

Body size, reproductive allocation, and maximum reproductive rate of two species of aphidophagous Coccinellidae exploiting the same resource

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Abstract

To test the predictions of allometric analyses of laboratory data on aphidophagous ladybirds, a study was carried out on a small [*Propylea quatuordecimpunctata* (L.); dry female body mass 3.7 mg] and large species (*Coccinella septempunctata* L.; 15.4 mg) (both Coleoptera: Coccinellidae) of predatory ladybird, which regularly exploit cereal aphids. In 2003–2006, females of *C. septempunctata* and in 2006 *P. quatuordecimpunctata* were collected at 2- to 5-day intervals during the 30-day period around the peak in cereal aphid abundance, and the number of eggs they laid in the following 24 h in the laboratory was recorded. In addition to the number of eggs laid, clutch mass, live weight, and scutum width of ovipositing females and the sizes of the clutches laid in the field were recorded. As predicted, the reproductive allocation in both species was similar. The weight of the eggs of *C. septempunctata* (0.20 mg) and *P. quatuordecimpunctata* (0.18 mg) differed little, and the proportion of body mass allocated to daily reproduction (ca. 12%) was identical in both species. In addition, the maximum number of eggs laid per day in the field by the large species was, as predicted, greater than by the small species. Interestingly, the size of the egg clutches laid by *C. septempunctata* in the field was similar to the daily oviposition of field-collected adults recorded in the laboratory, whereas for *P. quatuordecimpunctata* it was significantly smaller. The role of morphology and physiology of ladybirds in structuring aphidophagous ladybird guilds is discussed.

Introduction

As in most animals, reproduction in predatory Coccinellidae is determined by morphological constraints and environmental factors. Studies based mainly on laboratory results indicate that (i) small species of predatory ladybird lay proportionally larger eggs than large species, and (ii) the proportion of body mass allocated to reproduction is constant for a wide range of species of different sizes (Dixon, 2000). If this is the case, then a corollary of the first and second predictions is that small species should lay smaller clutches and fewer eggs per unit time than large species. That is, although small species can begin laying eggs at a lower aphid population density (Dixon, 2007),

their maximum rate of egg-laying is less than that of a large species (Stewart et al., 1991; Dixon, 2007). The few laboratory data that are available indicate that the relationship between the numbers of eggs laid per day and aphid density first increases and then stabilizes at a particular level, with large species laying more eggs per unit time than small species (Dixon, 2007).

This theoretical perspective of ladybird foraging is based on interspecific and intraspecific comparisons derived from a small and not fully representative data set. Most of the data are from laboratory studies, as reproduction in the field has been poorly studied. New data are needed to test these predictions. Therefore, the reproductive activity of two common aphidophagous species, one small [*Propylea quatuordecimpunctata* (L.); mean dry mass 3.7 (mg)] and one large (*Coccinella septempunctata* L.; 15.4 mg) (both Coleoptera: Coccinellidae) exploiting the same resource, was investigated under natural conditions. Reproduction

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of both species was compared when living together in one of their preferred breeding habitats, aphid-infested stands of cereals. Variation in clutch size and egg size were investigated in relation to female body size and aphid abundance.

The objective of this study was to test two of the predictions of allometric studies (Stewart et al., 1991; Dixon, 2007), in particular: (i) do both of these species allocate the same proportion of their body mass to reproduction, and (ii) is the maximum rate of egg-laying of the larger of the two species more constrained by prey abundance than that of the smaller species?

Materials and methods

Ladybirds studied

Both species are consistently among the most abundant species found in crops, on wild herbaceous plants and sometimes shrubs and trees, infested with various aphid species, in the Czech Republic (Honek & Rejmanek, 1982; Honek, 1985). Aphids are their preferred prey for egg production, but other types of prey, consumed when aphids are scarce, serve to fuel their survival and activity (Evans et al., 2004). For *C. septempunctata*, cereal crops are the most important breeding habitat (Honek, 1989). In spring, adults aggregate in aphid-infested crops (Elliott & Kieckhefer, 2000; Ninkovic et al., 2001; Evans, 2003), where they arrive shortly after the aphids (Honek, 1989) and the females may be attracting the males by means of sex pheromone (Schaller & Nentwig, 2000). The proportion of females laying eggs and the size of the egg clutches increases with increase in aphid abundance, peaking in mid-June (A Honek, AFG Dixon & Z Martinkova, unpubl.). *Propylea quatuordecimpunctata* is less dependent on aphid-infested cereals and it arrives in crops at the same time as *C. septempunctata*, but its oviposition behaviour is less affected by aphid abundance (A Honek, AFG Dixon & Z Martinkova, unpubl.).

Numerous laboratory and field studies on the reproduction of *C. septempunctata* indicate that food availability and temperature affect fecundity and clutch size (Kawauchi, 1985; Rhamhalinghan, 1985, 1986; Takahashi, 1987; Phoofolo et al., 1995; Xia et al., 1999). Studies on the less-investigated *P. quatuordecimpunctata* reveal similar environmental effects on reproduction (Quilici, 1981; Whittaker, 1987; Obrycki et al., 1993). In the laboratory, the fecundity of *P. quatuordecimpunctata* is not only lower than that of *C. septempunctata* (Morjan et al., 1999; Bazzocchi et al., 2004), but also that of *Adalia bipunctata* (L.) and *Hippodamia variegata* (Goeze), which are similar in size (Lanzoni et al., 2004). *Propylea quatuordecimpunctata* and *C. septempunctata* differ also in their oviposition dynamics (Phoofolo & Obrycki, 2000). Several studies of other coccinellid

species also reveal that environmental factors affect fecundity (Kawauchi, 1981; Agarwala & Yasuda, 2001; Osawa, 2003) and clutch size (Kawauchi, 1985; Stathas et al., 2001).

Study site

The study site was a field at Prague-Ruzyne (50°05'N, 14°10'E, 340 m above sea level). The area is divided into sections, each planted with different crops. The coccinellids were sampled in sections planted with winter wheat or spring barley. These stands were cultivated following agriculture practices recommended for the local conditions (Spaldon, 1982) and during the study period when no insecticides, fungicides, or fertilizers were applied. The stands were naturally colonized by the common aphid species *Metopolophium dirhodum* (Walker), *Sitobion avenae* (F.), and *Rhopalosiphum padi* (L.) in decreasing order of abundance. Aphid population densities were estimated at weekly intervals by a standard method (Honek & Martinkova, 2005). Each year, the aphids were counted on 6–10 plots established within the sections where the coccinellids were collected. Half of the plots were sown at the density recommended for commercial production, the other half thinned to ca. 5% of this density, in mid-April. Final density of thinned plots was ca. 50% of the dense plots, because the plants in the thinned plots produced ca. 10 times more tillers than those in the dense plots. This resulted in dense and sparse cereal crops, of which each favours different aphid species. The average abundance of aphids in these plots was similar to that in the surrounding area. As growth of aphid populations was similar in all cereal stands, estimates of aphid densities based on sampling plots give a good estimate of prey abundance in a particular year. In each year, the peak numbers of aphids of all species per shoot in each plot were summed and the average maximum aphid abundance calculated.

Sampling female ladybirds

Coccinella septempunctata was sampled from 2003 to 2006 and *P. quatuordecimpunctata* only in 2006. The coccinellid females were sampled at 2- to 3-day intervals, from 2–3 cereal stands, during the 20- to 30-day period around the peak of coccinellid reproduction. The beetles were sampled either by sweeping or by hand-collecting from leaves or from the ground, where they tend to bask in the sun. Preliminary experiments revealed that the reproductive output of these coccinellids was not affected by the time of collection (morning vs. evening). The coccinellids collected in this way were sexed based on the morphology of the last abdominal sternite (*C. septempunctata*) or coloration of head and scutum (*P. quatuordecimpunctata*) (Rogers et al., 1971). As sex determination in the latter species is not completely reliable, the sex of the individuals that did not oviposit was verified by dissection. Because both species

Table 1 Parameters measured or calculated for *Coccinella septempunctata* and *Propylea quatuordecimpunctata*

Parameter	Unit	Method of measuring or calculation
Daily oviposition	n	Number of eggs laid in the 24-h period following collection in the field (B)
Clutch size	n	Number of eggs per clutch in the field
Fresh body mass	mg	Measured on field collected females previously allowed to lay eggs for 24 h
Dry body mass	mg	Dry body mass after oviposition (C)
Scutum width	mm	Measured across the hind margin of scutum
Fresh egg mass	mg	Mass of a clutch of eggs/number eggs per clutch
Dry egg mass	mg	Fresh weight \times 0.259 (A)
Reproductive output	%	Percentage of body mass allocated to daily oviposition = $\{[A \times B]/[C + (A \times B)]\} \times 100$
Aphid abundance	n tiller ⁻¹	Mean of maximum abundances recorded in the different plots in a particular year

did not achieve peak reproduction until late in the season, only the results on oviposition collected between 1 June and 20 July were included in the analysis. The size of the egg clusters laid in the field was recorded over a period of 4 years (2003–2006) for *C. septempunctata* and 1 year (2006) for *P. quatuordecimpunctata*, with most data collected during the second 10-day period of June.

Determination of reproductive activity and body mass

Earlier, it was established that individual females of *C. septempunctata* kept in small Petri dishes with no food often lay eggs within 24 h of capture (Honek, 1986). The same oviposition behaviour was observed in a pilot experiment with *P. quatuordecimpunctata*. The eggs laid in this period are apparently those ready or nearly ready for oviposition at the time of capture. Measuring their potential fecundity in this way made it possible to determine the effect of body size on reproductive potential in the field. Prey availability and intra- and interspecific relations, which might also influence fecundity, were not studied. The females collected in the field were immediately placed individually in 55 \times 15 mm glass tubes, which were sealed with a plastic lid. The tubes were kept in the laboratory at 25 \pm 1 °C and the same photoperiod as in the field. No food was provided. Oviposition was recorded for a period of 24 h after collection. Eggs were counted and removed at 1- to 3-h intervals to prevent cannibalism. Each tube contained a 40 \times 13 mm piece of filter paper or floppy disk, which provided a substrate for oviposition. Both species readily laid eggs on filter paper, which was used when the numbers of eggs were counted. Pieces of floppy disk were used when egg mass (Table 1) was determined, because it provided a hard, non-wettable substrate from which complete eggs could easily be removed. Egg mass was determined in 2006, based on eggs collected on 6 June (41 ovipositing females of *C. septempunctata*), 19 June (55 females), and 28 June (112 females). On the same dates, females of *P.*

quatuordecimpunctata were each also provided with pieces of floppy disk; however, they were reluctant to oviposit on this substrate and laid most of their eggs on the walls of the glass tubes. As a consequence, only 18 egg clusters of *P. quatuordecimpunctata* were weighed. To determine the mass of each cluster of eggs, the eggs plus the immediate substrate on which they were laid were cut from the piece of floppy disk and weighed within 3 h of oviposition. The eggs were then counted, removed, and the cleaned piece of diskette weighed again. The mass of each clutch and average mass of one egg were then calculated. For *C. septempunctata*, seven of these clutches were dried to constant mass and the average proportion (\pm SE) of dry matter (0.259 \pm 0.008) was determined. This figure was used to calculate dry egg mass for both species. In 2003–2005, the live body mass of all females was determined after oviposition. Because fresh mass was poorly correlated with fecundity, dry body mass was determined in 2006. After depositing eggs, some females were killed, dried to constant weight at 80 °C, and weighed (Sartorius balance) to a precision of 0.01 mg. Because adult dry mass could be confounded by variations in gut content, female size was also measured in terms of the width of the hind margin of the scutum. The dried females were mounted on paper and the distance between the hind corners of the scutum was determined using an ocular micrometre (microscope SMZ 2T; Nikon, Tokyo, Japan) to a precision of 0.041 (*C. septempunctata*) or 0.033 mm (*P. quatuordecimpunctata*). There was a significant but not close relationship between log scutum width and log body mass in both *C. septempunctata* ($R^2 = 0.457$) and *P. quatuordecimpunctata* ($R^2 = 0.326$).

Analysis of results

Quantities determined or calculated are listed in Table 1 and the number of females (pooled over periods of 10 days, with three such periods in each month) used to determine reproductive activity in Table 2. Arithmetic means (\pm SE),

Table 2 Numbers of *Coccinella septempunctata* and *Propylea quatuordecimpunctata* females whose reproduction was established in particular 10-day periods. Non-ovipositing individuals are not included

	June I	June II	June III	July I	July II	Total
<i>C. septempunctata</i>						
2003			92	105	30	227
2004		7	202	119	44	372
2005			161	118	7	286
2006	123	161	118	31		433
<i>P. quatuordecimpunctata</i>						
2006	56	76	8			140

standard deviations (SDs), medians, 25 and 75% quartiles, and co-efficients of variation ($CV = SD/mean \times 100$) were calculated for particular sets of data. These results were further analysed using several tests.

One-way analysis of variance (ANOVA) was used to test for: (i) differences in mean egg size between species, using fresh egg mass (pooled over June I–June III periods of 2006) as response variable and species as factor, (ii) differences in daily oviposition between 10-day periods and between species, using daily oviposition of particular females as response variable and period (median day of June I–June III 2006) or species as factors, (iii) differences in reproduction between the two coccinellid species, using reproductive output as response variable and species as factor, and (iv) variation in oviposition among years, using daily oviposition of females over periods June II–July II as response variable and years as factor. Non-parametric Kolmogorov–Smirnov two-sample test (Sokal & Rohlf, 1981) was used to compare differences in egg size between the clutches laid in particular

10-day periods, namely, June I–June III, using the numbers of females laying eggs of a particular fresh mass as response variable. The test was made separately for each combination of June I–June III 2006 periods on data for *C. septempunctata*.

In 2006, a linear regression $y = a_0 + a_1x$ was calculated to establish the effect of mother's size (scutum width, explanatory variable) on daily oviposition (dependent variable). Multiple linear regression $z = a_0 + a_1x + a_2y$ was used to test for the effect of: (i) mother's body size (scutum width) and daily oviposition (explanatory variables) on fresh egg mass (dependent variable), and (ii) mother's body size and daily oviposition (explanatory variables) on reproductive output (dependent variable). The significance of the regression was tested using a t-test. Correlation (R^2) was calculated for simple regression relationships, and multiple R^2 and partial R_p^2 for multiple regression relationships. The statistics were calculated using Statistica for Windows (StatSoft, Tulsa, OK, USA).

Results

Daily oviposition and egg size

Daily oviposition, that is, the number of eggs laid in 24 h differed significantly in the two species (Table 3). In June 2006, the average size of an egg clutch laid by *C. septempunctata* (33.7 ± 1.01 eggs) was 3.6 times greater than that laid by *P. quatuordecimpunctata* (9.7 ± 0.36 eggs) ($F_{1,540} = 193.1$, $P < 0.001$). Average egg mass also differed significantly ($F_{1,174} = 5.326$, $P < 0.05$), but the eggs of *C. septempunctata* (0.20 mg) were only 1.1 times heavier than those of *P. quatuordecimpunctata* (0.18 mg) (Table 3). The average egg mass of *C. septempunctata* varied between clutches (Figure 1), but the distributions of the frequencies of egg masses did not differ between the three 10-day

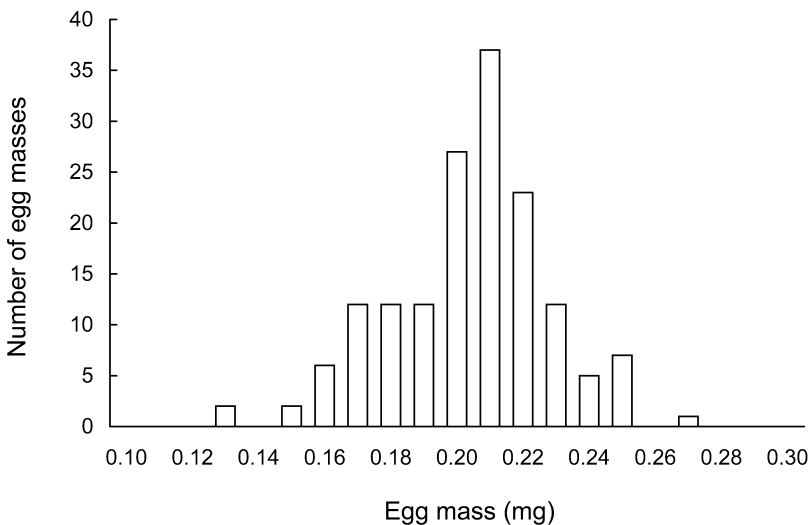


Figure 1 Frequency distribution of fresh mass (mean per cluster) of eggs laid by *Coccinella septempunctata*, pooled data for June I–June III 2006.

Table 3 Average fresh egg mass (mg) and daily oviposition (number of eggs) of *Coccinella septempunctata* and *Propylea quatuordecimpunctata* for each of the 10-day periods in June 2006

	Fresh egg mass		Daily oviposition	
	n	Mean ± SE	n	Mean ± SE
<i>C. septempunctata</i>				
June I	41	0.21 ± 0.004a	123	26.5 ± 1.49a
June II	55	0.19 ± 0.004a	161	40.2 ± 1.68b
June III	62	0.20 ± 0.003a	118	32.5 ± 1.80c
Average	158	0.20 ± 0.002a	402	33.7 ± 1.01c
<i>P. quatuordecimpunctata</i>				
Average	18	0.18 ± 0.005b	132	9.4 ± 0.35d

Means within a column followed by the same letter are not significantly different ($P > 0.05$), Kolmogorov–Smirnov two-sample test (fresh egg mass of June I–June III) and one-way analysis of variance (ANOVA).

periods in June (Kolmogorov–Smirnov two-sample test: for each of the combinations of periods June I–June III $P > 0.05$; Table 3). Egg mass in *C. septempunctata* (Figure 2) did not increase with size or daily oviposition of the mother ($R^2 = 0.020$, $F_{2,155} = 1.54$, and $P > 0.05$).

Reproductive output

The regression of daily oviposition on mother’s size (scutum width) was not significant in both *C. septempunctata*

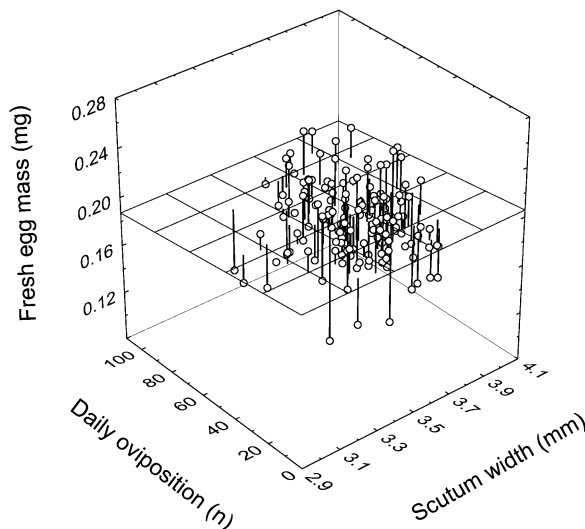


Figure 2 Scatterplot of the mean fresh mass of eggs laid by *Coccinella septempunctata* relative to their body size (scutum width) and daily oviposition (number of eggs laid in 24 h). Data for each female are represented by a point, the spikes indicate residuals of multiple linear regression (fitted surface).

($a_0 = -16.89$, $a_1 = 17.13$, $R^2 = 0.021$, $P > 0.05$; $n = 125$) and *P. quatuordecimpunctata* ($a_0 = -22.69$, $a_1 = 14.46$, $R^2 = 0.030$, $P > 0.05$; $n = 18$). Reproductive output, in terms of the percentage of body mass allocated daily to reproduction (Table 4), did not differ in the two species (ANOVA: $F_{1,174} = 0.0468$, ns). In *C. septempunctata*, reproductive output (multiple correlation: $R^2 = 0.903$, $F_{2,155} = 725.7$, $P < 0.001$; Figure 3) was positively related to daily oviposition ($R_p^2 = 0.950$, $P < 0.001$) and, unexpectedly, negatively to the size of the mothers ($R_p^2 = -0.564$, $P < 0.001$).

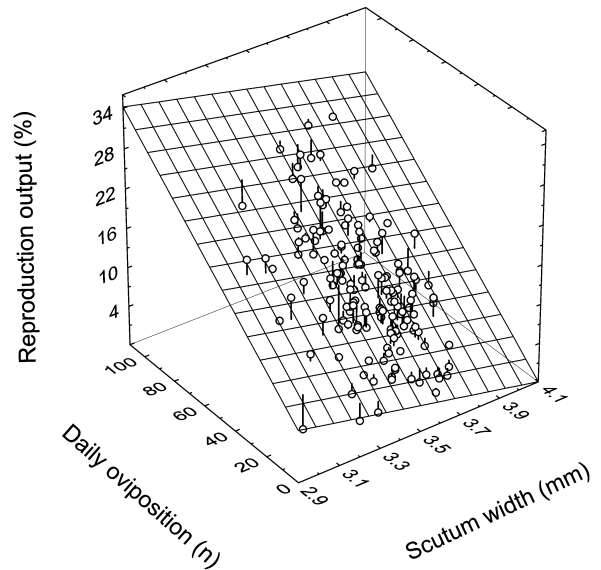


Figure 3 Scatterplot of the reproductive output (percentage of body mass allocated to reproduction per day; see Table 1) of *Coccinella septempunctata* relative to their body size (scutum width) and daily oviposition (number of eggs laid in 24 h). Plot layout and symbols as in Figure 2.

Variation in clutch size in the field

Clutch size of *C. septempunctata* in the field in the second 10-day period in June 2006 and daily oviposition of field collected adults determined at the same time in the laboratory (Table 5) did not differ significantly ($F_{1,239} = 2.738$, $P > 0.05$). In marked contrast, the clutch size of *P. quatuordecimpunctata* recorded in the field was significantly smaller ($F_{1,149} = 10.46$, $P < 0.005$) than its daily oviposition recorded in the laboratory (Figure 4).

Annual variation in daily oviposition

Daily oviposition in *C. septempunctata* averaged over the period June II to July II each year from 2003 to 2006 differed significantly ($F_{3,1395} = 96.78$, $P < 0.001$). This between-year variation in daily oviposition was clearly related to annual differences in aphid abundance (Figure 5), but the relationship

Table 4 Dry body mass (mg) and percentage of reproductive output (percentage of body mass allocated to reproduction in the 24 h following collection) in *Coccinella septempunctata* and *Propylea quatuordecimpunctata*

	n	Mean ± SE	Minimum	Maximum	CV
<i>C. septempunctata</i>					
Body mass	175	15.2 ± 0.19a	8.8	22.6	16.4
Percentage of reproductive output	158	12.3 ± 0.44c	1.5	25.1	44.8
<i>P. quatuordecimpunctata</i>					
Body mass	76	3.5 ± 0.09b	1.9	5.3	21.2
Percentage of reproductive output	18	12.6 ± 1.10c	6.6	23.0	37.2

CV, co-efficients of variation.

Means within a column followed by the same letter are not significantly different ($P > 0.05$), one-way analysis of variance (ANOVA).

is non-linear. Daily oviposition increased with aphid abundance at low aphid population densities of ca. <20 aphids per tiller, but not at the higher aphid population densities.

Discussion

The results accord with the predictions of allometric studies quantifying the relationship between body size and reproduction. Egg size relative to body size decreased with

adult body size for these two coccinellid species, although the slope of the regression of log-transformed results ($a_1 = 0.0704$) was smaller than the slope predicted by a multispecies study, which included both of these species ($a_1 = 0.63$) (Stewart et al., 1991). This is because the eggs of

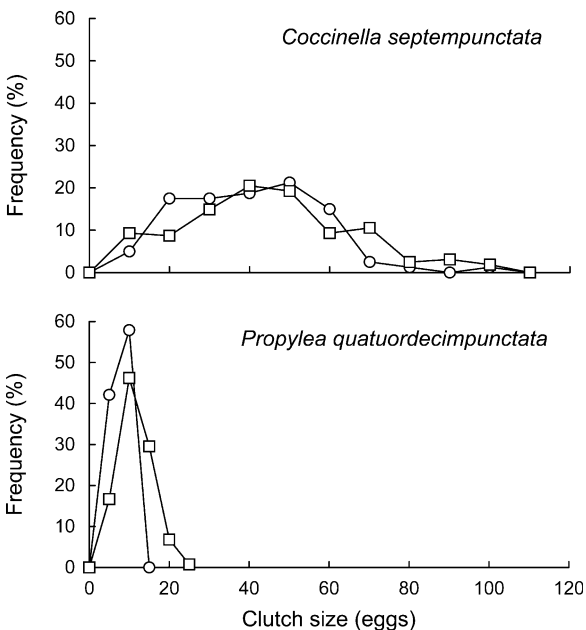


Figure 4 Frequency of different clutch sizes recorded in the field (circles) and daily oviposition (number of eggs laid in 24 h, squares) of *Coccinella septempunctata* and *Propylea quatuordecimpunctata*. As the numbers of clutches and numbers of females were different for each of the species (Table 5), the data are shown as a percentage of the total for each species.

Table 5 Clutch size in the field and daily oviposition in the laboratory of field collected adults of *Coccinella septempunctata* and *Propylea quatuordecimpunctata* in the second 10-day period in June 2006. Q25, 25% quartile; Q75, 75% quartile

	n	Mean ± SE	Q25	Median	Q75
<i>C. septempunctata</i>					
Clutch size	80	35.6 ± 1.92a	21.5	37.5	47.5
Daily oviposition	161	40.2 ± 1.68a	26	38	53
<i>P. quatuordecimpunctata</i>					
Clutch size	19	6.4 ± 0.57b	5	7	8
Daily oviposition	132	9.4 ± 0.35c	6	9	13

Means within a column followed by the same letter are not significantly different ($P > 0.05$): one-way analysis of variance (ANOVA).

the smaller *P. quatuordecimpunctata* (0.18 mg) are particularly large, being 95% of the size of the eggs of *C. septempunctata* (0.20 mg) while the average dry body mass of the former species (3.7 mg) is only 24% of that of the latter (15.4 mg). A major reason for small species to lay proportionally larger eggs than large species is that first instars must be large enough to be able to pursue and subdue aphids (Dixon, 1958; Ng, 1988; Stewart et al., 1991).

The daily allocation of body mass to reproduction is similar in *P. quatuordecimpunctata* (12.6%) and *C. septempunctata* (12.3%). This accords with another prediction of the allometric study: when allocation of resources to reproduction is measured in terms of both the biomass of eggs produced per day and reproductive biomass (ovariole number × egg weight), then the maximum investment in reproduction

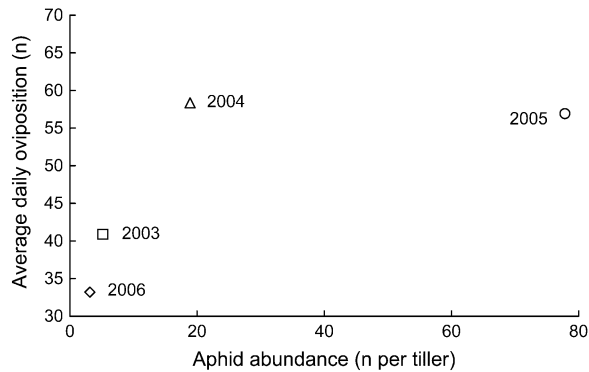


Figure 5 Daily oviposition (averaged over the period June II to July II) of *Coccinella septempunctata* in 2003–2006 plotted against aphid abundance.

should scale with body weight with an exponent of 1 (Stewart et al., 1991). Consequently, as the egg sizes of these two species are similar, the average daily oviposition (2006) in the field of *C. septempunctata* (40.2 eggs) was significantly higher than that recorded for *P. quatuordecimpunctata* (9.4 eggs).

The expected relationship (Honek, 1993) between mother's body size (scutum width) and fecundity (daily oviposition) was, however, not found. Daily oviposition is probably modified by external conditions (previous availability of prey, intra- and interspecific contacts, microclimate, etc.) that may become more significant than the allometric relationship between body size and fecundity (Leather, 1988).

Surprising was the large variation in average mass of an egg of both *P. quatuordecimpunctata* (0.13–0.22 mg) and *C. septempunctata* (0.13–0.27 mg). This is likely to reflect what is occurring in the field as the eggs weighed were the first to be laid after collection, that is, within the first 6 h. Thus, it is likely that egg size was already determined at the moment of collection and unlikely that it was affected by starvation. This does not conform with the results of a laboratory study on *C. septempunctata*, which tested the hypothesis that in ladybirds, as in birds (cf. Lack, 1986), egg size is likely to be the least and clutch size the most variable reproductive trait (Dixon & Guo, 1993). The latter study indicates, as predicted, that both the number of eggs laid per day and the size of the individual clutches are greatly affected by the availability of food. When food is supplied in excess, beetles lay twice as many eggs per day and larger clutches than when they are fed at a third of this rate. In marked contrast, the average size of the eggs laid by individual females is not affected by varying their food supply. This lack of conformity between a laboratory study (Dixon & Guo, 1993) and the results of this field study is surprising, because, as previously stated, egg size is likely to

be an important factor determining first instar survival. The factors that may have determined the variation in egg size are puzzling. Surprisingly, egg mass increased with clutch size, although this relationship only borders on significance ($P = 0.08$). This indicates that only a small proportion of the variation is determined trophically and both clutch size and average egg size change in parallel with trophic conditions experienced before oviposition. However, it is likely that these field results are confounded by the fact that the eggs were not produced by the same adults but by different batches of adults in each period and that these adults may differ genetically as well as in their metabolic condition and age.

The tendency of *P. quatuordecimpunctata* to lay clutches of eggs in the field that are smaller than their daily oviposition recorded in the laboratory, whereas in *C. septempunctata* it is the same, may be related to the different reproductive strategies of these two species. Theory (Dixon, 2007) and a field study (A Honek, AFG Dixon & Z Martinkova unpubl.) indicate that small species of ladybird lay a greater proportion of their eggs at lower aphid population densities than large species that are exploiting the same resource. When aphid densities are low, the best strategy may be to lay many small clutches of eggs rather than one large clutch per day and so spread the risk in space. When aphids are abundant, however, the better strategy may be to lay one large clutch per day. This requires further testing in the laboratory.

The prediction that the maximum rate of egg-laying of the larger of the two species is more constrained by prey abundance than that of the smaller species is also supported by our results. Daily oviposition by *C. septempunctata* was closely associated with prey availability in the 4 years of study. In the 2 years when aphids were relatively scarce, daily oviposition was 64% of that in the 2 years when aphids were more abundant. The increase in daily oviposition with increase in aphid abundance is not linear, since there is an upper limit to the rate at which *C. septempunctata* can produce eggs, which is determined by physiological and morphological constraints.

Species of ladybird that attack aphid colonies early in their development would appear to be at an advantage. Being small not only enables them to attack aphid colonies early in their development (Dixon, 2007), but may also enable them to exploit aphids even when they are still relatively uncommon. Large species on the other hand could be at a disadvantage when aphids are generally uncommon, but when abundant they can more effectively exploit the more numerous very large aphid colonies, because they can lay more eggs per unit time than small species of ladybird. In addition, the tendency of the immature stages of syrphids to attack colonies of aphids earlier and later in the year

than those of coccinellids is possibly determined by the difference in the lower developmental threshold of these two groups of predators (Dixon et al., 2005). This might mean that the morphology and physiology of insect predators is more important in determining the structure of aphidophagous guilds in the field than is generally appreciated.

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