey size and instead negatively correlated with size class (Table 1). One explanation is
263 that the dome shape may only be observed if the experiment had additional intermediate predator size
264 classes. Therefore, attack rate may yet hold a dome shaped function of predator size, which may exist
265 between the small and medium size classes measured in this study. Another explanation for the negative
266 correlation could be that the prey are already at the optimal size for maximum attack rate in small sized
267 predators. There is also a possibility that the relative fitness gain from small prey items is too small to
268 make it worthwhile for larger foragers to be active.

269

270 Milonas *et al.* (2011) found different feeding modes in a predatory ladybird (*Nephus includens*) in which
271 smaller instars (2nd instar, 2 mm) were found to partially consume prey of different sizes, whereas larger
272 instars (4th instar, 3.3 mm) consumed prey whole. The differences in feeding mode between the large and
273 small predators led to differences in handling time when prey size was increased. Smaller predators were
274 able to maintain a constant handling time, whereas larger predator's handling time increased with prey
275 size. However, in our study all predators completely consumed prey; thus the mosquito larvae were not
276 too large for the smallest frogs to consume. The lower capture success rate found in medium and large
277 predators was most likely due to their limited ability to hold relatively small prey (CJT pers. obs.), similar
278 to observations made on fish (Persson, 1987). Observation data also showed a response from predators to
279 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 predator size (hatchling to larval ambystomatid salamanders), with smaller predators (adult ambystomatid salamanders) being more limited by handling times than large predators. In other words, smaller predators tended to exhibit a Type II functional response while 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 the 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 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 predator-prey dynamics given fast handling times and a reduction in consumption 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 overall they have a much lower handling time, and therefore a higher 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; Lobos and Measey 2002; Faraone *et al.* 2008), but also in natural assemblages (de Villiers *et al.* 2016). The present study 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 prey 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

Studies often compare functional responses of native and invasive predators and important inferences are made about the potential impacts of these invaders (reviewed by 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. Similarly, it could be asked how prey traits (e.g. activity, shape, colour, etc.) affect functional response curves when size is kept constant. It is therefore important to answer these questions so that a predator population's functional response is correctly represented. 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 both predator and prey size, foraging strategy and prey species.

Acknowledgements

We would like to thank members of the MeaseyLab for their help in preparation and harvesting of experiments: Erin Jooste, Ana Nunes, Giovanni Vimercati, Nitya Mohanty, Marike Louw, Mohlamatsane Mokhatla, Alex Rebelo. We thank Donald Kramer, Peter Abrams, and an anonymous reviewer for their constructive comments. We would like to thank staff at Welgevallen Experimental Farm for facilitating the experimental work.

References

- Alexander ME, Dick JTA, O'Connor NE, Haddaway NR, Farnsworth KD (2012) Functional responses of the intertidal amphipod *Echinogammarus marinus*: effects of prey supply, model selection and habitat complexity. *Mar Ecol Prog Ser* 468:191–202.
- Alexander, ME, Dick, JTA, Weyl, OL, Robinson, TB, Richardson, DM (2014) Existing and emerging high impact invasive species are characterized by higher functional responses than natives. *Biol. Lett.* 10: 20130946.
- Anderson, TL, Linares, C, Dodson, KN, Semlitsch RD (2016) Variability in functional response curves among larval salamanders: Comparisons across species and size classes. *Can J Zool* 94: 23-30
- Aljetlawi, AA, Sparrevik, E, Leonardsson, K (2004) Prey–predator size-dependent functional response: derivation and rescaling to the real world. *J. Anim. Ecol.* 73: 239-252.
- Asquith, C M, Vonesh, J R (2012) Effects of size and size structure on predation and inter-cohort competition in red-eyed treefrog tadpoles. *Oecologia* 170: 629-639
- Avila, V L, Frye, P G (1978) Feeding behavior of the African clawed frog (*Xenopus laevis* Daudin):(Amphibia, Anura, Pipidae): effect of prey type. *J. Herp.* 12: 391-396.

358

359 Barr, AR (1967) Occurrence and distribution of the *Culex pipiens* complex. Bull World Health Organ.
360 1967; 37(2): 293–296.

361

362 Barrios-O'Neill D, Dick JTA, Emmerson MC, Ricciardi A, HJ MacIssac (2015) Predator-free space,
363 functional responses and biological invasions. Func. Ecol. 29: 377-384.

364

365 Beauchamp, DA, Whal, DH, Johnson, BM (2007) Predator-prey interactions. In Analysis and
366 interpretation of freshwater fisheries data. (Eds) CS Guy and MJ Brown. American Fisheries Society,
367 Bethesda, Maryland, pp 765-842.

368

369 Bollache, L, Dick, JT, Farnsworth, KD, Montgomery, WI (2008) Comparison of the functional responses
370 of invasive and native amphipods. Biol. Lett. 4:166-169.

371

372 Brooks, J L, Dodson, S I (1965) Predation, body size, and composition of plankton. Science 150: 28-35.

373

374 Brose, U, Cushing, L, Berlow, E L, Jonsson, T, Banasek-Richter, C, Bersier, L-F, Blanchard, J L, Brey,
375 T, Carpenter, S R, Blandenier, M-F C, Cohen, J E, Dawah, H A, Dell, T, Edwards, F, Harper-Smith, S,
376 Jacob, U, Knapp, R A, Ledger, M E, Memmott, J, Mintenbeck, K, Pinnegar, J K, Rall, B C, Rayner, T,
377 Ruess, L, Ulrich, W, Warren, P, Williams, R J, Woodward, G, Yodzis, P, Martinez, N D (2005) Body
378 sizes of consumers and their resources. Ecology, 86: 2545.

379

380 Carlson, B E, Langkilde, T (2014) Predation risk in tadpole populations shapes behavioural responses of
381 prey but not strength of trait-mediated indirect interactions. Oikos 123: 1519-1527.

382

Carpenter, S R, Kitchell, JF, Hodgson, JR (1985) Cascading trophic interactions and lake productivity. BioScience 35: 634-639.

Claessen, D, Van Oss, C, de Roos, AM, Persson, L, (2000) The impact of size-dependent predation on population dynamics and individual life history. Ecology 83:1660-1675.

Cohen, JE, Pimm, SL, Yodzis, P, Saldana, J (1993) Body sizes of animal predators and animal prey in food webs. J. Anim. Ecol. 62: 67-78.

Courant, J, Vogt, S, Marques, R, Measey, J, Secondi, J, Rebelo, R, De Villiers, A, Ihlow, F, De Busschere, C, Backeljau, T, Rödder, D, Herrel, A (2017) Are invasive populations characterized by a broader diet than native populations? PeerJ 5: e3250.

Cundall, D, Fernandez, E, Irish, F (2017) The suction mechanism of the pipid frog, *Pipa pipa* (Linnaeus, 1758). Journal of Morphology. DOI: 10.1002/jmor.20707

Dean, MN (2003) Suction feeding in the pipid frog, *Hymenochirus boettgeri*: kinematic and behavioral considerations. Copeia, 2003: 879-886.

De Villiers, FA, de Kock, M, Measey, GJ, (2016) Controlling the African clawed frog *Xenopus laevis* to conserve the Cape platanna *Xenopus gilli* in South Africa. Cons. Evidence, 13, 17.

De Villiers, FA, Measey, J. (2017) Overland movement in African clawed frogs (*Xenopus laevis*): empirical dispersal data from within their native range. PeerJ 5: e4039

408 Dick, JT, Gallagher, K, Avlijas, S, Clarke, H.C, Lewis, S.E, Leung, S, Minchin, D, Caffrey, J, Alexander,
 409 ME, Maguire, C, Harrod, C (2013) Ecological impacts of an invasive predator explained and predicted by
 410 comparative functional responses. *Biol. Invasions*, 15: 837-846.
 411
 412 Eggers, DM (1978) Limnetic feeding behavior of juvenile sockeye salmon in Lake Washington and
 413 predator avoidance. *Limnol. Oecnaogr.* 23: 1114-1125.
 414
 415 Ebenman, B (1988) Competition between age classes and population dynamics. *J. Theor. Biol.* 131: 389-
 416 400.
 417
 418 Englund, G, Öhlund, G, Hein, C. L, Diehl, S (2011) Temperature dependence of the functional response.
 419 *Ecol. Lett.* 14: 914–921.
 420
 421 Elepfandt, A, (1996) Sensory perception and the lateral line system in the clawed frog, *Xenopus*. In *The*
 422 *Biology of Xenopus: Symposia of the Zoological Society of London* (No. 68) Eds. H.R. Kobel & R.C.
 423 Tinsley. Oxford: Clarendon Press, pp 97-120.
 424
 425 Elton, CS (1927) *Animal Ecology*. Sidgwick and Jackson, London
 426
 427 Eveleigh, ES, Chant, DA (1981) Experimental studies on acarine predator-prey interactions: effects of
 428 predator age and feeding history on prey consumption and the functional response (Acarina:
 429 Phytoseiidae). *Can J. Zool.* 59: 1387-1406.
 430
 431 Faraone, FP, Lillo, F, Giacalone, G, Valvo, ML (2008) The large invasive population of *Xenopus laevis* in
 432 Sicily, Italy. *Amphib. Reptil.* 29: 405-412.
 433

434 Griffiths, D, (1980) Foraging costs and relative prey size. *Am. Nat.* 116: 743-752.

435

436 González-Suárez, M. , Mugabo, M. , Decencière, B. , Perret, S. , Claessen, D. and Le Galliard, J (2011),

437 Disentangling the effects of predator body size and prey density on prey consumption in a lizard.

438 *Functional Ecology*, 25: 158-165.

439

440 Haddaway, NR, Wilcox, RH, Heptonstall, RE, Griffiths, HM, Mortimer, RJ, Christmas, M, Dunn, AM

441 (2012) Predatory functional response and prey choice identify predation differences between

442 native/invasive and parasitised/unparasitised crayfish. *PloS One* 7: p.e32229.

443

444 Hassell, MP (1978) The dynamics of arthropod predator-prey systems. Princeton University Press.

445

446 Holling, CS (1959) The components of predation as revealed by a study of small mammal predation of

447 the European pine sawfly. *Can. Entomol.* 91: 293-320.

448

449 Holling, CS, (1965) The functional response of predators to prey density and its role in mimicry and

450 population regulation. *Mem. Entomol. Soc. Can.* 97: 5-60.

451

452 Hyatt, KD (1979) Feeding Strategy. In W.S. Hoar, D.J. Randall and J.R. Brett *Fish Physiology volume 8:*

453 *Bioenergetics and Growth* pp71-119.

454

455 Jansson, M, Persson, L, De Roos, AM, Jones, RI, Tranvik, LJ (2007) Terrestrial carbon and intraspecific

456 size-variation shape lake ecosystems. *Trends Ecol. Evol.* 22: 316-322.

457

458 Jeschke, JM, Kopp, M, Tollrian, R (2002) Predator functional responses: discriminating between handling

459 and digesting prey. *Ecol. Monogr.* 72: 95-112.

460

461 Juliano, SA (2001) Nonlinear curve fitting: predation and functional response curves. In: Scheiner SM,
 462 Gurevitch J (eds) Design and analysis of ecological experiments. Oxford University Press, Oxford, pp
 463 178–196.

464

465 Keast, A, Webb, D. (1966) Mouth and body form relative to feeding ecology in the fish fauna of a small
 466 lake, Lake Opinicon, Ontario. J. Fish. Res. Board Can. 23: 1845-1874.

467

468 Lavery, C, Dick, JTA, Alexander, ME, Lucy, FE (2015) Differential ecological impacts of invader and
 469 native predatory freshwater amphipods under environmental change are revealed by comparative
 470 functional responses. Biol. Inv. 17: 1761-1770

471

472 Lotka, AJ (1956) *Elements of mathematical biology*. Second edition. Dover Publications, New York.

473

474 Luecke, C, Vanni, MJ, Magnuson, JJ, Kitchell, JF, Jacobson, PT (1990) Seasonal regulation of *Daphnia*
 475 populations by planktivorous fish—implications for the spring clear water phase. Limnol. Oceanogr. 35:
 476 1091-1100.

477

478 Lobos, GA, Measey, GJ (2002) Invasive populations of *Xenopus laevis* (Daudin) in Chile. Herpetol. J. 12:
 479 163-168.

480

481 Márquez, R, Esteban, M, Castanet, J (1997) Sexual size dimorphism and age in the midwife toads *Alytes*
 482 *obstetricans* and *A. cisternasii*. J. Herp. 52-59.

483

484 McCoy, MW, Bolker, BB, Warkentin, KM, Vonesh, JR (2011) Predicting predation through prey
 485 ontogeny using size-dependent functional response models. Am. Nat. 177 (6): 752-766.

486

487 Measey, GJ (1998) Terrestrial prey capture in *Xenopus laevis*. *Copeia*, 787-791.

488

489 Measey, GJ (2001) Growth and ageing of feral *Xenopus laevis* (Daudin) in South Wales, UK. *J. Zool.*

490 254: 547-555.

491

492 Measey, GJ (2004) Genus *Xenopus* Wagler, 1827 (Family Pipidae). In: Minter, LR, Burger, M, Harrison,

493 JA, Braack, HH Bishop, PJ, Kloepfer, D (eds.) Atlas and Red Data Book of the Frogs of South Africa,

494 Lesotho and Swaziland: pp 266-267.

495

496 Measey, J. (2016) Overland movement in African clawed frogs (*Xenopus laevis*): a systematic review.

497 *PeerJ* 4: e2474.

498

499 Miller, TJ, Crowder, LB, Rice, JA, Marschall, EA (1988) Larval size and recruitment mechanisms in

500 fishes: toward a conceptual framework. *Can. J. Fish. Aquat. Sci.* 45: 1657-1670.

501

502 Milonas, PG, Kontodimas, DC, Martinou, AF (2011) A predator's functional response: Influence of prey

503 species and size. *Biol. Control* 59: 141-146.

504

505 Mittelbach, GG (1981) Foraging efficiency and body size: a study of optimal diet and habitat use by

506 bluegills. *Ecology* 62(5): 1370-1386.

507

508 Oaten, A, Murdoch, WW (1975) Switching, functional response, and stability in predator-prey systems.

509 *Am. Nat.* 299-318.

510

511 Paine, RT (1992) Food-web analysis through field measurement of per capita interaction strength. *Nature*
512 355: 73-75.

513

514 Persson, L (1987) The effects of resource availability and distribution on size class interactions in perch,
515 *Perca fluviatilis*. *Oikos* 48: 148-160.

516

517 Persson, L Leonardsson, K, de Roos, AM, Gyllenberg, M, Christensen, B. (1998) Ontogenetic scaling of
518 foraging rates and the dynamics of a size-structured consumer-resource model. *Theor. Popul. Biol.* 54:
519 270-293.

520

521 R Core Team (2013) R: A language and environment for statistical computing. R Foundation for
522 Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>.

523

524 Real, LA (1977) The kinetics of functional response. *Am. Nat.* 111: 289–300.

525

526 Ridewood, WG (1897) On the structure and development of the hyobranchial skeleton and larynx in
527 *Xenopus* and *Pipa*; with remarks on the affinities of the Aglossa. *J. Linn. Soc. Lon, Zoology*, 26: 53-128.

528

529 Rindone, RR, Eggleston, DB (2011) Predator–prey dynamics between recently established stone crabs
530 (*Menippe* spp.) and oyster prey (*Crassostrea virginica*). *J. Exp. Mar. Biol. Ecol.* 407: 216-225.

531

532 Ringeis, A, Krumscheid, B, Bishop, P J, De Vries, C, Elepfandt, A (2017) Acoustic communication and
533 reproductive behaviour in the aquatic frog *Xenopus laevis* (Pipidae), a field study. *African Journal of*
534 *Herpetology* 66: 122-146.

535

536 Rosenzweig, ML, MacArthur, RH, (1963) Graphical representation and stability conditions of predator-
537 prey interactions. Am. Nat. 97: 209-223.

538

539 Samhouri, JF Steele, MA, Forrester, GE (2009) Inter-cohort competition drives density dependence and
540 selective mortality in a marine fish. Ecology 90: 1009-1020.

541

542 Scharf, FS, Juanes, F, Rountree, RA (2000) Predator size-prey size relationships of marine fish predators:
543 interspecific variation and effects of ontogeny and body size on trophic-niche breadth. Mar. Ecol.:
544 Progress Series 208: 229-248.

545

546 Schoener, TW (1969) Models of optimal size for solitary predators. Am. Nat. 122: 240-285.

547

548 Schoonbee, HJ, Prinsloo, JF, Nxiweni, JG (1992) Observations on the feeding habits of larvae, juvenile
549 and adult stages of the African clawed frog, *Xenopus laevis*, in impoundments in Transkei. Water-SA. 18:
550 227-236.

551

552 Schröder, A, Nilsson, KA, Persson, L, Van Kooten, T, Reichstein, B (2009) Invasion success depends on
553 invader body size in a size structured mixed predation-competition community. J. Anim. Ecol. 78:1152-
554 1162.

555

556 Sih, A (1982) Foraging strategies and the avoidance of predation by an aquatic insect, *Notonecta*
557 *Hoffmanni*. Ecology 63: 786-796.

558

559 Skelly, DK (2002) Experimental venue and the estimation of interaction strength. Ecology 83(8): 2097-
560 2101.

561

- Solomon, ME (1949) The natural control of animal populations. J. Anim. Ecol. 18:1-35.
- Soluk, DA (1993) Multiple predator effects: predicting combined functional response of stream fish and invertebrate predators. Ecology 219-225.
- Thompson, DJ (1978) Towards a realistic predator-prey model: the effect of temperature on the functional response and life history of larvae of the damselfly, *Ischnura elegans*. J. Anim. Ecol. 757-767.
- Toscano BJ, Griffen BD (2013) Predator size interacts with habitat structure to determine the allometric scaling of the functional response. Oikos, 122: 454-462.
- Trexler JC, McCulloch CE, Travis J (1988) How can the functional response best be determined? Oecologia 76: 206–214.
- Tripet, F, Perrin, N. (1994) Size-dependent predation by *Dugesia lugubris* (Turbellaria) on *Physa acuta* (Gastropoda): experiments and model. Funct. Ecol. 458-463.
- Tucker MA, Rogers TL. (2014) Examining predator–prey body size, trophic level and body mass across marine and terrestrial mammals. Proc. Roy. Soc. B 281:20142103.
- Turell, MJ (2012) Members of the *Culex pipiens* complex as vectors of viruses. J Am Mosq Control Assoc. 28:123-6.
- Vogt, S, De Villiers, FA, Ihlow, F, Rödder, D, Measey, J, (2017) Competition and feeding ecology in two sympatric *Xenopus* species (Anura: Pipidae). PeerJ, 5, p.e3130.

Volterra, V, (1928) Variations and fluctuations of the number of individuals in animal species living together. J. Cons. Int. Explor. Mer, 3: 3-51.

Vonesh J, McCoy M, Altwegg R, Landi P, Measey J (2017) Functional responses can't unify invasion ecology. Biol. Invasions 19:1673-1676.

Vucic-Pestic O, Rall BC, Kalinkat G, Brose U (2010) Allometric functional response model: body masses constrain interaction strengths. Journal of Animal Ecology 79: 249-256.

Walls, M, Kortelainen, I, Sarvala, J. (1990) Prey responses to fish predation in freshwater communities. Ann. Zool. Fennici. 27: 183-199.

Werner, EE (1988) Size, scaling, and the evolution of complex life cycles. In: Ebenman B, Persson L. (eds) *Size-structured populations* pp. 60-81. Springer Berlin Heidelberg.

Werner, EE (1994) Ontogenetic scaling of competitive relations: size dependent effects and responses in two anuran larvae. Ecology 75:197-213.

Wilbur, HM (1988) Interactions between growing predators and growing prey. In Ebenman B, Persson L. (eds) *Size-structured populations* pp157-172. Springer Berlin Heidelberg

Wootton, RJ, Allen, JRM, Cole, SJ (1980). Effect of body-weight and temperature on the maximum daily food consumption of *Gasterosteus aculeatus* L. and *Phoxinus phoxinus* (L)—Selecting an appropriate model. J. Fish Biol. 17: 695-705.

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

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Size class	Intercept (p-value)	1 st order (p-value)	2 nd order (p-value)	Functional 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

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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 ± 0.202	0.005 ± 0.0001	Fixed at 0
Medium	0.212 ± 0.064	0.001 ± 0.0003	0.320 ± 0.069
Large	0.117 ± 0.080	0.004 ± 0.0003	0.738 ± 0.109

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 ± 0.67	0.0016 ± 0.0001
Medium	3.73 ± 0.43	0.0009 ± 0.0002
Large	3.75 ± 0.39	0.0023 ± 0.0002

Figure Legends

Fig. 1. 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.

Fig. 2. 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% CIs.

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645 Fig. 1.

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650 Fig. 2.

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