Chapter 3

LIFE HISTORY AND DEVELOPMENT

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3.1 INTRODUCTION

Coccinellids are **holometabolous**, i.e. they have a 'complete metamorphosis', and pass through the following stages: egg, larva, pupa and adult. Egg stage lasts 15–20% of the total preimaginal developmental time, larva 55–65% and pupa 20–25% (Honěk & Kocourek 1990, Dixon 2000).

3.2 EGG

3.2.1 Egg morphology

Coccinellid eggs are usually elongate, oval or elliptic. They vary in **colour** from almost transparent (*Scymnus louisianae*; Brown et al. 2003), light grey (*Stethorus*), yellowish (*Halyzia*) through bright yellow (most species) to dark orange (Chilocorini), sometimes greenish (Klausnitzer 1969b). They are laid either upright, attached (glued) to the substrate by the lower end (Coccinellinae) or lying on their side (Scymninae, Coccidulinae, Chilocorinae). The 'upper' or anterior pole bears a ring of **micropyles** (Fig. 3.1) – pores in the chorion (the egg shell) through which spermatozoa from spermatheca (receptaculum seminis) can enter during oviposition, and for oxygen diffusion. *A. bipunctata* possesses 40–50 pores in two rings, *Platynaspis luteorubra* have clusters of pores at both ends of the egg. Chilocorini have trumpet shaped structures besides the tube like micropyles (Ricci & Stella 1988). The egg of *Scymnus sinuanodulus* has a rosette of 4–11 cup-shaped and 13–20 semicircular structures that are like micropyles (Lu et al. 2002).

The surface of the coccinellid egg (**chorion**, egg shell) is usually smooth, except for the eggs of Epilachninae which bear a polygonal sculpture (Klausnitzer 1969b; Fig. 3.1c), and *Rhyzobius* with a granular surface (Ricci & Stella 1988). The smooth surface may be soaked with an oily **excretion** provided by accessory glands of the mother. The excretion is colourless, or rarely red (as in *Calvia quatuordecimguttata*; Klausnitzer & Klausnitzer 1986) and contains defensive or signalling alkanes (Hemptinne et al. 2000; Chapter 9.).

The yolk of the egg contains many **nutrients**. During embryonic development of the *A. bipunctata* egg mass, lipid and glycogen contents decline strongly, while egg protein decline more slowly. Free carbohydrates decline early in egg development and increase

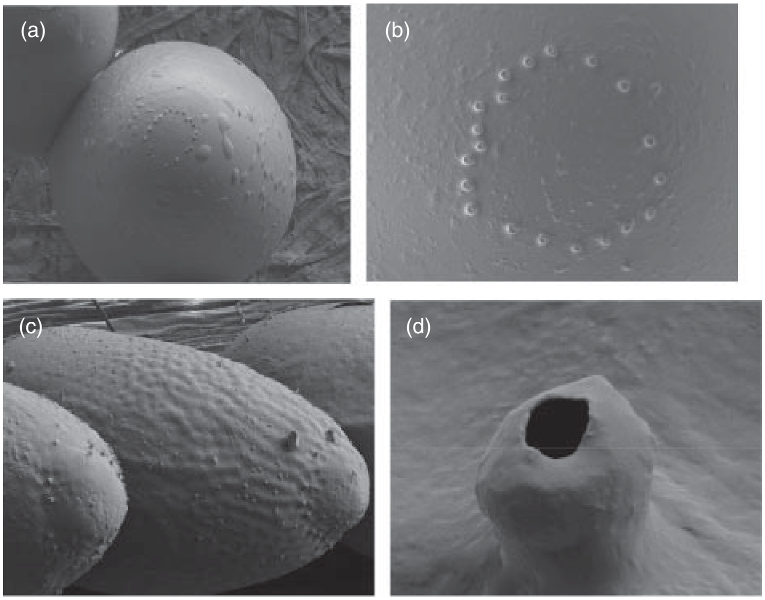

Figure 3.1 SEM photographs of ladybird eggs. (a, b) *Harmonia axyridis*, (c, d) *Cynegetis impunctata*. (a, c) upper parts of eggs with ring of micropyle openings; (b) ring of micropyles; (d) detail of a micropyle opening.

before hatching (Sloggett & Lorenz 2008). Energy per unit egg mass is lowest in the generalist *A. bipunctata*, which also has relatively large eggs, and is highest in the specialized *Anisosticta novemdecimpunctata*, which has small eggs.

A few days or hours before hatching the eggs become greyish, because the larvae are visible through the chorion. The first instar larvae of Coccinellinae and Epilachninae may possess special structures on head and prothorax called **egg teeth** which probably help the larva in hatching. Hatched larvae rest some time on the empty egg shells, and may eat them.

Ladybird eggs are defended chemically against predation, including that which is intra-guild, and they are suitable to varying degrees as food for other ladybirds (Rieder et al. 2008; Chapter 7).

3.2.2 Egg size

Insect species have a genetically fixed maximum number of ovarioles related to egg cluster size (see below) and/or a **fixed maximum size** of each single egg – traits expressed with ample food and other favourable environmental conditions. With a limited food supply, the size of eggs may be reduced and their number maintained, or decreased and their size maintained. Coccinellids adopt the second strategy (Stewart et a1. 1991a, b; Dixon & Guo 1993; see also 5.2.3). This is similar to birds, for example, where egg weight (*E*) across species increases in direct proportion (almost isometrically) to **body weight** (*W*) of the female and inversely to the **ovariole number** (*O*): $\log E = 0.83 \cdot \log(W/O) - 0.44$ (Stewart et al. 1991b).

The size of eggs is thus related to the average body size of the species; it is less than 0.4 mm in the smallest genera and over 2 mm in the largest genera. Eggs of *Scymnus louisianae* are 0.5 mm long and 0.2 mm wide (Brown et al. 2003). Adult *Clitostethus oculatus* are only 1.26 mm long and the eggs are 0.41 mm long and 0.18 mm wide, greenish to yellowish-white, with a reticulate chorion; whereas adult *Delphastus pusillus* are 1.39 mm long, the eggs are 0.43 mm long and 0.23 mm wide, white and smooth (Liu & Stansly 1996a). Eggs of *Stethorus pusillus* are 0.4 mm long, eggs of *A. bipunctata* 1.0 mm long, eggs of *C. septempunctata* 1.3 mm long, eggs of *Henosepilachna argus* 1.7 mm long, and eggs of *Anatis ocellata* 2.0 mm long (Klausnitzer & Klausnitzer 1986). Egg volume (V) in microlitres may be calculated as: $V = LW^2\pi/6$, where L is length and W is the width of the egg (Takakura 2004).

The weight of the eggs of large species *C. septempunctata* (15.4 mg adult dry mass) and small species *P. quatuordecimpunctata* (3.7 mg adult dry mass) differed little (0.20 versus 0.18 mg) (Honěk et al. 2008). *C. septempunctata* produces a larger number of individually smaller eggs than *C. transversoguttata* (Kajita et al. 2009) which has the same body size. Similarly, *Har. axyridis* produces larger egg clusters with smaller eggs (0.28 mm^3) than *Har. yedoensis* (0.36 mm^3) (Osawa & Ohashi 2008). Species of similar adult size laying smaller eggs may incur higher costs per unit mass than species laying larger eggs. More specialized species reproducing at lower aphid densities may provide neonate larvae with more nutrients to facilitate the finding of an aphid colony (Sloggett & Lorenz 2008).

The **fitness** of young larvae is positively related to egg size. Starving first instar larvae survived substantially longer (using only each individual's **yolk reserves**) in large *Coelophora bissellata* (with egg volume 1.53 mm^3) than did three other Malayan species with egg volumes of 0.81–1.20 mm^3 (Ng 1988). However, small eggs have a higher **rate of embryonic development**, which decreases the risk of egg predation (Majerus 1994). Developmental time was 3.0 days in *Har. yedoensis* possessing larger eggs and 2.7 days in *Har. axyridis* with smaller eggs (Osawa & Ohashi 2008). There is a strong selection pressure on fast development and **hatching synchrony** in cannibalistic ladybirds. Minimum egg size is, however, constrained by the minimum size at which first instar larvae can find (by extended walking) and kill prey (Stewart et al. 1991b).

Small inter-individual variation in egg size was reported in *Har. axyridis*: mean egg mass was 0.246 mg, with the minimum average in offspring of individual females 0.196 and the maximum 0.278 (Prevolsek & Williams 2006). About 30 small eggs were laid compared with only about 20 large eggs. Intra-individual variation in egg size with varying food levels was minimal.

3.2.3 Cluster size

Eggs are either laid **singly** (Scymninae, Coccidulinae, Chilocorinae – mostly coccidophagous groups) or in clusters (**batch**, **clutch** – Coccinellinae – aphidophagous, Epilachninae –phytophagous) (Klausnitzer & Klausnitzer 1986). There are a few exceptions. In Chilocorinae, the coccidophagous *Orcus chalybeus* lay eggs in clusters (Thompson 1951); *Exochomus quadripustulatus* usually lay their eggs in small groups but sometimes also individually (Sengonca & Arnold 2003). Within Coccinellinae, *Synonycha grandis* lay **sparse clusters** with the eggs a few millimetres apart; *Megalocaria dilatata* lay eggs in two **rows** (Iablokoff-Khnzorian 1982). In the adelgid eating specialist *Aphidecta obliterata*, 20% of 'clusters' contain a single egg, and a maximum cluster size observed on spruce needles was five eggs (Timms & Leather 2007).

The eggs in clusters of Coccinellinae are typically tightly packed in an upright position. The cluster size is anatomically determined by the number of **ovarioles** (3.5.5), which is similar in the left and right ovaries. The usual number of eggs per cluster in optimal conditions is equal to about half of the total ovariole number. This may be because the female lays eggs from one of the two ovaries at a time. Stewart et al. (1991a) proposed that about half the ovarioles are active in egg production at any time, while the rest are preparing for new oviposition. This interchange of activity might enable more continuous egg production. The maximum number of eggs laid in one cluster in optimal conditions is close to the total number of ovarioles. However, dissections showed no significant correlation between ovariole number and egg cluster size in intraspecific data sets of *Har. axyridis* and *A. bipunctata* (Ware et al. 2008; 5.2.3).

Baungaard and Hämäläinen (1984) attest that the **maximum cluster size** is limited by the number of ovarioles in a single ovary, since only one fully developed egg within an ovariole can be laid, and all eggs in a cluster originate from the same ovary. They suggested that larger clusters are a result of laying a second cluster in very close proximity to the first one. However, Majerus (1994) reported egg clusters which contained numbers well in excess of the maximum numbers of ovarioles recorded for the respective species (*C. septempunctata* and *A. bipunctata*). He suggested that a cluster may include eggs from **both ovaries**, and that more than one egg may be deposited from one ovariole. Ware et al. (2008) reported egg clusters laid by an individual female that were bigger than the number of ovarioles in both ovaries together. We suggest that the count of ovarioles during dissection may have been underestimated, because some of them had been emptied recently, therefore had not developed a second large maturing oocyte, and thus were overlooked.

In interspecific comparisons, there is a general linear correlation between the number of ovarioles and the cluster size (Dixon & Guo 1993). However, adult size is strongly determined by food availability during previous larval development (Rhamhalinghan 1985) while cluster size is affected by food availability during the development of oocytes. **Oocyte development** and maturation takes a few days and there are several oocytes of different stages in each ovariole sequentially ordered in chambers or **follicles**, so that the female is able to lay a full clutch of eggs from both ovaries daily. The total **egg load** is usually split into two or more clusters. It is uncertain whether eggs of such small clusters come from one ovary only, or from a combination of both.

Fois and colleagues (unpublished) found 5–72 eggs in clusters laid by a single female of *Har. axyridis*, the median and average being 28 eggs. This was a usual cluster size in this highly fertile species; well-fed young females laid two such clusters daily. However, the number of eggs laid per day was often lower than the total number of ovarioles of the female, which was 53–77 in this sample of *Har. axyridis*. The decrease in the number of eggs may have been due to **suboptimal feeding** with progressive **ageing**, and may vary with the **frequency of mating**. The average cluster weight of *Har. axyridis* is 5.6 mg (21 eggs) (Prevolsek & Williams 2006).

The egg cluster size of *Har. axyridis* fed with eggs of *Ephestia kuehniella* is 29–32 and 28–39. Females fed with honey bee pollen oviposited only 8–14 eggs per cluster, while those fed with the pea aphid, *Acyrthosiphon pisum*, laid 29–48 eggs per cluster (Berkvens et al. 2008a, b). A larval diet of unlimited aphids resulted in the largest clusters of eggs being laid by the resulting *Har. axyridis* and *A. bipunctata* females (Ware et al. 2008), irrespective of the constant number of ovarioles. For more examples on the **effect of food** on cluster size see Table 3.1.

Egg cluster size is on average smaller (about 30 versus 40 eggs) for a short **photoperiod** (12 h light) than for a long one (16 h) in both the laboratory strain and wild population of the red *succinea* morph of *Har. axyridis* (Berkvens et al. 2008b), while it is larger (34 versus 28) in the melanic morph. The average cluster size in a melanic **colour morph** of *C. septempunctata*

Table 3.1 Egg cluster size (C), daily fecundity (D) and lifetime fecundity (F) of coccinellids. References for individual rows are numbered and listed below the table.

C	D	F	Prey, conditions	Ref.
Adalia bipunctata				
11–17	—	—	—	8
11–16 (1–47)	—	—	—	10
—	—	250	*Aphis fabae*	14
—	—	676	*Myzus persicae*	14
11–14	—	—	—	15
15 (2–43)	—	—	—	25
—	10	—	*Myzus persicae* on *Brassica napus*	28
—	4	—	*Myzus persicae* on *Sinapis alba*	28
—	7	—	*Myzus persicae* on *Vicia faba*	28
14	—	—		34
—	9.3	738	*Aphis fabae*	35
—	20.4	max. 1535	*Microlophium carnosum*	35
15 (3–25)	—	—	—	37
—	12–20	—	—	40
—	—	63	*Aphis fabae*	52
—	—	1011	*Phorodon humuli*	52
14–28	—	—	*Euceraphis betulae*, 25°C, 18L:6D	53
16–28	—	—	*Eucallipterus tiliae*, 25°C, 18L:6D	53
14–24	—	—	*Tuberculatus annulatus*, 25°C, 18L:6D	53
18–26	—	—	*Liosomaphis berberidis*, 25°C, 18L:6D	53
14–22	—	—	*Acyrthosiphon ignotum*, 25°C, 18L:6D	53
12–18	—	—	*Macrosiphoniella artemisiae*, 25°C, 18L:6D	53
12–21	—	—	*Cavariella konoi*, 25°C, 18L:6D	53
12–21	—	—	*Aphis fabae*, 25°C, 18L:6D	53
12–16	—	—	*Aphis farinosa*, 25°C, 18L:6D	53
0	—	—	*Aphis cirsiiacanthoidis*, 25°C, 18L:6D	53
0	—	—	*Aphis spiraephaga*, 25°C, 18L:6D	53
—	16	537	*Myzus persicae*, 25°C	63
—	—	600	—	95
—	—	39	*Acyrthosiphon caraganae*	97
—	—	264	*Aphis pomi*	97
—	—	94, 241	*Hyalopterus pruni*	97
—	—	161	*Rhopalosiphum padi*	97
30	—	—	—	108
31	20	—	*Acyrthosiphon pisum*, 22°C, 14L:10D, 30 days period; mean of individual maxima	115
—	16.7	978	19°C	51
—	22.5	835	23°C	51
—	25.9	759	27°C	51
—	18.3	501	pollen + *Ephestia kuehniella* eggs	51
—	23.0	992	*Acyrthosiphon pisum*	51
—	23.7	1079	*Myzus persicae*	51
—	28.1	796	*Acyrthosiphon pisum*	122
—	33.3	1864	pollen + *Ephestia kuehniella* eggs	122
—	11.3	890	pollen + *Artemia franciscana*	122
—	6.3	265	pollen + lyophilized artificial diet	122
—	10.8	468	pollen + lyoph. art. diet + *A. franciscana*	122

Table 3.1 (*Continued*)

C	D	F	Prey, conditions	Ref.
Adalia decempunctata				
11	—	—	—	21
Aiolocaria hexaspilota				
26 (3–74)	—	881 (784–1036)		47
Anatis ocellata				
—	—	300	—	58
Anegleis cardoni				
—	6.8	397	*Aphis gossypii*, 27°C, 14L:10D	84
—	6.3	328	*Aphis craccivora*, 27°C, 14L:10D	84
—	5.1	137	*Lipaphis pseudobrassicae*, 27°C, 14L:10D	84
Axinoscymnus cardilobus				
—	—	125	17°C	43
—	—	211	23°C	43
—	—	20	32°C	43
Brumoides suturalis				
—	—	142	*Ferrisia virgata* + *Planococcus minor*	29
—	—	182	*Ferrisia virgata*	29
—	—	18	*Phthorimaea operculella*	29
—	—	214	*Planococcus minor*	29
Callicaria superba				
—	—	237	—	49
Calvia decemguttata				
—	—	162–257	—	62
Calvia duodecimmaculata				
—	—	165	*Rhopalosiphum padi*	62
—	—	127	*Aphis pomi*	62
—	—	193	*Psylla mali*	62
Calvia quatuordecimguttata				
—	—	185	*Psylla alni*	62
—	—	247	*Psylla mali*	62
—	—	114–133	*Rhopalosiphum padi*	62
—	—	122 (106–142)	*Aphis pomi*	98
—	—	38 (28–46)	*Hyalopterus pruni*	98
—	—	158 (147–183)	*Psylla alni*	98
—	—	219 (198–243)	*Psylla mali*	98
18 (10–27)	—	142 (113–168)	*Psylla ulmi*	98
—	—	114 (98–128)	*Rhopalosiphum padi*	98
Ceratomegilla undecimnotata				
—	—	139	spring	47
—	—	73	summer	47
—	20	—	aphids	102
—	9–14	—	*Ephestia kuehniella* eggs	102
30	—	—	—	108

(*Continued*)

Table 3.1 (*Continued*)

C	D	F	Prey, conditions	Ref.
Chilocorus bipustulatus				
—	4.2	529	*Aspidiotus nerii*	114
Chilocorus nigritus				
—	3	—	*Aonidiella orientalis*	3
—	—	24	*Melanaspis glomerata*	22
—	—	370	*Aulacaspis tegalensis*	32
—	5	—	*Aspidiotus nerii*	36
—	—	57–93	—	50
—	—	151	*Parlatoria blanchardi*	72
—	3	564	*Abgrallaspis cyanophylli*, 20°C	88
—	6	1361	*Abgrallaspis cyanophylli*, 24°C	89
—	8	1008	*Abgrallaspis cyanophylli*, 26°C	88
—	6	872	*Abgrallaspis cyanophylli*, 30°C	88
—	3.5	432	*Aspidiotus nerii*, 26°C	88
—	—	81	*Aonidiella aurantii*, 27°C	50
—	—	86	*Diaspidiotus perniciosus*, 27°C	50
—	—	93	*Aspidiotus desctructor*, 27°C	50
—	—	87	*Aulacaspis tubercularis*, 27°C	50
—	—	72	*Chrysomphalus aonidum*, 27°C	50
—	—	79	*Hemberlesia lataniae*, 27°C	50
—	—	71	*Lepidosaphes cornutus*, 27°C	50
—	—	79	*Melanaspis glomerata*, 27°C	50
—	—	194	*Aonidiella aurantii*, 26°C	100
—	—	483	*Aspidiotus nerii*, 26°C	100
—	—	151	*Parlatoria blanchardii*, 27°C	72
—	—	292	*Aonidiella orientalis*, 24°C	3
—	—	57	*Aonidimytilus albus*, 27°C	3
—	—	121	*Aspidiotus desctructor*, 30°C	9
—	—	102	*Hemberlesia lataniae*, 30°C	9
—	—	136	*Melanaspis glomerata*, 30°C	9
—	—	370+	*Aulacaspis tegalensis*, 21°C	32
Clitostethus arcuatus				
—	—	181	*Siphoninus phillyreae*	125
Clitostethus oculatus				
—	3	—	*Bemisia tabaci*	64
—	0.6	52	20°C	92
—	1.0	81	26°C	92
—	0.7	33	31°C	92
Coccinella leonina transversalis				
16	—	—	—	74
—	—	915	*Aphis craccivora*	80
—	21	1400	lifetime mating	81
—	23	376	single mating	81
Coccinella novemnotata				
18	11.9	302	*Brevicoryne brassicae*, 25°C	24

Table 3.1 *(Continued)*

C	D	F	Prey, conditions	Ref.
Coccinella septempunctata				
25	18	—	15 mg *Acyrthosiphon pisum* daily	20
41	34	—	*Acyrthosiphon pisum* ad libitum	20
17	12.3	201	*Brevicoryne brassicae*, 25°C	24
34	—	—	in the laboratory, field collected	120
36	—	—	field observation	120
—	19	—	20 *Acyrthosiphon pisum* / day	26
—	32	—	30 *Acyrthosiphon pisum* / day	26
—	28 (23–37)	—	105 aphids / day	30
—	7 (3–10)	—	50 aphids / day	30
—	—	514–719	aphids	41
—	—	34–228	artificial diets	41
—	—	283–1182	aphids, 12–27 mg/day	46
—	—	0.3–50	artificial diet, 4.5–9.1 mg/day	46
—	—	1428 (268–2386)	*Acyrthosiphon pisum*, 25°C, 16L:8D	54
—	—	1286 (218–2291)	*Sitobion avenae*, 25°C, 16L:8D	54
—	—	626 (98–1528)	*Aphis fabae*, 25°C, 16L:8D	54
—	—	683 (134–1839)	*Aphis craccivora*, 25°C, 16L:8D	54
—	—	893	*Aphis spiraephila*	62
—	—	356	*Rhopalosiphum padi*	62
—	—	759	*Sitobion avenae*	62
—	—	513	*Schizaphis graminum*	62
—	—	476	*Aphis gossypii*	62
—	—	448	*Aphis pomi*	62
—	—	1061	*Aphis craccivora*	79
—	—	739	*Aphis gossypii*	79
—	—	203	*Aphis nerii*	79
—	—	1764	*Lipaphis pseudobrassicae*	79
—	—	1199	*Myzus persicae*	79
—	—	488	*Uroleucon compositae*	79
—	—	1061	*Aphis craccivora*	80
—	25	1764	lifetime mating	81
—	13	298	single mating	81
—	—	552	—	93
—	—	668	—	93
—	—	79–313	varied with parental age	105
—	—	705	melanic female + melanic male	106
—	—	396	typical female + typical male	106
50	—	—	—	108
	—	814	—	110
33–44	—	—	—	111
	22.4	287	*Aphis gossypii*, 25°C	118
15–84		718–1485 (max. 1953)	Tashkent	119
—	27	—	seasonal peak, alfalfa	127
Coccinella transversoguttata				
—	15	—	seasonal peak, alfalfa	127
Coccinella trifasciata				
10	—	—	—	108

(Continued)

Table 3.1 (*Continued*)

C	D	F	Prey, conditions	Ref.
Coccinella undecimpunctata				
21	12.4	371	*Brevicoryne brassicae*, 25°C	24
—	max. 40	85–135	Palestina	33
1–37	max. 89	451–746	Egypt	48
—	—	742–983	*Aphis craccivora*, single mated	132
Coelophora biplagiata				
20	—	—	—	99
Coelophora bissellata				
10	—	—	—	74
Coelophora inaequalis				
9	—	—	—	74
Coelophora saucia				
—	26 (max. 51)	785	16L:8D	76
—	16 (max. 40)	478	24L:0D	76
—	10 (max. 39)	311	8L:16D	76
—	2–3 (max. 50)	230–1044	varied with light colour	76
—	—	120	10 s mating	83
—	—	310	1 min mating	83
—	—	380	one hour mating	83
—	—	393	*Aphis craccivora*, newly emerged female	126
—	—	1980	*Aphis craccivora*, 20 days old female	126
—	—	240	*Aphis craccivora*, 60 days old female	126
—	—	1506	*Aphis craccivora*, 1 mating	129
—	—	2192	*Aphis craccivora*, 20 matings	129
Coleomegilla maculata				
—	2.6–3.0	—	pollen	23
—	1	—	*Leptinotarsa decemlineata* eggs	38
—	4	—	*Myzus persicae*	38
5–7	—	—	the first clutch	67
—	6.2	—	pollen + *Ephestia kuehniella* eggs	131
—	6.8	—	maize pollen	131
Delphastus catalinae				
—	34	—	—	103
Epilachna vigintisexpunctata				
24–28		—	—	94
Exochomus quadripustulatus				
—	2.6	91	*Acyrthosiphon pisum*	91
—	4.3	173	*Dysaphis plantaginea*	91
—	1–16	139	12/24°C	101
—	1–11	97	9/19°C	101

Table 3.1 *(Continued)*

C	D	F	Prey, conditions	Ref.
Harmonia axyridis				
—	5	257	*Pectinophora gossypiella* eggs	1
—	13	—	single pair in container	2
—	1.6–8.8	—	10–40 females per container	2
—	15	715	fresh eggs of *Sitotroga cerealella*	2
—	13	607	frozen eggs of *Sitotroga cerealella*	2
—	—	834	*Aphis fabae*	6
—	—	1536	*Diuraphis noxia*	6
29–32	—	—	*Ephestia* eggs	11
8–14	—	—	pollen	11
29–48	—	—	*Acyrthosiphon pisum*	12
28–39	—	—	*Ephestia* eggs	12
27	—	—	—	21
28 (5–72)	—	—	*Acyrthosiphon pisum*	27
—	—	751	*Aphis gossypii*, 14.5–18°C	39
—	—	164	artificial diet	42
—	25	3819	*Hyperomyzus carduellinus*, 25°C	44
—	14	945	*Hyperomyzus carduellinus*, 30°C	44
—	27	2310	*Myzus persicae*, 25°C	44
—	22	778	*Myzus persicae*, 30°C	44
—	16	—	*Aphis gossypii*	59
—	18	561	*Myzus persicae*, 25°C	63
—	—	400–800	6 weeks, 18°C	65
—	—	900–1300	6 weeks, 24°C	65
—	—	800–1100	6 weeks, 30°C	65
—	—	719	*Acyrthosiphon pisum*, 27°C	69
20	—	—	*Aphis spiraecola*	85
21	—	—	—	90
26	—	—	*Acyrthosiphon pisum*	86
12–52	20	100–200	*Hyalopterus pruni*	96
—	23	—	aphids	102
—	34–41	—	*Ephestia kuehniella* eggs	102
30	27 (max. 78)	1642 (703–2263)	*Aphis fabae*	107
23	—	—	alfalfa	111
31	—	—	weeds	111
47	19	—	*Acyrthosiphon pisum*, 22°C, 14L:10D, 30 days period; mean of individual maxima	115
39	—	455	frozen *Ephestia kuehniella* eggs	121
—	—	128	*Aphis glycines* susceptible soybean	68
—	—	22	*Aphis glycines* resistant soybean	68
—	10.3	—	flightless strain, 36. generation	130
—	19.3	—	control strain, 36. generation	130
—	—	888	*Ephestia kuehniella* eggs	136
—	—	823	*Schizaphis graminum*	136
Harmonia yedoensis				
24	—	401	frozen *Ephestia kuehniella* eggs	121

(Continued)

Table 3.1 *(Continued)*

C	D	F	Prey, conditions	Ref.
Henosepilachna sumbana				
21–32	—	—	—	94
Henosepilachna vigintioctopunctata				
26	—	—	—	94
Hippodamia convergens				
—	—	max. 1550	—	47
19	—	—	—	116
—	—	589–851	*Aphis craccivora*, single mated	132
Hippodamia tredecimpunctata				
10–40	—	107–407	USA	47
—	—	316	*Aphis gossypii*	62
—	—	345	*Aphis spiraephila*	62
—	—	158	*Brevicorine brasicae*	62
—	—	452	*Schizaphis graminum*	62
—	—	327–504	*Sitobion avenae*	62
Hippodamia variegata				
19	10.6	276	*Brevicoryne brassicae*, 25°C	24
—	21	842	*Myzus persicae*, 25°C	63
20	—	—	—	108
11–20	—	960 (789–1256)	*Dysaphis crataegi*, 25°C, 16L: 8D	61
Megalocaria dilatata				
2 × 14	—	—	—	47
Menochilus sexmaculatus				
—	—	861	multiple mating	13
—	—	70	single mating	13
—	44 (peak)	—	after 10 matings	75
—	55 (peak)	—	after 20 matings	75
—	55 (peak)	—	after 5 matings	75
—	—	1998	*Aphis craccivora*	80
—	32	1898	lifetime mating	81
—	24	1268	single mating	81
—	16–27	92–275	old females	82
—	16–33	214–555	old males	82
—	4–6	43–64	senescent males	82
—	22–30	767–1318	young females	82
—	23–30	1118–1464	young males	82
—	—	110	1 min mating	83
—	—	40	10 s mating	83
—	—	620	one hour mating	83
—	17.2	—	*Aphis craccivora*, 15L:9D, 18°C	109
—	9.9	—	*Aphis gossypii*, 15L:9D, 18°C	109
—	—	max. 2388	—	47
12	—	—	—	74
Micraspis discolor				
—	—	385	20°C	77
—	—	563	25°C	77
—	—	750	27°C	77
—	—	622	30°C	77

Table 3.1 *(Continued)*

C	D	F	Prey, conditions	Ref.
Nephus reunioni				
—	2.6 (max.)	177	*Planococcus citri*, 25°C	134
Nephus includens				
—	—	151	—	135
Oenopia conglobata				
5	—	—	—	21
8–15	—	—	—	47
—	—	439	*Aphis spiraephila*	62
—	—	643	*Rhopalosiphum padi*	62
—	—	327	*Aphis pomi*	62
—	—	349–453	Central Asia	119
Oenopia lyncea				
—	—	40	—	117
Olla v-nigrum				
27	—	—	—	108
17	5.7	72	*Acyrthosiphon pisum*, 15°C, 12L:12D	137
13	8.1	200	*Acyrthosiphon pisum*, 20°C, 12L:12D	137
13	12.4	269	*Acyrthosiphon pisum*, 25°C, 12L:12D	137
14	6.4	329	*Acyrthosiphon pisum*, 20°C, 18L:6D	137
Propylea dissecta				
—	—	150	interference with 4 females	71
—	—	336	single female	71
—	37 (peak)	—	after 10 matings	75
—	19 (peak)	—	after 20 matings	75
—	33 (peak)	—	after 5 matings	75
—	—	278–710	1 to multiple matings	78
—	—	942	*Aphis craccivora*	80
—	—	867	20 day old females after single mating	87
Propylea japonica				
—	—	644	—	47
7–9	—	—	—	56
Propylea quatuordecimpunctata				
1–24	20 (max. 65)	1308 (max. 1800)	England, laboratory	47
10	—		field collected in laboratory	120
6.4	—		field	120
—	—	386	*Myzus persicae* on Bt potatoes	55
—	—	345	*Myzus persicae* on non-Bt potatoes	55
—	—	278	*Aphis craccivora*	55
—	—	431	*Aphis craccivora* + *Myzus persicae* on Bt potatoes	55
—	—	119	*Aphis gossypii*	62
—	—	351	*Sitobion avenae*	62
—	—	211	*Aphis spiraephila*	62
12	—	—	—	108

(Continued)

Table 3.1 (*Continued*)

C	D	F	Prey, conditions	Ref.
Propylea quatuordecimpunctata × *Propylea japonica*				
—	—	149	—	47
Psyllobora confluens				
—	17	440	*Erysiphe cichoracearum*	18
Sasajiscymnus tsugae				
—	2.9	280 (max. 513)	*Adelges tsugae*, 25°C	45
Scymnus frontalis				
—	—	151	22°C	31
—	7.3	—	*Diuraphis noxia*, 26°C	73
Scymnus hoffmanni				
—	—	127	25°C	57
Scymnus interruptus				
—	—	88	20°C	133
—	—	402	24°C	133
Scymnus levaillanti				
—	4.9	428	20°C	113
—	5.9	456	25°C	113
—	8.3	393	30°C	113
—	2.6	83	35°C	113
Scymnus louisianae				
—	—	122	*Aphis glycines*, 23°C, 15:9 L:D	16
Scymnus marginicollis				
—	—	75	20–25°C	17
Scymnus marinus				
—	—	1.7	15°C	70
—	—	602	30°C	70
Scymnus sinuanodulus				
—	2.5	130 (max. 200)		66
Scymnus subvillosus				
—	—	99	*Hyalopterus pruni*, 5 aphids. per day	7
—	—	232	*Hyalopterus pruni*, 80 aphids per day	7
Scymnus syriacus				
—	—	588	*Aphis spiraecola* on *Citrus sinensis*	104
—	—	658	*Aphis spiraecola* on *Spirea* sp.	104
Serangium parcesetosum				
—	—	28	*Trialeurodes vaporariorum*	5
Serangium japonicum				
—	—	387	*Bemisia tabaci*, 20°C	124
Stethorus bifidus				
—	1	2–33	10 mites / day	19
—	2	24–67	20 mites / day	19
—	6	308–438	50 mites / day	19

Table 3.1 (*Continued*)

C	D	F	Prey, conditions	Ref.
Stethorus gilvifrons				
—	4.4	149	*Oligonychus coffeae*	123
Stethorus japonicus				
—	8.1	—	*Amphitetranychus viennensis*, 27°C: 16L8D	60
—	5.4	—	*Panonychus mori*, 27°C: 16L:8D	60
—	7.1	—	*Tetranychus urticae*, 27°C: 16L:8D	60
Stethorus pussilus				
—	—	54–60	—	4
—	—	122	Bt-maize	128
—	—	111	non-Bt-maize	128
Subcoccinella vigintiquatuorpunctata				
—	—	200–300	—	112
Synonycha grandis				
3–60	—	360	—	47

1, Abdel-Salam et al. 1997; 2, Abdel-Salam and Abdel-Baky 2001; 3, Ahmad 1970; 4, Alvarez-Alfageme et al. 2008; 5, Al-Zyoud et al. 2005; 6, Anonymous 1997; 7, Atlıhan and Güldal 2009; 8, Banks 1955, 1956; 9, Baskaran and Suresh 2006; 10, Baungaard and Hämäläinen 1981; 11, Berkvens et al., 2008a; 12, Berkvens et al., 2008b; 13, Bind 2007; 14, Blackman 1965; 15, Blackman 1967; 16, Brown et al. 2003; 17, Buntin and Tamaki 1980; 18, Cividanes et al. 2007; 19, Collyer 1964; 20, Dixon and Guo 1993; 21, Dobzhansky 1924; 22, Dorge et al. 1972; 23, Duan et al. 2002; 24, ElHag and Zaitoon 1996; 25, Ellingsen 1969; 26, Evans et al. 2004; 27, Fois and Nedvěd, unpublished; 28, Francis et al. 2001; 29, Gautam 1990; 30, Ghanim et al. 1984; 31, Gibson et al. 1992; 32, Greathead and Pope 1977; 33, Hafez in Iablokoff-Khnzorian 1982; 34, Hämäläinen and Markkula 1977; 35, Hariri 1966; 36, Hattingh and Samways 1994; 37, Hawkes 1920; 38, Hazzard and Ferro 1991; 39, He et al. 1994; 40, Hemptinne et al. 1992; 41, Hodek 1996a; 42, Hong and Park 1996; 43, Huang et al. 2008; 44, Hukushima and Kamei 1970; 45, Cheah and McClure 1998; 46, Chen et al. 1980; 47, Iablokoff-Khnzorian 1982; 48, Ibrahim 1955; 49, Iwata 1932; 50, Jalali and Singh 1989; 51, Jalali et al. 2009; 52, Kalushkov 1994; 53, Kalushkov 1998; 54, Kalushkov and Hodek 2004; 55, Kalushkov and Hodek 2005; 56, Kawauchi 1981; 57, Kawauchi 1985; 58, Kesten 1969; 59, Kim and Choi (1985); 60, Kishimoto 2003; 61, Kontodimas and Stathas 2005; 62, Kuznetsov 1975; 63, Lanzoni et al. 2004; 64, Liu et al. 1997; 65, Lombaert et al. 2008; 66, Lu and Montgomery 2001; 67, Lundgren and Wiedenmann 2002; 68, Lundgren et al. 2009; 69, McClure (1987); 70, M'Hamed and Chemseddine 2001; 71, Mishra and Omkar 2006; 72, Muralidharan 1994; 73, Naranjo et al. 1990; 74, Ng 1986; 75, Omkar and Mishra 2005b; 76, Omkar and Pathak 2006; 77, Omkar and Pervez 2002; 78, Omkar and Pervez 2005; 79, Omkar and Srivastava 2003; 80, Omkar et al. 2005a; 81, Omkar et al. 2005b; 82, Omkar et al. 2006b; 83, Omkar et al. 2006a; 84, Omkar et al. 2009; 85, Osawa 2005; 86, Perry and Roitberg 2005; 87, Pervez et al. 2004; 88, Ponsonby 2009; 89, Ponsonby and Copland 1998; 90, Prevolsek and Williams 2006; 91, Radwan and Lovei 1983; 92, Ren et al. 2002; 93, Rhamhalinghan 1986; 94, Richards and Filewood 1988; 95, Savoiskaya 1965; 96, Savoiskaya 1970; 97, Semyanov 1970; 98, Semyanov 1980; 99, Semyanov and Bereznaya 1988; 100, Senal 2006; 101, Sengonca and Arnold 2003; 102, Schanderl et al. 1988; 103, Simmons et al. 2008; 104, Soroushmehr et al. 2008; 105, Srivastava and Omkar 2004; 106, Srivastava and Omkar 2005; 107, Stathas et al. 2001; 108, Stewart et al. 1991b; 109, Sugiura and Takada 1998; 110, Sundby 1968; 111, Takahashi 1987; 112, Tanasijevic 1958; 113, Uygun and Atlıhan 2000; 114, Uygun and Elekcioglu 1998; 115, Ware et al. 2008; 116, Williams 1945; 117, Witsack 1971; 118, Xia et al. 1999; 119, Yakhontov 1958; 120 Honěk et al. 2008; 121, Osawa and Ohashi 2008, 122, Bonte et al. 2010, 123, Perumalsamy et al. 2010, 124, Yao et al. 2010, 125, Tavadjoh et al. 2010, 126, Omkar et al. 2010b, 127, Kajita and Evans 2010, 128, Li and Romeis 2010, 129, Omkar et al. 2010a, 130, Seko and Miura 2009, 131, Pilorget et al. 2010, 132, El-Heneidy et al. 2008, 133, Tawfik et al 1973, 134, Izhevsky and Orlinsky 1988, 135, Transfaglia and Viggiani 1972, 136, dos Santo et al. 2009, 137, Kreiter 1985.

in India was 8.9 eggs, while the same in typical morphs was 14.34 (Rhamhalinghan 1999).

3.2.4 Hatching rate

The percentage of eggs in a cluster that develop fully and from which larvae eventually hatch is called hatching rate, **egg viability**, or percentage fertility (100–progeny loss). It is often substantially less than 100%. The hatching rate differentiates fecundity (number of eggs per female) from **fertility** (number of viable progeny per female).

Some eggs are non-fertile due to low **sperm volume and quality**. Other eggs are fertilized but do not develop or fail to hatch due to **infection** by various bacteria. In most species of invertebrates, **male-killing** occurs during embryonic stages (early male-killing) and is associated with cytoplasmic bacteria, including *Wolbachia*, *Spiroplasma*, *Rickettsia*, *Flavobacterium* and gamma proteobacteria (Nakanishi et al. 2008; Chapter 8). These bacteria kill only, or mostly, male embryos, giving a hatching rate close to 50%. The female larvae of ladybirds, especially Coccinellinae, i.e. the sisters of the killed males, have a nutritive advantage over the females from uninfected clusters, because they **cannibalize** those undeveloped 'male' eggs (Majerus 1994).

Most authors do not discriminate between 'non-fertile' and 'non-developing' eggs and record the proportion of hatched eggs. Under optimal conditions this is high: 100% eggs of *C. septempunctata* and *C. leonina transversalis* fed with *Lipaphis pseudobrassicae*, *Myzus persicae* or *Aphis nerii* hatched (Gupta et al. 2006). There were 6% unhatched eggs in *P. quatuordecimpunctata* in England in the field (Banks 1956). They were consumed by newly born larvae. Laboratory progeny loss ranged from 5% in *C. leonina transversalis*, 6% in *P. dissecta*, through 10% in *Menochilus sexmaculatus* to 25% in *C. septempunctata* (Omkar et al. 2005) when the ladybirds were reared on a **suboptimal prey**, *Aphis craccivora*. In *A. bipunctata* fed with optimal prey, *Myzus persicae*, the hatching rate was 89%, associated with high **fecundity** (676 eggs per female), while both measures decreased on a suboptimal prey, *Aphis fabae* (56%, 250 eggs; Blackman 1965). The decrease of hatching rate of *C. septempunctata* among six prey species was clearly correlated with a decrease of lifetime fecundity (Fig. 3.2; Omkar & Srivastava 2003).

Hatching rate varied with **temperature** in *Har. axyridis*. Between 18 and 24°C, the rate was 65–90%. At 30°C, it decreased to 30–65% (Lombaert et al. 2008). The highest temperature, 30°C, was lethal for most eggs of a population from the Czech Republic, regardless of humidity (O. Nedvěd, unpublished). In *Micraspis discolor* in India, the egg hatch rate was lowest (65%) at the lowest experimental temperature (20°C), highest (95%) at optimum temperature (27°C), and decreased (83%) at the highest temperature (30°C) (Omkar & Pervez 2002).

High **humidity** is favourable for embryonic development and larval hatching; 99% of the eggs of *Delphastus catalinae* hatched at 85% RH, while 85% hatched at 25% RH (Simmons et al. 2008).

There was no consistent difference in the hatching rate of *Har. axyridis* at long (16L:8D) and short (12L:12D) **photoperiod**s (Berkvens et al. 2008b). Wild populations hatched better than the laboratory strain. Nor in *Coelophora saucia* was the hatching rate very different (92–97%) under different photoperiods or under continuous light (Omkar & Pathak 2006).

Hatching rate was high (76–90%) when the eggs of *Menochilus sexmaculatus* were fertilized by young males (4–50 days), and low (12–25%) when fertilized by **old males** (60–110 days) (Omkar et al. 2006b). A similar pattern was found in *C. septempunctata* (Srivastava & Omkar 2004). Hatching rate of *A. bipunctata* remained high (80–90%) for 1 or 2 months old males and then decreased to 20–30% (Jalali et al. 2009a) and that of *Anegleis cardoni* increased from almost zero to more than 80% at a **female age** of 2 weeks (Omkar et al. 2009).

Multiple matings enhanced the total egg output and the percentage of hatching (Kesten 1969, Semyanov 1970, Omkar & Pervez 2005, Bind 2007). Hatching rate gradually decreased to 50% after the female of *P. dissecta* has been separated from the male (Omkar & Mishra 2005). However, the hatching rate was high in *Menochilus sexmaculatus*, *C. septempunctata* and *C. leonina transversalis* even when females mated only once (Omkar et al. 2005b). The level of **crowding** had a small detrimental effect on egg viability of *P. dissecta* (Mishra & Omkar 2006).

To describe **hatching synchrony** in individual species, three indices have been proposed (Perry &

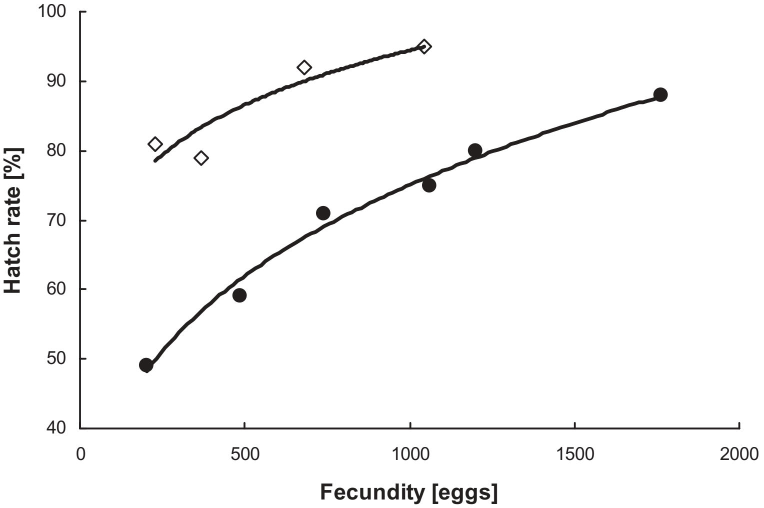

Figure 3.2 Relationship between average egg hatching rate (%) and lifetime female fecundity (eggs). The parallel increase in both parameters in *Coccinella septempunctata* (dots, lower line) was recorded simultaneously when six prey species were offered (after Omkar & Srivastava 2003). The increase in *Coelophora saucia* (diamonds, upper line) was recorded at (from the left) red, blue, yellow, and white light (after Omkar & Pathak 2006). Trend lines plotted as power functions.

Roitberg 2005): (i) total hatch time, related to batch size; (ii) the average interval between two sequential hatching larvae; (iii) the proportion of eggs per cluster, weighted by cluster size, that are vulnerable to sibling cannibalism by hatching later than the quiescent period of the first larva (141 min). The total duration of hatching of the first instar larva from an egg lasted 1 to 3.5 hours in *Har. axyridis*, and the total hatch time of the whole cluster (i) ranged from 61 to 203 minutes (Perry & Roitberg 2005). Hatching was synchronized within a cluster; the interval between hatching of successive larvae (ii) was 7–15 minutes. The proportion of eggs which showed a delayed hatch (iii) ranged from 0 to 7%.

The mean duration of hatching of larvae within the same batch (i) ranged between 1.01 hours in *Coelophora inaequalis* and 1.36 hours in *C. leonina transversalis* (Ng 1986). There were 45% (*Coelophora inaequalis*) to 83% (*C. leonina transversalis*) egg clusters which took longer to hatch than the duration between emergence of a larva and its cannibalization of eggs (a similar measure to (iii)).

Although hatching of ladybird larvae often occurs in daytime, most egg clusters (73%) of *P. dissecta* hatched during the night (Mishra & Omkar 2004; Fig. 3.3).

3.2.5 Trophic eggs

Apart from viable hatching eggs, ladybirds also produce non-hatching eggs, which may be either **infertile** (not fertilized by sperm) or non-viable, where an embryo develops for some time but the larva does not emerge from the egg capsule. Non-hatching eggs are sometimes considered as trophic eggs that serve as the first food for the newly born sibling larvae. Egg **cannibalism** (5.2, Chapter 8) is undoubtedly advantageous to *A. bipunctata* larvae both in terms of faster development and increased survival (Roy et al. 2007). Perry and Roitberg (2005) showed that laying infertile eggs is also an active part of the maternal strategy in *Har. axyridis*. Females produced 56% more infertile eggs (23 versus 15% of the cluster) in low versus high food treatments; they manipulated the proportion of trophic eggs in favour of young first instar larvae that might have problems in finding essential prey (aphids). The oviposition sequence of infertile eggs within a cluster did not differ from random.

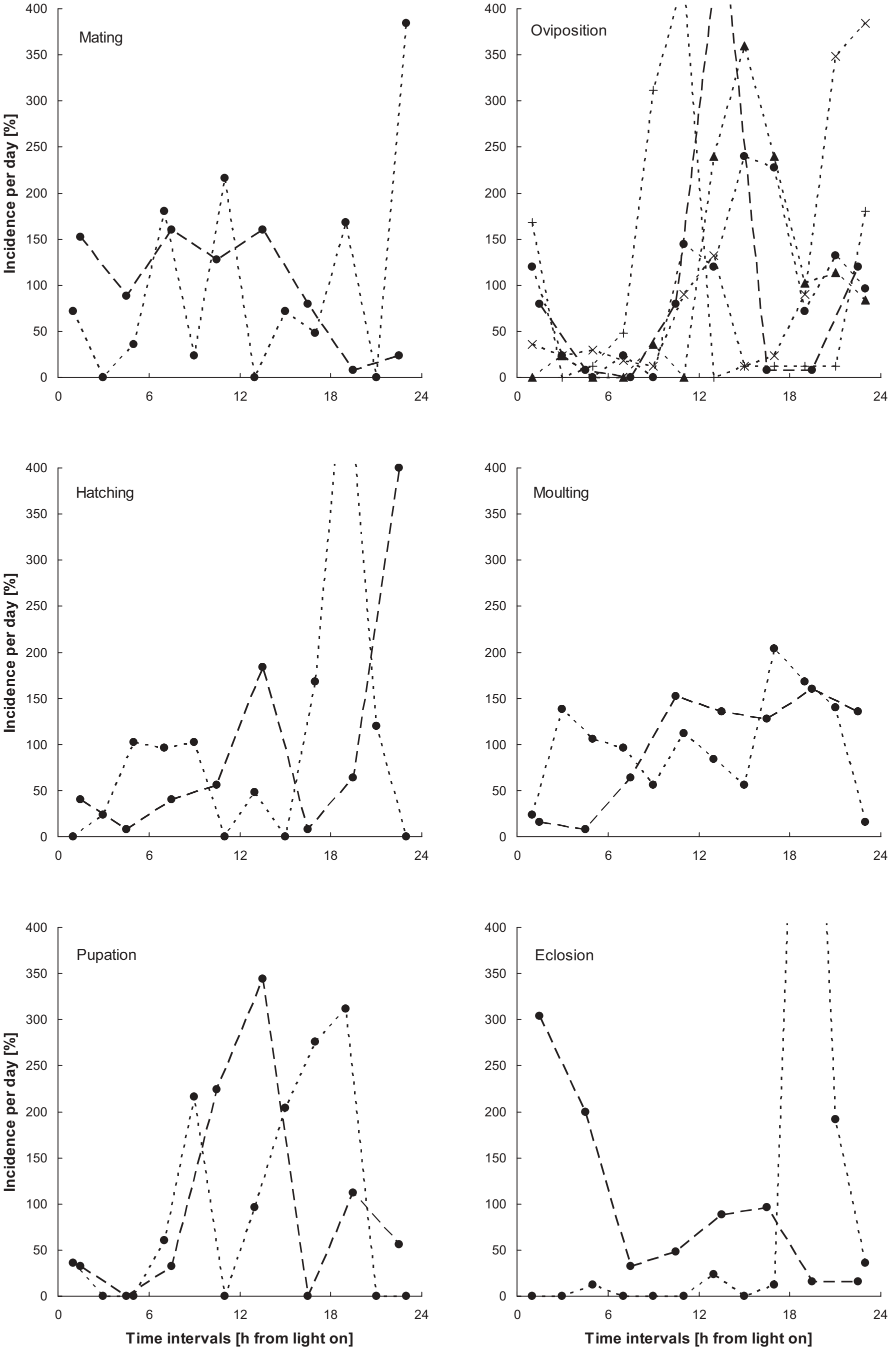

Figure 3.3 Circadian rhytmicity in life events of aphidophagous ladybird beetles (Coccinellini) in India. Dashed line and solid circles, *Menochilus sexmaculatus* (Omkar & Singh 2007); dotted line and open circles, *Propylea dissecta* (Mishra & Omkar 2004); dotted line and diagonal crosses, *Coccinella septempunctata*; dotted line and straight crosses: *Coccinella transversalis*; dotted line and triangles, *Propylea dissecta* (all three Omkar et al. 2004). Photophase: 0–12 h, scotophase: 12–24 h. All values are expressed in relative incidence, mean is 100%. Mating occurs more frequently around sunrise and around sunset; oviposition take place mainly during scotophase with two peaks (beginning and late scotophase); hatching from eggs occurs mainly during the second half of scotophase; larval moulting is more regularly distributed, with slight prevalence in scotophase; pupation occurs mainly during early or mid scotophase; adult emergence take place either during morning or during the second half of scotophase.

3.3 LARVA

3.3.1 Larval morphology

Larvae of most coccinellid tribes have an elongate body (Coccinellinae, Scymnini). It is ellipsoidal in the Hyperaspidini and Noviini and hemispherical in the Platynaspidini. The pronotum has two or four sclerotized plates (six in *Tetrabrachys*; Klausnitzer 1969a). The meso- and metanotum each have two plates, but in the Scymninae they are weakly developed or absent. The first eight abdominal segments bear six rows of characteristic structures as dorsal, dorsolateral and lateral pairs. These structures are well developed in the third and fourth instars and differ according to their shape, with seven types: seta, chalaza, tubercule, struma, parascolus, sentus and scolus (Gage 1920). These structures are important in taxonomy and identification. Larvae of Hyperaspidini and Platynaspidini are covered by chalazae and setae, the Scymnini and Noviini have tubercules, the Psylloborini and Tytthaspidini strumae, the Chilocorini senti and the Epilachninae scoli. Genera of Coccinellini have variable structures (Savoiskaya & Klausnitzer 1973). The more elaborate structures have a defensive role.

Larvae of most Scymninae, Telsimiini and Azyini (including *Cryptolaemus*) are covered with a white waxy exudation (filaments) as a defensive adaptation (Liere & Perfect 2008). Many larvae exhibit defensive reflex bleeding similar to that of adults, but the droplets exude from specific sutures or structures on the abdomen or thorax. Larvae of *Scymnus sinuanodulus* exhibit reflex bleeding of orange viscous droplets from thoracic tubercles (Lu et al. 2002). Larvae of third and fourth instars, namely of Coccinellinae, are brightly coloured.

The mandibles of larvae in the Hyperaspiidini, Platynaspidini, Stethorini, Scymnini and *Exochomus* have an apex ending with a single point; they have two apical teeth in the Coccinellini, Noviini and also in the larvae of *Chilocorus*, though in this genus the adults possess a mandible terminating in only a single point. In the phytophagous Epilachninae, mandibles are equipped with four or five large teeth. There is a row of smaller teeth or thick setae in the mycophagous Psylloborini and Tytthaspidini (Savoiskaya & Klausnitzer 1973). The larvae of *Scymnus levaillanti*, which employ pre-oral digestion, were more efficient in converting food to body mass than larvae of *Cycloneda sanguinea*, which use chewing and sucking (Isikber & Copland 2001).

The legs are elongate in the Epilachninae and Coccinellinae, but shorter in the Scymninae. The antennae are very short, 1–3 segmented; the first segment is short and wide (Savoiskaya & Klausnitzer 1973).

3.3.2 Instars

The individual substages during larval development separated by moulting (ecdysis) are called instars. The number of instars in the whole family is almost always four, independent of the species size, developmental conditions, etc. The constant and same number of instars in both aphidophagous and coccidophagous ladybirds, otherwise strongly different in many life history characteristics, was considered surprising by Dixon (2000). Fast development, typical and adaptive for aphidophagous Coccinellinae, would be better achieved by fewer instars, but their number seems to be phylogenetically constrained.

The last, fourth, instar eventually stops feeding and attaches to a substrate, forming the so-called prepupa. This pseudostage has sometimes been erroneously referred to as a fifth instar (Smith et al. 1999). Three instars were surprisingly reported in the coccidophagous *Hyperaspis campestris* (McKenzie 1932) and in an Egyptian population of *C. undecimpunctata* (while European populations of this species have four (Iablokoff-Khnzorian 1982)). Four larval instars were usually observed in *Clitostethus oculatus*, although a significant proportion of third instar larvae moulted directly to the pupal stage at 29°C or above (Ren et al. 2002). For these latter individuals, the third larval instar was prolonged to almost the length of the combined third and fourth instars of 'normal' beetles (6.1 days versus 6.3 days at 29°C, 3.4 days versus 4.9 days at 31°C and 4.7 days versus 5.0 days at 33°C).

However, a true higher number of instars, five, was reported for *Callicaria superba* (Iwata 1932), a large ladybird (12 mm) which feeds on Sternorrhyncha, Auchenorrhyncha and chrysomelid larvae. There is also a report of five larval instars in *Chil. nigritus* (Fitzgerald 1953, Chazeau 1981), a species feeding on coccids, aphids and whiteflies (Omkar & Pervez 2003). A small proportion of larvae of *Col. maculata* (Warren & Tadić 1967) and *Chil. bipustulatus* (Yinon 1969) went through five instars in the laboratory.

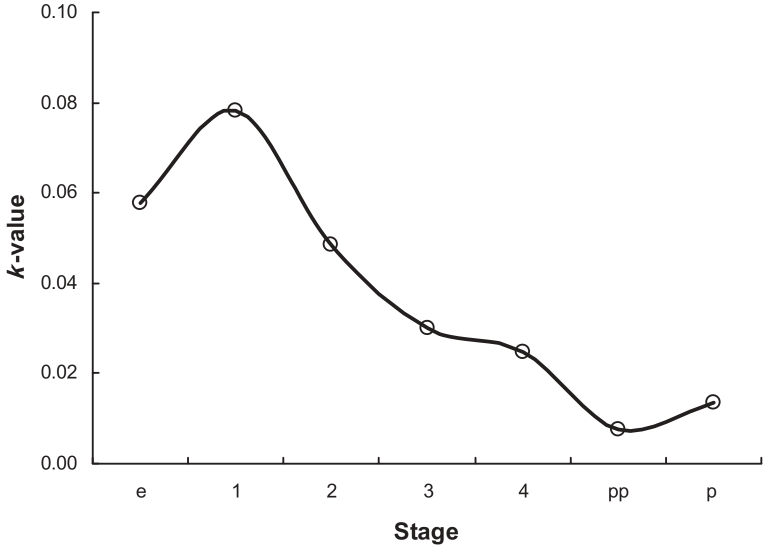

Figure 3.4. Stage specific mortality (k-values = $\log_{10}a_x - \log_{10}a_{x+1}$, where a_x is the initial number of individuals and $a_{x+1}$is the number of individuals surviving to the next stage) of *Propylea dissecta*. Average for five generations reared on five different aphid species. The first instar and eggs are most vulnerable to death, prepupa is the most resistant 'stage' (after Omkar & Pervez 2004).

A fifth larval instar occurred in 33% of the individuals of a Canadian population of the large invasive aphidophagous *Har. axyridis*. This extra instar had the same developmental time as ordinary fourth instars, but showed increased voracity and weight gain compared to the fourth larval instar, suggesting an increased fitness of those individuals and contributing to the invasiveness of the species (Labrie et al. 2006). A fifth instar was found to occur rarely also in European population of *Har. axyridis* at 20°C with an excess of food. Only females developed from these larvae (Ungerová, unpublished).

Moulting between instars occurs at any time of day, although in *P. dissecta* 61–77% of larvae moulted during the scotophase (Mishra & Omkar 2004).

During pre-adult development, mortality is highest in the first instar, possibly higher than in eggs, is least in prepupae and increases somewhat during the pupal stage (Fig. 3.4; Omkar & Pervez 2004b).

3.3.3 Development

The duration of larval development is species specific and strongly dependent on the ambient temperature (3.6), and also on the quality and quantity of food (5.2).

Larval development of coccinellids is direct with no diapause. An exception is the fourth instar of the phytophagous *Epilachna admirabilis* which is sensitive to photoperiod (Takeuchi et al. 1999). The fourth instar larvae of *Scymnus abietis* have been observed very early in the spring, suggesting that they overwinter in this stage (Nedvěd & Kovář, unpublished).

In well-fed larvae, the first instar takes about 24% of the total developmental time, the second 17%, the third 19% and the fourth 40% (Honěk 1996). There was higher variation in these percentages in *A. bipunctata* (Obrycki & Tauber 1981) than in *Col. maculata* (Wright & Laing 1978). Even when the prepupa (8–11%) is not included, the last instar is always longer than any of the others.

Immune responses to microbial infection may cause developmental delay. The mean larval duration of *Serangium parcesetosum* was longest (22.5 days) when sprayed with medium and high dosages of *Beauveria bassiana*, intermediate (20 days) with a low dosage of *B. bassiana*, and lowest (18 days) for the blank control and the *Paecilomyces fumosoroseus* treatments (Poprawski et al. 1998). *B. bassiana* strain ATCC 44860 increased the development time of *Col. maculata* fed with Colorado potato beetle larvae, whereas the strain ARSEF 2991 reduced the development time (Todorova et al. 1996).

Development of phytophagous species may depend not only on the quality but also on the surface structure of the host plant. Larvae of the Mexican bean beetle, *Epilachna varivestis*, completed the first instar most quickly on pubescent soybean plants, whereas the duration of the third instar was shortest on glabrous plants. Larval mortality was 2.5–5 times greater on a densely pubescent isoline than on glabrous and normal soybean isolines (Gannon & Bach 1996).

The duration of pre-imaginal development differed among several isofemale lines (progeny of individual females, from several egg batches) of field-collected *Hip. convergens*, the values ranging from 223 to 273 degree days above the lower temperature threshold (Rodriguez-Saona & Miller 1999). Accordingly it is recommended that experiments on the effects of environmental factors on coccinellids should be (i) conducted with siblings (the progeny of one female) distributed into all treatments and (ii) repeated with the progeny of several unrelated females.

The duration of larval development further depends on **population density**. In *Chil. bipustulatus*, duration of development increased at higher density (Fomenko 1970). Rearing *P. dissecta* larvae at a moderate density of four larvae in a half litre beaker shortened developmental time and increased immature survival when compared with both single larvae and higher densities of larvae (Omkar & Pathak 2009). Mean developmental time of *Har. axyridis* in small (7 cm) Petri dishes was 13.7 days; in 15 cm Petri dishes it was 11.5 days; and 11.7 days in 0.5 l jars (Ungerová et al. 2010).

The effect of diverse environmental conditions on development may be mediated through the quality of prey. Duration of larval development of *P. japonica* was significantly longer if fed *Aphis gossypii* from cotton grown at elevated than at normal CO_2 concentrations (Gao et al. 2008).

3.3.4 Body size

When fed *ad libitum*, the body mass increases exponentially with the age of the larva, peaking in the late last instar larva. Due to the cessation of further weight gain at the end of the last larval instar (Ng 1991) the function of weight increase is sigmoid (Fig. 3.5). Weight increases again in adults once they start to feed after emergence (Omkar et al. 2005a). The size of cuticular structures of successive instars increases in constant proportions. Weight increases exponentially, e.g. in *A. bipunctata* it is 0.04, 0.17, 0.52, 1.51 and 4.85 mg at the beginning of the first, second, third and fourth instar and prepupa, respectively (Jalali et al. 2009b).

The final size of the ladybird is largely determined during the fourth instar (Honěk 1996). For comparative purposes, the mean relative growth rate (RGR) may be calculated as RGR = dry weight gained during the feeding period / (length of feeding period in days · mean dry weight of predator during feeding period) (Waldbauer 1964). RGR values in *A. bipunctata* fed with *Myzus persicae* were 0.45, 0.70, 0.55 and 0.35 per day in the successive instars (Jalali et al. 2009b).

The relative food consumption of different larval instars is compared in 5.2. For example, Okrouhla et al. (1983) gave average values of 6, 11, 21 and 62% for the total food eaten by larvae of *Cheilomenes sulphurea*. In *A. bipunctata*, the percentages of food eaten by the four larval instars differed between food treatments. When fed with aphid *Myzus persicae,* they were 4, 9, 14 and 73% and with factitious food (a mixture of *Ephestia kuehniella* eggs and fresh bee pollen) they were 5, 8, 20 and 67% (Jalali et al. 2009b).

3.4 PUPA

3.4.1 Prepupal stage

The last (fourth) instar larva attaches itself by the tip of its abdomen ('anal organ', pygopod) to the substrate and prepares for pupation. The prepupae of particular species are as or more vulnerable to predation than their fourth instar larvae. Their physical defence structures are essentially the same, but they are practically **immobile** (Ware & Majerus 2008). Phorids attack host prepupae and parasitize them at the time of ecdysis to the pupal stage (Hurst et al. 1998). In life tables, the prepupa is often listed as one of the developmental stages, but strictly speaking it should be considered as a part of the **last instar larva**. For practical reasons, especially the differences between feeding larva and inactive prepupae, we recommend that these substages are separated in experiments.

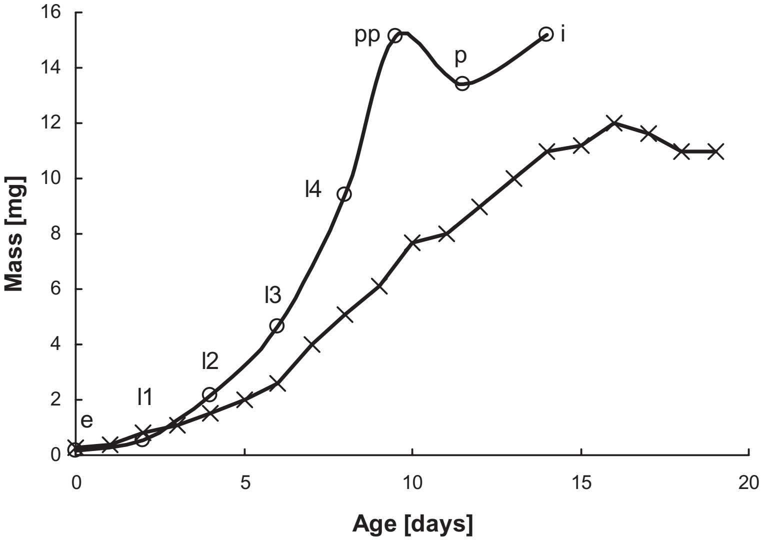

Figure 3.5 Growth curves of ladybirds. Crosses, growth of *Exochomus quadripustulatus* from egg to pupa at 25°C, fed with *Pulvinaria regalis* (after Sengonca & Arnold 2003). Circles, growth of *Coelophora biplagiata* from egg (e) through four larval instars (i), prepupa (pp), pupa (p) to adult (a); reared on *Aphis craccivora* at 27°C (after Omkar et al. 2005, mass was in fact double, but the values were reduced to a similar scale as the other species). Body mass increases exponentially from hatching to the fourth instar. This last instar stops to feed and grow and form a prepupa. The pupa is lighter than prepupa because the larval cuticle is shed, and some of the nutrients are spent through intensive metabolism. Part of the body water may be lost during the resting stage. Adults continue to grow, especially the females during egg production.

3.4.2 Pupal morphology

Pupae of coccinellids are of the type **pupa adectica obtecta**, which means that all appendages (antennae, limbs, wing pads) are glued to the body by exuvial fluid. The pupa is attached to the substrate (vegetation) by the tip of the abdomen. The **exuviae** (remains of the old cuticle) of the last larval instar are crumpled around the tip of abdomen in the Coccinellinae and Sticholotidinae. In the Chilocorinae, Scymninae and Ortaliinae the larval cuticle ruptures on the dorsal side, stretches and splits lengthwise, but is not shed and forms a **protective chamber** around the pupa. There are exceptions such as *Scymnus sinuanodulus* where the pupa is **naked** with the larval exuviae attached only to the last abdominal segment (Lu et al. 2002). In the Epilachninae, only the posterior third of the pupa is covered by the spiny larval exuviae. The pupal cuticle itself is either covered in long hairs (Epilachninae, Scymninae) or is apparently smooth, with only sparse very short glandular hairs (Coccinellinae).

The **size** of the pupa of particular species is highly dependent on prey quality and quantity during larval development, as well as on the temperature during development. The largest pupae develop at **medium temperatures**. The mean weight of pupae of *Exochomus quadripustulatus* was 11.9 mg at 9/19°C (thermoperiod), 12.5 mg at 12/24°C and 10.7 mg at a constant 25°C (Sengonca & Arnold 2003). The heaviest pupae of *Hip. convergens* were reared at 22°C as compared with 18, 26 and 30°C (Rodriguez-Saona & Miller 1999).

Har. axyridis larvae reared on *Acyrthosiphon pisum* produced heavier pupae (27.8 mg) than their siblings reared on the less **suitable prey** *Aphis craccivora* (20.8 mg) or on artificial diet (22.0 mg) (Ueno 2003). *Coleomegilla maculata* larvae fed with corn pollen gave much heavier pupae (13 mg) than individuals fed on the aphid *Rhopalosiphum padi* (7.3 mg) (Lundgren & Wiedenmann 2002). *Epilachna varivestis* reared on glabrous soybean plants had by 14–29% greater dry pupal weights than did individuals reared on the densely pubescent and normal isolines (Gannon & Bach 1996).

Male and female pupae cannot be distinguished by their external morphology. **Females** tend to be larger and heavier than **males** in the pupal stage: *Har. axyridis* females on average weighed 28.5 mg while males were 27.2 mg (Ueno 2003). Moreover, Ueno (2003) found slight intraspecific genetic variation (**family effect**) in pupal weights and an interaction of this genetic background with the type of prey. Based on these finding we suggest (i) strict use of siblings in all treatments of an experiment where effects of several environmental factors are to be studied, and (ii) the parallel use of several unrelated females/families for such experiments.

3.4.3 Timing of pupation

The development of pupae generally takes about 24% of the total pre-imaginal development time, i.e. less than in other Aphidophaga (Neuroptera: 33%, Syrphidae: 39%) (Honěk & Kocourek 1990). It may, however, exceed 40% in *Axinoscymnus cardilobus* (Huang et al. 2008) feeding on whiteflies. The **development rate** of pupae is linearly and positively related to **temperature** (3.6), and is usually **independent on the prey** quality and quantity in the preceding larval stage (Ahmad et al. 2006); by contrast, pupal and adult weight are dependent on previous feeding. Pupae of *Col. maculata* from larvae fed with pollen reached 14 mg and lasted 3.2 days while those fed on artificial diet weighed less (11 mg) and lasted for a comparable time (3.4 days) (Lundgren & Wiedenmann 2002). The complete pre-imaginal development of *Hip. convergens* on *Thrips tabaci* lasted 30 days, and 24 days on *Acyrthosiphon pisum*, while the duration of the pupal stage was not affected by the food (Schade & Sengonca 1998).

Under conditions of artificially elevated **CO_2 concentration**, the pupal development time was affected; both the larval and pupal durations of *Har. axyridis* fed *Aphis gossypii* were significantly shorter than at the normal concentration (Chen et al. 2005). A high level of **crowding** (35 larvae per beaker) shortened subsequent pupal development in *P. dissecta* (2.2 days in comparison to 3.4 days at low densities) (Omkar & Pathak 2009).

A relatively high incidence of pupation was observed during the late **photophase** (09:00–12:00 hours, where 0 hours is the time the light was switched on) and early **scotophase** (12:00–15:00 hours) in *Menochilus sexmaculatus* (Omkar & Singh 2007; Fig. 3.3).

Mass-specific **respiration** rates in *Har. axyridis* increased with increases in pupal age (while it decreased in the other stages) (Acar et al. 2004). Below 10°C, CO_2 was produced primarily from non-oxygen-consuming reactions. CO_2 production gradually shifted more to oxygen-consuming reactions with increasing temperature.

The **abundance** of pupae is widely underestimated in the field because they are attached to the vegetation and thus unavailable for common **sampling methods** (sweeping, Kalushkov & Nedvěd 2005; beating, Kula & Nedvěd unpublished; sticky traps, Kaneko et al. 2006).

3.4.4 Places of pupation

The usual place for pupation is on the vegetation where the larva developed, so that the prepupae and pupae are exposed to **cannibalism** or **intraguild predation**. The prevalence of **parasitization** of ladybird pupae by *Phalacrotophora* flies increases strongly with the population density of the pupae, reaching up to 40% (Durska et al. 2003). Larvae of the genus *Chilocorus* aggregate before pupation (Fomenko 1970, Fomenko & Zaslavskii 1970).

In **aphidophagous** ladybirds, the place for pupation is mainly **foliage**, while some **coccidophagous** species pupate on the **bark** of branches and on tree trunks. **Cryptically** coloured pupae tend to be hidden on the underside surface of the leaves, while **aposematically** coloured ones may be exposed on the upper side and take advantage of basking in the sun (see thermal melanism, 3.4.6).

In central Honshu, hibernating and reproductive adults of *C. septempunctata* coexist in the same habitat during the mild winter. Although natural substrates were available, the beetles preferred to use **artificial substrates** such as metal cans (iron or aluminium), papers, and wooden materials discarded on the sunny slope as oviposition and pupation sites. They were warmed by solar radiation and served as **thermal microhabitats** (Ohashi et al. 2005). About 90% of the larvae of *Col. maculata* left the potato plant to pupate. They selected shelters that effectively reduced their intraguild predation by the lacewing *Chrysoperla rufilabris* (Lucas et al. 2000). The larvae and pupae of the ladybird *Thalassa saginata* develop inside **colonies of the ant** *Dolichoderus bidens* (Orivel et al. 2004).

3.4.5 Pupal defence

Pupae covered by the **larval skin** are protected **mechanically**, especially when the larva is spiny (Chilocorinae, Epilachninae) or covered by waxy exudations (Scymninae). The pupal cuticle also has its own **hairs**, which are especially long in the Epilachninae and Scymninae, and often have a **glandular** function, containing defensive compounds. Transparent viscous **droplets** are visible on the tips of the setae of the pupa of *Scymnus sinuanodulus* (Lu et al. 2002). The white pupa of *Clitostethus oculatus* has tiny clear droplets on the tips of the setae at high relative humidity. Larval exuviae together with whitefly debris cover the tip of the pupal abdomen. The yellowish pupae of *Delphastus pusillus* are covered by short hairs without any secretion, and several abdominal segments are enclosed within an unfragmented larval skin (Liu & Stansly 1996a).

The surface of the pupa of the phytophagous *Subcoccinella vigintiquatuorpunctata* bears glandular hairs producing three polyazamacrolide alkaloids. The secretion serves as a potent anti-predator defence against the predatory ant *Crematogaster lineolata* (Smedley et al. 2002). Comparative studies of the defensive chemistry of eggs, larvae, pupae and adults showed both qualitative and quantitative differences in **alkaloid** composition between the life stages of *Epilachna paenulata* (Camarano et al. 2006). The polyazamacrolide epilachnene, the principal component of the secretion of the pupal defensive hairs of *Epilachna varivestis*, proved to be a **deterrent** for *Har. axyridis* (Rossini et al. 2000). The oily droplets on the pupal integumental hairs of the squash beetle *Epilachna borealis* contain a mixture of tocopheryl acetates (Attygalle et al. 1996) and **polyazamacrolides** (Schroder et al. 1998). (more on semiochemicals in Chapter 9).

The pupa is not entirely immobile. If irritated by a predator or parasitoid, it quickly **raises** itself **upwards** several times. Pupae are better protected against predation than prepupae, but in most species they are still susceptible to attack. The **tough** pupal **integument** affords better protection than the soft larval skin (Ware & Majerus 2008).

3.4.6 Colouration and thermal melanism

Many coccinellid pupae are **cryptically coloured**, while in some large Coccinellinae the colours are bright and probably have a **warning** function. Species such as *C. septempunctata* and *Har. axyridis*, which mostly pupate exposed on the upper leaf surface, combine a bright orange background with black spots. The extent of **melanization** and the darkness of the orange-brown background increases in both species with decreasing **temperature** and increasing humidity. The pupa is light orange at 35°C and dark brown at 15°C in *C. septempunctata* (Hodek 1958, Okuda et al. 1997). In *C. septempunctata*, the percentage of the area from dorsal and lateral views which is black decreases linearly (from 45–55% to almost zero) with increasing temperature (from 20 to 36°C) (Rozsypalova 2007). Unlike the larvae and adults, which can control their body temperature behaviourally, the pupa relies on heating by the sun.

The **sensitive stage** for the determination of the extent of melanization is the late prepupa. Elements of the future **elytral pattern** may be visible on the pupal **wingpads**. In *Har. axyridis*, there is a similar trend as in *C. septempunctata*, but shifted to lower temperatures (17 to 33°C) (Ungerová & Nedvěd, unpublished). The extent of melanization of the adult is independent of the melanization of the pupa.

Blackening of the pupal case may also be caused by infection, **injury** or intoxication. This was observed in pupae of *C. septempunctata* whose larvae had been treated with azadirachtin (Banken & Stark 1997).

Although the colouration of ladybird pupae is less variable and less striking than that of adults, pupae can still be identified to species. For example, the colour and spotting of prepupae and pupae provide identification characters to distinguish two sympatric ladybirds, *Henosepilachna pusillanima* and *H. boisduvali* that have indistinguishable adult colouration (Nakano & Katakura 1999).

3.5 ADULT

3.5.1 Teneral development

Teneral development may include **sexual maturation** and the acquisition of **flight ability**. In many coccinellids, the activity of the follicular tissue in the **testes** starts in the pupa (Hodek & Landa 1971, Hodek 1996). After emerging from the pupa, females, and sometimes also males, show a **refractory period** of a few days in their mating behaviour. This was found to be equal in males and females of *A. bipunctata* (Hemptinne et al. 2001). Slight **protogyny** (the first mating of females taking place at earlier age) could theoretically occur when females mate before sexual maturity and store sperm, while males mate only after maturity. Mating of sexually non-mature females is common in many species with reproductive diapause (Chapter 6). Long refractory periods were observed in *Sasajiscymnus tsugae*: at 25°C when males matured at 19 days, whereas the female pre-oviposition period was 22.4 days (Cheah & McClure 1998). Omkar & Srivastava (2002) report **protandry** in Indian *C. septempunctata*. Males were ready to mate within 9 days at 27°C, while females took 11 days. Rana & Kakker (2000) reported an average pre-mating period in *C. septempunctata* of 6.4 days.

Temperature requirements for completing the teneral period may be calculated as for immature development (3.6) and may be prolonged by unsuitable prey (Hukushima & Kamei 1970) or prey scarcity (Kawauchi 1981).

The basic **sex ratio** in coccinellids is close to 50:50, except where there is an infection by a male-killing agent (Chapter 8). An increased proportion of males was found at high temperatures: in *Har. axyridis* at 30°C (62–82%) (Lombaert et al. 2008) and in *P. dissecta* at 35°C (62%) (Omkar & Pervez 2004b).

3.5.2 Wings and flight

The ability to **take-off** matures within a short period after the moult to adult. Adults of *C. septempunctata* began attempts to fly 40 hours after emergence at 26°C (Honěk 1990). Confinement of ladybirds in a limited space increased both the willingness to take-off and the **duration of flight** in *C. septempunctata* (Nedvěd & Hodek 1995).

There have been a few reports of the occasional occurrence of wingless or brachypterous individuals among normally winged ladybirds. Winglessness in *A. bipunctata* is determined by a single locus with the **wingless** allele recessive to the winged wildtype allele (Lommen et al. 2005) (Chapter 2). The occurrence of flightless ladybirds might increase biocontrol because flightless beetles have a longer **residence time** on the plants, even at lower prey density (Lommen et al. 2008). A homozygous **flightless** (but fully winged) strain of *Har. axyridis* was obtained by laboratory selection and used in biological control (Tourniaire et al. 2000). This strain had not only a longer residence time on aphid-infested plants but also a minimal potential to become invasive. Artificially, flightless ladybirds may be induced in a culture by limiting space during the emergence of adults from pupae individually placed into small chambers; this results in deformation of elytra and wings (N. Osawa, personal communication).

3.5.3 Pre-oviposition period

The number of days between female emergence and the laying of the first egg batch is called the pre-oviposition period. Its duration can be used to measure the intensity of diapause (Chapter 6). In dormant females, it can last weeks or even months.

Interspecific variation in the pre-oviposition period can be substantial. In **Coccinellinae**, it ranges between 0 and 10 days: in *Har. axyridis* it was 6–10 days, in *A. bipunctata* 3–8 days and in *Hip. variegata* it was surprisingly reported to be only 0–4 days (Lanzoni et al. 2004), which would indicate that some females of this species completed the development of their eggs while in the **pupal stage**. A short pre-oviposition period of 2–3 days was also found in *Anegleis cardoni* (Omkar et al. 2009). Adults of *C. septempunctata* fed on *Sitobion avenae* started mating 4–11 days after emergence, with an average **pre-mating period** of 6.4 days (Rana & Kakker 2000).

In **Scymninae**, the pre-oviposition period varies even among closely related species. In *Scymnus frontalis* it was 10–11 days (Gibson et al. 1992), while it was only two days in *S. louisianae* (Brown et al. 2003). In contrast, long pre-oviposition periods of 13 days at 31°C and 23 days at 20°C were observed in *Clitostethus oculatus* (Ren et al. 2002), and of 22 days at 25°C in *Sasajiscymnus tsugae* (Cheah & McClure 1998).

The pre-oviposition period generally increases at lower **temperatures**: it ranged from 20.5 days at a mean temperature of 15°C to 7.7 days at 30°C in *Scymnus frontalis* (Naranjo et al. 1990), from 9 days at 20° to 4 days at 35°C in *S. levaillanti* (Uygun & Atlıhan 2000) and from 24 days at 15°C and 3.5 days at 35°C in *S. marinus* (M'Hamed & Chemseddine 2001). **Food suitability** also modifies the pre-oviposition period: this was shorter in *Menochilus sexmaculatus* fed with *Aphis craccivora*, *Aulacorthum solani*, *Sitobion akebiae*, and *Myzus persicae* (7.3–8.0 days) than when fed with *A. gossypii* (11.6 days) (Sugiura & Takada 1998).

3.5.4 Size

Females are generally larger and heavier than males, although often not significantly so, due to high variability. The fresh weight of emerged **females** of *Anegleis cardoni* was constantly 1.16-times higher than that of **males** when reared on three different prey species, while the difference in weight within each of the two sexes between being fed the most and the least **suitable prey** species was 1.35 times (Omkar et al. 2009). Newly emerged females of *Har. axyridis* were 1.1 to 1.2-times heavier than males (Ungerová et al. 2010).

The positive relationship between male and female weight under the same conditions is linear after log–log transformation, giving the equation log $W_M = -0.07 + 0.97$ log W_F. for *A. bipunctata* and $W_M = -0.043 + 0.96$ log W_F. for *P. japonica* (Dixon 2000). **Crowding** of larvae in a small space reduced adult size of *P. dissecta*: 7 mg with single individuals, 11 mg at 4 individuals per beaker (0.7 l), and only 5 mg at 35 per beaker (Omkar & Pathak 2009). In small (7 cm) Petri dishes, the mean mass of *Har. axyridis* was 18.8 mg; in 15 cm Petri dishes 21.2 mg; in 0.5 l jars 25.1 mg (Ungerová et al. 2010).

Body length and width decreased as constant temperatures increased from 22 to 34°C in *Chil. nigritus*, but were highest at an alternating **temperatures** regime of 20/34°C (Ponsonby 2009). Females were only 1.03-times longer than males.

Apart from using body length and weight, the ventral body area (mm^2) may be calculated by measuring the body length and width and using the formula [½(body length)] × [½(body width)] (Obrycki et al. 1998, Giles et al. 2002, Phoofolo et al. 2007).

In interspecific comparisons among aphidophagous ladybirds, body size of a species is related to the body size and density of the prey. Small ladybirds can feed on small aphid species when these are in both high and low densities, but on large aphid species only at high densities, where young instars of the aphids are abundant. Large ladybirds cannot be sustained by low densities of small aphids due to the food limitation (Sloggett 2008).

3.5.5 Ovarioles

The ovarioles of Coccinellidae are of the **meroistic telotrophic** type. The number of ovarioles is species-specific, as well as dependent on the conditions during the larval development of the female (Table 3.2). There is a higher **number of ovarioles** in larger species; the number increases with body length by the power function with the exponent of 1.14 ± 0.02 (Fig. 3.6). Species with few ovarioles lay larger eggs than similar-sized species with many ovarioles (Stewart et al. 1991b; 5.2.3). The number of ovarioles has been reviewed from the viewpoint of taxonomy, evolution and fecundity by Rathour and Singh (1991). In species with a high number of ovarioles, there is a smaller number of chambers (follicles) with ripening oocytes (three in *C. septempunctata*) than in species with a small number of ovarioles (eight in *Stethorus* sp.) (Dobrzhansky 1926).

Intraspecific comparisons in *C. septempunctata* showed a positive linear relationship between the number of ovarioles and female **body weight** (Dixon & Guo 1993). The mean number of ovarioles in *C. septempunctata* females of 24 mg body weight was 80, while it was 139 in females weighing 31 mg (Rhamhalinghan 1985, 1986). In contrast, no correlation of the number of ovarioles with either **body length** or body weight of females was found in *Har. axyridis* (Nalepa et al. 1996, Osawa 2005).

Effects on the reproductive output of the resulting females of the **diet** provided to larvae have been reported. The number of ovarioles was 10% lower in *A. bipunctata* fed on the suboptimal prey *Aphis craccivora* than in females fed with the high quality prey *Acyrthosiphon pisum* (Ferrer et al. 2008). However, Ware et al. (2008b) reported no effect of larval diet on ovariole number in *Har. axyridis* and *A. bipunctata*, although maximum clutch size and oviposition rate were affected. Starvation does not alter the total number of ovarioles, it only changes the percentage of oosorptive and mature ovarioles (Osawa 2005). In those individuals of *C. septempunctata* with less than 100 ovarioles per female, almost all of the ovarioles (99.8%) were healthy and functional. By contrast, in individuals with a high ovariole number (102 to

Table 3.2 Number of ovarioles per ladybird female, female weight (mg) and size (mm). Indicated are ranges or mean numbers of ovarioles in both ovaries together, if directly referred to in the literature source in the right column, or double the number of ovarioles per one ovary if given so in the source. Size and fresh weight of each species are either original unpublished data measured by Nedvěd, or measured by Rhamhalinghan (four rows marked by asterisk *); averaged literature data on body length are given for other species. See also Fig. 3.6.

Species	Weight	Size	Ovarioles	Reference
Adalia bipunctata	—	—	45–51	Dobrzhansky (1926)
Adalia bipunctata	—	—	47	Ferrer et al. (2008)
Adalia bipunctata	13.5	4.9	43	Ferrer et al. (2008)
Adalia bipunctata	—	—	48	Ware et al. (2008)
Adalia decempunctata	10.7	4.6	48–52	Dobrzhansky (1926)
Adalia tetraspilota	—	4.5	34–48	Rathour & Singh (1991)
Afidenta misera	—	5.4	40–48	Rathour & Singh (1991)
Afissula rana	—	—	26	Rathour & Singh (1991)
Afissula sanscrita	—	—	18	Rathour & Singh (1991)
Aiolocaria hexaspilota	—	9.7	91	Dobrzhansky (1926)
Aiolocaria hexaspilota	—	9.7	88–96	Rathour & Singh (1991)
Alloneda dodecaspilota	—	6.8	32–44	Rathour & Singh (1991)
Anatis ocellata	60.7	8.5	56	Dobrzhansky (1926)
Anegleis cardoni	—	3.7	20	Rathour & Singh (1991)
Anisosticta novemdecimpunctata	—	3.5	24	Dobrzhansky (1926)
Apolinus lividigaster	—	4.0	14–26	Anderson (1981)
Callicaria superba	—	11.5	52–60	Rathour & Singh (1991)
Calvia albida	—	8.0	18–24	Rathour & Singh (1991)
Calvia decemguttata	27.3	6.6	29	Dobrzhansky (1926)
Calvia quatuordecimguttata	22.7	5.4	40	Dobrzhansky (1926)
Calvia quatuordecimguttata	22.7	5.4	40	Semyanov (1980)
Calvia shiva	—	—	28–36	Rathour & Singh (1991)
Calvia shiva pasupati	—	—	22	Rathour & Singh (1991)
Calvia shiva pinaki	—	—	18	Rathour & Singh (1991)
Calvia shiva trilochana	—	4.9	22	Rathour & Singh (1991)
Calvia sp.	—	—	24–28	Rathour & Singh (1991)
Ceratomegilla undecimnotata	44.0	6.6	42–62	Dobrzhansky (1926)
Chilocorus bijugus	—	—	40–48	Rathour & Singh (1991)
Chilocorus bipustulatus	—	3.5	25	Dobrzhansky (1926)
Chilocorus breiti	—	—	18–24	Rathour & Singh (1991)
Chilocorus hauseri	—	—	30–40	Rathour & Singh (1991)
Chilocorus nigritus	—	4.0	18	Rathour & Singh (1991)
Chilocorus rubidus	—	6.5	72–80	Rathour & Singh (1991)
Chilocorus sp.	—	—	32–40	Rathour & Singh (1991)
Chilocorus sp.	—	—	24–32	Rathour & Singh (1991)
Coccinella hieroglyphica	—	3.5	34	Dobrzhansky (1924)
Coccinella hieroglyphica	—	—	28	Dobrzhansky (1926)
Coccinella luteopicta	—	5.8	44–52	Rathour & Singh (1991)
Coccinella magnifica	—	7.4	69–74	Dobrzhansky (1926)
Coccinella septempunctata	—	—	96–119	Dobrzhansky (1926)
Coccinella septempunctata	44.4	7.2	102	Klausnitzer & Klausnitzer (1986)
Coccinella septempunctata	—	—	108–124	Rathour & Singh (1991)
Coccinella septempunctata	30.5*	—	129 (57–82 pairs)	Rhamhalinghan (1985)
Coccinella septempunctata	23.6*	—	86 (26–61 pairs)	Rhamhalinghan (1985)
Coccinella septempunctata	31.6*	—	149	Rhamhalinghan (1986)
Coccinella septempunctata	24.2*	—	74	Rhamhalinghan (1986)

(*Continued*)

Table 3.2 (*Continued*)

Species	Weight	Size	Ovarioles	Reference
Coccinella undecimpunctata	—	5.0	68	Dobrzhansky (1926)
Coccinula quatuordecimpustulata	—	3.5	20	Dobrzhansky (1926)
Coccinula redimita	—	4.0	20	Dobrzhansky (1926)
Coelophora bissellata	—	5.3	26–36	Rathour & Singh (1991)
Coelophora duvaucelii	—	—	36–44	Rathour & Singh (1991)
Cryptogonus ariasi	—	2.2	14	Rathour & Singh (1991)
Cryptogonus orbiculus	—	—	14	Rathour & Singh (1991)
Cryptogonus postmedialis	—	—	14	Rathour & Singh (1991)
Cryptogonus quadriguttatus	—	—	14	Rathour & Singh (1991)
Epilachna dumerili	—	—	24–32	Rathour & Singh (1991)
Epilachna marginicollis	—	—	32–36	Rathour & Singh (1991)
Epilachna mystica	—	—	44–52	Rathour & Singh (1991)
Exochomus quadripustulatus	9.7	4.3	26	Dobrzhansky (1926)
Halyzia sanscrita	—	—	38–44	Rathour & Singh (1991)
Halyzia straminea	—	7.3	56–64	Rathour & Singh (1991)
Harmonia axyridis	—	—	54–78	Dobrzhansky (1924)
Harmonia axyridis	34.7	6.5	64–76	Dobrzhansky (1926)
Harmonia axyridis	—	—	53–77	Fois & Nedvěd, unpubl.
Harmonia axyridis	—	—	62 (44–84)	Nalepa et al. (1996)
Harmonia axyridis	—	—	62	Ware et al. (2008)
Harmonia dimidiata	—	8.3	50–60	Rathour & Singh (1991)
Harmonia eucharis	—	8.0	48–164	Rathour & Singh (1991)
Harmonia quadripunctata	22.3	6.1	36–40	Dobrzhansky (1926)
Harmonia sedecimnotata	—	6.5	54–64	Rathour & Singh (1991)
Henosepilachna dodecastigma	—	—	56–60	Rathour & Singh (1991)
Henosepilachna indica	—	—	44–54	Rathour & Singh (1991)
Henosepilachna ocellata	—	—	58–64	Rathour & Singh (1991)
Henosepilachna processa	—	9.1	54–58	Rathour & Singh (1991)
Henosepilachna pusillanima	—	8.1	63	Dobrzhansky (1926)
Henosepilachna sp.	—	—	34	Rathour & Singh (1991)
Henosepilachna vigintioctomaculata	—	—	55	Dobrzhansky (1926)
Henosepilachna vigintioctomaculata	—	7.4	48–56	Rathour & Singh (1991)
Henosepilachna vigintioctopunctata	—	6.4	56–72	Rathour & Singh (1991)
Henosepilachna vigintioctopunctata	—	—	84	Dobrzhansky (1926)
Hippodamia septemmaculata	—	6.0	40–46	Dobrzhansky (1926)
Hippodamia tredecimpunctata	—	5.9	48–60	Dobrzhansky (1926)
Hippodamia variegata	10.3	4.8	45–49	Dobrzhansky (1926)
Hippodamia variegata	—	—	42–48	Rathour & Singh (1991)
Hyperaspis campestris	4.7	2.9	19–21	Dobrzhansky (1926)
Hyperaspis reppensis	—	2.8	17–20	Dobrzhansky (1926)
Illeis cincta	—	4.0	38–44	Rathour & Singh (1991)
Jauravia quadrinotata	—	2.2	18	Rathour & Singh (1991)
Megalocaria dilatata	—	13.0	40–52	Rathour & Singh (1991)
Menochilus sexmaculatus	—	5.0	40–52	Rathour & Singh (1991)
Micraspis allardi	—	4.5	28	Rathour & Singh (1991)
Myrrha octodecimguttata	11.3	4.3	16–17	Dobrzhansky (1926)
Myzia oblongoguttata	39.0	7.5	41–46	Dobrzhansky (1926)
Nephus redtenbacheri	—	1.6	12	Dobrzhansky (1926)
Oenopia billieti	—	3.9	24	Rathour & Singh (1991)
Oenopia conglobata	—	—	24	Dobrzhansky (1926)
Oenopia conglobata	11.0	4.6	24	Nedvěd, unpubl.
Oenopia kirbyi	—	3.3	24	Rathour & Singh (1991)

Table 3.2 (*Continued*)

Species	Weight	Size	Ovarioles	Reference
Oenopia sexareata	—	—	24	Rathour & Singh (1991)
Palaeoneda auriculata	—	10.5	84–88	Rathour & Singh (1991)
Pania luteopustulata	—	5.1	24–32	Rathour & Singh (1991)
Platynaspis luteorubra	—	3.0	19–22	Dobrzhansky (1926)
Priscibrumus uropygialis	—	—	24	Rathour & Singh (1991)
Propylea quatuordecimpunctata	13.0	4.1	23	Dobrzhansky (1926)
Psyllobora vigintiduopunctata	7.7	3.8	22–24	Dobrzhansky (1926)
Lindorus lophanthae	—	2.5	20	Stathas et al. 2002)
Rodolia guerini	—	—	40	Rathour & Singh (1991)
Rodolia sp.	—	—	24	Rathour & Singh (1991)
Scymnus ater	—	1.5	8	Dobrzhansky (1926)
Scymnus frontalis	3.1	2.5	12	Dobrzhansky (1926)
Scymnus haemorrhoidalis	1.3	2.1	10–12	Dobrzhansky (1926)
Scymnus interruptus	—	2.2	12	Dobrzhansky (1926)
Scymnus nigrinus	3.0	2.6	12	Dobrzhansky (1926)
Scymnus rubromaculatus	1.9	2.2	10–12	Dobrzhansky (1926)
Scymnus suturalis	0.9	1.8	14	Dobrzhansky (1926)
Stethorus pusillus	0.6	1.4	4	Dobrzhansky (1926)
Subcoccinella vigintiquatuorpunctata	13.3	3.8	33–35	Dobrzhansky (1926)
Tytthaspis sedecimpunctata	5.3	3.0	20–21	Dobrzhansky (1926)
Vibidia duodecimguttata	—	4.0	24	Dobrzhansky (1926)

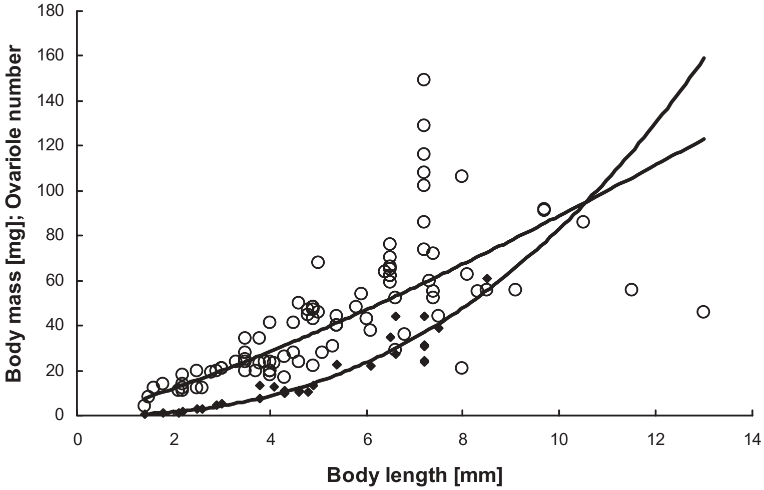

Figure 3.6 Relationships between body length (mm), body mass (mg, diamonds) and number of ovarioles (open circles) in Coccinellidae. Sources of the numbers of ovarioles are listed in Table 3.2. Fresh body masses are data measured by Nedvěd (unpublished), body length are either measured by Nedvěd or averaged literature data. Body mass increases with body length with the power function $M = 0.27 \cdot L^{2.46}$, number of ovarioles follow the power function (close to linear) $NO = 6 \cdot L^{1.14}$.

200 ovarioles per female), approximately 5.6% of the ovarioles were dysfunctional. The efficiency of the ovarioles (percentage of simultaneously active ones) was high in the summer generation and low in the winter generation. Crowding and competition among the ovarioles and inadequate nutrition were the factors affecting ovarian dysfunction (Rhamhalinghan 1986).

A five-stage rating system to describe ovarian development is based on the length of the terminal **follicle**, the number and shape of developing follicles in each ovariole, and the presence of yellow colour (**yolk**) in the terminal **oocyte** (Okuda et al. 1986, Phoofolo et al. 1995). Fully developed oocytes are **vitellinized** (yolk is deposited) and **chorionated** (covered by a chitinous envelope). A positive linear relationship has been observed between ovarian developmental rate and temperature. Oocytes gradually grow and ripen in individual ovarioles, and may then be laid synchronously from one or both ovaries. The number of eggs laid is positively correlated with the number of ovarioles, body length and body weight.

The rates of ovarian development and **oosorption** in predatory *Har. axyridis* are much higher than in herbivorous ladybirds. During **starvation**, the nutrients were found to be resorbed back from developing eggs. This oosorption mainly occurred during the intermediate developmental stage of the ovarioles, and the ovarian development and oosorption were asymmetric in the right and left ovaries in *Har. axyridis* (Osawa 2005).

3.5.6 Mating

3.5.6.1 Frequency and duration of mating

Ladybirds mate often and for a long time, and change partners (i.e. they are **promiscuous**). A **mating frequency** of about 20% at any given time was recorded for *A. bipunctata* in the field (Haddrill et al. 2007). The male uses his legs to hold himself onto the elytra of the female and is carried by her. Body shaking by males is essential for insemination. The spermatophore is formed in the bursa copulatrix (Obata 1988). Within 1 hour of mating the spermatophore is emptied, the envelope ejected from female's reproductive organs and is usually eaten by the female (Obata & Hidaka 1987).

The **mating duration** was recorded as 54 minutes with a range of 41–62 minutes in *C. septempunctata* (Rana & Kakker 2000). The duration was higher (51 minutes) when a melanic female mated with a melanic male of Indian *C. septempunctata* and lower (39 minutes) when a typical female mated with a typical male (Srivastava & Omkar 2005). Typical duration of mating of *Har. axyridis* in laboratory was between 2 and 3 hours (Awad & Nedvěd, unpublished). The mating posture in *Aiolocaria hexaspilota* may last several days (Iwata 1932). Manipulating the mating duration artificially had a dramatic influence on hatching rate in *Menochilus sexmaculatus* and *Coelophora saucia* (Omkar et al. 2006a). No eggs were fertilized after copulation lasting only 10 seconds, about 35% of eggs after a 1 minute copulation, and 80–90% after copulation lasting 1 hour or a natural long copulation.

Mating rhythmicity. Mating in *Menochilus sexmaculatus* (Omkar & Singh 2007) and *P. dissecta* (Mishra & Omkar 2004) in India occurred at all times of the day or night with a slight prevalence (66%) during the **photophase**.

The **willingness to mate** of both males and females of *P. dissecta* increased until their **age** had reached 10–30 days (Pervez et al. 2004). In *C. septempunctata* in India, females started to mate at 2 days and males at 4 days after emergence. Ten day old males and females were the most willing to mate (Srivastava & Omkar 2004). Mating of young (1–5 day old) adult *P. dissecta* lasted about 200 minutes; mating of those 20 days old lasted about 300 minutes (Pervez et al. 2004). The willingness to mate strongly increases when adults have no chance to mate. *Col. maculata* where the genders were isolated for only 1 day were 26 times more likely to mate than individuals kept in a mixed-sex group; isolating males had a stronger effect than isolating females (Harmon et al. 2008).

Multiple matings usually **enhance** the total egg output and percentage of eggs that hatch, even though one copulation is sufficient for permanent fertility of the female (except in some species such as *Stethorus pusillus* that lack a spermatheca; Putman 1955). Mating had a repeated stimulatory effect on the number of eggs laid in *A. bipunctata* (Semyanov 1970). The hatching rate in *Menochilus sexmaculatus* was 64% after multiple matings and 37% after only a single mating (Bind 2007). Egg hatching rate in this species decreased after separation of the female and male: hatching was reduced to 50% by 50, 40 and 30 days after the separation (following 5, 10 and 20 matings, respectively) (Omkar & Mishra 2005a). Results with *P. dissecta* (Omkar & Pervez 2005) were even more striking: 65% eggs hatched after a single mating, 72% after two, 78% after three and 93% after further multiple mating. However, the physical interference between individuals in a **limited space** had a small **detrimental effect** on egg viability of *P. dissecta*: 96% of the eggs laid by a single mated female hatched, while only 88% of the eggs hatched when laid by a female sharing a 9 cm Petri dish with four unmated males (Mishra & Omkar 2006).

Mating (or repeated mating) refusal by ladybird females has been observed frequently, but the causes and consequences of such behaviour have rarely been revealed. Two prominent hypotheses are that resistance is (i) a means of **avoiding costly** and **dangerous mating** and (ii) a means for the **selection of high-quality males**. Female refusal may be decreased by a nutritious **nuptial gift**, i.e. a spermatophore, provided by the male. The above hypotheses were investigated in *A. bipunctata*, in which females frequently display strong **copulation rejection** behaviour and ingest a **spermatophore** after copulation (Perry et al. 2009). Females deprived of food for 96 hours resisted mating more frequently and for longer periods than less starved females (starved for only 16 hours) and so they re-mated less frequently. The finding that starved females were more resistant suggests that mating is energetically costly, and that nuptial consumption of spermatophores does not offset these costs (Perry et al. 2009).

Female **longevity** decreased with increasing number of matings in both *Menochilus sexmaculatus* and *P. dissecta,* indicating there is a cost to mating. Thus very high mating activity, typical of many ladybirds, may have a deleterious effect on their fitness (Omkar & Mishra 2005a). Longevity decreased from 118 days for single, once-mated females to 76 days for repeatedly mated females of *Har. axyridis*. Due to this difference, once-mated females had higher lifetime fecundity (1326 eggs, hatchability 58%) than repeatedly mated ones (977 eggs, 51%; Fois et al. unpublished).

There was a transient benefit from **polyandry** (mating with several different males) in the reproductive success of *A. bipunctata* females. Fecundity and hatching rate were lower in females mated 10 times with one male than in females mated once with 10 different males (Haddrill et al. 2007). Promiscuous females of *P. dissecta* were also more fecund and laid more viable eggs than monogamous ones, which had been confined in a cage with a single male. Amongst promiscuous females, those mated with several males (i.e. there was freedom of mate choice) had a significantly higher reproductive output than those mated daily with a new unmated male with no choice (Omkar & Mishra 2005a).

3.5.6.2 Sperm competition

Earlier studies suggested that most often it was the sperm of the last male (of many that copulated with the female) that fertilized the eggs (Ueno 1994, 1996). De Jong et al. (1993) provided evidence for almost complete second male sperm precedence in experiments with melanic and non-melanic *A. bipunctata* providing that the results were not obscured by female **rejection behaviour**. In a repeated experiment, however, there was a highly variable degree of paternity of the second male (de Jong et al. 1998).

Behavioural and molecular genetic data were used to examine how sperm from several males was used over time by females of *A. bipunctata*, and to link mating with **fertilization** (Haddrill et al. 2008). In the laboratory, the number of mates (males that copulated with the observed female) was usually similar to the number of fathers (males that passed their genes to the progeny), suggesting that females have little post-copulatory influence on the **paternity** of their eggs. Longer copulation resulted in a higher probability of paternity for any particular male, probably due to the transfer of larger numbers of sperm in multiple **spermatophores** (Haddrill et al. 2008).

3.5.6.3 Female choice and melanism

Hodek and Ceryngier (2000) regarded the finding that at least some coccinellid species do not mate at random as the most important among the sexual activities of coccinellids.

To find out whether ladybird females prefer a specific male phenotype, e.g. a colour morph in polymorphic species, **choice** and **no-choice mating tests** can be conducted. Also, observations can be made of **seasonal changes** in the frequency of colour morphs (individuals) and of pairs of different composition in the field.

Lusis (1961) observed that matings of *A. bipunctata* recorded near Riga and Moscow involved fewer matings between red females and red males and significantly more black males in pairs than would be expected with random mating. He hypothesized that the higher sexual activity of the melanic forms was due to their higher metabolic rate, as the result of higher absorbance of solar radiation. However, Creed (1975) did not observe this phenomenon in a population of *A. bipunctata* near Birmingham. Also in England, Muggleton (1979) found that mating preference was affected by the frequency of the different forms: regardless of colour, the rarer morph was preferred by females of both morphs. Majerus et al. (1982a) reported a preference for melanic males in another English population in 1981: while 34% of the non-mating males of *A. bipunctata* in North Staffordshire were melanics, the melanic proportion of mating males was 49%. For melanic females, however, the proportion was about 35% for both mating and non-mating ones. The authors (Majerus et al. 1982b) demonstrated a genetic basis for such preferential mating; differential competitiveness among males was not involved. However, the mechanism whereby females recognize melanic males remains unknown.

Female *Har. axyridis* expressed **visible mate preference**, by rejecting less-preferred phenotypes, and cryptically by **retaining eggs** for longer periods after mating with less-preferred males, apparently in order to replace their sperm later by that of a more-preferred male. Whereas **pair formation** was under female control, the **duration of copulation** was under male control. Males invested more time in mating with dissimilar females (Wang et al. 2009). Which males were preferred was not clear-cut, because there was a pleiotropic effect whereby female choice varied between the spring and autumn **generations**. The prevalence of melanics in spring decreased in summer because females preferred mating with the pale *succinea* morph (Osawa & Nishida 1992). In the summer generation, melanics were more successful.

Several studies based on mate-choice experiments have shown that most females seemed to prefer to mate with **melanic** morphs, especially the *conspicua* morph. Thus melanics dominate in laboratory cultures and **biocontrol stocks** although they remain relatively rare in the wild due to a set of selection pressures (Seo et al. 2008).

Two alternative hypotheses have been offered to explain why gender-specific reproductive behaviour may vary between generations: (i) **maternal factors** (epigenetic) that influence the expression of genes in progeny, and (ii) linkage disequilibria among **allele frequency** that cycle seasonally as a function of **assortative mating** (Wang et al. 2009).

In **field populations** of *Har. axyridis* in China, red phenotypes outnumbered melanics by 5:1 in the autumn, but melanics became equally abundant in the spring, suggesting that melanism is advantageous in winter, but costly in summer (Wang et al. 2009). In *A. bipunctata*, melanic forms were more abundant in the autumn than in the spring but not significantly so (Majerus & Zakcharov 2000, Honěk et al. 2005). The representation of melanic males in mating pairs observed in a **cage experiment** was higher than would be expected from random mating (Majerus et al. 1982a). Though it is still unknown how females recognise melanic males, as pointed out above, O'Donald and Majerus (1989) were able to show that **visual discrimination** by females was not involved. Specific cuticular alkanes (Hemptinne et al. 1998) may be responsible for the recognition, and higher body temperature and **activity** in melanic *A. bipunctata* under most conditions has been recorded (De Jong et al. 1996).

In the related *A. decempunctata*, the proportion of the three main colour morphs (*typica*, spotted; *decempustulata*, chequered; *bimaculata*, melanic) was found to be very stable both in space and time, with no environmental selection or female choice (Banbura & Majerus in Majerus 1998, Honěk et al. 2005).

Females of *Har. axyridis* uninfected with the ectoparasitic fungus *Hesperomyces virescens* were preferred by males as mating partners over **infected** ones (Nalepa & Weir 2007).

Melanic as well as typical individuals of *C. septempunctata* in India preferred to mate with melanic forms of the opposite sex. Mate choice was mainly determined by females and to a lesser degree by males (Srivastava & Omkar 2005). While Osawa (1994) suggested that the colour of the elytra of *Har. axyridis* is the most important factor in mate choice by females, Ueno (1994) stressed that size and activity were important.

Perry et al. (2009) investigated whether the extent of active choice/rejection of males by females depended on **male size** or whether unspecified rejection passively favoured large males that overwhelmed the females. They found that the extent of female resistance was independent of the size of the male, but that limited resistance resulted in a bias towards large males in copulations. A side effect of imperfect female resistance would be expected to result in **selection** for large male size. However, in all ladybirds, males are still slightly smaller than females, as also applies for the majority of animals, reflecting the higher energetic and nutritional cost of producing eggs in comparison with sperm.

3.5.6.4 Hybridization

Cases of spontaneous **interspecific mating** in the wild are rarely reported but may occur relatively often in a limited space in the laboratory. Cases of successful interspecific reproduction, i.e. **hybridization** are even rarer. Majerus (1997) listed the observations of interspecific matings in the field (five combinations, including taxonomically distant species) and laboratory (eight combinations, also with unrelated species). There were either no progeny after such mating or the progeny were apparently of the same species as the female, suggesting that the female was already mated with the same species male. The only **hybrid progeny** were reported for a couple consisting of an *A. bipunctata* female and an *A. decempunctata* male. In other hybridization combinations using previously isolated females, eggs showed signs of development but did not hatch (**embryonic mortality**), or larvae died in the first instar (*Anatis ocellata* × *An. labiculata*). A hybrid between *P. quatuordecimpunctata* and *P. japonica* had decreased fecundity (Iablokoff-Khnzorian 1982).

Reproductive isolation between two related *Henosepilachna* species is achieved by a combination of two mechanisms: (i) there is a choice for conspecific females by *Henosepilachna vigintioctomaculata* males; (ii) there is a difference in the intensity of male rejection between *H. vigintioctomaculata* females (strong) and *H. pustulosa* females (weak) (Matsubayashi & Katakura 2007). Host fidelity functioned as a strong **barrier** against gene flow between two other species *Henosepilachna niponica* and *Henosepilachna yasutomii*, but occasional interspecific mating has been achieved by addition of common host plant (Hirai et al. 2006).

3.5.7 Oviposition

3.5.7.1 Oviposition substrate

Ovipositing females have to select a suitable place for their eggs. This selection involves balancing several requirements which may sometimes even be conflicting: optimum **microclimate** for embryonic development, proximity of **food** for the hatched larvae, and **protection** from predators, parasites and competitors (5.4.1.3).

The Coccidulini lay eggs freely on the leaf surface (Klausnitzer & Klausnitzer 1986). *Megalocaria dilatata* (Coccinellini) lays eggs on the spines of plants and makes a barrier preventing an access to the egg cluster with a sticky secretion from the abdomen (Liu 1933). The aphidophagous generalist *A. bipunctata* laid more eggs (91%) on filter paper than on spruce needles (9%; Timms & Leather 2007), while the conifer adelgid-eating specialist *Aphidecta obliterata* laid more eggs on needles (77%). Many aphidophagous coccinellids lay eggs on the underside of **filter paper** when in laboratory containers, as in the field they lay eggs on the **underside** of the leaves on broad-leaved plants. In this way the coccinellids may reduce the risk of predation and rain washing off the eggs. Ladybirds specialised on conifer trees lay eggs on the **needles** or into bark crevices.

In Japan, *C. septempunctata* used for oviposition artificial insolated objects during the winter (Ohashi et al. 2005). *A. bipunctata* avoided laying eggs in patches with *Lasius niger* **ants** (Oliver et al. 2008).

Scymninae often hide their eggs in crevices of the substrate, or use an artificial **protection**. Females of *Sasajiscymnus kurohimae*, feeding on eusocial aphids, which have a soldier caste that defend their colonies, protect their eggs beneath undigested remnants of eaten aphids (Arakaki 1988). *Scymnus hoffmanni* similarly covers its eggs with cuticles of predated aphids (Kawauchi 1985). Eggs of *Scymnus louisianae* are laid predominately on the undersides of leaves, nestled among the leaf hairs (Brown et al. 2003).

Females of Chilocorinae (e.g. *Chil. rubidus*) lay one egg at a time under the scale of a larval prey coccid (Pantyukhov 1968). *Exochomus flavipes* have occasionally been observed laying eggs into a conspecific empty pupae from which a parasitoid had emerged (Geyer 1947).

Two whitefly predators, *Clitostethus oculatus* (Scymninae) and *Delphastus pusillus* (Microweiseinae) lay eggs singly or in groups of 2–4 on leaf surfaces, where whitefly eggs and nymphs are abundant (Liu & Stansly 1996a).

In **Epilachninae** that feed on plants as both adults and larvae, it is often difficult to distinguish oviposition preference from adult feeding preference, because oviposition is likely to occur at or near feeding sites. In laboratory assays, the distance between adult feeding scars and egg masses of *Henosepilachna niponica* was long (25 cm) and the females often placed eggs on artificial substrates rather than leaf discs (Fujiyama et al. 2008).

3.5.7.2 Oviposition rhythmicity

Many activities of ladybirds take place during the day, whereas they rest during the night (5.4.1.1). However, the oviposition activity of several species in India showed the opposite trend (Fig. 3.3). There, it was found that *C. septempunctata* females preferred to oviposit at the end of the scotophase and in the early photophase hours (21.00–1.00, where 0.00 means the beginning of the photophase), *P. dissecta* laid 86% eggs during the early half of scotophase (Mishra & Omkar 2004) or that they laid most eggs in the middle of the scotophase (15.00–17.00). *C. leonina transversalis* laid most by dusk, i.e. at the beginning of the scotophase (11.00–13.00) (Omkar et al. 2004). In *Menochilus sexmaculatus* (Omkar & Singh 2007), the peak of oviposition (62%) was attained during early scotophase (12:00–15:00).

3.5.7.3 Oviposition rate

The number of eggs laid per day, i.e. daily oviposition or reproductive rate, increases rapidly during several days after adult eclosion, to reach a maximum (which may equate to the number of ovarioles in both ovaries of the female) at about two or three weeks, and then slowly decreases during the remaining life span of the female, which might be several months.

These changes in oviposition rate (rapid increase followed by slow decrease) during adult life can be described by a **triangular fecundity function** (Dixon 2000). The pattern can be fitted by a third order power function (see fig. 2.11b in Dixon 2000) or by the Bieri model (Bieri et al. 1983, for its use see Lanzoni et al. 2004, and Fig. 3.7c). The Bieri model ($Or = (a \cdot (age - b))/(\exp(c \cdot (age - b)))$) provides a calculation for the time of **peak oviposition rate**. The age specific oviposition rate can also be fitted by a lognormal or other asymmetric distribution curve.

The increase and decrease of oviposition rate (**age specific fecundity**) can also be almost symmetric, as in *Anegleis cardoni*, where it was fitted simply by a second power curve (Omkar et al. 2009). The estimation of age at peak oviposition tends to be higher when fitted by this parabolic curve than when using an **asymmetric** distribution, and higher for treatments giving long (usually in better conditions) than short oviposition periods (less suitable conditions). Omkar & Mishra (2005) distinguished between short-lived females, that distributed their reproduction **uniformly** in their lifetime, and long-lived females which showed a high burst of reproductive activity followed by a gradual decline.

Egg production in *Scymnus louisianae* was found to decrease slowly, and it was rather equally distributed over a female lifespan of 80 days, though there was a rapid increase during 6 days after adult eclosion and a rapid drop during last 10 days of life (Brown et al. 2003, Fig. 3.7g). The females of *Exochomus quadripustulatus* laid eggs in an irregular pattern, with the number of eggs deposited within a single day ranging from 1 to 11 at a thermoperiod of 9/19°C and from 1 to 16 eggs at 12/24°C; the oviposition rate had a rather bimodal appearance (Sengonca & Arnold 2003; Fig. 3.7h). The rate of egg production of *Chil. nigritus* followed a cyclical pattern that lasted for approximately 22 days (Ponsonby & Copland 2007).

The daily oviposition rates of *C. septempunctata* and *P. quatuordecimpunctata* were not related to **female size** (Honěk et al. 2008).

Natality (m_x), which is the mean number of female offspring produced per surviving female during age interval x (Birch, 1948), is sometimes used instead of oviposition rate. The natality of *Clitostethus oculatus* fluctuated many times during the lifespan of females (Fig. 3.7b), and did not follow the typical triangular fecundity function referred to above (Ren et al. 2002).

3.5.7.4 Oviposition period

The duration of the period between the first and the last egg batch, the oviposition period, is a good measure of individual **fitness**. The number of days between the last oviposition and death of the female is called the **post-oviposition period**. It can be zero, when a female dies during its reproductive phase, or can last from a few days to weeks in **senescent** females. When a mean oviposition rate is calculated from the total lifetime fecundity of a female, only the reproductive (=oviposition) period should be used in the denominator.

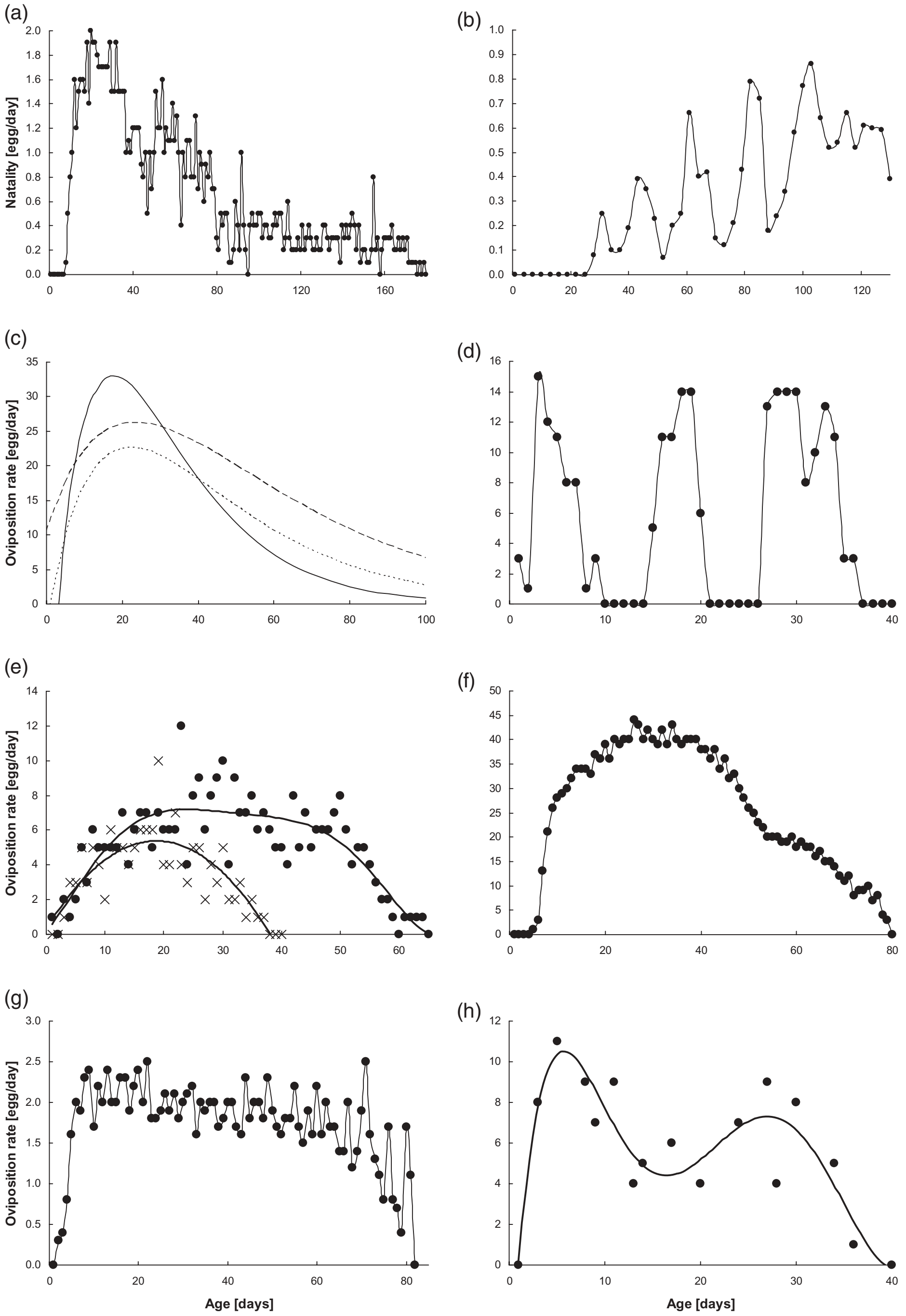

Figure 3.7 Age specific oviposition rates calling into question the general occurrence of the triangular fecundity function (Dixon 2000). (a) Triangular natality (m_x) with tail, *Axinoscymnus cardilobus* at 20°C fed with *Bemisia tabaci* (after Huang et al. 2008); (b) polymodal increasing natality of *Nephaspis oculatus* at 31°C fed with *Bemisia tabaci* and *B. argentifolii* (after Ren et al. 2002); (c) Bieri function calculated for *Harmonia axyridis* (solid line), *Hippodamia variegata* (dashed line) and *Adalia bipunctata* (dotted line) reared on *Myzus persicae* at 25°C (after Lanzoni et al. 2004); (d) polymodality in *Chilocorus nigritus* at 30°C, RH 62% and fed with *Abgrallaspis cyanophylli* (after Posonby & Copland 2007); (e) parabolic (second order power) function in *Anegleis cardoni* fed with *Lipaphis erysimi* (crosses) and long plateau of *Anegleis cardoni* fed with *Aphis craccivora* (dots; both after Omkar et al. 2009); (f) two levels in *Harmonia axyridis* at 25°C fed with *Aphis fabae* (after Stathas et al. 2001); (g) monotonous level (almost constant) in *Scymnus louisianae* fed with *Aphis glycines* (Brown et al. 2003); (h) bimodality in *Exochomus quadripustulatus* at thermoperiod 9/19°C fed with *Pulvinaria regalis* (Sengonca & Arnold 2003).

The length of the oviposition period is species-specific and decreases rapidly with increasing **temperature**, since **longevity** then decreases. The oviposition period of *Scymnus levaillanti* lasted 87, 76, 47 and 32 days at 20, 25, 30 and 35°C respectively (Uygun & Atlıhan 2000). No eggs were deposited at 15°C, even though the development thresholds for eggs and larvae were between 11–12°C. The oviposition periods of *Axinoscymnus cardilobus* lasted 109, 61, and 17 days at 17, 26 and 32°C, respectively (Huang et al. 2008).

The oviposition period may vary with **food** quality. The oviposition period was 22.4 days in *C. septempunctata* fed with the cereal aphid *Sitobion avenae* (Rana & Kakker 2000), but only 16 days when reared on *Brevicoryne brassicae* (ElHag & Zaitoon 1996). In *Anegleis cardoni*, it was twice as long (58 days) on *Aphis gossypii* than on *Lipaphis pseudobrassicae* (27 days) (Omkar et al. 2009).

While the average pre-oviposition and oviposition periods in melanic **colour morph** of *C. septempunctata* in India were 10.2 and 68.9 days, respectively, they were 14.6 and 76.9 days respectively in normal morphs (Rhamhalinghan 1986).

3.5.8 Fecundity

The total lifetime egg production (fecundity) is **species-specific**, increasing with the **size** of the ladybird, and dependent on **temperature** and on the quality and quantity of **food** both during the pre-imaginal development of the female and during reproduction. Fecundity is also influenced by **mating frequency**, **age** of the parents, **population density**, illumination, **photoperiod**, phenotype; it also changes with generation, etc. (Table 3.1). It is the product of daily fecundity (**oviposition rate**) and the duration of the **oviposition period**.

The relationship between food quantity and fecundity or fertility is called the **numerical response** (5.3). The shape of the relationship is usually a convex curve. In *Scymnus subvillosus* the numerical response was similar to its functional response that matched Holling's type II (Atlıhan & Güldal 2009). A twofold increase in **prey density** (*Aphis gossypii*) brought about a twofold increase in lifetime oviposition and mean oviposition rate in *C. septempunctata* (Xia et al. 1999).

The fecundity of *Anegleis cardoni* changed with **food suitability**: it was three times higher on *Aphis gossypii* than on *Lipaphis pseudobrassicae*, while the oviposition period was twice as long and the mean reproductive rate 1.34 times higher (Omkar et al. 2009). The fecundity of *C. septempunctata* was 35% higher when fed with *Aphis fabae* reared on a susceptible cultivar of *Vicia faba* than when the aphid had been fed on a resistant one (Shannag & Obeidat 2008).

A decrease in **prey density** (the scale *Abgrallaspis cyanophylli*) caused a significant but transient decline in egg production in *Chil. nigritus*. A heterogeneous prey population (mix of diverse developmental stages) elicited significantly higher levels of oviposition at similar host densities than homogeneous population (cohort of equally aged individuals), irrespective of the growth stage of the prey (Ponsonby & Copland 2007).

Of five generations of *Cer. undecimnotata* produced in experimental cages during a year, the greatest numbers of eggs were laid by females of the first and second **generations** (Katsoyannos et al. 1997).

Crowding has an adverse effect on fecundity. Individual females of *Har. axyridis* laid an average of 13 eggs per day, while females grouped as 10, 20, 30 and 40 per container laid 9, 6, 3 and 2 eggs per day, respectively (Abdel-Salam & Abdel-Baky 2001).

The parasitoid *Dinocampus coccinellae* has been reported as having a great effect on the fertility of mature female ladybirds. The **parasitoid** larva normally **castrates** the host ladybird and usually causes death. However, at relatively high temperatures (25°C), it was found that daily numbers of coccinellid eggs increased during two days after parasitization and then gradually decreased to stop 8–9 days after parasitization. Although mortality of the females was high (71%), half of those that survived began to oviposit again 12 days after the parasitoid larvae had emerged (Triltsch 1996).

Melanic females of *C. septempunctata* in India laid more eggs (302–412) than the females of the typical **colour morph** (278–379) (Rhamhalinghan 1986). In *Micraspis discolor* in India, fecundity was the lowest at the lowest experimental **temperature** of 20°C, highest at the optimum temperature, and decreased at the highest temperature of 30°C (Omkar & Pervez 2002) (3.6.4; Fig. 3.8b). In *Chil. nigritus*, no oviposition occurred at the low temperature of 18°C. The lifetime fecundity increased from 20 to 24°C and then

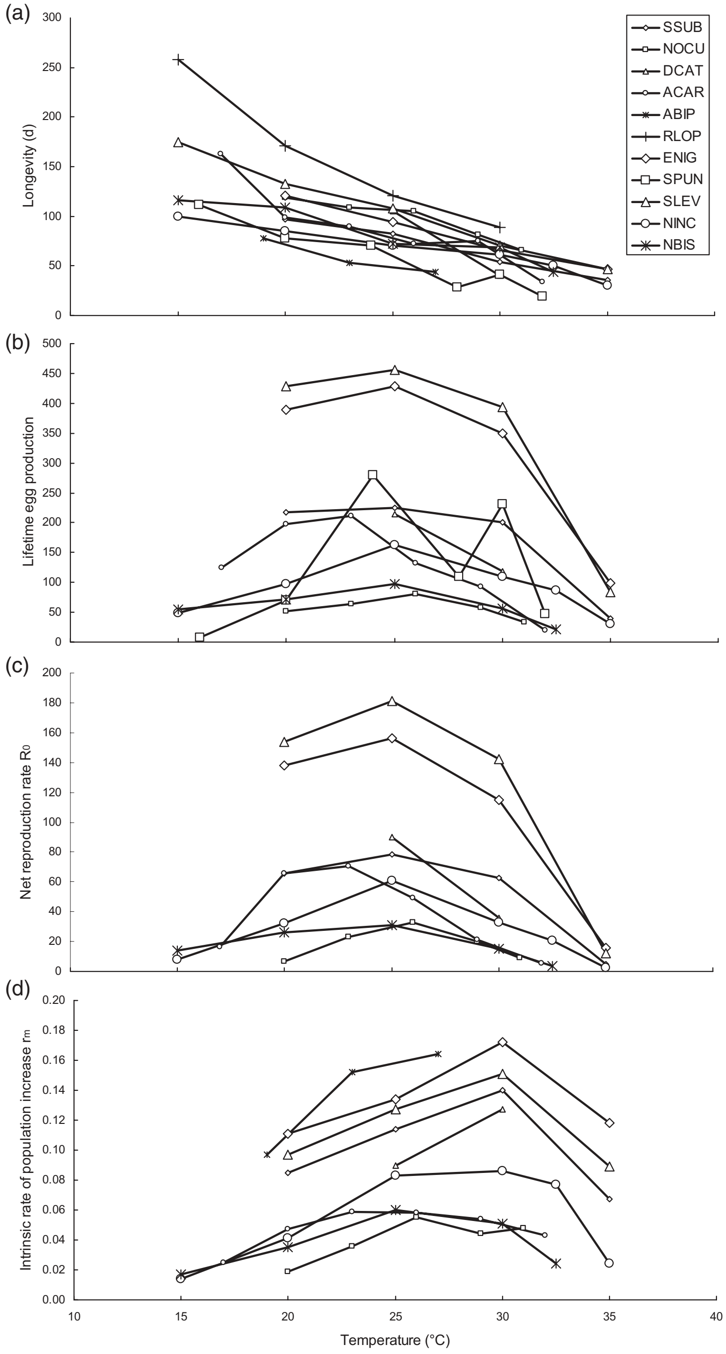

Figure 3.8 Temperature effects on selected parameters of adult life. (a) longevity; (b) lifetime egg production; (c) net reproduction rate R_0 (Andrewartha & Birch 1954); (d) intrinsic rate of population increase r_m (Andrewartha & Birch 1954). Data for 12 coccinellid species: *Adalia bipunctata,* ABIP (Jalali et al. 2009); *Axinoscymnus cardilobus*, ACAR (Huang et al. 2008); *Delphastus catalinae*, DCAT (Kutuk & Yigit 2007); *Diomus austrinus*, DAUS, (Chong et al. 2005); *Parexochomus nigromaculatus*, ENIG (Atlıhan & Özgökce 2002); *Clitostethus oculatus*, NOCU (Ren et al. 2002); *Nephus bisignatus*, NBIS (Kontodimas et al. 2007); *Nephus includens*, NINC (Kontodimas et al. 2007), *Lindorus lophantae*, RLOP (Stathas 2000); *Scymnus levaillanti*, SLEV (Uygun & Atlıhan 2000); *Scymnus subvillosus*, SSUB (Atlıhan & Chi 2008); *Stethorus pusillus*, SPUN (Roy et al. 2003).

decreased up to 30°C. No eggs were produced at 34°C. However, daily fecundity was highest at 30°C (Ponsonby 2009).

The **reproductive output** (percentage of body weight allocated to reproduction during 24 h) was similar (12.5%) in large *C. septempunctata* and small *P. quatuordecimpunctata* (Honěk et al. 2008).

3.5.9 Longevity

3.5.9.1 Voltinism

The number of generations per year and the lifespan of ladybirds depend on the **climatic conditions** in the region. However, many species, even in warmer climates, normally have a single generation (are **univoltine**), and live for one year including several months in **dormancy** (also Chapter 6).

In several species, a second overwintering has been reported in a minority of individuals. Thus there are records of a **second hibernation** in *Calvia quatuordecimgutta* (Kanervo 1946), in *P. quatuordecimpunctata* (Hariri 1966), in *Stethorus pusillus* (Putman 1955), in *Aiolocaria hexaspilota* (Iwata 1932, Savoiskaya 1970) and *C. septempunctata* (Sundby 1968). Savoiskaya (1970) reported that 15–20% of a *Har. axyridis* population in Kazakhstan may live and oviposit for 3 years.

Epilachna admirabilis is univoltine in northern Japan and hibernates as the final (fourth) instar larva. Some of the resulting adults then enter a second hibernation together with their own larvae (Katakura 1976).

Scymnus sinuanodulus regularly lives for **2 years** and the fecundity is the same in both years (Lu & Montgomery 2001). In *Pseudoscymnus tsugae* the mean longevity in the laboratory was 163 and 126 days for females and males, respectively, while some individuals of both sexes lived more than 300 days (Cheah & McClure 1998), suggesting the potential for a 2-year lifespan in the field.

While central European populations of *Cer. undecimnotata* are obligatorily univoltine (Ceryngier et al. 2004), at least a portion of the *Cer. undecimnotata* population in central Greece may complete two or more overlapping generations per year under artificial conditions in shaded outdoor cages (Katsoyannos et al. 1997; 6.2.8). *Hip. variegata* may complete seven generations between April and November under artificial conditions in outdoor cages in Greece. Adults of the 6th and 7th generations formed the hibernating population (Kontodimas & Stathas 2005).

Coccinella quinquepunctata, *C. septempunctata* and *C. magnifica* are potentially **polyvoltine** (Ceryngier et al. 2004). Heterogeneous voltinism (6.2.1.6) appears to be one of the factors responsible for the predominance of *C. septempunctata* in most habitats of the Palaearctic and for its successful invasion of the Nearctic Region (Hodek & Michaud 2008). The very successful invader *Har. axyridis* regularly has two generations per year, even in colder temperate countries (Brown et al. 2008), and unlike other ladybirds even reproduces late in the season.

The lifespan of the sequential generations of polyvoltine species usually decreases in the laboratory, probably due to inbreeding (6.2.1). Thus, in four successive generations of *Menochilus sexmaculatus* longevity was respectively 87, 89, 63 and 50 days in males, and 111, 101, 90 and 50 days in females (Hukushima & Kouyama 1974).

The overlap of generations in bivoltine species (such as *A. bipunctata* in Central Europe) enables the spread in the population of pathogens and parasites such as the mite *Coccipolipus hippodamiae* (Webberley et al. 2006; 8.3).

3.5.9.2 Effect of temperature, photoperiod and humidity

In coccinellids, as in other exotherms, **life span** shortens with increasing temperature. There are cases of a **linear decrease** of life span with temperature (3.6.4; Fig. 3.8a). For example, the linear decrease was clear in *Axinoscymnus cardilobus* reared at six temperatures; the longest longevity was 163 days at 17°C compared with only 34 days at 32°C (Huang et al. 2008). Adult *C. novemnotata* lived for 62, 48 and 21 days at 21, 27 and 32°C, respectively (McMullen 1967). *Olla v-nigrum* lived for 172 days at 15°C and only 51 days at 25°C (Kreiter & Iperti 1984). Males of Iranian population of *Stethorus gilvifrons* reared at various temperatures from 15 to 35°C had longest and shortest longevities of 18 and 13 days, and 17 and 9 days for females (Taghizadeh et al. 2008). The longevity of this coccinellid in Turkey also decreased with increasing temperature (20, 25, 30°C) and this was not affected by two different **photoperiod**s (16L:8D and 8L:16D) (Aksit et al. 2007). *Chil. nigritus* lived for 100–280 days at temperatures of 22–26°C, 65–115 days at 30°C and only 17–29 days at 34°C (Ponsonby 2009).

In contrast, in *Col. maculata* no such a clear tendency was recorded: longevity was 73, 74, 77, 45 and 80 days at 19, 21, 23, 25 and 27°C, respectively (Wright & Laing 1978). The mean adult longevities of *Delphastus catalinae* were 40 days at a constant 30°C and 42 days at **fluctuating temperatures** of 25/35°C (Kutuk & Yigit 2007).

The longevity of females of *Chil. nigritus* increased with increasing **relative humidity** (162 days at 40%, 220 at 80%), but net reproductive rate (R_0) and the maximum intrinsic rate of increase ($r_{\max}$) were higher at the lower humidity (Senal 2006).

3.5.9.3 Effect of food

Adult longevity tends to be longer on a more suitable diet. Longevity of *Anegleis cardoni* was almost double when fed the more **suitable prey** *Aphis gossypii* than when fed the less suitable *Lipaphis pseudobrassicae* (Omkar et al. 2009). A diet of *Myzus persicae* increased the adult longevity and fecundity of *C. undecimpunctata* compared with one of *Aphis fabae* (Cabral et al. 2006). In contrast, however, the longevity of *Chil. nigritus* was almost twice when fed *Aspidiotus nerii* than *Abgrallaspis cyanophylli*, although the latter would appear the more suitable prey since it more than doubled fecundity (Ponsonby 2009). Moreover, the adult longevities of *Har. axyridis* and *A. bipunctata* females did not differ significantly when reared as larvae on different diets (either natural or artificial) and then on artificial diet as adults (120 to141 or 74 to 118 days, respectively; Ware et al. 2008). The longevity of females (59–76 days) and males (54–64 days) of *P. quatuordecimpunctata* was only little affected by seven aphid species provided as different food (Kalushkov & Hodek 2005).

The longevity of *Har. axyridis* fed with *Aphis glycines* reared on three susceptible varieties of soybean was greater (12.5 days) than on three **resistant varieties** (7.3 days) (Lundgren et al. 2009). In contrast, the adult longevity of *C. septempunctata* was not affected by whether *Aphis fabae* was reared on a susceptible (major) or on a partially resistant (79S4) cultivar of *Vicia faba* (Shannag & Obeidat 2008). No significant differences were reported in longevity or other characteristics of *Col. maculata* fed with **Bt-transgenic** corn pollen, non-Bt pollen, or *Schizaphis graminum* (Ahmad et al. 2006). Also *P. japonica* was not affected when fed with *Aphis gossypii* reared on either transgenic or non-transgenic cotton (Zhu et al. 2006).

The **quantity** of food has inconsistent effects on longevity. Increased prey (*Hyalopterus pruni*) consumption did not change the longevity of *Scymnus subvillosus*, but did result in a higher intrinsic rate of increase (Atlıhan & Güldal 2009). When the food provided to *Har. axyridis* was limited, mean longevity increased although mean reproductive life span and fecundity were reduced (Agarwala et al. 2008). However, there was a difference between groups of individuals, with one group showing a positive correlation and the other group a negative correlation between reproduction and longevity.

3.5.9.4 Effect of sexual activity

Males may have a longer or shorter longevity than females. Female *Psyllobora confluens* lived 46 days, but males 59 days, when fed with *Erysiphe cichoracearum* (Cividanes et al. 2007). In contrast, the mean longevity of female *Serangium parcesetosum* was longer (71 days) than that of males (60 days) (Al-Zyoud et al. 2005). There was no significant difference between the longevities of male and female *P. quatuordecimpunctata* (Kalushkov & Hodek 2005), but in *Chil. nigritus*, males are on average longer-lived than females (Ponsonby 2009).

Ageing trends were sex dependent in *P. dissecta*, with reproductive performance declining later in females than in males (Mishra & Omkar 2006).

There is a strong trade-off between the number of matings and longevity. Longevity decreased with an increasing number of matings in both *Menochilus sexmaculatus* and *P. dissecta* indicating a **cost of mating** (Omkar & Mishra 2005). Post-hibernation longevity was much shorter (76 days) in females of *Har. axyridis* that lived with male in limited space and mated regularly than in females mated before hibernation and then maintained without a male (107 days) and also much shorter than in virgin females (135 days) (Fois et al. unpublished).

3.6 TEMPERATURE AND DEVELOPMENT

Finally, we provide a general account of the more recent research on the main factor influencing coccinellid development, namely temperature. Earlier data have been reviewed by Honěk (1996). The life of exotherms, with their limited capacity for thermoregulation, is dependent on the external temperature. This restricts the range of conditions in which they can survive, determines the rate at which life processes proceed within this range and, together with body size (Gillooly et al. 2002), controls the fitness of the organism (Kingsolver & Huey 2008). Temperature determines the length of development of the immature stages, the length of the teneral period from adult ecdysis to first oviposition, the quantity and duration of oviposition and the length of life. The role of temperature in survival during hibernation and aestivation is described in 6.4.4.

3.6.1 Thermal constants

Growth and development of pre-adult stages occur only across a specific range of temperature. Within this range the **development time** and **rate of development** (a reciprocal of development time) vary with temperature. The l**ower temperature threshold** is the temperature below which a particular stage of an animal cannot develop. After some time (3.6.4.1) it dies, probably because of the loss of correlation between physiological and behavioural functions. At the other extreme, the range of tolerated temperature is limited by the **upper temperature threshold** at which the animal dies from heat.

The relationship between the rate of development and temperature is linear only within the range of what are called the **ecologically relevant temperatures** at which most of the life activities of the animals take place. Close to the upper development limit, the relationship becomes non-linear, attains its highest point at the **temperature optimum** where development rate is highest (i.e. development time shortest), and it then decreases sharply as the upper lethal temperature limit is approached. The relationship between the rate of development and temperature thus typically has the shape of a right skewed peak, whose left slope also may divert from linearity near the lower development threshold (Gilbert & Raworth 1996). Several models which have been proposed to approximate this course of development rate with temperature, e.g. those of Lactin et al. (1995) and Briere et al. (1999) which enable the calculation of temperature optima and upper lethal temperatures, were reviewed by Kontodimas et al. (2004).

A **linear model** approximates the course of development rate in the ecologically relevant temperature range and enables the calculation of two thermal constants. The first of these is the above-mentioned **lower development threshold** (LDT; Honěk & Kocourek 1988), also known as the **basal temperature** Tb (Trudgill et al. 2005), and which is the temperature below which development ceases. The other constant is the **sum of effective temperatures** SET or, in other words, the thermal time T which is the number of day degrees [dd] above LDT for completion of a developmental stage). It has to be remembered that LDT is a virtual value, but it is convenient for predicting temperature effects under ecologically relevant temperatures. Under real conditions development is already seriously impaired below a temperature higher than the LDT by some 2–4°C.

3.6.2 Relationship between LDT and SET

Recent results on the effects of temperature on preimaginal development (Table 3.3) contain data for 44 populations of 25 coccinellid species. The results confirm the conclusion of the earlier review of Honěk (1996) that coccinellids are warm-adapted species with a relatively high LDT (mostly between 9–15°C; 17°C for tropical *Chil. nigritus*; Ponsonby 2009) and a low SET (200–320 dd for total development; but over 500 dd for small coccidophagous species; Table 3.3). For the whole family Coccinellidae, the average LDT calculated from Table 3.3 for eggs, larvae, pupae and total development, respectively, is 9.8, 9.3, 10.1 and 10.1°C and the average SET is 64, 167, 78 and 304 dd. Another plot of data for many species, both aphidophagous and coccidophagous, resulted in a LDT of about 10°C (Dixon et al. 1997).

The combination of a high LDT and a low SET guarantees a fast development at high temperatures, in contrast to cold adapted species whose LDT is low and SET high (Trudgill 1995). This adaptive covariance of thermal constants results in a **negative relationship** between LDT and SET (Honěk & Kocourek 1988), and this also holds for data presented in this chapter (Fig. 3.9). Interpretation of this correlation is difficult, because the negative slope of the regression of the LDT on the SET is both a consequence of biological variation and a statistical artefact. For a detailed discussion of this matter, see Honěk (1996).

Table 3.3 Thermal constants, lower development threshold LDT (°C) and sum of effective temperatures SET (dd) for the development of egg, larva, pupa and total pre-adult development. Calculated using a linear model of the development rate vs. temperature relationship and data of temperatures ≤30°C. Development time of the prepupae included in the larval stage.

	Egg		**Larva**		**Pupa**		**Total**		
	LDT	**SET**	**LDT**	**SET**	**LDT**	**SET**	**LDT**	**SET**	**Reference**
Adalia bipunctata	11.4	34.5	5.9	166.1	10.7	67.8	9.4	246	Olszak (1987)
*Adalia bipunctata**	7.8	52.0	7.7	180.2	9.4	86.1	8.4	314	Schuder et al. (2004)
*Adalia bipunctata**	6.2	56.5	9.7	119.4	9.5	81.2	9.2	252	Schuder et al. (2004)
*Adalia bipunctata**	10.4	44.0	11.4	114.0	11.7	71.1	11.2	232	Jalali et al. (2009a)
*Adalia bipunctata**	11.9	39.2	9.3	148.4	11.2	73.0	10.8	254	Jalali et al. (2009a)
*Adalia bipunctata**	11.5	39.8	13.3	108.8	12.1	67.6	12.6	218	Jalali et al. (2009)
*Adalia bipunctata**	—	—	—	—	—	—	10.3	268	Jalali et al. (2010)
*Adalia bipunctata**	—	—	—	—	—	—	10.4	266	Jalali et al. (2010)
Axinoscymnus cardilobus	8.8	63.7	8.9	128.5	9.5	114.7	9.3	302	Huang et al. (2008)
Calvia quatuordecimguttata†	6.5	52.6	7.5	171.6	8.5	64.3	7.7	288	LaMana & Miller (1995)
Calvia quatuordecimguttata †	5.8	55.9	7.1	174.1	8.2	68.3	7.3	294	LaMana & Miller (1995)
Calvia quatuordecimguttata†	8.3	45.3	8.2	166.0	9.4	60.8	8.5	271	LaMana & Miller (1995)
Calvia quatuordecimguttata†	7.2	52.4	7.7	173.9	8.3	66.5	7.5	292	LaMana & Miller (1995)
Chilocorus bipustulatus	—	—	—	—	—	—	11.1–13.0	475	Eliopoulos et al. (2010)
Chilocorus nigritus	13.9	88.3	16.2	241.8	13.4	79.0	15.6	363	Ponsonby & Copland (1996)
Clitostethus arcuatus	8.2	65.4	7.1	164.9	8.2	74.3	7.9	289	Mota et al. (2008)
Clitostethus oculatus	7.6	105.7	1.7	309.4	13.5	53.8	6.9	424	Ren et al. (2002)
Coccinella septempunctata	9.9	48.4	10.2	165.3	10.8	78.8	10.2	297	Katsarou et al. (2005)
Coccinella septempunctata	6.9	55.2	–2.1	270.6	0.9	90.8	0.7	405	Srivastava & Omkar (2003)
Delphastus catalinae	7.4	80.1	12.6	217.7	19.2	43.4	13.4	258	Kutuk & Yigit (2007)
*Diomus austrinus**	12.4	65.4	13.9	156.9	14.4	55.4	14.3	266	Chong et al. (2005)
*Diomus austrinus**	12.9	64.9	13.0	135.7	14.8	51.5	13.9	240	Chong et al. (2005)
Harmonia axyridis	10.2	47.0	10.9	162.9	10.9	69.2	10.8	279	LaMana & Miller (1998)
Harmonia axyridis	10.7	42.8	10.6	157.4	10.8	72.9	10.4	232	Schanderl et al. (1985)
Hippodamia convergens	8.7	50.4	10.8	121.9	11.3	50.0	10.6	224	Katsarou et al. (2005)
Hippodamia convergens	—	—	—	—	—	—	13.6	230	Rodriguez-Saona & Miller (1999)

(*Continued*)

Table 3.3 (*Continued*)

	Egg		Larva		Pupa		Total		
	LDT	**SET**	**LDT**	**SET**	**LDT**	**SET**	**LDT**	**SET**	**Reference**
Lindorus lophanthae	—	—	—	—	12.8	56.2	13.5	242	Cividanes & Gutierrez (1996)
*Lindorus lophanthae**	8.7	114.0	8.0	240.4	8.3	90.0	8.2	444	Stathas (2000)
*Lindorus lophanthae**	7.9	132.9	8.0	262.4	8.0	100.7	8.3	419	Stathas et al. (2002)
Nephus bisignatus	12.1	103.1	8.2	269.7	10.6	102.5	9.3	512	Kontodimas et al. (2004)
Nephus bisignatus	—	—	—	—	—	—	9.3	513	Kontodimas et al. (2007)
Nephus includens	11.8	101.9	10.4	196.8	11.1	103.8	11.0	403	Kontodimas et al. (2004)
Nephus includens	—	—	—	—	—	—	10.9	408	Kontodimas et al. (2007)
Nephus reunioni	16.4	100	8.4	274	9.2	116.0	11.9	469	Izhevsky & Orlinsky (1988)
Olla v-nigrum	9.0	46.2	11.9	133.1	12.5	45.8	11.4	220	Kreiter (1985)
Parexochomus nigromaculatus	11.5	57.7	7.9	140.4	6.6	89.7	8.8	284	Atlıhan & Ozgokce (2002)
Propylea dissecta	1.2	58.7	4.2	176.2	3.2	65.4	3.6	299	Omkar & Pervez (2004)
Rodolia cardinalis	10.0	77.8	10.9	138.0	10.9	69.7	10.7	285	Grafton-Cardwell et al. (2005)
Sasajiscymnus tsugae	10.7	95.9	12.8	140.2	13.6	62.7	12.6	295	Cheah & McClure (1998)
Scymnus argentinicus	17.0	26.1	14.2	118.0	14.6	69.0	14.9	210	dos Santos (1992)
Scymnus levaillanti	11.8	64.6	8.2	142.5	10.7	88.8	10.0	296	Uygun & Atlıhan (2000)
Scymnus levaillanti	6.3	77.4	15.1	65.9	6.3	72.4	11.3	201	Allawi (2006)
Scymnus marinus	13.7	28.1	—	—	—	—	10.6	657	M'Hamed & Chemseddine (2001)
Scymnus sinuanodulus	—	—	8.1	260.5	1.4	231.7	—	—	Lu & Montgomery (2001)
Scymnus subvillosus	9.8	66.1	5.5	136.4	11.9	138.0	5.5	329	Atlıhan & Chi (2008)
Scymnus syriacus	16.0	41.1	7.9	119.1	7.9	102.4	11.5	236	Allawi (2006)
Stethorus japonicus‡	12.6	51.9	12.3	102.8	12.4	42.5	12.4	197	Mori et al. (2005)
Stethorus japonicus‡	12.8	50.4	12.4	99.9	12.4	42.3	12.5	193	Mori et al. (2005)
Stethorus pusillus	—	—	—	—	—	—	11.7	159	Raworth (2001)
Stethorus pusillus	11.5	61.5	11.4	102.5	11.0	52.1	11.4	215	Roy et al. (2002)

* different food type.

† different geographic populations.

‡ sex differences.

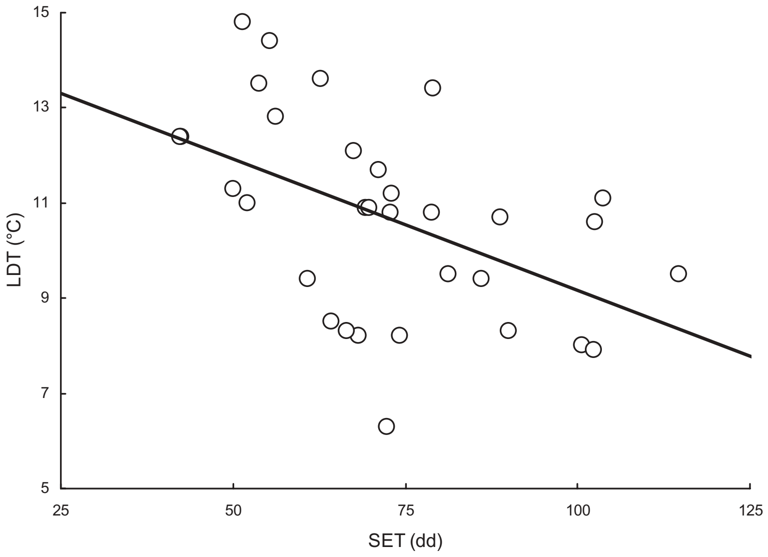

Figure 3.9 Lower development threshold LDT plotted against sum of effective temperatures SET in pupae of 32 species of coccinellid listed in Table 3.3 (data for three outlier species excluded). LDT = 14.7 – 0.0553 SET, $R^2 = 0.239$, $P < 0.005$.

3.6.3 Thermal window and development rate isomorphy

Two recent developments have provided rules that govern the temperature relationships of different species. A meta-analysis of data for many insect species has revealed that the span between the LDT and the optimum temperature for each individual species is about 20°C, regardless of whether the species are adapted to cold (i.e. have a low LDT) or warm conditions (Dixon et al. 2009). The existence of this **thermal window**, an intrinsic limit on thermal requirements, stresses the necessity of adaptation to the thermal conditions prevailing in the geographic area and in the ecological niche inhabited by the population. Another study (Jarosik et al. 2002) revealed that, in a population of any particular species, the LDT of the egg, larva and pupa is, in fact, identical and any experimentally established differences are probably caused by an observational bias. As a result, each developmental stage takes a constant proportion of the total development time and this proportion of development time does not change with temperature. This phenomenon was called **development rate isomorphy** and was tested with 426 populations belonging to 342 species of insects and mites. In a rigorous test, development rate isomorphy was demonstrated for 243 (57%) of the populations and any violation of this principle in the rest of the species was very small. The existence of the 'thermal window' and 'development rate isomorphy' was tested and demonstrated to be true for a number of coccinellid species (Jarosik et al. 2002).

3.6.4 Other events affected by temperature

The prevailing temperature during pre-adult development influences adult **body size** but its effect is difficult to separate from the effect of the rate of food consumption. Recent results from *Diomus austrinus* (Chong et al. 2005) and *Aphidecta obliterata* (Timms & Leather 2008) were ambiguous, since temperature affected the body weight of males and females in a different way in the two species.

Temperature further determines the course of events of adult life. The thermal requirements for completing **teneral development**, i.e. the time from moult to adult to the first oviposition, can also be approximated by a linear relationship between development rate and temperature, but of course only if dormancy does not take place. The average threshold temperature LDT calculated from data in Table 3.4 (without the outlier at

Table 3.4 Thermal constants, lower development threshold LDT (°C) and sum of effective temperatures SET (dd) for teneral pre-oviposition period. Calculated using a linear model of development rate vs. temperature relationship, and data of temperatures ≤30°C.

Species	LDT	SET	Reference
*Adalia bipunctata**	10.9	69.1	Jalali et al. (2009)
*Adalia bipunctata**	1.3	142.4	Jalali et al. (2009)
Axinoscymnus cardilobus	7.8	127.4	Huang et al. (2008)
Clitostethus oculatus	5.1	317.3	Ren et al. (2002)
Delphastus catalinae	10.9	93.0	Kutuk & Yigit (2007)
Nephus bisignatus	10.0	102.1	Kontodimas et al. (2004)
Nephus includens	10.7	86.5	Kontodimas et al. (2004)
Olla v-nigrum	13.5	138.8	Kreiter (1985)
Scymnus subvillosus	10.9	93.0	Atlıhan & Chi (2008)

* different food type.

1.3°C LDT) is 9.5°C, which is similar to the LDT for immature stages. The average sum of effective temperature SET for teneral development is 127 dd.

Further important effects of temperature concern **reproduction**. Temperature influences **longevity**, the number of eggs laid and the distribution of oviposition through adult life. The data for nine species (Fig. 3.8) reveal a uniform trend. Mean longevity decreases monotonically with increasing temperature (Fig. 3.8a) but the production of eggs peaks at around 25°C (Fig. 3.8b). Using the distribution of mortality and oviposition in time, it is possible to calculate the **innate capacity for increase**, which also depends on temperature, of a coccinellid population (for details see e.g. Andrewartha & Birch 1954).

Parameters of offspring production, **net reproduction rate** R_0 (Fig. 3.8C) and **intrinsic rate of population increase** r_m (Fig. 3.8d) are also temperature sensitive and peak between 25–30°C as in *P. japonica*, where the highest r_m of 0.113 occurred at 25°C (Chi & Yang 2003). In *Stethorus pusillus*, the r_m followed a typical asymmetrical dome-shape pattern, as temperature increased, with maximum values of 0.196 per day at 30°C (Roy et al. 2003). Nevertheless, there exist warm-adapted species like *Stethorus gilvifrons* (Mulsant) whose fecundity, R_0 and r_m peak at 35°C (Taghizadeh et al. 2008). While R_0 was highest (130) at 26°C and lower at both lower (22°C, 115) and higher temperatures (30°C, 82), r_m was greatest at the highest temperature in *Chil. nigritus* (Ponsonby 2009).

3.6.4.1 Tolerance to extreme temperatures

The **supercooling point** (SCP; Chapter 6) is naturally low for non-feeding stages, i.e. eggs and pupae, and high for larvae and adults. The mean SCP of *Har. axyridis* **eggs** was −27°C, and −21°C for **pupae**, while it was −14°C for larvae and −1.9°C for adults (Koch et al. 2004). The mean SCP of fresh eggs of *C. septempunctata* was −27°C and for older eggs it was −24.5°C, probably due to accumulation of metabolic water in the embryo (Nedvěd 1994). Wild-collected pupae of *C. septempunctata* in June and July had a SCP of −19°C. The mean SCP increased during larval development in *Cer. undecimnotata* (Nedvěd 1994): from −20°C in the second instar, through −16°C in the third , to −9°C in the fourth instar. In contrast, older and larger fourth instar larvae of *Exochomus quadripustulatus* had a lower SCP (−17°C) than smaller larvae of the same instar (−10°C) (Nedvěd 1994).

The **survival** of third and fourth instar larvae of *C. undecimpunctata* was higher than that of first and second instars when exposed to 6°C for a week. Larval survival declined sharply after 15 days. There was only 25% adult emergence from pupae chilled for 30 days. Adults survived the extended periods of **cold storage** better than the other developmental stages (Abdel-Salam & Abdel-Baky 2000).

Adults and second instar larvae of *Har. axyridis* were **heat stressed** at 35°C, and showed high mortality at 40°C, but these hot conditions were tolerated by all other stages (Acar et al. 2004). In our experiments with *Har. axyridis* (Fois & Nedvěd, unpublished), 100% **mortality** occurred in the egg and pupal stages at 35°C. The supercooling point (−17°C) and lower lethal temperature (−16.7°C) remained relatively constant for the overwintering populations in the outdoor hibernaculum. In contrast, the supercooling point and lower lethal temperature of the population overwintering indoors clearly increased as the winter progressed, from −18.5 to −13.2°C and −16.7 to −14.1°C, respectively (Berkvens et al. 2010).

The lower and upper thresholds for survival for 24 hours of *Delphastus catalinae* were around 0 and 40°C, respectively. Survival of their pupae was similar to that of adults (Simmons & Legaspi 2004). The first three instars of *Scymnus marinus* had an **optimum temperature** for development of 30°C; they also developed at 35°C but all died at 40°C. In contrast, the fourth instar larvae, prepupae and pupae of this species did develop at 40°C, although at a slower rate. The temperature optimum in these stages remained 30°C (M'Hamed & Chemseddine 2001).

In conclusion, coccinellids are average athletes in the wrestling match that Life has with Ambient Temperature. Within the range of performance of insects, coccinellids are no extremophiles; they do not live in particularly cold or warm conditions – or at least no such species have as yet been discovered.

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