

Male–male competition and mating success in the orb-web spider, *Nephila clavata*, with reference to temporal factors

TADASHI MIYASHITA

*Laboratory of Forest Zoology, Faculty of Agriculture, University of Tokyo,
Bunkyo-ku, Tokyo, 113 Japan*

Seasonal occurrence patterns of adults of both sexes, intensity of male–male interactions, and mating success in the spider, *Nephila clavata*, were examined in the field. Adult males began to attend female webs about 2 weeks before female maturation. Large adult males were abundant in the early breeding season, but small males increased later in the season. From the distribution of males among female webs and size relationship of males within a web, male–male interactions seemed to be more intense when most females were still subadult. This was verified by a field experiment in which males were artificially introduced to female webs that were attended by other males. It was found that the probability of introduced males remaining on subadult female webs was lower than that on adult webs. As mating occurred mostly in the period shortly after the female final molt and first male sperm precedence was known in all spiders reported so far, intense male–male competition on subadult female webs seemed to be reasonable. Male longevity had an important influence on the mating success of males with just-molted females. Mating success was also affected by the relative body size of males present in a given period. Since larger males occupied the position closest to females within a web and stayed there longer, relative body size appeared to influence mating success through male–male competition. Female body size at maturation declined with time; hence, males that attained sexual maturity earlier had the advantage of mating with larger and more fecund females. Therefore, early maturation as well as large size seem to be two important traits influencing the reproductive success of males.

Key words: male–male competition; mate guarding; mating success; reproductive success; spider.

INTRODUCTION

Many animals show mate guarding and male–male competition for females. Whether males guard before or after copulation largely depends on sperm precedence, that is first male sperm precedence leads to precopulatory guarding while last male precedence causes postcopulatory guarding. All species of spiders that have been reported so far exhibit a first male sperm priority unlike most other insects (Jackson 1980; Vollrath 1980; Austad 1982; Christenson & Cohn 1988; Watson 1991). Therefore, precopulatory male–male competition was observed in spiders (e.g. Christenson & Goist 1979; Robinson & Robinson 1980; Jackson 1986; Watson 1990). Several authors have demonstrated that

body size affected the result of combat between males, which often ensured successful copulation for winners (Christenson & Goist 1979; Vollrath 1980; Austad 1983; Rubenstein 1987; Watson 1990).

Most of these studies did not deal with the temporal change in intra- and intersexual relations. The carnivorous nature of spiders often constrains their foraging success and hence produces variation in timing of maturation as well as body size (Turnbull 1962; Vollrath 1987). This may cause a change in the number of receptive females, size of potential competitors, and size of mates, which may affect reproductive success of males.

The orb-web spider, *Nephila clavata*, exhibits conspicuous sexual dimorphism in body size; females are about twice as large as males in body length. Previous reports have shown that larger females and males tend to mature sexually earlier

than smaller ones (Miyashita 1990, 1991). Also, in a closely related species, *N. clavipes*, males guard females even after copulation (e.g. Cohn *et al.* 1988). The major objective of the present paper is to clarify the importance of temporal factors on the male–male competition and reproductive success of males. Firstly, seasonal occurrence patterns of adults of both sexes are described. Next, factors that affect male mating success are explored, and finally, temporal change in the intensity of male–male competition is evaluated by field experiments.

METHODS

Nephila clavata is a common univoltine species in Japan and is distributed widely except for Hokkaido, the northernmost main island. After overwintering in the egg stage, eggs hatch in May and spiderlings emerge from egg cocoons in early June in central Japan. Spiderlings live in clusters for about a week and then disperse to live individually. Spiders reach sexual maturity from late August to early October. Oviposition takes place from mid-October to November, and only one egg sac is produced per female in central Japan. Clutch size varies considerably among sites depending on the feeding conditions, the average ranging from 200 to 600 eggs (Miyashita 1992b). Most feeding is observed during daytime and web-building occurs mostly at night (Miyashita 1992a).

Field observations were conducted in the University Forest Experimental Station in Tanashi (UFT), located in the western suburbs of Tokyo. Its elevation is 60 m, and average annual temperature and rainfall are 14.3 °C and 1390 mm, respectively (meteorological report at UFT; 1966–1985). In 1988, preliminary observations of the seasonal occurrence pattern of adults of both sexes were recorded at site B. This site was located at the forest edge near a research building and consisted mainly of evergreen (*Quercus myrsinaefolia*, *Ilex* spp.) and deciduous (*Magnolia kobus*) trees. From late August to early November, all females and males present on the female's web which were found along the forest edge (18 m long × 2 m wide × 2 m high) were counted every 2 to 5 days. All females ($n = 33$) were marked individually with fast-drying paint on the dorsal part of the abdomen and/or legs, and their date of final molt was recorded. In 1989, field

observations were made at site A from late August to early November. Site A was a young red pine plantation (*Pinus densiflora*) with tree height of about 3 m. One to six censuses were taken every day between 10.00 and 17.00 h except on rainy days. At each census, all newly appeared and recently molted female spiders present in a 14 m × 3 m area were marked ($n = 51$) and their body length (cephalothorax–abdomen length) was measured. For males, only adults present on female webs were marked ($n = 104$). The author also recorded on which female's web a male was found and the position of males on that web. The position of males on a web was classified into two groups according to Christenson and Goist (1979); that is hub (near the center of the web) and peripheral males. Behavioral observation of spiders was also conducted on each female's web for a few minutes. If males touched the female's epigynum with their palps, the author checked whether hematodochal bulb contraction occurred. If this was observed, it was regarded as a copulation. In 1990, observations were conducted at sites A and C. Site C was a garden with rather sparse vegetation and consisted of maple and pine trees. The census area at site C was 18 m × 10 m. Census schedules before 7 October were the same as those in 1989, but they were reduced to every 2–4 days thereafter. Numbers of individuals within the two sites were counted and all females and adult males were marked. In addition to these individuals, several spiders which were found at the area surrounding the study sites were also marked from early September. A total of 98 males and 53 females were marked at site A, and 58 males and 34 females at site C. At site A, several subadult males were also marked at random to know when, and at what size, males mature to adulthood. All other observation items were the same as those in the previous year.

To evaluate the dispersion of adult males with respect to females, I used I_δ index as a measure of the aggregation pattern of males (Morishita 1959). I_δ is given as follows:

$$I_\delta = n \times \frac{\sum x_i (x_i - 1)}{N(N - 1)}$$

where x_i is number of males on i th female's web, N and n are total number of males and females, respectively. The distribution is random when I_δ equals unity, uniform and clumped when I_δ is smaller than unity and larger than unity, respec-

tively. The number of males and females used for the calculation of the index in 1988 and 1989 is shown in Fig. 1. In 1990, marked individuals at the area surrounding each site were also included and the total number of individuals is shown in the appendix.

Since average body length of males varied during the course of the breeding season (Fig. 4), relative body length of males was calculated. The breeding season was divided into three periods, each of which was about 10 days in length. Relative body length of

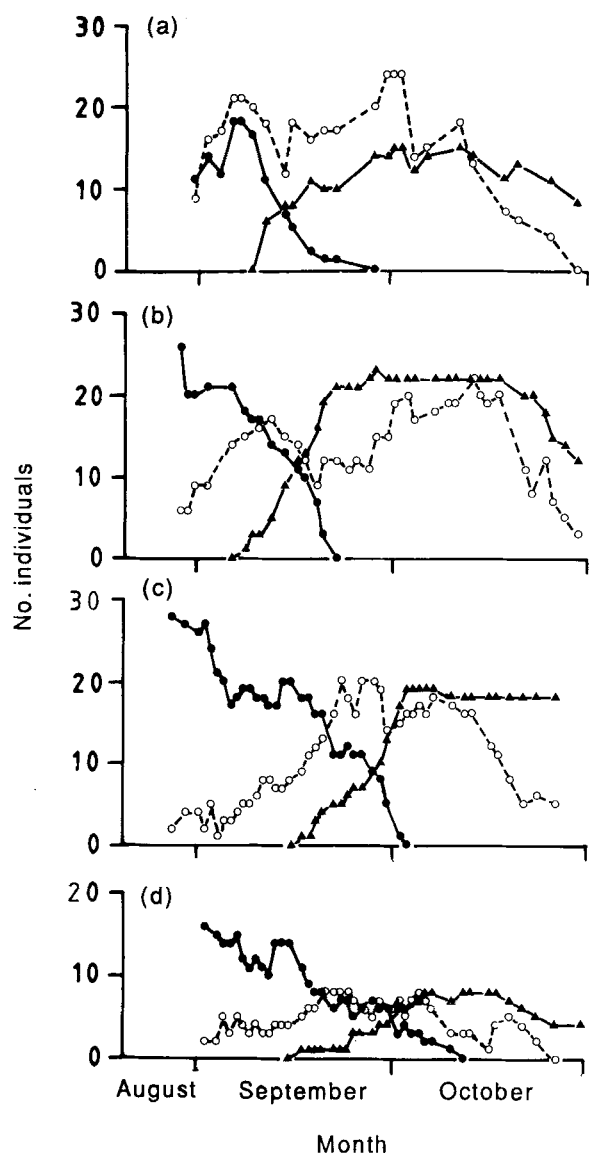


Fig. 1. Seasonal change in the number of adult males (O), subadult females (●), and adult females (▲) at the study sites. (a) Site B in 1988; (b), site A in 1989; (c) site A in 1990; (d), site C in 1990.

a male was the proportion of other males that were smaller than he was during a given period (Elgar & Pierce 1988). The three periods differed among sites or years due to the different maturation period of adult females (89A: to 5 Sept., 6–15 Sept., 16–25 Sept.; 90A: to 9 Sept., 10–19 Sept., 20–30 Sept.; 90C: to 15 Sept., 16–25 Sept., 26 Sept.–5 Oct.). Each male was assigned to one of the three periods depending upon which period was most representative of his life.

The field experiment was performed in UFT in 1990 and 1991. Three periods were involved in this experiment: period 1, when all females were subadult (late August); period 2, when subadult and adult females were present (mid September); and period 3, when all females were adult (early October). Males were collected from the field, marked with a fast-drying color paint, and measured for body length. In periods 1 and 3, each male was introduced to the web of a female which was occupied by either: (i) no male; (ii) one larger male; or (iii) one smaller male. In period 2, each male was introduced to a subadult or an adult female web on which a larger resident than the intruder was already present. The fate of the introduced males on the following day was recorded, that is whether they were absent or present, and if present, whether they occupied the hub position. Cases in which females had disappeared from the web on the following day were excluded from the analysis. All adult females used in this experiment had already copulated before the experiment.

RESULTS

Seasonal patterns of maturation and male attendance on female webs

Females molted to sexual maturity between early September and early October, though this varied among sites and years (Fig. 1). Adult males began to attend female webs from late August, which was nearly 2 weeks before the start of the female's final molting period. This means that males attended both subadult and adult females.

Seasonal pattern of the final molt of males was obtained at site A in 1990 and is presented in Fig. 2, together with that of females. Although the start of the molting period of males was earlier as described

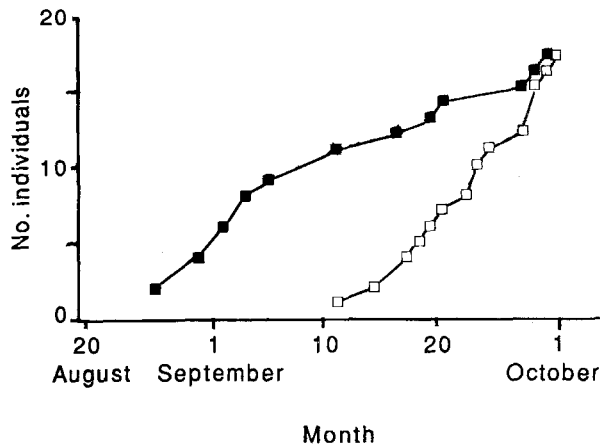


Fig. 2. Seasonal change in the cumulative number of males (■) and females (□) that molted to adulthood at site A, 1990.

before, the end of it was almost the same for both sexes. Levene's test using 'median-log' (Schultz 1985) reveals that the variation was significantly larger in males than in females ($t = 3.14$, $P < 0.005$).

The distribution of males with respect to females tended to be uniform from early to mid-September, and thereafter became random or clumped (Fig. 3). Of fourteen cases which showed statistically significant uniform distributions, twelve were recorded by the early part of the female molting period, which suggests the high intensity of male-male interactions during this period.

Males were classified into three classes based on the body length. Change of their numbers over the season is presented in Fig. 4. In the early season, males of the largest size class were abundant, while none of the smallest class was observed. As the season progressed, large males declined gradually and intermediate and small sized males increased. This can be partly explained by the fact that large males molt to adult earlier than smaller ones (Miyashita 1991). The decline in the number of large males may be caused by their death, since a similar tendency was widely observed outside the study area (T. Miyashita, pers. obs.). Thus the longevity of adult males seems to be shorter than that of females.

Mating frequency

Copulations were observed for 39 males and 38 females, which were the total figures of all the field

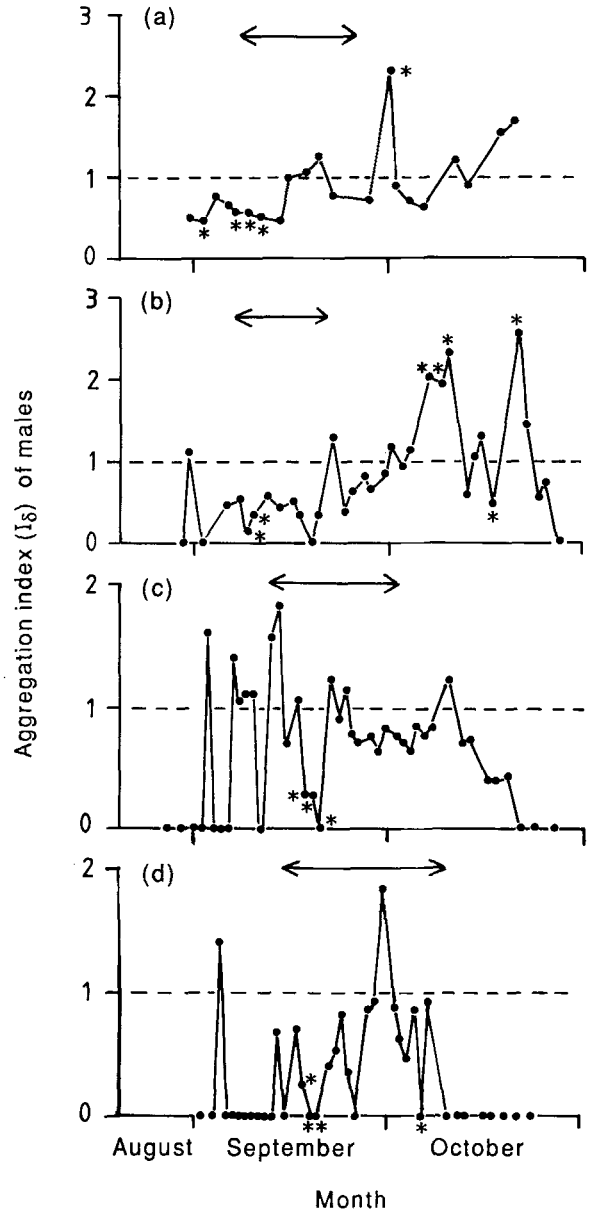


Fig. 3. Seasonal change in the distribution pattern (I_5 -index) of adult males per female web (including both subadult and adult females). Arrows show the range of final molting period of females, and asterisks denote the distribution significantly different from random distribution below 5% level. (a)-(d) labels are the same as for Fig. 1.

surveys. All males mated once while one female mated twice. Matings were observed either within 2 days of the female's final molt or while females were feeding. Six females were observed mating while feeding. Of these females, one was non-virgin before that mating and three were probably non-virgin because males had attended their webs at the time of

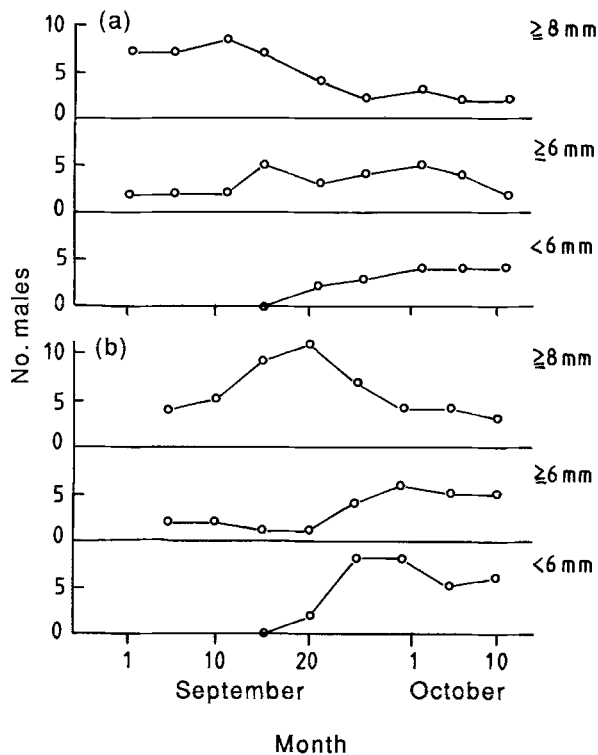


Fig. 4. Seasonal change in the number of adult males of different body length classes. (a) Site A in 1989; (b) site A in 1990.

the final molt. The remaining two had no males at their molt, so they might have been virgin.

The likelihood of a male mating was evaluated by dividing the number observed mating by the total number of males observed during a given period. The same individual at different observation times was counted separately. Most matings were observed within the two days of female final molt (Table 1). Since first male sperm priority was known for a congener *N. clavipes* (Christenson & Cohn 1988), mating with just molted females seems to be important for males.

Male status on female's web

The body lengths of hub and peripheral males were compared in Table 2. The breeding season was divided into two or three parts: the early period in 89A, and the early and middle period in 90A were before and during the female molting period. Hub males were significantly larger than peripheral ones during that period, whereas there was no such difference after the female molting period. This may

imply that size-related hierarchies degenerate with increasing female age.

Days of residence on a female's web were significantly longer for hub males (x_h) than for peripherals (x_p) (89A: $x_h = 3.3$, $n = 112$, $x_p = 1.5$, $n = 48$, $P < 0.001$; 90A: $x_h = 4.5$, $n = 101$, $x_p = 1.8$, $n = 54$, $P < 0.001$; 90C: $x_h = 4.4$, $n = 59$, $x_p = 1.7$, $n = 19$, $P < 0.001$, Mann-Whitney *U*-test). This suggests that peripheral males were banished from the web by hub males or left the web voluntarily to search for another female.

Correlates of mating success

Four measurements for males were chosen as possible correlates of male mating success, that is, date of first appearance in the study site, longevity (number of days from their appearance to disappearance at the study site in general), body length, and relative body length. Males that appeared prior to the end of the female's final molting period were used for the analysis, because mating with just molted females seems to be important for male reproductive success.

Table 3 compares traits of males that copulated with just-molted females and those that did not copulate. The date of first appearance did not differ between the two groups of males on three occasions. Males that copulated had greater longevity than those that did not copulate. Also, copulated males were significantly larger than those that did not copulate in 89A and 90A for body length and relative body length, while only the latter was significant in 90C. Thus, relative body length appeared to be more important for mating success of males.

The relationship between body length and longevity is presented in Table 4. In 89A, the correlation was not significant, while it was significant in 90A and 90C.

Body size of mates

Since it has already been reported that the size of females at their final molt decreased with time (Miyashita 1990), early maturing males may mate with larger females. Thus, the relation between date of appearance of males in the study site and body length of their mates was examined (Fig. 5). A significant negative correlation was found in two out of three instances (89A: $r = -0.762$, $P < 0.005$; 90A: $r = -0.688$, $P < 0.01$; 90C: $r = -0.613$, NS).

Table 1. Seasonal change in mating frequency of males (%) ((no. observed mating)/(no. observed males) × 100) of *N. clavata*

Female status when mating	September					October		Mean	
	6–10	11–15	16–20	21–25	26–30	1–5	6–10		11–15
89A									
Molt	4.5	9.6	4.4	0.9	0.0	0.0	0.0	0.0	2.4
Feed	0.0	0.0	0.0	0.9	0.9	1.8	0.0	0.0	0.5
<i>n</i>	111	104	45	108	116	57	93	144	
90A									
Molt	—	1.9	7.3	2.3	5.3	0.6	0.0	0.0	2.2
Feed	—	0.0	0.0	0.0	0.0	0.3	0.0	0.6	0.1
<i>n</i>		53	82	172	113	352	130	168	
90C									
Molt	—	—	—	7.1	2.9	2.7	0.0	0.0	1.6
Feed	—	—	—	0.0	0.0	1.4	0.0	0.0	0.2
<i>n</i>				56	35	74	12	10	

Molt: within 2 days of the molt of females; feed: while females are feeding; *n*: total no. males observed; —: no adult females are present.

Table 2. Comparison of body length (mean ± SD (mm)) of hub-males and peripheral males by Wilcoxon's test.

	89A		90A		
	to Sept. 20	from Sept. 21	to Sept. 20	Sept. 21–30	from Oct. 1
Hub	8.7 ± 1.1	6.8 ± 1.2	8.3 ± 0.6	7.6 ± 1.0	5.9 ± 1.2
Peripheral	7.5 ± 1.1	6.0 ± 1.0	7.4 ± 0.5	6.4 ± 1.4	5.3 ± 1.3
<i>P</i>	< 0.01	> 0.05	< 0.02	< 0.03	> 0.1
<i>n</i>	13	11	8	9	14

Experiment

Table 5 shows the result of the experiment.

Period 1: the probabilities that smaller intruders occupy the hub position and that they remain on the web were significantly lower than those of larger intruders. The fates of intruders with a small resident and without a resident were very similar.

Period 2: introduced males had a lower probability of remaining on subadult than on adult female webs, while they had little chance of occupying the hub position on the web at either stage of the females.

Period 3: smaller intruders had a lower probability of occupying the hub position than larger intruders, which was consistent with the result in period 1. However, the probability of remaining on webs was not significantly different between small and large intruders, which was inconsistent with the result in period 1. Also, there was no difference in the

probability of remaining on webs with and without resident males.

The above results can be summarized as: (i) whether intruders can remain on subadult female webs was largely affected by the relative body size between intruders and residents, but not so on adult female webs; and (ii) whether intruders can occupy the hub position was determined by the relative size irrespective of the female stage. These results suggest the strong male–male competition for virgin females and the importance of relative body size.

DISCUSSION

Mating chance and male–male competition

Mating in this species was restricted to two periods: shortly after the female's final molt and while

Table 3. Comparison of several traits (mean \pm SD) between copulated and not-copulated males

Site		Copulated	Not-copulated	P
89A	DE	36.7 \pm 6.5	40.2 \pm 7.6	NS**
	LN*	13.5	3.1	< 0.001
	BL	8.6 \pm 1.0	7.7 \pm 1.0	< 0.025
	RBL	0.60 \pm 0.19	0.38 \pm 0.30	< 0.025
	n	13	23	
90A	DE	44.1 \pm 6.8	48.3 \pm 8.7	NS
	LN*	18.9	5.0	< 0.001
	BL	8.0 \pm 0.8	6.7 \pm 1.3	< 0.003
	RBL	0.72 \pm 0.18	0.38 \pm 0.26	< 0.001
	n	13	36	
90C	DE	47.3 \pm 8.2	50.1 \pm 9.1	NS
	LN*	14.0	4.9	< 0.001
	BL	7.3 \pm 1.1	6.7 \pm 0.8	< 0.1
	RBL	0.63 \pm 0.23	0.42 \pm 0.28	< 0.05
	n	7	28	

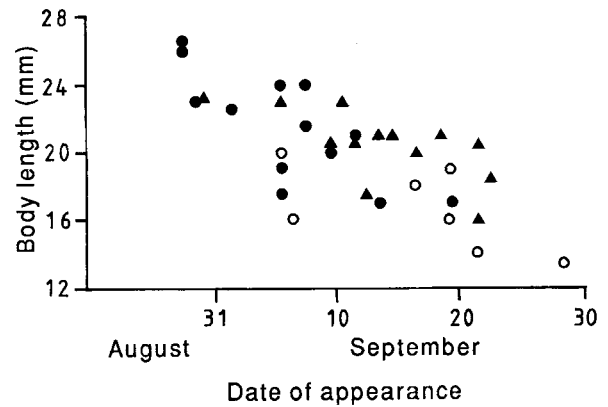
*Only mean values are shown because distributions are highly skewed; ** $P > 0.1$. DE: date of first appearance (days from August 1); LN: longevity at the site (days); BL: body length (mm); RBL: relative body length; n: sample size. Statistical test was performed by *t*-test or *U*-test (for LN).

Table 4. Correlation coefficients between body length or relative body length and longevity of males in the study sites

		r	P	n
89A	BL	0.247	NS	36
	RBL	0.270	NS	36
90A	BL	0.258	< 0.1	49
	RBL	0.418	< 0.005	49
90C	BL	0.452	< 0.01	36
	RBL	0.344	< 0.05	36

Abbreviations the same as for Table 3.

females were feeding. This is consistent with the observations of two congeners, *N. maculata* and *N. clavipes* (Robinson & Robinson 1973; Christenson *et al.* 1985). Females did not construct orb-webs and were not active during the 2 days after their final molt. While feeding, they are relatively insensitive to disturbance. Since males are much smaller than females and they have no apparent courtship behaviour, mating may be restricted to the time when females are not aggressive. Mating success with

**Fig. 5.** Relationship between the date of the first appearance of adult males at the study sites and body length of their mates. (●) Site A in 1989; (▲) site A in 1990; (○) site C in 1990.

females shortly after their final molt appeared to be important for the reproductive success of males because most of the matings concentrated on that period and first male sperm priority was reported in *N. clavipes* (Christenson & Cohn 1988). Thus, it is advantageous for males to mature earlier than females and attend webs of subadult females. On the other hand, adult females are usually non-virgin in the field, having already mated just after the final molt. Adult females may not be as valuable for males as subadult females, and hence male–male competition may be more intense for subadult females. This was supported by field observations; that is, the uniform distribution of males among females changed into random or clumped and the size difference between hub and peripheral males became smaller after the female's molting period. Also, field experiments provided more direct evidence that introduced males remained on adult female webs more frequently than on subadult webs. This was probably caused by the strong agonistic behavior of resident males, not by the voluntary departure of intruders from the web, because voluntary departure from virgin female webs would bear few benefits for the intruders when both virgin and non-virgin females are present (period 2 in Table 5). Thus, it appears that the tenacity of males on female webs and intensity of male–male interaction changes with the age of females.

Unlike the present results, the male–male interactions for subadult females were no more intense than those for adult females in *N. clavipes* (Cohn *et al.*

Table 5. Fates of introduced males on the day following their introduction. Left-hand tables: whether introduced males 'remained' on the web or 'disappeared'; right-hand tables: whether introduced males became 'hub males' or not

Period 1 (All females were subadult)			
Fate	I < R	I > R	R absent
Remained	3	6	6
Disappeared	5	0	1
(I < R) vs (I > R); $P = 0.028$ (I < R) vs (R absent); $P = 0.084$ (I > R) vs (R absent); $P = 0.462$			

Fate	I < R	I > R	R absent
Hub male	0	6	6
not	8	0	1
(I < R) vs (I > R); $P < 0.001$ (I < R) vs (R absent); $P = 0.001$ (I > R) vs (R absent); $P = 0.462$			

Period 2 (Sub-adult and adult females were present. Intruders were always smaller; I < R)		
Fate	Subadult	Adult
Remained	1	7
Disappeared	10	3
(Sub-adult) vs (Adult); $P = 0.007$		

Fate	Subadult	Adult
Hub male	1	0
not	10	10
(Sub-adult) vs (Adult); $P = 0.476$		

Period 3 (All females were adult)			
Fate	I < R	I > R	R absent
Remained	5	7	6
Disappeared	3	1	1
(I < R) vs (I > R); $P = 0.285$ (I < R) vs (R absent); $P = 0.339$ (I > R) vs (R absent); $P = 0.267$			

Fate	I < R	I > R	R absent
Hub male	0	5	6
not	8	3	1
(I < R) vs (I > R); $P = 0.013$ (I < R) vs (R absent); $P = 0.001$ (I > R) vs (R absent); $P = 0.339$			

I < R: introduced males were smaller; I > R: introduced males were larger; R absent: residents were absent at the time of introduction. Statistical test between rows were made by Fisher's Exact probability test.

1988). The reason why the results of the two *Nephila* species disagree is not yet clear.

Enhanced male-male competition on virgin female webs was reported by Austad (1983) and Watson (1990) in two *Linyphid* spiders. Assessment of virginity by males was made by pseudocopulation (intromission with no sperm transfer, Austad 1983) or by female behavior (Jackson 1980; Watson 1990). In *N. clavata*, pseudocopulation is unlikely because intromission with subadult females is impossible. Female behavior and/or sex pheromones seem to be the possible cues for virginity.

In spite of the first male sperm priority, why do males of *N. clavata* defend non-virgin females? Christenson (1989) reported that males of *N. clavipes* depleted sperms after copulation with just-molted females. If this is true for *N. clavata*, there is little reason for copulated males to search for another mate.

Mating success

Males that mated with just-molted females were larger and their longevity at the study site in general was longer than that of non-mated males. The statistical significance of longevity was so high in all study sites that longevity may be a more direct factor for male mating success. Longevity and days of residence on a web were correlated with body size; hence, it appears that body size influences mating success through competition among males. Males of large size appeared earlier but they gradually disappeared, so that average size of males in the sites decreased with time. Therefore male body size relative to potential competitors in a given period may be a more reliable predictor of mating success (Table 3).

Variance in the date of final molt was larger in males than in females. This might reflect 'making

the best of a bad situation' by males with poor foraging success; that is, such males delay the date of final molt to enhance the chance of mating by increasing their relative body size. However, those males must have lower reproductive success compared with males with high foraging success. In contrast, males mature more synchronously than females in the sierra dome spider *Linyphia litigiosa* (Watson 1990). This suggests that being large may be even more important than early maturation in *N. clavata* and vice versa in sierra dome spiders.

Among males that mated with just-molted females, those that appeared early in the season mated with larger females (Fig. 5). This is because large females tend to mature early in the season. Since there was a strong positive correlation between female body size and fecundity (Miyashita 1990), early maturation in males has a potential advantage in fathering more offspring than late maturation. The extent of variation in fecundity per female, for example, ranged from 335 to 971 eggs with the average of 606 at site A in 1990 (estimated by the size–fecundity equation presented by Miyashita 1990). Thus, selection favors males of large size and early maturation. As reported in other spiders (e.g. Vollrath 1987), well-fed males molted to adulthood earlier and at a larger size than poorly-fed males in *N. clavata* (Miyashita 1991). This implies that the two important traits for reproductive success of males, large size and early maturation, are positively correlated and are not apparently in a trade-off relationship due to the nutritional effects during nymphal stages. However, it seems highly possible that there is a negative genetic correlation between timing of maturation and size at maturation, which suggests that phenotypic evolution of these traits may already have reached a state of equilibrium.

ACKNOWLEDGEMENTS

I thank T. E. Christenson, P. J. Watson, K. Tanaka for helpful comments on an earlier version of the manuscript, and S. Lawson for improving the English. I also thank K. Katagiri and K. Furuta for encouragement during the course of this study, and staff of the Tokyo University Forest Experimental Station at Tanashi for providing undisturbed re-

search sites. This work was supported in part by a grant (02760088) from the Ministry of Education, Science and Culture, Japan.

REFERENCES

- AUSTAD S. N. (1982) First male sperm priority in the bowl and doily spider, *Frontinella pyramitela* (Walckenaer). *Evolution* **36**: 777–85.
- AUSTAD S. N. (1983) A game theoretical interpretation of male combat in the bowl and doily spider (*Frontinella pyramitela*). *Anim. Behav.* **31**: 59–73.
- CHRISTENSON T. E. (1989) Sperm depletion in the orb-weaving spider *Nephila clavipes*. *J. Arachnol.* **17**: 115–18.
- CHRISTENSON T. E., BROWN S. G., WENZL P. A., HILL E. A. & GOIST K. C. (1985) Mating behavior of the golden-orb-weaving spider, *Nephila clavipes*: I. Female receptivity and male courtship. *J. Comp. Psychol.* **99**: 160–6.
- CHRISTENSON T. E. & COHN J. (1988) Male advantage for egg fertilization in the golden orb-weaving spider, *Nephila clavipes*. *J. Comp. Psychol.* **102**: 312–18.
- CHRISTENSON T. E. & GOIST K. C. (1979) Costs and benefits of male–male competition in the orb-weaving spider, *Nephila clavipes*. *Behav. Ecol. Sociobiol.* **5**: 87–92.
- COHN J., BALDING F. V. & CHRISTENSON T. E. (1988) In defence of *Nephila clavipes*: Postmate guarding by the male golden orb-weaving spider. *J. Comp. Psychol.* **102**: 319–25.
- ELGAR M. A. & PIERCE N. E. (1988) Mating success and fecundity in an ant-tended Lycaenid butterfly. In: *Reproductive Success* (ed. Clutton-Brock) pp. 59–75. The University of Chicago Press, Chicago.
- JACKSON R. R. (1980) The mating strategy of *Phidippus johnsoni* (Araneae: Salticidae): II. Sperm competition and the function of copulation. *J. Arachnol.* **8**: 217–40.
- JACKSON R. R. (1986) Cohabitation of males and juvenile females: A prevalent mating tactic of spiders. *J. Nat. Hist.* **20**: 1193–1210.
- MIYASHITA T. (1990) Decreased reproductive rate of the spider, *Nephila clavata*, inhabiting small woodlands in urban areas. *Ecol. Res.* **5**: 341–51.
- MIYASHITA R. (1991) Direct evidence of food limitation for growth rate and body size in the spider *Nephila clavata*. *Acta Arachnol.* **40**: 17–21.
- MIYASHITA T. (1992a) Variability in food consumption rate of natural populations in the spider, *Nephila clavata*. *Res. Popul. Ecol.* **34**: 15–28.

- MIYASHITA T. (1992b) Food limitation of population density in the orb-web spider, *Nephila clavata*. *Res. Popul. Ecol.* 34: 143–53.
- MORISHITA M. (1959) Measuring of the dispersion of individuals and analysis of distributional patterns. *Mem. Fac. Sci. Kyushu Univ., Ser. E* 2: 215–35.
- ROBINSON M. H. & ROBINSON B. (1973) Ecology and behavior of the giant wood spider *Nephila maculata* (Fabricius) in New Guinea. *Smiths. Contr. Zool.* 149: 1–76.
- ROBINSON M. H. & ROBINSON B. (1980) Comparative studies of the courtship and mating behavior of tropical araneid spiders. *Pacific Insects Monographs* 36, Honolulu, Bishop Museum.
- RUBENSTEIN D. I. (1987) Alternative reproduction tactics in the spider *Meta segmentata*. *Behav. Ecol. Sociobiol.* 20: 229–37.
- SCHULTZ B. B. (1985) Levene's test for relative variation. *Syst. Zool.* 34: 449–56.
- TURNBULL A. L. (1962) Quantitative studies of the food of *Linyphia triangularis* Clerck (Araneae: Linyphiidae). *Can. Entomol.* 94: 1233–49.
- VOLLRATH F. (1980) Male body size and fitness in the web-building spider *Nephila clavipes*. *Z. Tierpsychol.* 53: 61–78 (in German).
- VOLLRATH F. (1987) Growth, foraging and reproductive success. In: *Ecophysiology of Spiders* (ed. W. Nentwig) pp. 357–70, Springer-Verlag, Berlin.
- WATSON P. J. (1990) Female-enhanced male competition determines the first mate and principal sire in the spider *Linyphia litigiosa* (Linyphiidae). *Behav. Ecol. Sociobiol.* 26: 77–90.
- WATSON P. J. (1991) Multiple paternity and first mate sperm precedence in the sierra dome spider, *Linyphia litigiosa* Keyserling (Linyphiidae). *Anim. Behav.* 41: 135–48.

APPENDIX I

Number of males and females used for calculating aggregation index (I_g -index) of males per female at sites A and C in 1990

90A																						
Date	Aug 2	29	31	Sep 1	2	3	4	5	6	7	8	9	10	11	12	13	14	16	17	18	19	21
Sub-adult ♀	28	27	26	27	24	24	23	20	21	22	23	23	23	21	21	25	24	22	22	20	19	14
Adult ♀	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	2	2	4	6	7
Adult ♂	2	4	5	3	6	2	4	5	6	7	7	7	10	10	8	8	9	10	14	14	15	20

90B																						
Date	22	23	24	25	27	28	29	Oct 1	2	3	4	5	6	9	11	12	15	16	18	20	22	25
Sub-adult ♀	13	14	12	12	10	9	6	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Adult ♀	7	8	10	11	13	14	17	22	24	24	24	24	24	23	23	23	23	23	23	23	23	23
Adult ♂	23	22	19	22	24	23	19	18	19	20	22	20	22	18	22	20	16	16	11	8	9	8

90C																						
Date	Sep 1	3	4	5	6	7	8	9	10	11	12	13	14	16	17	18	19	21	22	23	24	25
Sub-adult ♀	16	15	14	16	17	14	15	16	15	15	19	19	19	15	13	13	13	9	8	8	6	7
Adult ♀	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	2	4	4	7	7
Adult ♂	2	2	5	3	5	4	6	6	5	6	7	8	7	10	11	9	12	11	10	10	9	6

90D																	
Date	27	28	29	Oct 1	2	3	4	5	6	9	11	12	15	16	18	20	22
Sub-adult ♀	6	5	5	2	2	2	2	1	1	1	0	0	0	0	0	0	0
Adult ♀	7	8	8	10	11	11	11	12	12	9	10	10	10	10	10	10	10
Adult ♂	6	8	7	11	7	8	10	8	8	4	4	4	2	4	5	4	3