*Entomologia Experimentalis et Applicata* **75**: 99–107, 1995.



# Variations in body length, weight, fat content and survival in *Coccinella septempunctata* at different hibernation sites

X. Zhou[1], A. Honek[2], W. Powell & N. Carter[3]
[1]*Farmland Ecology Group, Institute of Arable Crops Research, Rothamsted Experimental Station, Harpenden, Herts AL5 2JQ, UK*
[2]*Institute of Plant Protection, Drnovska 507, CS-161 06, Praha 6, Czech Republic*
[3]*Present address: The British Trust for Ornithology, The National Centre for Ornithology, The Nunnery, Thetford, IP24 2PU, UK*

Accepted: August 24, 1994

*Key words:* body size, weight, fat content, altitude, *Coccinella septempunctata*, winter mortality

## Abstract

Adults of *Coccinella septempunctata* L. (Coleoptera; Coccinellidae) were sampled in four overwintering sites: one in England and three at different altitudes in the Czech Republic (350–1420 m above sea level) in autumn 1992 and spring 1993. Body length, dry weight and fat weight were measured. There were significant differences in body length between sampling sites in spring 1993, but not in autumn 1992. The average sex ratio (♀:♂) in all samples was 1:0.60 in 1992 and 1:0.72 in 1993. Females were significantly larger and heavier, and contained more fat than males in both sampling periods. Dry weight and fat weight were positively correlated to body length at all sampling sites except at Ruzyne, in the Czech Republic. Adults hibernating at higher altitudes and away from their breeding and feeding habitats had significantly more fat than those hibernating at lower altitudes. Fat reserves were reduced by 30% during the hibernation at the top of the Krkonose mountain, in the Czech Republic, where temperatures were much lower, but more than half of the fat reserves were consumed during the overwintering period at the other sampling sites. The significance of body length and fat reserves in relation to adult hibernation sites and overwintering survival is discussed.

## Introduction

Body size and metabolic reserves are important factors affecting insect fitness attributes, such as reproductive rate, mating success and survival (Crespi, 1989; Hodek, 1973; Stewart *et al.*, 1991; Wickman & Karlsson, 1989). Most studies of intraspecific variation in body size in insects have concentrated on its effects on mating success (McCauley, 1979; Juliano, 1985; Crespi, 1989) and reproductive rate (Johnson, 1982; Stewart *et al.*, 1991; Honek, 1993). Results from these studies indicate that large males have a mating advantage over small males and large females have a higher fecundity or reproductive rate than small females. There is much less information on the effect of body size and energy reserves on overwintering survival in insect populations.

*Coccinella septempunctata* is a large coccinellid species with a world-wide distribution (Hodek, 1973). It is an important aphid-specific predator and can prevent aphid pests reaching outbreak levels in some years (Cooke, 1991). Adult *C. septempunctata* are able to fly long distances and often hibernate away from their foraging and breeding habitats (Hagen, 1962; Hodek, 1973; Zhou & Carter, 1992). Fat reserves accumulated in the body before hibernation influence hibernation success (Hodek, 1973). More than half of the fat reserve can be consumed during hibernation depending on temperature (El-Hariri, 1966). Also, adult *C. septempunctata* hibernating at higher altitudes on mountains are larger on average than those hibernating at lower altitudes (Honek, 1989).

This study investigates the effects of geographic location and altitude on body size and fat reserves of overwintering adults and their relationship to the adult overwintering survival.

## Materials and methods

Several hundred adult *C. septempunctata* were collected at each of four hibernation sites: 1) NN; a coniferous forest, at Norwich, England (50 metres above sea level) sampled in the autumn (29 September 1992) and the following spring (15 April 1993), 2) RU; forest margins at Ruzyne (350 altitude m) sampled on the soil surface and vegetation on 12 September 1992, and in leaf litter on 15 April 1993, 3) RN; grass tussocks on hills at Rana (400 altitude m) sampled on 10 September 1992 and 11 April 1993, and 4) MT; under or between rocks on the top of the Krkonose mountain (1420 altitude m) sampled 15 September 1992 and 8 May 1993 (Sites 2–4 were in the Czech Republic). These adults were kept at a low temperature (*c.* 10 °C) and were transported to Rothamsted Experimental Station by air (the Czech samples) or by post (Norwich samples) within 10 days of collection. To study the effects of feeding and starvation on fat content and overwintering survival, a proportion (*c.* 300) of the adults from Norwich were put in each of two cages, each containing two pots of bean plants (*Vicia faba* L.), in an insectary at a constant temperature of 23 °C for 10 days. The ladybirds in one cage were supplied with an excess of aphids (*Acyrthosiphon pisum* (Harris)) as food (NF) whilst those in the other cage were starved (NS).

Fifty adults from each site, NF and NS had been randomly chosen for release in an overwintering site. Then, fifty adults were taken randomly from the samples from these sites, plus the remaining 38 and 40 alive adults in the NF and NS treatments respectively for measuring water, dry and fat weights. The adults were sexed and body length of each adult (from mesosternum to the last abdominal segment) was measured using a stereo-microscope with an ocular micrometer. Individual fresh weights were measured using a Sartorius microgram balance (0.00000 g) and then the adults were stored individually in labelled glass tubes, and oven-dried (55 °C) for five days and weighed again. Fat content was estimated by rinsing each adult in petroleum ether to remove fats once every day for five days at laboratory temperatures, oven-drying at 55 °C again for five days and reweighing (Mills, 1981). These adults selected for release were sexed and their body length was measured. Then, they were individually confined in small net cages which were labelled and placed in a natural coccinellid hibernation site in leaf litter at the south side of a woodland on the Rothamsted estate on 9 October 1992. These adults were examined on 15 January and 11 April 1993 and the numbers of living and dead individuals were recorded.

To remove the effects of body size on the water and fat contents, water weight per unit of dry body weight (water unit weight) and fat weight per unit of dry body weight after fat extraction (fat unit weight) were calculated:

$$Water\ unit\ weight\ (y_1) = \frac{fresh\ weight - dry\ weight}{dry\ weight}$$

$$Fat\ weight\ (y_2) = dry\ weight - dry\ weight\ after\ fat\ extraction$$

$$Fat\ unit\ weight\ (y_3) = \frac{y_2}{dry\ weight\ after\ fat\ extraction}$$

We believe that the water unit weight is a more direct measure of water content in the adults and statistical analyses can be done without the need of data transformation compared with percentage of water weight (Sokal & Rohlf, 1981).

Analysis of variance on the effects of sex, location and sample date on these parameters was done using the Genstat program (Genstat 5 Committee, 1987). To linearize the relationship between body length and weight, data on body length were transformed on a $\log_{10}$ scale. As there was no significant difference in the linear relationship between body length and dry weight after fat extraction, between the sexes or locations, data from all sites and sexes were pooled to obtain the regression parameters between body length and the dry weight. The relationships between body length and fat unit weight were analyzed and compared between locations and sampling dates.

To study distributions of coccinellid adults with different body sizes at sampling sites, the body length of the adults was divided into seven classes, which presented the best possible contrast in body size distribution between sampling sites (Fig. 1). The relationship between adult overwintering survival and body size was also studied using data from those hibernating adults of only MT, RU and NN, which were released in the overwintering site, as the diapause of the adults from the other two treatments: NS and NF might be affected by laboratory rearing. Because the number of adults of small and large size was small, the body length was divided into four classes so that similar numbers of adults in each of these size classes were obtained (Fig. 2).

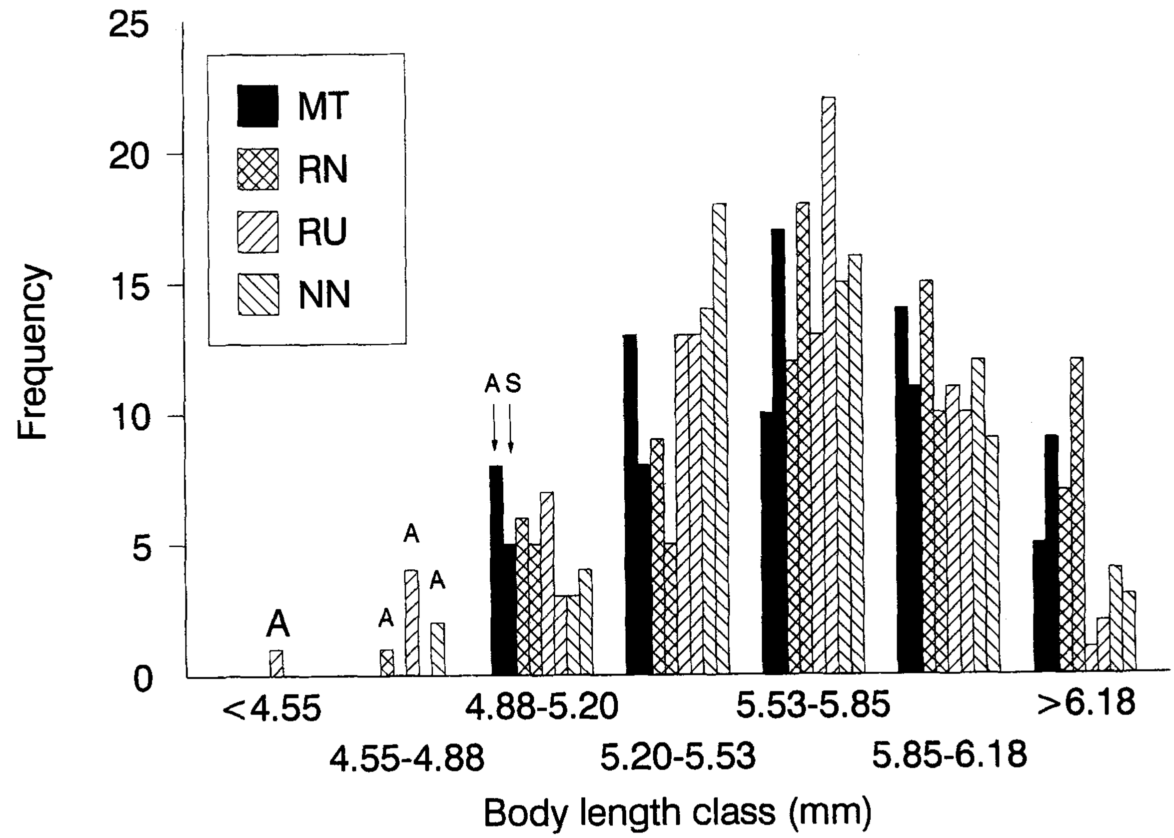


*Fig. 1.* Body size frequency distribution of *Coccinella septempunctata* adults sampled at MT, RN, RU and NN in autumn 1992 (A) and spring 1993 (S) (where MT is the Krkonose mountain, RN Rana and RU Ruzyne in the Czech republic, and NN Norwich, England).

**Results**

The average sex ratio (♀:♂) in samples from the four hibernation sites was 1:0.60 in adults sampled in autumn 1992 and 1:0.72 in spring 1993 (Tables 1, 2). More adults sampled at MT, RN and NN were female than at RU in 1992 while those sampled at MT, RN and RU had a higher proportion of females than those at NN, in 1993 (Tables 1, 2). In the analyses of variance of the measurement parameters (body length, water unit weight, fat unit weight and fat weight), there were no significant interactions between factors (sex, sampling site and sampling date) on these parameters. Therefore, only direct effects of these individual factors on the respective parameters are presented.

*Body length.* Female adults were significantly longer ($P<0.001$) on average than males (Tables 1, 2) in autumn 1992 ($F_{1/192}=231.02$) and in spring 1993 ($F_{1/266}=235.56$). There were no significant differences in mean body length between different locations in autumn 1992 ($F_{5/266}=1.87$) but adults were significantly larger ($P<0.01$) at MT and RN than at RU and NN in spring 1993 ($F_{3/192}=4.96$). Mean body length of adults sampled in autumn 1992 was significantly smaller ($P<0.05$) than that of adults sampled in spring 1993 at MT ($F_{1/96}=4.61$), and RN ($F_{1/96}=3.78$), but not at RU and NN (Tables 1, 2). There were more smaller adults (<4.88 mm) at RU than at the other sites but such small adults were not present at MT in autumn 1992 or in spring 1993 (Fig. 1). After overwintering, such small adults were not present at any of the sites (Fig. 1).

*Water unit weight.* There were no significant differences in mean water unit weight between males and females sampled (Tables 1, 2) either in autumn 1992 ($F_{1/266}=0.01$) or in spring 1993 ($F_{1/192}=1.04$), at three of the sites, MT ($F_{1/96}=0.09$), RU ($F_{1/96}=2.51$) and NN ($F_{1/96}=0.93$). However, at the fourth site RN, the mean water unit weight of males was significantly greater ($P<0.05$) than that of females ($F_{1/96}=5.34$).

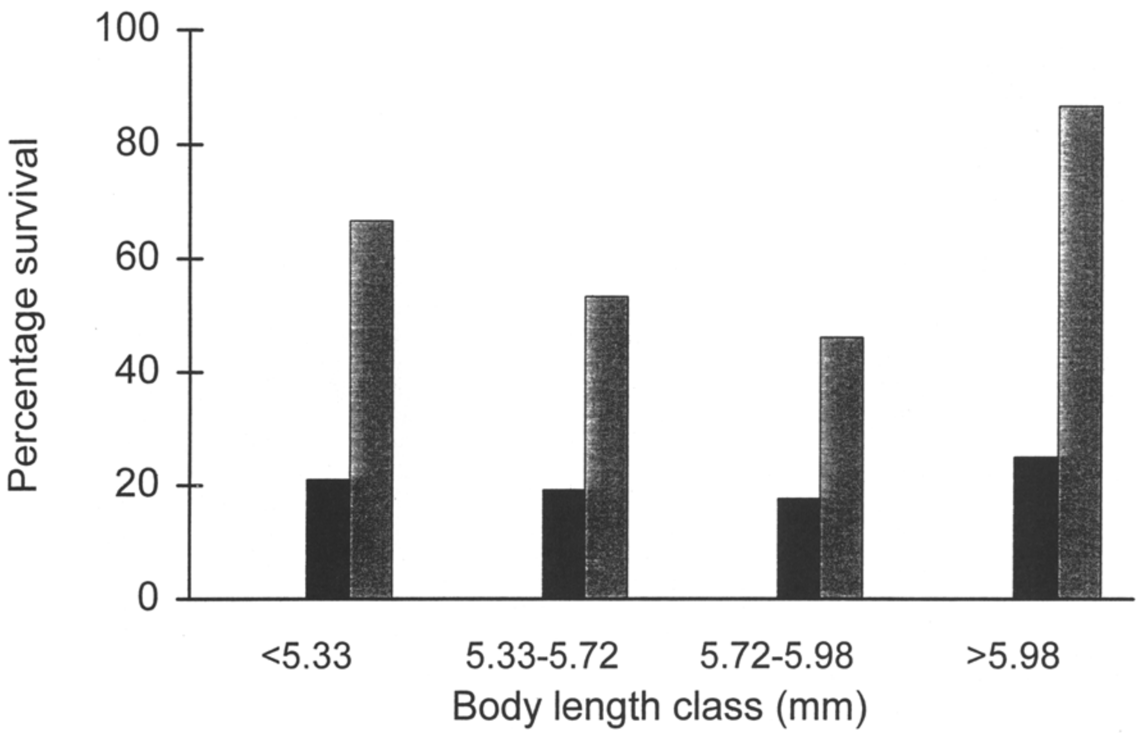


*Fig. 2.* Percentage of adults survived during hibernation for each body size class of the adults released at an overwintering site and inspected at mid January (filled bar) and mid April (shaded bar) in 1993.

*Table 1.* Measurements of mean body length, water unit weight, fat unit weight and fat weight of female and male *Coccinella septempunctata* adults at different hibernation sites (MT, Krkonose mountain: RN, Rana; RU*; Ruzyne in the Czech Republic; NN, Norfolk, England) (± variance) in autumn 1992 (observations on 50 adults per site)

| | | Body length (cm) | | | Water unit weight (g/g) | | |
|---|---|---|---|---|---|---|---|
| Location | ♀:♂ | ♀ | ♂ | Means | ♀ | ♂ | Means |
| MT | 1:0.52 | 0.589±0.0013 | 0.532±0.0006 | 0.569±0.0018 | 1.111±0.1035 | 1.115±0.0523 | 1.112±0.0847 |
| RN | 1:0.52 | 0.596±0.0008 | 0.534±0.0006 | 0.575±0.0016 | 1.105±0.0911 | 1.144±0.0269 | 1.118±0.0687 |
| RU | 1:0.79 | 0.576±0.0015 | 0.527±0.0008 | 0.555±0.0018 | 1.471±0.2502 | 1.325±0.1006 | 1.407±0.1863 |
| NN | 1:0.61 | 0.590±0.0007 | 0.534±0.0005 | 0.569±0.0014 | 1.102±0.0379 | 1.108±0.0310 | 1.104±0.0346 |
| means | 1:0.60 | 0.587 | 0.531 | 0.567 | 1.197 | 1.173 | 1.185 |

| | Fat weigh/unit dry weight (g/g) | | | Fat weight (mg) | | |
|---|---|---|---|---|---|---|
| Location | ♀ | ♂ | Means | ♀ | ♂ | Means |
| MT | 0.705±0.0823 | 0.601±0.0399 | 0.670±0.0693 | 9.351±22.650 | 6.639±5.694 | 8.429±18.335 |
| RN | 0.672±0.0454 | 0.596±0.0218 | 0.646±0.0381 | 8.933±9.796 | 6.912±4.970 | 8.246±8.956 |
| RU | 0.3132±0.0681 | 0.322±0.0382 | 0.317±0.0539 | 3.648±11.718 | 3.590±5.780 | 3.623±8.935 |
| NN | 0.602±0.0342 | 0.518±0.0147 | 0.570±0.0281 | 7.067±5.227 | 5.244±1.883 | 6.374±4.691 |
| means | 0.573 | 0.509 | 0.551 | 7.250 | 5.596 | 6.688 |

* Samples from RU contained some pre-diapause adults, which might not accummulate full fat reserve before hibernation

*Table 2.* Measurements of body length, water unit weight, fat unit weight and fat weight of female and male *Coccinella septempunctata* adults at different hibernation sites (MT, Krkonose mountain: RN, Rana; RU, Ruzyne in the Czech Republic; NN, Norfolk, England) (± variance) in spring 1993 (observations on 50 adults per site)

| | | Body length (cm) | | | Water unit weight (g/g) | | |
|---|---|---|---|---|---|---|---|
| Location | ♀ : ♂ | ♀ | ♂ | Means | ♀ | ♂ | Means |
| MT | 1:0.72 | 0.603±0.0008 | 0.543±0.0006 | 0.578±0.0016 | 1.263±0.0496 | 1.264±0.0263 | 1.263±0.0391 |
| RN | 1:0.67 | 0.606±0.0008 | 0.545±0.0006 | 0.582±0.0016 | 1.248±0.1009 | 1.469±0.1452 | 1.336±0.1280 |
| RU | 1:0.61 | 0.585±0.0005 | 0.540±0.0003 | 0.568±0.0009 | 1.376±0.1073 | 1.278±0.0427 | 1.339±0.0837 |
| NN | 1:0.92 | 0.585±0.0007 | 0.540±0.0003 | 0.563±0.0010 | 1.475±0.0466 | 1.475±0.0556 | 1.475±0.0499 |
| means | 1:0.72 | 0.595 | 0.542 | 0.573 | 1.337 | 1.3761.353 | |

| | Fat weigh/unit dry weight (g/g) | | | Fat weight (mg) | | |
|---|---|---|---|---|---|---|
| Location | ♀ | ♂ | Means | ♀ | ♂ | Means |
| MT | 0.540±0.0330 | 0.472±0.0157 | 0.512±0.0264 | 6.607±6.789 | 4.878±2.733 | 5.881±5.738 |
| RN | 0.404±0.0366 | 0.282±0.0291 | 0.356±0.0366 | 4.930±6.687 | 2.874±3.222 | 4.107±6.242 |
| RU | 0.368±0.0340 | 0.343±0.0134 | 0.359±0.0259 | 4.194±5.136 | 3.548±1.651 | 3.949±3.851 |
| NN | 0.366±0.0117 | 0.341±0.0069 | 0.354±0.0094 | 4.135±1.879 | 3.415±1.022 | 3.789±1.570 |
| means | 0.420 | 0.360 | 0.395 | 4.975 | 3.682 | 4.432 |

*Table 3.* Measurements of body length, water unit weight, fat unit weight and fat weight of female and male *Coccinella septempunctata* adults fed (NF) and starved (NS) in laboratory but originating from Norfolk, England (± variance) in autumn 1992 (observations on 50 adults per site)

| | | Body length (cm) | | | Water unit weight (g/g) | | |
|---|---|---|---|---|---|---|---|
| Location | ♀ : ♂ | ♀ | ♂ | Means | ♀ | ♂ | Means |
| Fed | 1:3.75 | 0.598±0.0006 | 0.537±0.0005 | 0.550±0.0012 | 1.291±0.0215 | 1.186±0.0187 | 1.209±0.0206 |
| Starved | 1:0.74 | 0.579±0.0012 | 0.534±0.0006 | 0.560±0.0014 | 1.275±0.1033 | 1.326±0.1020 | 1.297±0.1008 |

| | Fat weigh/unit dry weight (g/g) | | | Fat weight (mg) | | |
|---|---|---|---|---|---|---|
| Location | ♀ | ♂ | Means | ♀ | ♂ | Means |
| Fed | 0.568±0.0200 | 0.633±0.0143 | 0.620±0.0157 | 7.527±4.283 | 7.510±3.099 | 7.514±3.239 |
| Starved | 0.443±0.0314 | 0.381±0.0230 | 0.417±0.0281 | 5.436±6.776 | 4.099±3.141 | 4.868±5.559 |

*Table 4.* Survival of overwintering female (♀) and male (♂) *Coccinella septempunctata* adults collected from MT, Krkonose mountain: RU, Ruzyne in Czech Republic; NN, Norwich, England; NF, Norwich (fed with aphids) and NS, Norwich (starved), and released in a hibernation site on Rothamsted estate, south England in autumn 1992 [data in square brackets are percentages of surviving adults]

| | Time of inspection | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Origin | Autumn(9/10/92) | | | Winter(15/1/93) | | | Spring(11/4/93) | | |
| | ♀ | ♂ | Total | ♀ | ♂ | Total | ♀ | ♂ | Total |
| MT | 36 | 14 | 50 | 26[72.2] | 12[85.7] | 38[76] | 12[33.3] | 4[28.6] | 16[32] |
| RU | 29 | 21 | 50 | 16[55.2] | 8[38.1] | 24[48] | 4[13.8] | 6[28.6] | 10[20] |
| NN | 32 | 18 | 50 | 22[68.8] | 10[55.6] | 32[64] | 2[6.3] | 2[11.1] | 4[8] |
| NF | 28 | 22 | 50 | 16[57.1] | 14[63.6] | 30[60] | 2[7.1] | 6[27.3] | 8[16] |
| NS | 30 | 20 | 50 | 12[40.0] | 16[80.0] | 28[56] | 2[6.7] | 2[10] | 4[8] |
| Total | 15 | 95 | 250 | 92[59.4] | 60[63.2] | 152[61] | 22[14.2] | 20[21.1] | 42[17] |

The mean water unit weight of both females and males was greater in autumn samples from RU than in autumn samples from MT, RN and NN ($F_{5/266} = 8.74$, $P<0.01$), while in the spring sample, 1993, it was the greatest for the adults from NN, but smallest for those from MT ($F_{1/192} = 5.20$, $P<0.05$). Mean water unit weight was also greater for adults sampled in spring 1993 than in autumn 1992 at MT, RN and NN, but not at RU (Tables 1, 2). The mean water unit weight was larger in adults from the NF and NS cages than those from MT, RN and NN in autumn 1992 (Tables 1, 3).

*Fat unit weight.* Overall, mean fat unit weight was significantly greater ($P<0.05$) in female than male adults in both autumn 1992 and spring 1993 (Tables 1, 2). Only at RU were there no significant differences in the fat unit weight of males and females. The mean fat unit weight was similar from the adults sampled from MT, RN and NN ($F_{2,147} = 3.02$) in autumn 1992. In spring 1993, the adults from MT had a higher mean fat unit weight than those from the other sites (Tables 1, 2). The mean fat unit weight was significantly less ($P<0.001$) for adults collected in spring 1993 than for those collected in autumn 1992 at MT ($F_{1/96} = 12.08$), RN ($F_{1/96} = 56.67$) and NN ($F_{1/96} = 60.27$). Feeding, or starving the adults significantly ($P<0.001$) increased or decreased their fat unit weight respectively (Table 3).

*Fat weight.* Females contained significantly more ($P< 0.001$) fat than males in both autumn 1992 ($F_{1/266} = 15.26$) and spring 1993 ($F_{1/192} = 20.72$). In both autumn and spring samples, sampling sites significantly affected the fat content ($F_{5,266} = 22.20$, $P<0.001$ in 1992 and $F_{3/192} = 12.00$, $P<0.01$ in 1993). The adults from MT and RN had greater fat content than those from NN in autumn 1992 (Tables 1, 2). In spring 1993, the fat weight was similar in the adults from RN, RU and NN, but was significantly greater at MT (Tables 1, 2). Feeding with aphids or starvation also significantly ($P<0.01$) increased or decreased the fat weight in the adults respectively (Table 3). The adults sampled in spring 1993 contained significantly less fat than those sampled in autumn 1992 at MT, RN, and NN (Tables 1, 2). The percentage of fat depletion during hibernation was similar between females and males from MT and NN, but about 15% greater in males than females from RN. The greatest percentage depletion of fat after hibernation occurred at RN (50.2%), then at NN (40.6%) and the least at MT (30.2%).

*Overwintering survival.* Less than half of the adults introduced into hibernation sites were dead by mid January 1993, but by mid April, when coccinellids would normally come out of hibernation, very few of these adults were still alive (Table 4). However, more adults originating from MT and RU survived than those from NN (Table 4). There were no significant differences in the overall survival rate between females and males in mid January ($F_{1,8} = 0.13$) or in mid April 1993 ($F_{1,8} = 1.3$), but there were considerable differences in the survival of females and males in groups originating from different collection sites (Table 4). Although the survival rate varied from 46% to 87% between different size classes at mid January, it became similar after hibernation by mid April (Fig. 2).

*Relationship between body length and weight measurements.* Dry weight of adults after fat extraction was positively correlated with body length (Fig. 3). The fat unit weight in adults also increased significantly with body length at MT and RN, but not at NN and RU in both 1992 and 1993 (Fig. 4).

## Discussion

Body length of adult *C. septempunctata* varies geographically, it is largest in the Far East and smallest in the Middle East (Dobzhansky & Sivertzev-Dobzhansky, 1927). In Czechoslovakia, Honek (1989) found that the hind width of the scutum of adult *C. septempunctata* ranged from 2.75 to 4.25 mm and larger adults were collected as altitude increased. In this study, adults of *C. septempunctata* in Britain and the Czech Republic were of similar length. This may be because in a warm year, favourable weather conditions in late July and August, such as occurred in 1992, may enable small adults to fly long distances to hibernate at higher altitudes (Roff, 1990), and adults could then breed and hibernate there. In cold years, large hibernating adults at high altitudes may be migrant adults from breeding habitats far away as large individuals are able to fly longer distances (Honek, 1989). The significantly greater proportion of large adults found in samples collected after overwintering at MT and RN suggests that smaller adults are more likely to die during the overwintering period at these higher altitude sites.

The significantly greater water content in autumn 1992 in adults from RU, compared with those from the other sites, may be due to differences in the progress of their diapause states. Adults from RU were collected

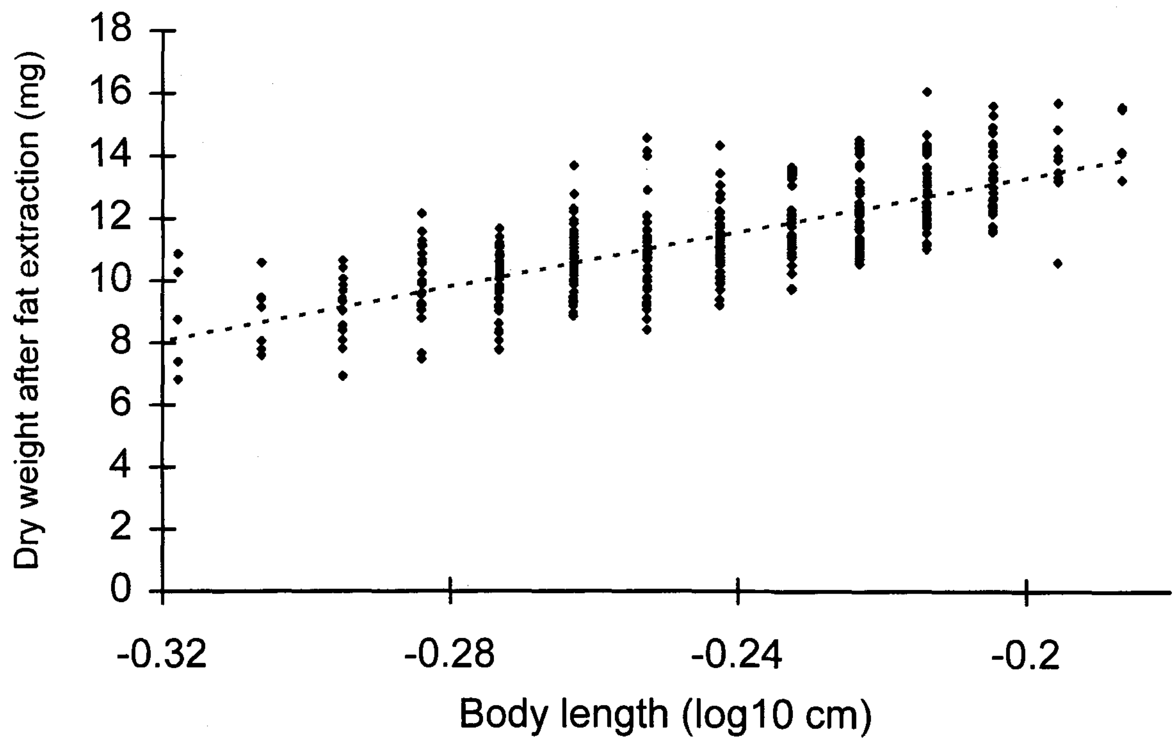


*Fig. 3.* Relationship between $\log_{10}$ (body length, cm) (X) and dry weight after fat extraction (mg) (Y) on data combined from the four sampling sites (the Krkonose mountain, Rana and Ruzyne in the Czech republic, and Norwich, England) in autumn and spring; Y = 22.11 (±0.471) + 43.9 (±1.90) X, $F_{1/398} = 531.59$.

on vegetation and may not have been in a diapause state in contrast to those collected from the high altitude sites (MT and RN). Water unit weight generally increased after overwintering, which is similar to data recorded for *Adalia bipunctata* (L.) (Mills, 1981). Other studies found that adult water content showed only small fluctuations during the overwintering period, but increased after emergence from hibernation sites in the spring in *C. septempunctata*, *A. bipunctata*, *Propylea quatuordecimpunctata* (L) (El-Hariri, 1966), and *Semiadalia undecimnotata* Schneid. (Hodek & Cerkasov, 1963). Adults were able to maintain their water level by drinking and/or by oxidation of metabolic reserves (El-Hariri, 1966). Therefore, fresh weight measurements of coccinellid adults cannot be used as an indicator of their fat levels (Mills, 1981).

Intraspecific body size variation is largely non-genetically determined (Alcock, 1984; Johnson, 1982, 1983), being primarily influenced by food intake and temperature during the immature stages (Juliano, 1985). Lepidopteran insects also accumulate the nutrients and energy reserves used for reproduction mainly during larval stages (Boggs, 1981) while these reserves in coccinellids have to be accumulated during the adult stage (Hodek, 1973). The amount and quality of the reserves in the adult body significantly affect survival during the winter and fecundity in the breeding season (Hodek, 1973; Stewart *et al.*, 1991). This study indicates that adults, hibernating far away from their feeding and breeding sites, accumulated the largest fat reserves. The adults hibernating at the lower altitude sites in the Czech Republic and England lost 50% of their fat reserves which is similar to that reported before (Hodek & Cerkasov, 1963; El-Hariri, 1966; Mills, 1981), while those hibernating at the high altitude site in the Czech Republic (MT) lost only 30% of their fat during the same period. This indicates that adults hibernating at high altitudes, where the temperature is low, may be able to conserve more fat during the hibernation period. Therefore, they are more likely to survive the period between emergence from the overwintering sites and finding the first aphid colonies (Mills, 1981) and to have a reproductive advantage in the spring (Stewart *et al.*, 1991). The similar survival rate between different body size classes in adults, released in an overwintering site, indicates that the

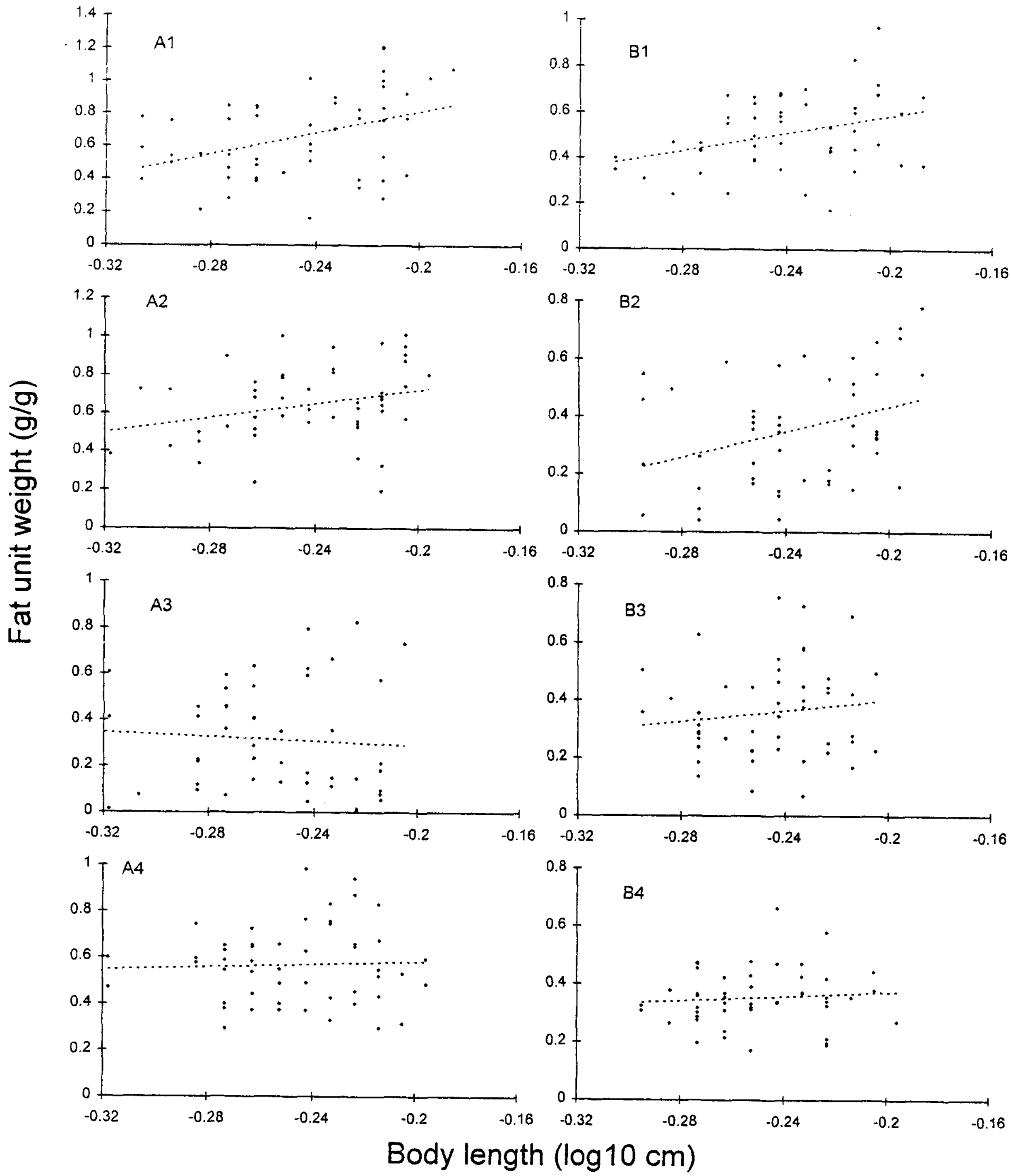


*Fig. 4.* Relationship between $\log_{10}$ (body size (X, cm)) and fat unit weight (g/g, Y)) of adult *Coccinella septempunctata* at MT (1), RN (2), RU (3) and NN (4) in autumn 1992 (A) and spring 1993 (B): (A1) Y = 1.485 (±0.265) + 3.32 (±1.07)X, $F_{1/48} = 9.6$; (B1) Y = 0.979 (±0.175) + 1.95 (±0.725)X, $F_{1/48} = 7.24$; (A2) Y = 1.088 (±0.215) + 1.829 (±0.0.882)X, $F_{1/48} = 4.30$; (B2) Y = 0.882 (±0.203) + 2.225 (±0.852)X, $F_{1/48} = 6.83$; (A3) Y = 0.192 (±0.0.248)–0.486 (±0.994)X, $F_{1/48} = 0.24$; (B3) Y = 0588 (±0.241) + 0.93 (±0.974)X, $F_{1/48} = 0.91$; (A4) Y = 0.642 (±0.208) + 0.294 (±0.838)X, $F_{1/48} = 0.12$; (B4) Y = 0.447 (±0.145) + 0.37 (±0.576)X, $F_{1/48} = 0.41$.

amount of fat reserve in the hibernating adults at the beginning of hibernation is more important than body sizes in adult survival at low altitudes where larger amount of fat reserve is depleted after hibernation.

There was no difference in average fat reserves before and after overwintering at the low altitude site (RU) in the Czech Republic (Table 1). This could be explained by the fact that the adults were collected in the autumn from the soil surface and vegetation at that site. The adults hibernating there may have consisted of a mixture of individuals which had accumulated maximum fat reserves and individuals which bred late in the season and so had very little fat and were not yet prepared to hibernate. This is indicated by the larger variance of fat unit weight recorded in the sample at this site (Fig. 4 and Table 1). Also, some adults with sufficient fat reserves may have already hidden in the leaf litter and might have escaped sampling, whereas all adults were sampled only from the leaf litter in spring 1993. Thus, the increase rather than decrease in mean fat reserves after overwintering at RU may have been affected by a higher mortality of those adults with low fat reserves and by sampling outside hibernation sites in autumn.

There have been very few studies of the direct effects of fat reserves on coccinellid adult overwintering survival. The overall mortality recorded in this study at the midhibernation period (mid-January) was similar to that recorded for coccinellids hibernating in an artificial hibernacula (El-Hariri, 1966). However, it was much greater at the end of hibernation than that recorded in the latter study. Similar levels of mortality were estimated in a separate study (Zhou *et al.*, 1994). This study also indicated that adults with greater fat reserves had higher survival rates such as those from MT (Tables 1, 4). Mills (1981) recorded 36% overwintering mortality for *A. bipunctata*, but the primary cause of the mortality was the fungal pathogen *Beauveria bassiana* (Bals.). This was independent of the depletion of the fat reserves even though there was 65% fat depletion after hibernation.

## Acknowledgments

The work was supported by the NERC through the Joint Environmental and Agricultural Programme. Thanks are due to S. Clark and J. Perry for help in statistics and using the Genstat programme and Dr. M. Majerus of Cambridge University for collecting those adults from Norwich, England.

## References

Alcock, J., 1984. Long term maintenance of size variation in two populations of *Centris pallida* (Hymenoptera: Anthophoridae). Evolution 38: 220–223.

Boggs, C. L., 1981. Nutritional and life history determinants of resource allocation in holometabolous. American Naturalist 117: 692–709.

Cooke, D. A., 1991. Growth of the UK sugar-beet crop in 1990. AFRC Institute of Arable Crops Research Report for 1990 pp 81–82.

Crespi, B. J., 1989. Variable selection and size-related mating patterns in natural populations of *Elaphrothrips tuberculatus*: a path analysis. American Naturalist 122: 142–150.

Dobzhansky, T. & N. P. Sivertzev-Dobzhansky, 1927. Die geographische Variabilität von *Coccillella septempunctata*. Biologisches Zentralblatt 47: 556–569.

El-Hariri, G., 1966. Studies of the physiology of hibernating Coccinellidae (Coleoptera): changes in the metabolic reserves and gonads. Proceedings of the Royal Entomological Society, London 41: 133–144.

Genstat 5 Committee, 1987. Genstat 5 Reference Manual. Oxford University Press, New York.

Hagen, K. S., 1962. Biology and ecology of predaceous Coccinellidae. Annual Review of Entomology 7: 289–326.

Hodek, I., 1973. Biology of Coccinellidae. Dr W. Junk N.V., The Hague, Academy of Sciences, Prague, Czechoslovakia, 260 pp.

Hodek, I. & J. Cerkasov, 1963. Imaginal dormancy in *Semiadalia undecimnotata* Schneid. (Coccinellidae, Col.). II. Changes in water, fat and glygogen content. Acta Societatis Zoologicae Bohemoslovenicae 60: 298–318.

Honek, A., 1989. Overwintering and annual changes of abundance of *Coccinella septempunctata* in Czechoslovakia (Coleoptera, Coccinellidae). Acta Entomologica Bohemoslovaca 86: 179–192.

Honek, A., 1993. Intraspecific variation in body size and fecundity in insects: a general relationship Oikos 66: 483–492.

Johnson, L. K., 1982. Sexual selection in a tropical brentid weevil. Evolution 36: 251–262.

Johnson, L. K., 1983. Reproductive behavior of *Claeoderes bivittata* (Coleoptera Brentidae). Psyche 90: 135–149.

Juliano, S. A., 1985. The effects of body size on mating and reproduction in *Brachinus lateralis* (Coleoptera: Carabidae). Ecological Entomology 10: 271–280.

McCauley, D. E., 1979. Geographic variation in body size and its relation to the mating structure of *Tetraopes* populations. Heredity 42: 143–148.

Mills, N. J., 1981. The mortality and fat content of *Adalia bipunctata* during hibernation. Entomologia Experimentalis et Applicata 30: 265–268.

Roff, D. A., 1990. The evaluation of flightlessness in insects. Ecological Monograph 60: 389–421.

Sokal, R. R. & F. J. Rohlf, 1981. Biometry. W. H. Freeman and Company, San Francisco.

Stewart, L. A., J. L. Hemptinne & A. F. G. Dixon, 1991. Reproductive tactics of ladybird beetles: relationships between egg size, ovariole number and developmental time. Functional Ecology 5: 380–385.

Wickman, P. O. & B. Karlsson, 1989. Abdomen, body size and reproductive effort of insects. Oikos 56: 209–214.

Zhou, X. & N. Carter, 1992. Ecology of coccinellids on farmland. Aspects of Applied Biology 31: 133–138.

Zhou, X., N. Carter & W. Powell, 1994. Seasonal distribution and aerial movement of adult coccinellids on farmland. Biocontrol Science and Technology 4: 167–179.