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Food intake and number of eggs laid by the carrion beetle, *Eusilpha japonica* (Coleoptera: Silphinae), collected using pitfall traps

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Abstract

The carrion beetle, *Eusilpha japonica*, is a carrion feeder that roams on forest floors searching for carrion. A field survey using pitfall traps with putrefied meat or without meat was carried out to examine the effect of carrion odor on the attraction of adults in the cedar forest. The sex distribution of the beetles captured in the pitfall traps suggested that the carrion odor might attract females more strongly than males. The distribution pattern showed that males might search for mates as well as for food. The daily food intake of adults collected in the field was measured in the laboratory. Lone females fed on the meat twice as much as lone males. A positive relationship between the cumulative quantity of food intake until the first brood and the clutch size suggested that the quantity of food intake during the pre-oviposition period was critical.

Key words: Carrion feeder; clutch size; food intake; pitfall traps; pre-oviposition period

INTRODUCTION

Because animals move about in their habitat widely and die due to aging, starvation, parasitoidism, injury by intra- and inter-specific fighting and so on, dead carcasses are found on the ground where many kinds of scavengers, including predatory vertebrates and carrion-feeding invertebrates (mainly Coleoptera and Diptera), are actively living (Putman, 1983). Thus, carrion quickly disappears due to the activities of such scavengers and is consequently an ephemeral resource, being temporally and spatially unpredictable for scavengers on the ground (Atkinson and Shorrocks, 1981). Putman (1978) stated that vertebrate scavengers removed a whole carcass lying exposed on the ground during winter and spring, while 10% of carcasses in woodlands in summer and autumn were decomposed by insects before being eliminated by vertebrate scavengers. Payne (1965) described changes in insect scavenger communities established on a pig carcass, where blowflies first arrived to oviposit in the fresh stages of the carcass, carrion beetles appeared during its active decay stages, and the larvae of those species remained on the carcass until its end (then dry) stages when all adults had left.

There is great variety in the size of carrion between vertebrates and invertebrates. Although small vertebrate carcasses, such as birds and rodents, contain highly nutritious food for the carrion beetles (Putman, 1983), such carcasses are very rarely found on forest floors (Atkinson and Shorrocks, 1981) due to the low population density of the animals. Thus, it might be difficult for *Eusilpha japonica* to encounter vertebrate carrion by walking (Nagano, 2003), although they rely on their olfactory sense to search for carrion (Pukowski, 1933). On the other hand, invertebrate carcasses, i.e., earthworms, caterpillars and snails, are relatively common on the ground (Suzuki, 2006), and are probably widely available resources that are easily accessed by the beetles (Ikeda et al., 2007), although an individual invertebrate carcass seems to offer poor nutrition because of its small size.

The carrion beetle, *Eusilpha japonica*, is a carrion feeder, and both adults and larvae roam on the

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ground to search for carrion, which is used to maintain their own bodies and for reproduction (Nagano, 2003). Wilson and Knollenberg (1984) reported that females of *Nicrophorus* spp. started to develop ovaries after encountering carrion. Trumbo (1990b) pointed out that *N. tomentosus* females regulated the number of eggs laid based on the carcass size, particularly in their first brood, and cared for the larvae until they became pupae. On the other hand, females of *E. japonica* showed no parental care and left their eggs after ovipositing them underneath the carrion (Nagano and Suzuki, 2003b). As soon as they were hatched, the larvae came out onto the ground, fed on the carrion, and then began to search for food after the carrion was exhausted (Suzuki, 2006). Probably due to a low food supply, Harusawa (1996) observed a low clutch size of each brood of *E. brunnicollis* throughout the oviposition period, which continued for six weeks. However, there is little information on the relationship between the number of offspring and the quantity of food intake of adult carrion beetles which show no parental care. The purpose of this study was to clarify the amount of food required by wild adults and the number of offspring produced in relation to their daily food intake.

MATERIALS AND METHODS

A field survey of the attraction of carrion for *E. japonica* adults was carried out 7 times from May to September, 2006, in Ibaraki Prefecture, in the warm temperate zone of Japan. Twenty pitfall traps were prepared at 2-m intervals along 4 lines with 5 sites in each line on a cedar forest floor, where litter derived from the leaves and branches of the cedar was abundant. Since the forest crown was closed, forest floor vegetation was poor. A few saplings of *Hedera rhombea*, *Rhus succedanea* and *Ilex crenataeach*, and low coverage of herbs such as *Pleioblastus chino* were found, all of which were less than 40 cm in height. Each sampling included consecutive capturing for two days, i.e., using traps containing putrefied chicken meat for 24 h followed by traps without any meat for 24 h. No individuals that fell into the former traps fed on the chicken meat because a cup with 20 small holes was placed on top of the cup containing meat.

Adults collected from the field were starved for over 72 h in a rearing container (5 cm in height, ϕ=11.5 cm) filled with sand and then allowed to feed on 1.00 g chicken meat on a 2.5 cm square piece of aluminum foil placed on the surface of the sand and changed every 24 h. To maintain the humidity in the container as well as to supply water to the adults, we misted water once a day. The containers were placed at room temperature (ca. 26°C) with the light condition of 16L8D.

Ten each of sexually mature females and males collected in July were singly reared for four days to estimate their daily food intake. Chicken meat of known weight (accuracy 0.01 mg) was supplied to each adult, while five containers with misted sand but without adults were prepared to compare their drying process with that of the chicken meat. After 24 h, the weight of the meat was measured again, and the daily food intake was estimated.

The relationship between daily food intake and reproductive output was examined for 19 pairs captured in late May. Because eggs of *E. japonica* are laid underground, the number of eggs just deposited cannot be counted directly. Thus, the number of first instar larvae was counted immediately after they appeared on the ground. The larvae were then removed from the container. Data for pairs that produced no offspring during the experiment were discarded. Males that had died during the experiment were removed and another individual was placed in the container.

Statistical analyses were performed using the SPSS statistical package (Version 12.0 J).

RESULTS

Three species of carrion beetles were captured throughout the survey period. The majority were *E. japonica* (397 individuals), followed by *Nicrophorus quadripunctatus* (3 individuals) and *N. concolor* (2 individuals). The latter two species were captured in traps with carrion in June and July. The daily number of *E. japonica* females captured in traps without carrion was low in May and September but high in July, while that in the traps with carrion was low in May and increased until September. As shown in Table 1, the average daily number of females in 20 traps with carrion was ca. 20, which was 3.7 times larger than that without carrion, that is, females were attracted by the carrion due to its odor in the reproductive period. The

Table 1. Daily number of adults captured in 20 pitfall traps with and without carrion (±SE), from May to September. Wilcoxon's test was used

	With carrion	Without carrion	
Female	29.7±9.0 (n=6)	9.3±2.1 (n=6)	Z=1.99, p<0.05
Male	19.2±9.2 (n=6)	8.1±1.7 (n=6)	Z=0.41, n.s.
	Z=2.00, p<0.05	Z=0.11, n.s.	

n: number of sampling days.

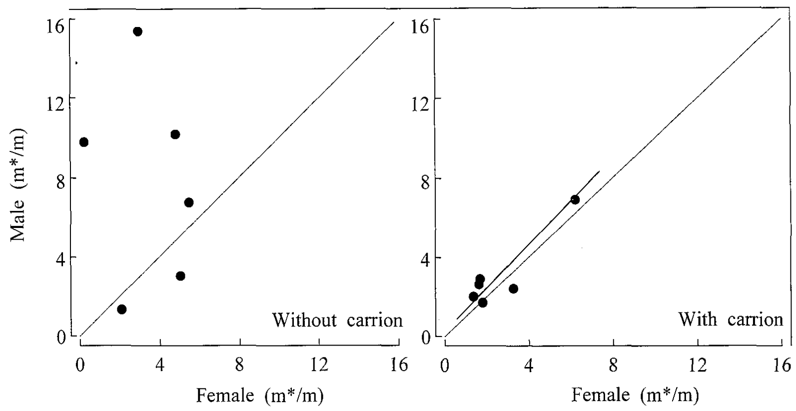

Fig. 1. Relationship in m^*/m between males and females for 20 traps with and without carrion. Using Pearson's correlation coefficient, there was no significant relationship (r=−0.14, n.s.) for traps without carrion, but a significant relationship (r=0.92, p<0.01) for traps with carrion. Each broken line represents a diagonal.

number of males captured in traps without carrion also showed a similar trend, low in May and September but high in July. Since the number of males captured in the traps with carrion fluctuated, there was no significant difference in the average daily number of males captured in the traps between traps containing carrion and those without, although the daily number of males in traps with carrion was about 2 times that in traps without carrion.

There was no significant difference between sexes in the number of adults in traps without carrion (Table 1). Such similar capture efficiencies for pitfall traps without carrion showed that both sexes walked about in a similar way on the forest floor and that the sex ratio was close to unity; however, the odor of carrion attracted significantly more females than males. The pronotum width of females was 9.0±0.16 mm (n=16, SE) and showed no significant difference from that of males, 9.2±0.11 mm (n=16, SE) (Mann-Whitney U-test, U=97.5, n.s.) in the reproductive period.

The number of adults captured in a trap varied from 0 to 15 throughout the survey period. The m^*/m index (Iwao, 1968) was used to determine the distribution pattern of adults captured in 20 traps for each sampling. When the m^*/m was more than unity, the adults were captured patchily in the traps. The m^*/m for females in traps without carrion was 5.6 (May), 2.0 (June), 5.1 (early July), 3.0 (late July), 4.9 (August) and 0 (September), indicating that females aggregated on the forest floor except in September. Thus, the averaged m^*/m for females was 3.4±0.9 (SE). On the other hand, the m^*/m for males was always more than unity and was 15.6 at its maximum in late July (mean: 7.9±2.1, SE). As shown in Fig. 1, the m^*/m for males was larger than that for females in 4 of 6 samplings, suggesting that males tended to aggregate rather than females. There was no significant relationship in m^*/m between sexes.

The m^*/m for females in traps with carrion was 1.6 (May), 6.2 (June), 3.3 (early July), 1.3 (late July), 1.5 (August) and 1.8 (September), while that for males changed from 1.7 to 6.7 (Fig. 1). The averaged m^*/m values for females and males were 2.6±0.8 (SE) and 3.0±0.7 (SE), respectively. The m^*/m for males captured in traps with carrion was significantly smaller than that in traps without carrion (Mann-Whitney U-test, U=7, p<0.05). A sig-

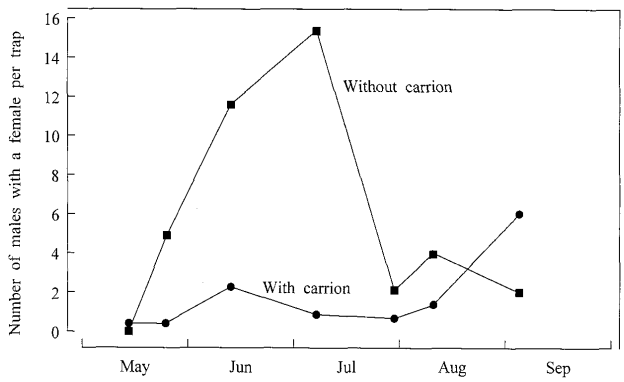

Fig. 2. Seasonal changes in the number of males with a female per trap, adopting the index of interspecies mean crowding methods (m^*_{FM}). Each sampling time includes 20 pitfall traps with (circle) and without (square) carrion from May to September.

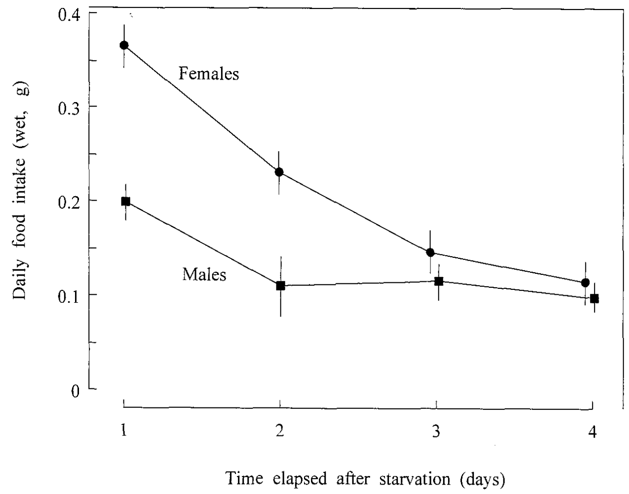

Fig. 3. Changes in the daily food intake of lone females ($n=7$) and lone males ($n=10$) after starvation for 72 h (±SE).

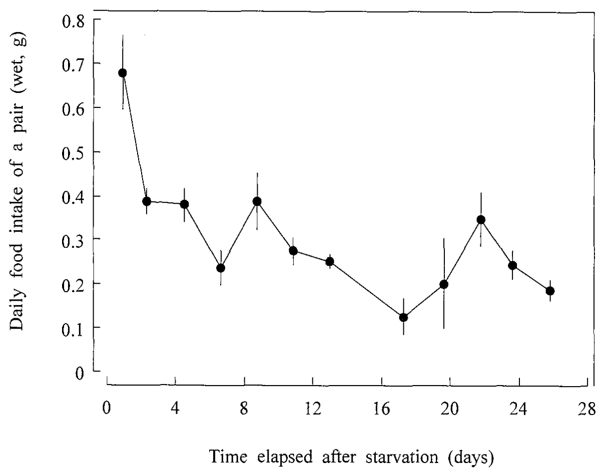

Fig. 4. Changes in the daily food intake of pairs ($n=14$) after starvation for 72 h (±SE).

nificant relationship in m^*/m between sexes was also found; therefore, both sexes showed a similar distribution pattern on the forest floor, where they were attracted in the same way to the odor of meat.

The interspecies mean crowding method (Iwao, 1977) was used to determine the number of males coexisting with a female in a trap. The m^*_{FM} was calculated using two parameters. One was the number of females per trap, F, and the other was the number of males in the same trap, M. The denominator is assumed by adding all traps of FM. The numerator is the sum of F for all traps. Thus, when there is at least one female with males, the m^*_{FM} is more than 0. As shown in Fig. 2, the m^*_{FM} of traps without carrion increased from May to July and then decreased. The number of males with a female was more than 10 in June and July. On the other hand, the m^*_{FM} of traps with carrion was constantly low irrespective of the sampling times, except in September.

Starved lone adults actively walked around immediately after they were placed in the plastic container with meat, and most individuals started to feed on the meat within 30 min. The daily food intake of lone adults on the first day was 0.37±0.02 g (SE) for females and 0.20±0.02 g (SE) for males (Fig. 3). Females fed on a significantly larger quantity of food than males on the first day (Mann-Whitney U-test, $U=3$, $p<0.01$). Although the daily food intake of both sexes decreased with time, the average daily food intake of lone males was 0.13±0.01 g (SE), while lone females fed on 0.23±0.02 g (SE), which was twice as much as the males.

A male and female placed together in the container started to actively walk around the container immediately. Within 30 min, some pairs started to feed on the meat independently. Copulation was observed within the day. During such copulation, each female continued to feed on the meat, but their mates continued to mount by holding the antenna of the female by the mandible without feeding. The daily food intake of a pair on the first day was 0.67±0.12 g (SE), as shown in Fig. 4. The average daily food intake of a pair was 0.31±0.02 g (SE), which was not very different from the sum of the daily food intake of a lone male and female.

It took 13.3±0.7 days (SE, $n=14$) to produce the first brood for pairs captured in late May. The sum of the eggs laid by the female and the quantity of food intake throughout the experiment showed a significant relationship ($r^2=0.58$, $p<0.05$). The

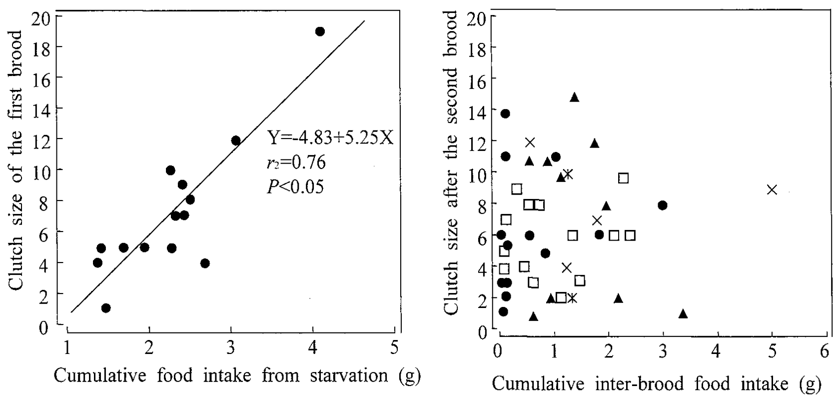

Fig. 5. Clutch sizes in relation to the cumulative food intake of a pair (wet, g). A significant relationship was found between the clutch size in the first brood and food intake before the first brood. The clutch size of the second (circle), third (open square), fourth (triangle), fifth (cross) and sixth (asterisk) broods had no significant relationship with each inter-brood food intake (r^2=0.01, 0.06, 0.02, 0.24 and 0.65, respectively).

clutch size of the first brood varied widely, and a positive relationship between the cumulative quantity of food intake of the pair before until the first oviposition and the first clutch size was observed, as shown in Fig. 5, indicating that more than 1.11 g was needed to lay an egg with somatic maintenance of the parents. Thereafter, the pairs successively produced 3.2±0.3 (SE) broods during 18.9±0.7 days (SE, n=14), up to the end of the experiment. The size of each clutch had no significant relationship with cumulative food intake during the inter-clutch interval.

DISCUSSION

Baited traps are commonly used to capture insects that walk around on the ground to search for food by odor (Southwood and Henderson, 2000). Even if Silphidae, Catopidae, Histeridae, Scarabaeidae, Geotrupidae and Trogidae commonly fall into pitfall traps without carrion, baited traps are much more attractive to carrion feeders (Kamimura et al., 1964). The structure and function of insect communities captured in baited traps have been reported (Wilson et al., 1984; Trumbo, 1990a; Hosoda, 1996; Wolf and Gibbs, 2004), and the population parameters have been estimated for ground beetles (Wallin, 1986; Günther and Assmann, 2004) and carrion beetles (Nisimura et al., 2002).

The sampling techniques for carrion beetles in the fields have exclusively focused on traps with carrion (Wilson and Fudge, 1984; Trumbo, 1990a). Traps hanging from branches were also used to capture flying beetles searching for food by odor (Wilson et al., 1984; Nagano and Suzuki, 2003a); however, individuals that fall into pitfall traps due to attraction to the odor of carrion have not been discriminated from individuals just walking about, and both were found together in the same pitfall traps. Baars (1979) pointed out that only individuals that were very active were captured in traps without bait. Thus, changes in the daily number of both sexes of *E. japonica* captured in traps without carrion could reflect changes in walking activity. In July, both sexes of the beetle showed a high capture number in traps with and without carrion, suggesting that July must be a high mating season on the forest floor under such a univoltine life cycle of the carrion beetle. Both sexes visit carcasses in order to eat for somatic maintenance and to copulate, while females also need to obtain energy to produce offspring from the resources (Steiger et al., 2007). Thus, the capture efficiency of *E. japonica* females by traps with carrion was higher than that of males, and females searched for food more intensely than males on the forest floor throughout the survey period.

In September, most adults captured in the pitfall traps seemed to be newly emerged individuals because they had soft elytrum. In addition, no first or second instar larvae were found in the fields, suggesting that the reproductive period had passed. High and low numbers of adults captured with and without carrion, respectively, indicated that newly emerged adults were strongly attracted to food, probably in order to hibernate.

Differences in the aggregation pattern of *E.*

japonica males captured between non-carrion and carrion traps suggested that males might change their walking activity in relation to the odor of carrion in the field. Although carrion beetle copulation was observed in fields without carrion (Eggert, 1992), sex pheromones were used by males of *Nicrophorus* spp. to wait for their mates on a carcass (Pukowski, 1933). Since most male *E. japonica* were found in traps into which more than one female had fallen, and it is likely that one had mated with the females before the traps were examined, males might search for food as well as mates, attracted not by the odor of carrion but that of female pheromones. On the other hand, the fact that there was little difference in the distribution pattern between carrion and non-carrion traps indicated that females always searched for food irrespective of the presence of carrion odor on the forest floor.

Tominaga (1991) stated that *E. japonica* larvae appeared on the ground one month after the adults had been captured in the field, which was in mid-May. In the present study, laboratory-reared females captured by pitfall traps in May produced the first clutch in early June, when first instar larvae had appeared in the field. A positive relationship between the cumulative quantity of food intake of a pair before the first oviposition and the first clutch size was found. Thus, the pre-oviposition period of *E. japonica* might be at least two weeks, during which the quantity of food intake is critical for female reproduction. There have been several reports on the relationships between food intake in the pre-oviposition period and egg production in the carrion beetle, *Nicrophorus vespilloides* (Steiger et al., 2007), and in the dung fly, *Scathophaga stercorallia* (Reim et al., 2006). *E. japonica* females found in May on the forest floor seemed to have a great need for food and fed much more than males, probably in order to produce eggs.

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