

## Development of ovaries, allometry of reproductive traits and fecundity of *Episyrphus balteatus* (Diptera: Syrphidae)

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**Abstract.** *Episyrphus balteatus* only matures eggs after emergence. Ovaries develop in 4 stages. In the absence of oviposition sites, females refrain from ovipositing and their ovaries progressively fill the abdomen and then egg resorption occurs. The potential fecundity, which is expressed by the ovariole number, the reproductive biomass and the abdomen volume, scales isometrically with the size of females. Egg size is much less variable and does not rise proportionally to body size. In laboratory conditions, females of *E. balteatus* might lay between 2,000 and 4,500 eggs during their life-time at a rate of 1 to 2 eggs per ovariole per day. Both life-time fecundity and rate of egg production are directly related to the size of females. The potential and realized fecundities are likely to be limited by the availability of food resources during larval and adult life, respectively.

### INTRODUCTION

Larvae of *Episyrphus balteatus* (De Geer, 1776) are potential biological control agents of many aphid species (Chambers & Adams, 1986; Nawrocka, 1988; Tenhumberg & Poehling, 1995). They have a very high growth rate and develop in less than 10 days at 20°C, when food supply is optimal (Ankersmit et al., 1986; Hart et al., 1997).

Like other hoverflies, *E. balteatus* only matures eggs after adult emergence. That is, females hatch with an immature reproductive system and must feed on pollen to complete the maturation of their ovaries. The preoviposition period lasts for about a week (Schneider, 1948; Stürken, 1964; Geusen-Pfister, 1987). If they do not experience food shortages, females continuously lay eggs from the start of the oviposition period until death. Their longevity frequently exceeds one month under laboratory conditions (Geusen-Pfister, 1987; Kan, 1988). As is the case for *Eupeodes corollae* (F.), another hoverfly species with predacious larvae, realised fecundity is directly linked to female longevity (Scott & Barlow, 1984).

At birth, the larvae of aphidophagous predators must be of a minimum size to succeed in subduing and eating their first prey (Dixon, 1959a; Wratten, 1973; Rotheray, 1983; Stewart et al., 1991b). Therefore, these predators produce anhydropic eggs that contain enough yolk to support the development of relatively large embryos. As is expected from the classical trade-off between the size and the number of eggs (Lack, 1954; Smith & Fretwell, 1974; Sibly & Calow, 1986), one can predict that hoverfly females with aphidophagous larvae must (1) have ovaries with few ovarioles, short oviducts and low storage capacity, and (2) be strongly egg limited because of their small maximum egg load (Price, 1973; Jervis & Copland, 1996), compared with species laying hydropic eggs.

The aim of this paper is to test the above predictions, determine the relationship between the reproductive investment and body size, and measure the realised fecundity of females of *E. balteatus* kept under laboratory conditions.

### MATERIAL AND METHODS

#### Ovary structure and development

The developmental stages of the ovaries of *E. balteatus* were determined by dissecting females reared in the laboratory (photoperiod of 16L : 8D; temperature: 21 ± 1°C) as described in Branquart et al. (1997). These females were F2 and F3 progeny of adults collected in Gembloux (Belgium). Groups of 20 to 30 males and females that emerged on the same day were kept in 30 × 30 × 60 cm cages consisting of a wooden frame covered with gauze. The light intensity varied from 12,000 lux at the top to 2,000 lux at the bottom of the cages. The hoverflies had access to wet absorbent paper and an artificial diet consisting of a mixture of sucrose, honey and ground pellets of pollen. Adult hoverflies from half of the cages were daily offered two broad bean plants (*Vicia faba* L.), approximately 15 cm high, infested with *Acyrtosiphon pisum* (Harris). This was the first treatment. The other adults were deprived of an egg laying stimulus, which was the second treatment. Five females from each treatment were dissected every other day, following the technique described by Gilbert (1993), to assess the development of their ovaries from hatching to 20 days after emergence. The ovaries were gently removed and stained with toluidine blue before further examination. The volume of the ovaries expressed as a percentage of the total abdomen volume, as well as the number of ovarioles, the number of follicles per ovariole, the number of mature and resorbed oocytes in the ovarioles and the lateral oviducts were recorded. Mature oocytes were easily distinguished because they stained less readily and were larger than immatures ones. Moreover, they had a characteristic net-like patterning resulting from the presence of the chorion. Resorbed oocytes were either shrunk to some extent or appeared rather

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enlarged when dissected out in distilled water (Gilbert, 1993; Jervis & Copland, 1996).

### Allometry of reproductive traits

Thirty-three mature females of *E. balteatus*, caught in Gembloux during the summer of 1998, were induced to lay eggs by keeping them individually for 2 h in a 9 cm diameter Petri dish with a piece of broad bean heavily infested with *A. pisum*. Fifteen eggs per female were weighed to 0.0001 mg on a Supermicro Sartorius balance. The reproductive biomass is defined as the egg weight multiplied by ovaride number. The length, width and depth of the abdomen of each female were measured and the volumes of their abdomens estimated using the formula for an ellipsoid. The females were dissected, the ovaries removed from the abdomen, the ovarioles counted and both the somatic and thoracic dry masses of the females determined after drying at 60°C for 24 h. Crops full of pollen were removed before drying to avoid overestimation of the somatic dry weight. The dry mass of the thorax, without wings and legs, was used as an approximation for flight muscle mass. Using the technique described by Marden (1987), we separated thoracic exoskeleton from wing muscles on a sample of ten females and determined that muscle mass corresponds to 82.5% of the thoracic dry mass.

The relationship between each reproductive trait (egg weight, ovariole number, reproductive biomass and abdomen volume) and respectively the somatic and thoracic dry mass was estimated by the following equation:

$$\log(Y) = a + b \log(X)$$

with Y standing for the value of the reproductive trait, X for the somatic or thoracic dry mass and a and b being constants.

Reduced major axis regression was applied to estimate the slope of the relationship and to test for isometry ( $\beta = 1$ ) (LaBarbera, 1989; Harvey & Pagel, 1991).

### Life-time fecundity

The daily fecundity of 8 females was determined over a period of 30 days from the beginning of oviposition. After emergence, each female was kept singly with 2 males in a cage (30 × 30 × 60 cm) and reared as described above. Every day, two 20 cm high broad bean plants heavily infested with *A. pisum* were introduced in the cages to trigger egg laying by the hoverflies. They were removed 24 h later and the eggs counted. After 30 days, the females were dissected and their ovarioles counted. The realized fecundity was described by the mean fecundity, the maximum fecundity, the mean daily rate of egg production and the maximum daily rate of egg production. The mean daily fecundity is the average number of eggs laid per day for the 30 day period; the maximum daily fecundity is the average of the three highest values of daily egg laying. The mean rate of egg production is the average number of eggs produced per ovariole and per day for the 30 day period; the maximum rate of egg production is similarly calculated for the three highest values of daily egg laying. The relationships between the mean daily fecundity and the ovariole number, and between the maximum daily fecundity and the ovariole number

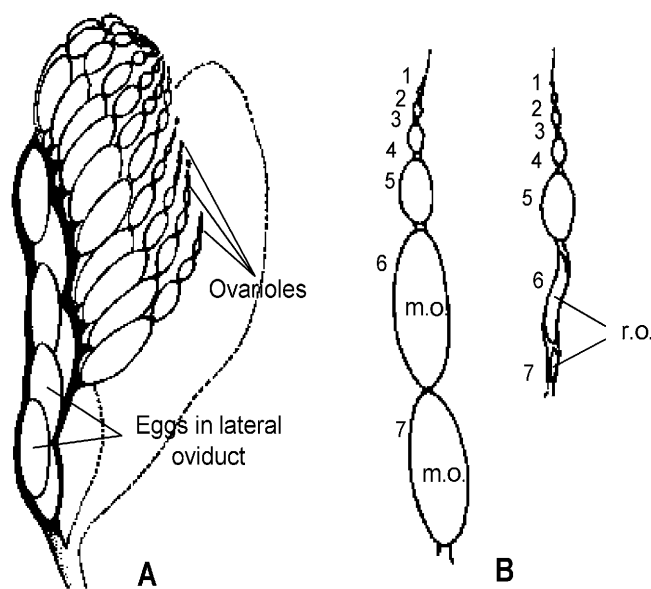


Fig. 1. Schematic representation of (A) an ovary and (B) the structure of a mature ovariole and one showing egg resorption in *Episyrrhus balteatus* (m.o. – mature oocytes; r.o. – oocytes being resorbed).

were determined in an attempt to use the number of ovarioles as an indicator of potential fecundity (Jervis & Copland, 1996).

## RESULTS

### Ovary structure and development

Oocytes grow and mature in progression in each ovariole. The number and size of the follicles in the ovarioles enable assessment of ovary development (Table 1). The ovaries of females deprived of an oviposition stimulus display four developmental stages: (1) maturation; (2) early maturity with a maximum of one mature oocyte per ovariole; (3) late maturity with one or two mature oocytes in each ovariole, and finally (4) ovaries with oocytes showing signs of resorption (Fig. 1). There are differences in the timing of sexual maturity between the females. Most of them lay eggs 8 or 10 days after emergence but some of them have a preoviposition period of 14 days.

The volume of the ovaries and the number of follicles in the ovarioles increase progressively during the maturation phase. Maturity is reached when oocytes are released into the lateral oviducts and when there is one fully developed oocyte in each ovariole. At this stage, there are six follicles per ovariole (Fig. 1). Oocytes continue to accumulate in the lateral oviducts and at the base of the ovarioles even if females do not oviposit. Females can then

TABLE 1. Features of the different stages of ovarian development in *Episyrrhus balteatus* when deprived of oviposition sites for up to 20 days after emergence. Values given hereafter refer to a female with 80 ovarioles.

| Stage of development | Days after emergence | Follicles per ovariole | Number of mature eggs |             | Egg load | Ovary volume (% abdomen) |
|----------------------|----------------------|------------------------|-----------------------|-------------|----------|--------------------------|
|                      |                      |                        | per ovariole          | per oviduct |          |                          |
| 1                    | 0–12                 | 1–5                    | 0                     | 0           | 0        | 0–30                     |
| 2                    | 8–14                 | (5)–6                  | (0)–1                 | 2–10        | 50–100   | 40–70                    |
| 3                    | 10–16                | (6)–7                  | (1)–2                 | 10–15       | 100–130  | 80–100                   |
| 4                    | 12–20                | 5(–6)                  | 0(–1)                 | 10–15       | 20–30    | 20–40                    |

TABLE 2. The relationships, expressed as  $\log(Y) = a + b \log(X)$ , between the somatic dry weight (SDW), the egg weight (EGW), the ovariole number (OVN), the reproductive biomass (RB) and the abdomen volume (ABV), and between the thoracic dry weight (TDW), the reproductive biomass (RB) and the abdomen volume (ABV) in *Episyrphus balteatus*.

| X-value  | Y-value                | Mean  | PSD   | Correlation |                | Regression |                |
|----------|------------------------|-------|-------|-------------|----------------|------------|----------------|
|          |                        |       |       | r           | P <sub>r</sub> | b          | P <sub>b</sub> |
| SDW (mg) |                        | 4.86  | 30.6% |             |                |            |                |
|          | EGW (µg)               | 67.20 | 9.7%  | 0.51        | **             | 0.29       | ***            |
|          | OVN                    | 80.50 | 22.6% | 0.93        | ***            | 0.75       | ***            |
|          | RB (mg)                | 5.47  | 29.3% | 0.90        | ***            | 0.96       | ns             |
|          | ABV (mm <sup>3</sup> ) | 12.72 | 33.0% | 0.94        | ***            | 1.08       | ns             |
| TDW (mg) |                        | 2.68  | 30.8% |             |                |            |                |
|          | RB (mg)                | 5.47  | 29.3% | 0.91        | ***            | 0.95       | ns             |
|          | ABV (mm <sup>3</sup> ) | 12.70 | 33.0% | 0.93        | ***            | 1.07       | ns             |

PSD = percentage standard deviation; \* –  $P < 0.05$ ; \*\* –  $P < 0.01$ ; \*\*\* –  $P < 0.001$ ; ns – not significant; P<sub>r</sub> – significance of the coefficients of correlation ( $H_0 : \rho = 0$ ); P<sub>b</sub> – significance of the slopes of regression lines ( $H_0 : \beta = 1$ ).

have a very high oocyte load, and the ovaries may occupy nearly all the abdominal cavity: this is the late maturity stage (Fig. 1). Later still, oocytes show signs of resorption at the proximal end of the ovarioles, resulting in a marked decrease in the volume of the ovaries (Fig. 1). Therefore, mature oocytes can only be retained for a brief period of time in the ovarioles.

In the presence of oviposition sites, females started to oviposit when their ovaries were at the second developmental stage. As long as oviposition sites were available, oviposition occurred every day and the ovaries remained in this stage.

#### Allometry of reproductive traits

The somatic dry mass of the females varied from 2.5 to 7.3 mg and its percentage standard deviation is 31%. All the other variables, but the ovariole number and the egg mass, display the same range of variation. The egg mass is clearly the less variable reproductive trait (Table 2).

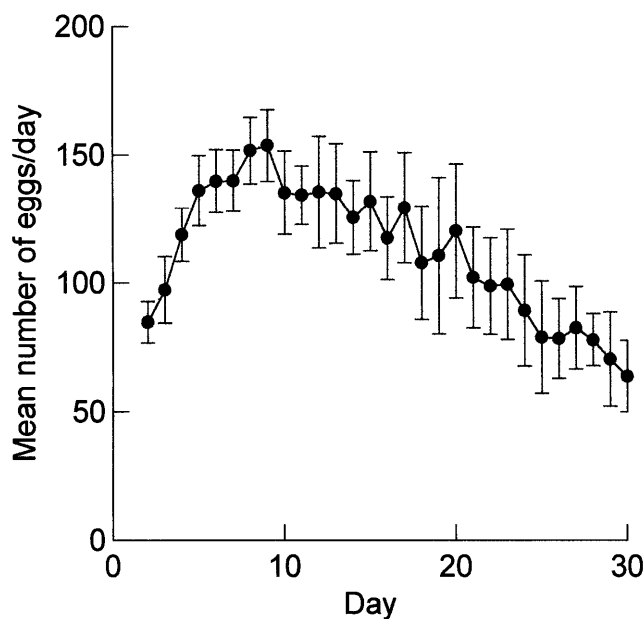


Fig. 2. Daily fecundity of *Episyrphus balteatus* over the 30 days following the onset of oviposition. Mean and standard deviation of eight replicates.

There are strong allometric relationships between all the traits (Table 2). There is a weak but significant correlation between the egg mass and the somatic dry mass. Both the reproductive biomass, which is the ovariole number multiplied by the egg mass, and the abdomen volume scale isometrically with the somatic and the thoracic dry mass (Table 2). That is, flight performance and muscle power are directly proportional to the size of the females and to the egg mass they carry when their ovaries are fully developed. The ovariole number has a slight negative allometry with the somatic dry mass, which means that the ovariole number per unit of somatic dry mass decreases as the somatic dry mass increases. Finally, the egg mass has a marked negative allometry with the somatic dry mass.

#### Life-time fecundity

The age fecundity function of *E. balteatus* is triangular shaped (Fig. 2). Fecundity rises in the first week of egg laying, reaches a maximum and slowly decreases until death. The hatching rate of the eggs was between 80 and 100% and the females survived for up to 6 weeks.

A female of *E. balteatus* lays an average 174 eggs/day at the peak of the oviposition period and 108 eggs/day over the whole oviposition period (Table 3). These values correspond to a rate of production between 1 and 2 eggs per ovariole per day. Fitting a linear regression to the points on the decreasing side of the fecundity curve,

TABLE 3. Potential fecundity, daily fecundity and rate of egg production of *Episyrphus balteatus*: number of replicates (N), mean, percentage standard deviation (PSD), minimum (Min) and maximum (Max) values. The maximum values correspond to the average of the three highest values of daily egg laying; the mean values are calculated for the 30 day period.

|  | N | Mean  | PSD  | Min   | Max   |
|--|---|-------|------|-------|-------|
| Potential fecundity                        |   |       |      |       |       |
| Number of ovarioles                        | 8 | 91.1  | 9.8  | 80    | 106   |
| Fecundity (eggs/day)                       |   |       |      |       |       |
| Maximum (3 days)                           | 8 | 174.1 | 18.0 | 130.3 | 214.3 |
| Mean (30 days)                             | 6 | 108.0 | 32.0 | 66.1  | 149.2 |
| Rate of egg production (eggs/ovariole/day) |   |       |      |       |       |
| Maximum (3 days)                           | 8 | 1.90  | 11.0 | 1.52  | 2.14  |
| Mean (30 days)                             | 6 | 1.16  | 25.0 | 0.83  | 1.57  |

revealed that oviposition continues for 50 days after the start of egg laying, and that life-time fecundity is about 3,900 eggs. The value for the realized fecundity are closely correlated to ovariole number ( $r_{\text{ovariole number/maximum fecundity}} = 0.887$ ;  $n = 8$ ;  $P < 0.01$ ;  $r_{\text{ovariole number/mean fecundity}} = 0.869$ ;  $n = 6$ ;  $P < 0.05$ ).

## DISCUSSION

Compared to other aphid predators, females of *E. balteatus* lay small eggs, have many ovarioles and an egg load that can exceed 100 eggs. They achieve a high fecundity under optimal laboratory conditions. The maximum daily egg production and life-time fecundity reported here are six times greater than quoted by Khan & Yunus (1970), Geusen-Pfister (1987), Kan (1988) and Ngamo Tinkeu (1998). Suboptimal rearing conditions in these studies might account for this discrepancy. However, the production of 1 to 2 eggs per ovariole per day, as recorded for *E. balteatus* in this study, is typical of other Diptera (Collins, 1980; R'kha et al., 1997).

The ovariole number, the rate of egg production per ovariole and the life-time fecundity are greater in *E. balteatus* than in similar sized predacious ladybird beetles and lacewings (Stewart et al., 1991a, b; Zheng et al., 1993b; Carvalho et al., 1996; Canard et al., 1996). For example, the ladybird beetle *Adalia bipunctata* (L.) whose larvae feed on the same prey as *E. balteatus*, has 46 ovarioles, lays 0.5 eggs per ovariole per day and a life-time fecundity of 1,200 eggs during its life under laboratory conditions (Stewart et al., 1991b; Branquart et al., unpubl.). *A. bipunctata* lays bigger eggs and lives longer than *E. balteatus*. The total egg production in both species is about ten times the adult fresh mass. The reproductive effort in these two species, however, is distributed differently. *E. balteatus* lays many eggs over a period of about 40 days whereas *A. bipunctata* lays eggs for 90 to 100 days. Under the experimental conditions of this study, the ovariole number is a good indicator of the daily and life-time fecundity, as it is for Coccinellidae, Drosophilidae, Tachinidae and Ichneumonidae (David, 1970; Price, 1975; Stewart et al., 1991a, b).

Pollen supply and aphid availability are likely to affect fecundity in the field. Pollen is a crucial resource for *E. balteatus* females as it provides a nitrogen source to mature the ovaries and sustain egg production (Schneider, 1948; Stürken, 1964). It is probably a limiting factor in areas of intensive agriculture, where vegetation at field margins has been impoverished in recent years (Rothery, 1994; Hickman & Wratten, 1996). Aphid availability affects fecundity directly and indirectly. A shortage of aphids leads to egg resorption, which occurs in *E. corollae* and *Scaeva pyrastris* (L.) (Schneider, 1969; Gilbert, 1993) but not in *Eupeodes lumiger* (Meigen) (Dixon, 1959b). Food shortage during the larval stages induces emergence of small adults with few ovarioles and a low fecundity (Cornelius & Barlow, 1980; Scott & Barlow, 1984; Dixon & Guo, 1993; Zheng et al., 1993a, b). Are females of *E. balteatus* limited by their rate of egg production and egg storage capacity or by the time available

to search for oviposition sites? A question that need to be addressed if we are to manage farmlands in order to enhance the impact of hoverflies on aphid populations. This problem can be addressed by checking the impact of management practices on the frequency distribution of the stages of ovary development in wild hoverflies.

Ovariole number, reproductive biomass and abdomen volume display a wide range of variation and are strongly related to female size. The correlation between reproductive investment and body size is not surprising since large females have proportionally more resources to allocate to reproduction than small females (Bennettova & Fraenkel, 1981; Reiss, 1985; Sibly & Calow, 1986; Marshall, 1990; Roff, 1992; Dixon & Guo, 1993, but see Klingenberg & Spence, 1997). Egg size is normally independent of both clutch and female size within a population living in the same environment (Smith & Fretwell, 1974; Parker & Begon, 1986; Godfray & Parker, 1991). Although egg mass is the least variable reproductive trait in *E. balteatus*, our results show an allometric relationship between egg and female size. This has been documented for other invertebrates and some recent studies show that some species living in variable environment exhibit a plasticity in the size of their eggs (Kaplan & Cooper, 1984; review in Roff, 1992; Yafuso, 1994; Fox et al., 1997; Guntrip et al., 1997; Ito, 1997; Roosenburg & Dunham, 1997). The adaptive significance of egg size plasticity in *E. balteatus* deserves further investigation.

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## REFERENCES

- ANKERSMIT G.W., DIJKMAN H., KEUNING N.J., MERTENS H., SINS A. & TACOMA H.M. 1986: *Episyrphus balteatus* as a predator of the aphid *Sitobion avenae* on winter wheat. *Entomol. Exp. Appl.* **42**: 271–277.
- BENNETTOVÁ B. & FRAENKEL G. 1981: What determines the number of ovarioles in a fly ovary? *J. Insect Physiol.* **27**: 403–410.
- BRANQUART E., HEMPTINNE J.-L., BAUFFE C. & BENFEKIH L. 1997: Cannibalism in *Episyrphus balteatus* (Dipt.: Syrphidae). *Entomophaga* **42**: 145–152.
- CANARD M., GRIMAL A. & CARVALHO C.F. 1996: Weight changes during preimaginal development in green lacewings (Insecta: Neuroptera: Chrysopidae). In Canard M., Aspöck H. & Mansell M.W. (eds): *Pure and Applied Research in Neuropterology. Proceedings of the Fifth International Symposium on Neuropterology, Cairo Egypt*. Sacco, Toulouse, pp. 87–101.
- CARVALHO C.F., CANARD M. & ALAUZET C. 1996: Comparison of the fecundities of the Neotropical green lacewing *Chrysoperla externa* (Hagen) and the West-Palaeartic *Chrysoperla mediterranea* (Hölzel) (Insecta: Neuroptera: Chrysopidae). In Canard M., Aspöck H. & Mansell M.W. (eds): *Pure and Applied Research in Neuropterology. Proceedings of the Fifth International Symposium on Neuropterology, Cairo Egypt*. Sacco, Toulouse, pp. 103–107.
- CHAMBERS R.J. & ADAMS T.H.L. 1986: Quantification of the impact of hoverflies (Diptera: Syrphidae) on cereal aphids: an analysis of field populations. *J. Appl. Ecol.* **23**: 895–904.

- COLLINS N.C. 1980: Developmental responses to food limitation as indicators of environmental conditions for *Ephydra cinerea* Jones (Diptera). *Ecology* **61**: 650–661.
- CORNELIUS M. & BARLOW C.A. 1980: Effect of aphid consumption by larvae on development and reproductive efficiency of a flower fly, *Syrphus corollae* (Diptera: Syrphidae). *Can. Entomol.* **112**: 989–992.
- DAVID J. 1970: Le nombre d'ovarioles chez *Drosophila melanogaster*: relation avec la fécondité et valeur adaptative. *Arch. Zool. Exp. Gén.* **111**: 357–370.
- DIXON A.F.G. 1959a: An experimental study of the searching behaviour of the predatory coccinellid beetle *Adalia decempunctata* (L.). *J. Anim. Ecol.* **28**: 259–281.
- DIXON T.J. 1959b: Studies on oviposition behaviour of Syrphidae (Diptera). *Trans. R. Entomol. Soc. Lond.* **111**: 57–81.
- DIXON A.F.G. & GUO Y. 1993: Egg and cluster size in ladybird beetles (Coleoptera: Coccinellidae): The direct and indirect effects of aphid abundance. *Eur. J. Entomol.* **90**: 457–463.
- FOX C.W., THAKAR M.S. & MOUSSEAU T.A. 1997: Egg size plasticity in a seed beetle: an adaptive maternal effect. *Am. Nat.* **149**: 149–163.
- GEUSEN-PFISTER H. 1987: Studies on the biology and reproductive capacity of *Episyrphus balteatus* (Diptera: Syrphidae) under greenhouse conditions. *J. Appl. Entomol.* **104**: 261–270.
- GILBERT F. 1993: *Hoverflies*. Richmond, Slough, 67 pp.
- GODFRAY H.C.J. & PARKER G.A. 1991: Clutch size, fecundity, and parent-offspring conflict. *Phil. Trans. R. Soc. Lond. (B)* **32**: 67–79.
- GUNTRIP J., SIBLY R.M. & SMITH R.H. 1997: Controlling resource acquisition to reveal a life history trade off: egg mass and clutch size in an iteroparous seed predator, *Prostephanus truncatus*. *Ecol. Entomol.* **22**: 264–270.
- HART A.J., BALE J.S. & FENLON J.S. 1997: Development threshold, day-degree requirements and voltinism of the aphid predator *Episyrphus balteatus* (Diptera: Syrphidae). *Ann. Appl. Biol.* **130**: 427–437.
- HARVEY P.H. & PAGEL M.D. 1991: *The Comparative Method in Evolutionary Biology*. Oxford University Press, Oxford, 239 pp.
- HICKMAN J.M. & WRATTEN S. 1996: Use of *Phacelia tanacetifolia* strips to enhance biological control of aphids by hoverfly larvae in cereal fields. *J. Econ. Entomol.* **89**: 832–840.
- ITO K. 1997: Egg-size and number variations related to maternal size and age, and the relationship between egg size and larval characteristics in an annual marine gastropod, *Haloa japonica* (Opisthobranchia, Cephalaspidea). *Mar. Ecol. Prog. Ser.* **152**: 187–195.
- JERVIS M.A. & COPLAND M.J.W. 1996: The life cycle. In Jervis M. & Kidd N. (eds): *Insect Natural Enemies, Practical Approaches to their Study and Evaluation*. Chapman & Hall, New York, pp. 63–161.
- KAN E. 1988: Assessment of aphid colonies by hoverflies. I. Mapple aphids and *Episyrphus balteatus* (Diptera: Syrphidae). *J. Ethol.* **6**: 39–48.
- KAPLAN R.H. & COOPER W.S. 1984: The evolution of developmental plasticity in reproductive characteristics: an application of the “adaptive coin flipping” principle. *Am. Nat.* **123**: 393–410.
- KHAN S. & YUNUS M. 1970: Biology of *Syrphus balteatus* (Diptera: Syrphidae). *Pakist. J. Zool.* **2**: 215–217.
- KLINGENBERG C.P. & SPENCE J.R. 1997: On the role of body size for life-history evolution. *Ecol. Entomol.* **22**: 55–68.
- LABARBERA M. 1989: Analyzing body size as a factor in ecology and evolution. *Annu. Rev. Ecol. Syst.* **20**: 97–117.
- LACK D. 1954: *The Natural Regulation of Animal Numbers*. Clarendon Press, Oxford.
- MARDEN J.H. 1987: Maximum lift production during takeoff in flying animals. *J. Exp. Biol.* **130**: 235–258.
- MARSHALL L.D. 1990: Intraspecific variation in reproductive effort by female *Parapediasia teterrella* (Lepidoptera, Pyralidae) and its relation to body size. *Can. J. Zool.* **68**: 44–48.
- MILLS N.J. 1981: Some aspects of the rate of increase of a coccinellid. *Ecol. Entomol.* **6**: 293–299.
- NAWROCKA B. 1988: Effectiveness of aphidophagous syrphids in controlling the cabbage aphid, *Brevicoryne brassicae* L. In Niemczyk E. & Dixon A.F.G. (eds): *Ecology and Effectiveness of Aphidophaga*. SPB Academic Publishing, The Hague, pp. 289–294.
- NGAMO TINKEU L.S. 1998: *Atouts biologiques, écologiques et morphologiques précisant l'utilité d'Episyrphus balteatus* (Diptera: Syrphidae) dans la lutte biologique. PhD. thesis, U.C.L., Louvain-la-Neuve, 207 pp.
- PARKER G.A. & BEGON M. 1986: Optimal egg size and clutch size: effect of environment and maternal phenotype. *Am. Nat.* **128**: 573–592.
- PRICE P.W. 1973: Reproductive strategies in parasitoid wasps. *Am. Nat.* **107**: 684–693.
- PRICE P.W. 1975: Reproductive strategies of parasitoid. In Price P.W. (ed.): *Evolutionary Strategies of Parasitic Insects and Mites*. Plenum Press, New York, pp. 87–111.
- REISS M.J. 1985: The allometry of reproduction: why larger species invest relatively less in their offspring. *J. Theor. Biol.* **113**: 529–544.
- R'KHA S., MORETEAU B., COYNE J.A. & DAVID J.R. 1997: Evolution of a lesser fitness trait: egg production in the specialist *Drosophila sechellia*. *Genet. Res.* **69**: 17–23.
- ROFF D.A. 1992: *The Evolution of Life Histories*. Chapman & Hall, New York, 535 pp.
- ROOSENBERG W.M. & DUNHAM A.E. 1997: Allocation of reproductive output: egg- and clutch-size variation in the diamond-back terrapin. *Copeia* **2**: 290–297.
- ROTHERAY G.E. 1983: Feeding behaviour of *Syrphus ribesi* and *Melanostoma scalare* on *Aphis fabae*. *Entomol. Exp. Appl.* **34**: 148–154.
- ROTHERY F.A. 1994: Hoverfly foraging on hedgerow flowers. *IOBC/WPRS Bull.* **17**: 148–155.
- SCHNEIDER F. 1948: Beitrag zur Kenntnis der Generationenverhältnisse und Diapause räuberischer Schwebfliegen (Syrphidae: Diptera). *Mitt. Schweiz. Entomol. Ges.* **21**: 249–285.
- SCHNEIDER F. 1969: Bionomics and physiology of aphidophagous Syrphidae. *Annu. Rev. Entomol.* **14**: 103–124.
- SCOTT S.M. & BARLOW C.A. 1984: Effect of prey availability during development on the reproductive output of *Metasyrphus corollae*. *Environ. Entomol.* **23**: 669–674.
- SIBLY R.M. & CALOW P. 1986: *Physiological Ecology of Animals*. Blackwell Science, Oxford, 179 pp.
- SMITH C.C. & FRETWELL S.D. 1974: The optimal balance between size and number of offspring. *Am. Nat.* **108**: 499–506.
- STEWART L., DIXON A.F.G., RŮŽIČKA Z. & IPERTI G. 1991a: Clutch and egg size in ladybird beetles. *Entomophaga* **36**: 93–97.
- STEWART L., HEMPTINNE J.-L. & DIXON A.F.G. 1991b: Reproductive tactics of ladybird beetles: relationships between egg size, ovariole number and developmental time. *Funct. Ecol.* **5**: 380–385.
- STÜRKEN K. 1964: Die Bedeutung der Imaginalernährung für das Reproduktionsvermögen der Syrphiden. *Z. Angew. Entomol.* **25**: 385–417.

- TENHUMBERG B. & POEHLING H.M. 1995: Syrphids as natural enemies of cereal aphids in Germany: aspects of their biology and efficacy in different years and regions. *Agric. Ecosyst. Environ.* **52**: 39–43.
- WRATTEN S. 1973: The effectiveness of the coccinellid beetle *Adalia bipunctata* (L.) as a predator of the lime aphid *Eucalipterus tiliae* L. *J. Anim. Ecol.* **42**: 785–802.
- YAFUSO M. 1994: Life history traits related to resource partitioning between synhospitolic species of *Colocasiomysia* (Diptera, Drosophilidae) breeding in inflorescences of *Alocasia odora* (Araceae). *Ecol. Entomol.* **19**: 65–73.
- ZHENG Y., HAGEN K.S., DAANE K.M. & MITTLER T.E. 1993a: Influence of larval dietary supply on the food consumption, food utilization efficiency, growth and development of the lacewing *Chrysoperla carnea*. *Entomol. Exp. Appl.* **67**: 1–7.
- ZHENG Y., DAANE K.M., HAGEN K.S. & MITTLER T.E. 1993b: Influence of larval consumption on the fecundity of the lacewing *Chrysoperla carnea*. *Entomol. Exp. Appl.* **67**: 9–14.

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