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**A THESIS FOR THE DEGREE OF  
MASTER OF SCIENCE**

**Development and oviposition models, life table, and  
functional response of *Amblyseius eharai*  
(Amitai et Swirski) (Acari: Phytoseiidae)**

**긴꼬리이리응애(진드기아강: 이리응애과)의 발육과 산란 모형,  
생명표 및 기능 반응에 관한 연구**

**By**

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**SEOUL NATIONAL UNIVERSITY**

**February 2017**

**Development and oviposition models, life table, and  
functional response of *Amblyseius eharai*  
(Amitai et Swirski) (Acari: Phytoseiidae)**

**UNDER THE DIRECTION OF ADVISER JOON-HO LEE  
SUBMITTED TO THE FACULTY OF THE GRADUATE SCHOOL  
OF SEOUL NATIONAL UNIVERSITY**

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## **ABSTRACT**

### **Development and oviposition models, life table, and functional response of *Amblyseius eharai* (Amitai et Swirski) (Acari: Phytoseiidae)**

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Many species of Phytoseiidae have been used to control the pest such as mites, thrips and white flies in agricultural crop systems. *Amblyseius eharai* is a native Phytoseiidae in Korea and known for a biological control agent of spider mites in the early season in apple orchards. To evaluate the potential of *A. eharai* as a biological control agent, ecological characteristics of *A. eharai* were studied by using *Tetranychus urticae* (Koch) (Acari: Tetranychidae) as prey. First, development and fecundity of *A. eharai* were studied at different temperatures and its temperature-dependent development and oviposition models were developed. Second, life table of

*A. eharai* was constructed at various temperatures to analyze its population growth characteristics. Third, functional response of *A. eharai* was studied against larvae of *T. urticae*.

Development of *A. eharai* was examined at 11 constant temperatures (18.0, 20.1, 21.6, 24.0, 24.1, 27.4, 28.6, 30.2, 32.0, 33.2 and 35.9 °C) and oviposition of *A. eharai* was examined at six constant temperatures (18.0, 21.6, 24.1, 27.4, 30.2 and 33.2 °C). Development of *A. eharai* was well described by the Briere 1 function. Lower threshold, optimal, and upper threshold temperatures of development of total immature stage were 13.2, 30.6, and 35.9 °C, respectively. Developmental variation of immature stages was well described by the two-parameter Weibull function. Fecundity was well described by the Extreme Value function. Optimal and  $B_{80}$  temperatures of fecundity were 24.3 and 20.5 ~ 27.4 °C, respectively. Adult developmental rate model, cumulative oviposition model and age-specific survival rate model were well described by the equation from the TableCurve 2D library, Weibull function and reverse sigmoid function, respectively.

Life table analysis of *A. eharai* was conducted at six constant temperatures (18.0, 21.6, 24.1, 27.4, 30.2 and 33.2 °C) according to the age-stage, two-sex life table theory. Age-stage specific survival rate, age-stage specific fecundity, age-stage specific reproductive value, age-specific

survival rate, age-specific fecundity and population projection were estimated. The intrinsic rate of increase was the highest at 27.4 °C as 0.2619. Mean generation time was longest at 18.0 °C as 26.9 days, and shortest at 30.2 °C as 10.5 days.

Functional response of *A. eharai* was conducted at 10, 30, 50, 70 and 130 larvae of *T. urticae*. Functional response of *A. eharai* was the Type 2. The attack rate of female and male *A. eharai* was 0.109 and 0.019, respectively. The handling time of female and male was 0.164 h and 0.234 h, respectively. The attack rate was significantly different between males and females at 95% confidence interval. However, handling time was not statistically different.

**Key words:** *Amblyseius eharai*, development model, oviposition model, life table, functional response, Phytoseiidae, biological control, *Tetranychus urticae*

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# 1. General introduction

The mites in Phytoseiidae are generally considered as very useful biological control agents against small-sized pests (McMurtry and Croft 1997). Phytoseiid mites have five life stages, egg, larva, protonymph, deutonymph, and adult. Phytoseiid mites can be divided into four types according to the prey preference (McMurtry and Croft 1997). Type 1 is a specialist to *Tetranychus* spp. Type 2 is broadly specific and tetranychids are most favored. Type 3 is a generalist. Type 4 is a generalist and a pollen feeder. *A. eharai* is a type 3 generalist species (McMurtry and Croft 1997). In addition, for the larval stage, Phytoseiidae can be classified to three types according to feeding traits, obligatory feeding larva (OFL), nonfeeding larva (NFL) and facultative feeding larva (FFL), and *A. eharai* is the OFL type (Chittenden and Saito 2001).

*Amblyseius eharai* (Amitai et Swirski) (Acari: Phytoseiidae) is a native species and most common in the early crop season in Korea (Kim et al. 2003). *A. eharai* is also native in Japan, China, Taiwan, and Malaysia (Ehara 2002). *A. eharai* had been misidentified to *A. newsami*, *A. cantonensis*, *A. deleoni*, or *A. largoensis* until 1980s (Waite and Gerson 1994). Then, Amitai and Swirski distinguished and classified *A. eharai* from

them through the difference of dorsal setae length (Amitai and Swirski 1981). *A. eharai* was known for a biological control agent of *Panonychus citri* (McGregor) (Acari: Tetranychidae) (Ji et al. 2013), which could damage citrus. *A. eharai* is also known for a biological control agent of spider mites in apple orchards in the early season (Kim et al. 2003). *A. eharai* prefers to glabrous leaves as a habitat (McMurtry et al. 2013) even though they are frequently found on various plants such as deciduous trees, conifers, shrubs, herbs and vines (Ryu et al. 1997). Moreover, *A. eharai* is the most abundant phytoseiid mites in Korea (Ryu et al. 1997) and may maintain their lives with their minor preys such as thrips, whiteflies, spider mites, rust mites, and so on (Waite and Gerson 1994, Kakimoto et al. 2004, Ji et al. 2013). Thus, *A. eharai* can be a good candidate as a biological control agent for controlling various pest species. However, no detailed ecological studies such as development and fecundity characteristics, life table at various temperature conditions and its functional response were not conducted before. These are important ecological characteristics for evaluating *A. eharai* as a biological control agent as well as for understating its population dynamics.

Thus, ecological characteristics of *A. eharai* were studied by using *Tetranychus urticae* (Koch) (Acari: Tetranychidae) as prey. First, development and fecundity of *A. eharai* were studied at different temperatures and its temperature-dependent development and oviposition

models were developed. Second, life table of *A. eharai* was constructed at various temperatures to analyze its population growth characteristics. Third, functional response of *A. eharai* was studied against larvae of *T. urticae*.



## **2. Temperature-dependent development and oviposition models of *Amblyseius eharai* (Amitai et Swirski) (Acari: Phytoseiidae)**

### **2-1. Introduction**

Population dynamics of insects and mites is significantly affected by temperature because it changes their behavior, development, survivorship, and fecundity (Bale et al. 2002, Crozier 2004). This is because they are ectotherms and thus their physiological function is determined by environmental temperature (Chapman 1982).

*Amblyseius eharai* is natural enemy of phytophagous insects and mites such as thrips, whiteflies, spider mites, and rust mites (Waite and Gerson 1994, Kakimoto et al. 2004, Ji et al. 2013). Temperature-dependent development and oviposition models are important to understand population dynamics of *A. eharai* in the agricultural crop systems because these two components are essential for the population model. In addition, by these models, we can estimate threshold temperature of development and fecundity, optimal temperature, and  $B_{80}$  which is operative thermal

range with over 80% performance of maximum (Lutterschmidt and Hutchison 1997).

In this part, temperature-dependent development and oviposition models of *A. eharai* were developed.

## **2-2. Materials and Methods**

### **2-2-1. Mite culture**

*A. eharai* were collected from overwintering grapevine buds in rainshield vineyards in Hwaseong, Korea in 2015. Rearing was started with 150 individuals of female *A. eharai*. To maintain vitality of the *A. eharai* colony, 30 ~ 50 individuals of wild *A. eharai*, which were also collected at the same vineyards in Hwaseong, were supplemented to the colony at 3 to 4 months interval. *A. eharai* were reared in petri dishes (93 mm diameter, 42 mm height, SPL Life Science, Pocheon-si, Korea) on which a water-saturated cotton pad was placed and excised kidney bean leaves were placed. Rearing condition was 26 ~ 28 °C, 60 ~ 80% RH and a photoperiod of 16:8 (L:D) h. Before the experiment began, at least 10 generations were cycled.

## 2-2-2. Development

For development experiments of *A. eharai*, 18 ~ 20 female *A. eharai* from the stock colony were randomly selected and transferred to 10 petri dishes each (93 mm diameter, 42 mm height) on which a water-saturated cotton pad was placed and then a kidney bean leaf disc (70 mm diameter) with *T. urticae* was placed on the cotton pad. Thus, total 180~200 females were prepared. Then, they were allowed to lay eggs for eight hours. Total twenty-five eggs were randomly collected from 10 dishes. The collected 25 eggs were transferred individually to 25 test petri dishes (50 mm diameter, 15 mm height, SPL Life Science, Pocheon-si, Korea) on which a water-saturated cotton pad was placed and a kidney bean leaf disc (35 mm diameter) with *T. urticae* was placed on the pad as prey. Thus, one egg was placed per dish. This procedure was executed two or three times for each temperature to meet the required number of eggs for experiment.

Development experiments were conducted in two sets. The first experiment was conducted at 5 temperatures (20.1, 24.0, 28.6, 32.0, and 35.9 °C). This experiment examined only development of immatures. The second experiment was conducted at 6 temperatures (18.0, 21.6, 24.1, 27.4, 30.2, 33.2 °C). This experiment examined development of immatures,

longevity of adults, and adult fecundity. In addition, the data were used for the life table analysis. Both experiments were conducted in incubators (HAN BAEK Scientific Technology, Bucheon-si, Korea) at 60 ~ 80% RH and a photoperiod of 16:8 (L:D) h. The initial sample size were 72, 41, 74, 47, 66, 67, 42, 70, 40, 57, and 50 individuals at 18.0, 20.1, 21.6, 24.0, 24.1, 27.4, 28.6, 30.2, 32.0, 33.2 and 35.9 °C, respectively. The temperature inside the incubator chambers was measured using a temperature logger (HOBO, OnSet Computer, Pocasset, MA, USA). Development and survivorship were checked every eight hours until completion of their development or deaths. The effect of temperatures on the development time was analyzed by the PROC GLM in SAS (SAS Institute 2013).

### **2-2-3. Oviposition**

Oviposition experiment was successively conducted from the second development experiment. Thus, examined temperatures were 18.0, 21.6, 24.1, 27.4, 30.2, and 33.2 °C at 60~80 % RH and a photoperiod of 16:8 (L:D) h. Newly molted female and male adults were transferred to petri dishes (50 mm diameter, 15 mm height) on which a water-saturated cotton was placed and a kidney bean leaf disc (35 mm) with *T. urticae* was placed

on it. In each petri dish, one female and one male adults were placed. When females or males were missing or dead, new individual was replenished. For replenishment, more than 30 eggs were reared individually at each temperature condition when the second development experiment was conducted. If the 8 hourly molted male and female numbers were not matched, then individual adults from the reared spawning petri dishes were added to match the numbers of male and female for mating. For all replaced or added adult individuals, their longevity and fecundity were not checked. Fecundity and survival of each adult individuals that were not replenished were checked every eight hours until they died. The effect of temperatures on longevity, pre-oviposition, oviposition, and post-oviposition periods, and fecundity of adults was analyzed by the PROC GLM in SAS (SAS Institute 2013).

## **2-2-4. Development and oviposition models**

### **Development rate model**

Development rates were expressed as reciprocals of development times (1/day) of each immature stage. Development rates of linear portion for each stage were fitted against temperature using TableCurve 2D

(SYSTAT Software Inc. 2002). The lower threshold temperatures for development of each stage were calculated as the  $x$ -intercept of the fitted equation for each stage (Arnold 1959). The equation is:

$$r(T) = aT + b \quad (\text{Equation 1})$$

where  $r(T)$  is the mean development rate at temperature  $T$  ( $^{\circ}\text{C}$ ).  $a$  and  $b$  are the parameters.

For construction of non-linear development rate model, development rates at each temperature were fitted against temperatures with the Briere1 model (Briere et al 1999) using TableCurve 2D (SYSTAT Software Inc. 2002):

$$r(T) = \alpha T(T - T_0)(T_L - T)^{1/2} \quad (\text{Equation 2})$$

where  $r(T)$  is the mean development rate at temperature  $T$  ( $^{\circ}\text{C}$ ).  $T_0$  is the lower threshold temperature, and  $T_L$  is the upper threshold temperature.  $\alpha$  is the parameter.  $B_{80}$  also was determined (Lutterschmidt and Hutchison 1997).

## Distribution model of development time

The variation in the development time of each immature stage was fitted with the two-parameter Weibull function (Wagner et al. 1984) against the physiological time ( $px$ ) using the cumulative proportion of daily transferred individuals from one stage to the next stage at a particular physiological time.

$$F(px) = 1 - \exp[-(px/\alpha)^\beta] \quad (\text{Equation 3})$$

where  $F(px)$  is the cumulative proportion of development completion at a physiological time  $px$ .  $\alpha$  and  $\beta$  are parameters. Parameter estimation was conducted using TableCurve 2D (SYSTAT Software Inc. 2002).

The physiological time ( $px$ ) of each stage was calculated by the rate summation method:

$$px = \sum_{i=1}^n r(T_i) \quad (\text{Equation 4})$$



where  $r(T_i)$  is the development rate at temperature  $T$  (°C) of  $i$ th day for a particular stage.

### **Fecundity model**

The mean total number of eggs laid per female was fitted against temperatures with an Extreme Value function (Kim and Lee 2003) using TableCurve 2D (SYSTAT Software Inc. 2002):

$$f(T) = a \exp\left[1 + \left(\frac{b - T}{k}\right) - \exp\left(\frac{b - T}{k}\right)\right] \quad (\text{Equation 5})$$

where  $f(T)$  is the total number of eggs laid by a female at temperature  $T$  (°C).  $a$  is the maximum fecundity of female individuals and  $b$  is the optimal temperature of fecundity,  $k$  is the parameter.

### **Adult longevity and physiological time**

Adult longevity was regarded as adult development, and thus the reciprocal of mean longevity (1/day) of adult *A. eharai* was used as adult

development rate, and fitted against temperature with a function from the library of TableCurve 2D (SYSTAT Software Inc. 2002):

$$r(T) = 1/(a + bT^2) \quad (\text{Equation 6})$$

where  $r(T)$  is the mean development rate at temperature  $T$  ( $^{\circ}\text{C}$ ).  $a$  and  $b$  are parameters. Parameter estimation was conducted by using TableCurve 2D (SYSTAT Software Inc. 2002). The physiological time of female adults was calculated by the rate summation method (eq. 4) using this model (eq. 6).

### **Age-specific cumulative oviposition rate model**

The cumulative oviposition rate was fitted against the adult physiological time by the three-parameter Weibull function (Wagner et al. 1984):

$$p(px) = 1 - \exp[-\{(px - \gamma)/\alpha\}^{\beta}] \quad (\text{Equation 7})$$

where  $p(px)$  is cumulative oviposition rate at a physiological time ( $px$ ) of a female adult.  $\gamma$ ,  $\alpha$ , and  $\beta$  are parameters. Parameter estimation was conducted by using TableCurve 2D (SYSTAT Software Inc. 2002).

### **Age-specific survival rate model**

The adult survival rate at a particular physiological time was calculated by dividing the number of adults alive at a given physiological time with the initial number of adults, and was fitted to the reverse sigmoid function:

$$S(px) = \exp[-\{(px - a)/b\}^c] \quad (\text{Equation 8})$$

where  $S(px)$  is adult survival rate at a physiological time ( $px$ ).  $a$ ,  $b$ , and  $c$  are parameters. Parameter estimation was conducted by using TableCurve 2D (SYSTAT Software Inc. 2002). Data of survival rate at 33.2 °C was excluded in model fitting because mortality occurred very high in early time and thus the shape was significantly different from those at other temperatures examined.

## Daily egg production

The number of eggs laid by an adult female at  $i$ th day was calculated with the oviposition model (Kim and Lee 2003):

$$f(T)[p(px_{i+1}) - p(px_i)][\{S(px_i) + S(px_{i+1})\}/2] \quad (\text{Equation 9})$$

## 2-3. Results

### 2-3-1. Development model

*A. eharai* successfully developed from eggs to adults at 18.0 ~ 33.2 °C (Table 1). Survival rates of each immature stages of *A. eharai* are presented in Table 2. No eggs survived at 35.9 °C, and all eggs survived at 20.1 and 24.0 °C. Low survival rate of total immature stage was observed at 18.0 and 33.2 °C, and was 55.56 and 38.60%, respectively. Development time was significantly different according to the temperature (egg,  $F_{9, 530} = 960.70$ ,  $P < 0.0001$ ; larva,  $F_{9, 481} = 96.46$ ,  $P < 0.0001$ ; protonymph,  $F_{9, 454} = 52.19$ ,  $P < 0.0001$ ; Deutonymph,  $F_{9, 437} = 89.42$ ,  $P < 0.0001$ ; total immature,  $F_{9, 437} = 387.04$ ,  $P < 0.0001$ ; total immature (female),  $F_{9, 243} = 237.17$ ,  $P < 0.0001$ ; total immature (male),  $F_{9, 193} = 160.20$ ,  $P < 0.0001$ ). Development time of the total immature stage was longest at 18.0 °C (14.84 days), and shortest at 30.2 °C (4.40 days).

Linear development relationship against temperature for each stage of *A. eharai* and estimates of model parameters are shown in Fig. 1 and Table 3, respectively. Non-linear development relationship against

temperature was well described by the Briere 1 model (Fig. 2). Estimates of model parameters are given in Table 4. Lower threshold, optimal, and upper threshold temperatures, and  $B_{80}$  are presented in Table 5. Lower threshold, optimal, and upper threshold temperatures of total immature stage were 13.2, 30.6, and 35.9 °C, respectively. Developmental variation model and estimates of model parameters for each stage are shown in Fig. 3, and Table 6, respectively.

**Table 1. Development times (days, mean  $\pm$  SEM) of immature stages of *Amblyseius eharai***

Temperature (°C)	Egg	Larva	Protonymph	Deutonymph	Total Immature	Total Immature (Female)	Total Immature (Male)
18.0 (n = 72)	4.31 $\pm$ 0.045a (n = 48)	5.05 $\pm$ 0.289a (n = 43)	3.15 $\pm$ 0.154a (n = 41)	2.43 $\pm$ 0.059a (n = 40)	14.84 $\pm$ 0.393a (n = 40)	14.54 $\pm$ 0.386a (n = 26)	15.40 $\pm$ 0.869a (n = 14)
20.1 (n = 41)	3.20 $\pm$ 0.052b (n = 41)	2.58 $\pm$ 0.193b (n = 35)	2.49 $\pm$ 0.121b (n = 32)	2.01 $\pm$ 0.036b (n = 31)	10.33 $\pm$ 0.211b (n = 31)	10.70 $\pm$ 0.247b (n = 18)	9.82 $\pm$ 0.330b (n = 13)
21.6 (n = 74)	2.85 $\pm$ 0.028c (n = 71)	2.17 $\pm$ 0.124b (n = 69)	2.13 $\pm$ 0.108bc (n = 69)	1.67 $\pm$ 0.073c (n = 69)	8.81 $\pm$ 0.174c (n = 69)	9.15 $\pm$ 0.279c (n = 39)	8.37 $\pm$ 0.138c (n = 30)
24.0 (n = 47)	2.13 $\pm$ 0.028d (n = 47)	1.51 $\pm$ 0.094c (n = 47)	1.52 $\pm$ 0.066cd (n = 45)	1.23 $\pm$ 0.028de (n = 44)	6.41 $\pm$ 0.090d (n = 44)	6.58 $\pm$ 0.097d (n = 26)	6.17 $\pm$ 0.155d (n = 18)
24.1 (n = 66)	2.22 $\pm$ 0.030d (n = 61)	1.65 $\pm$ 0.095c (n = 48)	1.85 $\pm$ 0.089c (n = 43)	1.39 $\pm$ 0.049d (n = 41)	7.10 $\pm$ 0.106d (n = 41)	7.18 $\pm$ 0.120d (n = 22)	7.00 $\pm$ 0.184de (n = 19)
27.4 (n = 67)	1.62 $\pm$ 0.018e (n = 66)	1.15 $\pm$ 0.053cd (n = 64)	1.26 $\pm$ 0.041d (n = 60)	1.02 $\pm$ 0.019ef (n = 60)	5.06 $\pm$ 0.062e (n = 60)	5.12 $\pm$ 0.093e (n = 33)	4.99 $\pm$ 0.076f (n = 27)
28.6 (n = 42)	1.41 $\pm$ 0.038f (n = 41)	0.85 $\pm$ 0.050d (n = 39)	1.15 $\pm$ 0.070d (n = 38)	1.04 $\pm$ 0.051ef (n = 38)	4.44 $\pm$ 0.099ef (n = 38)	4.40 $\pm$ 0.101e (n = 19)	4.47 $\pm$ 0.173f (n = 19)
30.2 (n = 70)	1.35 $\pm$ 0.026f (n = 66)	0.92 $\pm$ 0.040d (n = 63)	1.26 $\pm$ 0.055d (n = 60)	0.94 $\pm$ 0.025fg (n = 58)	4.40 $\pm$ 0.062f (n = 58)	4.50 $\pm$ 0.088e (n = 28)	4.31 $\pm$ 0.086f (n = 30)
32.0 (n = 40)	1.32 $\pm$ 0.023f (n = 38)	1.15 $\pm$ 0.070cd (n = 36)	1.10 $\pm$ 0.059d (n = 35)	0.98 $\pm$ 0.045eg (n = 35)	4.56 $\pm$ 0.112ef (n = 35)	4.67 $\pm$ 0.144e (n = 19)	4.44 $\pm$ 0.174f (n = 16)
33.2 (n = 57)	1.38 $\pm$ 0.021f (n = 52)	1.32 $\pm$ 0.065cd (n = 38)	1.31 $\pm$ 0.079d (n = 32)	1.26 $\pm$ 0.076de (n = 22)	4.97 $\pm$ 0.087ef (n = 22)	4.90 $\pm$ 0.081e (n = 14)	5.08 $\pm$ 0.197ef (n = 8)
35.9 (n = 50)	- (n = 50)	-	-	-	-	-	-

Means followed by the same letter within a column are not significantly different at  $\alpha=0.05$ , Tukey's studentized range test.

**Table 2. Survival rate (%) of each stages of *A. eharai* at different temperatures**

Temperature (°C)	Egg	Larva	Protonymph	Deutonymph	Total Immature
18.0 (n = 72)	66.67 (48 / 72)	89.58 (43 / 48)	95.35 (41 / 43)	97.56 (40 / 41)	55.56 (40 / 72)
20.1 (n = 41)	100 (41 / 41)	85.37 (35 / 41)	91.43 (32 / 35)	96.88 (31 / 32)	75.61 (31 / 41)
21.6 (n = 74)	95.95 (71 / 74)	97.18 (69 / 71)	100 (69 / 69)	100 (69 / 69)	93.24 (69 / 74)
24.0 (n = 47)	100 (47 / 47)	100 (47 / 47)	95.74 (45 / 47)	97.78 (44 / 45)	93.62 (44 / 47)
24.1 (n = 66)	92.42 (61 / 66)	78.69 (48 / 61)	89.58 (43 / 48)	95.35 (41 / 43)	62.12 (41 / 66)
27.4 (n = 67)	98.51 (66 / 67)	96.97 (64 / 66)	93.75 (60 / 64)	100 (60 / 60)	89.55 (60 / 67)
28.6 (n = 42)	97.62 (41 / 42)	95.12 (39 / 41)	97.44 (38 / 39)	100 (38 / 38)	90.48 (38 / 42)
30.2 (n = 70)	94.29 (66 / 70)	95.45 (63 / 66)	95.24 (60 / 63)	96.67 (58 / 60)	82.86 (58 / 70)
32.0 (n = 40)	95.00 (38 / 40)	94.74 (36 / 38)	97.22 (35 / 36)	100 (35 / 35)	87.50 (35 / 40)
33.2 (n = 57)	91.23 (52 / 57)	73.08 (38 / 52)	84.21 (32 / 38)	68.75 (22 / 32)	38.60 (22 / 57)
35.9 (n = 50)	0 (0 / 50)	-	-	-	-



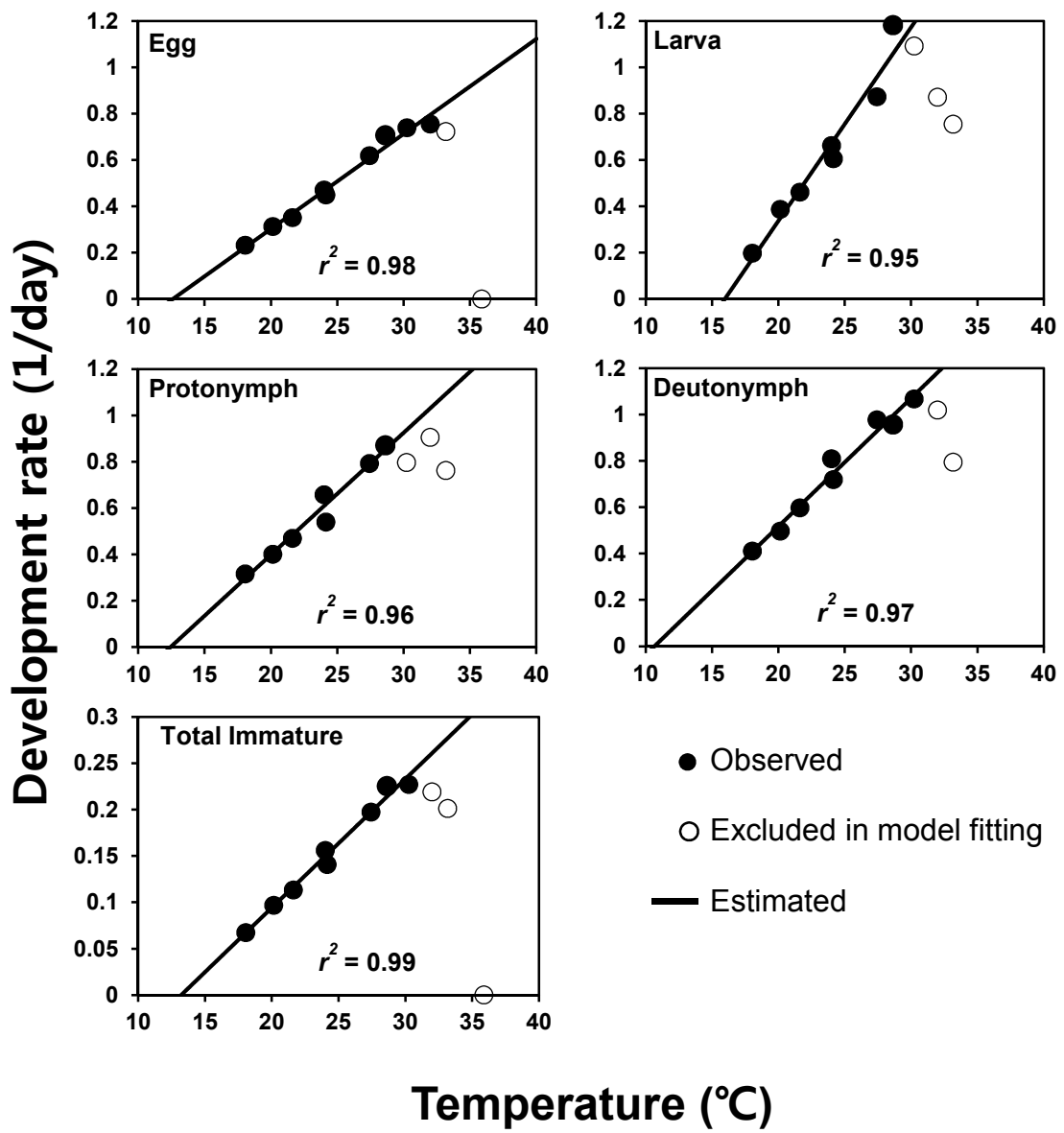


Fig. 1. Linear development rate model of *A. eharai*

**Table 3. Estimates of parameters of linear development rate model**

Stage	Parameters (Estimate $\pm$ SEM)	
	<i>a</i>	<i>b</i>
Egg	0.0410 $\pm$ 0.00207	-0.5156 $\pm$ 0.05276
Larva	0.0836 $\pm$ 0.00840	-1.3337 $\pm$ 0.19897
Protonymph	0.0527 $\pm$ 0.00462	-0.6547 $\pm$ 0.10947
Deutonymph	0.0554 $\pm$ 0.00376	-0.5897 $\pm$ 0.09237
Total Immature	0.0139 $\pm$ 0.00070	-0.1836 $\pm$ 0.01717

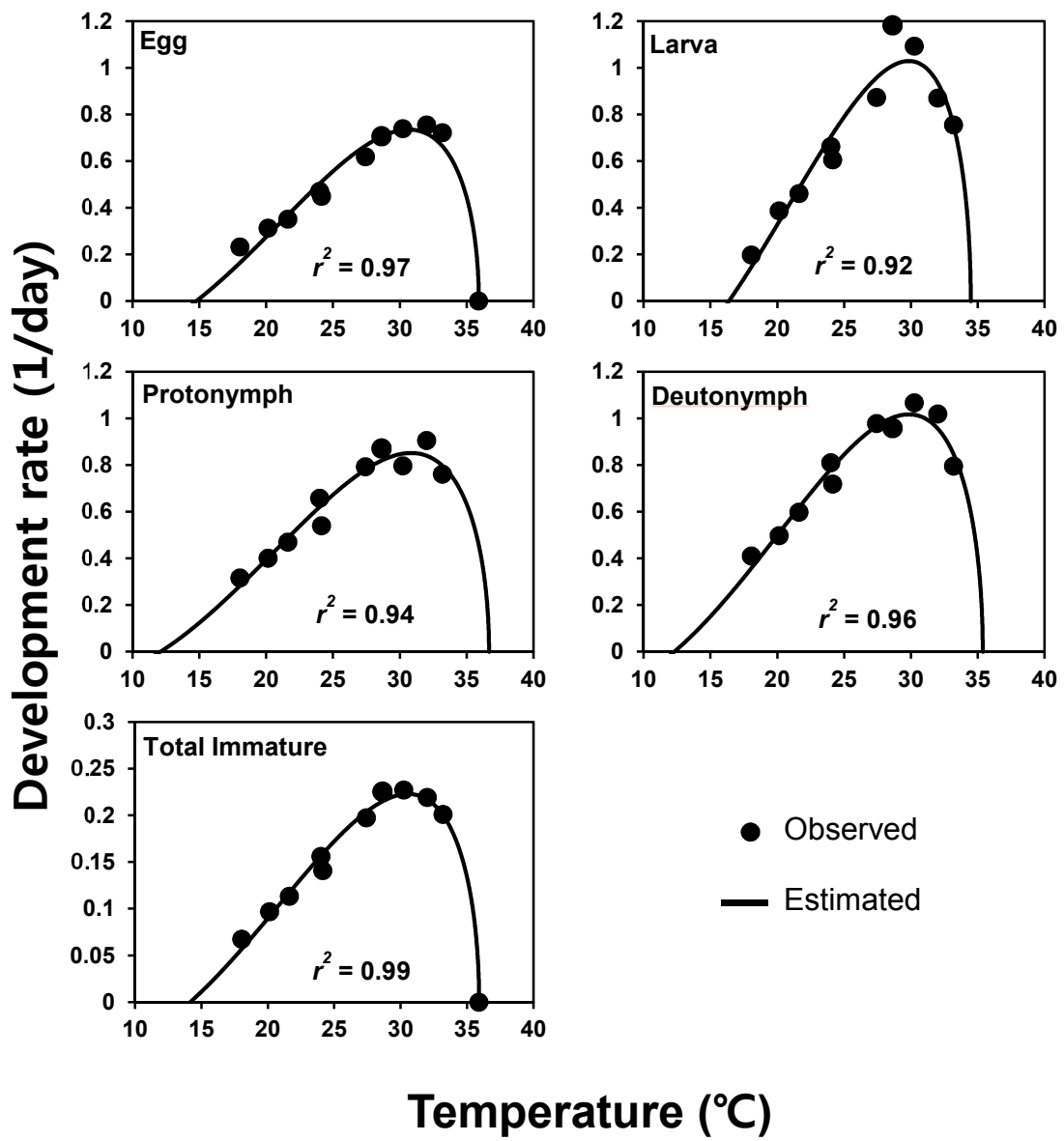


Fig. 2. Non-linear development rate model of *A. eharai*

**Table 4. Estimates of parameters of the non-linear development rate model**

Stage	Parameters (Estimate $\pm$ SEM)		
	$\alpha$	$T_0$	$T_L$
Egg	0.0007 $\pm$ 0.00004	14.7526 $\pm$ 0.75002	35.8900 $\pm$ 0.00136
Larva	0.0012 $\pm$ 0.00016	16.3650 $\pm$ 0.91591	34.4671 $\pm$ 0.45810
Protonymph	0.0006 $\pm$ 0.00011	12.0767 $\pm$ 1.63957	36.6620 $\pm$ 1.05299
Deutonymph	0.0008 $\pm$ 0.00010	12.2721 $\pm$ 1.15005	35.3528 $\pm$ 0.47943
Total Immature	0.0002 $\pm$ 0.00001	14.1353 $\pm$ 0.51310	35.8900 $\pm$ 0.00086

**Table 5. Threshold, optimal and  $B_{80}$  temperatures ( $^{\circ}\text{C}$ ) of development of immature stages of *A. eharai***

Stage	Lower threshold	Optimal	Upper threshold	$B_{80}$
Egg	12.6	30.7	35.9	25.7 ~ 34.0
Larva	16.0	29.8	34.5	25.5 ~ 32.8
Protonymph	12.4	30.8	36.7	25.2 ~ 34.6
Deutonymph	10.7	29.8	35.4	24.5 ~ 33.4
Total Immature	13.2	30.6	35.9	25.5 ~ 34.0

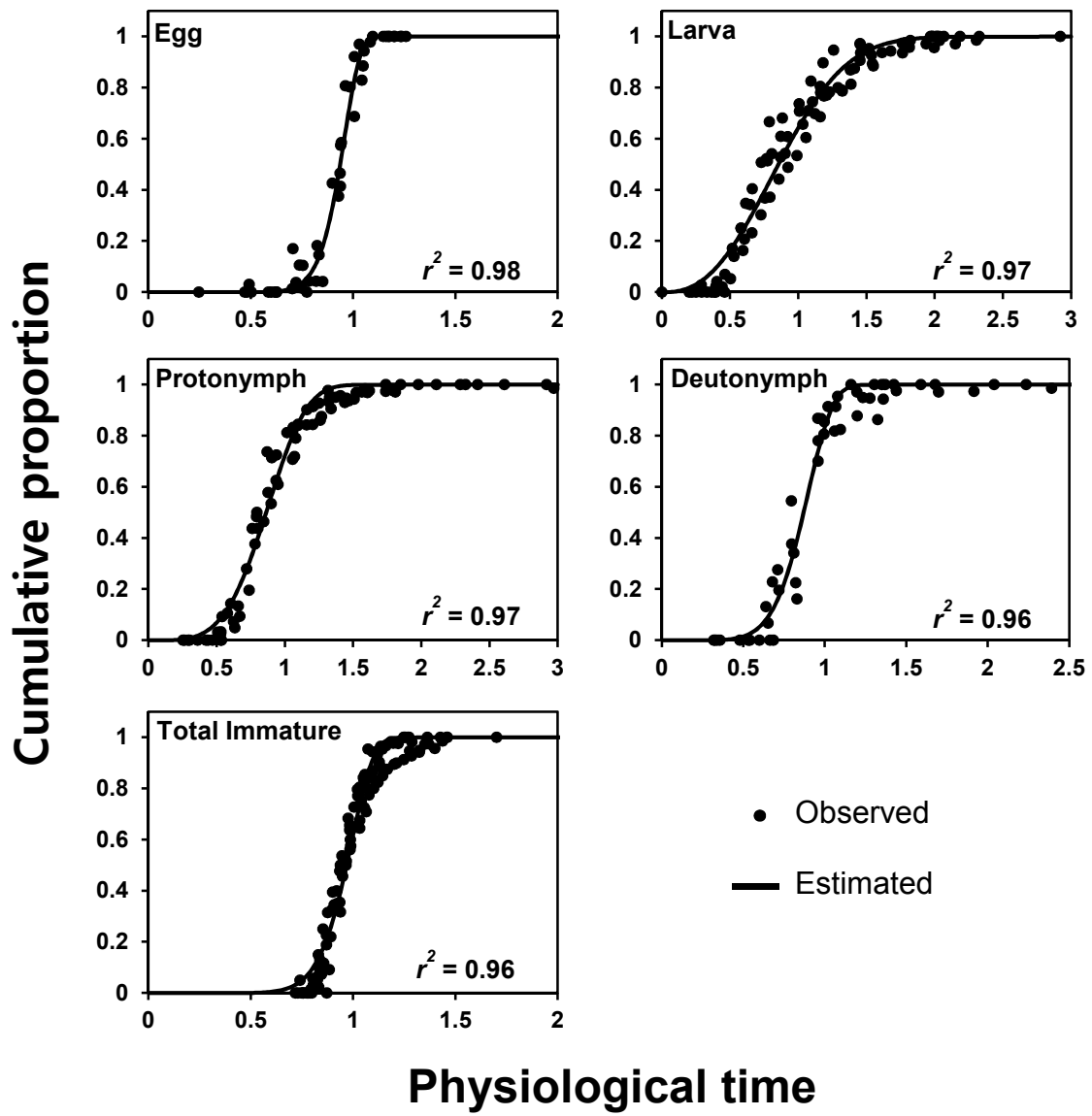


Fig. 3. Distribution model of development time of each stage of *A. eharai*

**Table 6. Estimates of parameters of distribution model of development time of *A. eharai***

Stage	Parameters (Estimate $\pm$ SEM)	
	$\alpha$	$\beta$
Egg	0.9621 $\pm$ 0.00416	13.0809 $\pm$ 1.02647
Larva	0.9869 $\pm$ 0.01196	2.5134 $\pm$ 0.10975
Protonymph	0.9414 $\pm$ 0.00853	4.1562 $\pm$ 0.20825
Deutonymph	0.9170 $\pm$ 0.00920	6.8172 $\pm$ 0.54998
Total Immature	1.0029 $\pm$ 0.00317	10.1467 $\pm$ 0.42688

## 2-3-2 Oviposition model

Mean adult longevity, oviposition periods, fecundity, and number of daily laid eggs of *A. eharai* at each temperature are given in Table 7. They were significantly affected by temperatures except for the post-oviposition period (adult longevity,  $F_{5, 198} = 41.11$ ,  $P < 0.0001$ ; adult longevity (female),  $F_{5, 114} = 22.44$ ,  $P < 0.0001$ ; adult longevity(male),  $F_{5, 83} = 20.76$ ,  $P < 0.0001$ ; pre-oviposition period,  $F_{4, 99} = 27.60$ ,  $P < 0.0001$ ; oviposition period,  $F_{4, 99} = 15.87$ ,  $P < 0.0001$ ; post-oviposition period,  $F_{4, 99} = 2.22$ ,  $P = 0.0728$ ; fecundity,  $F_{5, 114} = 26.02$ ,  $P < 0.0001$ ; number of daily laid eggs per female,  $F_{5, 114} = 43.76$ ,  $P < 0.0001$ ). Adult longevity decreased as temperature increased, and it decreased sharply above 30.2°C. Thus, it was longest at 18.0 °C (30.04 days), and shortest at 33.2 °C (3.73 days). Pre-oviposition period was 3.57 days at 18.0 °C, and 1.21 days at 27.4 °C. Oviposition period was 24.20 days at 18.0 °C, and 9.20 days at 30.2 °C. Fecundity was highest at 24.1 °C as 42.31 eggs, and no eggs were laid at 33.2 °C.

Components of the oviposition model of *A. eharai* (adult development rate, fecundity, age-specific cumulative oviposition rate, and age-specific survival rate) were well described by respective models (Figs. 4, 5, 6, 7, respectively; Table 8). Simulated daily egg production curve of *A.*



*eharai* in relation to adult age (days) and temperature (°C) was presented in Fig. 8. Highest daily reproduction was observed at 23 ~ 28 °C within 10 days.

**Table 7. Longevity, oviposition period and fecundity of *A. eharai* (mean  $\pm$  SEM)**

Temperature (°C)	Longevity (day)			Pre-oviposition period (day)	Oviposition period (day)	Post- oviposition period (day)	Fecundity (egg number)	Daily eggs per female
	Adult	Female	Male					
18.0	30.04 $\pm$ 2.725a (n = 28)	30.19 $\pm$ 3.567a (n = 19)	29.70 $\pm$ 4.183a (n = 9)	3.57 $\pm$ 0.174a (n = 18)	24.20 $\pm$ 2.734a (n = 18)	4.07 $\pm$ 1.278a (n = 18)	26.53 $\pm$ 2.841bc (n = 19)	0.87 $\pm$ 0.064a (n = 19)
21.6	29.76 $\pm$ 1.933a (n = 39)	31.38 $\pm$ 2.748a (n = 20)	28.05 $\pm$ 2.735a (n = 19)	2.40 $\pm$ 0.144b (n = 20)	22.85 $\pm$ 2.114a (n = 20)	6.13 $\pm$ 1.768a (n = 20)	36.40 $\pm$ 3.247ab (n = 20)	1.22 $\pm$ 0.079a (n = 20)
24.1	24.00 $\pm$ 1.463a (n = 28)	25.33 $\pm$ 1.791a (n = 16)	22.22 $\pm$ 2.432ab (n = 12)	1.52 $\pm$ 0.096c (n = 16)	19.65 $\pm$ 1.344a (n = 16)	4.17 $\pm$ 1.361a (n = 16)	42.31 $\pm$ 2.731a (n = 16)	1.73 $\pm$ 0.112b (n = 16)
27.4	16.28 $\pm$ 0.822b (n = 46)	15.41 $\pm$ 1.168b (n = 25)	17.30 $\pm$ 1.136b (n = 21)	1.21 $\pm$ 0.066cd (n = 24)	12.29 $\pm$ 1.109b (n = 24)	2.44 $\pm$ 0.639a (n = 24)	33.80 $\pm$ 3.057ab (n = 25)	2.15 $\pm$ 0.139b (n = 25)
30.2	10.61 $\pm$ 0.876bc (n = 37)	13.26 $\pm$ 0.597bc (n = 22)	6.73 $\pm$ 1.508c (n = 15)	2.08 $\pm$ 0.273bc (n = 22)	9.20 $\pm$ 0.793b (n = 22)	1.98 $\pm$ 0.393a (n = 22)	16.86 $\pm$ 1.653c (n = 22)	1.25 $\pm$ 0.104a (n = 22)
33.2	3.73 $\pm$ 0.709c (n = 21)	5.18 $\pm$ 0.936c (n = 13)	1.38 $\pm$ 0.231c (n = 8)	-	-	-	0d (n = 13)	0c (n = 13)

Means followed by the same letter within a column are not significantly different at  $\alpha=0.05$ , Tukey's studentized range test.

Daily eggs per female was fecundity divided by female longevity.

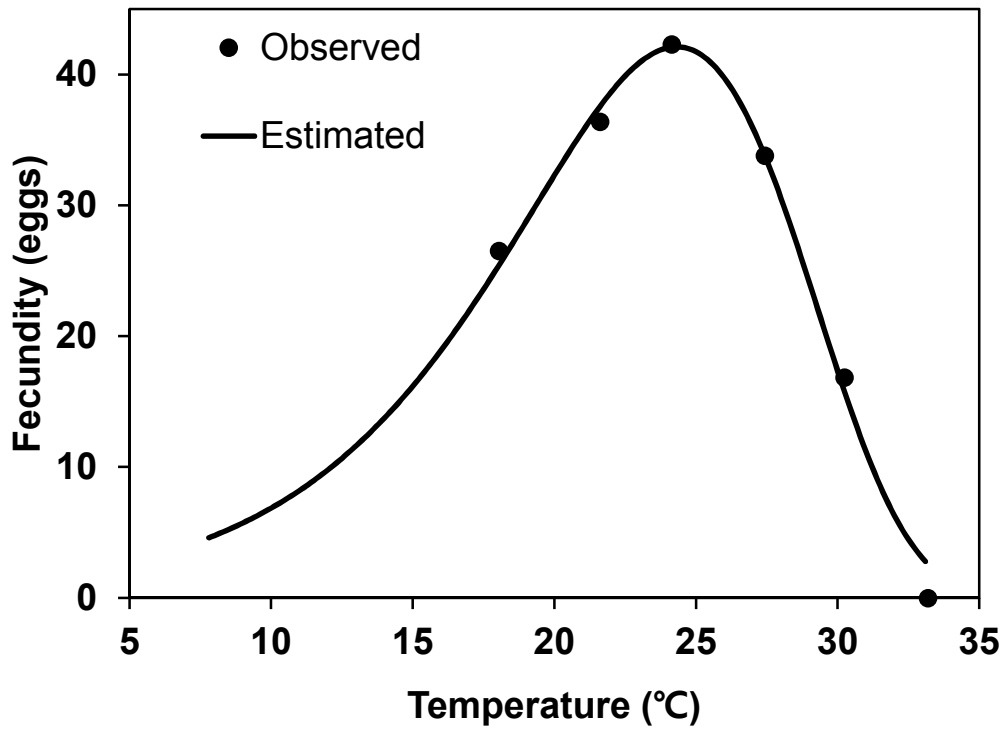


Fig. 4. Fecundity model of *A. eharai*

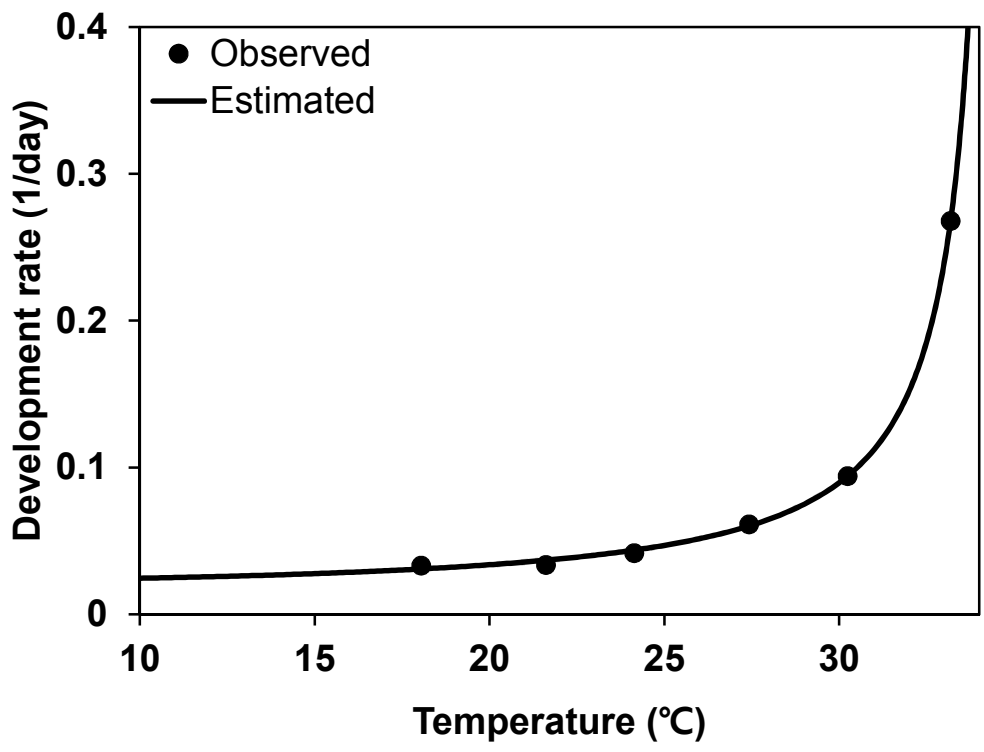


Fig. 5. Adult development rate model of *A. eharai*

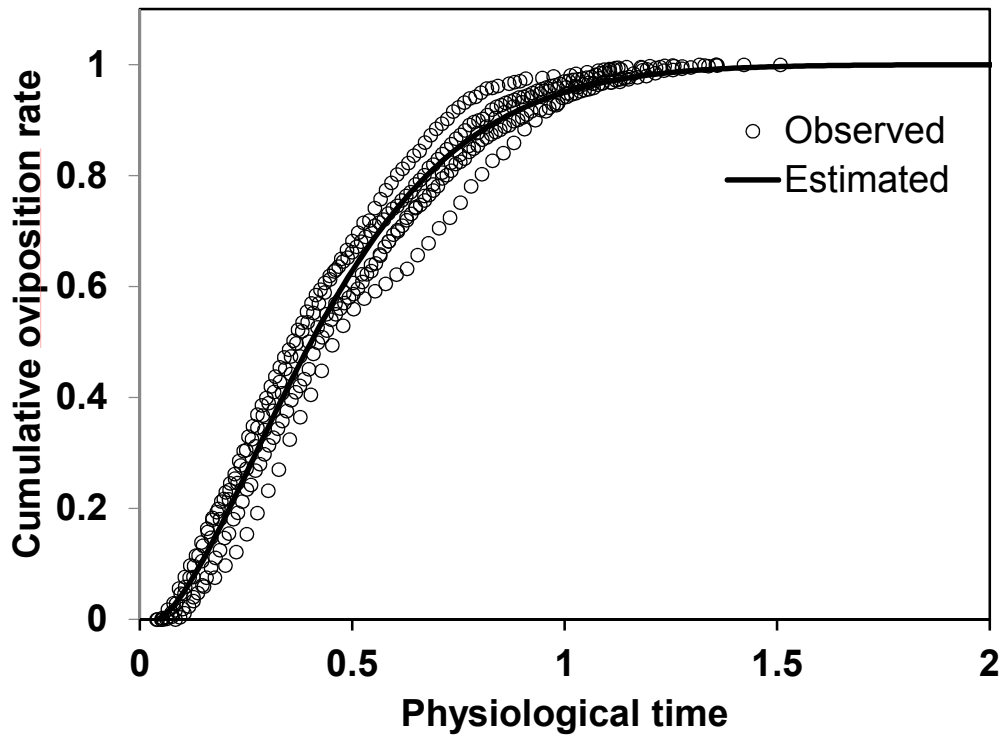


Fig. 6. Age-specific cumulative oviposition rate model of *A. eharai*

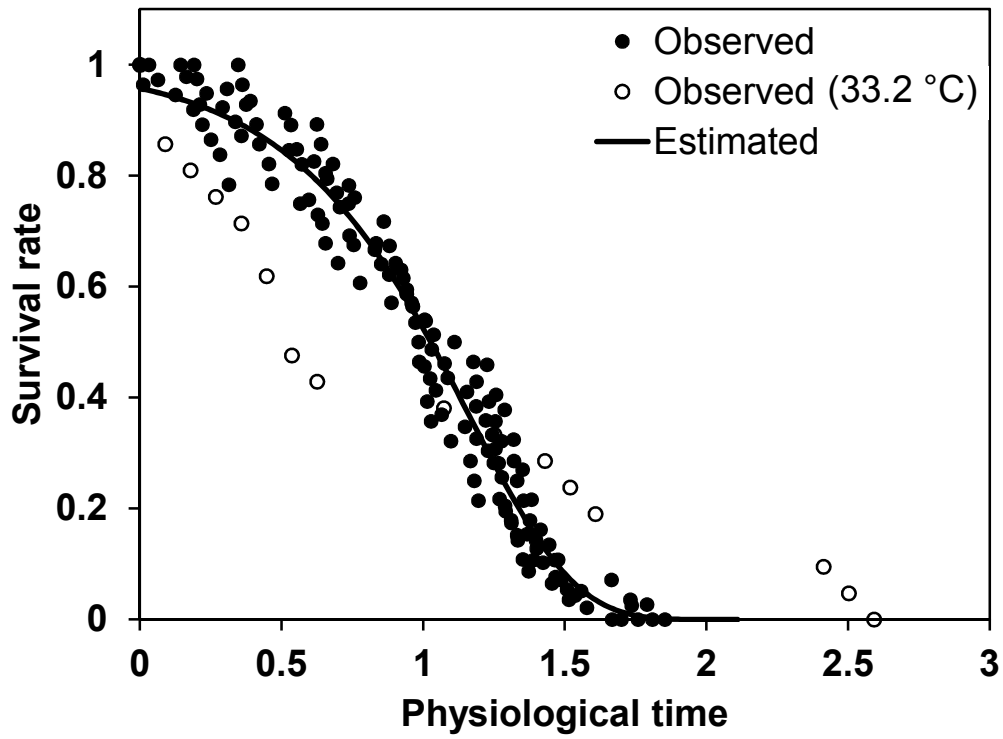
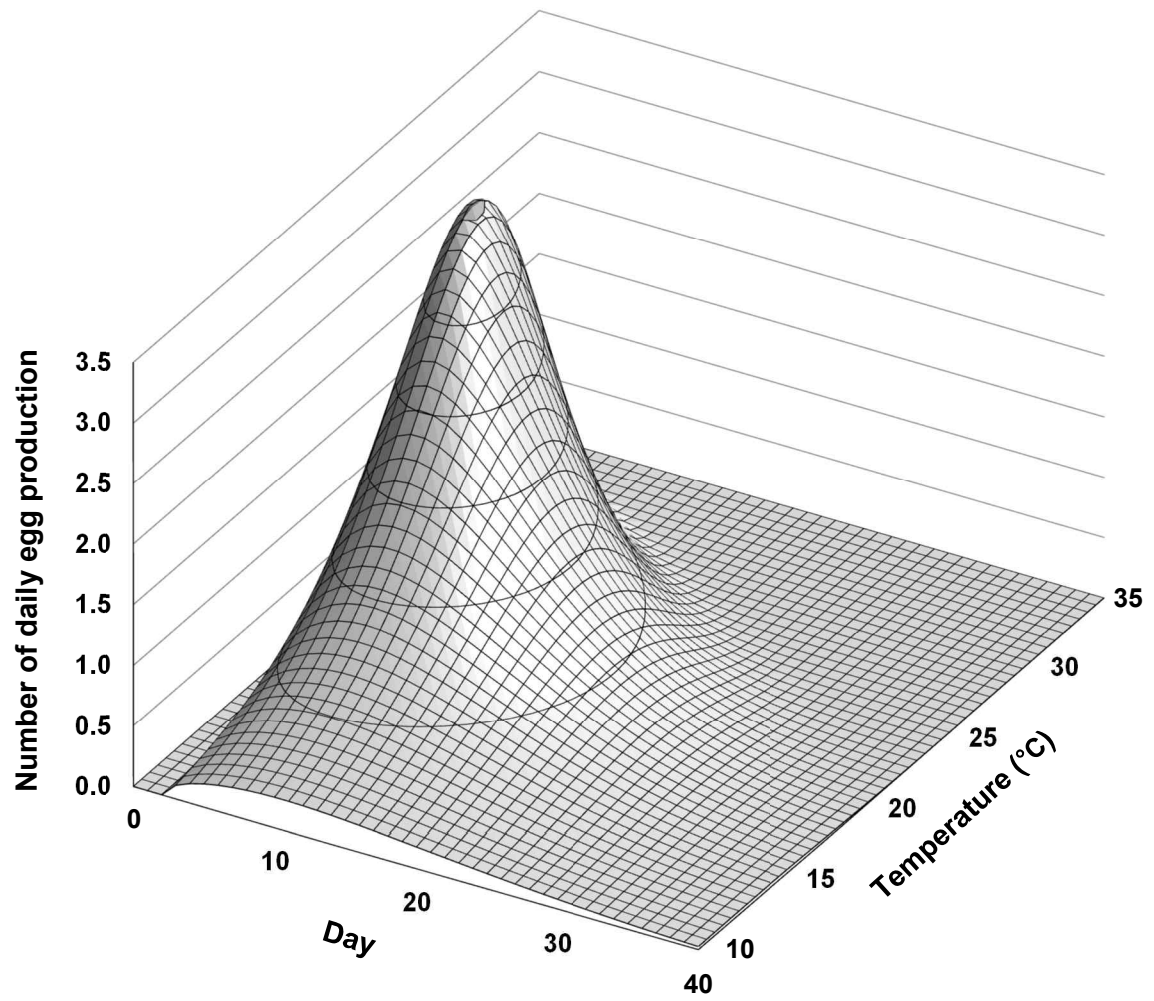


Fig. 7. Age-specific survival rate model of adult *A. eharai* (observed data of 33.2 °C was excluded for model fitting)

**Table 8. Estimates of parameters of oviposition models**

Models	Parameters	Estimate ( $\pm$ SEM)	$r^2$
Fecundity	<i>a</i>	42.1307 $\pm$ 1.36221	0.99
	<i>b</i>	24.3166 $\pm$ 0.24145	
	<i>k</i>	-5.2075 $\pm$ 0.28455	
Adult development rate	<i>a</i>	44.3108 $\pm$ 1.01863	0.99
	<i>b</i>	-0.0369 $\pm$ 0.00093	
Age-specific cumulative oviposition rate	$\gamma$	0.0385 $\pm$ 0.01065	0.98
	$\alpha$	0.4642 $\pm$ 0.01222	
	$\beta$	1.5083 $\pm$ 0.04834	
Age-specific survival rate	<i>a</i>	448.9095 $\pm$ 22.90661	0.97
	<i>b</i>	-447.7471 $\pm$ 22.91110	
	<i>c</i>	-1209.5671 $\pm$ 137.94086	



**Fig. 8. Predicted daily egg production curve of *A. eharai* in relation to age (day) and temperature**



## 2-4. Discussion

In larval stage, the lower development threshold temperature, 16.0 °C, was higher than other immature stage (egg, 12.6 °C; protonymph, 12.4 °C; deutonymph, 10.7 °C; total immature, 13.2 °C) and upper development threshold temperature, 34.5 °C, was lower than other immature stage (egg, 35.9 °C; protonymph, 36.7 °C; deutonymph, 35.4 °C; total immature, 35.9 °C). Thus, larval stage seems to be most susceptible to temperature. The optimal development temperature of total immature stage, 30.6 °C, was similar to other phytoseiid mites such as *Galendromus occidentalis* (Nesbitt) (Tanigoshi et al. 1975), *Neoseiulus fallacis* (Garman) (Kwon et al. 1998), *Iphiseius degenerans* (Berlese) (Tsoukanas et al. 2006), and it was lower than *N. californicus* that of which was 34.4 °C (Kim et al. 2009), and *N. womersleyi* that of which was 33 °C (Lee and Ahn 2000). Development time of *A. eharai* appeared to vary according to the prey species. For example, development time of *A. eharai* fed with *Panonychus citri* was 6.5 days at 25 °C. In this study, when fed on larval *T. urticae* estimation by using the development rate model at 25 °C was 5.8 days. Optimal and threshold temperature of development were compared

with *Tetranychus urticae* (Kim et al. 2001) and *Calepitrimerus vitis* (Walton et al. 2010) as prey. Their optimal temperatures were in range of  $B_{80}$  of *A. eharai* (*T. urticae*, 32.5 °C; *C. vitis*, 31.3 °C). Upper threshold temperature of *C. vitis*, 34.2 °C, was lower than that of *A. eharai*. Thus, *A. eharai* seems to be good biological agent of *T. urticae* and *C. vitis*.

*A. eharai* successfully laid eggs at temperature range of 18.0 ~ 30.2 °C. The optimal temperature of total fecundity was 24.3 °C, and it was similar to *N. californicus*, 25 °C (Kim et al. 2013), and it was lower than *N. womersleyi*, 32.1 °C (Lee and Ahn 2000). Other phytoseiid mites such as *N. womersleyi* (Lee and Ahn 2000), *A. swirskii* (Lee and Gillepie 2011) and *N. californicus* (Kim et al. 2013) successfully laid eggs over 33.2 °C. However, adult *A. eharai* showed high mortality within few days and no fecundity at 33.2 °C, this results was similar to *Euseius finlandicus* (Broufas and Koveos 2001). In this results, *A. eharai* might be not suitable at high temperature. It may be explanation about report of Kim et al. (2003) that *A. eharai* occurred at early season. Combined  $B_{80}$  range of development and fecundity was 25.5 ~ 27.4 °C. In this results, *A. eharai* seems to be suitable natural enemy for early and late crop seasons in Korea.

### **3. Age-stage, two-sex life table of *Amblyseius eharai* (Amitai et Swirski) (Acari: Phytoseiidae)**

#### **3-1. Introduction**

Life table is a useful tool for comparison of population potential at specific condition (Krebs 2009). Through the life table, we can predict the population dynamics for a target insect or mite at particular condition (Krebs 2009, Huang and Chi 2012). Moreover, it is possible to decide optimal conditions for population growth among various condition (Krebs 2009, Huang and Chi 2012). For insects and mites, a cohort life table is commonly employed (Jones and Parrella 1984, Abou-Setta and Childers 1987, Lee and Ahn 2000, Tsai and Wang 2001, Farhadi et al. 2011, Huang and Chi 2012).

A traditional life table is biased to females, and certain age-specific (Chi and Liu 1985, Chi 1988). However, males do not exist just for mating. Males can also damage plants in the pest species and feed on the prey in the predator species. Insects and mites have distinctive life stages through

molting. Each life stages may differ in biological traits (i.e., active stages such as instars and adults; inactive stages such as eggs or pupae) (Istock 1981, Carey 1993). Thus, traditional life table seems to insufficient for mites and insects (Chi and Liu 1985, Chi 1988).

In this study, age-stage, two-sex life table studies of *A. eharai* were conducted at different constant temperatures.

## **3-2. Materials and Methods**

### **3-2-1. Data**

Data for the life table analysis of *A. eharai* were obtained from the second experiment of the development of immatures and the oviposition experiment of adults in Chapter 2. Since the experimental procedure was described in detail in Chapter 2, here brief description is presented. Experimental conditions were six temperatures (18.0, 21.6, 24.1, 27.4, 30.2 and 33.2 °C) at 60 ~ 80% RH and a photoperiod of 16:8 (L:D) h. Development, survivorship, fecundity, oviposition period, and longevity of each individuals were observed from eggs to later stages until they died. In the life table analysis, the data of missed individuals during the adult stage was excluded.

### **3-2-2. Life table analysis**

Life table analysis was conducted using by TWSEX – MSChart (Chi 2016) that was based on age-stage, two-sex life table theory (Chi and Liu 1985, Chi 1988). The age-stage specific survival rate ( $S_{xj}$ ,  $x$  = age in days,  $j$  = stage), the age-stage specific fecundity ( $f_{xf}$ ,  $f$  = adult female stage), the age-stage specific reproductive value ( $v_{xj}$ ), the age specific survival rate ( $l_x$ ) and the age specific fecundity ( $m_x$ ) at each temperature were estimated. Population projection at each temperature was made using TIMING – MSChart (Chi 2008).

### **3-2-3. Population parameters**

The intrinsic rate of increase ( $r$ ), finite rate of increase ( $\lambda$ ), net reproductive rate ( $R_0$ ) and mean generation time ( $T$ ) were calculated. To calculate standard error of population parameters, the bootstrap method (100,000 times repeated) (Efron and Tibshirani 1993, Chi 2016) was used. To verify effects of temperature on population parameters, the paired

bootstrap test (Efron and Tibshirani 1993, Chi 2016) was conducted. All analyses were conducted by using TWOSEX – MSChart (Chi 2016).

### The intrinsic rate of increase ( $r$ )

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1 \quad (\text{Equation 10})$$

$$l_x = \sum_{j=1}^n S_{xj} \quad (\text{Equation 11})$$

$$m_x = \frac{\sum_{j=1}^k S_{xj} f_{xj}}{\sum_{j=1}^k S_{xj}} \quad (\text{Equation 12})$$

where  $x$  is age, and  $k$  is the number of stages.

### The finite rate of increase ( $\lambda$ )

$$\lambda = e^r \quad (\text{Equation 13})$$

**The net reproductive rate ( $R_0$ )**

$$R_0 = \sum_{x=0}^{\infty} l_x m_x \quad (\text{Equation 14})$$

**The mean generation time ( $T$ )**

$$T = (\ln R_0 / r) \quad (\text{Equation 15})$$



### 3-3. Results

Age-stage specific survival rates ( $S_{xj}$ ) at each temperature are presented in Fig. 9. The survival rates were expressed separately by stage and sex. Low survival rate was observed at 33.2 °C. Age-stage specific fecundity ( $f_{xf}$ ), age-specific survival rate ( $l_x$ ) and age-specific fecundity ( $m_x$ ) at each stage are given in Fig. 10. Fecundity showed a decreasing tendency with increasing age. Age-stage specific reproductive value ( $v_{xj}$ ), that indicates the effect of individuals of age  $x$  and stage  $j$  to future population, at each temperature are presented in Fig. 11. The value was high at young female and old-aged deutonymph. Population projections, population growth at age-stage specific, at each temperature are given in Fig. 12. Population growth rate at 27.4 °C was highest.

Population parameters and standard error are presented in Table 9. Estimates of population parameters were significantly different among temperatures at 95% confidential limit. The intrinsic rate of increase was highest at 27.4 °C as 0.2619 days<sup>-1</sup>, and lowest at 18.0 °C as 0.0792 days<sup>-1</sup>. The net reproductive rate was 16.55 eggs at 21.6 °C, and was 7.57 eggs at 30.2 °C. Mean generation time was longest at 18.0 °C as 26.86 days, and

shortest at 30.2 °C as 10.47 days. However, there was no significant difference between 27.4 °C, and 30.2 °C.

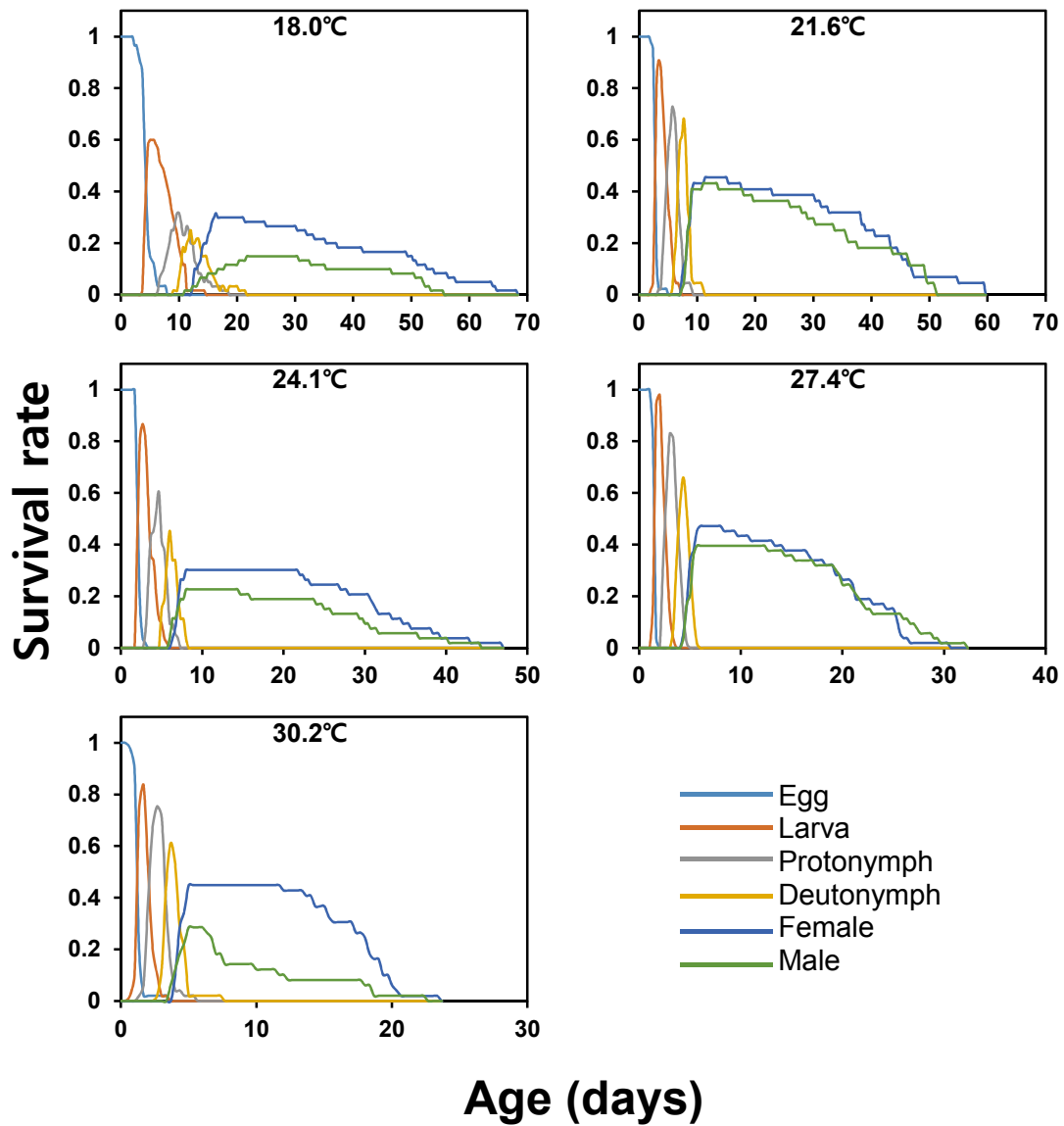


Fig. 9. Age-stage specific survival rate ( $S_{xj}$ ) of *A. eharai* at different temperatures

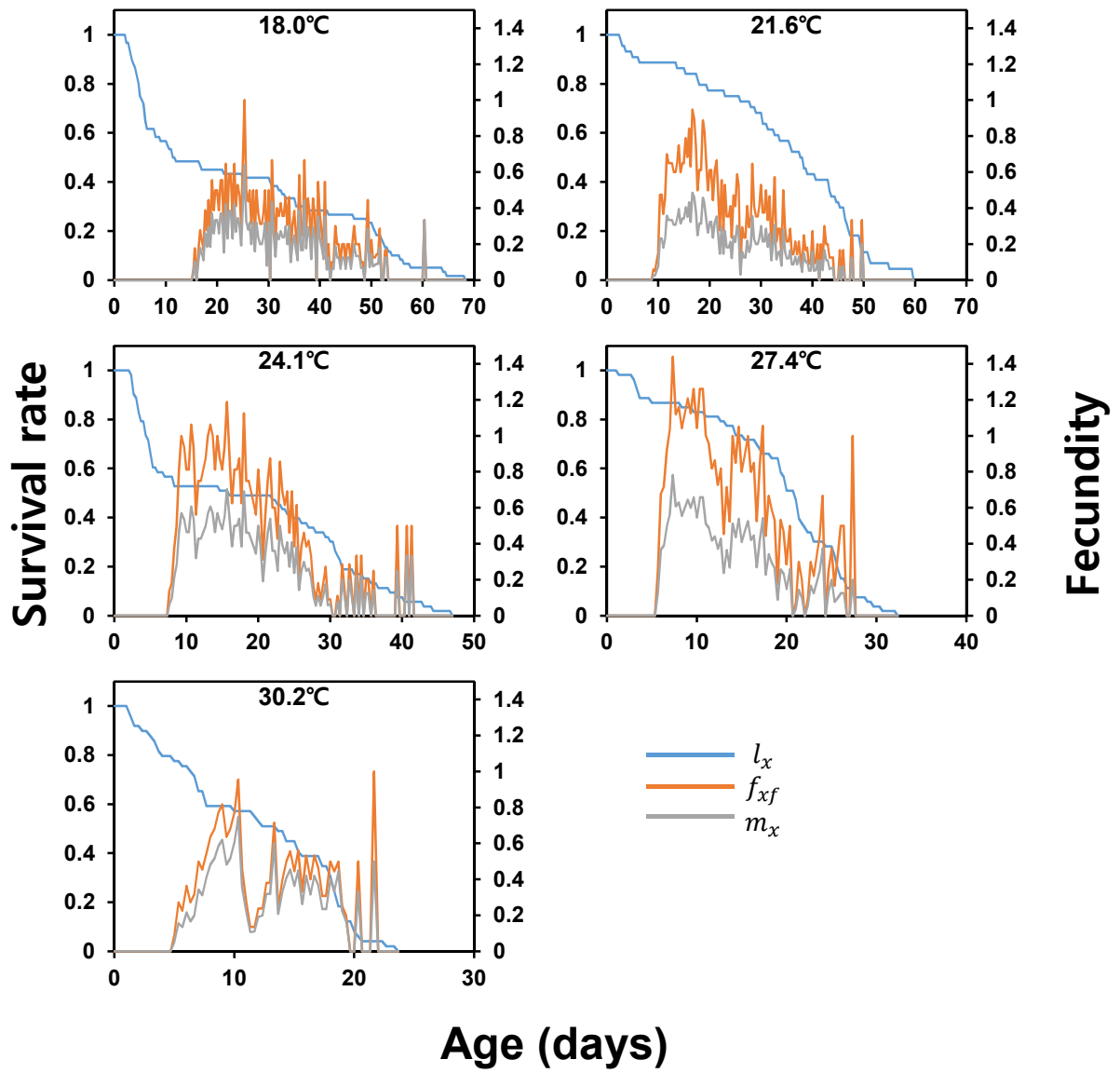


Fig. 10. Age-stage specific fecundity ( $f_{xf}$ ), age specific survival rate ( $l_x$ ) and fecundity ( $m_x$ ) of *A. eharai* at different temperatures

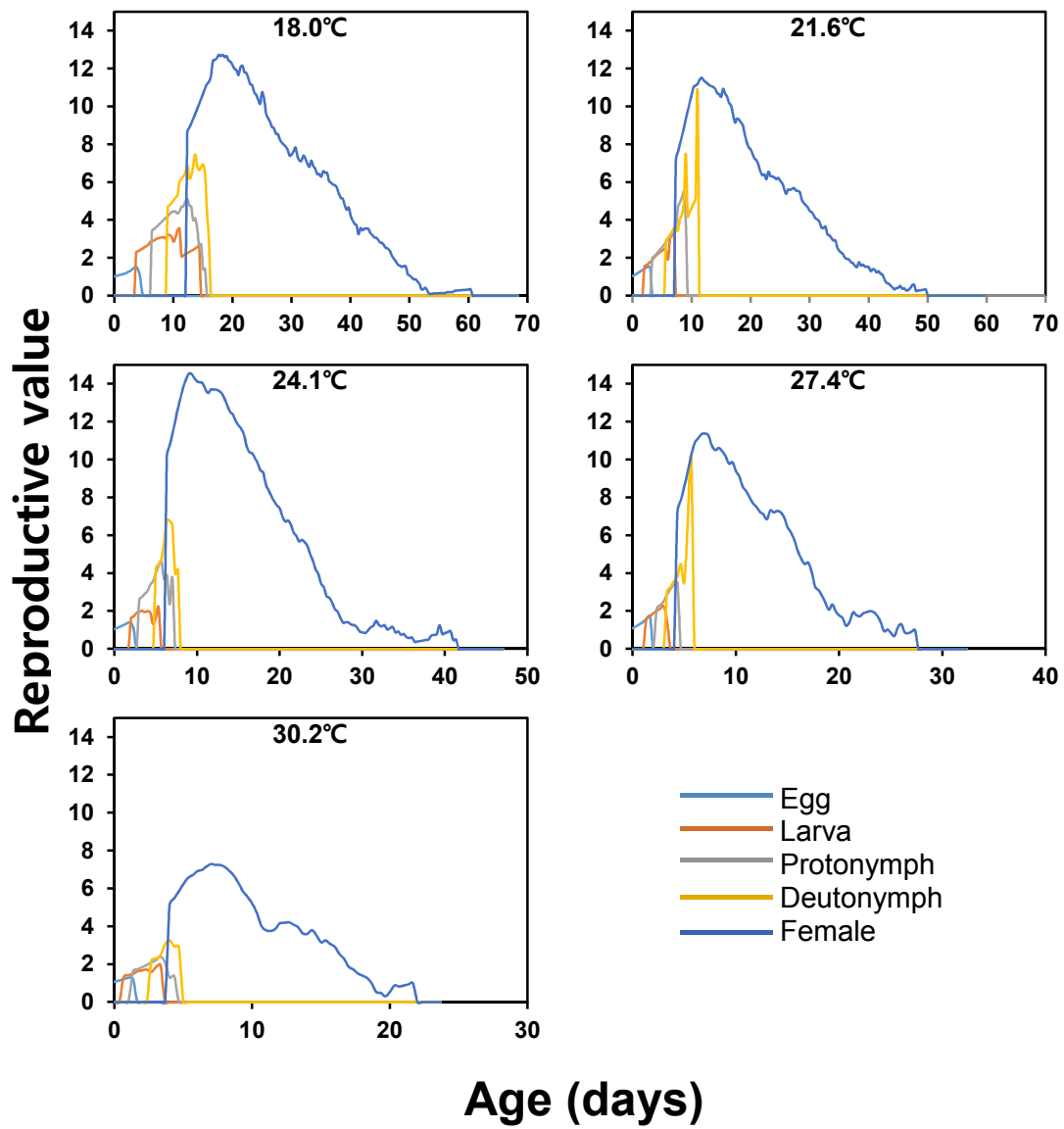


Fig. 11. Age-stage specific reproductive value ( $v_{xj}$ ) of *A. eharai* at different temperatures

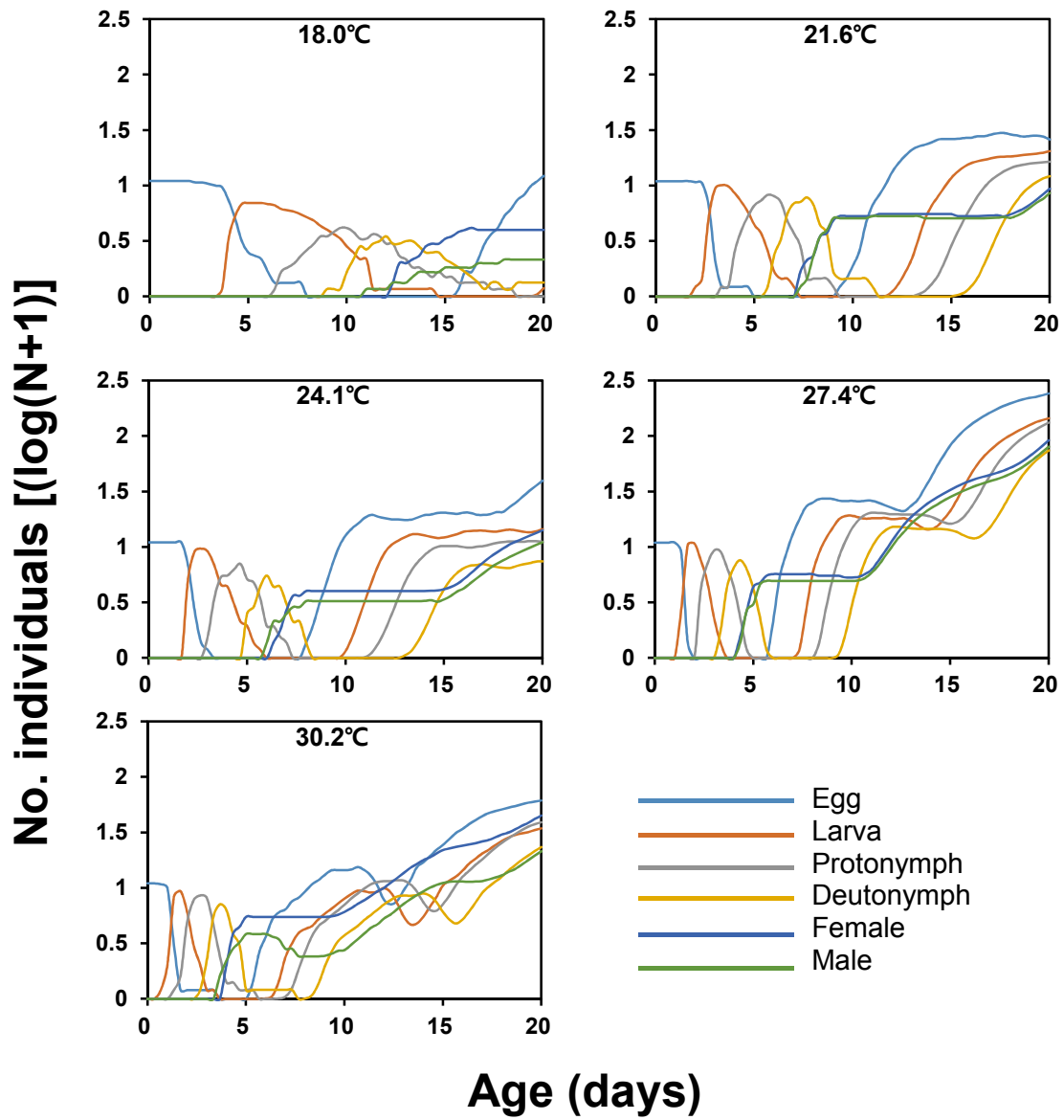


Fig. 12. Population projection of *A. eharai* of each stage at different temperatures

**Table 9. Estimates of population parameters of *A. eharai* (mean  $\pm$  SEM)**

Population parameters	18.0 °C	21.6 °C	24.1 °C	27.4 °C	30.2 °C
Intrinsic rate of increase ( $r$ )	0.0792 $\pm$ 0.00003c	0.1538 $\pm$ 0.00004b	0.1679 $\pm$ 0.00005b	0.2619 $\pm$ 0.00006a	0.1933 $\pm$ 0.00006b
Finite rate of increase ( $\lambda$ )	1.0825 $\pm$ 0.00003c	1.1663 $\pm$ 0.00004b	1.1828 $\pm$ 0.00006b	1.2994 $\pm$ 0.00007a	1.2133 $\pm$ 0.00008b
Net reproductive rate ( $R_0$ )	8.4 $\pm$ 0.006b	16.5 $\pm$ 0.010a	12.8 $\pm$ 0.009ab	15.9 $\pm$ 0.009a	7.6 $\pm$ 0.004b
Mean generation time ( $T$ )	26.9 $\pm$ 0.002a	18.2 $\pm$ 0.002b	15.2 $\pm$ 0.001c	10.6 $\pm$ 0.001d	10.5 $\pm$ 0.001d

Means followed by the same letter within a row are not significantly different at  $\alpha=0.05$ , Paired bootstrap test.

### 3-4. Discussion

In traditional life tables, stage and sex are ignored. In that case, some problems can be occurred. For example, when calculating  $m_x$ , some female individuals laid eggs at age  $x$ , but some individuals could be still in the pre-adult stage (Chi and Liu 1985, Chi 1988). Thus, it cannot correctly calculate the intrinsic rate of increase. In this study, the age-stage, two-sex life table theory (Chi and Liu 1985, Chi 1988) was applied. To calculate  $l_x$  and  $m_x$ , difference of stage and sex were considered.

Ji et al. (2013) constructed the life table of *A. eharai* at 25 °C using *Panonychus citri* as prey. The intrinsic rate of increase from Ji et al. (2013) was 0.1711. In the present study, the similar value was at 24.1 °C as 0.1679. The difference could be due to various factors such as different prey species and life stages of prey used.

The mean generation time of *A. eharai* decreased with increasing temperature. The intrinsic rate of increase was highest at 27.4 °C, and then decreased above 27.4 °C. This indicates that *A. eharai* may not be proper to control pests during the high temperature season or in the high temperature region. Using the population parameter of *A. eharai* at each



temperature, we can estimate the future population size. Estimated future population size can apply to decision the condition for mass-rearing. Thus, 27.4 °C is recommended for mass-rearing temperature.

In comparison with the intrinsic rate of *N. womersleyi* (Lee and Ahn 2000), which is a commercialized native phytoseiid mite against *T. urticae* (Fig. 13), similar rate was observed at medium temperature range (24 ~ 27 °C). At high temperature, the intrinsic rate of *N. womersleyi* increased until 33 °C and could be calculated until 38 °C. At low temperature (below 24.0 °C), the intrinsic rate of *A. eharai* was slightly higher than that of *N. womersleyi*. *A. eharai* could be a more effective biological agent against *T. urticae* than *N. womersleyi* at low temperature conditions. *A. eharai* might be a good candidate as a native natural enemy in early or late crop seasons, and low temperature cultivation farm lands.

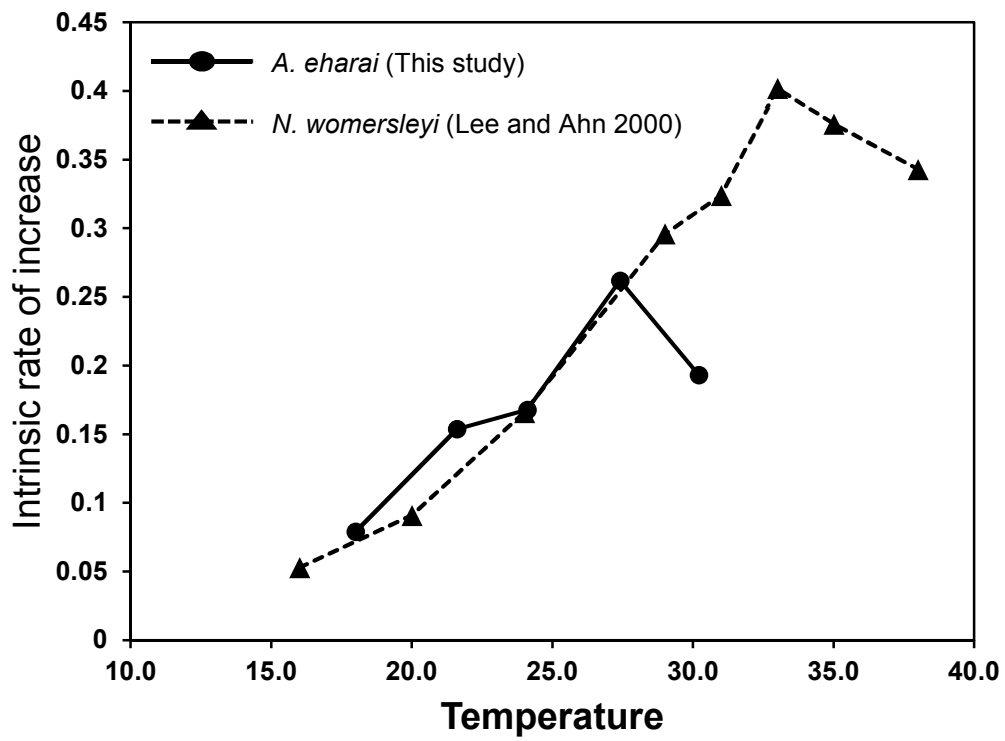


Fig. 13. Comparison of the intrinsic rate of increase of *N. womersleyi* and *A. eharai*

## **4. Functional response of *Amblyseius eharai* (Amitai et Swirski) (Acari: Phytoseiidae) to larval *Tetranychus urticae* (Koch) (Acari: Tetranychidae)**

### **4-1. Introduction**

*T. urticae* is one of most notorious pests in agricultural and ornamental systems (Hussey and Parr 1963, van de Vrie et al. 1972, Raworth 1986, Kim et al. 2001, Khanjani 2005, Lim et al. 2008). For controlling *T. urticae*, use of predatory mites has been continuously increasing (Port and Scopes 1981, Cross 1984, Nihoul et al. 1991, Greco et al. 1999, Opit et al. 2004, Fitzgerald et al. 2007).

Predation ability of predators can be altered by environmental factors and prey densities, and is frequently evaluated as functional responses (Krebs 2009). The functional response is a relationship between predation rates of single predator and different prey densities per unit time (Solomon 1949). Predation amount, attack rate, and handling time, that are estimated by functional response analysis (Juliano 2001), are basic information for evaluation of biological agents (Price 1997, Price et al. 2011,

Seiedy et al. 2012).

There has been only one study (Kakimoto et al. 2004), related with predation abilities of *A. eharai*, in which thrips were used as a prey. However, Kakimoto et al. (2004) did not reveal all important parameters in the functional responses of *A. eharai*. Thus, in this study, the feeding abilities of adult *A. eharai* were studied according to different densities of *T. urticae* to estimate important parameters related with the functional responses of *A. eharai*.

## **4-2. Materials and Methods**

### **4-2-1. Experiments**

To obtain same aged adult females and males of *A. eharai*, 60 eggs were randomly selected from the stock colony at each test group (2 preference test group, 5 different prey density group). Randomly selected eggs were transferred to petri dishes (90 mm diameter, 42 mm height, SPL Life Science, Pocheon-si, Korea) on which a water-saturated cotton pad was placed and a kidney bean leaf disc (70 mm diameter) with *T. urticae* was placed on the pad as prey. Development of these eggs was observed every day. Newly molted adults were transferred to new petri dishes and they were allowed to mate and consume prey for 3 days. After 3 days, they were transferred to petri dishes with no prey for starvation. Adults starved during 24 hours were used for tests.

Before the functional response experiments, a preference test between eggs and larvae of *T. urticae* was conducted, and the life-stage of *T. urticae* as a prey was determined. Prey preference and functional response test were conducted at petri dishes (50 mm diameter, 15 mm height, SPL Life Science, Pocheon-si, Korea) on which a water-saturated

cotton pad was placed and a kidney bean leaf disc (35 mm diameter) with *T. urticae* was placed on the pad as prey. Environmental conditions are 26.4 °C, 60 ~ 80% RH, and a photoperiod of 16:8 (L:D) h. The temperature and relative humidity inside the incubator chambers were measured using a temperature logger (HOBO, OnSet Computer, Pocasset, MA, USA). Starved adults *A. eharai* were allowed to feed on prey for 24 hours. Prey preference test of *A. eharai* was conducted between eggs and larvae of *T. urticae*. In the experiment 1, on separate petri dishes, 50 eggs or 50 larvae of *T. urticae* were transferred by using brush, and number of prey consumed by female *A. eharai* was observed. Ten replications were conducted for experiment 1. In the experiment 2, on the same petri dishes, 25 eggs and 25 larvae of *T. urticae* were transferred by using brush, and numbers of prey consumed by adult *A. eharai* was observed. Eleven replications for females, and ten replications for males were conducted in the experiment 2.

Since *A. eharai* preferred larval *T. urticae* in the preference test, functional response experiments for female and male *A. eharai* were conducted with larvae of *T. urticae*. Treated prey densities were 10, 30, 50, 70, and 130 larvae. Ten to twelve replications were conducted for each treatment. Number of consumed prey was checked.

## 4-2-2. Data analysis

To determine preference of *A. eharai* to prey life-stages and effects of prey densities on predation amount, ANOVA test was conducted by using PROC GLM in SAS (SAS Institute 2013).

Functional response was analyzed in two steps according to Juliano (2001) by using PROC GENMOD in SAS (SAS Institute 2013). To determine the shape of the functional response, a logistic regression was conducted. The equation is:

$$\frac{N_e}{N_0} = \frac{\exp(P_0 + P_1 N_0 + P_2 N_0^2 + P_3 N_0^3)}{1 + \exp(P_0 + P_1 N_0 + P_2 N_0^2 + P_3 N_0^3)} \quad (\text{Equation 16})$$

where  $N_e$  is the number of preys consumed per predator,  $N_0$  is the initial prey number,  $N_e/N_0$  is the probability of being consumed.  $P_0$ ,  $P_1$ ,  $P_2$  and  $P_3$  are parameters. Maximum-likelihood estimates of parameters  $P_0$  to  $P_3$  was obtained by using the logistic regression. The parameter of logistic model was evaluated by log likelihood test and it determined the type of functional response. If  $P_1 < 0$ , it describes a type two functional response. If  $P_1 > 0$  and  $P_2 < 0$ , it describes a type three functional response (Juliano 2001). Values of  $P_1$  of female and male *A. eharai* in this study were negative. Thus, random

predator equation (Rogers 1972) was used to present the type two functional response. The equation is:

$$N_e = N_0[1 - \exp(\alpha T_h N_e - \alpha T)] \quad (\text{Equation 17})$$

where  $N_e$  is the number of prey consumed per predator during test period  $T$  (24 h),  $N_0$  is the initial number of the prey,  $\alpha$  is the attack rate and  $T_h$  is the handling time of predator. The attack rate and handling time between male and female were compared at 95% confidence interval.



### 4-3. Results

Female *A. eharai* consumed significantly more number of larvae than eggs of *T. urticae* ( $T_{18} = 4.71$ ,  $P = 0.0002$ ) (Table 10), and both female and male adult *A. eharai* appeared to prefer larvae (female,  $T_{20} = 2.52$ ,  $P = 0.0204$ ; male,  $T_{18} = 2.16$ ,  $P = 0.0447$ ) (Table 11).

The number of consumed larvae of *T. urticae* per adult *A. eharai* at different larval densities is shown in Table 12. The consumed prey number was significantly different among prey densities (female,  $F_{4, 51} = 90.73$ ,  $P < 0.0001$ ; male,  $F_{4, 52} = 24.37$ ,  $P < 0.0001$ ). Female consumed significantly more larvae of *T. urticae* than male at all larval density levels (10 larvae,  $T_{19} = 4.15$ ,  $P = 0.0005$ ; 30 larvae,  $T_{19} = 17.52$ ,  $P < 0.0001$ ; 50 larvae,  $T_{20} = 16.19$ ,  $P < 0.0001$ ; 70 larvae,  $T_{18} = 10.69$ ,  $P < 0.0001$ ; 130 larvae,  $T_{19} = 6.90$ ,  $P < 0.0001$ ). Maximum likelihood estimates from logistic regression are presented in Table 13. Values of  $P_1$  of female and male adult *A. eharai* were negative, indicating type II functional response. The functional response curves of female and male, and parameter estimates are presented in Figs. 14 and 15, and Table 14, respectively. The attack rate ( $\alpha$ ) of female was 0.109 and male was 0.019. The handling time ( $T_h$ ) of female was 0.164 h and male was 0.234 h. The attack rate ( $\alpha$ ) was significantly different but

handling time ( $T_h$ ) was not different between males and females at 95% confidence level.

**Table 10. Comparison of consumed eggs and larvae number ( $\pm$  SEM) by female *A. eharai* at 50 initial density**

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Eggs	Larvae
$26.9 \pm 2.29a$ (n = 10)	$39.6 \pm 1.43b$ (n = 10)

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Means followed by the same letter within a row are not significantly different at  $\alpha=0.05$

**Table 11. Comparison of consumed eggs and larvae number ( $\pm$  SEM) by adult *A. eharai* at 25 eggs and 25 larvae**

Sex	Eggs	Larvae
Female (n = 11)	19.1 $\pm$ 1.30a	22.7 $\pm$ 0.62b
Male (n = 10)	7.8 $\pm$ 1.19a	11.8 $\pm$ 1.42b

Means followed by the same letter within a column are not significantly different at  $\alpha=0.05$

**Table 12. Number ( $\pm$  SEM) of larval *T. urticae* consumed by adult *A. eharai***

Prey density	Female	Male
10	9.4 $\pm$ 0.20a* A** (n = 11)	6.1 $\pm$ 0.80a B (n = 10)
30	26.7 $\pm$ 0.30b A (n = 11)	12.4 $\pm$ 0.79ab B (n = 10)
50	39.6 $\pm$ 1.43c A (n = 10)	13.0 $\pm$ 0.91ab B (n = 12)
70	58.1 $\pm$ 2.74d A (n = 10)	21.2 $\pm$ 2.10b B (n = 10)
130	85.5 $\pm$ 6.47e A (n = 10)	33.9 $\pm$ 4.04c B (n=11)

\* mean separation by prey density at 95% confidence level, Tukey's studentized range test.

\*\* mean separation by sex at 95% confidence level.

**Table 13. Maximum likelihood estimates ( $\pm$  SEM) from logistic regression of the proportion of *T. urticae* larvae consumed by adult *A. eharai* as a function of initial prey densities**

Sex	Parameters	Estimated values	$\chi^2$	P
Female	P <sub>0</sub>	4.179 $\pm$ 0.7199	33.7	< 0.0001
	P <sub>1</sub>	-0.124 $\pm$ 0.0387	10.23	0.0014
	P <sub>2</sub>	0.002 $\pm$ 0.0006	8.63	0.0033
	P <sub>3</sub>	-8.1E-06 $\pm$ 2.76E-06	8.66	0.0033
Male	P <sub>0</sub>	1.510 $\pm$ 0.3619	17.4	< 0.0001
	P <sub>1</sub>	-0.105 $\pm$ 0.0216	23.73	< 0.0001
	P <sub>2</sub>	0.001 $\pm$ 0.0004	15.24	< 0.0001
	P <sub>3</sub>	-6.0E-06 $\pm$ 1.72E-06	12.03	0.0005

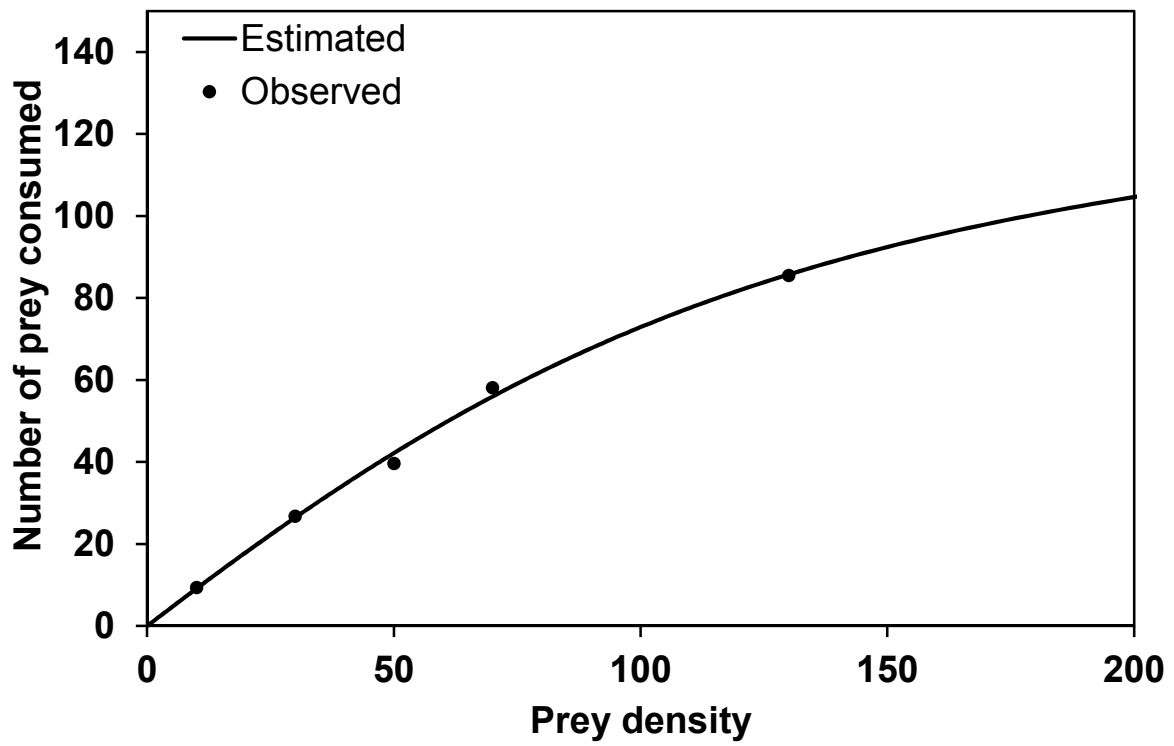


Fig. 14. The functional response of female *A. eharai* to *T. urticae* larvae on 35 mm leaf disc for 24 hours

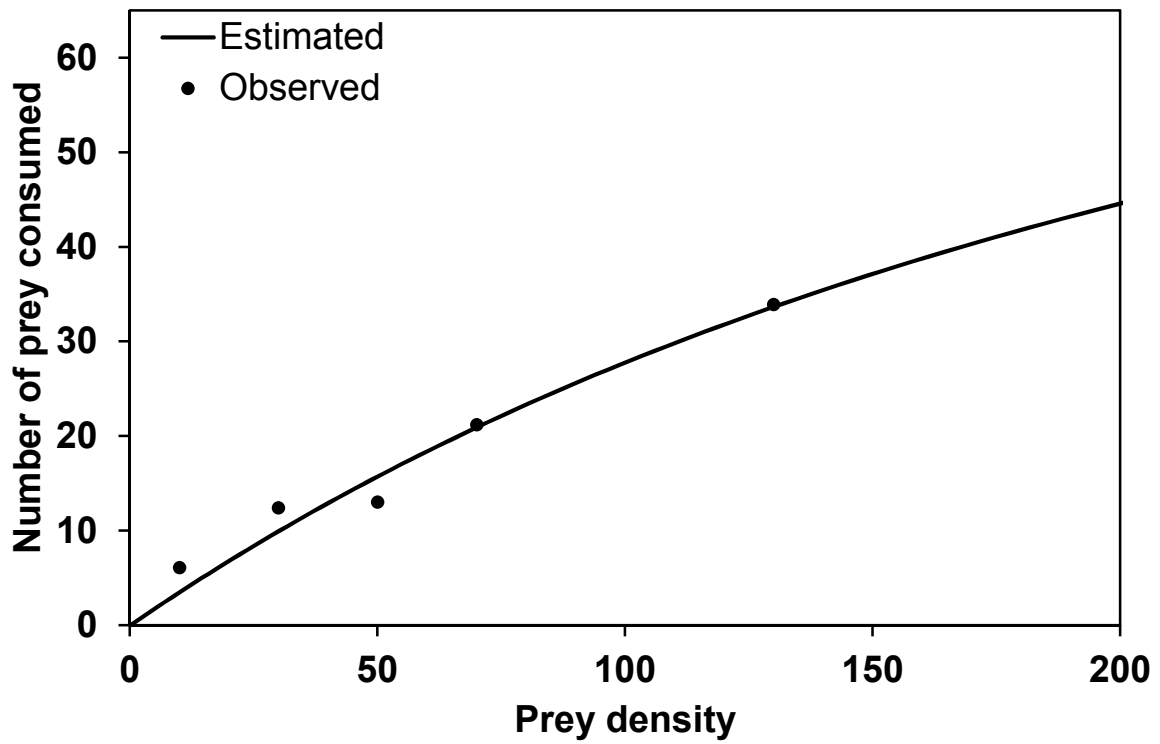


Fig. 15. The functional response of male *A. eharai* to *T. urticae* larvae on 35 mm leaf disc for 24 hours



**Table 14. Parameter estimates ( $\pm$  SEM) of the random predator equation for *A. eharai* preying on *T. urticae* larvae at different prey densities**

Sex	Attack rate ( $\alpha$ )	Handling time ( $T_h$ )	$r^2$	P
Female	0.109 $\pm$ 0.0231a	0.164 $\pm$ 0.0310a	0.97	<.0001
Male	0.019 $\pm$ 0.0037b	0.234 $\pm$ 0.1227a	0.89	<.0001

mean separation by sex at 95% confidence level.

## 4-4. Discussion

The attack rate and handling time can be differently estimated as the prey species and prey stage because of the preference to a certain life-stage and species of preys (Xiao et al. 2013, Ganjisaffar and Perring 2015, Song et al. 2016). In this study, *A. eharai* preferred larvae than eggs of *T. urticae*. Appearance was not much different between starved females (A) and egg consumed females (B). However, the larva consumed females (C) look more healthier than starved or egg consumed females (Fig. 16). For normal development of *A. eharai*, *T. urticae* eggs may have less nutritional values than larvae.

In many functional response test, male predatory mites were not often tested (Laing and Osborn 1974, Shipp and Whitfield 1991, Koveos and Broufas 2000, Gotoh et al. 2004, Ahn et al. 2010, Seiedy et al. 2012, Xiao et al. 2013, Ganjisaffar and Perring 2015, Song et al. 2016). However, in the present study both sexes were tested to compare their predation efficacy, and female *A. eharai* consumed more than males. It might be due to the larger body size and requirement of more nutrients for oviposition in females. The functional response test by using male seems to be fully worthy, because they exist with female and they have predation ability. The

functional response type of *A. eharai* was estimated as the type II, which is the common type of predatory mites (Laing and Osborn 1974, Shipp and Whitfield 1991, Koveos and Broufas 2000, Gotoh et al. 2004, Ahn et al. 2010, Seiedy et al. 2012, Xiao et al. 2013, Ganjisaffar and Perring 2015, Song et al. 2016).

In comparison with *N. californicus* (Ahn et al. 2010) (Table 15), attack rate and handling time of *A. eharai* were better than *N. californicus*. Even though there were differences in plant leaf disc and temperature between this experiment and experiment of Ahn et al. (2010), the handling time and attack rate of *A. eharai* were much higher than those of *N. californicus*. However, further study is necessary to compare feeding abilities between *A. eharai* and *N. californicus* against *T. urticae* in the field conditions. The present information on the functional response of *A. eharai* should be helpful for evaluation of *A. eharai* for a biological control agent against *T. urticae*.

**Fig. 16. Photo comparison of female *A. eharai* as the condition of prey consumed**



- (A) Starved female for 24 hours.
- (B) Female that consumed *T. urticae* eggs for 24 hours.
- (C) Female that consumed *T. urticae* larvae for 24 hours.

**Table 15. Comparison of functional response parameters of *A. eharai* and *N. californicus* both of which feed on *T. urticae* larvae**

Species	Attack rate ( $\alpha$ )	Handling time ( $T_h$ )	Reference
<i>A. eharai</i>	0.1087	0.1642	This study
<i>N. californicus</i>	0.0678	1.5855	Ahn et al. 2010

Ahn et al. (2010) conducted at 25 °C and strawberry leaf disc (30 mm diameter).

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**긴꼬리이리응애(진드기아강: 이리응애과)의 발육과 산란 모형,**

**생명표 및 기능 반응에 관한 연구**

**박영균**

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**초록**

많은 이리응애들은 상업화되어 농경지 내에서 응애, 총채벌레, 가루이 방제를 위해 이용되고 있다. 긴꼬리이리응애는 국내 토착 이리응애로, 사과원 내 잎응애류의 초기방제원으로 알려져 왔다. 천적으로서 긴꼬리

이리응애의 잠재성 평가를 위해, 점박이응애를 먹이로 하여 긴꼬리이리응애의 생태적 특성에 관한 연구가 진행되었다. 먼저, 온도 별 긴꼬리이리응애의 발육과 산란에 관한 연구와 그것을 이용하여 발육과 산란 모형이 만들어졌다. 두번째로, 여러 온도 조건에서 긴꼬리이리응애의 개체군 성장 특성을 분석하기 위해 생명표가 작성되었다. 세번째로, 점박이응애 유충을 이용하여 긴꼬리이리응애의 기능 반응 연구가 진행되었다.

긴꼬리이리응애의 발육 실험은 11개 온도(18.0, 20.1, 21.6, 24.0, 24.1, 27.4, 28.6, 30.2, 32.0, 33.2, 35.9 °C)에서 진행되었고, 산란 실험은 6개 온도(18.0, 21.6, 24.1, 27.4, 30.2, 33.2 °C)에서 진행되었다. 발육 모형은 Briere<sup>1</sup> 식을 이용하여 표현되었다. 미성숙기 발육 모형의 발육영점온도, 적정온도, 발육한계온도,  $B_{80}$ 은 각각 13.2, 30.6, 35.9, 25.5 ~ 34.0 °C 였다. 미성숙기의 발육 완료 모형은 Weibull 식을 사용하여 표현되었다. 산란수 모형은 Extreme Value 식을 이용하여 표현되었다. 산란에 대한 적정온도,  $B_{80}$ 은 각각 24.3, 20.5 ~ 27.4 °C 였다. 성충의 발육 모형, 누적 산

란 모형, 나이에 따른 생존율 모형은 각각 TableCurve 2D의 목록에 있는 식과 Weibull 식, reverse sigmoid 식을 이용하여 표현되었다.

긴꼬리이리응애의 생명표 분석은 6개 온도 (18.0, 21.6, 24.1, 27.4, 30.2, 33.2 °C) 그리고 Age-stage, two-sex life table 이론에 따라서 분석되었다. 연령 - 발육 단계 별 생존율, 연령 - 발육 단계 별 산란 수, 연령 - 발육 단계 별 번식가, 연령 별 생존율, 연령 별 산란 수 그리고 개체군 증가율 예측이 측정되었다. 내적 자연 증가율은 0.2619로 27.4 °C 에서 가장 높게 나타났다. 평균 세대 기간은 18.0 °C 에서 26.9일로 가장 길었고, 30.2 °C 에서 10.5일로 가장 짧았다.

긴꼬리이리응애의 기능 반응 실험은 점박이응애 유충 10, 30, 50, 70, 130마리에서 진행되었다. 긴꼬리이리응애는 2형 기능 반응을 나타냈다. 공격율은 암컷은 0.109 였고, 수컷은 0.019 였다. 처리 시간의 경우 암컷은 0.164 h 그리고 수컷은 0.234 h 였다. 공격율의 경우 암컷과 수컷이 95% 신뢰 구간에서 통계적으로 유의미한 차이를 보였지만, 처리 시

간의 경우 유의미한 차이를 보이지 않았다.

핵심어: 긴꼬리이리응애, 발육 모형, 산란 모형, 생명표, 기능 반응, 이리  
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