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ECOLOGICAL RESEARCH

Decreased Reproductive Rate of the Spider, *Nephila clavata*, Inhabiting Small Woodlands in Urban Areas

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Abstract

The reproductive characteristics and feeding conditions of the spider, *Nephila clavata*, were examined at some urban and non-urban woodland sites. More than 80% of females were gravid by late October in both non-urban and large urban woodlands, whereas only 10%–30% were gravid in small urban woodlands. The expected number of eggs per female in mid-October was also lower in the small urban woodlands, although body length was not reduced. This suggests that reproductive failure was not caused by food shortage during the nymphal stage. Relative food consumption rate, prey size, biomass and size of potential prey during the adult stage all tended to be lower in small urban woodlands. These results suggest that decreased reproduction of *N. clavata* in small urban woodlands is caused by food shortage during the adult stage, particularly a shortage of large insects.

Key words: Feeding condition; Reproductive rate; Spider; Urban habitat.

Introduction

The urban woodland is characterized by small area, a high degree of human disturbance, and poor species composition of plants and animals. Since web-building spiders are sedentary and consume various kinds of insects, their growth and reproductive patterns will reflect the characteristics of urban ecosystems.

Spiders in the field often suffer food shortage (e.g. Miyashita, 1968; Anderson, 1974; Wise, 1975, 1979). In addition, the amount of food consumed by spiders varies among habitats or microhabitats (e.g. Riechert and Tracy, 1975; Morse and Fritz, 1982; Miyashita, 1986; Gillespie and Caraco, 1987). These two factors lead to local variability in growth and/or reproduction, which may influence the population consequences. However, the extent of such local variability has not been well studied, especially in urban habitats.

The spider, *Nephila clavata* Koch, is abundant throughout lowland forests in the Kanto plain, Japan, and it can also inhabit building spaces in the vicinity of small urban woods. Spiderlings emerge from egg cocoons in June and the largest female grows as large as 1000 mg in body weight by late October (Miyashita, 1986). Thus it can be expected that a food shortage for this large spider would be more severe in urban areas than in non-urban areas. To elucidate this point, I investigated the reproductive characteristics and feeding conditions of *N. clavata* at several sites in Tokyo and its suburbs.

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Study Sites and Methods

Observations were carried out at the following locations: Yayoi campus of the University of Tokyo (site code: U1), the Tokyo University Forest Experimental Station at Tanashi (U2), Nature Conservancy of the National Institute of Agro-environmental Sciences in Tsukuba (N1) and the Tokyo University Forest in Chichibu (N2) (Fig. 1). Site U1 is surrounded by buildings and streets, being located in the middle to Tokyo. The extent of the wooded area is only *ca.* 1 ha. The vegetation consists predominantly of *Castanopsis cuspidata*, *Zelkova serrata* and *Cornus controversa*. Site U2 is in the western suburbs of Tokyo and has about 10 ha of forest. The study site consists predominantly of *Zelkova serrata*, *Cinnamomum camphora*, *Pinus densiflora* and *Aucuba japonica*. Site N1 lies about 45 km northeast of Tokyo and is surrounded by woods and agricultural fields. The study site consists predominantly of *P. densiflora*, *Quercus serrata*, *Castanea crenata* and *Pleioblastus chino*. Site N2, lying about 70 km northwest of Tokyo, consists of a young plantation of *Abies firma* and is surrounded by deciduous broadleaved forest on a hillside.

Growth and reproductive patterns of *N. clavata* were recorded at N1, U1 and U2, but only reproductive pattern was recorded at N2. Body length was adopted as an indicator of growth because female body weight is more variable than body length due to egg maturation. Body length was obtained from either dorsal view photographs or by direct measurement with a pair of calipers.

Formation of mature eggs is easily recognized by the swollen abdomens of gravid females. This state was adopted as evidence of successful reproduction, because egg cocoons of this spider are seldom found in the field. To estimate the reproductive success of females at study sites U1, U2 and N2, I marked each adult female with paint and pursued their fates. The percentage of gravid females was estimated on the basis of the cumulative number of gravid females among the marked females present in mid-October, which was just before the oviposition period. For individuals which disappeared before becoming gravid, I assumed that they had the same probability of becoming gravid as resident females which were non-gravid at the previous census. The fecundity of a female was estimated using the following regression equation between body length and the number of ovarian eggs.

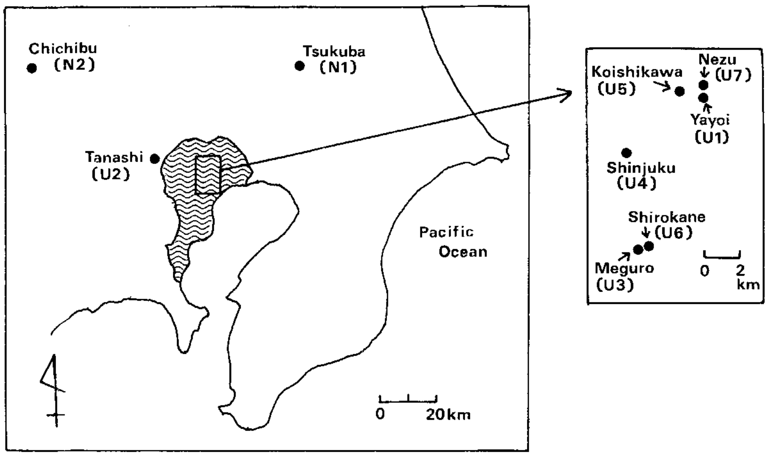

Fig. 1. Map showing location of the study sites. Shaded area denotes densely built-up area.

$$\ln E_0 = 2.394 \ln L - 0.967 \ (r = 0.938, p < 0.001, n = 31),$$

where E_0 is the number of eggs and L is the body length. This equation was derived by adding new data to those already obtained by Miyashita (1986). The expected number of eggs per female in mid-October (E), which represents the mean reproductive success of females, was calculated as follows:

$$E = E_a\, a/N + E_d\, d/N,$$

where a and E_a are the number of gravid fmales actually observed and their estimated mean number of eggs, respectively; d and E_d are the estimated number of females which became gravid after their disappearance and their estimated mean number of eggs, respectively, and N is the number of females in mid-October. The mean number of eggs of females that disappeared was estimated from their body length prior to disappearance.

The relative food consumption rate was estimated from the feeding frequency, which was the ratio of the number of feeding individuals to the total number of individuals observed (Miyashita, 1986). To obtain these estimates, 15 to 30 individuals were observed each time. Since there is no distinct trend in diurnal feeding frequency in this species (unpublished data), the time of observation was not fixed within the day. Prey caught by spiders were identified by taxonomic order or family, and their body size was also measured to the nearest mm. In 1988, the relative food availability at the study sites was surveyed by setting traps to capture flying insects (see Fig. 2). Four (U2) and three (U1) traps were set about 1 m above the ground for five periods: 17–22 August, 4–9 and 17–22 September, 5–10 and 19–24 October. The biomass index of captured insects was estimated from the following allometric equation for adult insects used by Spiller and Schoener (1988); Mass = $(\text{length (mm)})^{2.62}$. Large insects which spiders could not capture were excluded from the calculation.

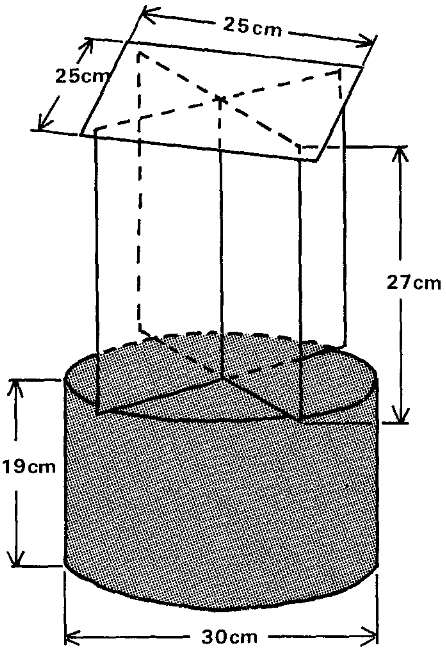

Fig. 2. Trap for arthropods (mainly flying insects) used to estimate the relative food availability for spiders. The shaded part is a white plastic bucket and the other parts are transparent acrylic plates.

To obtain more information on reproductive characteristics in urban areas, the following five additional sites other than U1 were investigated on 22 October 1988. These were the Institute for Nature Study at Meguro (Meguro, U3), Shinjuku-Gyoen National Garden (Shinjuku, U4), Koishikawa Botanical Garden (Koishikawa, U5), The Institute of Medical Science (Shirokane, U6) and Nezu Shrine (Nezu, U7). The first three had a much larger area of woodland than the latter two (see Table 2). The vegetation of the study sites consists mainly of *Castanopsis cuspidata*, *Z. serrata*, *Cornus controversa* and *Aucuba japonica* at U3; *Castanopsis cuspidata*, *Cinnamomum camphora*, *Z. serrata* and *A. japonica* at U4; *Cornus controversa*, *Z. serrata*, *Prunus* sp. and *A. japonica* at U5; *Cedrus deodara*, *Prunus* sp. and *Rhododendron* sp. at U6; *Z. serrata*, *Ginkgo biloba*, *Eurya japonica* and *Rhododendron* sp. at U7.

Results

Growth and reproduction

Figure 3 shows seasonal growth patterns in the mean body length for *N. clavata* populations in different years and study sites. Though there were considerable spatio-temporal variations in mean body length, the seasonal growth patterns showed similar trends between urban and non-urban populations.

Figure 4 shows body length of females at the time of their final molt. Except for one female at N1, all the females at N1 and U2 molted for the last time in September, while most of the females at U1 did so in October. A negative correlation between body length and the day of

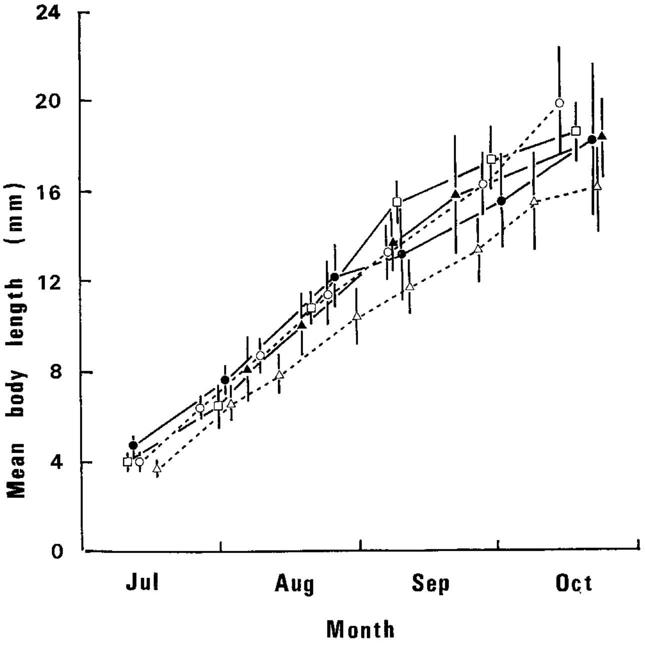

Fig. 3. Seasonal changes in the mean body length of spiders (Sample sizes range 7–23). Vertical bars represent 95% confidence limits. For the locations of study sites, see Fig. 1. ○: N1 in 1983; △: N1 in 1984; ▲: U1 in 1987; ●: U1 in 1988; □: U2 in 1988.

final molt was found by excluding seven large females for which the final molt occurred in October at U1 ($r = -0.635, p<0.001, n = 26$). Most of these large females did not become gravid in November because of the scarcity of prey.

Changes in the percentage of gravid females are shown in Fig. 5. From this it is clear that ovarian maturation did not proceed normally at U1. The percentage of gravid females at U1 hardly exceeded the 30% level throughout October to November in spite of the rapid rise observed at the other sites.

Table 1 shows the average reproductive performances of marked females in mid-October.

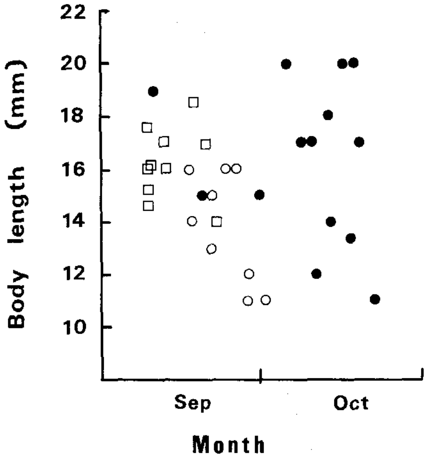

Fig. 4. Body length of females as a function of the day of the final molt. For the locations of study sites, see Fig. 1. ○: N1 in 1984; ●: U1 in 1987 and 1988; □: U2 in 1988.

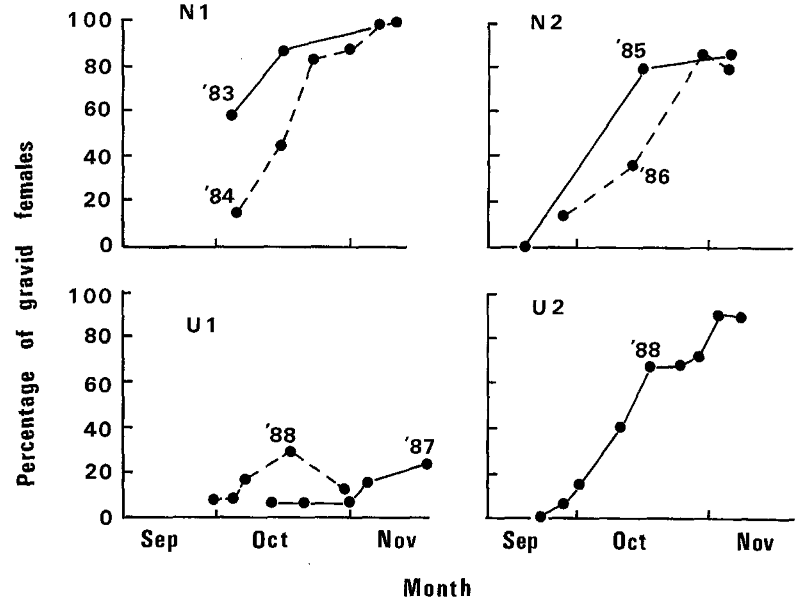

Fig. 5. Seasonal changes in the percentage of gravid females.

Table 1. Average reproductive performances of marked females observed in mid-October. Figures in parentheses represent percentages of individuals against the number of individuals in mid-October.

Site	Year	No. in mid-October	No. gravid	No. non-gravid	No. disappearing before becoming gravid	Estimated no. of c becoming gravid	Total no. gravid females	Expected no. eggs per female
		N	a	b	c	d	a+d	
N2	1985	43	37 (86.0)	1 (2.3)	5 (11.6)	2	39 (90.7)	367
	1986	16	14 (87.5)	1 (6.3)	1 (6.3)	0	14 (87.5)	310
U1	1987	15	2 (13.3)	3 (20.0)	10 (66.7)	2	4 (26.7)	121
	1988	15	4 (26.7)	2 (13.2)	9 (60.0)	0	4 (26.7)	195
U2	1988	16	14 (87.5)	2 (12.5)	0 (0)	0	14 (87.5)	424

Table 2. Reproductive status of female *Nephila clavata* individuals at several urban populations in late October, 1988.

Site	Wooded area (ha)	No. observed	Gravid (%)	Non-gravid (%)	Oviposited (%)
U3	18	24	62.5	29.2	8.3
U4	26	25	64.0	36.0	0.0
U5	15	27	63.0	37.0	0.0
U6	1	16	18.8	81.2	0.0
U7	1	15	26.7	73.3	0.0
U1	1	17	29.4	70.6	0.0
U2	10	21	66.7	33.3	0.0

As compared to N2 and U2, the percentage of gravid females was much lower and the percentage of individuals which disappeared before becoming gravid was much higher at U1. The estimated number of gravid females among those which disappeared in a non-gravid state was very small, because only a few non-gravid residents became gravid. Thus the total percentage of gravid females including those which disappeared was also smaller at U1. The expected number of eggs per female in mid-October was also lower at U1 than at the other sites (Table 1).

Table 2 compares the percentages of gravid females in several urban populations including U1 and U2. The percentages of gravid females at U1, U6 and U7 all remained below 30%, whereas those at the other sites were above 60%. Such a contrasting difference is apparently correlated to the difference in woodland area between the above two groups.

Frequency distributions of body length of females and their reproductive conditions are shown in Fig. 6. Female body length at urban sites was not smaller than that at non-urban sites; in fact females at some urban sites were significantly larger. A significant difference was found between N1 and all urban sites except U6 ($p<0.03$, t test), and between N2 and U4 ($p = 0.01$, t test). At N1 and N2 (non-urban sites), there was a tendency for females with a body length of less than 15 mm to have a lower probability of becoming gravid, whereas all females were gravid above this threshold. However, the probability of large females becoming gravid seemed to be negatively related to the degree of urbanization.

Feeding conditions

Adult females of *N. clavata* were found between early September and early November, and thus feeding conditions during this period seem to be very important for successful reproduc-

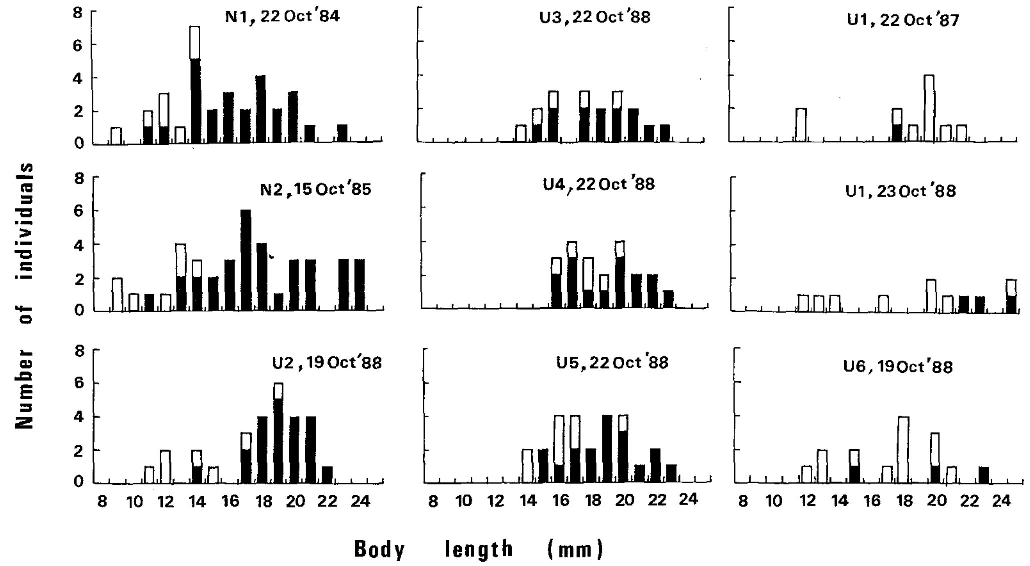

Fig. 6. Frequency distributions of body length of females. Clear and solid bars represent non-gravid and gravid females, respectively.

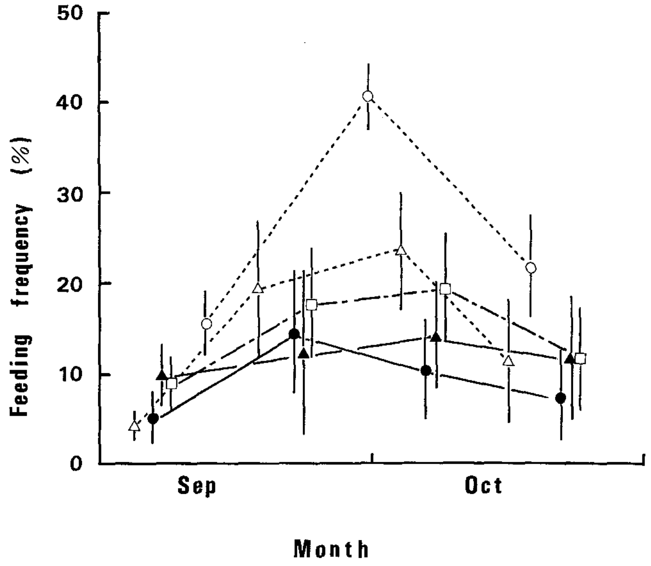

Fig. 7. Mean feeding frequency of spiders from September to October (Sample sizes range 5–13). Vertical bars represent 95% confidence limits. For the locations of study sites, see Fig. 1. ○: N1 in 1983; △: N1 in 1984; ●: U1 in 1987; ▲: U1 in 1988; □: U2 in 1988.

tion. Figure 7 shows temporal trends in the feeding frequency of spiders at N1, U1 and U2. A rise and a fall in the feeding frequency was commonly observed in late September and late October, respectively. However, the feeding frequency from late September to early October tended to be lower at U1 than at N1 and U2, although the difference was only significant between U1 and N1 ($p<0.05$, *F* test).

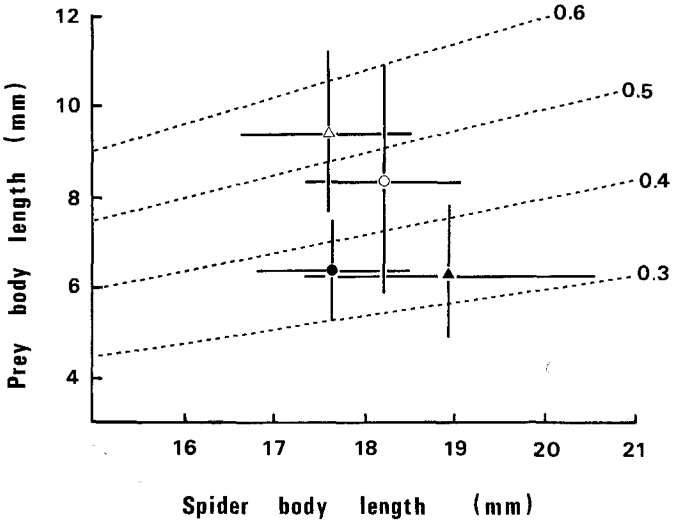

Fig. 8. Relationship between the body length of spiders and their prey captured from mid-September to mid-October (Sample sizes range 20–42). Vertical and horizontal bars represent 95% confidence limits and dashed lines represent isoclines of the relative size of prey. Numerals indicate relative prey size (prey/predator). For the locations of study sites, see Fig. 1. △: N1 in 1983; ▲: U1 in 1987; ●: U1 in 1988; ○: U2 in 1988.

Figure 8 shows the relationship between spider body length and prey body length. There was a significant difference in prey size between N1 in 1983 and U1 in 1987 or 1988 ($p<0.01$, t test). Prey size tended to be greater at U2 than at U1, although the difference was not significant ($p = 0.09$, t test). Relative prey size (prey length/predator length) is more important for spiders, because the benefit gained from a particular prey differs according to the size of the spider. Isoclines of relative prey size are indicated by dashed lines in the figure. The statistical significance of prey size mentioned above was not affected by using relative prey size. These results suggest that the different feeding frequencies shown in Fig. 7 were related to the difference in prey size.

The biomass indices of arthropods captured by traps at U1 and U2 in 1988 were compared (Fig. 9). No significant difference in the index was detected between the two sites due to the large variation of the values. However, the values at U2 tended to be higher from mid-September ($p = 0.1$, F test). This coincides well with the trend of greater feeding frequency observed at U2 (see Fig. 7).

The size distributions of arthropods captured by traps are compared in Fig. 10. Two-way analysis of variance revealed that the number of arthropods larger than 5 mm in body length was higher at U2 ($p<0.05$), although the mean number of individuals of all size classes was slightly higher at U1 (U1:38.5; U2:31.9).

Discussion

The genus *Nephila* is widely distributed from tropical to temperate zones (Austin and Anderson, 1978). Many authors have reported that members of this genus live mainly in forests and on their edges (e.g. Robinson and Robinson, 1973; Moor, 1977; Brown et al., 1985). The native habitat of *N. clavata* also seems to belong to this category, although this

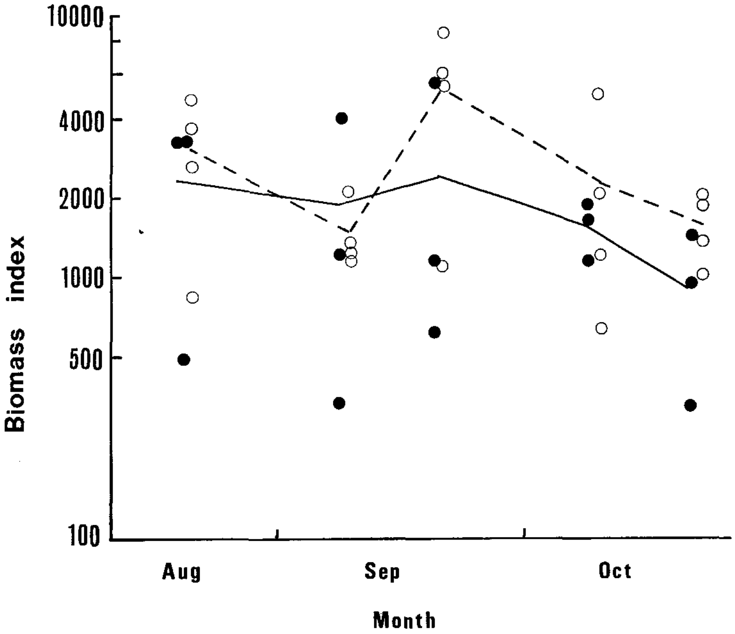

Fig. 9. Index of biomass of arthropods captured by traps in 1988. Solid and dashed lines represent mean values of U1 and U2, respectively. For the locations of study sites, see Fig. 1. ●: U1; ○: U2.

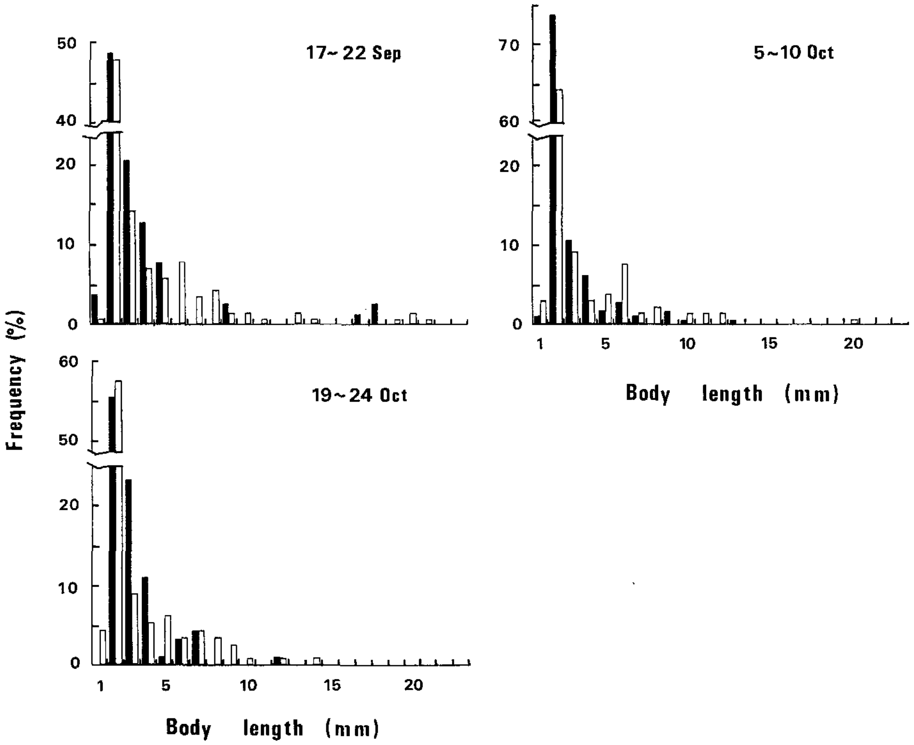

Fig. 10. Frequency distributions of the body length of arthropods captured by traps. Solid and clear bars represent percentage of U1 and U2, respectively. For the locations of study sites, see Fig. 1.

species is rarely seen at elevations above 700 m in the Kanto region (Miyashita, unpublished). It is considered that observation sites N1 and N2 both closely represent the typical native habitat. More than 80% of the females at these two sites became gravid by late October (Fig. 5). However, nearly 10% of the females still failed to become gravid (Table 1). It seems that even in such favorable habitats, prey availability is not sufficient to allow all females to reproduce successfully.

The reproductive status of spiders living in urban areas differed markedly according to the habitat characteristics (Table 2 and Fig. 6). In urban habitats with a relatively large wooded area, both the percentage of gravid females and the expected number of eggs per female were higher than those in habitats with smaller wooded areas (Tables 1 and 2). The lower reproductive success of females at U1 was due to the large number of disappearances and their lower probability of becoming gravid. Thus the assumption that both disappeared and resident non-gravid females have the same probability of becoming gravid may be contentious. One might imagine that the individuals which disappeared had a higher probability of successful reproduction than residents by emigrating to a better-quality site. However, this seems to be unlikely because only a few gravid females were observed at the periphery of the census area, and some disappearances must have been due to death rather than emigration. Therefore it seems that the above assumption does not underestimate the reproduction of disappeared females.

It should be noted that the lower reproduction at U1 was not caused by growth retardation since the frequency distribution of body size was not small in comparison with those at the other sites (Fig. 6). This suggests that feeding conditions during the nymphal stage were not so poor at U1. It has beeen pointed out that although the adult size of some arthropod predators determines their potential fecundity, scarcity of food during the adult stage can lead to reduced egg production (Kessler, 1973; Eisenberg et al., 1981; Matsura and Morooka, 1983). This can also be applied to the situation for *N. clavata* in small urban woodlands.

The adult female of *N. clavata* is so large that it requires a considerable amount of food for self maintenance and reproduction. Thus prey size is an especially important factor for this large ambush predator. The main large prey items at N1 and U2 were bees, wasps and dragonflies. These large insects are in general more abundant in urban habitats with large wooded areas than in those with small wooded areas. This seems to be the main reason for the differences in reproductive performance among the urban habitats. Since the intensity of human disturbance depends reciprocally on the size of a woodland through edge effects, it appears that woodland size may impose critical effects on the population persistence of *N. clavata* in urban areas.

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References

ANDERSON, J. F. (1974) Responses to starvation in the spider. *Lycosa lenta* (Hentz) and *Filistata hibernalisis* (Hentz). Ecology **55**: 576–585.

AUSTIN, A. D. & ANDERSON, D. T. (1978) Reproduction and development of the spider *Nephila edulis* (Koch) (Araneidae: Araneae). Aust. J. Zool. **26**: 501–518.

BROWN, S. G., HILL, E. B., GOIST, K. E., WENZL, P. A. & CHRISTENSON, T. E. (1985) Ecological and seasonal variations in a free-moving population of the golden-web spider, *Nephila clavipes*. Bull. Br. Arachnol. Soc. **6**: 313–319.

EISENBERG, R. M., HURD; L. E. & BARTLEY, J. A. (1981) Ecological consequences of food limitation for adult mantids (*Tenodera aridifolia sinensis* Saussure). Am. Midl. Nat. **106**: 209–218.

GILLESPIE, R. G. & CARACO, T. (1987) Risk-sensitive foraging strategies of two spider populations. Ecology **68**: 887–899.

KESSLER, A. (1973) A comparative study of the production of eggs in eight *Pardosa* species in the field (Araneae, Lycosidae). Tijdschrift voor Entomologie **116**: 23–41.

MATSURA, T. & MOROOKA, K. (1983) Influences of prey density on fecundity in a mantis, *Paratenodera angustipennis* (S.). Oecologia **56**: 306–312.

MIYASHITA, K. (1968) Growth and development of *Lycosa T-insignita* Boes et Str. (Araneae: Lycosidae) under different feeding conditions. Appl. Ent. Zool. **3**: 81–88.

MIYASHITA, T. (1986) Growth, egg production, and population density of the spider, *Nephila clavata* in relation to food conditions in the field. Res. Popul. Ecol. **28**: 135–149.

MOORE, C. W. (1977) The life cycle, habitat and variation in selected web parameters in the spider *Nephila clavipes* Koch (Araneidae). Am. Midl. Nat. **98**: 95–108.

MORSE, D. H. & FRITZ, R. S. (1982) Experimental and observational studies of patch choice at different scales by the crab spider, *Misumena vatia*. Ecology **63**: 172–182.

RIECHERT, S. E. & TRACY, C. R. (1975) Thermal balance and prey availability: bases for a model relating web-site characteristics to spider reproductive success. Ecology **56**: 265–284.

ROBINSON, M. H. & ROBINSON, B. (1973) Ecology and behavior of the giant wood spider *Nephila maculata* (Fabricuis) in New Guinea. Smithon. Contrib. Zool. **149**: 1–76.

SPILLER, D. A. & SCHOENER, T. W. (1988) An experimental study of the effect of lizards on web-spider communities. Ecol. Monogr. **58**: 57–77.

WISE, D. H. (1975) Food limitation of the spider *Linyphia marginata*; experimental field studies. Ecology **56**: 637–646.

WISE, D. H. (1979) Effects of an experimental increase in prey abundance upon the reproductive rates of two orb-weaving spider species. Oecologia **41**: 289–300.