



Path Analysis as a Tool To Identify Indicators of Fitness Traits

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ABSTRACT

Path Analysis As a Tool To Identify Indicators Of Fitness Traits. Karakter kebugaran, seperti keperidian, lama hidup, dan fertilitas sering digunakan untuk menggambarkan kapasitas reproduksi suatu spesies. Oleh karena itu, kebugaran parasitoid sering digunakan sebagai indikator potensial dari suatu kualitas dan keberhasilan di lapangan. Karakter tersebut dapat pula menggambarkan persistensi populasi parasitoid di lapangan selama periode tertentu. Dalam pengelolaan hama, kebugaran parasitoid menjadi indikator penting untuk kesuksesan pengendalian hayati. Beberapa faktor yang berkaitan dengan kualitas parasitoid adalah pengaruh inang, lama generasi dan asal-usul parasitoid. *Path analysis* digunakan untuk menganalisa pola hubungan dan keterkaitan antar variabel kebugaran. Tujuan penelitian ini adalah untuk mengidentifikasi indikator sukses dari perilaku parasitisasi serta mempelajari mekanisme hubungan sebab akibat (*causal mechanism*) antar beberapa karakter kebugaran dari (*T. armigera*) yang menyerang (*C. cephalonica*) dan *H. armigera*. Hasil analisis menunjukkan adanya korelasi koefisien yang tinggi antara jumlah telur dan laju parasitisme pada kedua jenis inang yang digunakan. Produksi telur juga mempunyai korelasi yang tinggi dengan lama hidup. Pada inang *Coeryra*, ditemukan bahwa panjang sayap depan memiliki nilai positif dengan parasitisme, sedangkan ukuran kepala dan laju keberhasilan hidup dapat dikategorikan sebagai *indirect indicators* melalui jumlah telur yang dihasilkan.

KATA KUNCI: Interaksi inang parasitoid, pengendalian hayati, ekologi reproduksi, karakter kebugaran

INTRODUCTION

Background

Several methods of pest control have been commonly used, for instance chemicals, mechanicals and biological. The methods that has been widely argued as safe for the environment is through biological, using natural enemies such as egg parasitoids.

A well-known and commonly used egg parasitoids is *Trichogramma*. *Trichogramma* are commonly reared commercially for control of pest moth and they have been used in biological control programs with variable success. These parasitoids are produced in unnatural conditions often in factitious hosts. One reason for mixed success in the field is that wasps reared in insectaries have biological

attributes that can reduce their performance under field conditions. This problem has led to a search for useful attributes that predict field success.

Parasitoid effectiveness is influenced by many factors, one of them is parasitoid fitness. Parasitoid fitness is frequently cited as a potential indicator of "quality" and hence field success. The failure of parasitoid released is caused by the low quality of the parasitoid itself. Some factors that relates to parasitoids quality are host influence, length of generation and history where the parasitoids came from. Female fitness is strongly related with the egg host quality that she attacked (Godfray 1994) and also influenced by the host size (Corrigan & Lashomb 1990). Female parasitoid size depends on host size where the parasitoids do its development. Bigger host can produce bigger parasitoids rather than smaller host.

Positive correlations between adult body size and fitness measures are ubiquitous in plants and animals. Non-positive correlations between size and adult fitness measures are uncommon and usually restricted to one fitness measure under some but not all test conditions (Kazmer & Luck 1995). In general, though, laboratory fitness data provides strong support for the "adult size-fitness hypothesis" i.e., that the fitness of males and females increases with increasing size. In solitary para-

sitoids (one wasps develops per host), adult size is positively correlated with host size, a measure of the resources available to the developing larvae. Knowledge of size-fitness hypothesis is important to basic and applied research on parasitoid wasp. Size-fitness relationships are important because the size and presumably fitness of a mother's progeny are affected by her oviposition "decisions" (Klomp & Teerink 1967). If size is a reliable indicator of fitness, we can take advantage of this easily measured variable to assess how progeny fitness varies for different oviposition strategies. Size-fitness relationships are also important to biological pest control. The size of the released wasps depends on the size of the host used for mass production and on the density of females parasitizing the hosts, which together influence how many progeny are laid in each host.

To analyze the relationships pattern among fitness variables, the common method introduce is regression analysis and simple correlation. But, if the relationships is involving causal relations, path analysis is considered more likely to perform.

The objectives of this research are to identify indicators and causal mechanism among fitness traits of *Trichogramma armigera* (*T. armigera*) that affects the parasitism success in *Corcyra cephalonica* (*C. cephalonica*) and *Heliothis armigera* (*H. armigera*) as

natal hosts. Two hosts were used because it will generate two different sizes of wasps. The ones reared from *Heliotis armigera* will be bigger compared to the ones reared from *Corecya cephalonica*.

MATERIAL AND METHODS

Fitness trait parameters observed (see Table 1):

1. Parasitoids size

Forewing length, head width and hind length can be use as parameters to know about the parasitoids size. The size was measured using *Tps dig.*

2. Percentage of parasitism

The percentage of parasitism was computed from the numbers of parasitized egg host each day. The parasitized eggs are shown by the changing of color from yellow to dark.

3. Length of development

Length of development was computed since the day when the eggs were laid to the egg host until the appearance of adult parasitoids.

4. Percentage of survival.

The percentage of survival numbers of appeared adult parasitoids (from parasitized hosts).

5. Longevity

Longevity is the length of a female appeared parasitoids until its death.

6. Egg numbers

Egg numbers is equal to total appeared parasitoids plus numbers of dead pupa and residual eggs in ovary.

Path Analysis

Path Analysis is a method for partitioning the correlations among variables. Sewall Wright first developed Path Analysis as a mean of interpreting qualitatively the causal relationships among a system of correlated variables. Wright distinguishes two distinct situation of special relevance to the analysis of selection: system ordered in time, in which there may be a cause-and-effect relation between 'earlier' and 'later' variables; and systems involving un measured common factors (Kingsolver & Schemske 1991).

Table 1. Fitness traits of *T. armigera*.

No	Variables	Explanation
1	X1	Head width (mm)
2	X2	Hind length (mm)
3	X3	Forewing length (mm)
4	X4	Longevity (days)
5	X5	Survival rate (%)
6	Y1	Egg numbers (number)
7	Y2	Length of development (days)
8	Y3	Parasitism rate (%)

Path Analysis begins with the construction of a path diagram showing the relationships among all variables in the system, based upon a priori knowledge of such relationship. In this sense, the path coefficient indicates the direct contribution of one variable to the variation observed in another. Path Analysis assumes that the relationships among variables are linear, so it is applicable only to the analysis of directional selection.

The Path Analysis intended to combine the qualitative information given by the correlation as may be at hand on causal relations to give a quantitative interpretation (Wright 1968).

The mechanism of Path Analysis obtained through decomposition of correlation coefficients to direct and indirect effects (Gravois & Helms 1992). The direct effect refers to path coefficient, which is used to see contribution of a variable to variance of another variable. This is possible, because the variance of a variable is sums of all path effect contribution in path diagram (Heise, 1975). Path coefficients determine based on multiple regression, as follow:

$$Y_i = \beta_0 + \beta_1 X_{i1} + \dots + \beta_t X_{it} + \dots + \beta_p X_{pi} + \varepsilon_i$$

Where:

$i = 1, 2, \dots, n.$

$t = 1, 2, \dots, p$

β_t = regression coefficient.

Y_i = dependent variable

X_{it} = independent variable

With:

ε_i = The i-th residual.

$$E(\varepsilon_i) = 0$$

$$E(\varepsilon_i^2) = \sigma^2$$

$$E(\varepsilon_i, \varepsilon_j) = 0$$

Afterwards, variables Y_i and X_{it} standardized to obtain path coefficient equations, as follow:

$$w_i = c_1 z_{1i} + \dots + c_k z_{ki} + \dots + c_m z_{mi} + c_u u_i$$

Where:

$$w_i = \frac{Y_i - \bar{Y}}{\sigma_y}, \quad z_{ki} = \frac{x_i - \bar{x}}{\sigma_x}$$

$$u_i = \frac{\varepsilon_i}{\sigma_i}$$

With:

w_i = standardized dependent variable

z_{ki} = standardized independent variable

u_i = standardized residual

u_k = path coefficient standardized independent variable

c_u = path coefficient residual variable

The path coefficient can derive from correlation coefficient among independent variables. In matrix notation it can be write as follow:

$$\begin{bmatrix} r_{11} & r_{12} & \dots & r_{1p} \\ r_{21} & r_{22} & \dots & r_{2p} \\ \vdots & & \ddots & \vdots \\ r_{p1} & r_{p2} & \dots & r_{pp} \end{bmatrix} \begin{bmatrix} c_1 \\ c_2 \\ \vdots \\ c_p \end{bmatrix} = \begin{bmatrix} r_{1y} \\ r_{2y} \\ \vdots \\ r_{py} \end{bmatrix}$$

$R_x \qquad \qquad \underline{C} \qquad \qquad R_y$

With:

R_x = correlations among independent variables from path equation model.

\underline{C} = path coefficient vector that shows direct effect from each independent variable to dependent variable.

\underline{R}_y = correlation coefficient vector among dependent variable.

The path coefficient vector can be computed through equation:

$$\underline{C} = \underline{R}_x^{-1} \underline{R}_y$$

Indirect effect from independent variables to dependent variables through another independent variables computed based on equation:

$$C_{k,r_{ik}}$$

With:

$i = 1, 2, \dots, m$

The residual effect that cannot explain by the Path Analysis model measure by:

$$C_s = \sqrt{1 - \sum_{i=1}^p c_k r_{ik}}$$

In this research, the methods to develop path diagrams are:

1. To obtain path diagrams, this research starts with checking the correlation coefficients and combines the information from correlation coefficients with causal relationships theory about fitness traits variables.
2. Predict path coefficients in each host.
3. Test the coefficients significance. First, with test the standardized re-

gression coefficients (β). If β shows significant value, so does the path coefficients (Kerlinger & Pendhazur 1973). Second, with path coefficient significance test. Path coefficients do not give any effect if the value is less than 0.05.

This research using software Minitab version 13.2 for windows and Microsoft Excel version 97.

Data resources

The data used in this research is a secondary data that resulted from research project of Pests and Plant Diseases Department, Bogor Agricultural University. The research held on November 2001 until October 2002 with 40 imago of *T. armigera* in each host, which is *C. cephalonica* and *H. armigera*.

RESULTS AND DISCUSSION

The correlation coefficients of *T. armigera* fitness traits in *C. cephalonica* (hereafter will be called as TaC) show that egg numbers (Y1) has the highest strength to parasitism rate (Y3). The second correlation is between egg numbers (Y1) and longevity (X4) (Appendix Table. 1) and the correlation coefficients of *T. armigera* fitness traits in *H. armigera* (hereafter will be called as TaH) also shows that egg numbers gives the highest degree of association to parasitism rate and the second

Table 1. Correlation Matrix of *T. armigera* fitness traits in *C. cephalonica*

	X1	X2	X3	X4	X5	Y1	Y2	Y3
X1	1.000							
X2	0.329	1.000						
X3	0.133	-0.050	1.000					
X4	0.047	-0.45	0.185	1.000				
X5	-0.085	0.193	0.129	0.038	1.000			
Y1	0.165	0.045	0.107	0.733	0.204	1.000		
Y2	0.096	-0.078	0.089	0.205	0.579	0.268	1.000	
Y3	0.151	0.030	0.110	0.728	0.193	0.997	0.250	1.000

Table 2. Correlation Matrix of *T. armigera* fitness traits in *H. armigera*

	X1	X2	X3	X4	X5	Y1	Y2	Y3
X1	1.000							
X2	0.378	1.000						
X3	0.195	0.498	1.000					
X4	-0.172	-0.079	-0.042	1.000				
X5	-0.052	-0.151	-0.149	0.184	1.000			
Y1	0.050	0.135	0.352	0.547	-0.009	1.000		
Y2	0.157	0.065	0.118	-0.324	0.231	-0.339	1.000	
Y3	0.089	0.209	0.302	0.506	0.033	0.910	-0.252	1.000

correlation also between egg numbers and longevity (Appendix Table. 2).

Discussion of Path Analysis results is divided into several path diagrams which are also based on two different hosts. The path diagram is constructed into four different models. It is assumed that these four models can represent the causal mechanism relationships among fitness traits of TaC and TaH.

Path Analysis of *T. armigera* fitness traits based on 1st model

1. Path Analysis of fitness traits on TaC

Path Analysis results (Figure 1) shows that head width (X1) gives

positive value of direct effect to egg numbers (Y1). It gives 0.154 direct effect values. Hind length (X2) gives -0.001 direct effect, while forewing length (X3) gives 0.087 direct effect to egg numbers. It means that increase in the head width and forewing length will increase the egg numbers, while the increase in hind length will decrease the egg numbers. The residual coefficient for this model is 0.983, which means that 96.63% of the total variance cannot be explained by the model. Length of development is also directly influenced by the imago size. Head width also gives a positive value. It gives 0.126 direct effect on length of development. Hind length once again

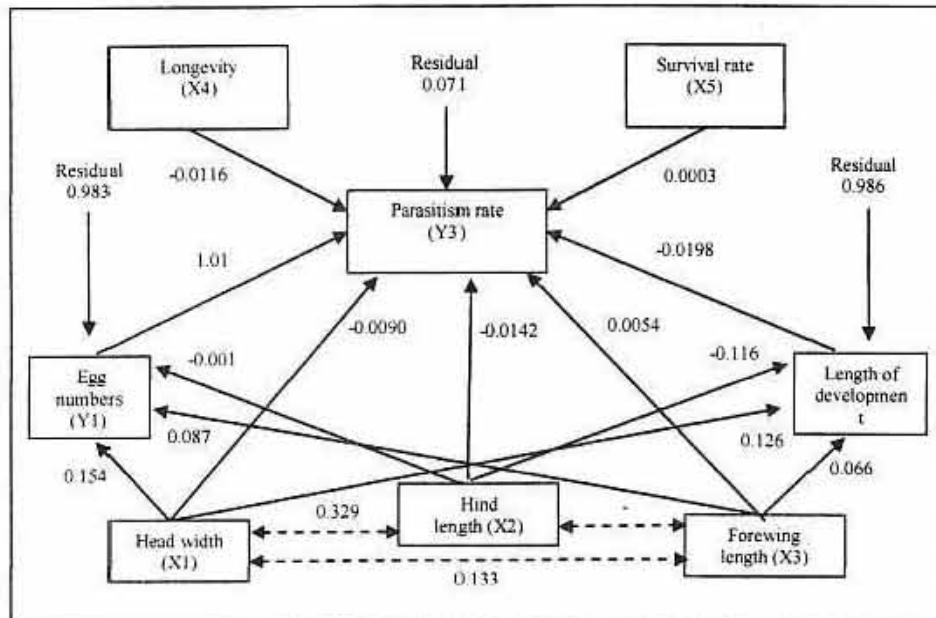


Figure 1. Path diagram of *T. armigera* fitness traits in *C. cephalonica*

gives a negative value. It gives -0.116. Forewing length gives 0.066 direct effect values. These results mean that the increase in head width and forewing length will increase the length of development, while the increase in hind length will decrease the length of development. The residual coefficient is 0.986. This means that 97.22% of the total variance cannot be explained by the model.

Parasitism rate (Y3) is directly influenced by imago size, longevity (X4), Survival rate (X5), egg numbers (Y1) and length of development (Y2). Head width as one of the imago size parameters gives -0.0090 direct effect to parasitism rate. Hind length also gives a negative value, it gives -0.0142

while forewing length gives 0.0054 direct effect. Egg numbers gives 1.01 direct effect to parasitism rate which is the highest value of all variables that directly affect the parasitism rate. Length of development and longevity give negative values.

Length of development gives -0.0198 and longevity gives -0.0116 to parasitism rate. Survival rate gives 0.0003 direct effect. These results indicate that the increase in egg numbers, forewing length and survival rate will increase the parasitism rate, while the increase in head width, hind length, length of development and longevity will decrease the parasitism rate. Indirect effect of imago size to parasitism rate (Appendix Table. 3) shows that head width gives 0.15554

Table 3. Path Coefficients of fitness traits on TaC (1st model)

Variables	Direct effects	Indirect effects		Total Indirect effects	Total effects
		Via Y1	Via Y2		
X1	-0.0090	0.15554	-0.0024948	0.1530452	0.1440452
X2	-0.00142	-0.00101	0.0022968	0.0012868	-0.0129132
X3	0.0354	0.08787	-0.013068	0.074802	0.080202
X4	-0.00116	-	-	-	-0.0116
X5	0.0003	-	-	-	0.0003
Y1	1.01	-	-	-	1.01
Y2	-0.0198	-	-	-	-0.0198

through egg numbers and -0.0024948 through length of development, while hind length gives -0.00101 indirect effect through egg numbers and 0.0022968 through length of development. Forewing length also gives a positive value through egg numbers (0.08787) and negative value (-0.013068) through length of development. The total indirect effects of the imago size give positive value, which indicates that for *C. cephalonica* as the first host of *T. armigera* forewing length is the only parameter of imago size that can directly effect the parasitism rate. Egg numbers also gives a positive and high value of direct effect to parasitism rate. The residual coefficient for this model is 0.071, which means that 99.5% of the total variance can be explained by the model. In this model for TaC indicates that egg numbers, forewing length and survival rate can be direct indicators to parasitism rate, while head width and hind length is indirect indicators through egg numbers.

2. Path Analysis of fitness traits on TaH

Path Analysis results (Figure 2) shows that for this host, head width (X1) gives negative value. It gives -0.009 direct effect to egg numbers (Y1), while hind length (X2) gives 0.039 and forewing length (X3) gives 0.324 direct effect to egg numbers. It means that the increase in hind length and forewing length will increase the egg numbers, while the increase in head width will decrease the egg numbers. The residual coefficient for this model is 0.947. Head width this time gives 0.198 direct effect to length of development. Hind length also gives positive value, it gives 0.072 while forewing length gives -0.209 direct effects to length of development. From these results it can refrained by stating explicitly that the increase in head width and hind length will increase the length of development, while increase in the forewing length will decrease the length of development. The residual coefficient for this model is 0.969 which is also a high value of

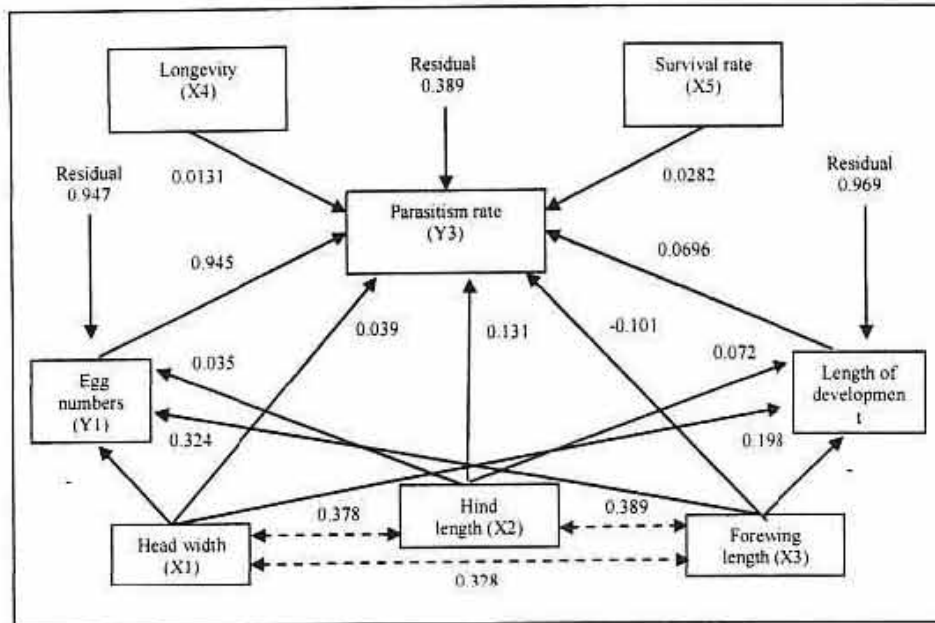


Figure 2. Path diagram of *T. armigera* fitness traits in *H. armigera*

residual. The egg numbers this time gives 0.945 direct effect to parasitism rate (Y3). Length of development, longevity and survival rate also give positive values each of the fitness traits gives 0.0096, 0.0131 and 0.0282 direct effects. Head width gives 0.039 and hind length gives 0.131 direct effect to parasitism rate, while forewing length this time gives -0.101 to parasitism rate. These results mean that the increase in head width, hind length, longevity and survival rate will increase the parasitism rate, and it will decrease along with the increase of forewing length.

Indirect effect from imago size through egg numbers (Appendix Table. 4) shows that head width this

time gives -0.065205 indirect effect and hind length gives 0.033075. Indirect effect from forewing length to parasitism gives 0.18711. The indirect effect of head width through length of development is 0.0137808 and hind length gives 0.0050112 indirect effect, while forewing length gives -0.0145464 to parasitism rate through length of development. Total indirect effects for this host show that head width gives negative value, while the other two give positive values. From these results the conclusion is that for this host, forewing length is not a direct indicator of parasitism rate, but head width and hind length can be direct indicators to parasitism rate.

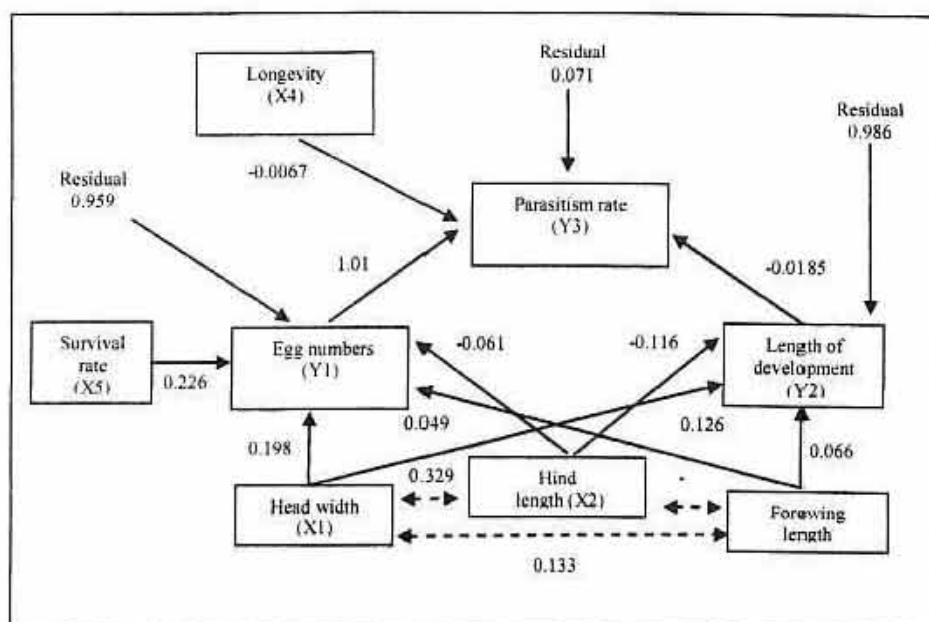


Figure 3. Path diagram of *T. armigera* fitness traits in *C. cephalonica*

longevity gives -0.0067 direct effect to parasitism rate.

Indirect effects (Appendix Table 5) from imago size through egg numbers shows that head width and forewing length give positive values and hind length gives the opposite value. Indirect effect through length of development shows that for this model the only parameter of imago size that gives positive value is hind length. Even though, total indirect effects shows that head width and forewing length give positive values and hind length gives negative value. Total effects of the imago size also indicate the same results. The conclusion that can be state from these results is that head width and forewing length can be

indicators that affects parasitism rate even only through egg numbers and length of development.

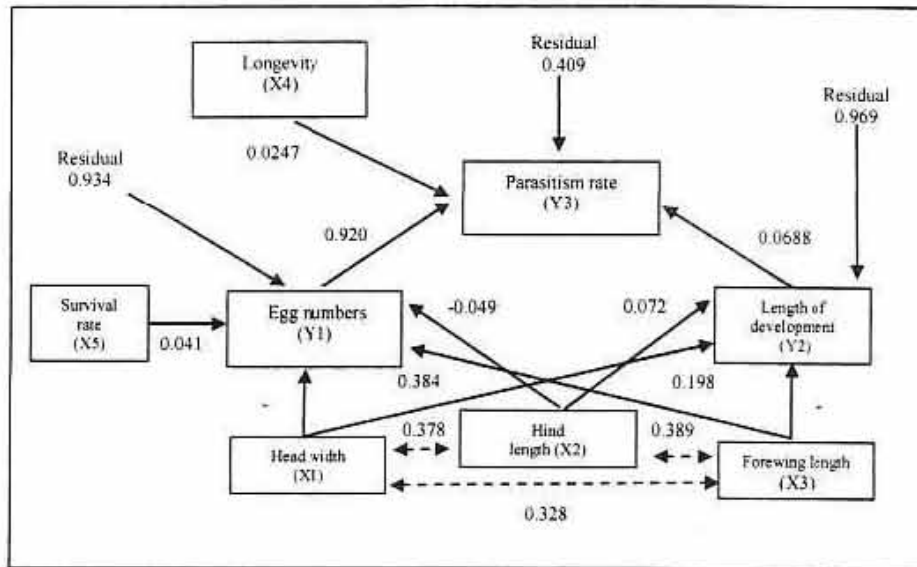
The residual coefficient for this model is 0.071, which means that 99.5% of the total variance can be explained by the model.

2. Path Analysis of fitness traits on TaH

Path Analysis results for this host (Figure 4) shows that head width gives -0.004 direct effect to egg numbers. Hind length gives -0.049, while forewing length gives 0.324 direct effect value. These results mean that the increase in head width and hind length will decrease the egg numbers, and it will increase along with the

Table 5. Path Coefficients of fitness traits on TaC (2nd model)

Variables	Direct effects	Indirect effects		Total Indirect effects	Total effects
		Via Y1	Via Y2		
X1	-	0.19998	-0.002331	0.197649	0.197649
X2	-	-0.06161	0.002146	-0.059464	-0.0059464
X3	-	0.04949	-0.001221	0.048269	0.048269
X4	-0.0067	-	-	-	-0.0067
X5	-	0.222826	-	0.222826	0.222826
Y1	1.01	-	-	-	1.01
Y2	-0.0185	-	-	-	-0.0185

Figure 4. Path diagram of *T. armigera* fitness traits in *H. armigera*

increase of forewing length. Survival rate also gives a positive value. it gives 0.041 direct effect to egg numbers. The residual coefficient for this model is 0.934. which indicates that almost 87.24% of the total variance cannot be explained by the model.

Head width this time gives 0.198 direct effect to length of development. Hind length gives 0.072 and forewing length gives -0.209 direct effect to length of development. These results

are similar to the first model. The path coefficient residual for this model is 0.969 which means that 93.89% of the total variance cannot be explained by the model. Egg numbers (Y1) gives 0.920 direct effect to parasitism. longevity gives 0.0247 and length of development gives 0.0688 direct effect to parasitism rate. These mean that the increase in the whole variables will increase the parasitism rate.

Table 6. Path Coefficients of fitness traits on TaH (2nd model)

Variables	Direct effects	Indirect effects		Total Indirect effects	Total effects
		Via Y1	Via Y2		
X1	-	0.19998	-0.002331	0.197649	0.197649
X2	-	-0.06161	0.002146	-0.059464	-0.0059464
X3	-	0.04949	-0.001221	0.048269	0.048269
X4	-0.0067	-	-	-	-0.0067
X5	-	0.222826	-	0.22826	0.22826
Y1	1.01	-	-	-	1.01
Y2	-0.0185	-	-	-	-0.0185

Indirect effects from imago size to parasitism rate through egg development (Appendix Table. 6) shows similar results as the first model. The total indirect effect shows that hind length gives negative value, while the other two variables give positive values. Total effects shows that both head width and forewing length give negative values just like in the first host. In this model, both of host point the same indicators.

The path coefficient residual for this model is 0.409 which is 88.2% of the total variance can be explained by the model.

Path Analysis results in the second model show that in TaC, egg numbers is still the direct indicators to parasitism rate, while head width, forewing length and survival rate is indirect indicators through egg numbers. Path Analysis results in TaH shows that for this host egg numbers also can be direct indicator to parasitism rate, while forewing length

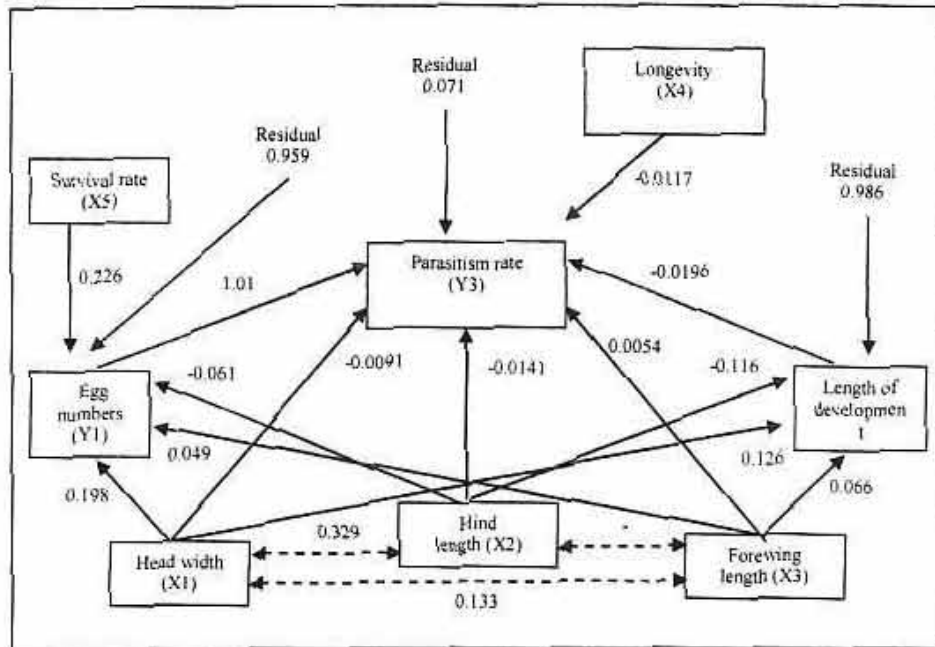
and survival rate is indirect indicators through egg numbers.

Path Analysis of *T. armigera* fitness traits based on 3rd model

1. Path Analysis of fitness traits on TaC

Path Analysis results (Figure 5) shows that head width (X1) gives 0.198 direct effects to egg numbers (Y1). Hind length gives 0.049 direct effect, while forewing length gives -0.061 direct effects to egg numbers. The increase in head width and forewing will decrease the egg numbers and the increase in hind length will decrease the egg numbers. Survival rate also gives positive direct effect to egg numbers. It gives 0.226. This value is the same as the second model value. The residual coefficient for this model is 0.959.

Length of development (Y2) is also influenced by imago size in this model. The head width gives 0.126 direct effects to length of development, while

Figure 5. Path diagram of *T. armigera* fitness traits in *C. cephalonica*

the hind length gives -0.116 direct effect to length of development. Forewing length in this model also gives 0.066. All of these results are the same values as the second model results. The path coefficient residual for this model is 0.986 which 97.22% of total variance cannot be explained by the model. This model also indicate the same thing just like former models, which always shows high value of residual in egg numbers and length of development that involving the imago size parameters.

Parasitism rate (Y3) in this model directly influenced by head width (X1), hind length (X2), forewing length (X3), egg numbers (Y1), length of development (Y2) and longevity

(X4). Head width gives -0.0091 direct effect to parasitism rate. Hind length gives -0.0141 direct effect, while forewing length gives 0.0054 direct effect. The egg numbers gives 1.01 direct effects which is a stable value in the whole models. Even though the construct or path diagram involving or not involving the direct effect from imago size to parasitism rate. Length of development in this model gives -0.0196 direct effect. These results are similar to those in the first model, except longevity in this model gives -0.0117 direct effect to parasitism rate. These results mean that the increase in egg numbers and forewing length will increase the parasitism rate, while the increase in head width, hind length,

length of development and longevity will decrease the parasitism rate.

Indirect effects from the imago size to parasitism rate through egg numbers and length of development (Appendix Table. 7) give the results that hind length is give -0.06161 indirect effects through egg numbers and also gives negative total indirect effects and total effects. Head width and forewing length give positive value of direct effect (0.19998 and 0.04949) through egg numbers. even these two parameters give negative values of indirect effect through length of development but they still give positive total indirect effect and indirect effect. Survival rate gives 0.222826 indirect effects to parasitism rate through egg numbers. The residual coefficient for this model is 0.071, which indicates that 99.5% of the total variance can be explained by the model.

Path Analysis results for this host show that egg numbers and forewing

length can be direct indicators to parasitism rate. while forewing length and survival rate is indirect indicators through egg numbers.

2. Path Analysis of fitness traits on TaH

In this host, the Path Analysis results (Figure 6) also give similar values as the first one. The head width gives -0.004 direct effect to egg numbers. Hind length gives -0.049, while forewing length gives 0.384 direct effect values. Survival rate this time gives 0.041, which is smaller than in *C. cephalonica*. The residual coefficient for this model is 0.946. The variance that cannot be explained by the model is 89.5%.

Head width gives 0.198 direct effect to length of development. Hind length gives 0.072 direct effects, while forewing length gives -0.209 direct effects to length of development. The residual coefficient for this model is 0.969,

Table 7. Path Coefficients of fitness traits on TaC (3rd model)

Variables	Direct effects	Indirect effects		Total Indirect effects	Total effects
		Via Y1	Via Y2		
X1	-0.0091	0.19998	-0.0024696	0.1975104	0.1884
X2	-0.0141	-0.06161	0.0022736	-0.0593364	-0.0734
X3	0.0054	0.04949	-0.0012936	0.0481964	0.0536
X4	-0.0117	-	-	-	-0.0117
X5	-	0.22826	-	0.22826	0.22826
Y1	1.01	-	-	-	1.01
Y2	-0.0196	-	-	-	-0.0196

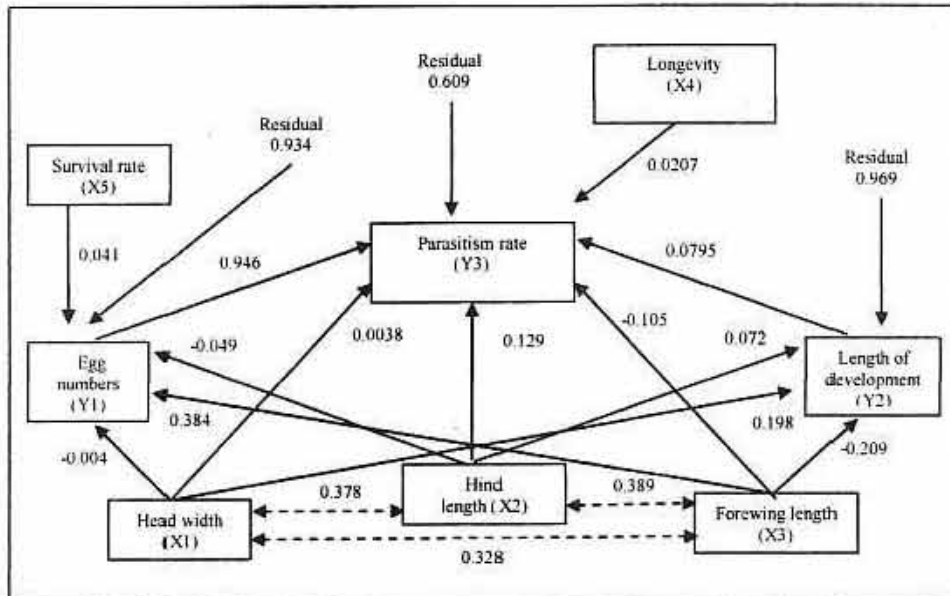


Figure 6. Path diagram of *T. armigera* fitness traits in *H. armigera*

The residual values in the whole models that involving imago size effect to egg numbers or length of development are showing high residual values.

Head width this time gives 0.0038 direct effect to parasitism rate. Hind length gives 0.129, while forewing length gives -0.105 direct effect. Egg numbers seems to have stable value in the three models. It gives 0.946, which is similar to values of the other three models. The length of development gives 0.0207 direct effect to parasitism rate. These results indicate that the increase in head width, hind length, egg numbers, length of development and longevity will increase the parasitism rate. But it will decrease along with the increase of forewing

length. This raise question why forewing length gives negative value also for the first model forewing length gives negative value of direct effect to parasitism.

The indirect effects (Appendix table. 8) from imago size through egg numbers shows that head width gives -0.003784 and hind length also gives negative values, it gives -0.046354. Forewing length is the only imago size parameter that gives positive and high value of indirect effect to parasitism rate. The indirect effect through length of development shows the opposite results. In this case, forewing length gives positive values.

The total effects show that all of the parameters give positive values and the highest value is given by forewing

Table 8. Path Coefficients of fitness traits on TaH (3rd model)

Variables	Direct effects	Indirect effects		Total Indirect effects	Total effects
		Via Y1	Via Y2		
X1	0.0038	-0.003784	0.0015741	0.0053581	0.00159
X2	0.129	-0.046354	0.005724	-0.04063	0.08837
X3	-0.105	0.363264	-0.0166155	0.3466485	0.24165
X4	0.0207	-	-	-	0.0207
X5	-	0.038786	-	0.038786	0.03879
Y1	0.946	-	-	-	0.946
Y2	0.0795	-	-	-	0.0795

length. Path coefficient residual for this model is 0.609 which is a higher value compared to the other residuals. This value means only 62.9% of the total variance that can be explained by this model.

This residual is the highest residual compared to other residuals in different models. even though the results indicate similar values in all the models. In this hosts, the direct indicators to parasitism rate are egg numbers, head width, hind length, length of development and longevity. Forewing length and survival rate is indirect indicators of parasitism rate through egg numbers.

Path Analysis results in the third model, shows that once again egg numbers give positive and stable value in TaC, and in TaH even it is not stable but still gives positive value of direct effect. In TaC, forewing length is also direct indicators to parasitism rate, while head width, hind length and survival rate are only indirect indicators through egg numbers. In

TaH, head width, hind length, length of development and longevity is direct indicators, while forewing length only indirect indicators through egg numbers.

Path Analysis of *T.armigera* fitness traits based on 4th model

The fourth model shows different construct of path diagram compared to the other three models. In this model parasitism rate is still the final outcome, but imago size parameter such as hind length does not directly effect parasitism rate. It is indirectly effects through egg numbers. Survival rate is also indirectly effect parasitism through egg numbers, while length of development indirectly effect parasitism rate through egg numbers and longevity. Fitness traits that directly effect parasitism rate are egg numbers, longevity, head width and forewing length. The head width and forewing length also indirectly effect parasitism rate through egg numbers.

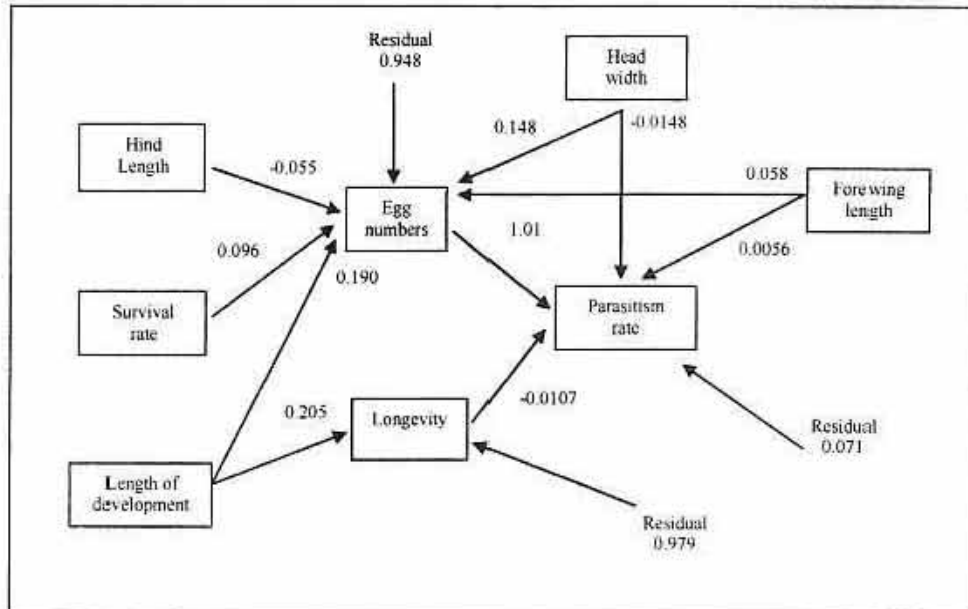


Figure 7. Path diagram of *T. armigera* fitness traits in *C. cephalonica*

1. Path Analysis of fitness traits on TaC

Path Analysis results (Figure 7) shows that for this host in this model head width gives 0.148 to egg numbers, forewing length gives 0.058 while hind length gives -0.005 . Survival rate gives 0.096 and length of development gives 0.190 to egg numbers. These results mean that the increase in head width, forewing length, survival rate and length of development will increase the egg numbers, while the increase in hind length will decrease the egg numbers. The residual coefficient for this model is 0.948, which means that 89.87% of the total variance cannot be explained by the model. Length of development gives 0.205 direct effect to longevity with residual coefficient is 0.979

Head width gives -0.0148 direct effect to parasitism rate, longevity also gives negative value. It gives -0.0107 direct effect. Forewing length and egg numbers once again gives positive direct effect to parasitism rate, each of them gives 0.0056 and 1.01 to parasitism rate. The residual coefficient for this model is 0.071, which means that 99.5% of the total variance can be explained by the model. This value is same as the other model residuals. Indirect effects to parasitism rate (Appendix Table. 9) shows that head width gives positive indirect effect through egg numbers, survival rate and length of development also give positive results.

Path Analysis in TaC based on fourth model shows that egg numbers and forewing length can be direct

Table 9. Path Coefficients of fitness traits on TaC (4th model)

Variables	Direct effects	Indirect effects		Total Indirect effects	Total effects
		Egg numbers	Longevity		
Head width	-0.0148	0.149	-	0.149	0.1342
Forewing length	0.0056	0.059	-	0.056	0.0642
Egg numbers	1.01	-	-	-	1.01
Longevity	-0.0107	-	-	-	-0.0107
Hind length	-	-0.056	-	-0.056	-0.056
Survival rate	-	0.097	-	0.097	0.097
Length of development	-	0.192	-0.0022	0.189	0.189

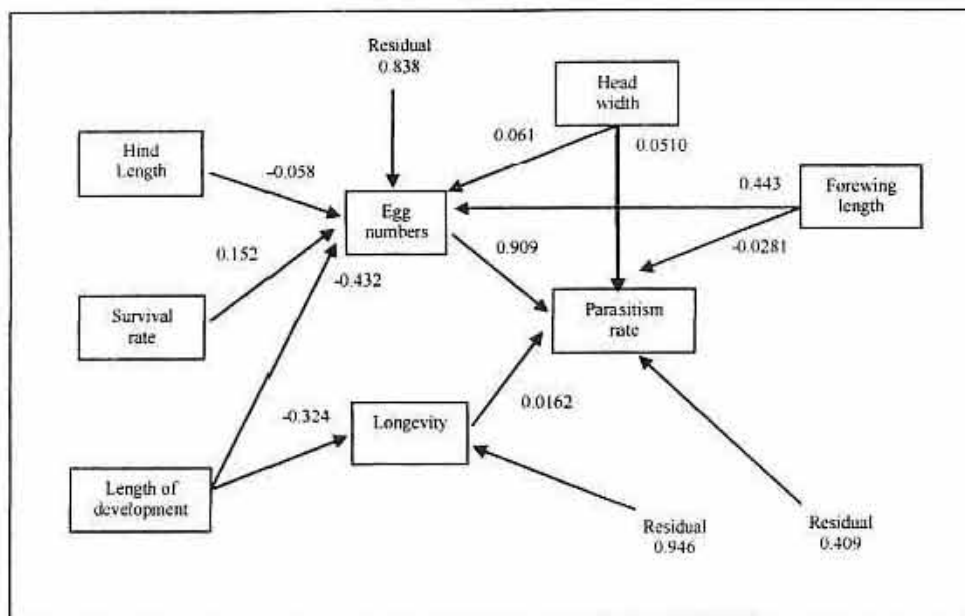


Figure 8. Path diagram of *T. armigera* fitness traits in *H. armigera*

Indicators to parasitism rate, while head width, survival rate and length of development are indirect indicators through egg numbers.

2. Path Analysis of fitness traits on TaH

Path Analysis results of TaH (Figure 8) shows that for this host, head width gives 0.061 direct effects to

egg numbers. Forewing length also gives positive result, it gives 0.443. Hind length gives negative value, it gives -0.058. Survival rate gives 0.152. Length of development in this host gives high value, but negative. It gives -0.432 direct effects to egg numbers. These results indicate that the increase in head width, forewing length and survival rate will increase

Table 10. Path Coefficients of fitness traits on TaH (4th model)

Variables	Direct effects	Indirect effects		Total Indirect effects	Total effects
		Egg numbers	Longevity		
Head width	0.0510	0.056	-	0.056	0.106
Forewing length	-0.0281	0.403	-	0.403	0.375
Egg numbers	0.909	-	-	-	0.909
Longevity	0.0162	-	-	-	0.0162
Hind length	-	-0.053	-	-0.053	-0.053
Survival rate	-	0.138	-	1.38	1.38
Length of development	-	-0.393	-0.005	-0.398	-0.398

the egg numbers, while the increase in hind length and length of development will decrease the egg numbers. The residual coefficient for this model is 0.838, which means that 70.22% of the total variance cannot be explained by the model. Length of development this time gives -0.324 to longevity with residual coefficient of 0.946, also indicates high residual.

Head width gives 0.0510 direct effect to parasitism rate, while forewing length gives negative value, it gives -0.0281 to parasitism rate. Egg numbers gives 0.909 direct effect and longevity gives 0.0162. These results mean that the increase in egg numbers, head width and longevity will increase the parasitism rate. Parasitism rate will decrease along with the increase of forewing length.

Indirect effects to parasitism rate (Appendix Table. 10) shows that head width, forewing length and survival rate gives positive values, while the rest of variables give negative values. From these results the conclusion that

can be stated is that in TaH, head width, egg numbers and longevity can be direct indicators to parasitism rate. Forewing length and survival rate only indirect indicators of parasitism rate through egg numbers.

The residual coefficient for this model is 0.409, which means that 83.2% of the total variance can be explained by the model.

To support the results of Path Analysis, standardized regression is used for each host (Appendix Table. 11 and Appendix Table.12). The results show that egg numbers gives significant value in each host (P-value=0.000).

CONCLUSIONS

All of the models developed indicate similar results. Path diagram on TaC always indicate that egg numbers is constantly positive value and stable, also high value in all of the models. It always gives 1.01 direct

Table 11. Standardized regressions of *T. armigera* fitness traits in *C. cephalonica*.

Variables	DF	Coefficients	SE Coefficients	T	P-Value
Intercept	1	-0.00000	0.01203	-0.00	1.000
Z1	1	-0.00905	0.01436	-0.63	0.533
Z2	1	-0.01417	0.01429	-0.99	0.329
Z3	1	0.00538	0.01288	0.42	0.679
Z4	1	1.01259	0.01917	52.82	0.000
Z5	1	-0.01981	0.01688	-1.17	0.249
Z6	1	-0.01164	0.01901	-0.61	0.545
Z7	1	0.00029	0.01766	0.02	0.987

R² = 99.5%

Table 12. Standardized regressions of *T. armigera* fitness traits in *H. armigera*

Variables	DF	Coefficients	SE Coefficients	T	P-Value
Intercept	1	-0.00000	0.06940	-0.00	1.000
Z1	1	0.01374	0.08000	0.17	0.856
Z2	1	0.09515	0.08103	1.17	0.249
Z3	1	-0.01848	0.08206	-0.23	0.823
Z4	1	0.90098	0.09114	9.89	0.000
Z5	1	0.04517	0.08102	0.56	0.581
Z6	1	0.03196	0.09075	0.35	0.727
Z7	1	0.03870	0.07634	0.51	0.616

R² = 84.2%%

effect value in all of the models, even though the construction of the model involving direct effects or not from imago size to parasitism rate, or even though the construct itself is different from other models (Figure 7 and Figure 8). Forewing length also gives positive value to parasitism rate, directly or indirectly, while head width and survival rate can be indirect indicators through egg numbers. Path diagrams of fitness traits on TaH shows that egg numbers is the one that gives positive and high value. The value of egg numbers in this host is not showing the same value as in the first host, but still gives highest value of all. For this host, head width as one of the

parameters should be considered as indicator for this host that affects the parasitism rate. Longevity also gives positive result to parasitism rate; this variable should be considered also as indicator to parasitism rate. For this host, forewing length can be indirect indicator through egg numbers.

Path Analysis of *T. armigera* in both host show that egg numbers has a significant effect to parasitism. This value is stable, because egg numbers in TaC and TaH gives positive and significant direct effect to parasitism (P-value=0.000), through standardized regression test. Even though the standardized regression test only shows that egg numbers is the only

variables that resulted in significant value. other variables should be considered also, because the variables still give contribution through third variables, and by itself will have indirect effect to parasitism rate.

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