

Offspring discrimination by female parents of the matrophagous spider *Cheiracanthium japonicum* (Araneae: Eutichuridae)

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ABSTRACT

The ability of females of the matrophagous spider *Cheiracanthium japonicum* to discern their own offspring was examined based on a comparison of her maternal care for her own eggs and spiderlings with other conspecific females as well as those of other congeneric species. *Cheiracanthium japonicum* females did not discern their own nest from those of conspecific and congeneric individuals. In addition, the female did not distinguish her own egg sac from those of other conspecific or congeneric individuals. On the other hand, the female clearly discriminated between her own spiderlings and those of other congeneric species only if the congeneric spiderlings were introduced into the breeding nest. Consequently, the female will allow conspecific spiderlings to predate her (i.e. cannibalism). However, it is hardly expected that spiderlings of a certain female would eat another female in the field, as the reproductive period is quite short and synchronised in a population. Considering that the female can only recognise spiderlings of other species, the recognition ability of *C. japonicum* females will be evolved only to work as a protection against intruders of other species into the breeding nest.

ARTICLE HISTORY

Received 25 December 2015

Accepted 28 June 2016

KEYWORDS

Japanese foliage spider; kin discrimination; maternal care; matrophagy; *Cheiracanthium japonicum*

Introduction

Parents of many organisms provide parental care for their offspring in various forms (Clutton-Brock 1991). Matrophagy represents an unusual self-sacrificial care in which offspring eat their own mother at the final stage of maternal care. This habit was noted by Kataoka (1939) on *Cheiracanthium japonicum* for the first time, and thereafter it has been reported many times in several spider species (Uyemura 1940; Yaginuma 1955; Bristowe 1958; Kullmann 1972; Jacson and Joseph 1973; Polis 1981; Crespi 1992; Evans et al. 1995; Schneider and Lubin 1997; Kim and Horel 1998; Toyama 1999, 2001, 2003; Kim et al. 2000; Salomon et al. 2005; Foelix 2011). Such an extreme form of maternal care can be interpreted as an altruistic behaviour (Hamilton 1964). In this context, a mother's ability to discriminate kin from non-kin offspring should be selectively advantageous because the mother can increase her fitness only if she is eaten only by her own offspring. Consequently, a female's offspring discrimination ability is

expected to be reinforced in a species with matrophagy. Nevertheless, studies on a female's ability to distinguish her own eggs and juveniles from those of others are quite limited (Kürpick 2000; Viera et al. 2007).

The Japanese foliage spider *Cheiracanthium japonicum* is a solitary hunting spider that inhabits grasslands throughout Japan. The female of this spider builds a closed nest with a plant leaf for laying her eggs and taking care of the eggs and juveniles until the second instar eats her (i.e. matrophagy), in the nest (Nakahira 1966). Toyama (1999, 2001, 2003) investigated the matrophagy of *C. japonicum* in detail and demonstrated that several advantages in offspring survival conferred by matrophagy contributed to high reproductive success for females of this species. The reproductive season of *C. japonicum* is from June to August in the field study (Hironaka and Abé 2012a), and the egg-laying period is limited to within one month, so the developmental progress of eggs in each breeding nest almost synchronises in the field. Therefore, it is hardly expected that spiderlings of a certain female would eat another female in the reproductive period. In that case, the ability of the female *C. japonicum* to discriminate conspecific spiderlings is not predicted to evolve in this recognition system. On the other hand, some predatory organisms including ants, parasitic wasps and other spider species have an opportunity to intrude into the female's breeding nest. Consequently, the discrimination ability of the female *C. japonicum* for the other species can be expected to be reinforced with such predation pressure. In regard to the kin discrimination ability of female parents of *C. japonicum*, however, no information has been obtained before now. Accordingly, the aim of the present study is to estimate ability of the female *C. japonicum* to discriminate her own offspring from that of others by comparing her maternal care for her own eggs and spiderlings with those of other conspecific females and other congeneric species.

Materials and methods

Study animal

The Japanese foliage spider *Cheiracanthium japonicum* Bösenberg and Strand, 1906 is known as a matrophagous spider that inhabits grasslands throughout Japan. The spider builds several kinds of nests from a monocotyledonous plant leaf for molting, mating and breeding during its life cycle (Figure 1a) (Nakahira 1966; Hironaka and Abé 2012a, 2012b). The female aggressively defends the eggs and juveniles against predators and parasitoids until the second instar eats her (i.e. matrophagy), in the breeding nest (Toyama 1999, 2001, 2003).

Cheiracanthium lascivum Karsch, 1879 is also common in the grasslands of Japan and is quite similar to *C. japonicum* in its appearance and life cycle. *Cheiracanthium lascivum* also makes several kinds of nests like those of *C. japonicum*, and the female takes care of her progeny in the breeding nest. However, matrophagy does not occur in *C. lascivum*, and the female leaves the breeding nest together with the second instar (Kikuchi and Ohkawara 2007).

Collecting and breeding

Sample collection was carried out from 4 to 24 July in 2008 and from 2 June to 1 August in 2009. A total of 128 gravid females of *C. japonicum* were collected in the grasslands of

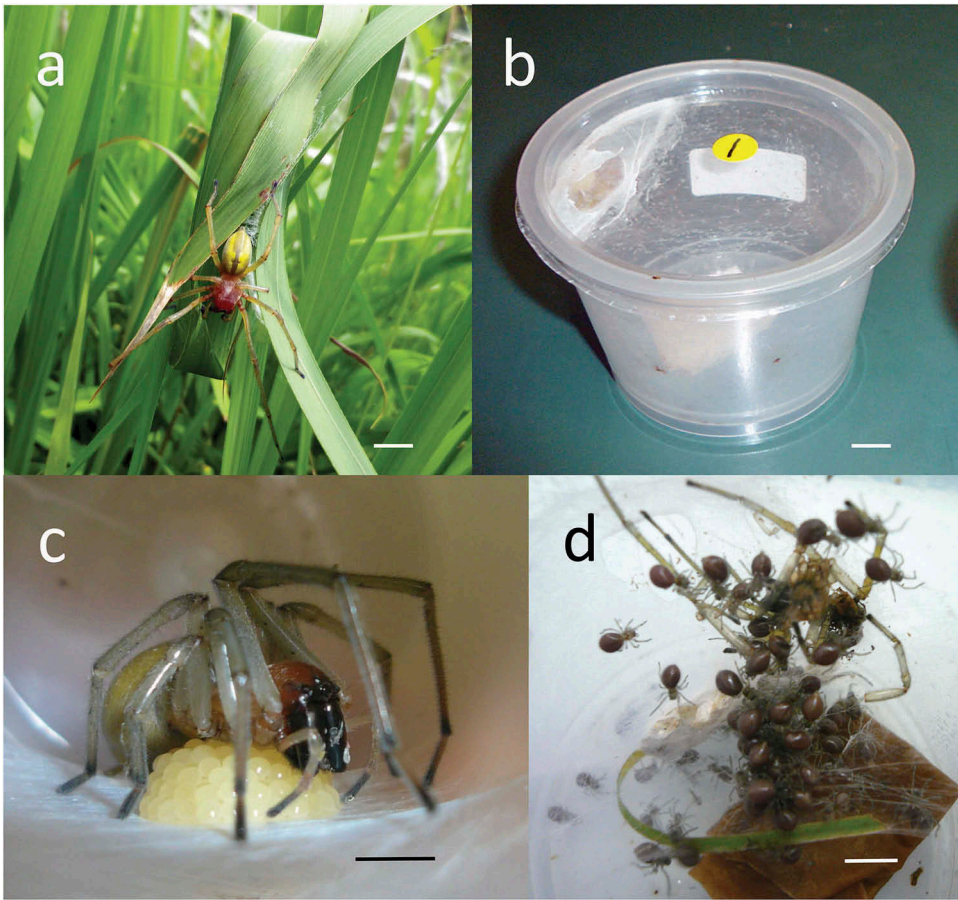


Figure 1. Matrifagous spider *Cheiracanthium japonicum*. (a) Male on a nest constructed with poaceous leaves in the field; (b) artificial breeding nest built by a female in a polypropylene container; (c) female laying her eggs in her breeding nest; (d) juveniles in the second instar eating their own mother (matrphagy). Scale bars = 5 mm.

Samukawa Town in Koza County, the Ohshima District in Sagami-hara City, and the Kameino District in Fujisawa City, Kanagawa Prefecture, Japan. Additionally, 62 gravid females of *C. lascivum* were obtained in the grasslands of Samukawa Town in Koza County and the Ohba District in Fujisawa City, Kanagawa Prefecture.

Breeding nests lodged with females were collected from each study area and transported to the Biological Laboratory of the College of Bioresource Sciences, Nihon University. Each female was transferred from the nest to a polypropylene container with a lid, 10 cm in diameter and 4.5 cm in height (A-Pet 200MB, Mineron Kasei Co., Ltd.), as an artificial breeding nest (Figure 1b) (Toyama 2001). The container was kept in an incubator (CR-14 C Hitachi Co. Ltd.) at 20°C with 16 h light:8 h dark conditions. A piece of 1 cm square paper soaked with water was set up in a container for a water supply, and a juvenile house cricket, *Acheta domestica*, was fed to the female every other day until she laid her eggs in the artificial nest (Figure 1c).

Experiments

After the egg laying was completed in the artificial nest, the following three kinds of experimental manipulations of females, egg sacs and the first instar spiderlings of *C. japonicum* and *C. lascivum*, and also artificial egg sacs made of a plastic eraser, were executed in the laboratory.

Female exchange between breeding nests

Objective

To clarify whether a female distinguishes her own nest from that of other females of *C. japonicum* and that of the congeneric species *C. lascivum*.

Procedure

A *C. japonicum* female was removed from a nest, and another *C. japonicum* female was also removed from another nest. Then, the females were exchanged and each placed in the other spider's nest (intraspecific exchange).

A *C. japonicum* female was removed from a nest, and a *C. lascivum* female was also removed from a nest. Then, the *C. japonicum* female was placed in the *C. lascivum* nest, and the *C. lascivum* female was placed in the *C. japonicum* nest (interspecific exchange).

A *C. japonicum* female was removed from a nest. Then, the female was returned to the same nest (control).

Egg sac exchange between breeding nests

Objective

To clarify whether a female distinguishes her own egg sac from those of other *C. japonicum* females and those of a congeneric species, *C. lascivum*. Additionally, to clarify whether a female discriminates her own egg sac from one made of artificial material.

Procedure

A *C. japonicum* egg sac was removed from a nest, and another one of *C. japonicum* was also removed from another nest. Then, the egg sacs of the two females were exchanged and each placed in the other spider's nest (intraspecific exchange).

A *C. japonicum* egg sac was removed from a nest, as was a *C. lascivum* egg sac. Then, the egg sacs were exchanged: the *C. japonicum* egg sac was placed in the *C. lascivum* nest, and that of *C. lascivum* was placed in the *C. japonicum* nest (interspecific exchange).

A *C. japonicum* egg sac was removed from a nest. Then, the egg sac was returned to the same nest (control).

A *C. japonicum* egg sac was removed from a nest. Then, an artificial egg sac made of a plastic eraser was placed back in the same nest instead of the spider's own egg sac (artificial exchange).

Spiderling exchange between breeding nests

Objective

To clarify whether a female distinguishes her own spiderlings from those of other *C. japonicum* females and those of the congeneric species *C. lascivum*.

Procedure

Cheiracanthium japonicum spiderlings were removed from a nest, and other *C. japonicum* spiderlings were also removed from another nest. Then, the spiderlings of each female were exchanged, being placed in the other spider's nest (intraspecific exchange).

The first instar spiderlings of *C. japonicum* were removed from a nest, and those of *C. lascivum* were also removed from a nest. Then, the spiderlings of *C. japonicum* were placed in the nest of *C. lascivum*, and those of *C. lascivum* were placed in the nest of *C. japonicum* (interspecific exchange).

Cheiracanthium japonicum spiderlings were removed from a nest. Then, the spiderlings were returned to the same nest (control).

Prior to each experimental manipulation described above, the target individual was fully anaesthetised with CO₂ gas. When the target individual was removed from a nest, the extent of physical damage to the nest was minimised. Each manipulation was completed within 10 minutes.

Observation

Although a *C. japonicum* female does not show radical offensive behaviour before she makes a breeding nest, the female becomes extremely aggressive after she confines herself to the breeding nest for egg laying, showing her fangs and attacking intruders. Therefore, the aggressive biting behaviour of the female against an intruder is regarded as protective behaviour for her progeny. The female's protection of various subjects was examined every other day from the day after each exchange manipulation of the subjects to the date of her fate by matrophagy (Figure 1d). The protectiveness of a female in the nest was judged by making an artificial invasion into the breeding nest with tweezers. If a female attacked the tweezers, that female was regarded to be protecting the object. On the contrary, if a female did not attack the tweezers, the female was regarded as not protecting the object.

After the egg sac exchange experiments described above were completed, maternal care for the first instar spiderlings hatched from the eggs was continuously observed until the females died.

Statistics

Multiple pairwise comparisons based on Tukey's test were performed to determine the existence of a female's protective behaviour on the dyad of each experimental pair. The existence of maternal care for an artificial egg sac was examined by Mann-Whitney U test. Statistical analyses were conducted using JMP v. 4.0 (SAS Institute Inc.) and Excel Statistics v. 7.0 (Esumi Co., Ltd.).

Results

Female exchange between breeding nests

The results are given in Table 1. In an intraspecific exchange, 29 of 30 *C. japonicum* females showed continuous maternal care for their conspecific eggs in the conspecific nests. In an interspecific exchange, all seven females protected other congeneric eggs in

Table 1. Existence of maternal care of the female for eggs in the female exchange experiment.

	Intraspecific exchange (<i>Chiracanthium japonicum</i> ↔ <i>C. japonicum</i>)	Interspecific exchange (<i>C. japonicum</i> ↔ <i>C. lascivum</i>)	No exchange (control)
Females showing maternal care (ind.)	29	7	10
Females showing no maternal care (ind.)	1	0	0
Total females (ind.)	30	7	10

the congener's nest. In a control (no exchange), all 10 females showed maternal care for their own eggs in their own nests. There were no significant differences between the results of each experiment ($P > 0.05$). These results indicate that the *C. japonicum* females pay no attention to the authenticity of the nests stored with eggs inside, even if the nests belong to another species, *C. lascivum*. Consequently, it is highly probable that a *C. japonicum* female does not discern her own nest.

Egg sac exchange between breeding nests

The results are shown in Table 2. In an intraspecific exchange, 49 of 52 *C. japonicum* females showed maternal care for their conspecific egg sacs. In an interspecific exchange, all 15 females continuously protected egg sacs of *C. lascivum*. In a control (no exchange), all 10 females showed protective behaviours for their own egg sacs. There were no significant differences between the results of each experiment ($P > 0.05$). These results indicate that *C. japonicum* females do not discern their own egg sacs from those of conspecific females or those of *C. lascivum*. Moreover, on the basis of the consecutive observation after the experiment, the females in each exchange experiment protected the spiderlings hatched from the eggs laid by other conspecific females and also those laid by the other species.

In an artificial egg sac exchange, maternal care for the egg sac of 15 *C. japonicum* females was continuously observed for 25 days until all of the females died (Figure 2). The number of females showing maternal care was significantly different from those showing no maternal care ($P < 0.05$). During most of the observation period, the number of females showing maternal care was well above those without maternal care. This means that *C. japonicum* females do not discern the genuineness of their eggs.

Spiderling exchange between breeding nests

The results are given in Table 3. In an intraspecific exchange, all 16 *C. japonicum* females showed continuous maternal care for the first instar spiderlings of other *C. japonicum* females. On the other hand, in an interspecific exchange, all 10 females of *C. japonicum*

Table 2. Existence of maternal care of the female for eggs in the egg sac exchange experiment.

	Intraspecific exchange (<i>Chiracanthium japonicum</i> ↔ <i>C. japonicum</i>)	Interspecific exchange (<i>C. japonicum</i> ↔ <i>C. lascivum</i>)	No exchange (control)
Females showing maternal care (ind.)	49	15	10
Females showing no maternal care (ind.)	3	0	0
Total females (ind.)	52	15	10

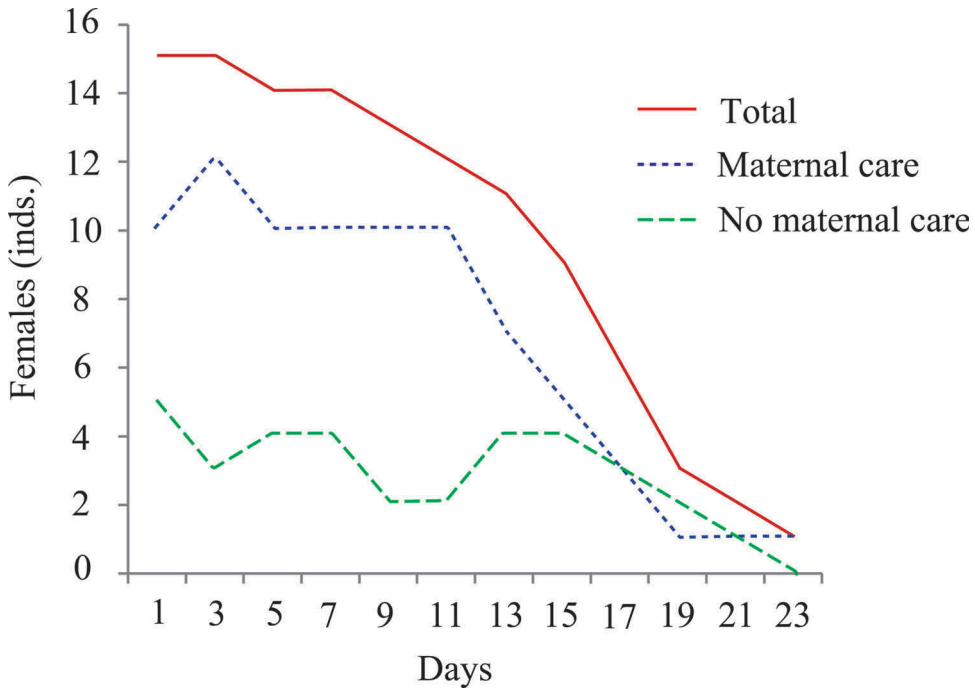


Figure 2. Temporal change of the number of surviving females of *Cheiracanthium japonicum* showing maternal care (broken line) and no maternal care (dashed line) for an artificial egg sac during the observing period of 25 days.

Table 3. Existence of maternal care of the female for spiderlings in the spiderling exchange experiment.

	Intraspecific exchange (<i>Chiracanthium japonicum</i> ↔ <i>C. japonicum</i>)	Interspecific exchange (<i>C. japonicum</i> ↔ <i>C. lascivum</i>)	No exchange (Control)
Females showing maternal care (ind.)	16	0	10
Females showing no maternal care (ind.)	0	10	0
Total females (ind.)	16	10	10

did not give maternal care for the spiderlings of *C. lascivum*. In a control (no exchange), all 10 females showed maternal care for their own spiderlings. There was no significant difference between the results of the control and intraspecific exchange experiments ($P > 0.05$). On the other hand, there was a significant difference between the results of the control and interspecific exchange experiments ($P < 0.05$), as well as those of the intra- and interspecific exchange experiments ($P < 0.05$). These results show that *C. japonicum* females clearly discriminate their own spiderlings from those of *C. lascivum*, but not from those of other conspecific females of *C. japonicum*.

Discussion

A *C. japonicum* female does not discern her own nest from the nests of conspecific and congeneric individuals. Morse (1989) reported that the semelparous crab spider

Misumena vatia accepted nests of conspecifics as readily as its own, but not those of other species. An *M. vatia* female makes her nest with a specific plant leaf and lays eggs in a nest. Morse (1989) suggested that *M. vatia* probably responds to tactile or visual cues in the nests. If a *C. japonicum* female also uses such cues to recognise her own nest, the results of the female exchange experiment in an artificial nest in the present study will be understandable.

According to the results of the egg sac exchange experiment, a *C. japonicum* female does not distinguish her own egg sac from that of other conspecific and congeneric species. The female always shows maternal care for the eggs and the spiderlings hatched from the eggs lodging with the female in the nest, even if the nest and eggs belong to another species. This means that once a *C. japonicum* female lodges in a breeding nest, regardless of its original constructor, she regards the eggs previously laid in the nest and the spiderlings hatched from the eggs as her own to protect. Viera et al. (2007) noted that the females of a sub-social spider, *Anelosimus* cf. *studiosus*, did not discriminate their own egg sacs from conspecific ones. Quite a few spider species were capable of recognising their own egg sacs: *Portia labiata* (Clark and Jackson 1994), *Loxosceles gaucho* (Japyassú et al. 2003) and *Stegodyphus dumicola* (Kürpick 2000). Additionally, in the case of *Loxosceles gaucho*, although they are able to recognise their own egg sacs, spiders with a single egg sac make no distinction between their own and conspecific egg sacs (Japyassú et al. 2003). If it is unlikely in nature for a female to encounter foreign eggs in her own nest, a system for discriminating her own eggs from those of others might not be so advantageous.

Moreover, an artificial egg sac exchange experiment indicates that a *C. japonicum* female does not discern the genuineness of the eggs. Consequently, it is highly probable that a *C. japonicum* female does not recognise her eggs on the basis of chemical substances, while Clark and Jackson (1994) referred to egg sac discrimination based on chemical cues in the cannibalistic *Portia labiata*. The reason that a *C. japonicum* female does not discern her own eggs might be related to the physical strength of the breeding nest and a range of protective behaviours of the female. The breeding nest is quite firmly constructed with a hard plant leaf backed entirely with strong spider silk, and the female has quite aggressive protective behaviour against an enemy (Nakahira 1966; Toyama 1999). It is almost impossible for a female to lay her eggs in another female's breeding nest. Therefore, it will be guaranteed that the eggs and spiderlings hatched from the eggs coexisting with the female in the breeding nest surely belong to the female in the nest; therefore, the female does not need to evolve a system for recognising her own eggs.

Considering the results of the spiderling exchange experiment, a *C. japonicum* female does not distinguish her own spiderlings from those of other *C. japonicum* females. On the other hand, the female clearly discriminates her own spiderlings from those of other congeneric species. However, the female accepts spiderlings hatched from the congeneric eggs lodging with the female in the nest. This indicates that a *C. japonicum* female can discriminate her own spiderlings from those of other species only if the female meets them first in their spiderling stage rather than at the egg stage in the breeding nest. And this mechanism is potentially possibly related to the familiarity (previous association) between parents and offspring (Hepper 1991). Kin recognition and discrimination (Hepper 1991) are known to occur in solitary spiders, *Coelotes terrestris*

(Bessékon 1997) and *Hogna helluo* (Roberts et al. 2003), as well as social spiders, *Delena cancerides* (Beavis et al. 2007) and *Diaea ergandros* (Evans 1998, 1999). The kin discrimination of these spider species is related to predatory or cannibalistic behaviour of the females or juveniles against non-kin individuals. In such a situation, kin recognition and discrimination might be adaptive; however, a *C. japonicum* female did not predate congeneric spiderlings.

In a temporal view of the developmental stages of the spider, the first instar spiderling is the final phase of a female spider's protectiveness, as the second instar eats its own mother in the breeding nest. If a female wishes to avoid being eaten by any organisms other than her own progeny in matrophagy, it is sufficient only to discern her own progeny in the spiderling stage. Therefore, it is reasonable that a *C. japonicum* female discerns her own progeny only in the spiderling stage in the later period of reproduction.

On account of a peculiar characteristic of *C. japonicum* (i.e. matrophagy), we expected that a female should have a definite discrimination system of her own progeny to make sure that she offers herself only to her progeny as a food resource, and that the female would be able to discern her own progeny from a relatively early period of reproduction. Contrary to our expectation, a *C. japonicum* female's ability to discriminate her own progeny from that of others is not so exclusive. In the recognition system of *C. japonicum* revealed in this study, a female will allow herself to become prey for the spiderlings of other conspecific females. The result corresponded with our predictions to some degree. A *C. japonicum* female does not need to discriminate her own spiderlings from those of other conspecific females, because spiderlings of a given female would not have a chance to eat another female in the quite short reproductive period. Considering that a female at least discerns spiderlings of other species and some predatory organisms inhabit sympatrically in the field, the females' ability to recognise others will be evolved only to work as a protection against other organisms intruding into the breeding nest.

Acknowledgements

The authors thank Dr. Masahiro A. Iwasa (Nihon University) and Dr. Yutaka Hironaka (NPO Seitai Koubou) for their helpful comments on the ecological study of spiders.

Disclosure statement

No potential conflict of interest was reported by the authors.

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