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Functional Response of *Amblyseius longispinosus* (Acari: Phytoseiidae) to *Tetranychus urticae* (Acari: Tetranychidae): Effects of Prey Density, Distribution, and Arena Size*

긴털이리응애의 점박이응애에 대한 기능반응 : 피식자 밀도, 분포 및 면적크기의 영향

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ABSTRACT Experiments were conducted to study the functional response of *Amblyseius longispinosus* Evans to egg densities (10-80) of *Tetranychus urticae* Koch under different egg distributions (clumped & uniform) and arena sizes (3, 9 & 16 cm^2). The searching success of *A. longispinosus* was affected by the spatial distribution and density of the prey but not by the arena size. There was a highly significant negative correlation ($r=-0.85$; $p=0.0001$) between predation amount and distances between preys. The predation response showed a type Ⅱ functional response. The random predator equation satisfactorily described *A. longispinosus*' predation. The search rate ranged from 0.1030 to 0.1504 under clumped distribution of the prey while it ranged from 0.0546 to 0.0276 under uniform distribution.

KEY WORDS Functional response, *Amblyseius longispinosus*, *Tetranychus urticae*, spatial distribution

초 록 점박이응애(*Tetranychus urticae*)의 알밀도(10~80), 공간분포(집중 및 균일분포) 및 서식면적크기(3, 9, 16 cm^2)에 따른 긴털이리응애(*Amblyseius longispinosus*)의 기능반응을 연구하여 다음과 같은 결과를 얻었다. 긴털이리응애의 점박이응애 발견효율은 밀도와 공간분포의 영향을 받았으나, 면적의 영향은 없었다. 포식량과 피식자간의 거리와는 매우 높은 역상관관계를 보였다($r=-0.85$; $p=0.0001$). 포식반응은 제2형의 기능반응을 보였다. 긴털이리응애의 기능반응은 random predator equation으로 잘 설명되었으며, 탐색률은 피식자의 집중분포하에서 반응면적에 따라 0.1030~0.1504였고 균일분포하에서는 0.0546~0.0276였다.

검 색 어 기능반응, 긴털이리응애, 점박이응애, 공간분포

In Korea, the two-spotted spider mite, *Tetranychus urticae* Koch, has become a serious pest in apple orchards where calendar spray programs are applied. The mite develops resistance rapidly to a wide range of pesticides and its natural enemies are suppressed by pesticides (Lee et al. 1985, Lee 1990). There has been a growing concensus that the pest control system for apple orchards should be changed. A recent study suggested that an effective mite

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control program for apple orchards needed to integrate biological control and chemical control (Lee 1990).

The value of predatory mites in controlling spider mite populations has been reported worldwide (Mori 1967, Huffaker et al. 1970, McMurtry et al. 1970, Dover et al. 1979, Sabelis 1981, Helle & Sabelis 1985). In Korea, *Amblyseius longispinosus* Evans is a predominant predator of spider mites in apple orchards. However, the biology of *A. longispinosus* has not been extensively studied until recently in spite of its important potential in mite control. The effectiveness of natural enemies can be assessed based on 1) the predator's ability to attack its prey, 2) the predator's life history in relation to its prey's and 3) environmental tolerance (Murdoch & Oaten 1975). Research has shown that *A. longispinosus* synchronizes its life history with *T. urticae* and has a considerable tolerance to adverse environments (Lee et al. 1985, Lee 1990).

For evaluation of this predator's ability to attack its prey, functional response studies quantify search rate (attack rate) and the response of the predator to prey densities. Functional responses can be used for determining control potential of predators by comparing relative effectiveness of predators on a common prey. However, under natural conditions, the prey may be distributed in various patterns because of the complexity of habitats, prey species characteristics, and other environmental factors. Therefore, the searching success of a predator should be evaluated in terms of the manner in which the prey population is distributed in different habitat sizes as well as in terms of prey density.

The ojective of this study was to illustrate the functional response of *A. longispinosus* to *T. urticae* densities under different distribution patterns and arena sizes.

MATERIALS AND METHODS

Origin of mites

All predators and prey used in this experiment were taken from labaoratory cultures maintained at Department of Agricultural Biology, College of Agriculture and Life sciences, Seoul National University, Suwon since 1990. These mites were obtained from Department of Entomology, Agricultural Sciences Institute, Suwon in 1990.

A. longispinosus was maintained on detached kidney bean, *Phaseolus vulgaris* var. *humilis* Alefeld, leaves with *T. urticae* as prey. The leaves with stem were inserted into a plastic plate with holes that was placed upside-down in a stainless-steel tray filled with water. *T. urticae* was reared on kidney bean plants with 3 to 6 fully developed leaves. The colonies were maintained under laboratory conditions (Temp. 23-30℃, RH 60-80%, and 16L : 8D). Kidney beans were grown in the growth room lighted by four 40W fluorescent lamps and two 60W light bulbs from 60 cm top (Temp. 18-32℃, RH 60-80%, and 16L : 18D).

Functional response study

Excised fresh bean leaf discs (arena) were placed upside-down on water saturated sponge in a petridish (9 cm in dia., and 1.4 cm high). Arena sizes were 3 (circle with 1 cm, dia.), 9 (3 × 3 cm), and 16 cm^2 (4 × 4 cm). The different prey densities offered to a single *A. longispinosus* female adult were 10, 20, 30, 50, and 80 eggs of *T. urticae*. Eggs were provided by following procedures: Three, 5, 7, 11, and 18 *T. urticae* female adults were placed on leaf discs where 10 to 80 eggs were needed, respectively. After 24 h, mites and webs were removed, and eggs were removed or replenished to meet required densities.

Uniform and clumped distribution patterns were used for eggs. For a uniform distribution, positions were regularly marked by pinpricks on leaf discs and eggs were placed on each position one by one using a fine brush. The distances between nearest neighbors in arena levels and egg densities were shown in Fig. 1. For a clumped distribution, natural egg laying by mites on leaf discs was used. The degree of clumping (k) ranged 0.417 to 0.146.

Two to three days old mated female adults of *A. longispinosus* were used as predators. It was assumed that their pre-experimental conditions were same since they were kept in a same colony.

All experiments were conducted in a labaratory (Temp. 25±1 ℃, RH 60-80%, and 16L : 8D) for 24 hours and replicated 6 to 17 times. Presence or absence of predators in experimental arenas were examined every 6 hours. The number of eggs consumed was recorded after 24 hours. Eggs were not replaced as they were killed during tests. Data of tests in which a predator escaped or was dead before 6 hours were excluded in analyses.

Data analyses

The search rate (a) and handing time (h) for the functional response at different prey distributions and arena sizes were estimated from the "random predator equation" developed by Royama (1971) and Rogers (1972). The equation is

$$y=x[1-\exp\{-ap_t(T-h(y/p_t))\}]$$

where, y = the number of prey consumed, x = initial prey density, a = search rate, h = handling time, p_t = the number of predator introduced, T = the total time of the interaction. The initial values of 'a' and 'h' were obtained by fitting a linear regression between y and $l_n\ (x-y)/y$ (Rogers 1972). Then, their final values were estimated by using Marqurdt methods of nonlinear regression between y and $l_n\ (x)$ (SAS Institute 1988).

Data were transformed by log (x + 1) and analyzed by the general linear model (GLM) procedures (SAS Institute 1988).

Results

The analysis of variance on factors affecting *A. longispinosus's* predation on eggs of *T. urticae* indicated that predation was affected by egg distribution ($F=18.07$; $df=1,132$; $p=0.0001$) and egg numbers ($F=15.79$; $df=4,132$; $p=0.0001$). However, arena sizes did not influence the predation amount ($F=2.25$; $df=2,132$; $p>0.1$). Also, there was a significant interaction between egg distribution and egg numbers ($F=5.43$; $df=4,132$; $p=0.0004$). This resulted in different functional response curves with different egg distributions (see Fig. 2).

The functional responses of *A. longispinosus* to prey numbers from 10 to 80 eggs per arena under different distributions are shown in Fig. 2. The response curves showed type Ⅱ functional response (Holling 1966). However, the shapes of curves were different between egg distributions. Under clumped distribution, the response curve rises rapidly to a plateau from a low prey density while the curve rises gradually to a plateau under uniform distribution.

The random predator equation (Royama 1971, Rogers 1972) satisfactorily described the *A. longispinosus's* predation (Table 1). The search rate ranged from 0.1030 to 0.1504 under clumped distribution of prey while it ranged

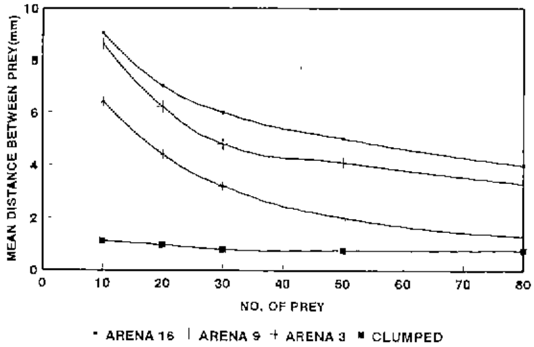

Fig. 1. Mean distance between *T. urticae* eggs at different densities and arena sizes.

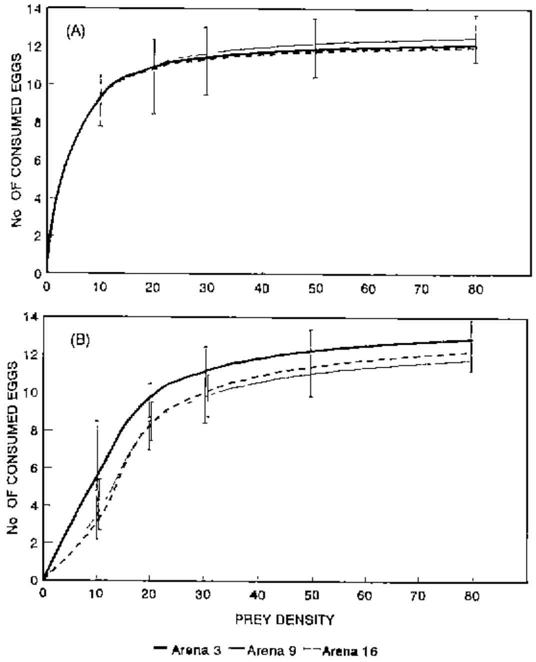

Fig. 2. Functional responses of adult female *A. longispinosus* to *T. urticae* eggs under clumped (A) and uniform (B) distributions.

from 0.0546 to 0.0276 under uniform distribution. Under uniform distribution of prey, the search rate of predator was lower in a larger arena than in a smaller one.

Discussion

Since a search rate in the random predator model is a parameter defining a slope of the curve (Holling 1959), differences in curves will produce different values in the search rate of a predator. Therefore, differences in predation processes of *A. longispinosus* under different prey distributions can be explained by differences in a predator's searching success. The effect of prey distribution seemed to related to the differences in distances between nearest neighbor prey eggs. Since mean distances between eggs stay constant (ca 1.2 mm) in clumped distribution regardless of egg numbers and arena sizes (Fig. 1), predation amount changed little with increasing egg numbers and arena sizes (Fig. 2). However, in uniform distribution, mean distances varied with egg numbers and arena sizes (1.5-9 mm) (Fig. 2). Thus, increasing distances resulted in decreasing egg finding, thus less consumption where less nmubers of eggs were placed uniformly in a larger arena (Fig. 2). There was a highly significant negative correlation ($r=-0.85$; $p=0.0001$) between predation amount and distances between eggs (Fig. 3). The distance between prey, however, may not be the only factor responsible for predation variation since *A. longispinosus* did not always stay in an experimental arena during experiment periods (24 hours). In other words, perdators escaped the arena where distances between eggs were high. Thus, differences in predation amount did not always resulted from differences in *A. longispinosus's* searching time which is defined as the time spent to search for another egg after preying on one. Fig. 4 shows the extent of escape of *A. longispinosus* in different arenas and prey numbers under different distri-

Table 1. Estimates of the parameters of functional responses of adult female *A. longispinosus* to *T. urticae* eggs

ARENA/DISTRIBUTION	SEARCH RATE	HANDLING TIME(Hr)	R^2
3 cm^2 ARENA			
CLUMPED	0.1030 ± 0.04370	1.6976 ± 0.08917	0.77
UNIFORM	0.0546 ± 0.00900	1.5270 ± 0.06940	0.97
9 cm^2 ARENA			
CLUMPED	0.1238 ± 0.06692	1.7323 ± 0.10264	0.71
UNIFORM	0.0276 ± 0.00316	1.3053 ± 0.09854	0.98
16 cm^2 ARENA			
CLUMPED	0.1504 ± 0.05086	1.8368 ± 0.04707	0.87
UNIFORM	0.0273 ± 0.00287	1.2824 ± 0.09140	0.99

*Values are Parameter ± SEM.

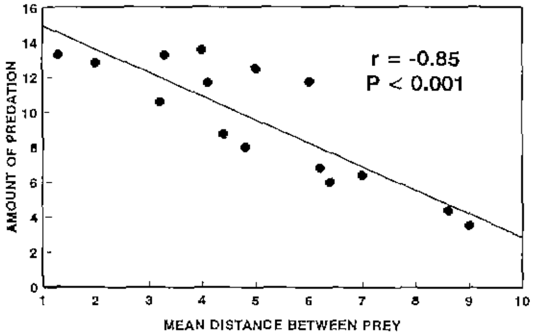

Fig. 3. Relationship between *A. longispinosus* predation amount and mean distance between *T. urticae* eggs.

butions. In overall, predator's escape from arena were more frequent and occurred earlier in uniform distribution of prey than in clumped distribution. This indicated that a predator escaped the arena when it faced difficulty in finding prey. This phenomenon was more prominent when distances between nearest neighbor eggs were longer. This induced escape of a predator might result in its reduced searching time. Under clumped distribution of eggs, escape of a predator occurred less at 18 hours and became prominant at 24 hours at low numbers of eggs. Since distances between eggs were close under clumped distribution, a predator might not have difficulty finding prey untill most eggs were consumed (after ca. 18 hours) even at low numbers of prey, so stay arena as far as it successfuly finds prey. Then a predator might escape after prey numbers became extremly low. This trend was more clear under uniform distribution of prey. Under uniform distribution, escape of a predator occurred more frequently and earlier at low numbers of prey and occurrence of escape decreased as prey numbers increased. This could characterize predation behavior of *A. longispinosus.* These differences in its predation behavior under different prey distributions were reflected in its search rates. Therefore, search rates of *A. longispinosus* were higher in clumped distribution' of prey than in uniform distribution (Table 1).

Not all predacious mites respond to the spatial distribution of the prey in a similar manner as *A. longispinosus.* Ths spatial distribution of the prey affected the functional response of *Phytoseiulus persimilis* Athias-Henriot but not of *A. degenerans* (Berlese) (Eveleigh & Chant 1982). The degree of prey aggregation affected the number of prey killed by *P. persimilis.* More

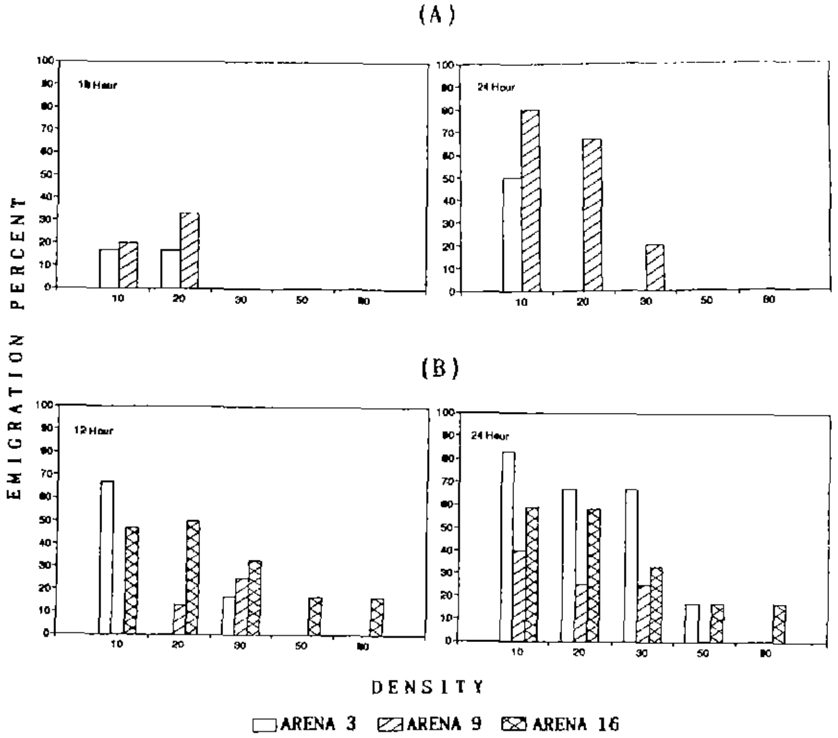

Fig. 4. Percent emigration of *A. longispinosus* under clumped (A) and uniform (B) distributions of *T. urticae* eggs at different arena sizes.

prey were killed when prey were clumped. In contrast, *A. degenerans* consumed prey in almost direct proportion to the prey density regardless of the spatial arrangement of the prey. More behavioral studies on predacious mites are needed to explain the reasons for these results.

The reduced searching effort at low prey density plays an important role in the functional response of a predator, generating a type Ⅲ shape (a sigmoid curve). This type has been known theoretically as the one that can contribute to the stability of a predator-prey interaction (Murdoch & Oaten 1975). Sabelis (1985) stated that the functional response was expected to have a sigmoid relationship with prey density if predators were allowed to leave the arena on their own accord. Takafuji & Deguchi (1980) also reported a sigmoid functional response of *P. persimilis* when arena sizes were relatively large (16 and 23 cm^2) since at low prey density predators spent less time for searching, but they moved around the border of arena instead. However, Ryoo (1986) reported a type Ⅱ response of *P. persimilis* in an open system where predators could disperse freely. In our study, *A. longispinosus* showed a type Ⅱ functional response where prey were distributed clumped regardless of arena sizes since escape of a predator was delayed. Even under conditions where prey were artificially overdispersed, it showed a type Ⅱ response though its predation pressure became less.

Our results may have important implications for studies on biological control of *T. urticae* by *A. longispinosus.* Although prey distribution under natural conditions may not correspond exactly to clumped distribution used in our study, our study indicated that *A. longispinosus* could devour preys at low density under clumped distribution. This fact might result in a unstable predator-prey interaction. Since a stable predator-prey interaction with low equilibrium is desirable for a successful biological control, it is important to find factors which may alter *A. longispinosus's* predation behavior. Further studies are needed on this aspect.

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