Digestion Limits the Functional Response of an Aphidophagous Coccinellid (Coleoptera: Coccinellidae)

NIKOS E. PAPANIKOLAOU,1,2,3 PANAGIOTIS G. MILONAS,2 NIKOS DEMIRIS,4 DIMITRIOS P. PAPACHRISTOS,2 AND YIANNIS G. MATSINOS1

ABSTRACT The dynamics of predator–prey systems are strongly affected by the predators feeding rate on increasing prey density, that is, its functional response. Holling’s assumptions concerning the biological process of handling time, that is, the time a predator spends on pursuing, subduing, eating, and digesting its prey, have been debated, as digestion represents a background component of predation. Therefore, predators are characterized either as digestion or handling limited. A study was initiated to identify the mechanism that limits the coccinellids’ predation ability. The 14-spotted ladybird beetle, Propylea quatuordecimpunctata (L.) (Coleoptera: Coccinellidae), and its prey, Aphis fabae Scopoli (Hemiptera: Aphididae), were used in long- and short-term functional response experiments. Results showed that P. quatuordecimpunctata adults exhibit a type II functional response. The estimated attack rates and handling times differed significantly between long- and short-term experiments, indicating that the digestion process limits predation ability of P. quatuordecimpunctata.

KEY WORDS Coccinellidae, digestion, handling time, predation, random predator equation.

Understanding the relation between the consumption rate of a predator and its prey density, that is, the functional response (Solomon 1949), remains a significant subject in insect ecology, as it affects the dynamics of communities, on the basis that it explicitly takes into account predator–prey interactions. The functional responses of predators proposed by Holling (1959) are characterized by two parameters, the attack rate that represents the per capita prey consumption at low prey densities, and the handling time, that is, the time a predator spends subduing, pursuing, eating, and digesting a prey item. The shape of the functional response curve is dependent on these parameters (Holling 1965, Hassell 1978). When handling time is minor, prey consumption up to a certain threshold prey density is density independent (linear functional response), beyond which it is constant (type I). When density dependence follows a continuous decelerating feeding rate (type II) or a sigmoid response (type III), functional response curve reach a plateau determined by handling time. Type II is considered to prevail in nature (Jeschke et al. 2004).

Because of the importance of functional responses on predator–prey dynamics, several modeling approaches for type II functional responses have been pursued with respect to the attack rate (see Jeschke et al. 2002 for a review). An aspect that has received considerable attention in functional response studies is the limit to the number of prey attacked at high prey densities. It has been considered that handling time is the limiting factor for parasitoids and satiation for predators (Getz and Mills 1996, Jeschke et al. 2002). The importance of digestion in shaping functional responses and thus foraging decisions has been increasingly acknowledged (Jeschke et al. 2002; Van Gils and Piersma 2004; Van Gils et al. 2005a,b). Digestion and handling prey are discrete biological processes that should be taken into account separately, as digestion influences the predators’ hunger level and its probability of searching for prey (Jeschke et al. 2002).

Discriminating digestion process from handling time is essential for a thorough understanding of the predation processes and the underlying foraging behavior and how it is affected by satiation-driven functions (van Rijn et al. 2005). There are several examples where predators are not time limited but digestion limited (Jeschke et al. 2002). In this article, we explore functional responses of the 14-spotted ladybird beetle, Propylea quatuordecimpunctata L. (Coleoptera: Coccinellidae), a common Palearctic species and a predator of various aphid pests (Kalushkov and Hodek 2005). Papanikolaou et al. (2011) has shown that P. quatuordecimpunctata larvae exhibit a type II functional response when preying on the black bean aphid, Aphis fabae Scopoli (Hemiptera: Aphididae). Following the approach proposed by Jeschke et al. (2002), we investigated the functional response of P. quatuordecimpunctata adults to determine whether it is limited by handling or by digestion. To test this, we designed and

1 Biodiversity Conservation Laboratory, Department of Environmental Sciences, University of the Aegean, Mytilene 81100, Greece.
2 Department of Entomology and Agricultural Zoology, Benaki Phytopathological Institute, St. Delta 8, 14561, Kifisia, Greece.
3 Corresponding author, e-mail: nepapanikolaou@yahoo.gr.
4 Department of Statistics, Athens University of Economics and Business, Patission 76, 10434, Athens, Greece.
developed functional response experiments at two time periods with predators in steady hunger state, to estimate short- and long-term attack rate and handling time. A long-term feeding experiment was performed at the daily foraging cycle of the predator, whereas in the short-term feeding experiment, the total exposure time of prey and predator was 3 h. If the estimated handling times did not differ significantly statistically, disclosing satiation effects in both time intervals, we had to test shorter time period(s), to identify if this predator is digestion or handling limited. The functional responses were run separately for males and females to accommodate for potential sex differences.

Materials and Methods

Insects. An A. fabae colony (originally from a stock colony at the Biological Control Laboratory, Benaki Phytopathological Institute) was reared on fava bean, Vicia faba L., plants under constant temperature and light regimes (20 ± 1°C, 65 ± 2% relative humidity [RH], and a photoperiod of 16:8 [L:D] h). P. quatuordecimpunctata adults were originally collected from corn, Zea mays L., plants infested by the corn leaf aphid, Rhopalosiphum maidis Fitch in Arta County (northwestern Greece, 21° 0’0” E, 39° 10’0” N) and were reared in cylindrical Plexiglas cages (50 cm in length by 30 cm in diameter) feeding on A. fabae mixed instars and adults at 25 ± 1°C, 65 ± 2% RH, and a photoperiod of 16:8 (L:D) h.

Functional Response Experiments. We followed Jeischke et al. (2002) in performing long- and short-term functional response experiments. The experiments were carried out at 25 ± 1°C, 65 ± 2% RH, and a photoperiod of 16:8 (L:D) h. The experimental arena consisted of a plastic container (12 cm in height by 7 cm in diameter) with a potted V. faba plant (at 8–9 cm height, top growth was cut) with different A. fabae densities (3- to 3.5-d-old immature aphids to avoid any reproduction during the experiments). Females and males of P. quatuordecimpunctata were starved for 12 h and placed individually into plastic containers. In long-term experiments, total exposure time was 24 h and A. fabae densities 4, 8, 16, 32, 64, and 128 aphids for both male and females. In short-term experiments, exposure time was 3 h and A. fabae densities 2, 5, 10, 15, and 20 and 2, 5, 10, 15, 20, and 25 aphids for males and females, respectively. We used 20- to 30-d-old P. quatuordecimpunctata adults. Ten replicates on each prey density were formed. At the end of each experimental period, we counted the number of aphids not eaten by the predator.

Statistical Analysis. The shape of the functional response was determined via logistic regression analysis of the proportion of aphids consumed as a function of available aphid density (Trexler et al. 1988, Juliano 2001). We fitted a polynomial function:

\[
N_e = \frac{\exp(P_0 + P_1N_0 + P_2N_0^2 + P_3N_0^3)}{1 + \exp(P_0 + P_1N_0 + P_2N_0^2 + P_3N_0^3)},
\]

where \(N_e\) is the number of prey consumed, \(N_0\) the initial prey number available, and \(P_0, P_1, P_2, P_3\) are the intercept, linear, quadratic, and cubic coefficients estimated using the method of maximum likelihood. The visual inspection of the observed versus fitted probabilities showed a close match, indicating that the proportion of prey eaten decreases with increasing prey density.

The integrated form of disc equation proposed by Rogers (1972), commonly known as the random predator equation, was used, as it allows for prey depletion:

\[
N_e = N_0[1 - e^{-(aT - N_e/T_e)}],
\]

where \(a\) denotes the attack rate; \(T_h\) the handling time; and \(T\) the total time that prey was exposed to predator. The parameters were estimated using Lambert’s W function, which provides a numerical solution of the equation \(W(x)e^{W(x)} = x\) (Corless et al. 1996). In terms of Lambert W, equation 1 can be written (Bolker 2008) as:

\[
N_e = \frac{W[aT_hN_0e^{(aT_hN_0-aT_h)}]}{aT_h}
\]

The fitting was performed using maximum likelihood (R Development Core Team 2010). Significant differences between estimated parameters were based on a 5% significance level. In addition, the maximum attack rate, that is, the maximum number of prey which can be attacked by a predator during the time interval under consideration (\(T/T_h\)) was calculated using the mean estimate of \(T_h\) (Hassell 2000).

Results

The outcome of the logistic regression, that is, the observed versus fitted probabilities (Fig. 1; Table 1), indicated that the proportion of prey eaten decreases with increasing prey density, in all bioassays. Thus, a type II functional response exhibited by P. quatuordecimpunctata females and males at the short- and long-term experiments was adequately described by the random predator equation in terms of Lambert W function (Fig. 2).

Estimated handling time differed between long- and short-term experiments for both males and females (Table 2; Fig. 3). At 24-h exposure time, the handling time for females was 0.256 h, decreasing to 0.161 h at 3-h exposure time, while for males decreased from 0.479 h at 24 h to 0.213 h at 3 h. Handling time was higher for males than females at the long-term experiment but not at the short-term experiment. In addition, the maximum numbers of prey that can be attacked by females were 93.56 and 18.62, and by males 50.11 and 14.07, at long- and short-term experiments, respectively.

Attack rates were higher during the short-term experiment for both females and males (1.006 and 0.540 h\(^{-1}\), respectively) compared with long-term (0.216 and 0.192 h\(^{-1}\) respectively). Attack rates did not differ between males and females in both long- and short-term experiments.
Discussion

Our study generated several clear findings. *P. quatuordecimpunctata* males and females exhibit a type II functional response to *A. fabae* prey. This decelerating increase in predation rate with prey density is quite common in invertebrate predators in general (Mansour and Heimbach 1993, Milonas et al. 2011, Vieira et al. 2012) and in aphidophagous ladybirds in particular (e.g., Cabral et al. 2009, Xue et al. 2009, Farhadi et al. 2010, Jalali et al. 2010, Papanikolaou et al. 2011, Aqueel and Leather 2012). There are, however, a few exceptions where linear or type III responses have been reported (e.g., Hassell et al. 1977, Luo 1987). Under type II functional response, stable population is unlikely to occur, as prey are either driven to extinction at low densities, or escape predation at high densities. However, when handling time is small in relation to the total time available for the predator, as is the case for long-lived species, it is assumed that handling time will be of minor importance in affecting stability (Hassell and May 1973, Hassell 1978).

We can exclude that under different biotic and abiotic factors the functional response of a predator might change. It would be possible that *P. quatuordecimpunctata* adults could show a different functional response when feeding on another prey species (Luo 1987, Seko and Miura 2008), on a mixture of prey species (Schenk and Bacher 2002), on different host

![Graph](https://example.com/graph.png)

**Fig. 1.** Observed versus fitted probabilities of *A. fabae* prey eaten by *P. quatuordecimpunctata* at long- (L. T.) and short-term (S. T.) experiments.

| Parameter | Female | Male |
|-----------|--------|------|
|           | Long term | Short term | Long term | Short term |
| $P_0$     | 3.631 ± 0.472 | 1.326 ± 0.170 | 1.927 ± 0.171 | 0.541 ± 0.145 |
| $P_1$     | $-14.744 ± 2.911$ | $-6.713 ± 1.558$ | $-10.962 ± 1.046$ | $-4.334 ± 1.158$ |
| $P_2$     | $4.688 ± 2.526$ | $0.807 ± 1.252$ | $2.403 ± 0.969$ | $1.793 ± 0.981$ |
| $P_3$     | $-4.348 ± 1.737$ | $-0.970 ± 0.872$ | $2.773 ± 0.865$ | $-0.167 ± 0.812$ |

Table 1. Estimated parameters of the logistic regression analysis of the proportion of *A. fabae* prey eaten by *P. quatuordecimpunctata* adults versus initial *A. fabae* density at two exposure times.
plants (Messina and Hanks 1998), or in the presence of an intraguild predator (Martinou et al. 2010). In nature, type III response is likely to occur by prey switching on the part of the predator. It is argued that the prevalence of type II functional responses under restricted laboratory conditions in a small arena or cage may overestimate their occurrence in field conditions, as laboratory studies do not take into account alternative prey (Oaten and Murdoch 1975, Schenk and Bacher 2002). Therefore, prey switching of a generalist predator could conceivably lead to a sigmoid response in the field (Begon et al. 1996). A different functional response type would affect our prediction of what actually occurs in the field.

In the current study, we disentangle the digestion process from handling time. According to Jeschke et al. (2002) when handling time does not change with duration of experimental set up, then it is probable

Fig. 2. Functional responses of females and males of *P. quatuordecimpunctata* to *A. fabae* at long- (L. T.) and short-term (S. T.) experiments.

| Exposure time (h) | Handling time (h) | Attack rate (h^{-1}) | AIC | Max attack rate |
|-------------------|-------------------|----------------------|-----|----------------|
|                   | Mean 95% CI       | Mean 95% CI          |     |                |
| Females 24 h      | 0.2565 0.2388-0.2744 | 0.2162 0.1896-0.2473 | 330.60 | 93.56 |
| 3 h               | 0.1611 0.1286-0.1913 | 1.0064 0.7603-1.3365 | 276.42 | 18.62 |
| Males 24 h        | 0.4789 0.4446-0.5139 | 0.1924 0.1629-0.2280 | 421.87 | 50.11 |
| 3 h               | 0.2132 0.1224-0.2929 | 0.5396 0.3661-0.8061 | 198.48 | 14.07 |
that the predator is handling limited. In our study, handling time was lower under a short-term than at a long-term experimental set up. This further indicates that the predator probably does not become satiated in the short-term feeding experiment, unlike the long-term. As Hodek and Honek (1996) stated, hungry aphidophagous coccinellids completely devour the first prey items they encounter and then become less competent at exploiting prey. This trait results from the digestion process, which acts parallel to predation activities of pursuing, subduing, and eating prey. Therefore, the predation efficiency of coccinellids may be limited by digestion time, setting the upper limit of resource consumption. In general, the majority of predators in nature, including predatory insects, seem to be digestion limited (Sabelis 1992, Jeschke and Tollrian 2000, Jeschke et al. 2002).

A critical aspect of predators’ decision of prey selection is the diet composition. Ecology theory supposes that predators are likely to maximize their long-term average energy intake rate, optimizing the ratio of the prey metabolizable energy content to required handling time (Van Gils et al. 2005a). We therefore expect that the amount of the aphids’ indigestible matter affect aphidophagous coccinellidae species foraging behavior, causing them to drop lower value prey from their diet. They may prefer to spend less time to pursue, subdue, and eat aphid prey, while they gain the most energy intake, with further effects in population’s fitness. Moreover, we expect that non-foraging activities, such as mating and egg production, are beneficial for the predator that results from purely digestion process. Digestion-limited predators could take an advantage of reduced interference competition, owing to digestive constraints (Van Gils and Piersma 2004).

Several studies have been conducted concerning the density effect of aphid species in the feeding rate of coccinellids (e.g., Athan and Guldal 2009, Farhadi et al. 2010, Inayat et al. 2011). Our estimated maximum attack rates of \( P. \) quatuordecimpunctata adults seem higher than of other aphidophagous coccinellids. This could be an effect of the relative sizes of the predator and prey. In the current study, we also observed a
difference in maximum attack rates between males and females at the long-term (24 h) experiment. Females might attack and subdue prey more efficiently and faster than males. However, attack rate within a species is limited by speed movement of the predator and the proportion of successful attacks (Hassell 1978).

In conclusion, we provide evidence that density-dependent predation rate of an aphidophagous coccinellidae species is limited by its digestion process. This is critically important for using functional response outcomes to accurately infer mortality rates imposed on prey in a population and community level, and also use functional response as a key component to dynamically couple prey and predator populations in models of predator–prey systems.

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