

**The Effects of Egg Production on Longevity in the Parasitoid *Mastrus ridibundus*
(Hymenoptera: Ichneumonidae)**

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Abstract Parasitoid behaviors are predicted by dynamic optimization models based on variables that describe the insects physiology and surrounding environment. Many of these models assume an interaction between the cost of reproduction and longevity. However, the details of this of the trade off function are still undescribed. This paper investigates the effects of egg production on longevity in a synovigenic parasitoid *Mastrus ridibundus*. Reproduction efforts were manipulated and their corresponding longevitys are analyzed with a series of linear regression tests. The results show a negative correlation between both egg production and the number of hosts attacked. However a conclusive trade-off function could not be described.

Introduction

Parasitoids are a group of insects whose larvae develop by feeding on arthropod hosts. Adult females often paralyze hosts with an injection of venom that is delivered via the ovipositor. Eggs are then deposited in or on the host, and the larvae feed on the host's hemolymph. They are a unique group, with a developmental strategy that distinguishes them from both predators and parasites. Unlike predators, the consumption of a single host facilitates development into an adult; they differ from parasites in that larval feeding usually kills the host (Gauld and Bolton 1988). Their diversity and ability to adapt is evident in the range of host stages exploited (Mills 1994). As a group, parasitoids comprise an invaluable component of terrestrial ecosystems and are represented in the orders Hymenoptera, Coleoptera, Diptera, Lepidoptera, Neuroptera, and Trichoptera (Eggleton and Belshaw 1992; Wells 1992).

Studies on parasitoids, have led to tremendous advancements in a number of academic fields. Their success in agricultural systems, as biological control agents in integrated pest management programs, has not only reduced the application of environmentally degrading insecticides but has proved that sustainable pest management can be achieved (Huffaker and Messenger 1976). Within the field of population biology, the host-parasitoid relationship contributed to the development of models that describe species interactions and ecosystem stability (Walde and Murdoch 1988). These models are designed to predict optimal behavioral responses in different environments.

However, details of the "currency" that is optimized, and thus the behavior carried out, remains an issue under contention. Jaenike (1978), Charnov and Skinner (1984), and Ives (1989) proposed models within the framework of the optimal foraging theory; behavior and reproduction are a function of the rate of energy gained by ovipositing on the host of marginal quality or by searching for an alternative host. In these models, time and environmental conditions are the primary factors governing behavioral responses. For example, the time spent locating and handling a host of poor quality is time that could be spent finding a more suitable host. Therefore, the poor host should be abandoned and a new one should be sought out because the rate of fitness gained by finding the better host outweighs the fitness incurred from the poor host.

Other studies contend that optimal behavior is based on a lifetime reproductive success (Iwasa 1984; Houston et al. 1988; Mangel 1988; Heimpel et al. 1996; Rosenheim 1996). These

dynamic state variable models emphasize the physiological state of the searching parasitoid. Thus, optimal behavior is a function of not only time and environmental conditions, but also a function of the parasitoid's age, egg load, and nutritional status. For example, an old female with a large egg load should deposit eggs on hosts of marginal quality because that would return a fitness gain, whereas dying having laid no eggs returns no fitness. Although many of these models include functions illustrating a trade-off between reproduction and longevity, there are only a few empirical studies directly supporting this assumption (Ellers et al. 2000).

The basis for a trade-off between the cost of reproduction and longevity lies within the nutrient limitation theory. In general, this theory assumes that all activities draw on a common resource pool. Any activities performed during the life of the insect compete for the same resources. Therefore, allocation of resources to any activity would reduce the amount of energy available for maintaining life (van Noordwijk and de Jong 1986; Boggs 1997). Several experiments conducted on other organisms support the nutrient limitation theory and phenotypic plasticity. For example, Tatar et al. (1993) and Tatar and Carey (1995) found that early reproductive efforts caused an increase in age-specific mortality in the beetle *Callosobruchus maculatus*. In waterstriders, Kaitala (1991) reported decreased longevity and increased egg production given high quality environments. In *Drosophila* species, multiple mating decreased female longevity (Partridge et al. 1987; Fowler and Partridge 1989; Chapman et al. 1995; Chapman et al. 1998). Scott and Barlow (1984) reported that greater flight activity decreased longevity in the Syrphid *Metasyrphus corollae*.

Applying the theory to parasitoids requires the use of species that exhibit the synovigenic method of egg production. These types of species are able to mature eggs throughout their adult stage (this contrasts the proovigenic strategy, where adult females have a fixed number of oocytes within their ovarioles). Therefore, increased egg production draws on the energy reserves that could be allocated to extending longevity.

Two theories predicting the trade-off function exist within the literature. Rosenheim (1996) proposed a reciprocal relationship, defined by the function $L = 1/(aR)$, where (L) is longevity, (a) is a constant, and (R) is the reproductive investment. This theory states that the first eggs laid cause a greater reduction in longevity relative to eggs laid later in life. The logic behind it involves a reduction in egg size as the parasitoid ages. Alternatively, Sevenster et al (1998) proposed a linear trade-off described by the equation $L = T - aE$, where (L) is longevity, (T) is

the total amount of available resources, (a) is a constant, and (E) is egg production. Here, each egg laid reduces the total amount of available resources by the same increment.

Ellers et al. (2000) is the only known study that directly assesses this trade-off function in parasitoids. Their results suggest a linear trade-off function. However, their analysis was based on a small data set, and the assumption of a trade-off between egg production and intrinsic mortality rate could not be confirmed. This experiment will assess the trade-off function between egg production and longevity in the parasitoid *M. ridibundus* (Hymenoptera: Ichneumonidae).

Experimental Subjects *M. ridibundus* is a synovigenic parasitoid that attacks the codling moth, *Cydia pomonella* (Lepidoptera: Tortricidae), during the prepupal stage of development. *M. ridibundus* is a gregarious ectoparasitoid (several eggs are deposited and the larvae feed from the surface of the host). The females are synovigenic. At 26° C, *M. ridibundus* develops, from egg to adult emergence, in approximately 18 days. We regulated their population with a weekly provision of cardboard strips containing codling moths suspended in the prepupal stage. The culture was supplied with an allotment of honey and water three times per week.

Cydia pomonella (Lepidoptera: Tortricidae) is a major pest of apples, walnuts, peaches, and other stone fruits. The Okanagan-Kootenay sterile insect release program in Canada supplied us with egg sheets. The larvae fed on thinned, fuji apples at a temp of 20° C. Specially designed cardboard strips served as pupation sites for the developing larvae. We induced diapause with a photoperiod of eight hours, and the strips were removed and placed into a refrigerator. This maximized the availability of the host stage needed for laboratory experiments.

Methods

To impose the treatments of differential reproductive efforts, I created five groups delimited by a spread of total eggs laid (control = 0 eggs laid; group 1 = 1-10 eggs; group 2 = 11-20 eggs; group 3 = 21-30 eggs; group 4 = eggs laid for entire life). I conducted three trials (see Table 1). Each treatment group in the three trials contained a proportion of the total number of females for that group. All of the females used in the control group came from trial 1. Small vials (diameter = 4cm, height = 7cm) equipped with either honey cards alone (control), or honey cards and four hosts (all treatments), housed the parasitoids. I ensured the highest potential longevity within my sample population by selecting newly emerged females. To limit the frequency of mating, I

placed each female and two males into a vial for 24 hours. All specimens were kept in an incubation chamber set at 22° C.

I randomly assigned parasitoids to groups after their first successful oviposition. Thus, all individuals that oviposited on the first day were distributed to a group; these individuals were excluded from further assignment. I followed this protocol daily, until every parasitoid was included in a group. This method of distribution across all groups controlled for Tatar et al.'s (1993) finding, which linked a high early reproductive effort to increased age-specific mortality. Females of each treatment were exposed to four hosts per day until the target number of eggs laid was reached. Daily examination of the hosts yielded the number of eggs laid by each parasitoid. Larvae that contained eggs but were paralysed yet lacked the deposition of eggs were scored as a host attacked. Once a female reached the target egg range, I discontinued the supply of available hosts and recorded total longevity in days since eclosion. Mortality was recorded and the honey cards were replenished daily. Upon death, I measured the female's hind tibia and dissected their abdomens to determine the total number of mature oocytes remaining in the ovarioles. Mature oocytes were scored based on their opaque, banana shaped appearance. Immature oocytes were transparent and flat (Alexander and Rozen 1987). For each female, I determined the total number of eggs laid, the total number of eggs produced (eggs laid plus mature oocytes contained in the ovarioles), the number of hosts attacked, the hind tibia length (HTL), and the longevity since eclosion.

I analyzed the data using a series of simple linear regression tests. Each variable was tested within each of the three trials. I also performed a linear regression with the combined data set.

Results

The results on the series of simple linear regression tests for each trial are summarized in Table 1. All of the variables were tested against the dependent variable, longevity. Neither the total number of eggs produced nor HTL had a significant effect on longevity in any of the three trials. In trial 1, only the number of hosts attacked had a significant effect ($p = 0.0311$, $R^2 = 0.0932$). None of the variables yielded a significant effect in trial 2. In trial 3, the number of hosts attacked and the number of eggs laid revealed significant effects on longevity ($p = 0.0014$, $R^2 = 0.587$ and $p = 0.0065$, $R^2 = 0.473$ respectively). Table 1 displays the results from the regression tests for the combined data set. The number of hosts attacked and eggs laid each had a

significant effect on longevity ($p < 0.001$, $R^2 = 0.10$ and $p = 0.005$, $R^2 = 0.087$ respectively; Fig. 1 and Fig. 2). There is a negative correlation between eggs laid and longevity. However, there is a stronger negative relationship between longevity and the number of hosts attacked.

treatment		HTL	Total eggs produced	Eggs Laid	Number hosts attacked
trial 1 n = 50	Rsqr =	0.0118	0.0224	0.067	0.0932
	P =	0.452	0.2994	0.0696	0.0311
trial 2 n = 26	Rsqr =	0.0015	0.00918	0.0355	0.0396
	P =	0.8535	0.6487	0.3673	0.34
trial 3 n = 13	Rsqr =	0.0747	0.251	0.473	0.587
	P =	0.3444	0.0681	0.0065	0.0014
complete set n = 89	Rsqr =	0.00166	0.038	0.087	0.1
	P =	0.7045	0.067	0.005	0.0025

Table1 displays the results of the linear regression tests for each trial and the entire data set. Each variable was tested against the dependent variable longevity. Eggs laid and number of hosts attacked both had significant effects on longevity for trial 1, 2, and the entire data set. The increasing R^2 values and the decreasing p-values following the variables HTL, total eggs produced, eggs laid, and number of hosts attacked.

An interesting pattern exists across all three trials and the combined data set. There was a gradual increase in the R^2 values and a decrease in the p-values following the variables from the total number of eggs produced, to eggs laid, and finally to the number of hosts attacked (Table 1). Thus, the number of hosts attacked had the largest impact in reducing longevity. Using this variable in a least squares regression model yielded a linear trade-off (Fig 2; $p = 0.0025$; equation Longevity = $25.1 - 0.283 * \text{the number of hosts attacked}$). I used the same variable to test the reciprocal model (Fig 3; $p > 1E20$; the statistical software failed to report an equation). The R^2 for the reciprocal fit had to be discarded because the sum of squares of the residuals was too large and resulted in a value greater than 1. Comparison of these tests suggests that the linear trade model better describes the trade off function.

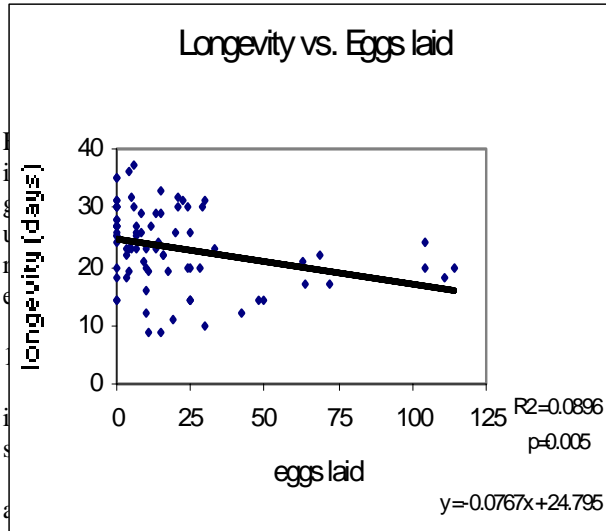


Figure 1 is a graph of longevity as a function of eggs laid for the entire data set. The regression line is significant, $R^2 = 0.087$; $p = 0.005$, displaying a negative correlation between longevity and eggs laid. The positive trend after day 15 displays the imposed treatment, and switching of the dependent and independent variables.

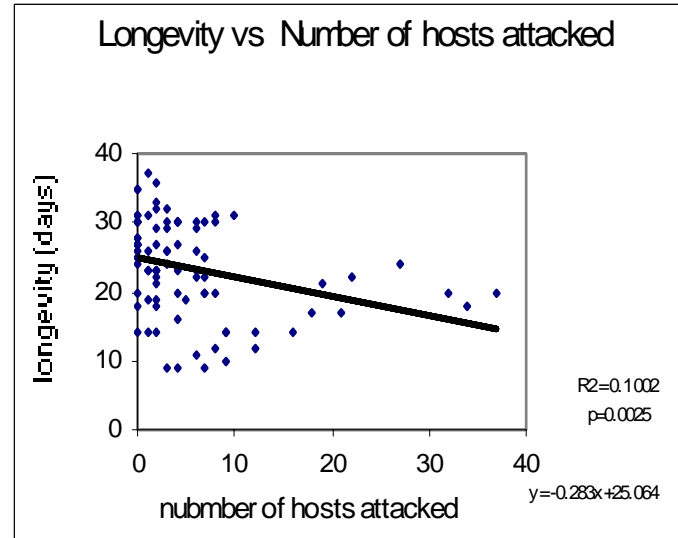


Figure 2 is a graph of longevity as a function of number of hosts attacked for the entire data set. The regression line is significant, $R^2 = 0.1$; $P = 0.0025$. There is a stronger negative relationship between the number of hosts attacked and longevity.

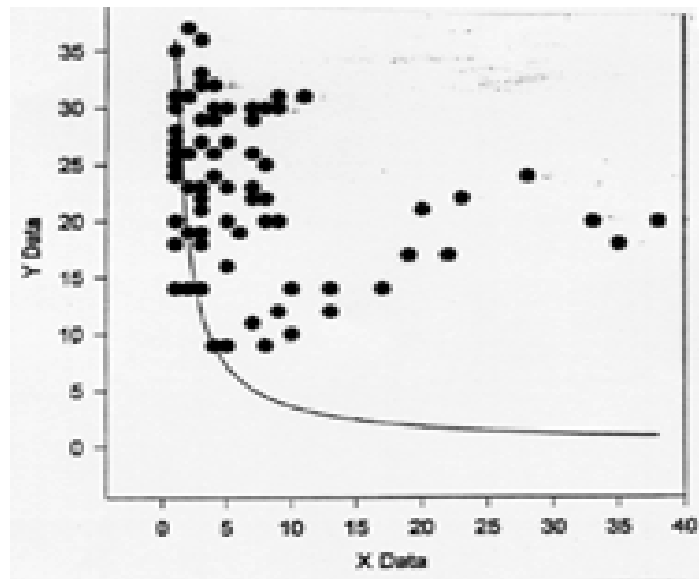


Figure 3 is a graph of the reciprocal fit line. The y axis is longevity, and the x axis is number of hosts attacked. When compared to the best fit line for longevity versus number of hosts attacked, it is clear that the linear model is a better representative of the trade-off function.

During the experiment, a number of specimens experienced premature mortality. This effect is a display of compositional heterogeneity (Vaupel and Yashin 1985; Vaupel and Carey 1993). I eliminated some of these individuals based on previous intrinsic mortality measurements. Mills (1999) found premature mortality inflicted a proportion of the population. He noted that the species gained stability at the 86th percentile measured in the cumulative survivorship curve (Fig. 4). I applied this to my experiment, and a cut-off point of 9 days was calculated. I discarded any individuals that died before this period. Consequently, all of the above tests were carried out on the reduced data set.

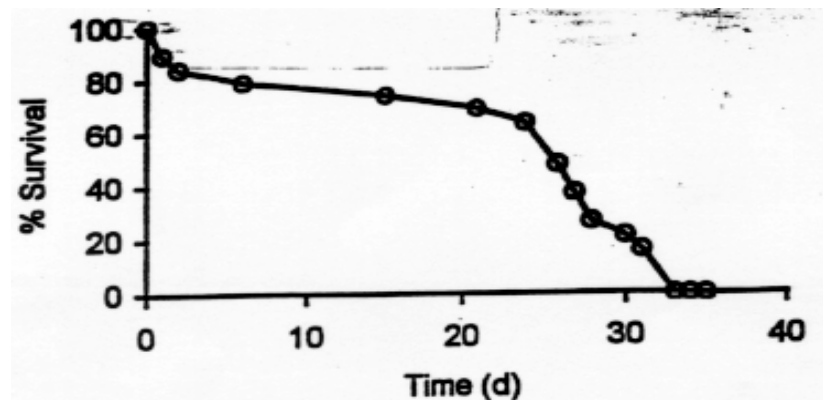


Figure 4 is a graph of the cumulative survivorship curve. The population experiences a sudden increase in mortality over the first 14th percentile. The population then approaches a stability. When applied to my data set, this percentile translates into a nine day cut-off threshold. All parasitoids that died within nine days were excluded from the analysis. The graph comes from Mills (1999).

Discussion

The lack of a consistent effect of any variables across all three trials and the low R^2 value of the linear trade-off function (based on the number of hosts attacked; see Fig. 2 and Table 1) prevent any inference of a concrete trade-off between egg production and longevity. The linear trade off model yielded the equation (Longevity = 15.1 – (0.283 * the number of hosts attacked)). Although the linear trade-off model is significant ($p = 0.0025$) the low R^2 value of 0.1 signifies that the cost of reproduction did not have the expected, large negative effect on longevity. One reason the data was inconclusive within the context of the model may be due to the large variability of mortality within the parasitoids that laid less than 30 eggs (Fig. 1 and Fig. 4). Although a reduced data set was used, I believe a large proportion of the sample population

still experienced premature mortality caused by factors other than a complete exhaustion of stored resources.

The high variation in mortality could be a result of desiccation. Relative humidity was not controlled within the incubation chamber, and throughout the experiment I observed that nearly all of the honey cards were dry within 24 hours. This suggests that individuals may have starved to death. Also, the presence of hosts may have caused humidity levels within the vials to rise, thereby preventing desiccation. This could have prevented early mortality in the groups that were exposed to hosts for a greater number of days.

Another source of variation that could have influenced longevity is compositional heterogeneity. Vaupel and Yashin (1985), Vaupel and Carey (1993), and Tatar and Carey (1995) reported treatment inappropriate responses that yielded a convergence of age-specific mortality of subgroups within cohorts. Thus, the mortality rates of individuals within different subgroups merged; as a result, there were no differences in their measured longevity. Other explanations for the variability in early deaths could be differential energetic expenditures related to flight. Scott and Barlow (1984) reported decreased longevity related to increased flight activity. I observed that the *M. ridibundus* often rested or hid inside the strips. Bernstein and Driessen (1996) reported that semiochemical markers of parasitoids can influence within patch searching behavior. The presence of hosts may have relaxed or arrested the parasitoids, whereas an absence of hosts might have induced increased flight activity in the hopes of escape.

Other costs that may have contributed to unrealized longevity potentials are linked to physiological regulation. Reproduction is known to cause a rise in certain hormones that are linked to decreases in the immune response of some insects (Sapolsky et al. 1986; Folstad and Karter 1992). Chapman et al. (1995) found that sperm can contribute to the decreased longevity in female *Drosophila* species. Harman (1981) reported that oxidative damage resulting from metabolic processes can damage tissues and cause premature mortality.

Despite this variation, analysis of the relationship between HTL and longevity reveals that reproductive processes and maintaining longevity compete for the same resource pool. Hardy et al. (1992) and Petersen and Hardy (1996) reported that larger parasitoids have longer life spans. They are able to store greater amounts of nutrients in fat body reserves (Ellers 1996). The fat body acts as a nutrient bank. It can be metabolized and the released energy can be allocated to sustain various activities. Bezemer and Mills (unpublished data) found a positive correlation

between HTL and longevity in non-reproducing females (Figure 5a; $R^2 = 0.18$; $p < 0.0002$). However, this correlation disappears in reproducing females (Figure 5b; $R^2 = 0.0027$; $p = 0.704$). This suggests that the energy requirements associated with longevity draw on a common resource pool, and that this stored energy can be allocated to reproduction or longevity.

The consistent pattern of gradually increasing R^2 values and decreasing p-values in the variables, total number of eggs produced, eggs laid, and the number of hosts attacked respectively (Table 1) may illustrate an interaction that has never been documented. Although it cannot be measured directly, the pattern suggests that the act of egg laying is more costly than the production of eggs. I believe that this increased cost can be attributed to the production of venom. Further, I theorize that venom production requires an allocation of resources that outweighs the investment associated with egg production. Because every oviposition bout is accompanied by an injection of venom, the results of Ellers et al. (2000) study are confounded with the potential cost of venom production. This could have a significant impact on the formation of dynamic optimization models, requiring different methodological approaches relative to gregarious and solitary parasitoid species. This is a fascinating aspect of my study and it warrants further research.

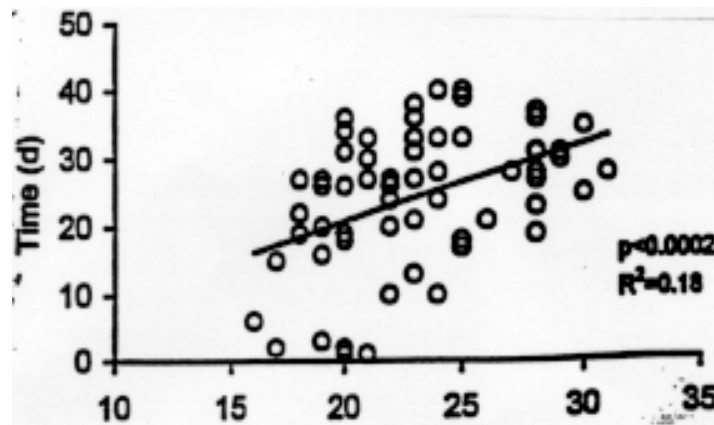


Figure 5a is a represents the positive correlation between longevity and HTL. $R^2 = 0.18$, $p < 0.002$.

This data is for non-reproducing females.

It was obtained from Bezemer and Mills Lab (unpublished data).

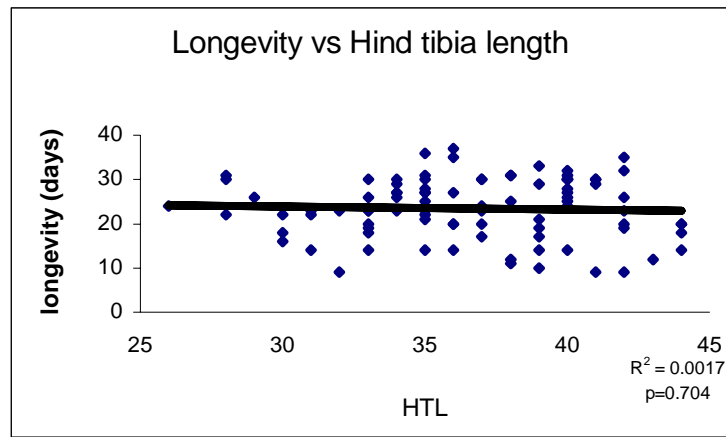


Figure 5b illustrates the disappearance of the positive correlation seen in Fig. 5a. This shows that reproduction and longevity must draw on the same resource pool.

A potential methodological problem was associated with the variables measured and the imposed treatment effect of differential egg laying. The variables measured are confounded, and there is a switch between the independent and dependent variable in group 4. The number of eggs laid is dependent on the number of oviposition bouts, and the number of oviposition bouts is dependent on the rate of egg laying (number of eggs per oviposition bout). For example, females in groups 1, 2, or 3 that had a high rate of egg laying reached their targeted egg production faster, thus, they had a fewer number of oviposition bouts. The slight positive trend after day 30 (Fig. 1) displays the switching of variables. After day 30, longevity is no longer a function of eggs laid, rather eggs laid becomes a function of longevity. A study conducted by Tatar et al. (1993) suffered from the same effect, however they did not address its importance in their study. However, in a later study Tatar and Carey (1995) altered their methodology. This leads me to believe that the imposed effect had a small, yet significant effect on the data. I believe the effect is small, because their first study was published, however in further research it must be corrected for.

New methods are needed to correct for this error. There are two possible approaches. First, egg production could be maximized the treatment groups, and the number of hosts available for attack would vary between groups. For example, low reproductive effort = 2 hosts and high reproductive effort = 10 hosts. They would be allowed to lay as many eggs as they could, and I would measure their corresponding longevity. This would not only eliminate the variable switching problem, it would also distribute the early mortality influence across all groups equally. A simple t-test could be applied to test for a difference in mean longevity between the

high and low reproductive groups. The second, varies the number of days that the parasitoid is exposed to hosts. Differential egg laying efforts should be imposed by supplying a varying number of hosts over the same number of days. For example, low reproductive effort = 2 hosts and high reproductive effort = 10 hosts. This might produce a varying number of eggs laid between groups, and their differences could be measured by an t-test.

However, there is a potential problem that might actually prove beneficial to other research. Bezemer and Mills (unpublished data) found that *M. ridibundus* varies the clutch size according to the availability of hosts. This might yield equal numbers of eggs laid between the groups. Although this would not be useful in the analysis of egg production on longevity, it could be used to analyze the effects of the cost of venom. If there is no difference between the number of eggs laid across the groups, there must be a difference in the number of hosts attacked. This would isolate the cost of venom production, and it could be tested by an ANCOVA with HTL as a covariant.

In conclusion, although there was an effect of eggs laid on longevity in the simple linear regression test for the combined data set, a linear trade-off could not be assumed. Little support was gained for the linear trade-off model. However, examination of the disappearing positive correlation between longevity and HTL in reproducing females reveals that reproduction and longevity draw on a common resource pool. The consistent pattern of increasing R^2 values and decreasing p-values following the variables total number of eggs produced, eggs laid, and the number of hosts attacked (Table 1) may illustrate a relationship that has never been documented in parasitoid literature. This pattern suggests that the costs incurred by the process of egg laying is greater than the costs associated with maturing oocytes. I believe that the cost of venom requires an allocation of resources that outweighs the cost of producing eggs.

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