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NESTING PATTERNS OF THE JAPANESE FOLIAGE SPIDER *CHEIRACANTHIUM JAPONICUM* (ARANEAE: MITURGIDAE)

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A female of the Japanese foliage spider *Cheiracanthium japonicum* lays her eggs in her breeding nest and guards them. The nesting patterns on the spatial distributions of breeding nests of this spider in Hokkaido and Honshu in Japan are analyzed on the basis of statistical and mathematical models. Analyses using Morisita's $I\delta$ index, modified *K*-function and *L*-function showed that *C. japonicum* builds a breeding nest on a plant at a specific site regardless of the density of nests, suggesting that it is crucial for *C. japonicum* to select the physical conditions for nest building and a female and her juveniles don't strongly compete.
KEY WORDS: Araneae, Miturgidae, spiders, nesting behavior, oviposition site, host plant, Japan.

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Самки японского листового паука (*Cheiracanthium japonicum*) откладывают яйца в гнезда и охраняют их. На основании статистических и математических

моделей проанализировано строение и пространственное распределение гнездовых камер этого паука в Японии (Хоккайдо и Хонсю). Анализ с использованием *Iδ* индекса Морисицы и модифицированных *K*- и *L*-функций показал, что *C. japonicum* устраивает гнездовые камеры на растениях в специфичных местах вне зависимости от плотности гнезд. Это позволяет предположить, что при выборе мест гнездования определяющим фактором является поиск подходящих условий, а не конкуренция самок и их потомства.

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INTRODUCTION

Herbivorous invertebrates generally lay their eggs on a plant, because the plant body might become an effective food resource for their juveniles. There are a lot of studies on the spatial distribution of eggs of herbivorous insects in Coleoptera, Diptera, Lepidoptera and Hemiptera (Iwao, 1968; Palumbo *et al*., 1991; Tonhasca *et al*., 1994; Fujiyama *et al*., 2003; Rohlfs & Hoffmeister, 2004; Arnaldo & Torres, 2005; Huang *et al*., 2005; Shimada *et al*., 2005). These studies analyzed the spatial distribution of eggs (i.e. aggregate, random, or uniform) on a particular substratum such as a leaf, a stem, a fruit of a plant. In these studies, the eggs on a substratum often resulted in uniform distribution (Iwao, 1968), because the substratum itself is regarded as a food for the herbivorous species and the juveniles might compete each other for their common food resource.

On the other hand, for carnivorous invertebrates in general, the substratum for egg-lying is not a food resource for their juveniles, but a suitable shelter from their enemies. For carnivorous invertebrates, the disposition of eggs might not be necessarily resulted in uniform distribution in the absence of a strong resource competition. Although egg-lying behaviors have been well studied in some parasitic wasps (Miura, 2003; Liljesthrom & Virla, 2004; Fathi *et al*., 2011; Nakajima *et al*., 2012), there are almost no studies on the widespread spatial distribution of eggs of carnivorous invertebrates.

Some species are known to make a particular construction, i.e. a nest, for the eggs and juveniles as well as for the adult itself. For some invertebrates which oviposit and guard their own eggs in their nests, the placement of a nesting site is an important decision. Not only must nests be placed where physical conditions permit the development of eggs and hatchlings but their location must also be satisfactory for the adults guarding them. Indeed, many species of animals exhibit precise site selection for egg deposition in a particular environment (Clutton-Brock, 1991).

Spiders represent a major group in the carnivorous terrestrial invertebrates, and some species make a nest for egg-lying. The Japanese foliage spider *Cheiracanthium japonicum* Bösenberg et Stramd, 1906 is a very common species inhabiting grasslands

throughout Japan. The female of this spider builds a breeding nest that is made of a plant leaf connected by spider silk for laying her eggs and taking care of the eggs and juveniles until the second instar eats her, i.e. matriphagy, in the nest (Nakahira, 1966). The breeding nest is easily found in a field and it is regarded as a preferable material for studying its spatial distribution over a wide range of a field.

The studies so far examining the spatial distribution of eggs of herbivorous invertebrates were based on the Morisita's I_δ (Morisita, 1962) and Lloyd's m^* (Lloyd, 1967). These two methods, however, don't take account of the spatial distribution of the substratum itself. On the contrary, Modified K-function and L-function (Ripley, 1976; Fortin & Dale, 2005; Baddeley, 2010) can analyze the spatial distribution of eggs in relation to the spatial distribution of the substratum. Consequently, for the study of the spatial distribution of eggs or nests, the modified K-function and L-function should be also employed in addition to the Morisita's I_δ and Lloyd's m^*.

Consequently, our intention in this study is to clarify the spatial distribution of breeding nests of *C. japonicum* on the basis of reliable statistical and mathematical models. In addition, we also throw light on the change of distribution patterns of breeding nests according to the increase in population density of the spider.

MATERIAL AND METHODS

Study species

The spider *Cheiracanthium japonicum* shows one annual reproductive cycle. The reproduction period is from early June to late August and the spider builds several kinds of nests in relation to seasons and purpose of nesting (Hironaka & Abé, 2012a, b). The female makes a breeding nest from August to September by using monocotyledonous plant leaves and produces eggs in an egg sac in the nest. In the present study, the breeding nest is called the "nest". The spider usually makes the nest on the following five plant species: *Miscanthus sacchariflorus* (Maxim.) Benth., *M. sinensis* Anersson, *Dactylis glomerata* L., *Phragmites australis* (Cav.) Trin. et Steud., *P. japonicus* Steud. and *Imperata cylindrica* (L.) Raeusch. var. *koenigii* (Retz.) Pilg. Therefore, the plant belonging to the above mentioned five species is referred to as the "plant" regardless of the existence of the nests. On the other hand, the plant on which the nest was actually made by the spider is referred to as the "host plant" for the sake of convenience.

Study sites

The field research was conducted in Hokkaido, northern Japan and Kanagawa, central Japan. Two study sites were established in each area. The precise locations of study sites are described as follows:

1. **Mi**: 42.96°N, 141.22°E. On the Toyohira River at Misumai in Sapporo City, Hokkaido, mainly dominated by *Miscanthus sinensis* and partly dominated by *Dactylis glomerata*.

2. **Sh**: 43.22°N, 141.33°E. The coastal plain near Ishikari River at Shibi in Ishikari City, Hokkaido, dominated by *Miscanthus sinensis*.

3

3. **Os-1**: 35.58°N, 139.32°E. The upper river bank of Sagami River at Oshima in Sagamihara City, Kanagawa Prefecture, dominated by *Miscanthus sinensis* and *Phragmites japonicus*.

4. **Os-2**: 35.57°N, 139.31°E. The lower river bank of Sagami River at Oshima in Sagamihara City, Kanagawa Prefecture, dominated by *Miscanthus sacchariflorus* and *M. sinensis*.

Distribution analysis using the index of I_δ and the K-function

To examine the site preference for nest building in relation to plant distribution, the number of nests on each plant in four study sites was counted from August to September during 2006 and 2008. The area size of each site was ranged from 260 m^2 to 580 m^2. To analyze the distribution pattern of nests, the index of I_δ (Morisita 1962) for the number of nests on each plant was calculated. The index of I_δ is defined with the following formula:

$$I_\delta = q \times \sum_{i=1}^q x_i(x_i - 1)/T(T-1),$$

where x_i is the number of nests in the i-th plant in research area ($i = 1, 2, 3, ...,$ q), q is the number of plants, and $T = \sum_{i=1}^q x_i$. If $I_\delta = 1$, the nests are randomly built on all plants. If $I_\delta > 1$, the nests are aggregately built on some specific plants. If $I_\delta < 1$, the nests are built on all plants.

When I_δ indicates that nests are aggregately built on some specific plants, the following two different patterns can be expected: 1) nests aggregate because host plants aggregate; 2) nests aggregate but host plants do not. The former pattern means that nests aggregate on several bunches of host plants with no relation to sites in an area (i.e., host-dependent distribution), and the latter one means that nests aggregate on few host plants at a specific site in an area (i.e., they have a site-dependent distribution).

To examine two patterns above in the spatial distribution of nests, specific study sites were established in Hokkaido and Kanagawa: 30 m x 18 m square area at Sh and 27 m x 10 m square area at Os-1 in September 2008. At each study site, the location of every plant species was mapped on a two-dimensional plane distinguishing a host plant from the others. The obtained spatial distribution of the host plants and the others was analyzed by using $K_\alpha - K$-function (Baddeley 2010). The K-function (Ripley 1976) is defined as follows:

$$\hat{K}(t) = |A| \sum_{i=1}^n \sum_{j=1}^n w_{ij}^{-1} I_t(u_{ij})/n^2,$$

where t is a certain distance from an arbitrary plant, n is the number of plants in a rectangular area A, $|A|$ denotes its area, u_{ij} is the distance between i-th and j-th plants, $I_t(u_{ij})$ is the counter variable: the number of plants within distance t from i-th

4

plant with radius u_{ij}, which lies within area A. The K_α-function is defined as follows:

$$\hat{K}_\alpha(t) = |A| \sum_{i=1}^{n_\alpha} \sum_{j=1}^{n} w_{ij}^{-1} I_t(u_{ij})/n_\alpha n.,$$

where n_α and n are the number of host plants and that of all plants in an area, respectively. If $\hat{K}_\alpha(t) - \hat{K}(t) = 0$, host plants are randomly distributed. If

$\hat{K}_\alpha(t) - \hat{K}(t) > 0$, host plants aggregate. If $\hat{K}_\alpha(t) - \hat{K}(t) < 0$, host plants are evenly distributed. By the Monte Carlo simulation (Besag and Diggle 1977), 95 percent confidence envelopes are defined as the highest and lowest values of

$\hat{K}_\alpha(t) - \hat{K}(t)$. The $\hat{K}_\alpha(t) - \hat{K}(t)$ values are shown in the $\hat{K}_\alpha(t) - \hat{K}(t)$ value

graph representing the relationship between the $\hat{K}_\alpha(t) - \hat{K}(t)$ values and a

distance t from an arbitrary host plant. In short, the graph represents the number of host plants within a certain radius from an arbitrary plant.

Density and crowding of nests on plants in an area

The relationship between the density (m) of nests on all plants and the crowding ($m*$) of nests on a host plant was examined. The nests on all plants in an area were counted. Then, the mean number of nests on a plant in an area was calculated as a density (m). The number of other nests per host plant per nest in an area was calculated as crowding ($m*$). In other words, crowding is the degree of concentration of nests on a host plant in an area. Crowding ($m*$) was defined by Lloyd (1967) as:

$$m* = \sum_{i=1}^{q} x_i (x_i - 1)/\sum_{i=1}^{q} x_i,$$

where x_i is the number of nests in the i-th plant in an area ($i = 1, 2, 3, ..., q$) and q is the number of plants in an area.

Distribution analysis using the L-function

To examine the geometric spatial distribution of nests in disregard of the plant distribution, study sites were established in a 30 m x 18 m square area at Sh and a 29 m x 10 m square area at Os-1 in September 2008 and a 29 m x 20 m square area at Mi and a 26 m x 10 m square area at Os-2 in September 2009. Localities of these study sites were exclusively same as those for examining the site preference for nest building in relation to plant distribution by using the K-function. At each study site, the location of every nest was mapped on a two-dimensional plane. The obtained data were then analyzed using an L-function (Fortin & Dale, 2005). The function is defined as:

$$\hat{L}(t) = t - \sqrt{\hat{K}(t)/\pi},$$

where t is a certain distance from an arbitrary nest. If $\hat{L}(t) = 0$, the nests are

randomly distributed. If $\hat{L}(t) < 0$, the nests aggregate. If $\hat{L}(t) > 0$, the nests are evenly distributed. By the Monte Carlo simulation, 95 percent confidence envelopes were defined as the highest and lowest values of $\hat{L}(t)$. The $\hat{L}(t)$ values are shown

in the $\hat{L}(t)$ value graph representing the relationship between the $\hat{L}(t)$ values and

distance t from an arbitrary nest. In short, the graph represents the number of nests within a certain radius from an arbitrary nest.

The statistical and mathematical analyses employed in the present study were conducted using computer program 'R' (R Foundation for Statistical Computing, Vienna, Austria).

RESULTS

Spatial distribution of nests in relation to the host plant distribution

The values of I_δ for each research area from 2006 to 2009 are shown in table 1. The value was not significantly different in each research area (one-way ANOVA, $F = 1.720, P = 0.273$). In all areas in all research years, the I_δ values were significantly higher than 1. This indicates that nests concentrate on some host plants in all research areas.

Table 1. Value of the I_δ index in each research site from 2006 to 2009. The F-test was carried out to test whether the value of I_δ was higher than 1.

Research site	Research year	Number of plant	Number of nest	I_δ	F	P
Mi	2006	64	194	2.427	5.372	< 0.05
	2007	33	80	3.230	6.498	< 0.05
	2008	36	81	2.933	5.419	< 0.05
	2009	66	43	4.166	3.046	< 0.05
Sh	2007	71	110	3.079	4.238	< 0.05
	2008	195	248	7.233	8.935	< 0.05
Os-1	2007	51	36	2.428	2.000	< 0.05
	2008	87	29	3.000	1.651	< 0.05

Then, whether or not host plants, not the nests themselves, concentrate at particular sites was examined. The spatial distribution of host plants, which is calculated by the number of host plants within a certain distance t (radius) from an arbitrary plant, is shown in fig. 1. In each research area, the observation values of $\hat{K}_\alpha(t) - \hat{K}(t)$

6

were lower than the estimated highest value of the 95 percent confidence envelopes at all distances. This indicates that host plants do not concentrate at particular sites. The results suggest that nests aggregate on few host plants at specific sites independently of the host plant distribution.
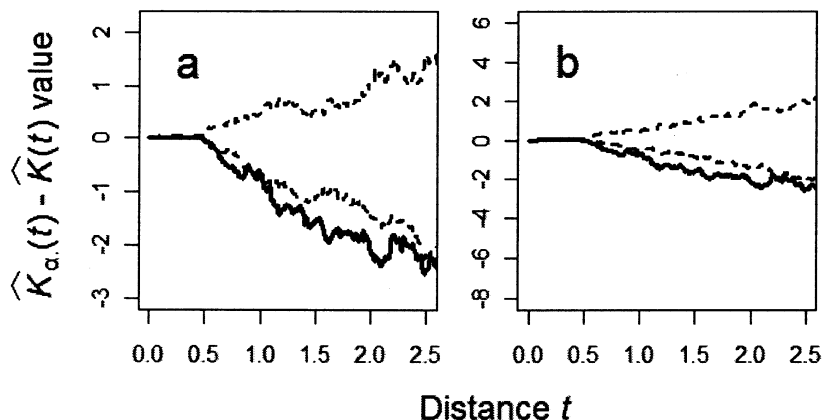

Distance t

Fig. 1. Distribution of the $\hat{K}_\alpha(t) - \hat{K}(t)$ value to a distance t between arbitrary host plants in a research area: Sh (a) and Os-1 (b). The solid line indicates the observation values of $\hat{K}_x(t) - \hat{K}(t)$ at distances ranging within a radius of 0 m to 2.5 m. The two broken lines indicate 95 percent confidence envelopes defined as the highest and lowest values of $\hat{K}_\alpha(t) - \hat{K}(t)$ at distances ranging within a radius of 0 m to 2.5 m.

Density and crowding of nests on plants in an area

The density of nests on all plants and the crowding of nests on a host plant in each research area in each year are shown in table 2. The crowding of nests was significantly higher in the Hokkaido than the Kanagawa populations (one-way ANOVA, $F = 8.274$, $P < 0.05$). On the other hand, clear differences on the densities of nests between the Hokkaido and Kanagawa populations could not be found (one-way ANOVA, $F = 4.074$, $P = 0.090$). However, this result could be influenced by the small sample size in Kanagawa ($n = 2$), but it appears that the density of nests tended to be higher in the Hokkaido than the Kanagawa populations (Table 2). The relationship between the density and the crowding of nests is shown in fig. 3. The linear regression line in fig. 2 is significantly fitted to the data (one-way ANOVA, $F = 7.993$, $P < 0.05$). The slope larger than 1 (2.199 ± 0.8534) is significantly fitted to the data (T test, t-value $= 2.576$, $P < 0.05$), but the intercept (1.600 ± 1.514) is not significantly different from zero (T test, t-value $= 1.057$, $P > 0.05$). If the regression line has a slope 1, the number of nests on each plant evenly increases as the density of nests in an area increases. The regression line with a slope larger than 1 indicates that the number of nests on host plants alone increases as the density of nests in an area increases.
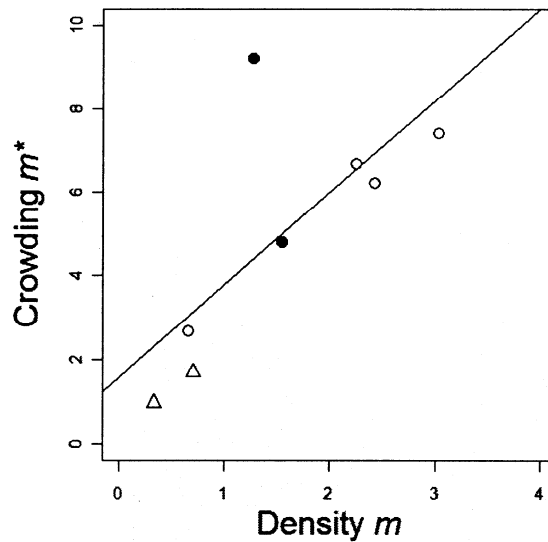
7

Fig. 2. Relationship between density (m) and crowding (m*) of nests. Each research area is marked with different symbols: Mi: circle, Sh: solid circle, Os-1: triangle. The solid line represents the simple regression: $Y = 2.398 X + 1.486$, $r^2 = 0.5712$.

Table 2. Density and crowding of nests in each research site from 2006 to 2009.

Research site	Research year	Density m	Crowding m*
Mi	2006	3.031	7.404
	2007	2.424	6.205
	2008	2.250	6.669
	2009	0.6515	2.697
(Average)		(2.089)	(5.744)
Sh	2007	1.549	4.787
	2008	1.272	9.207
(Average)		(1.411)	(6.997)
Os-1	2007	0.7059	1.706
	2008	0.3333	0.9845
(Average)		(0.5196)	(1.345)

Spatial distribution of nests in relation to the two-dimensional geometry

The geometric spatial distribution of nests, which is calculated by the $L(t)$ value representing the number of nests within a certain distance (radius) from an arbitrary nest, is shown in the $\hat{L}(t)$ value graph (Fig. 3). In all research areas, the observed

$\hat{L}(t)$ values were lower than the lowest value of the 95 percent confidence envelopes at distances ranging within a radius of 0.3 m to 2.5 m. This indicates that nests significantly aggregate at particular sites in all areas. In addition, the nests in Mi, Sh, and Os-2 were strongly aggregated at a distance of 1.0 m, 1.3 m, and 0.9 m, respectively (Fig. 3). This suggests that the patch of nests in Mi, Sh, and Os-2 has a radius of about 1.0 m, 1.3 m, and 0.9 m, respectively. The difference between the lowest observed $\hat{L}(t)$ value and the lowest 95 percent confidence value in Sh was
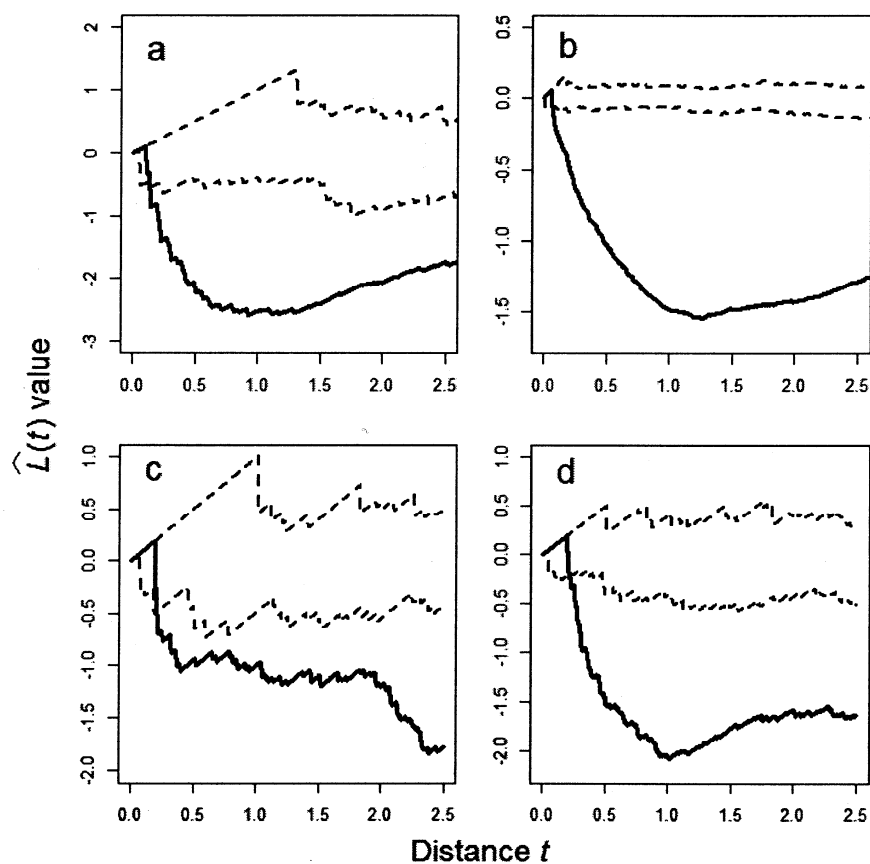

Fig. 3. Distribution of the $\hat{L}(t)$ value to a distance between arbitrary nests in a research area: Mi (a), Sh (b), Os-1 (c), and Os-2 (d). The solid line indicates the observed $\hat{L}(t)$ values at distances ranging within a radius of 0 m to 2.5 m. The two broken lines indicate 95 percent confidence envelopes defined as the highest and lowest $\hat{L}(t)$ values at distances ranging from 0 m to 2.5 m.

9

relatively larger than that in Mi and Os-2 (Fig. 3). This indicates that the patch size of nests in Sh was relatively larger than that in Mi and Os-2. On the other hand, the observed $\hat{L}(t)$ values in Os-1 did not show a distinct peak (Fig. 3). Furthermore, the differences between the observed $\hat{L}(t)$ values and the lowest 95 percent confidence value in Os-1 were relatively smaller than those in the other research areas (Fig. 3). Moreover, the observed $\hat{L}(t)$ values rapidly decreased at distances ranging within a radius of 0.2 m to 0.4 m, which suggests that the relatively small patch with 0.4 m radius aggregates in Os-1.

DISCUSSION

Eggs of some herbivorous arthropod species (e.g. the azuki bean weevil *Callosobruchus chinensis* (L.), seed beetle *Callosobruchus maculatus* (F.) and the queensland fruit fly *Dacus tryoni* (Frogg.)) exhibit a uniform distribution on plants (Iwao, 1968; Huang *et al.*, 2005). A female of *C. chinensis* has a strong tendency to avoid to lay eggs in fruits already used by the other females, because the female prevents her juveniles from the resource competition with the other offsprings due to the quite limited food resource, i.e. fruits (Yoshida, 1961; Shimada *et al.*, 2005). On the other hand, eggs of some lepidopteran and hemipteran species aggregate on particular plant leaves, and there is no resource competition among their offsprings due to almost unlimited food resource, i.e. leaves (Iwao, 1968; Palumbo *et al.*, 1991; Tonhasca *et al.*, 1994; Liang *et al.*, 1996; Arnaldo & Torres, 2005). Regarding the spatial distribution of nests of the spider *Cheiracanthium japonicum*, the nests concentrated on some plants in all research areas ($I_\delta > 1$). Although host plants did not concentrate at particular sites (positive low value of $\hat{K}_\alpha(t) - \hat{K}(t)$), the nests significantly aggregated at specific sites in all research areas ($\hat{L}(t) < 0$). Consequently, regardless of the plant distribution, nests aggregate on few plants at particular sites; i.e., they have a site-dependent distribution. The juveniles of the carnivorous spider *C. japonicum* do not use the nest consisting of plant leaves as a food resource. Therefore, the female spider does not need to build the nest keeping away from the other's nest owing to an absence of food resource competition for juveniles. And it is more probable that the female selects the most appreciable nesting site regardless of the existence of nests of the others.

The *L*-function analysis revealed the relative patch size of nests in each research area: Sh (1.3 m radius) > Mi = Os-2 (1.0 m radius) > Os-1 (0.4 m radius). While the patch size of nests varies more or less within local populations, the patch size is larger in the Hokkaido than the Kanagawa populations. In addition, the density of nests in an area and the crowding of nests on a host plant tended to be larger in the Hokkaido than the Kanagawa populations. Namely, the differences in the density and

10

the crowding of nests between the Hokkaido and Kanagawa populations coincided with those of the patch size of nests between them. Consequently, the differences in the crowding and patch size of nests between the Hokkaido and Kanagawa populations could be attributed to the differences in population densities between them. In general, as the population density increases, animals tend to enter vacant areas to avoid a competition. On the contrary, it is highly remarkable that as the spider population grows *C. japonicum* raises the crowding and the patch size of nests without intruding into neighbor vacant areas. Such unconventional nesting behavior of *C. japonicum* is considered to be caused by the rather strong selectivity for nesting sites of the female spider.

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11

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