



Density-dependent allometric functional response models



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ABSTRACT

Functional response models describe the relationship between predators and the rate at which prey are consumed. Traditional models are based on the density of prey and predators. More recently, the role of variables such as predator and prey size have received increased attention. This study presents several new modifications of existing functional response equations that incorporate predator size as a factor affecting capture rate and/or handling time. These models were tested on an experimental system in which we used several aquatic nepomorphans (Hemiptera: Heteroptera) predators of mosquito larvae. The models that best fitted our data were modified Beddington–DeAngelis and Hassell–Varley models in which predator size affected the handling time. Models in which predator size affected capture rates performed better than models without a predator size effect. This suggests that capture rates are also affected by predator size. This study shows that predator size is an important variable in functional response models, particularly when the size variation among predators is relatively large.

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1. Introduction

Predator–prey interactions play a central role in ecology because they drive community and food web structure (Addicott, 1974; Naeem, 1988; Turner and Mittelbach, 1990; Wellborn et al., 1996; Winkelmann et al., 2011) and are fundamental in the evolution of behavioural and morphological characteristics of prey species (Abrams, 1991, 1986; Dawkins and Krebs, 1979; Van Der Laan and Hogeweg, 1995). A wide range of mathematical models that describe the relationship between predators and prey has been developed (Aljetlawi et al., 2004; Beddington, 1975; Crowley and Martin, 1989; DeAngelis et al., 1975; González-Suárez et al., 2011; Hassell and Varley, 1969; Hewett, 1980; Holling, 1959; Vucic-Pestic et al., 2010); these population models are most commonly used to predict the outcomes of two-species, predator–prey interactions. Early models, such as Holling's functional response models, predict predation rates as a function of prey density (Holling, 1959). Holling's type II functional response is the most widely applied predator–prey model (Skalski and Gilliam, 2001). This model

assumes that predation rates are limited by capture rates¹ and handling time. Since this time, our understanding of predator–prey interactions has improved substantially and we now know that, although prey density is important, there are other factors involved in these functional responses.

Predator density is another important factor in the functional response of predators. Predators can interfere with the foraging behaviour of con-specifics via a wide range of behaviours that subsequently reduce the time that can be spent on foraging (Beddington, 1975; Sih et al., 1998). Intraspecific competition, cannibalism, mating, and other social behaviours are examples of such interference (Buskirk Van, 1989; Martín and López, 2004; Wissinger and Mcgrady, 1993). Thus, the Holling type II functional response model was further developed into a set of new models that include predator density (Beddington, 1975; Crowley and Martin, 1989; DeAngelis et al., 1975; Hassell and Varley, 1969). The Beddington–DeAngelis (BDA) and Crowley–Martin (CM) models are examples of such models and are based on the same assumptions as the Holling type II model, while also assuming that competition between predators occurs (Beddington, 1975; Crowley and

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¹ We use the term 'capture rates' for the coefficient in functional response models that represent the rate at which a predator can catch a prey (Skalski and Gilliam, 2001), sometimes also called the 'attack coefficient' (Holling, 1959). The term 'predation rate' is used for the total number of prey consumed over a specified amount of time and depends on the capture rate, but also the handling time (Holling, 1959).

Martin, 1989; DeAngelis et al., 1975). The difference between these two models is that the BDA model assumes that predator interference only affects prey-searching activities whereas the CM model assumes that predator interference can also affect handling time (Beddington, 1975; Crowley and Martin, 1989). The Hassell–Varley (HV) model is another model that includes predator densities (Hassell and Varley, 1969). However, this model assumes that predation rates are dependent on the ratio of predators to prey (Hassell and Varley, 1969). Ratio-dependency in predator–prey models does not add in the explanation of processes (Abrams and Ginzburg, 2000; Abrams, 1994). Nevertheless, using a ratio-dependent model might give a better fit to a given dataset than a density-dependent model (Médoc et al., 2013); ratio-dependent models tend to be a good fit when predation rates are unaffected by predator density because prey densities are high (Skalski and Gilliam, 2001).

Predation rates may also depend on predator size as well as prey size (González-Suárez et al., 2011; Hewett, 1980; Hirvonen and Ranta, 1996; Thompson, 1975). Larger predators need more food, therefore, predation rates should be higher and predators will require less prey when prey are larger. A number of studies have aimed to develop functional response models that include prey density, predator density, predator size and/or prey size (Aljetlawi et al., 2004; González-Suárez et al., 2011; Hewett, 1980; Kalinkat et al., 2013; Vucic-Pestic et al., 2010). González-Suárez et al. (2011) developed models that included predator and prey sizes and were based on the added assumption that capture rates and handling time are dependent on both predator and prey size. They extended this idea to generate new allometric models based on Holling's type I and II models and the HV model (González-Suárez et al., 2011). Their best model was a Holling type II functional response, which included allometric parameters for prey and predator, but did not include predator densities (González-Suárez et al., 2011). Predator size was a very important parameter in their models; this is also the case in other studies (Hewett, 1980; Kalinkat et al., 2013; Vucic-Pestic et al., 2010). Adding predator size in functional response models will thus increase the accuracy of the models. However, many of these models that include predator size neglected the effect of predator density on the functional response (Aljetlawi et al., 2004; Hewett, 1980; Kalinkat et al., 2013; Vucic-Pestic et al., 2010). Many of these studies use predator biomass as a model parameter (Aljetlawi et al., 2004; Kalinkat et al., 2013; Vucic-Pestic et al., 2010). It could be argued that when predator density increases, the biomass increases as well, and thus the interference between predators is accounted for. However, a single large predator with a high biomass will not be subjected to predator interference even though such a model would assume it does. Competition between predators can also be size-dependent (Arim et al., 2011). Large predators require more resources and thus the number of individuals that can be supported by environment is lower (Arim et al., 2011). This effect is referred to as cross-community scaling or self-thinning (Arim et al., 2011). It is thus important to include predator size as well as predator density.

The aim of this study was to develop a set of allometric functional response models that included prey density, predator density as well as predator size. In contrast to previous studies we used four predator-density-dependent functional response models, which have all been widely applied in the literature, but to which we added a predator size effect. These included models that assume either a predator interference or ratio-dependent functional response. Specifically, we compared a range of models that included a predator size interaction with capture rates, handling time, or both, resulting in a total of 16 tested models. These models can be very useful for predator–prey studies in which one deals with a single prey species and multiple predator species. We tested these models in an experimental aquatic predator–prey system in which we used mosquito larvae (Diptera: Culicidae: *Armigeres*

sp.) as prey with multiple aquatic Nepomorpha (Hemiptera) predators (*Diplonychus rusticus*, *Naucoris scutellaris* and *Heleocoris* spp.). Discrete aquatic assemblages are ideal modelling systems because they are easy to independently replicate (De Meester et al., 2005). In addition, mosquito-predator systems have widely been studied in the context of biological control (Saha et al., 2014; Shaalan et al., 2007; Streams, 1994). Thus, using this mosquito-predator system provides an appropriate test of the applicability of the presented models.

2. Methods

Between March 29th and April 1st 2013, nepomorphan specimens were caught by sweeping a hand-held net through the vegetation of a canal that runs parallel to the historic city wall in Kamphaeng Phet, Thailand (16°29' 27.5532"N, 99°31' 19.1604"E). All specimens were stored in 1.5 l plastic containers filled with water; individuals were separated by size to reduce predation and cannibalism. We also collected water plants from the canal (*Ceratophyllum* sp.), which were rinsed to remove predatory organisms such as dragonfly larvae and were added to the containers as a resting substrate for the Nepomorpha. In the laboratory, all nepomorphan specimens were stored in separate plastic containers filled with water and one plant. All containers were provided with mosquito larvae prior to the experiment to avoid starvation and consequent artificial inflation of the predation rates. Mosquito larvae were collected with a hand-held net from a roof drain in Kamphaeng Phet (16°29' 34.3314"N, 99°31' 0.123"E). The majority of larvae were from the genus *Armigeres* (95% or more). Larvae were stored in a 5 l plastic container filled with water from the canal in which the nepomorphan specimens were caught. The container was covered with mosquito netting to prevent emerging adults from roaming freely in the laboratory.

The experimental set up consisted of 21, 1.5 l cylindrical plastic containers filled with 1 l of water and one plant with an approximate length of 10 cm. Nepomorphan specimens were grouped by size and released into the containers; we did not distinguish among species, therefore, containers also contained mixed species. The density of Nepomorpha ranged from one to four specimens per container; we used a total of 48 nepomorphan specimens (Table 1). Finally, the

Table 1

Overview of experimental set-up in which predator and prey densities are given in numbers per unit (1 l). The last column display the combinations of predators species in an experimental unit; *Diplonychus rusticus* (D), *Naucoris scutellaris* (N) and *Heleocoris* spp. (H).

Unit	Predator density	Prey density	Predator size mm (SD)	Predator species
1	1	10	5.9 (0)	N
2	1	10	2.9 (0)	N
3	1	20	7.3 (0)	N
4	1	30	4.6 (0)	N
5	1	40	2.7 (0)	H
6	1	50	13.3 (0)	D
7	2	10	6.9 (0.7)	NN
8	2	10	3.8 (0.9)	DD
9	2	20	7.2 (2.4)	DN
10	2	30	6.2 (0.7)	NN
11	2	40	6.1 (0.9)	NN
12	2	50	6.6 (0.5)	NN
13	2	60	11.3 (1.0)	DD
14	3	20	4.9 (0.3)	DNN
15	3	20	6.6 (0.5)	DNN
16	3	40	6.6 (0.2)	NNN
17	3	60	7.1 (0.1)	NNN
18	4	20	3.3 (0.3)	DDDH
19	4	30	6.7 (0.5)	NNNN
20	4	40	4.5 (0.0)	DHNN
21	4	50	7.1 (0.1)	NNNN

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