Local interactions between predators and prey call into question commonly used functional responses

Toshinori Okuyama *

Department of Entomology, National Taiwan University, Taipei 106, Taiwan

ABSTRACT

Commonly used functional response models (Holling's type I and type II models) assume that the encounter rate of a predator increases linearly with prey density, provided that the predator is searching for prey. In other other words, aN (a is the baseline encounter rate and N is prey density) describes the encounter rate. This study examined whether the models are adequate when predators and prey interact locally by using a spatially explicit individual based model because local interactions affect the spatial distribution of predators and prey, which also affects the encounter rate. Predators were assumed to possess a spatial perception range that influenced their foraging behavior (e.g., if a prey is in the perception range, the predator moves towards the prey). The effect of antipredator behavior by prey was also examined. The results suggest that prey and predator densities as well as handling time affect the baseline rate (i.e., parameter a) as opposed to the common assumption that the parameter is constant. The nature of model deviations depended on both the antipredator behavior and the predators' perception range. Understanding these deviations is important as they qualitatively affect community dynamics.

© 2009 Elsevier B.V. All rights reserved.

1. Introduction

Functional response is a basic modelling unit in community ecology. It describes the relationship between the rate at which a predator consumes prey and the environmental condition. For example, type II functional response is described by $aR/(1 + ahR)$; encounter rate a and handling time h are the parameters of the model, and the environmental variable is described solely by the prey density, R. When there is no handling time ($h = 0$), the type II functional response is reduced to the type I functional response. These functional responses have mechanistic underpinnings (Holling, 1959; Royama, 1971; Stephens and Krebs, 1986; Case, 2000).

Community dynamics are sensitive to the form that the functional response takes (Oaten and Murdoch, 1975; Vos et al., 2001). Thus it is important that functional response models are appropriate approximations for predation processes. For example, whether functional responses are also influenced by the density of predators and other non-prey species in the community (in addition to prey density) qualitatively alters community dynamics (Vos et al., 2001; Kratina et al., 2007) although they are commonly assumed independent of predators and other non-prey densities (Vos et al., 2001; Jensen and Ginzburg, 2005). Empirical characterizations vary in their results (Mols et al., 2004; Fussmann et al., 2005; Schenk et

al., 2005) and the appropriate form of functional response has been debated (Abrams and Ginzburg, 2000; Vos et al., 2001; Fussmann et al., 2005; Jensen et al., 2007; Fussmann et al., 2007; Kratina et al., 2007). To better understand the appropriate representation of predation processes, further detailed examinations of ecological factors that affect functional response are needed.

In the conventional functional response model, prey and predators are assumed located randomly in space. However, local interactions (e.g., a predator can capture a prey that is located its vicinity) and the limited dispersal ability can make the spatial distribution of individuals deviated from the random distribution (Bolker and Pacala, 1999). Spatial variance and covariance between prey and predators are important ecological factors (Kareiva and Tilman, 2000; Keeling et al., 2000; Vos et al., 2002; Vos and Hemerik, 2003). Although we know that spatial parameters such as the perception ranges of prey and predators affect the parameter of a functional response (Hassell, 1978; Case, 2000), we know little about how the spatial variance arising from the local interactions affects the functional response. This is because most spatial community models have their main focus on the effect of the spatial pattern on community dynamics (de Roos et al., 1991; McCauley and Wilson, 1993; Cuddington and Yodzis, 2002; Murrell, 2005), and they pay relatively little attention to an individual predator's functional response (but see Petersen and DeAngelis, 2000; Travis and Palmer, 2005; Anderson et al., 2005). For example, by using an individual based model, de Roos et al. (1991) and Cuddington and Yodzis (2002) found that the spatial variance, clumped distribution,

---

* Tel.: +881 2 33665282.
  E-mail address: okuyama@ntu.edu.tw.

generally decreased predation rates. In other words, by adjusting the parameter a, the conventional model may adequately describe the spatial predation process.

Notwithstanding, the seemingly adequate fit of the models do not indicate that the model assumptions are valid. This is because prey density and predation rate generally have a positive relationship regardless of the mechanistic processes behind. Because the qualitative prediction is trivial, the two parameter model, $aR/(1 + ahR)$, can phenomenologically fit data well even when the mechanistic assumptions of the model may be violated. For example, empirically estimated parameters are often biologically unreasonable (Hassell, 1978), which suggests that assumptions of the model are violated. Hassell (1978) also discusses that spatial parameters may make the parameters of the model to vary with environmental variables (e.g., species densities). The effect of spatial parameters on functional responses may provide useful insights about the true relationship between predation processes and ecological variables.

In this study, I examined the effect of spatially explicit predator–prey interactions on functional response by using an individual based model (IBM). In particular, I examined whether the encounter rate parameter a is independent of predator and prey densities, and handling time. In addition, when the constancy assumption of the parameter was violated, I characterized the patterns of deviation to better understand the functional responses.

2. The model

An individual based model (IBM) was used to examine the effect of spatially explicit predator–prey interactions on functional response. Both predators and prey occupy a point in a two dimensional square environment. Each individual possesses an internal variable that represents its heading orientation (0 to 360°) and moves a specified distance (on average) to the direction at each time step. Predators have their circular perception range defined by its radius. When a prey is in the perception range, predators orient towards the prey. When there are multiple prey in the range, predators orient to the closest prey. When no prey is in the perception range, predator's heading direction randomly changes by $u = U_1 - U_2$ degrees where U_1 and U_2 are independent random variates from a uniform distribution whose domain is 0 to 50.

The effect of antipredator behavior was also studied by examining the scenarios where prey exhibited and did not exhibit antipredator behavior. When a prey is assumed to exhibit antipredator behavior and finds a predator in its perception range, it orients to the opposite direction of the predator. When prey are assumed to exhibit no antipredator behavior (i.e., perception range = 0) or do not find a predator in its perception range, their heading directions are randomly changed in the same way as that of predators (i.e., changed by u degrees). Because it was assumed that predators moved faster than prey (i.e., 1.6 times), even when the prey's perception range was larger than that of predators, predators were able to capture prey.

The experimental arena was a square environment (51×51 units) where an edge did not function as boundary; instead, individuals were allowed to move "through" this boundary to the other side of the arena. Predators were assumed to capture a prey that was within one unit radius of the predator. In other words, a predator always captured a prey once the prey was encountered (i.e., a prey is within one unit radius of a predator); encounter rate and predation rate are equal in the study. The model was built using NetLogo (Appendix A) (Wilensky, 1999).

2.1. Simulations

When a prey was consumed by a predator, a new prey was introduced at a random location in the environment to maintain

Table 1
Parameter values used in the simulations

Variable	Value
Number of prey	2, 4, 6, 8, 10
Number of predator	1, 3, 5, 7, 9
Prey speed	0.2, 0.5
Antipredator behavior	YES, NO
Predator perception range	5, 15, 25
Prey perception range	0.5, 1.0, 1.5
Handling time	20, 40, 60, 80, 100

Predator perception range is a radius of the circular region. Prey perception range is relative to the predator perception range. For example, when it is 1.5, the radius of prey's perception range is 1.5 times larger than that of predators. Prey speed describes the average value; each realization was changed by $s_1 - s_2$, where s_1 and s_2 are independent random variates from a uniform distribution whose domain was 0 to 0.1.

the same prey density throughout the experiment. When a predator captured a prey, the predator stopped at the location and did not forage for a given duration, representing the handling time. Each simulation was continued until 1000 prey were captured in total. Search time for each prey capture was recorded for the 1000 incidents. Parameter values used in the simulations are shown in Table 1.

2.2. Analysis

The analysis focused on how prey density, predator density, and handling time influenced the encounter rate (i.e., search time). In theory, the rate of prey capture is described as aR given that a predator is searching (e.g., as opposed to handling) where R is the density of prey. Thus the quantity a ($= aR/R$) is assumed to be constant. In this study, I call this quantity the baseline encounter rate and examined the constancy assumption. Because predators sequentially spend time on searching for a prey and on handling the prey, one sample of search time begins when a predator finishes handling a prey and ends when it captures a new prey (i.e., time required for a predator to capture a prey given it is searching for a prey). The average search time based on 1000 search time samples, was used to represent $1/aR$ to compute aR/R. In addition to the mean effect, the coefficient of variation was also quantified as such variations can also affect community level dynamics (Okuyama, 2008).

3. Results

When prey's perception range was half of that of predators', prey could not escape from predators once they were found by predators because predators were assumed to move faster than prey. Thus the simulation results were similar to the case where prey exhibited no antipredator behavior. Results were also similar between the scenario where the perception range of prey was 1 times and 1.5 times larger than that of predators. Thus, here only the results based on the largest prey's perception range are shown to represent the effect of antipredator behavior. Similarly, the prey speed also did not affect the qualitative patterns of the results. When the prey speed was slow (i.e., 0.2 unit/time), predation rates were generally lower than the case when it was faster (i.e., 0.5 unit/time). Here, I present the results from the latter situation. In addition to the mean effect on the baseline encounter rate, coefficient of variation (CV) for search time is also presented for the scenario without the antipredator behavior of prey.

The mean baseline encounter rate and the prey density were negatively correlated (Fig. 1). This qualitative pattern is robust to the duration of handling time. The baseline encounter rate was more sensitive to the density of prey when the perception range of predators was large. When the perception range was 15, there was a clear negative relationship between the baseline encounter