Optimal Clutch Size for Maximizing Reproductive Success in a Parasitoid Fly, *Exorista japonica* (Diptera: Tachinidae)

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The number of adults emerging from a host, their size in terms of puparium weight, mortality and sex ratio of *Exorista japonica* were examined in relation to clutch size per larva of the host, *Pseudalata separata*. Effects of female size on fecundity and longevity were also examined. The mean number of adults emerging from the host increased as clutch size increased up to 15. Body size, however, decreased markedly with increasing clutch size. Sex ratio was not significantly different from 0.5. Survival ratio of eggs to adults correlated negatively with clutch size. There was a positive correlation between the size of females and their fecundity, but no correlation between size and longevity. The relationship between clutch size and total number of eggs expected from female offspring was also examined. Reproductive success gained from one egg was maximized when clutch size was 1, while that gained from one host attained its maximum when clutch size was 10.

**Key words:** clutch size, *Exorista japonica*, fitness, reproductive strategy, Tachinidae

INTRODUCTION

Many types of animals produce eggs or offspring in clutches on discrete resources. The study of clutch size evolution is one of the oldest areas of behavioural ecology, and has recently been undertaken for insects, particularly parasitoids (reviews in Waage, 1986; Godfray, 1994). Predators can exploit other prey when the present one is insufficient to complete development. In contrast, once a female parasitoid oviposits on a host, the amount of food for the larvae is fixed, and oviposition decisions made by the female parasitoid are crucial to her reproductive success. This makes parasitoids excellent organisms for the study of reproductive strategy. If all the eggs deposited on a host produce normal adults, it would be adaptive for females to lay as many eggs as possible on the host, because searching for other hosts requires more time and energy. However, once supernumerary eggs are deposited on a single host, intraspecific competition occurs among larvae in the host, resulting in higher parasitoid mortality in the immature stages or stunted adults. As the benefit of laying more eggs is countered by the disadvantages caused by such deleterious effects, there should be an optimal clutch size for the female to produce a maximum number of offspring and to minimize the negative effects of intraspecific competition within the host (Takagi, 1985).

Although there has recently been a surge of interest in the theory of clutch size of insect parasitoids, there have been very few manipulative studies of clutch size (Hardy et al., 1992). In general, it is very difficult to manipulate clutch size of parasitoid wasps without affecting primary sex ratios, because of their haplodiploid reproduction systems. It is also difficult to count the number of eggs of endoparasitoids without dissection. In tachinid flies,
however, sex is probably determined by the random segregation of sex chromosomes, and
the sex ratio is usually 0.5 (Waage, 1986; Godfray, 1994, but see Clausen, 1940; Ziser et
al., 1977). Some tachinids lay heavy-shelled macrotype eggs on the host cuticle (Clausen,
1940; Shima, 1989). Since the egg shells remain on the host after hatching, it is possible to
count the number of eggs deposited on the host unless the egg shells drop from the host and
the host moults. Exorista japonica Townsend is an endoparasitic fly of caterpillars and some-
times deposits supernumerary eggs on a single host, not only in the laboratory (Nakamura,
1994) but also in the field (Takahashi and Sawaki, 1969). Therefore, an ideal way to carry
out manipulative experiments is to use tachinid flies laying macrotype eggs such as E.
japonica.

To determine the optimal clutch size for female E. japonica to oviposit on a host, last-
instar larva of Pseudaleia separata Walker, the author examined the effects of clutch size on
parasitoid mortality, adult size and sex ratio, and the effects of body size on the number of
ovarioles, fecundity and longevity of females.

MATERIALS AND METHODS

Host and parasitoid. Larvae of the common armyworm, P. separata, were obtained from
a stock culture and reared on an artificial diet after Hattori and Atsusawa (1980). E.
japonica culture was initiated from parasitized last-instar larvae of the fall webworm,
Hyphantria cunea Drury, which were collected at the National Institute of Agro-Environ-
mental Sciences, Tsukuba, Ibaraki, in September, 1990 and maintained after the method of
Nakamura (1994).

Clutch size manipulations. Day 1 last-instar larvae of P. separata of approximately the
same weight (135–165 mg: mean 150.3 mg, weighed soon after moulting to last-instar larva)
were given to mated and singly caged female E. japonica (day 4–14, n = 47) for oviposition for
3 min to 5 h. To adjust clutch size per host to 1, 2, 3, 6, 9, 12, 15 and 18 (n = 120, 90, 80,
60, 59, 60, 60 and 60, respectively), one or two excess eggs were removed with tweezers
when necessary. Hosts with more than 20 eggs were not used. Host larvae were kept
individually in plastic Petri dishes (9 cm dia., 2 cm depth) with an artificial diet of the army-
worm until parasitoid larvae emerged from the host. The number of puparia and adults of
the fly emerging per host, puparium weight, and sex ratio were recorded. All puparia were
weighed 7 days after puparium formation. A total of 47 female and 42 male adults were
used to examine the relationship between head width and puparium weight.

Number of ovarioles, fecundity and longevity of female. To determine the relationship between
puparium weight and the number of ovarioles of the emerging female, day 2 adult females
of E. japonica (n = 34) obtained from the above experiment were dissected and the total
number of ovarioles was counted. The following experiments were also carried out to
determine the effect of puparium weight on fecundity and longevity of the female. Newly
emerging and mated females (n = 45) obtained from the clutch size manipulations were
individually kept in a cage (plastic cylinder, 16 cm dia., 22 cm ht.) with a sugar cube and
distilled water. The females were provided with two day 1 last-instar hosts for oviposition
between 09:00 and 16:00. Hosts were recovered and the number of eggs deposited on the
hosts was counted daily until the fly died. The lines fitted in graphs were calculated using
the linear least squares method. All experiments were conducted under conditions of 25°C,
60% RH and a photoperiod of 16L–8D.
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Fig. 1. Relationship between the number of E. japonica eggs laid per host (clutch size) and the mean number of puparia formed (open circles) and adults emerging (solid circles) of the fly per host. Vertical lines indicate standard error. Regression for the mean number of adults emerging: $y = -0.0170x^2 + 0.554x + 0.937$, $r^2 = 0.99$, $p < 0.001$.

Fig. 2. Relationship between the number of E. japonica eggs laid per host (clutch size) and the mean puparium weight of males (open circles) and females (solid circles). Vertical lines indicate standard error. Asterisks show significant difference between the mean puparium weight of males and females in each clutch size (t-test, * $p < 0.05$, ** $p < 0.01$, ns: $p > 0.05$). Regression for the mean puparium weight of females: $y = -45.1 \log(x) + 78.4$, $r^2 = 0.95$, $p < 0.001$.

Fig. 3. Relationship between the number of E. japonica eggs laid per host (clutch size) and the survival rate to puparium (open circles) and adult (solid circles). Regression for survival rate of adults: $y = -0.0190x + 0.590$, $r^2 = 0.94$, $p < 0.001$.

Fig. 4. Relationship between the number of E. japonica eggs laid per host (clutch size) and the sex ratio of parasitoid offspring. Vertical lines indicate 95% confidence limits.

RESULTS

As clutch size increased, the mean number of adults emerging from the host formed a domed curve with a peak at clutch size 15 (Fig. 1). A quadratic polynomial regression was thus adapted to describe the relationship. On the contrary, the mean puparium weight of males and females dropped sharply as clutch size increased from 1 to 6 and decreased gradually afterwards, so that a logarithmic curve was fitted (Fig. 2). The mean puparium weight of males was significantly larger than that of females at all clutch sizes except for 9 (Fig. 2). The ratio of the number of emerging adults to the number of deposited eggs gradually decreased with clutch size (Fig. 3). Female sex ratio was not significantly different from 0.5 at any clutch size (Fig. 4, $\chi^2$-test, $p > 0.05$). Since puparium weight showed a highly
positive correlation with the cube of adult head width (Fig. 5), the weight of the puparium was used for a body size index. The size of females (puparium weight) showed a highly significant correlation with the number of ovarioles and fecundity (Fig. 6). However, body size had no relation to longevity (Fig. 7).

DISCUSSION

There is a trade-off between the number of offspring from a single host and size in
gregarious parasitoids, and an increase of numbers per host causes higher parasitoid mortality in the immature stages (van Alphen and Visser, 1990). The mean number of emerging adults of *E. japonica* increased until a clutch size of 15 and decreased, thereafter (Fig. 1). In a tachinid fly, *Archytas marmoratus*, all parasitoids die before emergence, once the number reaches a certain level (Hughes, 1975). Although this phenomenon did not occur in this study, there is the possibility that all maggots might die at clutch sizes much larger than 18. Body size (puparium weight) decreased sharply up to a clutch size of 6 and decreased gradually thereafter. The mean puparium weight of females at clutch size 6 was almost equal to 40% of that of females at clutch size 1 (Fig. 2). Thus, the early increase in clutch size greatly affected the body size of adults. Survival rate to the adult stage decreased with increasing clutch size (Fig. 3). In accordance with several reports that more than one parasitoid larvae per host might better enable the parasitoid to overcome host defences (Allee effect) in gregarious parasitoid wasps (e.g., Ikawa and Okabe, 1985), survival rate at clutch size 2 seemed to be higher than that at clutch size 1 (Fig. 3), although the difference was not statistically significant ($\chi^2$-test, $p > 0.05$).

The size of females showed no significant relationship to longevity (Fig. 7), although larger females generally tend to live longer in many parasitoid species (Godfray, 1994). Female size, however, had a highly significant correlation with the number of ovarioles and fecundity (Fig. 6).

To estimate optimal clutch size for maximizing parental fitness, the total number of eggs expected to be produced by female offspring emerging from hosts of various initial clutch sizes was calculated using the relationships shown in Figs. 1, 2, 3 and 6(b); it was assumed that the sex ratio was 0.5. The calculations were made for fitness gained per host and per egg (Fig. 8). The curve for fitness per host showed a dome shape, with the maximum value close to clutch size 10, while the curve for fitness per egg reached a maximum at clutch size 1.

Models which consider fitness gain per unit time (Jwasa, et al., 1984; Parker and Courtney, 1984; Skinner, 1985) predict that parasitoids should vary clutch size in response to the rate of host finding and oviposition ability at the time. If egg number is very large relative to the number of hosts available, the parasitoid should lay the clutch size which would maximize its fitness per host. But, if eggs are in short supply or severely limited, the parasitoid should produce the clutch size which maximizes its fitness gain per egg (Waage,
According to the models, the best strategy for $E. \text{japonica}$ is to oviposit 10 eggs on a host when host density is low and there are few prospects of finding enough hosts to deposit all the eggs of the parasitoid female. On the other hand, it is better to lay 1 egg per host when host density is high enough to deposit all of a female's eggs.

Predicted clutch sizes to maximize fitness gained from each host were often substantially larger than the observed ones (e.g., Waage and Ng, 1984). This discrepancy may be due to several factors (Charnov and Skinner, 1984), one of which is the frequent correlations between the number of eggs laid by a female and unknown third variables (Godfray, 1994). Manipulative studies are, thus, essential to control for these confounding variables (Hardy et al., 1992). Although many studies on insect clutch size were prompted by studies of hymenopterous parasitoids, it is very difficult to measure primary sex ratios of parasitoid wasps, and females tend to produce a more male biased sex ratio under certain experimental conditions (Suzuki and Iwasa, 1980; Takagi, 1985). It is also difficult to examine clutch sizes of endoparasitoids without dissection, and no one has directly manipulated clutch size in an endoparasitoid (Godfray, 1994). Since sexual composition and clutch size can influence offspring fitness and optimal clutch size (Waage and Ng, 1984), uncertainty of those factors could cause misleading results. In this sense, tachinids that are all endoparasitoids (Belshaw, 1994) and oviposit macrotype eggs on a host as $E. \text{japonica}$ constitute excellent organisms for clutch size studies, because of their sex ratio of 0.5 (Fig. 4 in this study and Waage, 1986; Godfray, 1994, but see Clausen, 1940; Ziser et al., 1977) and visible external eggs.

In most species of parasitoid wasps, females are usually larger than males (Hurlbutt, 1987), and the advantages of being larger are relatively less for males than females (Godfray, 1994). Therefore, many studies calculating optimal clutch size have used only the size of females, but not that of males (e.g., Waage and Ng, 1984; Takagi, 1985). The method for obtaining optimal clutch size in this study was also in accordance with those studies. However, larger males enjoy greater reproductive success in some other dipteran species (Burk and Webb, 1983; Churchill-Stanland et al., 1986; Cook, 1992), and the mean weight of male puparia in this study was significantly heavier than that of females at all clutch sizes except for 9 (Fig. 2). This phenomenon may explain how male size of $E. \text{japonica}$ is important in reproductive success, and suggests that the size of males should be considered as a factor in calculations of the clutch size in this species.

In hymenopterous parasitoids, there are many reports indicating that adult females have the ability to recognize host suitability, size and age, and are able to regulate clutch size according to the quality of the host (Waage, 1986; Godfray, 1994). However, since these characteristics have not yet been demonstrated in tachinid flies (but see Weseloh, 1976), further investigations on this in $E. \text{japonica}$ might enhance our understanding of clutch-size evolution of parasitoids.

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