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ORIGINAL RESEARCH PAPER

Seasonal fluctuations in offspring body size in the wolf spider, *Pardosa astrigera* (Araneae: Lycosidae)

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Abstract Seasonal fluctuations in body sizes of mother spiders, spiderlings, and clutch size in the wolf spider, *Pardosa astrigera* (L. Koch) (Araneae: Lycosidae), were investigated. Cephalothorax and abdomen widths were measured in females with egg sacs collected in Tsu, Mie Prefecture, from May 2009 to October 2013. Spiderlings that emerged from the egg sacs were counted and those widths measured. In addition, abdomen–cephalothorax size ratio, which could be correlated with seasonal adaptation of spiderlings, was calculated. Means for cephalothorax size of mothers and offspring tended to decrease from March to October. Mean cephalothorax and abdomen sizes of the spiderlings in March, April, May, and October were significantly larger than in July and August. Abdomen–cephalothorax size ratios in March, April, May, and June were significantly larger than in July and August. Environmental temperature in Tsu increases steadily from March to August and drops toward October. Significant negative correlations were detected between temperature and cephalothorax and abdomen widths of spiderlings. These results suggest that body size and abdomen–cephalothorax size ratio of spiderlings change seasonally, and environmental temperature would affect body size. Furthermore, considering that body size would put a limit on the available prey, food conditions could also be an influence.

Keywords *Pardosa astrigera* · Spiderling · Cephalothorax · Abdomen · Seasonal fluctuation · Body size

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Introduction

The relationship between offspring size and fitness in insects has been studied for many years. For example, in butterflies, larvae from larger eggs have higher fitness due to the bigger mandible in butterflies in the genus *Mycales* (Braby 1994); offspring from larger eggs develop faster and grow into larger adults in the seed beetle, *Callosobruchus maculatus* (Fabricius) (Coleoptera: Chrysomelidae) (Fox 1994). In spiders, benefits of the large body size in spiderlings have been reported: larger offspring of *Hogna helluo* (Simon) (Araneae: Lycosidae) (Walker et al. 2003) and *Pardosa pseudoannulata* (Boes. et Str.) (Araneae: Lycosidae) (Iida 2005) have greater hunting ability and greater starvation tolerance. Accordingly, mother spiders would attain higher fitness if they could produce larger and more spiderlings. However, since there is a tradeoff between number of offspring and their body size for a fixed amount of resources invested into offspring (Edgar 1971; Simpson 1995), mothers would need to have good balance between offspring size and number.

Adult females of *Pardosa astrigera* (L. Koch) (Araneae: Lycosidae) with an egg sac can be found successively from March to November in Mie Prefecture, Japan (Iida et al. 2012). During this period, abiotic and biotic conditions such as temperature, prey species, and prey density for young spiders would change seasonally; that is, since spiderlings would be exposed to various environmental conditions, body size of spiderlings could also change seasonally. Producing as many offspring as possible of sufficient size to adapt to their circumstances would make it extremely important for mothers to increase their own fitness under constraint of the trade-off.

In this study, we investigated the seasonal changes in body sizes of mother *P. astrigera* spiders and their offspring, as well as the number of offspring produced at one time. We measured cephalothorax width for mothers and cephalothorax and abdomen widths for spiderlings as indices of body size. Since cephalothorax and abdomen width could strongly influence their hunting ability and starvation tolerance, respectively (Iida 2005), appropriate allocation of resources between cephalothorax and abdomen would have great importance for the fitness of mother spiders. Hence, seasonal changes in abdomen-to-cephalothorax size ratio was also investigated. Using this method, we determined whether mother spiders produce a fixed number and size of offspring throughout their breeding season or adopt a reproductive strategy to produce offspring by adapting to the season.

Materials and methods

P. astrigera

Pardosa astrigera is a wandering spider inhabiting a range of environments from plains to mountainous regions and is one of the most common spiders in Japan (Chikuni 1989). *P. astrigera* was selected as one of the indicators of functional biodiversity in cabbage fields in Kinki district (Agriculture, Forestry and Fisheries Research Council, National Institute for Agro-Environmental Sciences and National Institute of Agrobiological Sciences 2012). An adult female lays eggs as a mass containing approximately 35–80 eggs (Iida et al. 2012) and makes an egg sac by wrapping the mass with her silk. Thereafter, she attaches the egg sac to her spinneret, which is positioned at the rear end of her abdomen, until the spiderlings simultaneously emerge from the egg sac. The emerged spiderlings climb their mother's abdomen, where they remain as a group. Several days later, young spiders gradually disperse from their mother.

Spider collection

Spiders carrying egg sacs were collected once a week from a field at an organic farm in Tsu, Mie Prefecture, Japan (~34.38°N, 136.24°E, 23 m above sea level) from May 2009 to November 2013. The investigated field is located ~130 m from the Kumozu River. Various seasonal vegetables are cultivated on a small scale, such as cabbage, spring onion, watermelon, pumpkin, etc. We measured cephalothorax width of the collected adult female spiders to the nearest 0.025 mm under a binocular microscope. Mother spiders were individually confined to cotton-plugged glass vials (20 ml) with moistened cotton wool and kept under conditions of 25 °C and 16:8 light:dark cycle until spiderlings emerged. Spiders were fed with planthoppers, *Laodelphax striatellus* (Fallen) (Homoptera: Delphacidae) ad libitum, which were reared with rice seedlings under conditions of 22 °C and 16:8 light:dark cycle.

Laboratory experiment

Two to 3 days after spiderlings emerged, all young spiders on the mother's abdomen were removed using a soft brush and counted. In cases where unhatched eggs were left in the egg sac, the sum of the number of unhatched eggs and emerged spiderlings was recorded as clutch size. Thirty spiderlings were randomly selected from every clutch and their cephalothorax and abdomen widths measured under a binocular microscope to the nearest 0.025 mm. Mean widths were calculated, and values were noted as indices of the spiderling size of each clutch. Mean values were calculated every month using the indices of each clutch and were statistically compared. Relationships between spiderling body size and monthly average temperatures in Tsu were analyzed using data on the website provided by the Japan Meteorological Agency (2015). Statistical analyses were performed using JMP 8.0.1 software (SASS Institute Inc.).

Results

Cephalothorax widths of mother spiders and clutch size

Females with egg sacs were successfully collected from March through October: the minimum number was 21 (in March) and the maximum was 112 (in July); no spiders with egg sacs were found in January and February in any year or in November 2012 and December 2009, 2011, 2012 and 2013. The number of spiders with egg sacs collected in November and December were ten and two, respectively. Since these sample sizes were too small to analyze statistically, November and December data were removed from analysis. Consequently, two-way analysis of variance (ANOVA) revealed that body and clutch size of mother spiders change seasonally and that the fluctuation pattern differed between investigated years (Tables 1, and 2). Seasonal changes in body size of mother and clutch size are shown in Figs. 1 and 2, respectively. Although statistical analysis showed that seasonal fluctuation patterns depends upon years and that, as a whole, mother spiders and clutch sizes collected from March to June were significantly larger than from August to October, showing a

Table 1 Two-way analysis of variance (ANOVA) for cephalothorax width of *Pardosa astrigera* mothers

Factor	*df*	SS	*F* value	*p* value
Year	4	0.0896	2.7512	<0.05
Month	5	0.55208	16.9482	<0.0001
Year × month	26	0.080385	2.4677	<0.0001
Residuals	614	0.03257		

Table 2 Two-way analysis of variance (ANOVA) for *Pardosa astrigera* clutch size

Factor	*df*	SS	*F* value	*p* value
Year	4	359.661	1.2372	0.2939
Month	5	4215.538	14.5007	<0.0001
Year × month	26	501.821	1.7262	0.0146
Residuals	601	290.712		

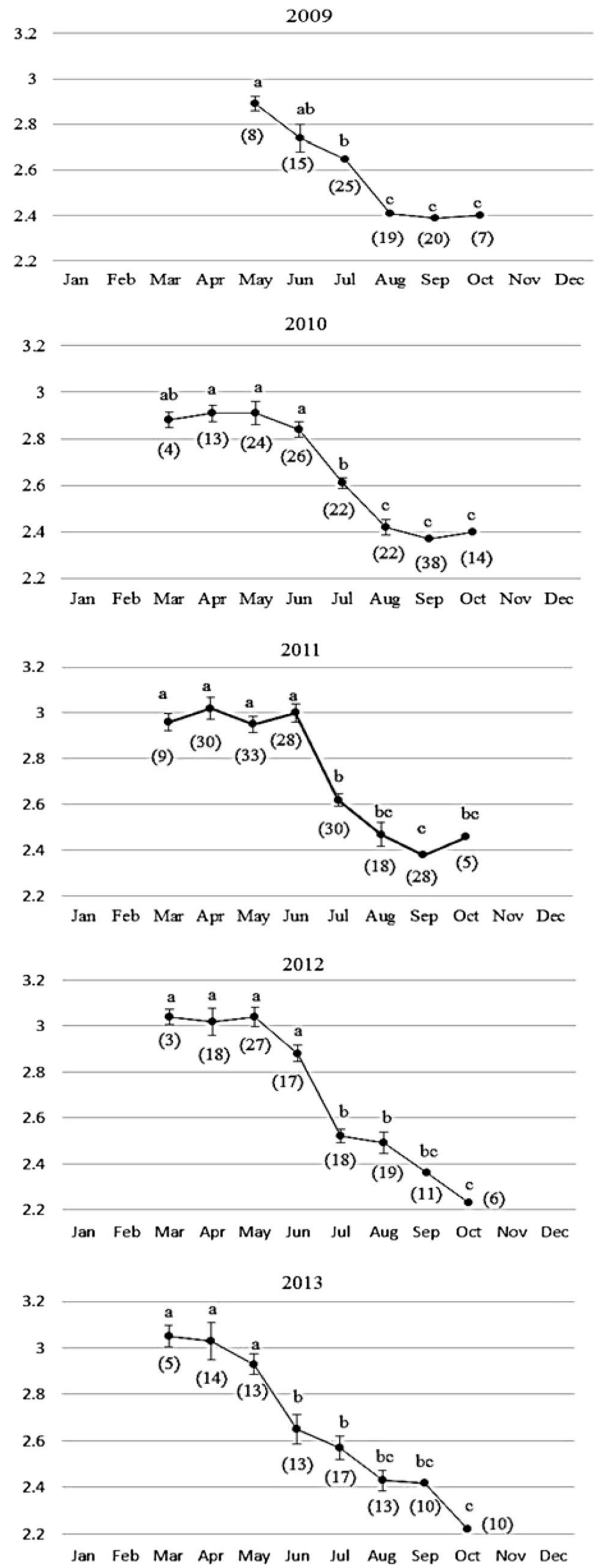

Fig. 1 Monthly means ± standard error (SE) of cephalothorax width of *Pardosa astrigera* mothers in 2009–2013. Means with the *same letters* are not significantly different [Tukey–Kramer honestly significant difference (HSD) test, $p < 0.05$]. *Numerals* in parentheses are the number of spiders examined

tendency to become smaller with seasonal progression [Tukey–Kramer honestly significant difference (HSD) test, $p < 0.05$].

Cephalothorax and abdomen widths of spiderlings

Since two-way ANOVA revealed that fluctuation patterns in cephalothorax and abdomen widths were not significantly different among investigated years (Tables 3, 4), combined data during the 5 years was analyzed (Tukey–Kramer HSD test, $p < 0.05$), spiderling widths fluctuated in a similar pattern (Fig. 3). From March to August, cephalothorax and abdomen widths continued to decrease significantly; both sizes reached a minimum in August. During this period, spiderling cephalothorax width showed significant and positive correlation with mothers' cephalothorax width in 2010, 2011, 2012, and 2013; on the other hand, spiderling abdomen width showed significant and positive correlation with cephalothorax width of mother spiders in 2010, 2011, and 2013 (Table 5). After this period, however, spiderling cephalothorax and abdomen widths suddenly started to increase and were significantly larger in October than in August.

Since two-way ANOVA revealed that fluctuation patterns of abdomen–cephalothorax size ratio is not significantly different among investigated years (Table 6), combined data during the 5-year study period was analyzed (Tukey–Kramer HSD test, $p < 0.05$). There was no significant difference in size ratios in March, April, May, and June; however, the ratio immediately and significantly fell in July and August (Tukey–Kramer HSD test, $p < 0.05$), after which it started to rise again in September and October (Fig. 4).

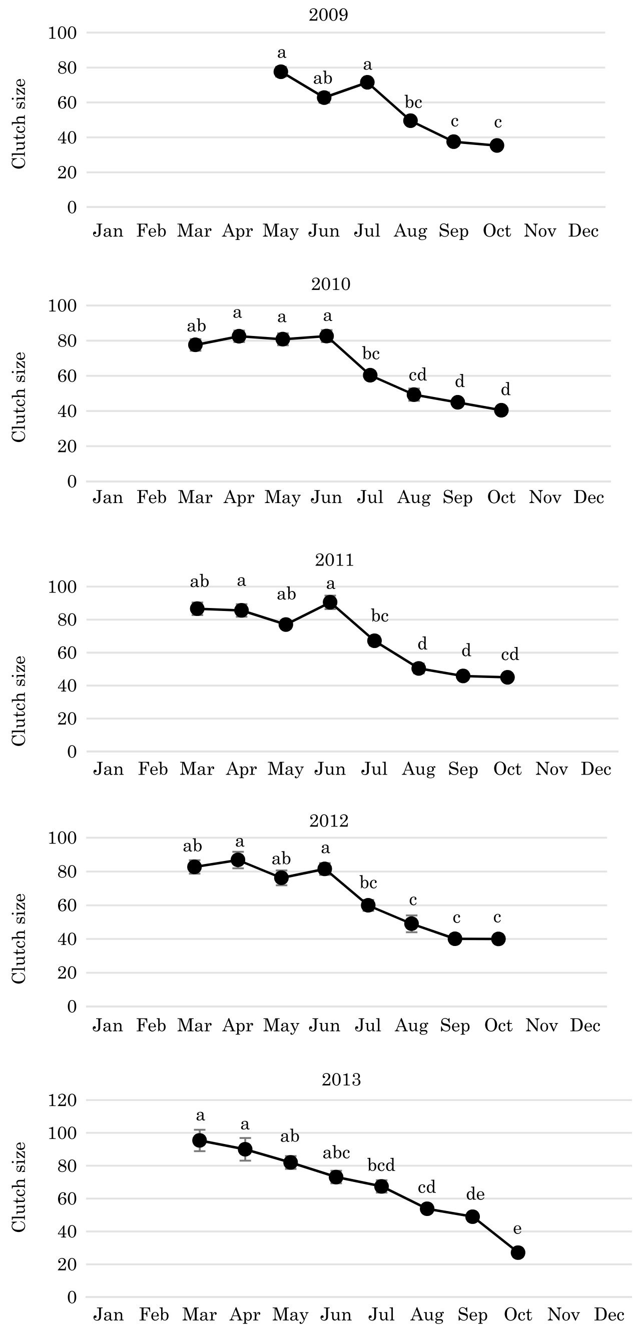

Fig. 2 Monthly means ± standard error (SE) of *Pardosa astrigera* clutch size 2009–2013. Means with the *same letters* are not significantly different [Tukey–Kramer honestly significant difference (HSD) test, $p < 0.05$]

Relationship between monthly average temperature and spiderling body size

Relationships between monthly average temperature in Tsu and monthly averages of spiderling cephalothorax and abdomen widths during the investigated period are shown in Fig. 5a, b, respectively. There were significant and

Table 3 Two-way analysis of variance (ANOVA) on cephalothorax width of *Pardosa astrigera* spiderlings

Factor	*df*	SS	*F* value	*p* value
Year	4	0.0005	1.4669	0.2107
Month	5	0.002634	7.7102	<0.0001
Year × month	26	0.000444231	1.3004	0.1467
Residuals	616	0.000341558		

Table 4 Two-way analysis of variance (ANOVA) on abdomen width of *Pardosa astrigera* spiderlings

Factor	*df*	SS	*F* value	*p* value
Year	4	0.000328	0.4649	0.7615
Month	5	0.005584	7.9068	<0.0001
Year × month	26	0.000705	0.9989	0.4669
Residuals	216	0.000706		

negative correlations between monthly average temperature and spiderling body size ($p < 0.0001$; Spearman's rank correlation coefficients −0.3958 for cephalothorax and −0.4307 for abdomen).

Discussion

We focused on seasonal fluctuation in body size of *P. astrigera* mothers and spiderlings in this study. From March to August, monthly means of cephalothorax and abdomen widths of spiderlings and cephalothorax width of mothers followed similar patterns. In fact, in arthropods, there is a tendency for larger mothers to lay larger eggs, though there are exceptions to this pattern (Fox and Czesak 2000). From August to October, however, seasonal fluctuation in body size of spiderlings revealed a completely different pattern from the former period—that is, body sizes of mother and spiderlings tend to become smaller from March to August; from August to October, however, though cephalothorax width of mothers remains small or continues to become smaller, body size of spiderlings becomes larger with progression of the season. Accordingly, it can be said that seasonal changes in spiderling body size cannot be explained only by the mother's body size fluctuation. Another possible explanation for the seasonal change in spiderling body size would be that temperatures during oviposition and growth determine progeny size. A review of the literature by Fox and Czesak (2000) found that females of many arthropod species lay larger eggs when exposed to lower temperatures during oviposition or rearing. For example, egg size increases at lower temperature in three *Drosophila* spp. (Avelar 1993) and in the butterfly *Bicyclus anynana* (Butler) (Lepidoptera:

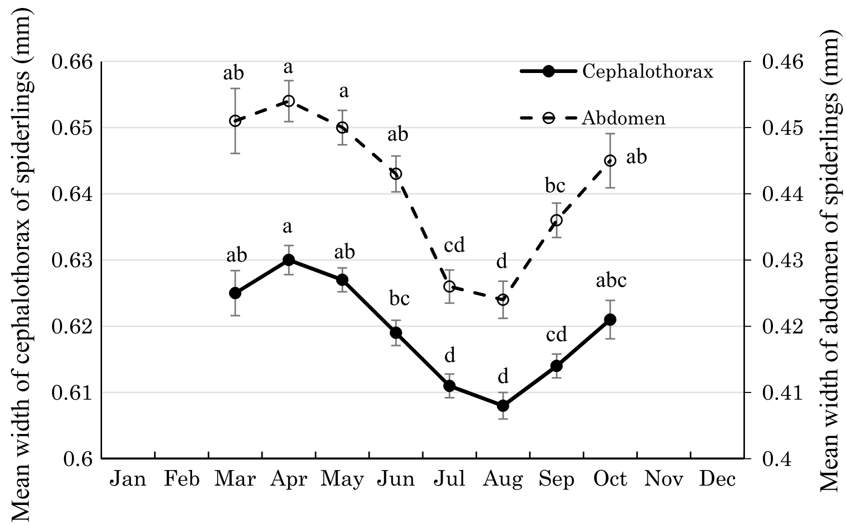

Fig. 3 Monthly means ± standard error (SE) of cephalothorax (*filled circles with a solid line*) and abdomen (*open circles with a dotted line*) of *Pardosa astrigera* spiderlings. Means with the *same letters* are not significantly different [Tukey–Kramer honestly significant difference (HSD) test, $p < 0.05$]

Table 5 Relationships between cephalothorax width of *Pardosa astrigera* mothers (A) and abdomen width of spiderlings (B) from March to August, 2009, 2010, 2011, 2012, and 2013

Year	Correlation coefficient	*P* value
A		
2009	0.929	0.071
2010	0.821	<0.05
2011	0.933	<0.01
2012	0.934	<0.01
2013	0.859	<0.05
B		
2009	0.943	0.057
2010	0.895	<0.05
2011	0.904	<0.05
2012	0.787	0.063
2013	0.959	<0.01

Table 6 Two-way analysis of variance (ANOVA) for abdomen–cephalothorax ratio of *Pardosa astrigera* spiderlings

Factor	*df*	SS	*F* value	*P* value
Year	4	0.0008012	0.6217	0.6472
Month	7	0.0044614	3.4621	<0.01
Year × month	28	0.0013031	1.0112	0.4497
Residuals	616	0.0012887		

Nymphalidae) (Fischer et al. 2004). In our study, significant and negative correlations were detected between temperature and spiderling cephalothorax and abdomen widths . These results suggest that the temperature experienced by mother spiders could determine spiderling body size. Thus, the seasonal change of temperature may play a vitally important role in seasonal change of *P. astrigera* spiderling body size.

This study revealed that body and clutch sizes of mother spiders fluctuate differently depending on researched years, while the pattern of spiderling body size fluctuation were not significantly different among years. Differences would be induced by the difference between factors that affect the determination of the mother spider's body and clutch sizes and factors affecting determination of spiderling body size. For example, generation may be a key factor affecting determination of spiderling body size. Miyashita (1969) reported that *P. astrigera* repeats two generations annually. Since generation of mother spiders most greatly works on the decision of body size of spiderlings, even if environmental factors significantly change every year, the fluctuation pattern of body size of spiderlings may not have significantly differed over the study period.

Temperature could be also associated with the reproductive strategy of *P. astrigera*. Yoshikura (1987) reported that spiders generally grow faster under higher temperatures and slower under lower temperatures within a certain temperature range. Hence, *P. astrigera* spiderlings hatched in July and August would be able to shorten their vulnerable period during higher temperatures. Mother spiders therefore could produce smaller offspring. On the other hand, availability of prey for spiderlings could also influence the reproductive strategy related to body size determination of offspring. In the wolf spider *P. pseudoannulata*, spiderling cephalothorax width strongly affects hunting ability and abdomen width greatly affects starvation tolerance (Iida 2005). In addition, *P. pseudoannulata* spiderlings with a larger abdomen–cephalothorax size ratio are able to molt into the subsequent instar under limited food condition (Iida and Fujisaki 2007). Seasonal changes in cephalothorax and abdomen widths and abdomen–cephalothorax size ratio of *P. astrigera* revealed in this study show similar patterns of seasonal change with those of *P. pseudoannulata*

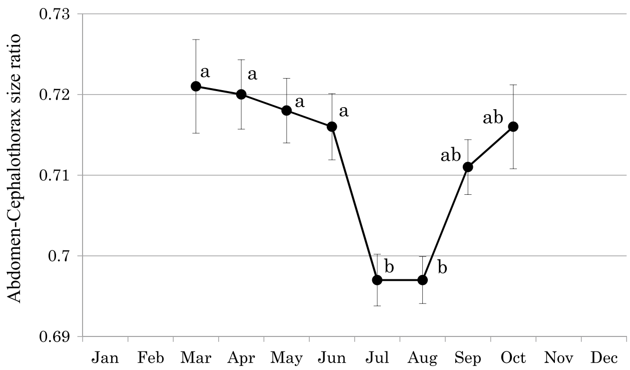

Fig. 4 Monthly means ± standard error (SE) of abdomen–cephalothorax size ratio of *Pardosa astrigera* spiderlings. Means with the *same letters* are not significantly different [Tukey–Kramer honestly significant difference (HSD) test, $p < 0.05$]

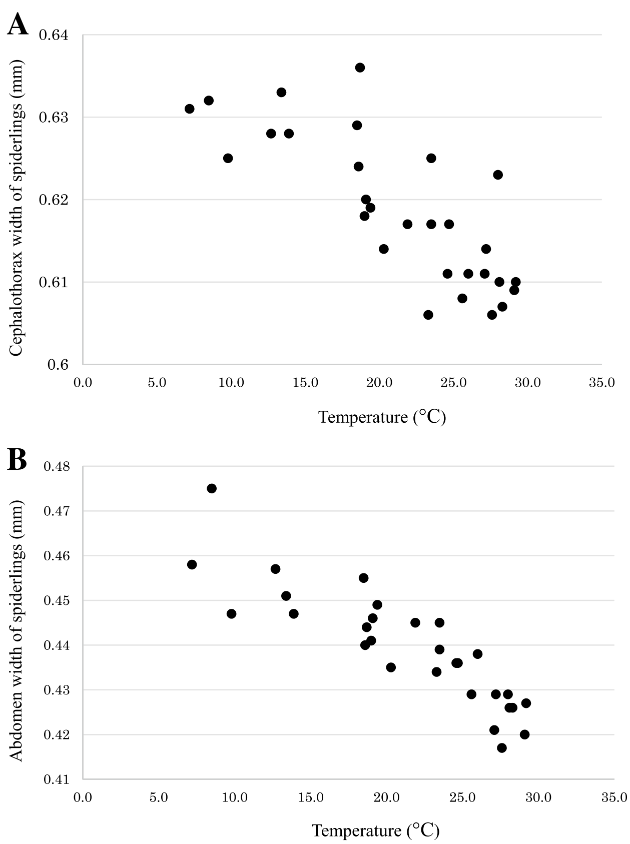

Fig. 5 Relationship between monthly average temperature in Tsu and **a** cephalothorax and **b** abdomen widths of *Pardosa astrigera* spiderlings. Significant negative correlations were detected between temperature and cephalothorax width ($p < 0.0001$; Spearman's rank correlation coefficients −0.3958) and abdomen width ($p < 0.0001$; Spearman's rank correlation coefficients −0.4307)

reported by Iida and Fujisaki (2007); body size and ratio tend to be smaller in summer than in autumn. Considering that both species belong to the genus *Pardosa* and the two species are sometimes observed in the same habitat, they may produce offspring under a similar reproductive strategy. In addition, there is a possibility that both temperature and availability of prey importantly influence reproductive strategy related to determination of offspring size. The determination mechanism on spiderling body size has not yet been elucidated.

Other factors that could influence determination of progeny body size, such as father's body size (Iyengar and Eisner 1999), heredity (Fischer et al. 2004), maternal food availability (Braby and Jones 1995), and maternal age (Wiklund and Persson 1983). A physiological approach and a survey of food conditions for spiderlings in their habitat would help elucidate the mechanisms that determine offspring size and control resource allocation of *P. astrigera* spiderlings.

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