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Consumption and Food Utilization by Individual Larvae and the Population of a Wood Borer *Phymatodes maaki* Kraatz (Coleoptera: Cerambycidae)

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Summary. The consumption and the utilization of food by the individuals and the population of a wood borer, *Phymatodes maaki* Kraatz feeding on the dead wood of a Japanese wild vine, *Vitis coignetiae* Pulliat were studied at Mt. Daibosatsu, Yamanashi Pref., central Honshu from 1974 to 1976.

As for individuals of *P. maaki*, the estimates of the ratio of growth to consumption and that of assimilation to consumption were very low, amounting to 1.24 and 3.23% in dry weight, 1.23 and 3.12% in carbon weight, and 16 and 13.6% in nitrogen weight respectively. The ratio of growth to assimilation was estimated at 35% in dry weight, 39% in carbon weight and 118% in nitrogen weight. Dry body weight of the adult was correlated with the amount of consumption of the larva.

The parasitism by two Ichneumonidae species seemed to be the main mortality factor of the population of *P. maaki*. A minimum estimate of mortality from egg stage till emergence was 75%.

As for the bioeconomy of the population, waste consumption i.e. the consumption of individuals that died before emergence amounted to 75% of total consumption. The growth efficiency (biomass of adults/total consumption) was 0.24% in dry weight, 0.26% in carbon weight and 3.4% in nitrogen weight. The waste efficiency (waste consumption/biomass of adults) was 310 in dry weight, 285 in carbon weight and 22 in nitrogen weight. Approximately 18% of the dead wood of *V. coignetiae* was decomposed by the feeding of the population.

The dry weight of an adult was inversely correlated with density of larvae in the dead wood from which it emerged, but not significantly correlated with the diameter of the wood. The ratio of adult emergence i.e. the survival rate was inversely correlated with density of larvae, but the mortality by parasitism was not density dependent. This seems to suggest that there was an intraspecific competition for the limited food.

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Introduction

It is well known that the larve of cerambycid beetles play an important role in the decomposition of wood litter in forest ecosystems. The amount of wood litter produced in the forest ecosystems was said to be nearly equal to or a little less than that of leaf litter (Kira and Shidei, 1967). Decomposition of wood litter has been studied by several workers (Kühnelt, 1976; Watanabe, 1966; Satchell, 1971; Yoneda, 1975a, 1975b). But the quantitative studies on primary decomposers are only a few (Mamaev, 1961; Savely, 1939). A large number of studies have been made on the consumption and utilization of food by phytophagous insects (cf. Waldbauer, 1968), and a majority of them have dealt with leaf or flour eating insects.

The present study was carried out on the individual animal and the population of a wood borer species, *Phymatodes maaki* Kraatz, dealing mainly with consumption and utilization of food by individuals, mortality, consumption, waste consumption of the population, and the decomposition rate of dead wood by feeding of the population and correlation among adult dry weight, density of larvae, diameter of wood and other factors.

I wish to thank Prof. Y. Kitazawa, Department of Biology, Tokyo Metropolitan University for encouragement and critical reading of the manuscript.

Study Site and Life History

Studies on the natural population of *P. maaki* were made at the study site selected in a deciduous forest of Mt. Daibosatsu 1,500 m above sea level in central Honshu, where the estimated mean air temperature is about 6° C. The study site was 64 m^2 (8m × 8m) in area.

P. maaki is distributed through Amur to Japan (Duffy, 1968 and others). In the present study area it required 2 years to complete its life cycle, but in the areas of less elevation the insect is univoltine. According to my observation it is also univoltine at Karuizawa about 1,000 m above sea level in central Honshu. *Vitis coignetiae* Pulliat, *Vitis vinifera* Linne and *Actinidia arguta* Planch have been found to be its food plants.

Adults emerge in June at Daibosatsu and in May at Karuizawa and lay eggs in cracks in the bark. Larvae develop immediately after hatching, eat beneath the bark, and the frass plugs the burrows tightly behind the larvae. They become mature larvae in early autumn of the same year for univoltine individuals and of the next year for those requiring 2 years for development. The species overwinters in the fullgrown larval or pre-pupal stage. The same two parasitic species of Ichneumonidae were found from the larvae at both Daibosatsu and Karuizawa.

Methods

The number of food plants, *V. coignetiae* in this study site was 9. All the food plants had been cut near the ground by May, 1974 before the emergence of adults of *P. maaki*, and set in the natural condition. They were collected in May, 1975 before the emergence of adults. It seems certain that the larvae of *P. maaki* have hatched in early summer in 1974. The population therefore can be regarded as a cohort.

Dead wood of *V. coignetiae* was left in the laboratory after being cut into twigs 30 to 40 cm in length. Diameter and length of each twig were determined and the volume was calculated. Some twigs were broken open in December, 1975 and the live weight of fullgrown larvae and pupae in them was determined. Adults emerged in March, 1976. The number of adults emerging from each twig was counted. After that all the twigs were broken open, and the numbers of adults, pupae, and larvae of *P. maaki* and those of other insects dead within each twig were counted. Fullgrown larvae, pupae and adults of *P. maaki* were dried at 70° C for 48 h to determine dry weight and the ratio of dry to live weight.

The dry weight of frass in the burrow per unit volume was determined as follows. Frass was removed from burrows and dried at 70° C for 48 h and the dry weight was determined. Silicon plaster was packed into burrows and the weight of the silicon plaster removed was determined. The weight of silicon plaster was 1.59 g/cm^3 (S.E. 0.00017, n=13). The volume of the burrow was calculated by using this value. The dry weight per unit volume of dead wood was determined as follows. The dead wood was dried at 70° C for 48 h and its dry weight was determined. The dead wood was covered by silicon plaster and total volume was determined by sinking it in water. Then the silicon plaster was separated from the dead wood and its volume was calculated by determining its dry weight. The difference between these was regarded as the volume of the dead wood. When the ratio of frass dry weight to volume of the burrow in which frass is plugged is denoted by $R1$ and that of wood dry weight to volume by $R2$, $R2/R1$ may be the mean ratio of consumption to feces of larva, because frass may consist almost entirely of feces.

Carbon and nitrogen contents per dry weight of larvae, pupae, adults, frass, and dead wood were determined with C N corder Yanaco MT 500, and the ratio C/N was calculated.

Consumption, Feces, and Efficiencies of Individual Larva

Consumption (C), feces (F), and growth (G) of an individual were determined for 12 individuals. The dry weight of an adult emerged was regarded as growth, the corresponding frass was dried and its dry weight was regarded as feces. Consumption of an individual was calculated as (the dry weight of frass) $\times R2/R1$. The conversion efficiency of ingested food to body substance (G/C), the efficiency with which assimilated food is converted to body substance [G/(C-F)] and the conversion efficiency of ingested food to assimilation [(C-F)/C] were calculated. These values in dry weight were also converted into those in carbon and nitrogen weight.

Population Productivity

Frass from each twig was gathered and the dry weight was determined. Total frass dry weight within all twigs was the feces of the population (FP). Consumption within each twig was calculated as (the dry weight of frass within each twig) $\times R2/R1$ and total consumption within all twigs was the consumption of the population (CP). By effective consumption (ECP) I mean the consumption of individuals alive and by waste consumption (WCP) I mean the consumption of dead individuals. So, ECP+WCP=CP (see Ikeda, 1976). Effective consumption within each twig was calculated as follows. Consumption of the larva was correlated with biomass of the adult, as represented by the following equation (see Fig. 1),

$$Y = 0.0347\,X + 0.589$$

where Y is consumption in g dry weight and X is biomass of the adult in mg dry weight.

Effective consumption in g dry weight within each twig is represented by,

$$\sum_{i=1}^{n} (0.0347\,X_i + 0.589)$$

where X_i is the mg dry weight of ith adult emerged from each twig and n is the total number of adults emerged from each twig. Effective consumption within total twig was regarded as that

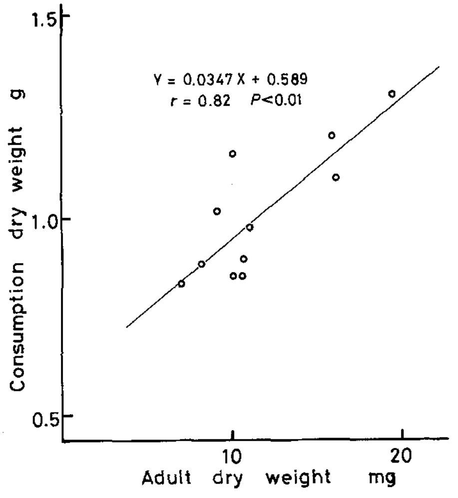


Fig. 1. Correlation between adult dry weight of *Phymatodes maaki* and wood dry weight of *Vitis coignetiae* consumed by it

of the population (ECP). Waste consumption of the population (WCP) was calculated as CP-ECP. The ratio of biomass of total adults emerged (BP) to consumption of the population, that is growth efficiency (BP/CP), the ratio of waste consumption to total consumption (WCP/CP), and the waste efficiency (WCP/BP), by which I mean the amount of waste consumption required to produce unit biomass (see Ikeda, 1976), were calculated. These values relating to population productivity in dry weight were also converted into those in carbon and nitrogen weight.

Results

Fecundity and Parasite within Abdominal Cavity

The ovariole number in all of the 13 specimens examined (5 from Daibosatsu and 8 from Karuizawa) was 12. Intraspecific variation in ovariole number was not recognized. The number of eggs detected in one ovariole was 4 to 5 and that of mature eggs per individual ranged from 12 to 42, 25 in the mean (S.E. 2.55). From 17 individuals of 27 specimens tested, a large number of parasitic Nematoda which ranged from 500 to 50,000, 5,900 in the mean (S.E. 2813), per individual were found within the abdominal cavity of the adult in both male and female from both Daibosatsu and Karuizawa.

Table 1. Mean dry weight per unit volume of dead wood of *Vitis coignetiae* and mean dry weight of frass of *Phymatodes maaki* in the burrow per unit volume with standard error (S.E.)

	Number of samples	Mean (g/cm^3)	S.E.
Wood	7	0.4334[a]	0.0087
Frass	10	0.4193[a]	0.014

[a] This difference is significant ($P < 0.001$)

Dry Weight of Dead Wood per Unit Volume and That of Frass

Table 1 shows the dry weight per unit volume of dead wood and the ratio of frass dry weight to the volume of the burrow in which the frass is plugged. The value of the former was slightly higher than that of the latter with significant difference ($P < 0.001$).

Live and Dry Weight, Carbon and Nitrogen Content of Larvae, Pupae and Adults

Table 2 shows live weight, dry weight and the ratio of dry to live weight of pupae and adults. Dry weight of adults ranged from 4.7 to 19.7 mg. Dry/live ratio was higher in adults than in pupae. Savely (1939) reported that dry/live

Table 2. Live weight, dry weight and dry weight/live weight in pupae and adults of *Phymatodes maaki*

		Pupa			Adult		
		male	female	total	male	female	total
Live wt	Mean	47.6 mg	44.60	45.87	24.01	21.42	22.62
	S.E.	1.79	3.70	2.25	0.98	0.84[a]	2.14[b]
Dry wt	Mean	15.58 mg	15.15	15.33	8.81	7.89	8.30
	S.E.	0.65	1.29	0.78	0.44	0.38	0.27
Dry/live	Mean	32.73%	33.97	33.41	36.73	35.93	36.20
	S.E.	0.38	0.44	0.33	0.77	0.38	0.39
No. of samples		8	11	19	42	53	95

[a] n=63
[b] n=110

Table 3. Carbon and nitrogen contents and C/N ratio per dry weight of *Vitis coignetiae* and frass, larvae, pupae and adults of *Phymatodes maaki*

		Wood	Frass	Full grown larva	Pupa			Adult		
					male	female	total	male	female	total
Carbon	Mean	47.44%	47.50	53.23	54.83	55.56	55.12	51.04	52.18	51.61
	S.E.	0.14	0.37	0.35	0.73	0.25	0.45	0.62	0.24	0.36
Nitrogen	Mean	0.740%	0.661	7.760	8.905	9.103	8.984	10.50	10.38	10.44
	S.E.	0.012	0.005	0.08	0.118	0.165	0.076	0.059	0.034	0.037
C/N	Mean	64.13	71.89	6.86	6.16	6.10	6.14	4.86	5.03	4.95
	S.E.	2.14	0.99	0.085	0.049	0.023	0.031	0.080	0.022	0.047
No. of samples		13	14	4	6	4	10	6	6	12

Table 4. Consumption (C), feces (F), biomass of adult (B) or growth (G) per individual and efficiency of conversion on dry weight basis of *Phymatodes maaki*. n = 12

	C	F	G(B)	(C–F)/C	G/(C–F)	G/C
Mean	1052 mg	1018 mg	11.92 mg	3.23%	35.07%	1.239%
S.E.	70.7	68.4	1.08		2.11	0.107

ratio of larvae of a cerambycid species *Callidium antennatum* Newman varied from 20.25 to 50.64, 31.6% on average. Table 3 shows carbon and nitrogen contents of wood, frass, larvae, pupae, and adults. Carbon contents of wood and frass were almost the same, but nitrogen content of the former was higher than that of the latter. Carbon content of adults was lower than that of pupae and larvae and nitrogen content increased with the progress of development.

Consumption and Feces of Individual Larva in Dry Weight and Efficiencies

Consumption (C) and Feces (F) of an individual larva and adult biomass (G or B) determined on 12 individuals are shown in Table 4. Consumption of the larva was correlated to biomass of adult as shown in Fig. 1. Savely (1939) also showed that the dry weight of larvae of *C. antennatum* and *Chrysobathris* sp. (Buprestidae) was correlated with the dry weight of wood they consumed. The conversion efficiencies, G/C, G/(C-F) and (C-F)/C are shown in Table 4. (C-F)/C and G/C were very low as compared with those of other phytophagous insects reviewed by Waldbauer (1968) ranging from 22 to 70% in leaf eating insects and 46 to 95% in non-leaf-feeders, mainly flour and powdered milk feeders. On the other hand, the value of G/(C-F) of about 35% was the middle of the values in other phytophagous insects.

Utilization of Carbon and Nitrogen by Larva

Table 5 shows the conversion efficiency of ingested carbon and nitrogen to assimilation [(C-F)/C], that of ingested carbon and nitrogen to body substance (G/C) and the efficiency with which the assimilated carbon and nitrogen are converted to body substance [G/(C-F)]. The values of (C-F)/C, G/C and G/(C-F) in carbon weight were almost the same as those in dry weight. The value of (C-F)/C of 13% in nitrogen weight was 4 times as large as that in dry weight, and that G/C of 16% was more than 10 times as large as in dry weight. In a grasshopper *Parapleurus alliaceus* Germer, the efficiency G/C in nitrogen weight was estimated at about 20% (Matsumoto, 1977).

Table 5. Utilization rates of carbon and nitrogen by larvae of *Phymatodes maaki.* (C–F)/C: the efficiency of conversion of ingested carbon and nitrogen to assimilation. G/(C-F): that of assimilated carbon and nitrogen to body growth. G/C: that of ingested carbon and nitrogen to body growth. n = 12

	Carbon			Nitrogen		
	(C–F)/C	G/(C–F)	G/C	(C–F)/C	G/(C–F)	G/C
Mean	3.12%	39.39%	1.233%	13.6%	117.62%	15.99%
S.E.		2.44	0.076		7.29	0.99

Table 6. The number of insects emerged from dead wood of *Vitis coignetiae* and that of dead insects found from them

Phymatodes maaki

adult emerged	adult dead in wood	pupa dead in wood	larvae dead in wood			total
			unknown	death by[a] small parasite	death by[a] large parasite	
92	12	8	55	53	10	230

Other insects

Scolytidae sp.		*Teratoclytus plavilstshikovi*		*Phymatodes albicinctus*	
adult	larva	adult emerged	larva dead in wood	adult emerged	adult dead in wood
95	5	5	2	2	1

[a] Both species belong to Ichneumonidae

Ratio of Emergence and Mortality Factors of Population

The number of twigs of *V. coignetiae* tested was 56 of which the diameter ranged from 0.55 to 2.7 cm. The number of twigs eaten was 51 and 5 other twigs were not eaten by any insects. The number of adults of *P. maaki* emerging from one twig ranged from 0 to 6. The number of total individuals of *P. maaki* found in one twig which is equal to the number of adults emerging from the twig plus that of dead individuals within the twig ranged from 0 to 20. However, this value should be less than the actual one, because dead eggs and dead young larvae were not found and dead larvae found in the wood were of middle or fullgrown stage. The ratio of emergence or the ratio of adult number emerged to the total number of individuals found in one twig ranged from 0 to 1, and that in the total twigs representing the value for the population is 0.4 (92/230 in Table 6). The apparent density of individuals or total number found per unit volume of the twig ranged from 0 to 0.345 ind./cm^3. This is equivalent to 0.057 ind./cm^3 on a population basis. Table 6

Table 7. Amounts in dry weight, carbon and nitrogen of total wood of *Vitis coignetiae* (TW), consumption (CP), feces (FP), effective consumption (ECP), waste consumption (WCP), biomass of adults (BP), ratio of waste consumption to consumption (WCP/CP), that of consumption to wood available (CP/TW), the growth efficiency (BP/CP), the waste efficiency (WCP/BP) of the population of *Phymatodes maaki*

	TW	CP	FP	ECP	WCP	BP	WCP/CP	CP/TW	BP/CP	WCP/BP
Dry wt.	1756.6 g	324.14 g	309.55 g	81.04 g	243.10 g	0.7826 g	75%	18.45%	0.2414%	310.63
Carbon	833.33	153.77	147.04	38.45	115.33	0.4039	75	18.45	0.2627	285.54
Nitrogen	12.995	2.398	2.045	0.600	1.798	0.0817	75	18.45	3.407	22.01

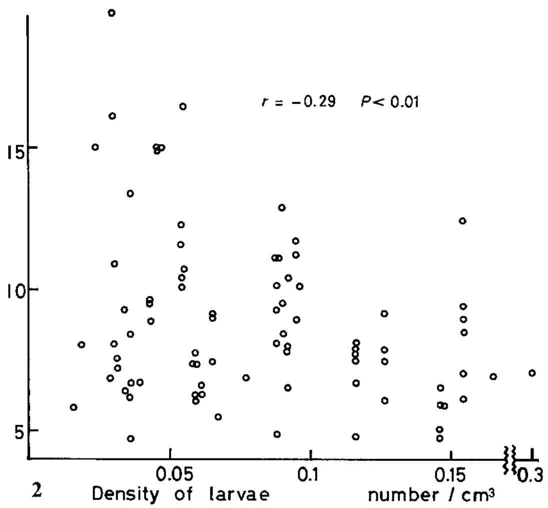
shows the total number of adults of *P. maaki* emerged, that of adults, pupae, and larvae that had died in wood and that of other insects. Two parasitic species of Ichneumonidae were found, one is large and monoparasitic, and the other is small and polyparasitic. The number of small parasites that emerged from one host ranged from 3 to 7. They caused more than a half of the total mortality of middle and fullgrown larvae of *P. maaki* found in the wood. Besides these, many individuals of Scolytidae species (about 2 mm in body length) and a few individuals of two cerambycid species, *Teratoclytus plavistshikovi* Zaitev and *Phymatodes albicinctus* Bates were found.

Population Productivity

Total amount of wood (TW), wood consumed by the larvae (CP), feces (FP), and that of biomass of emerged adults (BP) of the population of *P. maaki* in terms of dry matter, carbon, and nitrogen weight are shown in Table 7. Effective consumption (ECP) and waste consumption (WCP) of the population are also shown in Table 7. Since consumption of Scolytidae and Cerambycidae other than *P. maaki* seemed to be negligible, it was estimated that approximately 18% of dead wood of *V. coignetiae* was decomposed by feeding of the population of *P. maaki*. The growth efficiency (BP/CP) of the population in nitrogen was found to be more than 10 times as much as that in dry weight. The waste efficiency (WCP/BP) in dry weight was more than 10 times as large as that in nitrogen weight. The ratio of waste consumption to total consumption (WCP/CP) amounted to 75%.

Factors Affecting Adult Dry Weight

The correlation coefficient (r) of dry weight of an adult on apparent density of larvae in the twig from which it emerged was -0.29 ($P<0.01$) as shown in Fig. 2, and that on the ratio of consumption to food available (dry weight of the twig) was 0.27 ($P<0.05$) as shown in Fig. 3. However, adult dry weight was correlated neither with diameter of the twig nor with the ratio of waste consumption to consumption in the twig ($P>0.05$).



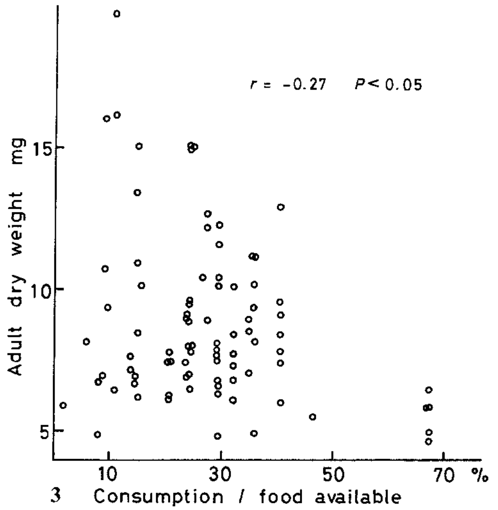
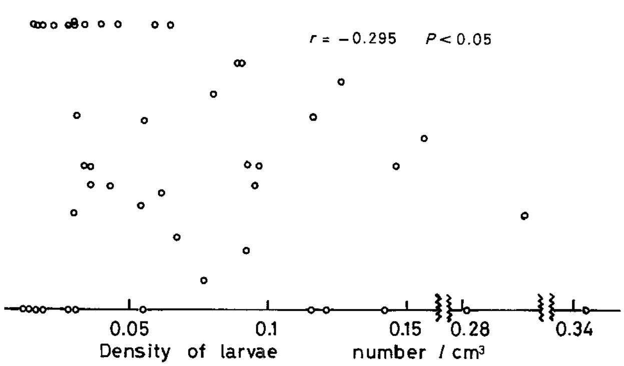


Fig. 2. Correlation between adult dry weight of *Phymatodes maaki* and the density of larvae of *P. maaki* in the twig of *Vitis coignetiae* from which the adults emerged

Fig. 3. Correlation between adult dry weight of *Phymatodes maaki* and the ratio of consumption to the amount of wood available for food in the twig of *Vitis coignetiae* from which the adults emerged



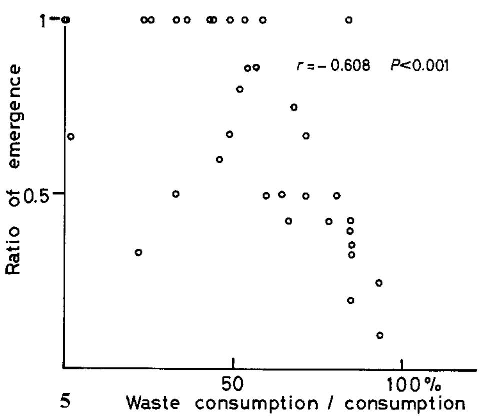


Fig. 4. Correlation between the ratio of numer of emerged adults to the total number of larvae of *Phymatodes maaki* in the twig of *Vitis coignetiae* and the density of larvae in the twig

Fig. 5. Correlation between the ratio of the number of emerged adults to the total number of larvae of *Phymatodes maaki* in the twig of *Vitis coignetiae* and the ratio of waste consumption to total consumption in the twig

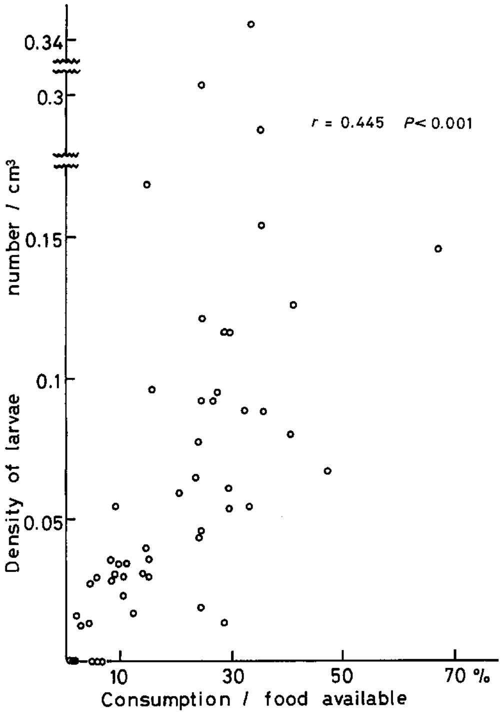


Fig. 6. Correlation between the density of larvae of *Phymatodes maaki* in the twig of *Vitis coignetiae* and the ratio of total consumption to food available in the twig

Correlation among Some Factors

The correlation coefficient of the ratio of emergence on apparent density was $r = -0.295$ ($P < 0.05$, Fig. 4), that on the ratio of waste consumption to consumption, $r = -0.608$ ($P < 0.001$, Fig. 5) and that of density on the ratio of consumption to the amount of the food available, $r = 0.445$ ($P < 0.001$, Fig. 6). However, the ratio of the number of larvae killed by parasitism to total mortality in one twig was not significantly correlated with apparent density of larvae ($P > 0.05$). The correlations between the ratios (waste consumption)/(consumption) and (consumption)/(food available), between density and diameter, between the ratio (consumption)/(food available) and diameter were not significant ($P > 0.05$).

Discussion

Carbon content in larvae and pupae was slightly higher than that in adults. This may be due to the large amount of fat storage in the former.

A very low value of (C-F)/C of about 3% in dry weight was probably due to poor food quality. It caused accordingly the very low value of G/C of 1.24%. Savely (1939) reported that G/C in dry weight was 1.27% for *Chrysobathris* sp. (Buprestidae) and Mamaev (1961) reported the values of 0.21 to 34.4% in a variety of invertebrate species fed on oak wood.

The ratios of (C-F)/C and G/C in nitrogen weight to those in dry weight in *P. maaki* were very high. This high effiency of nitrogen utilization of *P.maaki* may indicate one of the adaptations to food of low nitrogen content. The value of G/(C-F) of 117.6% is slightly higher than the theoretical value of 100% when nitrogen fixation, deamination or other agencies are not taken into account, but this difference seems not to be significant ($0.05 > P > 0.02$).

The ratio of the number of emerged adults to that of larvae of the population of *P. maaki* was 40%, that is, the apparent mortality was 60%. However the actual mortality should be more than the value of WCP/CP of 75%, because waste consumption of individuals that died in the younger stages is small. Therefore WCP/CP will be a ninimum estimate of the mortality in the cohort population. The mortality by parasitism in middle and mature larval stages was large, amounting to about a half of total mortality in these stages. So, the parasitism seemed to be the most important mortality factor.

The growth efficiency of the population (BP/CP) seemed to be low compared with those of populations of leaf-feeders, for example the values of two lepidopteran species *Luehdorfia puziloi inexpecta* (Ikeda, 1976) and *Nymphalis xanthomelas japonica* (Ikeda, 1978) were 7.6% and 9.6% respectively, which was mainly due to the small value of G/C of individual animals. The waste efficiency (WCP/BP) was high for the same reason. WCP/CP was higher than those of the populations of *L. puziloi inexpecta* and *N. xanthomelas japonica* but lower than that in the population of *Papilio xuthus* Linne (Lepidoptera) reported by Tsubaki (1977).

The ratio of total consumption to food available (CP/TW) in the population of *P. maaki* was 18%. In the actual situation where dead woods were set in the natural condition for 2 years, this value may become much higher, because dead wood of *V. coignetiae* was removed before the oviposition in 1975 would have taken place. It seems that the population of *P. maaki* plays an important role in the decay of dead wood of *V. coignetiae*. Watanabe (1966) reported the dry weight of sticks of red pine *Pinus densiflora* and beech *Fagus crenata* set in the natural condition was lost by 20 to 30% after a year and 35 to 55% after 2 years. The loss of dry weight of dead wood of *V. coignetiae* in the study field when set in the natural condition may be similar to these values of Watanabe.

It seems to be natural that the ratio of emergence was inversely correlated with the ratio of waste consumption to total consumption and that the density of larvae was correlated with the ratio of consumption to the amount of food available. The body weight of an emerged adult and apparent mortality of *P. maaki* seemed to be density dependent. This seemed to have resulted from the intraspecific competition for the limited food, because the mortality by parasitism was not density dependent. Dry weight of an adult of *Necydalis formosana* (Cerambycidae) increased with the increment of the diamter of dead wood of *Symplocos argutidens* Nakai from which it emerged (Yamagami, unpublished). As for eight species of *Agrilus* (Buprestidae) tested by Hespenheide (1976), body sizes of two species were significantly correlated with the diamter of branches from which they emerged. In the population of *P. maaki* such correlation was not recognized.

References

Duffy, E.A.J.: A monograph of the immature stages of oriental timber beetles (Cerambycidae), pp. 175–176. London: The British Museum 1968

Hespenheide, H.A.: Patterns in the use of single plant hosts by wood-eating beetles. Oikos **27**, 161–164 (1976)

Ikeda, K.: Bioeconomic studies on a population of *Luehdorfia puziloi inexpecta* Sheljuzko (Lepidoptera: Papilionidae). Jap. J. Ecol. **26**, 199–208 (1976)

Ikeda, K.: Bioeconomic studies of three phytophagous insects. Ph. D. Thesis, Tokyo Metropolitan University, Tokyo (1978)

Kira, K., Shideik T.: Primary production and turnover of organic matter in different ecosystems of the Western Pacific. Jap. J. Ecol. **17**, 70–87 (1967)

Kühnelt, W.: Soil biology, with special reference to the animal kingdom, 2nd ed., pp. 316–332. London: Faber and Faber 1976

Mamaev, B.M.: Activity of larger invertebrates as one of the main factors of natural destruction of wood. Pedobiologia **1**, 38–52 (1961)

Matsumoto, T.: The nitrogen budget in the natural population of a grasshopper, *Parapleurus alliaceus* Germer. In: JIBP Synthesis 17, Studies on methods of estimating population density, biomass and productivity in terrestrial animals (M. Morisita, ed.), pp. 161–169. Tokyo: University of Tokyo Press 1977

Satchell, J.E.: Feasibility study of an energy budget for Meathop Wood. In: Productivity of forest ecosystems (P. Duvigneaud, ed.), pp. 619–630. Paris: Unesco 1971

Savely, H.E.: Ecological relations of certain animals in dead pine and oak logs. Ecological Monographs **9**, 321–385 (1939)

Tsubaki, Y.: A bioeconomic study on the natural population of the swallow-tail butterfly, *Papilio xuthus* Linne. Report from Ebino Biol. Lab., Kyushu Univ. **2**, 37–54 (1977)

Waldbauer, G.P.: The consumption and utilization of food by insects. Adv. Insect Physiol. **5**, 229–288 (1968)

Watanabe, H.: Weight loss of red pine and beech test sticks and associated animals. Bull. Kyoto Univ. For. **38**, 1–14 (in Japanese 1966)

Yoneda, T.: Studies on the rate of decay of wood litter on the forest floor. I. Some physical properties of decaying wood. Jap. J. Ecol. **25**, 40–46 (1975a)

Yoneda, T.: Studies on the rate of decay of wood litter on the forest floor. II. Dry weight loss and CO_2 evolution of decaying wood. Jap. J. Ecol. **25**, 132–140 (1975b)

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