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Energy utilization by Adult Females of a
Hover fly *Eupeodes corollae* (Fab.) (Diptera: Syrphidae):
the effect of female size and reproductive state.

by

LOUISE M. H. CHARRON, B.Sc.

A thesis submitted to the Faculty of
Graduate Studies and Research in partial fulfilment
of the requirements for the degree of
Master of Science

Department of Biology
Carleton University
Ottawa, Ontario
May, 1988

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May, 1988

ABSTRACT

Energy budgets were constructed for small, large, mated and unmated female *Eupeodes corollae* (F.) fed pollen and 2 % sugar solution *ad libitum*. Consumption, respiration, production and rejecta were measured, energy allocations in the 4 categories were determined and ecological efficiencies calculated. Fecundity was not correlated with body size and mated flies laid significantly more eggs than unmated ones. Longevity was similar between the 4 categories. Flight affected longevity, with small flies affected most. Small and large flies apportion their energy in a similar manner. Small and large flies may contribute equally to population increase if flight is unnecessary. Mated flies allocate more energy to reproduction while unmated flies are heavier.

Consumption was highest in mated flies ($176.9 \text{ cal}\cdot\text{fly}^{-1}$) and lowest in unmated flies ($142.1 \text{ cal}\cdot\text{fly}^{-1}$). Large flies consumed more ($168 \text{ cal}\cdot\text{fly}^{-1}$) than small flies ($149.2 \text{ cal}\cdot\text{fly}^{-1}$). Mated flies produced more faeces than unmated flies and large flies produced more regurgitated pollen than did small ones. Large flies produced the most rejecta; they also consumed the most food. Unmated flies consumed the least and produced the least amount of rejecta. Assimilation efficiencies were similar in the 4 categories and ranged between 38.7 to 42.3 %. Gross production efficiency ($P/C = 11.3$ to 12.2%) and gross respiration efficiency ($R/C = 27.4$ to 30.1%) were similar among the four categories. Net respiration efficiency (R/A) of all 4 categories was 70.0 to 71.1 % and net production efficiency

(P/A) did not vary with size or reproductive state and ranged between 28.3 to 30.0 %.

ACKNOWLEDGMENTS

I would like to thank my supervisor Dr. C. A. Barlow for his intellectual and financial support throughout this thesis. I would also like to thank my committee members Dr. J. Houseman for his knowledge of insect physiology, and Dr. L. P. Lefkovitch for his statistical expertise. All 3 supervisors spent many hours during committee meetings and their own spare time setting me on the right track.

I have spent most of my laboratory hours working along side Jo Anne Whittingham who has not only helped me iron out technical problems, but has supported me through both the rough times when I was ready to give it all up and has laughed with me through the good times. I hope I have returned the favour.

I would like to thank Dr. A. J. Damman for his help with the little problems that arose day to day, and also for the use of his computers both in his laboratory and in my own home. This saved me many hours of time.

My friends were a great help and had to put up with me when I didn't even like my own self.

I especially want to thank William Ogilvie for his friendship and love; and who kept reminding me that there was an end to all these years of work.

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INTRODUCTION

The hoverfly, *Eupeodes corollae* (F.) (Diptera: Syrphidae) (Figure 1) (formerly *Metasyrphus corollae* (F.)), is an obligate predator of aphids in the larval stage. The nomenclature for *E. corollae* has been established by Vockeroth (Pers. Com, 1988). It has also been cited in the literature as *Syrphus corollae* (Schneider, 1948; Bombosch, 1962; Stürken, 1964; and Barlow 1979) and also *Eupeodes cognatus* (Luv. 1860, Vöckeroth Pers. Com. 1988). The species is widespread throughout Eurasia, North Africa, South Africa, Egypt, Tanzania, and Formosa..

In Denmark, fertilized females from Central Europe immigrate to start a new generation every spring (Torp, 1984). Migration has been observed also in Sweden (Svensson and Janzon, 1984) due to high aphid populations the year previous and patchy aphid populations in the year of migration. More than 50 % of the migrants were reproductively immature females and all the flies had consumed some pollen. *E. corollae* may hibernate in the pupal stage (Torp, 1984) or overwinter as larvae (Svensson and Janzon, 1984).

Since eggs are usually oviposited within, or on the edge of an aphid colony, freshly hatched larvae do not have to travel far to find food. Aphids and/or aphid honeydew are the oviposition stimuli (Scott, 1983). The larvae (Figure 2) of *E. corollae* apparently rely on touch to locate aphids. Larvae search for prey by first feeling the immediate area with the anterior part of the body. They start to move, always feeling the surroundings around them. The front half of the body is lifted completely from the substrate and swung from

Figure 1. Adult Female *Eupeodes corollae*. (Ruler is in mm).

Figure 2 Larva of *Eupeodes corollae*. (Ruler is in mm).

side to side. At first contact with an aphid, the larva exudes a sticky saliva which it uses to trap the aphid. The larva then pierces the aphid with its jaws and quickly lifts it off the substrate. The first two front segments of the larva are retracted and the aphid sits in a hollow of the contracted proboscis, like a cork. The aphid contents are sucked out and, when finished, the larva discards the aphid carcass (Schneider, 1969). Satiated larvae usually rest near aphid colonies so they can reach their food quickly. The larval stage lasts about 8 days at 20 °C. Energy budgets for the larval stage have been constructed by Bomboesch (1962, 1963) and Barlow (1979) with larvae feeding on the aphids *Aphis fabae* (Scop.) or *Acyrtosiphon pisum* (Harris). Pupation lasts for about a week at 20 °C and occurs in the soil or among the leaves of plants. Adults live for about 2 weeks at 20 °C, but some flies have lived up to a month (Scott, 1983).

Pollen consumption is necessary for oogenesis in *E. corollae* (Schneider, 1948; 1969) and nectar may be eaten as a carbohydrate source. In England and Sweden, *E. corollae* has been observed feeding on the pollen and nectar of Asteraceae (Gilbert, 1980; Svensson and Janzon, 1984).

Syrphid larvae can consume 100 or more aphids but the suitability of these predaceous insects as control agents depends on their reproductive output in low and high aphid populations. Since aphid populations are ephemeral, syrphid larvae may experience low aphid populations during development. Cornelius and Barlow (1980) observed that, with increased aphid consumption above 38 aphids per larva (55 cal.), fecundity in adult females increased linearly with

consumption up to 58 aphids/ larva. The mean weight of pupae and adult flies also increased with increased larval consumption (Barlow, 1979) and developmental time decreased (Cornelius and Barlow, 1980). Reproductive state greatly affected energy allocation in *Oncopeltus fasciatus* (Slansky, 1980a, b).

The energy supply of *E. corollae* probably fluctuates more than that of a herbivore because of the transitory nature of aphid populations. How then should they apportion their energy to reproduction if they encounter low aphid populations during the larval stage? A change in energy allocation in small and large adult *E. corollae* may influence the relative importance of growth, maintenance and reproductive output for overall fitness.

The reproductive state of mating in insects has many physiological affects on egg production (Englemann, 1970) The act of mating affects an increase in egg production (Riegert, 1965; Baudoin and Boivin, 1985); it induces oviposition ((Vennison and Ambrose, 1986; Rutowski and Gilchrist, 1987) and egg maturation (Englemann, 1970; Ladd, 1987)). The effect of reproductive state on energy allocation in female *E. corollae* will be discussed.

E. corollae require a sugar source for adult maintenance but if this is not obtained, flies can still survive for a few days. This ability to survive means that some energy from larval stores goes to adult maintenance (Scott, 1983). Insect size affects how much larval reserve is available for adult maintenance, and if this same energy is important for dispersal, then adult maintenance in small flies will be reduced more than large flies. If aphid populations are sparse when

a fly emerges, it will have to disperse to reproduce and dispersal decreases longevity of small flies more than large flies (Scott, 1983). Thus the cost of reproduction for small flies may be higher than for large flies because, when oviposition occurs over a period of time, fecundity will be affected also.

I compared the energy budgets of the reproductive stage of small and large female *E. corollae* to see if size affects how the flies apportion their energy. Mating has an effect on longevity (Slansky, 1980a, b), so I also compared the energy budgets of mated and unmated female *E. corollae*. Ecological efficiencies were calculated and energy flow diagrams constructed and compared among the four categories.

Energy budgets

Bioenergetics is the study of energy transformations occurring in living organisms (Downer, 1981). Ecological energetics "encompasses any bioenergetic approach which contributes to a fuller understanding of energy transformations by ecological units in the environmental conditions normally experienced by them" (Phillipson, 1975).

Lindeman (1942) first discussed the transfer of energy between populations. The common denomination used in these early publications was the calorie. Since 1948, the internationally accepted basic unit of heat energy has been the joule. However much of the literature on energetics has used the calorie which is equivalent to 4.1867 J. I will therefore use the calorie throughout for comparison.

Wiegert (1968) derived the classical equation for an energy budget from the equation for the First Law of Thermodynamics as follows.

$$C = P + R + FU \text{ where}$$

C = consumption

P = production (growth and reproduction)

R = Respiration

FU = Rejecta (F = Faeces and U = urine)

Petrusewicz, (1967) defined faeces, as that part of consumption that is rejected as nitrogenous waste and indigestible portions or regurgitated food. Assimilation is defined as ingestion - egestion. The food assimilated by a population includes respiration (life maintenance), and production (growth and reproduction). Growth is that part of production that is retained in the organism or the amount of tissue elaborated per defined time interval (Petrusewicz, 1967). In this study, the interval was the adult stage of *E. corollae* females from emergence to death.

METHODS

Stock Colony

The stock colony of *E. corollae* was kept in a 90 x 50 x 45 cm screened cage in a room maintained at $20 \pm 1^\circ\text{C}$, $70 \pm 10\%$ R.H with a 16 h photoperiod. Room lighting was provided by a combination of 84 % "cool white" fluorescent and 16 % incandescent of the total number of lamps giving an intensity of 9000 lux. at bench level. Adult flies were provided with pollen of mixed origin (a protein source for oogenesis) and diluted honey (a carbohydrate source) on the floor of the cage. Seven days after the flies emerged and at 2-day intervals thereafter a 12.5 cm pot containing small pea seedlings (*Pisum sativum*) infested with pea aphids (*Acyrtosiphon pisum*(Harris)) was placed in the cage. Females were stimulated to oviposit by the presence of aphids. When sufficient eggs had been deposited, the pot was removed and placed in a 19 x 19 x 31 cm screened cage. Eggs hatched 2-3 d later and the larvae were fed pea aphids *ad libitum*.. After 4-5 d, 100 larvae were transferred from the first pot to a second pot of aphid-infested peas which was then covered with 25.5 cm x 12 cm plastic cylinder. Screen covered holes in the wall of the cylinder allowed for air circulation; a removable screen-covered lid permitted addition of aphids. When larvae matured they pupated usually in the soil or on the leaves of plants.

Pea plans were cut down to soil level and pots containing pupae were placed in a 19 x 19 x 31 cm screened cage until adult flies emerged (3 d later). Upon emergence adult syrphids were collected and maintained in the stock colony cage.

Experimental Insects

Two different sizes of flies were raised. Some larvae were offered an average of 10 aphids per larva per day and developed into pupae which weighed between 12 and 20 mg. Pupae were collected from each pea pot by cutting off the pea plants and shaking the stalks gently in order to dislodge any pupae that did not pupate in the soil. The stalks were discarded and the soil was gently shaken away from the pea roots. Pupae were removed from the soil using feather forceps and kept in petri dishes, 5 pupae/dish.

Adult flies which subsequently emerged from these pupae were considered small adults ("starved"). Other larvae were fed aphids *ad libitum*. Adults from these pupae were called large ("well fed") and pupae weighed more than 25 mg. All pupae were weighed to ensure that they fell into the appropriate weight class.

Adults which emerged were kept individually in 450 mL Mason® jars. The bottoms of the jars were lined with teflon sheets cut to size (6.5 cm x 6.5 cm) and affixed with double sided tape.

Fly Mating

Small and large females were mated with large male flies to ensure equal mating chances of all flies either small or large. Two virgin males, (24 h old) were placed with one virgin female in a 450 mL jar with pollen and 2 % (w/v) sugar solution was supplied to allow feeding *ad libitum*. Females that were mated within 3 d of emergence were kept for experimental use. Mating was easy to observe since flies remained *in copula* for > 2 h.

Longevity was calculated from day of emergence but consumption was calculated from the time flies were placed in experimental jars with preweighed pollen and sugar. Unmated flies were placed in experimental jars on the day they emerged.

The components of the following equation were measured to determine energy budgets for the flies.

$$C = P + R + FU$$

Consumption (C) consisted of pollen (C_P) and a solution of sugar (C_S). Reproduction (egg production) (P_R) and fly growth (P_G) were measured as production (P). Respiration (R) was measured, and rejecta (FU) was the sum of faeces (FU_f) and regurgitated pollen (FU_{rp}). The equation for the total energy budget was then

$$C_P + C_S = P_R + P_G + R + FU_f + FU_{rp}$$

This was calculated in total calories·fly⁻¹.

Consumption

Sugar

A 2% sugar solution (sucrose:fructose:glucose in a ratio of 1:2:2) was presented in one-half dram screw cap vials (1.8 - 2 mL). Vials were prepared by placing three 0.1 cm long pieces of capillary tube held together with parafilm and inserted into the vial opening. A diamond pencil was used to scratch identifying numbers on the sides of the vials. A 1:1 acetone:water solution was used to clean the vials of finger prints and tiny glass shards. Clean empty vials were weighed on a microbalance (Metler Micro Gram-Atic, Fisher Scientific

Co.) and then covered with parafilm to keep the surface clean. A 1.0 mL plastic syringe was used to add 1.5 mL of sugar solution to each vial. After 7 d, 0.5 to 1.0 mL of sugar solution was added if necessary so that vials never went dry. Vials were inserted upside down into the jars, 1 vial per jar, and taped in place with masking tape. The sugar solution did not drip out and flies were able to drink *ad libitum*.

After the flies died, vials were removed from the jars and the tape and parafilm removed from the outside. The vials were then dried for 24 h in an oven at 50 °C, to evaporate some water out of the capillary tubes. This prevented the sugar solution from oozing out of the capillary tubes at low pressure during subsequent freeze-drying.

The vials were cleaned with an acetone:water solution and stored at -20°C until 30 - 40 vials were collected for freeze-drying. Vials were freeze-dried to constant mass. The vials were then weighed to obtain the mass of sugar remaining which was subtracted from the original amount of sugar added to the vials. The caloric content of the sugar mixture was calculated to be 3.784 cal•mg⁻¹ (Weast and Astle, 1981). Sugar consumption was calculated in total cal•fly⁻¹.

Pollen

Pollen of mixed specific origin (bee collected) was mixed in a blender until a very fine consistency was achieved. This was then presented to the flies in 2 mL polyethylene vials with snap tops (Bell Art Products, Pequannock, N. J.). The vials were prepared by heating

a finishing nail and melting 2 holes, one on each end and 2 rows of 3 holes on one side of each vial. The empty vials with caps attached were weighed on a microbalance, packed tightly with pollen and snapped closed. Excess pollen that stuck to the outside of the vial was brushed away. The pollen vials were freeze dried to a constant weight for 72 h and then reweighed. A small piece of masking tape affixed on the side opposite to the two rows of holes prevented the vial from rolling on the bottom of the jar. This set-up provided the flies with pollen *ad libitum*. After the flies died, the vials of remaining pollen were removed and freeze dried for 48 h. Faeces and regurgitated pollen were scraped off and collected. A damp, camel-hair brush was used to wash the pollen vial clean of regurgitated pollen and the brush was then dipped in acetone (in 100 ml vials) in order to collect all the regurgitated pollen produced by all the flies. Pollen vials were then freeze-dried to a constant weight. The caloric equivalent of the pollen is $6.20 \text{ cal} \cdot \text{mg}^{-1}$ (ash-free) (Barlow and Whittingham, Pers. Com.)

Jars were assembled as follows: a large square of teflon was affixed to the bottom of the jar, and small circles of teflon (1.5 cm diameter) were cut out and affixed to the bottoms of the sugar vials. Pollen dishes were taped to the bottom of the jar (Figure 3) then jars were covered with cheese cloth held in place with metal rings provided with the jars. Sugar vials were taped to the side of the jar, upside down. When jars were being disassembled, any pollen scattered on the bottom of the jar was collected and total pollen consumption adjusted accordingly.

Figure 3. Mason® jar (450 mL) used to maintain female *Eupeodes corollae*. The bottom of the jar and sugar vial were lined with teflon. A pollen dish was affixed to the teflon on the bottom of the jar, and a sugar vial was taped upside down on the side of the jar. The jar was covered with cheese-cloth and held in place with a Mason® jar ring.

Respiration

Oxygen utilization of flies 5, 8, 10 and 12 days after emergence was measured. Four to 5 flies from each group from each experiment were placed individually in 25 ml flasks in a Gilson Respirometer (Gilson Medical Electronics, Middleton, Wisconsin). Two identical flasks without flies served as controls. Each flask contained 0.4 mL of 20 % (w/v) KOH to absorb the CO_2 respired by the fly. A 1.0 cm diameter copper wire mesh screen was placed over the KOH receptacle to exclude the flies. A piece of Kimwipe® was placed in the bottom of the flask as a holdfast for the fly; flies became agitated if the tissue paper was not provided. Flies were weighed before being placed in the respiration flasks. The flasks were connected to the respirometer, sealed closed with stopcock grease and submerged in the water bath at 20 ± 1 °C. The flasks were equilibrated for 30 min, then the system was closed; O_2 utilization was measured after 1 h.

The barometric pressure (P) in mm Hg, time, room temperature (T) °K and the vapour pressure of water (Pw) (Weast and Astle, 1981) were noted in order to calculate a multiplying factor. The respiratory quotient (R.Q.) 0.85 ($1 \mu\text{l O}_2 = 4.683 \mu\text{cal}$) was used to convert μl of O_2 into calories (Southwood, 1978). Flies were weighed before being placed in the respiration flasks. Respiration rates were measured as $\text{cal} \cdot \text{day}^{-1}$. The statistical analyses for respiration followed the same format as pollen and sugar consumption.

Since flies generally remained relatively motionless in the flasks, the respiration measured was assumed to be basal respiration (Duncan and Klekowski, 1975).

If respiration was measured more than once for any individual fly, a mean fly mass was calculated. A mean mass was calculated for each group of flies.

Production

Growth (P_G)

To determine if mass gain occurred due to adult feeding, some newly emerged flies were kept in jars for 24 h with only water to allow the meconium to be expelled. Other females were subsequently fed *ad libitum* for 5 d or 10 d. Flies were weighed live and then frozen in preparation for freeze-drying. All flies were freeze-dried for 3 d then reweighed on a microbalance. The experimental design was factorial with 3 food regimes (no food, 5 d, and 10 d), two sizes small and large (S and L) and 2 status categories mated and unmated (M and U). The caloric equivalent of flies ($\text{cal}\cdot\text{mg}^{-1}$) was determined in a Phillipson microbomb calorimeter (Phillipson, 1964) (Gentry Instruments Inc., Aiken South Carolina). Benzoic acid (Fisher Scientific Company, Fairlawn, New Jersey) ($6,3189 \text{ cal}\cdot\text{mg}^{-1}$) was used to calibrate the bomb and the chart recorder.

Reproduction (P_R)

Eggs were collected in a petri dish three times per week beginning on the fourth day after emergence. Petri dishes were prepared by lining dishes with damp pieces of filter paper, one piece per dish. A piece of pea stem with 4 leaves infested with aphids was

placed on top of the filter paper. Aphids were left to settle on the leaves for 1 h before the flies were introduced, one fly per petri dish. Aphids were necessary as they provided an oviposition stimulus. Females were permitted to lay for 4 h and then were returned to their jars and the eggs counted. Eggs were collected, cleaned and stored in acetone in a freezer. The caloric content of the eggs was determined subsequently in a Phillipson microbomb calorimeter. Egg mass ($\mu\text{g}\cdot\text{egg}^{-1}$) was determined by weighing 25 samples of eggs for each group of flies (SU, SM, LU, and LM) on a microbalance. The number of eggs in each sample was counted and the mass per egg was calculated. Caloric equivalent of eggs produced by each fly was calculated and a mean for each group from each experiment was determined as $\text{total calories}\cdot\text{fly}^{-1}$.

Rejecta

Rejecta in these adult syrphid flies consisted of faeces (FU_f) and regurgitated pollen (FU_{rp}). The flies "play" with the pollen, secrete digestive juices and ingest part of the resulting liquid. The remainder was left behind on the teflon, or on the pollen dish. This was collected daily and stored in acetone. Faeces were collected and stored in the same manner (during the growth experiment). At the end of each experiment the faeces and regurgitated pollen were dried in glass petri dishes in a fume hood for 24 h to evaporate the acetone and then freeze dried for 3 d. The dried mass was weighed on a microbalance and the amount divided by the number of flies in each block. The $\text{cal}\cdot\text{ash-free}\cdot\text{mg}^{-1}$ and percent ash were determined and caloric equivalents calculated as $\text{total calories}\cdot\text{fly}^{-1}$. The means of

the caloric content and percent ash of faeces and regurgitated pollen were determined using the the statistical computer package SPSSX Kruskal-Wallis Chi Square test..

The experimental design was in the form of an incomplete factorial block with eight different experiments (Table 1) to test for differences between small (S), large (L), unmated (U), and mated (M) female flies. It was biologically impossible to raise enough syrphids to the adult stage to look at all four groups (SU LU SM and LM) at the same time so a series of eight experiments (two groups per experiment) was determined and tested with an ANOVA (Genstat) (See Appendix). Consumption, respiration, reproduction and rejecta were measured in the eight experiments to ensure that generation effects were balanced.

The means for SU, SM, LU and LM were not calculated because the design is a balanced incomplete block in which these terms are confounded with sequence; only the means of S, L, M, and U can be estimated.

Pellet formation

Freeze-dried faeces, regurgitated pollen, flies, and eggs, were prepared for the bomb calorimeter by grinding each sample in a Wig-L-Bug (Crescent Dental MFG. Co., Chicago, Illinois). The samples were freeze-dried to ensure that no volatile compounds were lost due to excess heat. The loss of these compounds and the chemical alteration of others would have lowered the caloric content. The samples were then made into firm pellets using a hammer and a pellet maker. The pellets were redried then and bombed.

Table 1: Order of syrphid categories in 8 different experiments to measure consumption, respiration, reproduction and rejecta in female *E. corollae*. S = small, L = large, U = unmated, and M = mated.

Experiment No.	Syrphid categories	
1	SU	LU
2	SM	LM
3	SU	SM
4	LU	LM
5	SU	SM
6	LU	LM
7	SU	LU
8	SM	LM

Approximately 5 pellets of each sample (except regurgitated pollen) were ashed in a muffle furnace at 650 °C for 12 h in Coors No. 4 crucibles. Ash-free masses were determined for regurgitated pollen, by weighing the platinum pans after combustion of the sample in the microbomb. The ash-free masses of all samples were used to calculate total calories·fly⁻¹ for consumption, rejecta and eggs.

Activity and Energy Use

Female *E. corollae* of 2 sizes (S, L) and 2 reproductive states (U, M) were maintained in small cages to determine consumption and fly weight in flies that had restricted flight. The data were compared to flies maintained in 450 mL jars because, during respiration readings, flies were kept in 25 mL flasks which restricted fly movement. Flies were placed in 40 mL plastic vials with sugar and pollen *ad libitum*. The vials were covered with cloth held in place at the top of the bottle with an elastic. Small, large, mated and unmated flies were weighed live and dry at 10 d in order to weigh a majority of the experimental flies.

To determine the effect of flight-activity on energy use, 20 small and 20 large unmated female flies were maintained in larger screened cages, 40 x 40 x 45 cm. Sugar and pollen consumption were measured and eggs collected but not counted. Sugar vials were prepared as previously described, and 8 vials were presented to each group of 20 flies. The vials were taped upside down on the outside of a preserving jar, 2 vials on each side of the jar. Pollen was presented in 2 shallow, covered plastic petri dishes, 5.5 cm in diameter and 0.5

cm high. The dishes were filled with pollen and sealed with parafilm. They were then freeze-dried for 3 d and subsequently weighed. Sixty small holes in the dish cover gave flies access to the pollen.

Mortality was noted and the total number of fly-days recorded. At 10 d post emergence the flies were weighed live and dry (3 d in a freeze-dryer).

The fresh and dry masses of flies from both small and large cage experiments were compared with masses of flies of the same age raised in jars from the growth experiment.

Energy Budgets and Ecological Efficiencies

Energy budgets were calculated for the 4 groups, small, large, unmated, and mated females. Consumption ($C_S + C_P = C$), production (P), respiration (R) and rejecta ($FU_f + FU_{rp} = FU$) were calculated in total cal·fly⁻¹ and energy flow diagrams were constructed.

The following food utilization efficiencies were calculated for female *E. corollae* (after Kohler *et al.*, 1987 and Randolph *et al.*, 1975). Assimilation (A) efficiency (digestibility) (A/C), net production efficiency (P/A), gross production efficiency (P/C), gross respiration efficiency (R/C), net respiration efficiency (R/A), and gross reproduction efficiency (P_R/C), net reproduction efficiency (P_R/A), gross growth efficiency (P_G/C), and net growth efficiency (P_G/A), were calculated for the four treatments (S, L, U, M).

Statistical analyses were completed using computer statistical analyses packages of SPSSX and Genstat. The assumptions of an ANOVA were met and they are random sampling, homogeneity of the variances, normality of the data, and the variance is independent of

the mean (Sokal and Rohlf, 1981). If the last three assumptions were not met, than the data were transformed.

RESULTS

Average fresh masses and longevities of female *E. corollae* from four different experimental categories are shown in Table 2. The data were back transformed from log x. Longevity was unaffected by size (ANOVA $F = 0.011$) or reproductive status (ANOVA $F = 0.008$). Masses of small and large flies were significantly different (ANOVA $F = 164.663$, $p < 0.001$), but not of unmated or mated flies (ANOVA $F = 2.063$).

Table 3 lists the caloric equivalents ($\text{cal} \cdot \text{mg}^{-1}$ ash-free dry wt) and percent ash of female *E. corollae* and fly products. Only whole flies showed a significant difference between the 2 treatments of mated and unmated flies (Kruskal-Wallis Chi Square $X^2 = 4.697$ $p < 0.05$). The caloric equivalents of unmated flies were higher than mated flies. It was unnecessary to transform the data. The caloric equivalent of whole flies was the same at emergence as at 5d and 10 d of age. Since there was no difference in energy equivalent of the tissues between the 3 ages, it is assumed that the amount of energy left in the carcass is accounted for in mass differences. Unmated flies did not lay as many eggs, but assimilated the same amount of energy. Since the caloric content of eggs was high, the extra energy in unmated flies might have been due to unlayed eggs or fat body (Table 3). The caloric contents ($\text{cal} \cdot \text{ash-free} \cdot \text{mg}^{-1}$) and % ash of faeces and regurgitated pollen were the same. They were collected separately but, due to the closeness in colours, some mixing might have occurred.

Table 2. Summary of fresh fly mass (mg) and longevity (d) of female *E. corollae*. n = No. of observations. Means and (95 % confidence intervals).

Treatment	Fresh fly mass (mg) ^a	n	No. days alive (d)	n		
Small	14.15 (12.05-16.63)	137	12.48 (7.18-17.78)	154		
Large	18.65 (15.88-21.92)	138	12.54 (7.24-17.84)	159		
Unmated	16.09 (13.70-18.90)	136	12.54 (7.24-17.84)	163		
Mated	16.69 (14.21-19.61)	139	12.47 (7.17-17.77)	150		
ANOVA	size ^c	d.f.	status	d.f.	interaction	d.f.
F ratios						
Fly masses	164.663***	1	2.063	1	6.535*	1
Days alive	0.011	1	0.008	1	0.558	1

(^aback-transformed from log x)

* p < 0.05, *** p < 0.001

Table 3: Caloric equivalents ($\text{cal} \cdot \text{mg}^{-1}$ ash-free dry wt), and percent ash of female *E. corollae*, and fly products. n = No. of observations. Means and (95 % confidence intervals) or means $\pm$ S.E. of mean. 1 cal = 4.187 joules.

Product	$\text{cal} \cdot \text{mg}^{-1}$	n	% Ash	n
Eggs ^a	7.501* (7.228-7.783)	11	8.95 $\pm$ 0.52	5
Faeces	5.910 $\pm$ 0.156	21	6.15 $\pm$ 0.43	17
Regurgitated Pollen	5.900* (5.720-6.086)	129		
Whole flies	-	-	5.12 $\pm$ 0.23	61
unmated	6.420 $\pm$ 0.141	62		
mated	6.112 $\pm$ 0.124	44		

*Back-transformed from log x

^a1 egg = 10.783 (10.708-10.859) μg .

Consumption

Analysis of covariance (ANCOVA) was adjusted for the covariates of fresh fly mass and longevity (No. of days alive). The ANCOVA removes a source of variability from the residual sums of squares and may result in a smaller S. E. of the treatments and an increase in precision of the experiment to (Allen and Cady, 1980).

Energy intake from consumption of sugar and pollen is summarized in Table 4. Small flies consumed less calories of sugar than large flies. The covariates of fresh fly mass (mg) and number of days were considered with only days being significant (ANOVA $F = 99.365$, $p < 0.001$). Mated flies consumed more pollen than did unmated flies. The covariates of fresh fly mass and days alive were significant (ANOVA $F = 19.689$, $p < 0.001$).

Respiration

Table 5 shows the calories allotted to maintenance for each category of fly. Oxygen utilization (total $\text{cal} \cdot \text{fly}^{-1}$) was not significantly different between the four treatments. The covariate of days (d) was significant according to the following relation with respiration (R):

$$R = 3.46 \pm 0.37 \text{ d}$$

$$(t = 9.326, p < 0.001; n = 307)$$

Total respiration ($\text{cal} \cdot \text{fly}^{-1}$) can be calculated if the age of the fly is known. There was, however, a significant difference in O_2 consumption between young and old flies. Five and 8 d old flies respired less than 10 and 12 d old flies (Table 6).

Table 4: Sugar and pollen consumption ($\text{cal}\cdot\text{fly}^{-1}$) by *E. corollae* females. n= No. of observations. 1 cal = 4.187 joules. Means and (95 % confidence intervals).

Treatment	Sugar (C_S)	n	Pollen (C_P)	n
Small	64.4 (36.4-72.4)	143	84.8 (49.0-133.8)	125
Large	72.4 (44.4-100.4)	154	95.6 (46.6-144.6)	144
Unmated	66.5 (38.5-94.5)	152	75.6 (26.6-124.6)	146
Mated	70.6 (42.6-98.6)	145	106.3 (57.3-155.3)	123
ANOVA				
F ratio	size	status	interaction	covariates ^a
C_S	5.287*	0.815	0.931	99.365***
C_P	2.914	14.091***	3.582	19.689***

(^acovariates are fresh mass and No. days alive)

* $p < 0.05$, *** $p < 0.001$

Table 5: Total eggs•fly⁻¹, production due to reproduction (P_R) and growth (P_G) and respiration (R) of female *E. corollae*. Means and (95 % confidence intervals) (total cal•fly⁻¹) 1 cal = 4.187 joules.

Treatment	No. Eggs•fly ⁻¹ ab	n	Reproduction(P _R)ab	n	Growth(P _G)	n	Respiration(R)	n
Small	100.4 (43.52-180.71)	112	8.56 (4.38-14.12)	113	9.57	98	44.5 (19.55-69.4)	99
Large	112.78 (51.80-197.21)	140	9.15 (4.81-15.66)	141	10.82	128	46.5 (21.6-71.5)	117
Unmated	82.99 (32.34-157.08)	132	6.72 (3.10-11.72)	132	10.65	122	42.8 (17.9-67.8)	104
Mated	137.59 (69.01-229.61)	120	11.51 (6.56-17.85)	122	8.54	104	48.4 (23.5-73.4)	112
ANOVA	size	d.f.	status	d.f.	interaction	d.f.	covariates ^c	d.f.
F ratios								
No. Eggs	0.979	1	17.11***	1	1.830			
P _R	0.893	1	34.35***	1	0.579	1	43.71***	2
R	0.374	1	1.87	1	8.626*	1	43.35*	2

(^aback-transformed from $\sqrt{x}$)

(^bflies with zero eggs were omitted from calculations)

(^ccovariates are fresh weight and days alive)

Table 6: Respiration of young and old female *E. corollae*. (Young = 5 and 8 d, old = 10 and 12 d) (total cal*fly⁻¹) 1 cal = 4.187 joules. Means and (95 % confidence intervals). n = No. observations.

Age	Respiration ^a	n
Young Flies (5-8 d)	27.597 (25.157-30.273)	151
Old Flies (10-12 d)	38.957 (35.577-42.657)	156

ANOVA F-Ratio = 3.58 $p < 0.001$ d.f. = 1
 (^acovariates are fresh mass and No. days alive)

Production

Growth (P_G)

Female flies gained significantly in mass between emergence and day 5 (S, Kruskal-Wallis $X^2 = 28.239$; L, $X^2 = 49.54$; U, $X^2 = 23.699$; M, 48.042), and emergence and day 10 (S, $X^2 = 13.171$; L, $X^2 = 49.675$; U, $X^2 = 30.180$; M, $X^2 = 46.196$) (Fig. 4a and 4b). Mass increase could be due to increases in 1) fat body, 2) flight muscles, and/or 3) egg formation. Growth was calculated by subtracting fly masses on day 1 and day 10 (Table 5). A significant mass loss was observed for large flies (Kruskal-Wallis $X^2 = 15.455$, $p < 0.001$) and mated flies ($X^2 = 24.350$, $p < 0.001$) between day 5 and day 10. Mass loss after day 5 in 3 categories could be due to 3 oviposition days in between 5 and 10 days. Unmated flies did not lose mass, but were slightly heavier in mass. This could be because unmated flies oviposited significantly less eggs than mated flies.

Reproduction (P_R)

The numbers of eggs oviposited by small, large, unmated and mated flies and the total amount of cal·fly⁻¹ are shown in Table 5. Flies with zero eggs oviposited were removed from the analysis. These flies did not lay eggs because it was assumed they were either too weak or were physically unable to lay eggs. Size did not significantly affect the total number of eggs oviposited but mated flies oviposited significantly more eggs than unmated flies.

Egg mass was the same between the four treatments (size: ANOVA $F = 0.792$, N. S.; and reproductive status: ANOVA $F = 1.235$, N. S.).

Figure 4a. Fresh fly masses (mg) of small and large female *E. corollae* weighed at 3 different ages.(1, 5 and 10 d).

Figure 4b. Fresh fly masses (mg) of unmated and mated female *E. corollae* weighed at 3 different ages (1, 5 and 10 d).

Rejecta

Faeces and regurgitated pollen were collected from flies from each of the four treatments. The amounts of calories in both kinds of rejecta produced by each treatment are recorded in Table 7. Caloric content of faeces did not differ between size (ANOVA $F = 1.116$, N. S.), but was significant in reproductive state (ANOVA $F = 3.421$, <0.05). The data were not transformed for both faeces and regurgitated pollen because it was not necessary due to the non parametric analyses.

Amounts of regurgitated pollen varied only between small and large flies (Kruskal-Wallis $X^2 = 6.494$, $p < 0.05$); large flies produced more.

Activity and Energy Use

The amount of sugar and pollen consumed by *E. corollae* females in small cages (40 mL) is shown in Table 8. Sugar and pollen consumption did not differ among the four categories of flies, maintained in small cages.

Average fresh masses of *E. corollae* after 10 d in 3 different cage sizes were significantly different (ANOVA $F = 17.43$, $P < 0.001$), (Table 9a). When flies were separated into small and large categories, it was obvious the main differences were among small flies (Table 9b).

Table 10 summarizes consumption of *E. corollae* females kept in 3 different sized cages. Mated flies in large cages consumed significantly more pollen and oviposited less eggs than mated flies in medium sized cages (Barlow and Whittingham Pers. Com.) When flies were maintained in large cages, no difference occurred between

Table 7: Energy from rejecta (FU) from female *E. corollae* (total cal·fly⁻¹) Note: FU_f = Faeces and FU_{rp} = Regurgitated Pollen. n = No. of flies (No. of samples). Means ± S. E. of the mean.

Treatment	FU _f	n	No. of samples ^a	FU _{rp}	n	No. of samples ^a
Small	19.167 ± 4.085	311	2	13.267 ± 1.410	164	7
Large	24.613 ± 3.143	342	2	20.635 ± 2.127	159	8
Unmated	18.276 ± 3.194	292	2	17.818 ± 1.562	163	8
Mated	25.50 ± 2.252	261	2	16.486 ± 2.916	150	7

^aDue to the small mass of FU_f and FU_{rp} for each fly, both were collected separately for large number of flies

ANOVA	Size	d.f.	Reproductive State	d.f.
F. Ratios				
FU _f	1.116	1	3.421*	1
Kruskal-Wallis				
X ²				
FU _{rp}	6.494*	1	0.272	1
* p < 0.05				

Table 8: Sugar and pollen consumption (total cal·fly⁻¹·d⁻¹) of female *E. corollae* from emergence to 10 d old. Cage size = 40 mL. Means and (95 % confidence intervals). n = No. of observations.

	Sugar (C _S)	n	Pollen (C _P)	n
Small	5.07 (3.45-6.69)	23	11.16 (6.09-16.23)	23
Large	4.35 (2.73-5.97)	15	10.24 (5.17-15.31)	15
Unmated	5.14 (3.52-6.76)	13	12.08 (7.01-17.15)	13
Mated	4.60 (2.98-6.22)	25	10.13 (5.06-15.20)	25

ANOVA	Size	d.f.	Status	d.f.	Interaction	d.f.	Covariate ^a	d.f.
F-Ratio								
C _S	0.982	1	0.906	1	0.614	1	0.965	1
C _P	0.160	1	1.192	1	0.656	1	0.000	1

(^aCovariate is fresh mass)

Table 9a: Fresh and dry fly masses (mg) of female *E. corollae* maintained in 3 cage sizes at 10 d of age. Means $\pm$ S. E. n = No. of observations which are the same for fresh and dry fly masses.

Cage size	Fresh (mg)	Dry(mg)	n
40 mL	16.593 $\pm$ 0.405	4.647 $\pm$ 0.121	38
450 mL	15.278 $\pm$ 0.343	4.477 $\pm$ 0.097	100
220.5 L	18.809 $\pm$ 0.801	5.402 $\pm$ 0.224	16
ANOVA F = 17.43 p < 0.001 d.f. = 2			

Table 9b: *E. corollae* separated into two size categories in three different cage sizes for 10 d. Means $\pm$ S. E. n = No. of observations. Fresh and dry fly masses (mg).

	Cage size	Fresh(mg)	Dry (mg)	n
Small	40 mL	15.341 $\pm$ 0.410	4.286 $\pm$ 0.130	24
	450 mL	12.649 $\pm$ 0.305	3.802 $\pm$ 0.096	51
	220.5 L	16.193 $\pm$ 1.946	4.962 $\pm$ 0.644	4
Large	40 mL	18.737 $\pm$ 0.446	5.266 $\pm$ 0.123	14
	450 mL	18.015 $\pm$ 0.299	5.179 $\pm$ 0.095	49
	220.5 L	19.681 $\pm$ 0.738	5.548 $\pm$ 0.215	12

Table 10: Fresh fly masses (mg) and consumption (C_S and C_P) ($\text{cal}\cdot\text{fly}^{-1}\cdot\text{d}^{-1}$) of *E. corollae* in three different cage sizes. Means and (95 % confidence intervals) or means $\pm$ S. E. of mean. n = No. of observations. Flies housed in large cages were maintained in groups of 20, all other flies were housed individually. C_S = sugar. C_P = pollen.

Cage Size	Fly wt	n	C_S	n	C_P	n
40 mL	16.593 ± 0.405	38	4.79 (3.17-6.41)	38	10.80 (5.73-15.87)	38
459 mL	15.278 ± 0.343	100	5.48 (3.24-7.72)	297	7.22 (3.30-11.14)	269
229.5 L	18.809 ± 0.801	16	4.76 ^a	20 (12.62-14.60)	13.57 ^a	40

^aOne pollen sample for 20 flies

mated and unmated flies in pollen consumption (Barlow and Whittingham, Pers. Com.)

Flight was more costly for small flies than large flies. Of 20 small flies maintained in a large cage, only 4 survived to 10 d. The mean age of flies that died before 10 d was 7.26 d. Flight takes a heavy toll on small flies. Twelve out of 20 large flies survived to 10 d in a large cage. There were no significant differences in body water content of flies kept in the 3 different sized cages. The relation between fresh and dry mass was:

$$1 \text{ g fresh mass} = 0.277 \pm 0.013 \text{ g dry mass}$$

$$(t = 21.30, p < 0.001; n = 154)$$

Energy Budgets and Ecological Efficiencies

The energy budgets for small, large, mated and unmated flies are shown in Figs. 5-8. Large flies consumed more energy, but the assimilation efficiencies were similar among the four categories. Mated flies produced more than unmated flies. Small and large flies produced about the same amount. Unmated flies used more energy for growth (storage) and less for reproduction than the other 3 groups. The four groups respire the same amount of energy but the gross respiration efficiency (R/C) was lower for mated flies because of the higher consumption. Between 32.3 and 37.6 % of the energy budgets are not accounted for.

Figures 9 and 10 show the amounts of energy used for production and respiration as a percent of assimilation. Net respiration efficiency (R/A), net production efficiency (P/A), net reproduction efficiency (P_R/A), and net growth efficiency (P_G/A) of

Figure 5. Energy flow (total cal*fly⁻¹) and % utilization efficiencies of small female *E. corollae*.

Consumption (C)

149.2 cal.

100 %

42

Rejecta (FU)

32.43 cal.

FU/C = 21.74 %

Assimilation (A)

62.63 cal.

A/C = 41.98 %

Production (P)

18.13 cal.

P/C = 12.15 %

Respiration (R)

44.50 cal.

R/C = 29.83 %

Reproduction (P_R)

8.56 cal.

$P_R / C = 5.74 \%$

Growth (P_G)

9.57 cal.

$P_G / C = 6.41 \%$

63.7 % of energy accounted for

Figure 6. Energy flow (total cal·fly⁻¹) and % utilization efficiencies of large female *E. corollae*.

Consumption (C)

168.0 cal.

100 %

44

Rejecta (FU)

45.25 cal.

FU/C = 26.93 %

Assimilation (A)

66.47 cal.

A/C = 39.57 %

Production (P)

19.97 cal.

P/C = 11.89 %

Respiration (R)

46.50 cal.

R/C = 27.68 %

Reproduction (P_R)

5.45 cal.

P_R /C = 3.24 %

Growth (P_G)

10.82 cal.

P_G /C = 6.44 %

66.5 % of energy budget accounted for

Figure 7. Energy flow (total cal·fly⁻¹) and % utilization efficiencies of unmated female *E. corollae*.

Consumption (C)

142.1 cal.

100 %

46

Rejecta (FU)

36.09 cal.

FU/C = 25.4 %

Assimilation (A)

60.17 cal.

A/C = 42.34 %

Production (P)

17.37 cal.

P/C = 12.22 %

Respiration (R)

42.80 cal.

R/C = 30.12 %

Reproduction (P_R)

6.72 cal.

$P_R/C = 4.73$ %

Growth (P_G)

10.65 cal.

$P_G/C = 7.49$ %

67.7 % of total energy budget accounted for

Figure 8. Energy flow (total cal•fly⁻¹) and % utilization efficiencies of mated female *E. corollae*.

Consumption (C)

176.9 cal.

100 %

48

Rejecta (FU)

41.99 cal.

$FU/C = 23.73 \%$

Assimilation (A)

68.45 cal.

$A/C = 38.68 \%$

Production (P)

20.05 cal.

$P/C = 11.33 \%$

Respiration (R)

48.40 cal.

$R/C = 27.35 \%$

Reproduction (P_R)

11.51 cal.

$P_R/C = 6.50 \%$

Growth (P_G)

Growth (P_G) 8.54 cal.

$P_G/C = 4.83 \%$

62.4 % of total energy budget

Figure 9. Percent energy of assimilation (A) used for respiration (R) and production (P) by small and large female *E. corollae*. P_G = production due to growth. P_R = production due to reproduction.

Figure 10. Percent energy of assimilation (A) used for respiration (R) and production (P) by unmated and mated female *E. corollae*. P_G = production due to growth. P_R = production due to reproduction.

small and large flies were similar (Fig. 9). With mated and unmated flies R/A and P/A were similar, but P_G/A and P_R/A were different. This resulted because of the significant differences in growth and reproduction observed earlier.

DISCUSSION

Eupeodes corollae is an efficient disperser and can migrate many miles (Svensson and Janzon, 1984). Scott (1983) observed that flight activity reduced longevity and fecundity (the two were inter-related) in small flies. Fecundity was also reduced in large flies that were able to fly in a large cage (Barlow and Whittingham, Pers. Com.). In this study, reduced flight activity (450 ml jars) allowed female *E. corollae* to hover and this did not effect longevity in small or large, and mated or unmated syrphids. Scott (1983) also observed no difference in longevity between small and large female *E. corollae* in reduced flight conditions. It has been observed in *Oncopeltus fasciatus* (Lener, 1967; Dingle, 1968; Slansky, 1980a) and in the paddy field grasshopper (*Oxya velox*) (Delvi and Pandian, 1971) that non-reproducing adults live longer than actively reproducing adults. But under optimal rearing conditions, Slansky (1980b) did not observe any difference in longevity due to reproductive state in *O. fasciatus*. This was also observed in this study in *E. corollae* females but the rearing conditions were not considered optimal.

Consumption

A sugar solution is necessary for adult maintenance in the pitcher-plant mosquito (*Wyeomyia smithii* Coquillett) (Moeur and Istock, 1980) and in female *E. corollae* (Scott, 1983). Large female *E. corollae* consumed more sugar (cal of sugar·mg⁻¹ fresh fly mass) than small flies perhaps because the sugar solution was the only available water source. Stürken (1964) observed an increase in longevity with increased sugar concentration (5 to 49 %) when fed to *E. corollae*. The

2 % sugar solution used in these experiments "may not have provided a sufficient amount of energy for adult maintenance. A mean age of 18 d was obtained for *E. corollae* fed on a dilute honey solution (Scott, 1983; Scott and Barlow, 1984). In England, *E. corollae* consumes nectar (Gilbert, 1980), and Murphy *et al.* (1983) determined that nectar of temperate zone flowers consists of a 20 % sugar solution.

Most of the pollen consumption occurs within the first week after adult emergence in *E. corollae* (Barlow and Whittingham, Pers. Com.). Mating also occurs within the first week, the first mating occurring within the first 3 d. Females will mate with different males for up to one week but the number of matings did not affect egg production (Barlow and Whittingham, Pers. Com.). *E. corollae* requires pollen for oogenesis and females are able to oviposit eggs 4 d post emergence at 20 °C, whether mated or unmated. Ross (1978) observed that mated *O. fasciatus* consumed and assimilated more food than did unmated bugs. In this study mated female *E. corollae* consumed more pollen than unmated ones but reproductive state did not affect assimilation. Slansky (1980b) suggested that interactions are present between reproduction, food consumption and assimilation. For *E. corollae*, this seems to be only between food consumption and reproduction. Mated flies also oviposited more eggs than unmated females and the extra pollen consumed by mated flies (a source of lipid for egg production) was probably diverted to egg formation. Newly emerged females have to "choose" whether or not to migrate depending on aphid density. Svensson and Janzon (1984)

noted low pollen contents in migrating *E. corollae*, and these flies were reproductively immature. Unmated flies may consume less pollen because they are in migration phase due to low resources.

Respiration

Respiratory rate is a sensitive measure of an organism's daily expenditure, and it is so sensitive that internal physiological factors such as body size, age, developmental stage, reproductive state, nutritional state or state of activity may affect the metabolism of animals (Duncan and Klekowski, 1975). Physiological changes occur in insects, particularly in the post mitotic tissues, such as nervous and striated muscle (Rockstein and Miquel, 1973). These aging effects cause an increase in respiration with time in female *E. corollae*, *A. pisum* (Randolph *et al*, 1975), and in worker honey bees (*Apis mellifera* L.) (Allen, 1959). This was observed in *E. corollae* females which increased respiration with increased age. This "senescence" includes "the sum total of those changes in structure and function which, by virtue of their deleterious and degradative nature, result ultimately in the failure of the individual to survive, and therefore, result in it's death" (Rockstein and Miquel, 1973).

Reproductive state did not affect respiration in female *E. corollae*, and respiration was the same in small and large flies when adjusted for fly mass.

Basal metabolism is the resting energy of non-active organisms (Duncan and Klekowski, 1975). This measurement of metabolism is not directly relevant for ecological studies of wild organisms under field conditions but is useful as a measure in minimally active

animals. Measurements of respiration in *E. corollae* in 25 mL flasks can be considered basal metabolism (Lawton and Richards, 1970). Flies respire more than basal respiration when feeding due to increased metabolic activity (Aidley, 1976; McEvoy, 1984), and skeletal muscular activity (Jones, 1974). Aidley (1976) and McEvoy (1984; 1985) attributed 3 % of total ingested food to energy expended during feeding. Activity which includes movement, ingestion and digestion and growth processes also contribute to metabolism in insects (McEvoy, 1984). Since only basal respiration was measured in *E. corollae*, a low respiration rate was measured and therefore input energy into the budget was higher than output.

Production

Mass increases over time observed in *E. corollae* females and *O. fasciatus* (Slansky, 1980b) were probably due to food intake, tissue growth (flight muscles, fat body) and development of eggs. Mass decreases were probably due to excretion, metabolism and egg oviposition. The overall positive net mass gain in the first 10 d observed in *E. corollae* was likely due to high pollen consumption in the first week and reduced flight in flies maintained in 450 mL jars. Flies were still able to hover but flight was restricted. Mass loss in mated flies between 5 d and 10 d was due to egg production. Some mass gain between 5 d and 10 d in unmated flies may have been caused by resorption of unlayed eggs or direct storage into the fat body (Slansky, 1980b). Female *E. corollae* oviposited the majority of their eggs within the first 15 d (Scott, 1983) and this could be

reflected in a higher pollen consumption within the first 7 d (Barlow and Whittingham, Pers. Com.)

Scott (1983) noted that flight activity in small syrphids had a greater effect on fecundity than on life-span. Fecundity was increased in both small and large flies if flight was restricted but low sugar concentration affected longevity. The lower longevity decreased overall fecundity in these experiments in comparison to Scott (1983). *Heliothis virescens* routed energy from eggs to fuel flight (Willers et al, 1987) and this is probably occurring in syrphids that are able to fly. If small flies emerge and experience low aphid populations, dispersal may be advantageous even though it incurs some reproduction cost. In both *E. corollae* (Scott, 1983) and *Ephydra cinerea* (Collins, 1980), small flies produced more ovarioles per mg fly mass than did large flies. Ovarioles are relatively inexpensive to produce (Collins, 1980) and body size may be unrelated to reproduction setting only an upper limit on egg production through its effect on ovary size or number of eggs that can be contained in the abdomen (Matsura et al., 1975; Mills 1981). Small *E. corollae* oviposited as many eggs as large flies if flight was restricted. If flight was unrestricted, then a trade-off between fecundity and flight energy occurred (Barlow and Whittingham, Pers. Com.). Longevity was greatly affected in small syrphids fed on low sugar concentrations. Small and large flies that consumed more concentrated sugar solution and were unrestricted in flight had lower fecundity than flies with restricted flight (Scott, 1983). If more energy is invested in fecundity, then longevity is reduced which in

turn causes a reduction in fecundity in future investments (Reznick, 1985).

Dispersing flies face increased risk of mortality if a suitable habitat to colonize is unavailable and a reproductive cost because of energy expended in flight (Roff, 1977). Small syrphids can make a greater contribution to population increase if aphid populations are high at emergence and extensive flight is unnecessary.

Many studies have been performed to compare body size and fitness in insects. Large *Psorophora columbiae* mosquitoes are more successful at obtaining a blood meal than small ones (Nasci, 1986). Large Jamaican gall midges (*Asphondylia boerhaaviae*) were more reproductively fit and 80 % were dispersive whereas none of the small morphs were dispersive (Freeman and Geoghagen, 1987).

Longevity and fecundity are affected in adult *Aedes triseriatus* with low larval feeding (Magnarelli, 1986) but this does not occur in *E. corollae* in these experiments if flight is restricted. Small and large flies exhibited similar longevity, P_R , R and pollen consumption. Only sugar consumption varied.

Rejecta

Large flies produced more faeces and regurgitated pollen than small flies. This is reflected in consumption. Small and large flies assimilated the same amount of energy but larger flies had a higher energy intake. Mated flies also produced more faeces than unmated flies. The amount of energy assimilated between mated and unmated is also similar. Larger and mated insects require more adult

maintenance and must consume more to produce the same amount of eggs (Matsura and Morooka, 1983).

Activity and Energy Use

Masses of female *E. corollae* raised in 3 different cage sizes were significantly different, especially among small flies. In medium sized jars *E. corollae* females weighed less than those kept in either smaller or larger cages. Small cages prevented flight and hovering but activity was not stopped completely as flies could still walk and feed. Reduced activity of flies in small cages caused an increase in mass to that greater than flies maintained in medium cages. Only consumption was measured and this was the same as that of flies maintained in medium sized cages. Flies maintained in large cages consumed more than those in small cages (Barlow and Whittingham, Pers. Com.). They also oviposited less eggs and the excess energy presumably was needed to power flight.

Energy Budgets

Calories allotted to production and respiration were similar for small and large flies. Large flies produced more rejecta, probably due to higher consumption. If small *E. corollae* do not have to disperse, then they can have an effect on population growth equal to large flies (Scott, 1983; Scott and Barlow, 1984) and therefore are potential biological control agents.

The shortfall in all energy budgets was a nearly constant 32.3 to 36.3 %. It is most probable that this error occurred in the measurement of respiration (Aidley, 1976; McEvoy, 1985). Humphreys (1978) estimated that respiration of active and feeding

spiders (*Geolycosa godeffroyi*) was 3 times higher than laboratory basal respiration measurements. The R_m (measured respiration) in feeding insects is 1.6 (McEvoy, 1984) to 2.05 times higher than R_m in starved ones. McEvoy (1985) stated that starving insects prior or during respiratory measurements will lower R_m . For ease of handling, *E. corollae* was starved during measurements since these only lasted 1 hr. If respiration (total cal.·fly⁻¹) values of non-feeding female *E. corollae* are multiplied by 2.1 to 2.4 then 100 % of all 4 energy budgets is accounted for.

Ecological Efficiencies

The assimilation efficiency (A/C) was 39 to 42 % for female *E. corollae*. Adult tulip tree aphids assimilated about 23 % of ingestion (calculated from Neilson and Van Hook, 1971). Meadow spittlebugs averaged 33 to 66 % (Wiegert, 1964) and an A/C of 28 to 36 % has been reported for the mirid bug *Leptoterna dolabrata* (McNeill 1971). An A/C of 64 % has been calculated for predatory larvae of *E. corollae* (Barlow, 1979). Average assimilation efficiency is usually somewhat higher for carnivores than for herbivores (Reichle, 1971).

The gross production efficiency (P/C) for *E. corollae* of 11 to 12 % was much lower than that observed in some terrestrial predaceous insects (22 - 53 % Calow, 1977) but similar to the pattern recorded for a number of poikilothermic herbivores such as *L. dolabrata* (16 - 20 %, McNeill, 1971) and spittlebug nymphs (19 %, Weigert, 1964). Fecundity of *E. corollae* was much lower in this work than in other studies (Scott, 1983; Scott and Barlow, 1984; Barlow and Whittingham, Pers. Com.). High consumption resulted in a low P/C;

however, net production efficiency ($P/A = 29$ to 30%) was within the range of $9.1 - 37.2\%$ observed in ten different insects (Golley, 1958). In this study, both P and R (see Respiration) are lower than expected.

Age affects P/A ; younger animals tend to have higher P/A ratios than older ones (Calow, 1977; Humphreys, 1979). The highest P/A ratios have been reported for herbivores and sit-and-wait predators (Calow, 1977). The P/A for larvae of *E. corollae* (84.7% , Barlow, 1979) is very high for searching predators (Calow, 1977) and much higher than for adult female *E. corollae*. This could have been due to the feeding regime where larvae were isolated on pea plants with aphids *ad libitum* and rarely had to search for food.

• Net respiration efficiency (R/A) for *E. corollae* was around 70% and would be higher if the estimate of R was low (See Respiration). Values of R/A of 26.9 to 95.9% have been calculated from 64 invertebrate studies in a review by Humphreys (1978). Gross respiration efficiency ($R/C = 27.4$ to 30.12%) was slightly lower than observed in recent literature for *Plodia interpunctella* ($R/C = 38.5\%$, Imura and Sinha, 1986) and eastern tent caterpillars ($R/C = 34.5\%$, Ruggiero and Merchant, 1986).

The gross reproductive efficiency ($P_R/C = 5.5$ to 8.6%) for *E. corollae* was higher than that observed by Cornelius and Barlow (1980). The highest mean pupal mass in the that study was 22.90 mg. This is slightly higher than the small category (12 to 20 mg) in the present work. P_R/C was higher in small flies (8.6%) than large flies (5.5%) and this trend was also observed by Cornelius and Barlow (1980) between pupal masses of 14.12 mg - 22.9 mg with a

P_R/C of 3.35 to 3.06 %. A greater proportion of larval consumption contributes to potential fecundity when food is scarce due to a higher number of ovarioles per mg mass in small pupae than in large ones (Scott, 1983).

If aphids could be fed radioactively labeled amino acids, or the nitrogen contents of aphids and syrphid larvae were analyzed as in 3 species of Heliconiine butterflies feeding on Passifloraceae (Boggs, 1981) and/or carbohydrates as in *Tipula paludosa* (Griffiths and Cheshire, 1987), then nitrogen and carbohydrates could be followed from aphids to syrphid larvae to adults to eggs. The influence of larval consumption on adult reproduction could then be estimated more accurately. Feeding adult *E. corollae* radioactively labeled food would also facilitate the study of how adults apportion their food.

Adult consumption did not affect longevity in female *E. corollae* with restricted flight. A larger gross reproduction efficiency (P_R/C) was noted in small flies because they ate less than in large ones; however the net reproduction efficiency (P_R/A) was the same. Small and large flies oviposited the same amount of eggs with restricted flight and it seems that only longevity affects the upper limit of egg production (Scott, 1983; Scott and Barlow, 1984). Larger flies consume more calories but assimilation is the same between small and large flies. Small flies make the same contribution to population growth as large flies if flight is not necessary. Energy allocation is different between mated and unmated flies. Mated flies reproduce and consume more pollen than unmated ones, but unmated flies grow more than mated ones. The effect of mating on energy

allocation has been observed also in other studies (Slansky, 1980a, b).

CONCLUSIONS

1. With flight restricted, large female *E. corollae* consumed more sugar (total cal•fly⁻¹) than small flies. Mated female *E. corollae* consumed significantly more pollen than unmated flies.
2. Consumption was highest in mated flies (176.9 cal•fly⁻¹) and lowest in unmated flies (142.1 cal•fly⁻¹). Large flies consumed more (168 cal•fly⁻¹) than small flies (149.2 cal•fly⁻¹).
3. Small and large flies laid the same number of eggs. Mated flies laid significantly more eggs than unmated ones.
4. Longevity was not affected by size or reproductive state.
5. Respiration (total cal•fly⁻¹) was similar between the four categories but was affected by age. Flies 10 to 12 d old respired more than flies 5 to 8 d old.
6. Flies in all 4 categories gained a significant mass between emergence and 10 d of age.
7. Flies maintained in small and large cages attained significantly greater mass than flies maintained in medium sized cages.
8. Flight greatly reduced longevity in small flies maintained in large cages.
9. Mated flies produced more faeces than unmated flies. Large flies produced more regurgitated pollen than did small flies. Large flies produced the most rejecta; they also consumed the most. Unmated flies consumed the least and produced the least amount of rejecta.
10. Assimilation efficiencies were similar in the 4 categories and ranged between 38.7 to 42.3 %.

11. Gross production efficiency ($P/C = 11.3$ to 12.2%) and gross respiration efficiency ($R/C = 27.4$ to 30.1%) were similar among the four categories.
12. Gross reproduction efficiency (P_R/C) ranged between 4.7 to 9.2% and gross growth efficiency (P_G/C) varied from 4.8 to 7.5% . The greatest range in P_G/C was observed between mated and unmated flies. The P_G/C for both small and large flies was 6.4% .
13. Net respiration efficiency (R/A) of all 4 categories was 70.0 to 71.1% . Net production efficiency (P/A) did not vary with size or reproductive state and ranged between 28.3 to 30.0% .
14. Net reproduction efficiency (P_R/A) and net growth efficiency (P_G/A) were similar between small and large female *E. corollae*. ($P_R/A = 13.7$ to 13.8% ; $P_G/A = 15.3$ to 16.3%).
15. P_R/A was 16.8% for mated flies and 11.2 for unmated flies. The trend for the ratio P_G/A was reversed, 12.5% for mated flies and 17.7% for unmated flies.

Appendix

The partitioning of the degrees of freedom for the 8 sequential experiments for female *E. corollae* is as follows:

ANALYSIS OF VARIANCE

SOURCE OF VARIATION	DF
EXPT STRATUM	
SIZE	1
STATUS	1
RESIDUAL	5
TOTAL	7

EXPT *UNITS* STRATUM	
TREATMENT	1
SIZE	1
STATUS	1
RESIDUAL	5
TOTAL	8

GRAND TOTAL	15
-------------	----

***** INFORMATION SUMMARY *****

MODEL TERM EF NON-ORTHOGONAL TERMS
EXPT STRATUM

SIZE	0.500
STATUS	0.500

EXPT *UNITS* STRATUM	
SIZE	0.500 EXPT
STATUS	0.500 EXPT

Data are stored on a 5.25 inch (130 mm) floppy disk, IBM compatible, at the National Archives of Canada. Title of disk "Energy budget data for *Eupeodes corollae* (Diptera: Syrphidae). April 28, 1988, Louise Charron".

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