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GROWTH, EGG PRODUCTION, AND POPULATION DENSITY OF THE SPIDER, *NEPHILA CLAVATA* IN RELATION TO FOOD CONDITIONS IN THE FIELD

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INTRODUCTION

It has been reported by many authors that arthropod predators are faced with food shortage in the field (MIYASHITA, 1968a, b; LAWTON, 1971; ANDERSON, 1974; WISE, 1975, 1979; MATSURA et al., 1975; MATSURA and MOROOKA, 1983; LENSKI, 1984; BAARS and VAN DIJK, 1984). Among them spiders are thought to be far from satiated food condition (MIYASHITA, 1968; ANDERSON, 1974), suggesting that their growth and reproduction are largely affected by the amount of food available to them. FUJII (1972) obtained the growth rates of the spider, *Agelena opulenta* at two different sites in a field and found that the difference in the rates was probably due to the difference in food conditions at the two sites. However, little has been known about the effects of food condition on growth and reproduction in the field, which may determine the density of spiders in the subsequent generations.

In the present study, seasonal changes in the population density, growth process and egg production of the spider, *Nephila clavata* KOCH, were examined and the effects of food abundance on the spider population were discussed based on these results. This species is one of the large orb-weaving spiders which rebuilds its web almost every day. According to NAKAMURA (1982), the group of spiders that renews webs frequently requires large amount of food for growth. This means that the effects of food shortage can be easily observed on these spiders. Therefore, *N. clavata* seems to be favorable subject for the study of the influence of food condition on a spider population.

MATERIALS AND METHODS

The species

Nephila clavata is widely distributed in Japan except for Hokkaido and is one of the biggest and most common spiders that build orb webs. It overwinters in the egg stage and eggs hatch in May. The second instar spiderlings emerge from egg cocoons and live in a cluster. The third instar spiderlings disperse from the cluster in June. They mature in September and females lay eggs from mid-October to November.

Study area

Field study was conducted at the Nature Conservancy of National Institute of Agro-

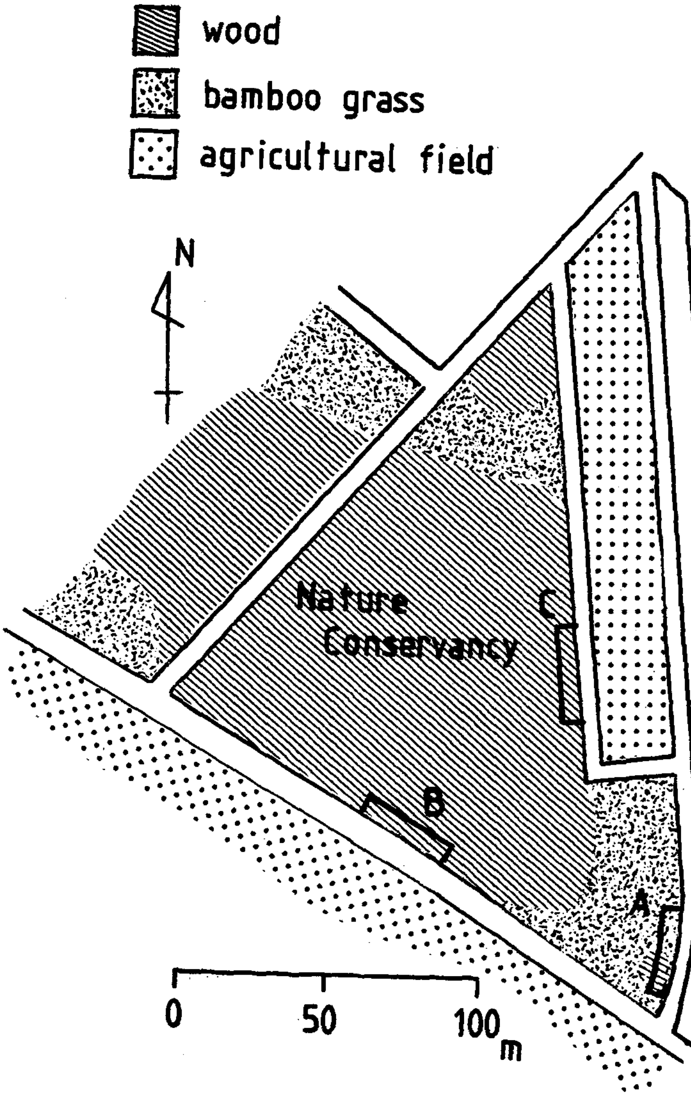

Fig. 1. Map of the study area. Rectangules show the three study plots examined.

environmental Sciences in Ibaraki Prefecture in 1983 and 1984 (Fig. 1). The Nature Conservancy covered an area of about 1.8 ha. In the study area, Japanese red pine, *Pinus densiflora*, and Japanese red cedar, *Cryptomeria japonica* formed the upper layer of vegetation and the undergrowth consisted of *Pleioblastus chino* (a species of bamboo grass), *Quercus serrata*, *Viburnum dilatatum*, *Castanea crenata*, and so on.

Mean monthly temperatures at National Institute of Agro-environmental Sciences from February 1983 to October 1984 are shown in Fig. 2. The mean temperatures from winter to spring were consistently lower in 1984 than those in 1983.

Three study plots, designated A, B and C were established as shown in Fig. 1. Plot A was an open habitat dominated by *P. chino* and plots B and C were located along the

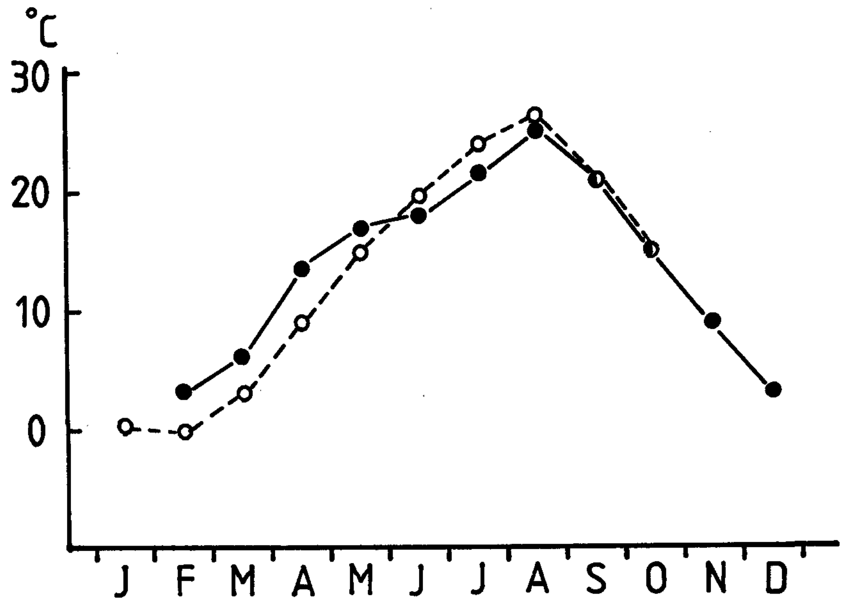

Fig. 2. Mean monthly temperatures at National Institute of Agro-environmental Sciences in 1983 (-●-) and 1984 (--○--).

forest edge.

Methods

The changes in the population density were obtained at two quadrats of 12 m×2 m which were established within study plots A and B, respectively. At each quadrat, the number of *N. clavata* found within a height of 2 m above the ground was recorded once a week from mid-June to early November.

Growth process of spiders was analyzed in the following ways. First, to measure the body length of those on webs, photos were taken from behind the spiders. These were magnified by a profile projector and body length of spiders was measured. In this paper, the body length means the sum of cepharothorax length and abdomen length. The photos were taken every other week in plots A and B in 1983 and in all three plots in 1984. The number of spiders photographed in each plot was about 20 by the end of August, while it was 10 to 15 thereafter because the spiders became scarcer.

Live body weights of these spiders were estimated from their body lengths. For this estimation, spiders were collected from the outer field of the Nature Conservancy, and the body lengths and weights were measured. The body weights of spiders in plots were calculated from the regression equation between these two measurements. As the abdomen of a gravid female swelled conspicuously, the body length-weight relationships were quite different between non-gravid and gravid females. Therefore, a different equation was needed for gravid females.

Gravid females which were collected from the outer field of the Nature Conservancy were dissected to count the number of eggs, which produced the regression equation between body length and number of eggs. However, as the eggs were often broken during dissection, their weight could not be measured. Therefore, the relationship between number of eggs and live weight per egg was estimated from egg cocoons already deposited in the field.

Potential prey abundance in study plot was estimated using paper sticky traps (90 cm × 35 cm). Two sticky traps were established in each of plot A and B, in 1983, but only one in each plot in 1984. The top of the trap was placed at a height about 1.8 m above the ground. These were left for three days in the field and then brought back to the laboratory.

Proportion of the number of spiders which were feeding to the total number of individuals observed was used to estimate the relative food abundance of spiders (Waldorf,

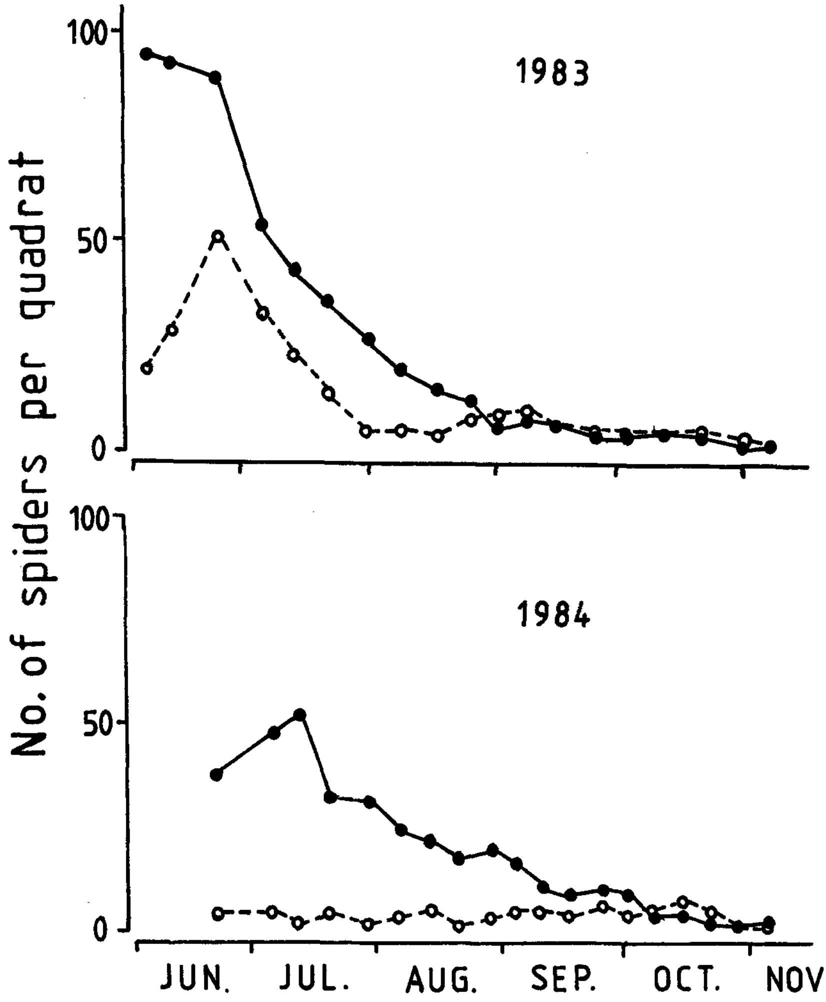

Fig. 3. Seasonal changes in the number of individuals per quadrat in plot A (-●-) and B (--○--).

1976; Horton and Wise, 1983; Smith, 1983). In the present paper, this proportion is termed "feeding frequency". The feeding frequency was measured twice in 1983 and eight times in 1984.

Results

Population density

Figure 3 shows seasonal changes in the number of individuals per quadrat in plots A and B. In both years, the number of individuals in plot A was much greater than that

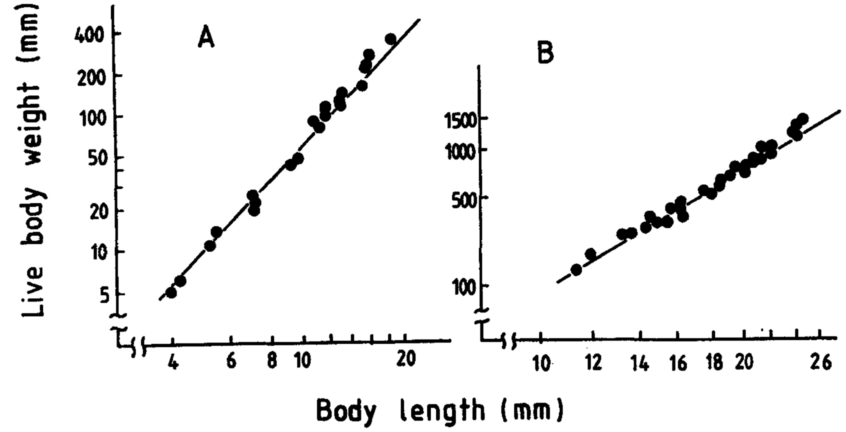

Fig. 4. Relationships between body length and live body weight in non-gravid spiders (left) and gravid females (right).

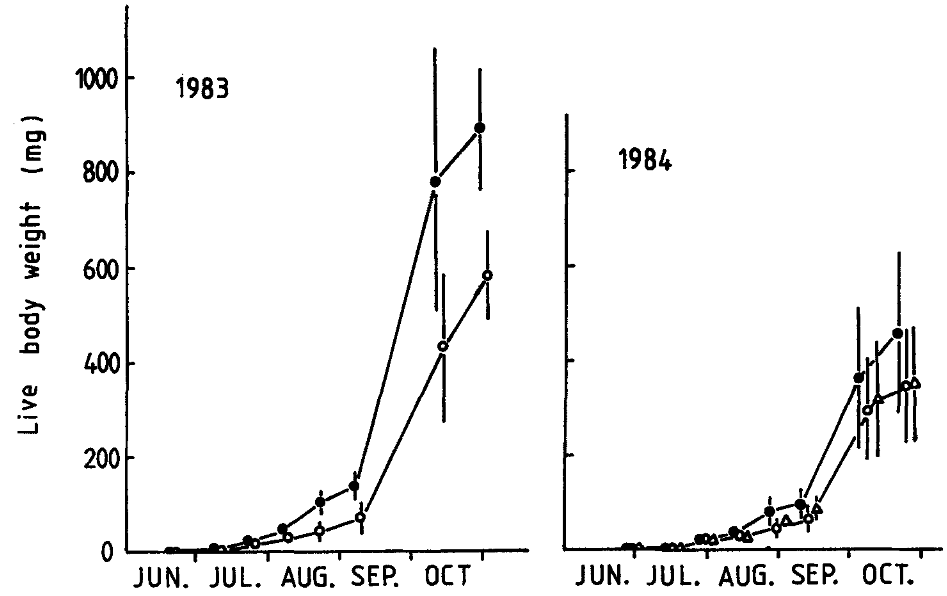

Fig. 5. Seasonal changes in the mean body weight of spiders in plot A (●), B (○) and C (△).

in plot B during the early part of the season. However, the difference became less after September when the spiders began to mature, indicating that the number of adult had little relation to the number of juveniles.

Growth

The relationships between body length and live body weight in non-gravid spiders and gravid females are shown in Figure 4. The regression lines for non-gravid spiders and gravid females, respectively, are as follows:

$$\ln W = 2.518 \ln L - 1.652 \ (r = 0.913,\ p < 0.001)$$
$$\ln W = 2.786 \ln L - 1.739 \ (r = 0.990,\ p < 0.001)$$

where L is the body length and W is the live body weight. Seasonal changes in the mean live body weight of spiders in each plot were estimated using these equations (Fig. 5). The mean body weight increased slowly until mid September, more rapidly thereafter. This rapid increase after mid September was due to egg maturation, indicating that females consumed much more food during this period than before. In 1983, spiders

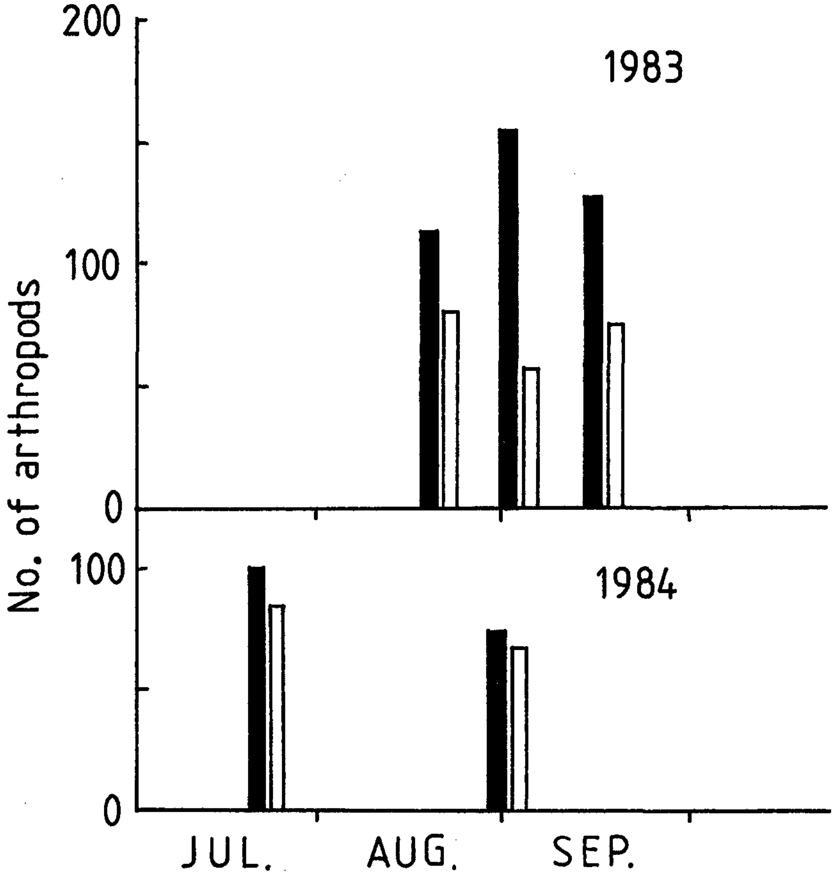

Fig. 6. The number of arthropods captured by sticky traps in plot A (■) and B (□).

grew significantly larger ($p<0.05$) in plot A than in plot B from August. This was probably because an abundance of leguminosean flowers attracted many hymenopterans and dipterans to this plot. In 1984, the growth rates were not significantly different among the plots. The mean body weights in October in 1984 were lighter than those in 1983. Probably both the lower availability of food (Fig. 7) and the delay of spiderling emergence from egg cocoons due to lower spring temperatures in 1984 (Fig. 2) were responsible for this.

Relative food abundance

The number of arthropods captured by sticky traps in plot A was greater than that in plot B in 1983, but the difference was not so great in 1984 as shown in Fig. 6. The feeding frequencies were also higher in plot A than those in plot B in 1983, but they did not greatly differ in 1984 (Fig. 7). These results agreed well with the results in the increase in body weight (Fig. 5). The feeding frequencies declined in August. Though the reason is not clear, it may be related to lower activity in summer of prey or predators, or both.

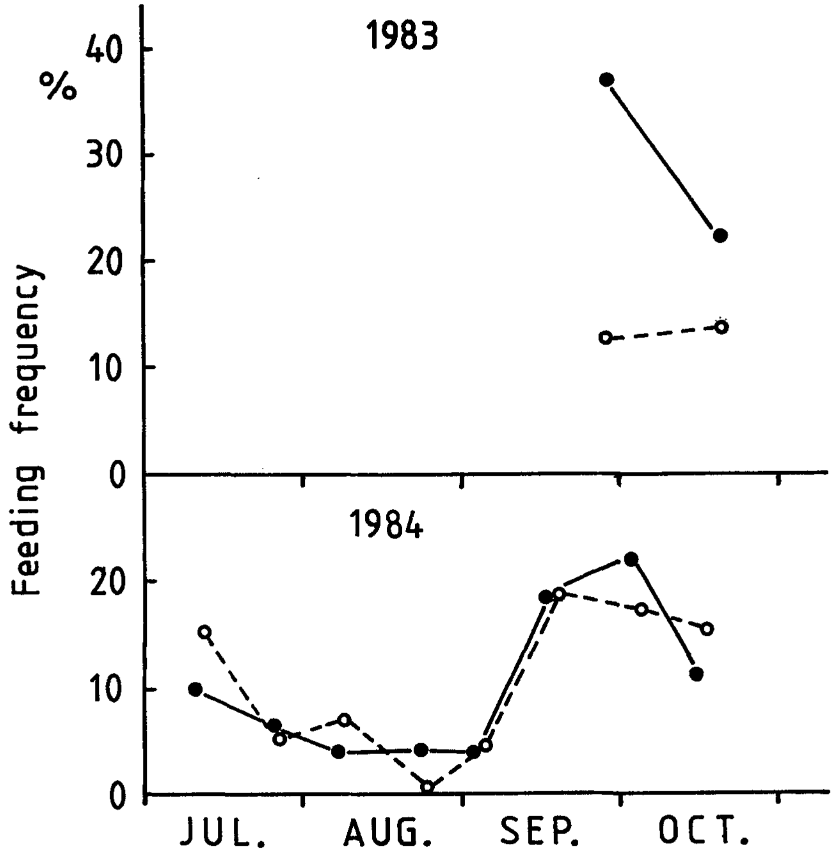

Fig. 7. Feeding frequencies of *N. clavata* in plot A (-○-) and B (--●--).

Egg production

Figure 8 shows changes in the proportion of gravid females to total females examined. From early to mid October, the percentages of gravid females in plot A in 1983 were much higher than those in plot B in 1983 and in all the plots in 1984: in early October, half of the females were already gravid in plot A in 1983, whereas only less than 10% were gravid in the other plots. This result indicates that females which have lived in a habitat with abundant food resource became gravid earlier.

Frequency distributions of the body lengths of females on September 26, October 8

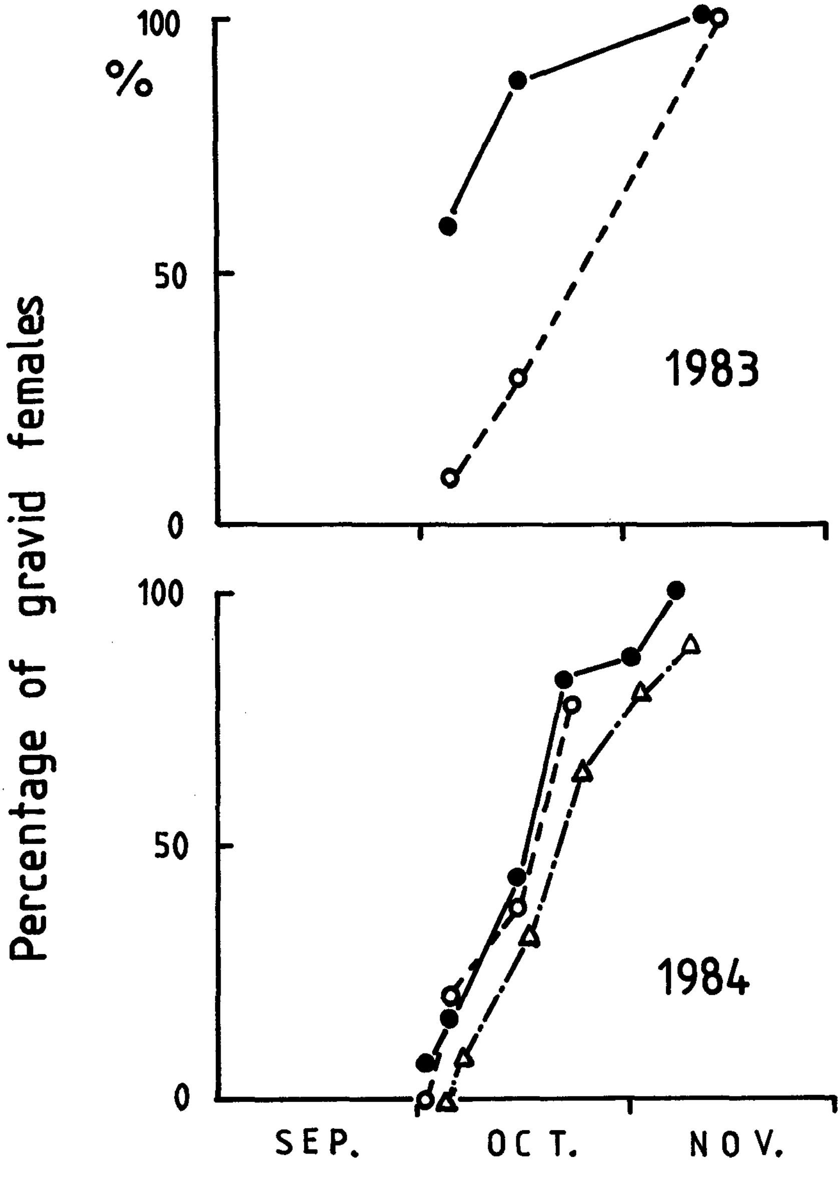

Fig. 8. Changes in the percentage of gravid females in plot A (-●-), B (--○--) and C (---△---).

and October 22 in 1984 are shown in Fig. 9. Since the growth patterns were similar in the three plots this year (Fig. 5), the distributions are shown collectively. Although very large individuals were present on September 26, no female was gravid, whereas the large females were gravid on October 8, and small individuals (about 11 mm in body length) also became gravid by October 22. These results suggest that the time of egg maturation is determined not only by body size but also by the length of development period. Therefore, even small individuals could become gravid with the passage of time.

Figure 10 shows the relationship between body length and number of eggs in gravid females. Since *N. clavata* lay only one egg mass in its life in this study area, the number of eggs presented in this figure represents the total number produced by a single female. The number of eggs was significantly correlated with the body length; the regression equation between the two was

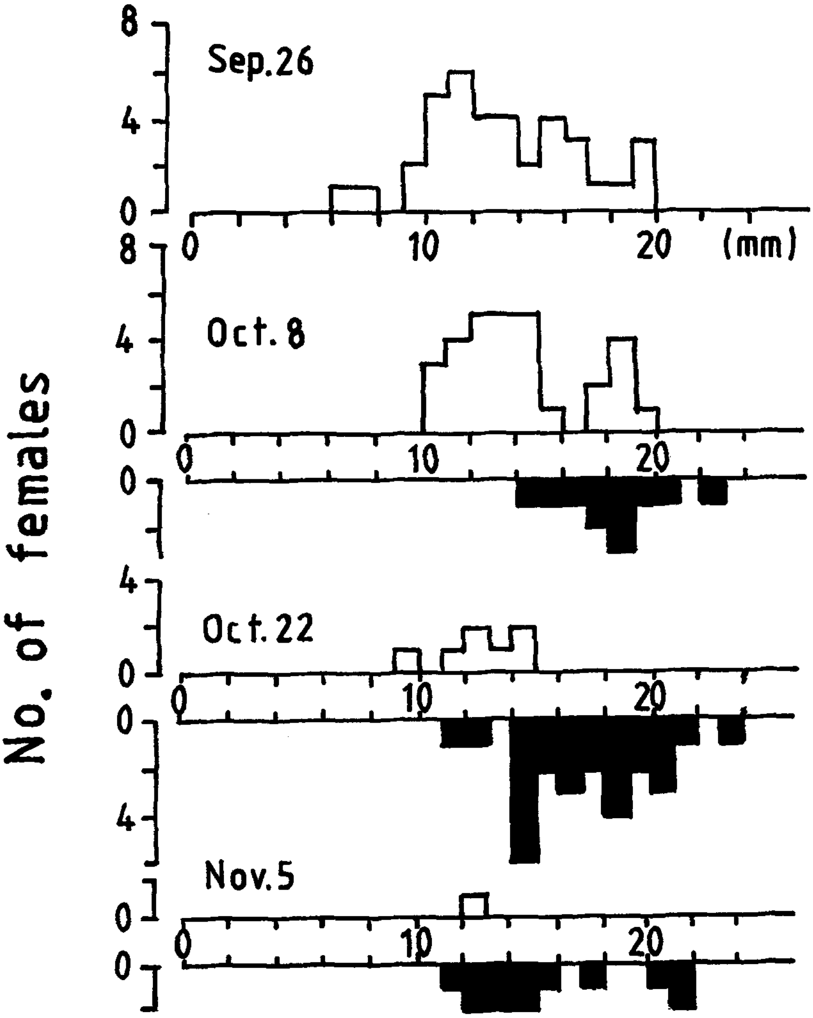

Fig. 9. Frequency distributions of the body lengths of non-gravid (□) and gravid (■) females in 1984.

$$\ln N = 2.245 \ln L - 0.503 \quad (r = 0.944, p < 0.001)$$

where N is the number of eggs and L is body length.

Figure 11 shows the relationship between number of eggs in an egg mass and live weight per egg. Live weight per egg was calculated from weight of an egg mass divided by the number of eggs. The regression equation was

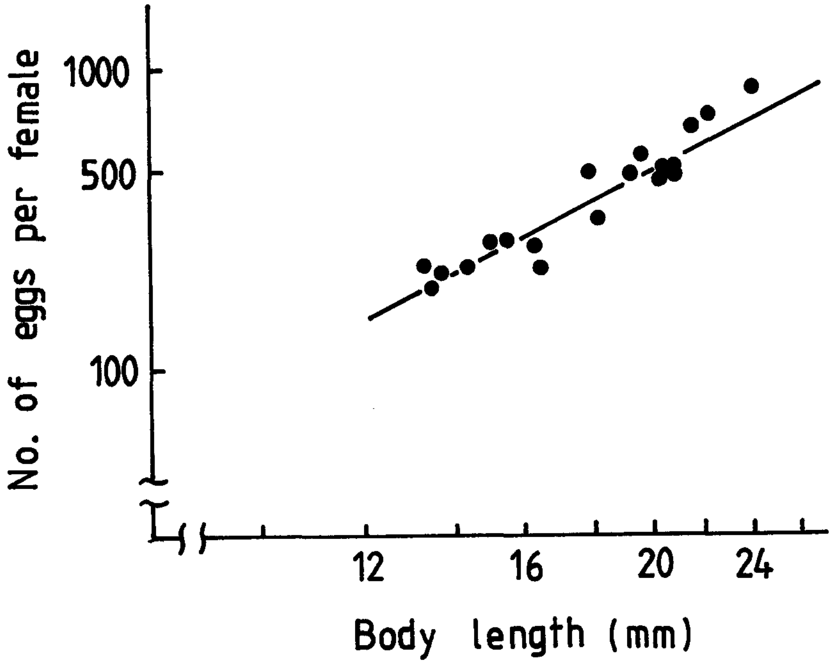

Fig. 10. Relationship between body length and number of eggs in adult females.

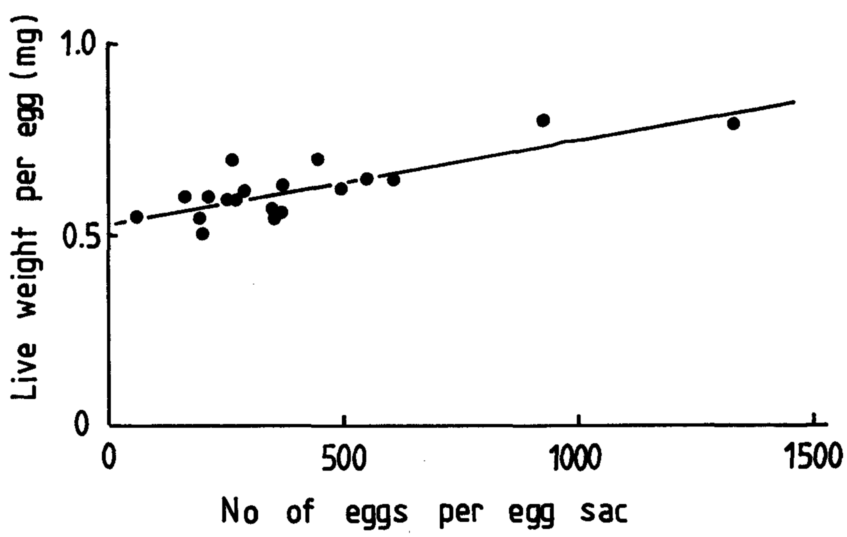

Fig. 11. Relationship between the number of eggs in an egg mass and live weight per egg.

Table 1. Mean numbers of eggs per female in the three study plots. They were estimated from the body length of gravid females. Values in parentheses are numbers of individuals examined.

Plot	Number of eggs*	
	1983 (Oct. 13)	1984 (Oct. 22)
A	555±77.8(8)	366±56.9(8)
B	345±61.8(6)	301±46.5(7)
C	—	345±42.1(7)

* mean±S.E.

$$y=2.149\times 10^{-4}x+0.531\ (r=0.799)$$

where y is the live weight per egg and x is the number of eggs in an egg mass. Slope of the regression line is only 2.149×10^{-4}, but is significantly different from zero ($p<0.01$), indicating that the eggs are heavier in larger egg masses than in smaller ones.

Table 1 shows the mean numbers of eggs per female in the three study plots. They were estimated from the regression equation between body length and the number of eggs. The mean number of eggs per female in plot A in 1983 was 1.5 to 1.9 times as many as those in the other plots. This is possibly due to the difference in food abundance between the study plots.

Discussion

Several authors have reported that growth rate and time of maturity of spiders were dependent on the food supply in the laboratory, i.e., the more food spiders consumed, the earlier they could mature (Turnbull, 1962; Miyashita, 1968). In *N. clavata*, larger individuals, which might have consumed more amount of food, matured earlier than smaller ones, which agrees with the results in other species. However, even smaller ones could mature in late October (Fig. 9). The ranges of body length and body weight in mature females were 11 to 25 mm and 150 to 1400 mg, respectively, and the ratios of maximum to minimum were 2.3 for body length and 9.3 for body weight. These differences in body length or body weight among mature females were greater than those reported in other species (Table 2). This fact may be due to the inability of *N. clavata* to grow larger by prolonging the development period considerably and delaying the time of maturation under poor food conditions, unlike *Linyphia triangularis*. In addition, the larger variance in prey availability compared to that in *Lycosa* T-*insignita* probably contributes to this fact. Since *N. clavata* cannot overwinter in the adult stage and development period is limited by winter, the species must have adapted so that small females mature and reproduce by late fall, even if their size is small and the number of eggs low. However, live weight per egg decreased slightly as the clutch size decreased (Fig. 11). Whether or not this difference in an egg weight affects hatching and survival

Table 2. Ratios of maximum to minimum in body length or body weight of mature females (values calculated from figures in the literatures).

Spider species	maximum/minimum		Author
	Length	Weight	
Linyphia triangularis	—	2.3[a]	Turnbull (1962)
Agelenopsis potteri	—	4.0[a]	Turnbull (1965)
Lycosa T-*insignita*	1.4[b]	—	Miyashita (1968a)
Nephila clavata	2.3	9.3	Present study

a: The ratio of body weight of spiders supplied *ad libitum* prey to minimum prey for survival.

b: The ratio of carapace width of spiders collected from a natural population.

rate of spiderlings must be studied in the future.

Studies of the effects of food abundance on a spider population are much fewer than those on individuals. A few authors found that there was no relationship between the number of spiders and their potential prey abundance in the field (Kajak, 1965; Turnbull, 1966; Greenstone, 1978), while Kobayashi (1975) succeeded in increasing some spider populations by releasing a number of fruit flies, *Drosophila melanogaster*, into dikes surrounding a paddy field. However, these studies were rather short term and did not deal with whole generation or successive generations. As revealed in this study, the difference in food abundance between the plots affected fecundity of *N. clavata*. The number of individuals in the early part of the development period was greater in the plot where food was more abundant in the previous year. Thus, reproductive numerical response was possibly recognized in the early part of the development period of the following year, but this effect disappeared after September when almost all spiders had matured. This indicates that the effects of food abundance on the number of individuals in the following year gradually disappeared with the developmental stage of the spider. The reason that the number of spiders in the two plots decreased to a similar level later is not clear. Hurd and Eisenberg (1984) also obtained a similar result in mantids, *Tenodera sinensis*, and attributed this to density dependent dispersal caused by food limitation. However, in the case of *N. clavata*, competition for food is possibly not important, because the feeding frequencies were not so low (Fig. 7) and the growth was not retarded in the plot where the number of individuals was greater (Fig. 5). Rypstra (1983) suggested that local population density of web-spinning spiders was determined by habitat structure if food abundance did not greatly differ between habitats. Therefore, other density dependent effects such as competition for web site, which may be related with habitat structure, and predation may be possible causes, but density independent dispersal can also depress the high population density and reduce the variation in density among populations if the species has relatively high dispersal ability (Iwao and Kuno, 1971). Further studies are required to solve this problem.

SUMMARY

Field studies were carried out to clarify the growth pattern, egg production and changes in the population density of the spider, *Nephila clavata*, in relation to food conditions.

1. Larger individuals, which might have consumed more amount of food, became gravid earlier (early October), but even smaller ones also became gravid by early November. The difference of body size in mature females was greater than those reported in other species.
2. The rate of growth and the fecundity were greater in the plot where food was more abundant, and the number of individuals in the early part of the development period in the following year was also greater in that plot.
3. Although the population densities in the early part of the development period differed considerably between the two study plots, the difference became obscure after September when almost all spiders had matured. This suggests that the number of adult individuals had little relation to that of juveniles.

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野外の餌条件と関係したジョロウグモの成長，卵生産，および個体群密度

宮下　直

ジョロウグモの野外個体群について，成長経過，卵生産，および個体群密度の変化を調べ，それらの餌量との関係について考察した.

1）より多くの餌を獲得したと思われる大型個体の方が早く卵成熟したが（10月上旬），小型個体でも11月上旬までには卵成熟した．成熟雌間での体のサイズの差異は，他に報告されている種よりも顕著であった.

2) 餌となる節足動物が多い調査区のほうが，クモの成長速度が速く，卵数も多くなり，翌年の発育初期の個体数ももう一方の区よりも多くなった．

3) 発育初期の個体群密度は調査区間でかなり異なっていたが，9月以後その差異は明らかではなくなった．よって，成体期の個体数とあまり関係していないようである．