

Conflict between optimal clutch size for mothers and offspring in the leaf miner, *Leucoptera sinuella*

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Abstract. 1. Clutch size in a leaf-mining moth, *Leucoptera sinuella* (Reutti), was examined to determine whether the clutch size in natural populations meets the prediction of an optimal strategy, through comparisons between the optimal clutch sizes for offspring and for a mother.

2. A field experiment revealed that premature leaf abscission, egg dropping, and larval competition were important selective forces in determining the clutch size of this leaf miner on its host plant, *Salix miyabeana*. Then, optimal clutch size was predicted using the theoretical model of Weis *et al.* (1983), from the data obtained in the field experiment.

3. The model predicts that the clutch size that maximises offspring fitness is two, and that the clutch size that maximises reproductive success of the female varies from two to four, depending on the female's survival rate between oviposition events. The predicted clutch size (two) was identical to the clutch size observed most frequently in the field, assuming > 95% survival rate of females. Suitability of the model of Weis *et al.* (1983) was discussed based on these results.

Key words. Leaf miner, life-history evolution, offspring fitness, optimal strategy, reproductive success.

Introduction

The mechanism of clutch size determination is one of the important components of life-history evolution (Stearns, 1992), and has been repeatedly examined in several taxonomic groups from both theoretical and empirical approaches (Godfray *et al.*, 1991; Wilson & Lessells, 1994; Monaghan & Nager, 1997). According to evolutionary theory, selective pressures determining clutch size act on both offspring fitness and oviposition efficiency of females (Godfray, 1987; Godfray *et al.*, 1991). In herbivorous insects, however, clutch size determination has been mainly examined from the perspective of offspring fitness, because clutch size observed in the field can be explained by the availability of food resources for larvae (Pilson & Rausher, 1988; Matsumoto, 1990; Vasconcellos-Neto & Monteiro,

1993), attack by natural enemies during the egg or larval period (Damman, 1991; Damman & Cappuccino, 1991; Siemsen & Johnson, 1992), and the maintenance of a suitable microclimate during the egg stage (Clark & Faeth, 1998). In these studies, oviposition efficiency of the female has received less attention as a determinant of clutch size; however, conflicts between offspring and parents over the determination of clutch size are probably common in herbivorous insects (Weis *et al.*, 1983; Desouhant *et al.*, 2000). For example, when searching for oviposition sites is costly, females should lay eggs in larger clusters to reduce the costs associated with multiple oviposition events (Courtney, 1984). In this case, laying large clutches would lead to increased reproductive success of the female even if the fitness of individual offspring decreased (Weis *et al.*, 1983). Hence, the clutch that maximises offspring fitness is not necessarily identical to the clutch that maximises reproductive success of the female. This indicates that analysis of clutch size on the basis of offspring fitness alone may overlook an important mechanism.

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In the present study, clutch size in a leaf-mining moth, *Leucoptera sinuella* (Reutti) (Lyonetiidae: Lepidoptera) was examined to determine whether it meets the prediction of an optimal strategy, through comparison of optimal clutch sizes for offspring and females. A field experiment was conducted to determine the performance of immature stages in a tri-trophic context, because leaf-mining insects are affected by host plant leaf abscission (Preszler & Price, 1993), competitors on a same leaf (Murai, 1974; Stiling *et al.*, 1984), and parasitoids (Valladares & Lawton, 1991; Conner & Beck, 1993). Then, a mathematical model was constructed to predict the clutch size that maximises the fitness of individual offspring and the lifetime reproductive success of the female using parameters estimated from the field experiment. Because it was difficult to determine adult performance of the leaf miner in the field, reproductive success of the female was predicted using several different values of survival in the model (see Weis *et al.*, 1983).

Materials and methods

Biology of the leaf miner

Leucoptera sinuella (*Paraleucoptera sinuella*: currently the genus *Paraleucoptera* is treated as a junior synonym of genus *Leucoptera*; Leraut, 1997) is distributed in northern areas of the Holarctic region (Kuroko, 1982). Adults appear in June and August in Hokkaido, Japan (H. Kagata, unpubl. data). Females lay one egg mass on the upper surface of a leaf per oviposition. Larvae feed gregariously on leaf mesophyll of several *Populus* and *Salix* species, making a communal mine. The larval period lasts about 20 days and the larvae do not emerge from the leaf until pupation.

Clutch size (number of eggs deposited during one oviposition event) ranged from one to six (mean \pm SD = 2.22 ± 0.84) on the host plant, *Salix miyabeana* (Seemen); the most frequent number of eggs being two (Kagata & Ohgushi, 2002a). There was a weak positive correlation between clutch size and leaf size (Kagata & Ohgushi, 2002a). In addition, oviposition by several females occurred frequently on the same leaf (mean number of egg masses per leaf \pm SD = 1.38 ± 0.81 ; Kagata & Ohgushi, 2002b).

Experimental design

An experiment to determine the selective forces affecting clutch size was conducted on the floodplains along the Ishikari River, Ishikari City, Hokkaido ($43^{\circ}11'N$, $141^{\circ}24'E$). *Salix miyabeana* is the most abundant of several *Salix* spp. in the area, and *L. sinuella* larvae are commonly observed on this host species. Sixteen *S. miyabeana* trees were chosen randomly for the experiment. Although these trees were isolated from each other, genetic relationships among them were unknown. Polypropylene mesh bags (26×30 cm) were used to enclose the adults for mating and oviposition. One pair of male and female moths collected at the study site were

introduced into each bag in early June, coinciding with the natural oviposition period of *L. sinuella*. Five to 10 bags per tree (in total 130 bags), each on a separate branch, were placed on 16 trees. Two or three days after bagging, all adult moths were removed from the bags, and leaves with eggs were marked with an oil marker.

Bagging yielded 552 leaves with egg masses used in the experiment. The size of egg masses varied from one to nine, and more than one egg mass per leaf occurred (i.e. multiple oviposition). Offspring performance and mortality factors were analysed relative to standardised egg density (eggs cm^{-2}) because leaves with eggs varied in size and ovipositing females adjusted clutch size in response to leaf size (Kagata & Ohgushi, 2002a). In addition, mortality factors were analysed based on absolute clutch size to detect any density-dependent relationship. The egg densities were divided into five classes: <0.2 , $0.2-0.4$, $0.4-0.6$, $0.6-0.8$, and ≥ 0.8 eggs cm^{-2} . To reduce egg masses to one per leaf, excess eggs were removed with a needle. However, to create higher density class (≥ 0.6 eggs cm^{-2}), two or three egg masses were left on a leaf, because few individual egg masses contained a sufficient number of eggs. After the length of the marked leaf was measured to estimate leaf area (see Kagata & Ohgushi, 2002a), each branch was enclosed again with a mesh bag to prevent additional oviposition. To determine the effects of natural enemies on larval performance, enemy-free (bagged) and enemy-exposed (control) treatments were used. Bagged branches were randomly assigned to the two treatments (50 enemy-free and 80 enemy-exposed treatments). At the end of the oviposition period, control bags were removed so that the leaf miners were exposed to attack by natural enemies. The 50 enemy-free branches were kept enclosed in bags to exclude predators and parasitoids until the end of the experiment. All marked leaves were collected 1 month after oviposition, sufficient for a larva to have developed to the final instar. Except where egg death or leaf abscission occurred, collected larvae were reared in the laboratory until eclosion of adult moths or parasitic wasps. Each of the leaves including larvae were put in plastic cases ($7 \times 12 \times 3$ cm). Moistened paper was placed on the bottom of each case to maintain humidity. The number of eclosed adult moths was recorded along with the causes of mortality. Deaths in leaf-mining insects are easily determined by characteristic traces on or within a leaf (Faeth & Simberloff, 1981). They were classified into the following five categories: (1) leaf abscission; (2) egg death due to egg dropping and egg predation; (3) larval predation; (4) parasitism, and (5) unknown causes.

Adults were fixed in 70% alcohol immediately after eclosion, and body length was measured under a microscope. Moreover, several females were dissected under a microscope to count mature eggs in ovarioles. Continued egg maturation after eclosion was disregarded because this is a short-lived species. The relationship between female body size and egg number in ovarioles was determined to estimate potential fecundity. Relative fitness of offspring at each density class was estimated by the following equation:

$$W_i = l_i/m_i, \quad (1)$$

where W_i = mean fitness per individuals on leaf i , l_i = total potential fecundity of all individuals that developed to adult on leaf i , and m_i = number of eggs on leaf i .

Statistics

Relationships between egg density and mortality factors were tested by Spearman's rank correlation. Effect of clutch size on parasitism was tested using a G -test. Differences in survival rate and relative fitness were tested using a two-way ANOVA with bagging treatment and egg density as the main effects. Survival rate data were arcsine-transformed prior to the analysis. Differences in adult body size were tested using a three-way ANOVA (factors = treatment, density, and sex). When a significant difference was detected, the Scheffé test was performed as a *post-hoc* test. Relationship between female body size and fecundity was determined by a linear regression analysis. Because preliminary analysis showed that larval performance did not differ significantly among study trees (e.g. Kruskal–Wallis test: $H = 19.07$, $P > 0.05$ for survival), pooled data across trees were used in the analyses to obtain replicates for each density class.

Results

Density-dependence in mortality factors

Density-related mortality factors were detected for both enemy-free (bagged) and enemy-exposed (control) treat-

ments (Fig. 1 and Table 1). Leaf abscission increased with increasing egg density, while egg death was inversely density dependent. The egg death in the enemy-free treatment resulted from egg disappearance, which was most likely due to eggs failing to adhere to the leaves. In addition, small clutches in the enemy-free treatment tended to disappear, although its significance was not tested due to its low frequency in large clutches (Table 2). In the control, egg death was caused by disappearance, which may reflect dropping, predation, or both, since their causes could not be distinguished from each other.

Larval mortality rate due to predation and parasitism was low (Fig. 1), and it was not significantly correlated with egg density (Table 1). In addition, clutch size was not correlated with parasitism ($G_3 = 0.94$, $P > 0.05$; Table 2). Although larval death or disappearance by unknown causes was the greatest mortality factor (Fig. 1), it was independent of egg densities in both enemy-free treatment and control (Table 1). Larval death due to interference competition or starvation was not observed in either treatment.

Offspring fitness

Survival rate until adult eclosion differed significantly between treatments, and among density classes (two-way ANOVA: Table 3, part a). An interactive effect between treatment and density was not detected, and a *post-hoc* test (Scheffé test, $P < 0.05$) was conducted for different density classes using pooled data for the experimental treatments (i.e. enemy-free treatment and control). The survival rate showed a convex curve, and there was a significant difference between the 0.2–0.4 and > 0.8 eggs cm^{-2} classes (Fig. 2a).

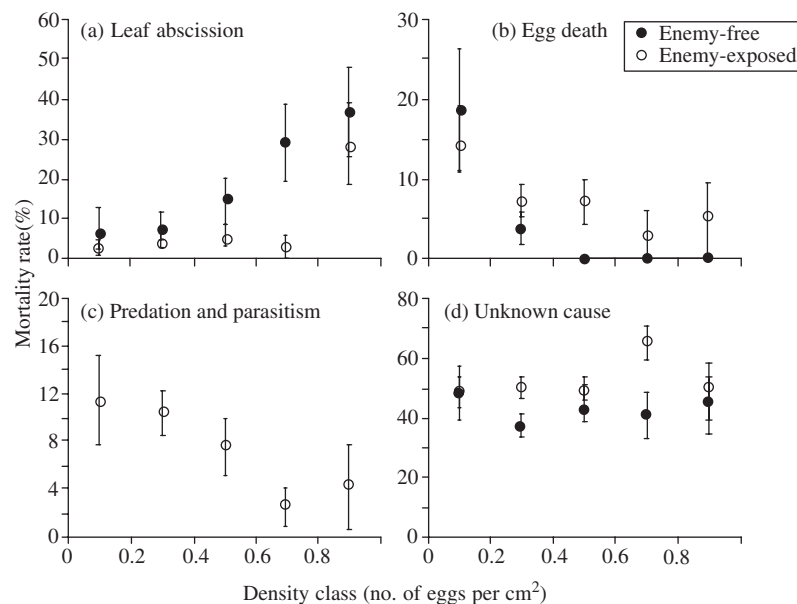


Fig. 1. Mortality rates from (a) leaf abscission, (b) egg death, (c) predation and parasitism, and (d) unknown causes, at different density classes. Vertical bars show SE. ●, Enemy-free (bagged) treatment; ○, enemy-exposed (control).

Table 1. Density dependence in mortality factors of *Leucoptera sinuella*. *n* = sample size.

Mortality factor	Enemy-free (bagged)			Enemy-exposed (control)		
	<i>n</i>	ρ	<i>P</i>	<i>n</i>	ρ	<i>P</i>
Leaf abscission	189	0.28	<0.0001	363	0.16	0.002
Egg death	189	-0.27	<0.0001	363	-0.11	0.037
Predation	189	-		363	0.05	0.321 NS
Parasitism	189	-		363	-0.08	0.126 NS
Unknown	189	0.03	0.724 NS	363	0.03	0.567 NS

Body size of adult moths differed significantly between treatments and sexes, and among density classes (three-way ANOVA: Table 3, part b). There were no interactions among the three factors. Body size was significantly larger in the control than in the enemy-free treatment. Females were significantly larger than males (mean body size \pm SE: female, 2.73 \pm 0.02 mm, *n* = 283; male, 2.50 \pm 0.02 mm, *n* = 284). The sex ratio of the adult moths was approximately 1:1 (male:female), and was not affected by egg density ($G_4 = 1.51$, $P > 0.05$). A *post-hoc* test (Scheffé test, $P < 0.05$) was conducted for different density classes using pooled data for experimental treatments and sexes because there were no interactions among the main factors. Body size decreased consistently with increasing density (Fig. 2b).

The number of mature eggs in ovarioles was positively correlated with female body size ($Y = -99.5 + 51.5X$, *n* = 51, $r^2 = 0.86$, $P < 0.0001$), indicating that larger females have a larger potential fecundity.

Relative fitness differed significantly among density classes; however, it was not affected by treatment or interactions between treatment and density class (two-way ANOVA; Table 3, part c). A *post-hoc* test (Scheffé test, $P < 0.05$) was conducted for different density classes using pooled data for experimental treatments because interactions were not significant. The highest fitness was found in the 0.2–0.4 eggs cm⁻² class with fitness decreasing in lower or higher density classes (Fig. 2c).

Optimal model

Model construction

The optimal clutch size that maximises offspring fitness, fitness per clutch, and reproductive success under different survival rates of the female was estimated using a model

Table 2. Rates of egg dropping for clutches in the enemy-free treatment and parasitised clutches in the enemy-exposed treatment for different clutch sizes. Numbers in parentheses show frequencies.

Clutch size	%	egg dropping	%	parasitised clutches
1	16.7	(4/20)	13.6	(8/51)
2	6.1	(2/31)	12.4	(11/78)
3	4.7	(2/41)	14.5	(12/71)
4	0	(0/31)	10.2	(6/53)
5	0	(0/25)	9.4	(3/29)

from Weis *et al.* (1983). For simplicity, it was assumed that (1) females lay eggs in clutches of the same size throughout their lifetime, and (2) all leaves for oviposition site are equal in size: the mean value of *S. miyabeana* leaves selected by the leaf miner for oviposition in the field was used (Kagata & Ohgushi, 2002a). Each parameter in the model was obtained from the field experiment described above. Mortality factors were partitioned between egg and larval mortality. Egg dropping is dependent on clutch size but not leaf size (see Discussion) and its rate was obtained from Table 2. In the model, all egg death was ascribed to dropping, since other causes of mortality could not be distinguished from egg dropping under natural condition. Larval mortality from premature leaf abscission, predation, parasitism, and unknown causes was estimated from the following equation, which was determined from the control treatment of the above experiment (Fig. 3a):

$$Q_c(\text{larva}) = 64.0 - 20.0 \times D_c + 42.8 \times D_c^2, \quad (2)$$

where $Q_c(\text{larva})$ = mortality rate (%) of larva, and D_c = density of clutch size *c* on mean leaf size (= 9.1 cm²). In transforming clutch size to density (D_c), the effect of increased density due to multiple oviposition was incorporated into the model because multiple oviposition was frequently observed in the field and the mean number of clutches per leaf was 1.38 (Kagata & Ohgushi, 2002b). Density of each clutch size was determined by the following equation:

$$D_c = (c \times 1.38) / 9.1. \quad (3)$$

Survival rate for each clutch size was estimated by the following equation:

$$P_c = 100 - [Q_c(\text{egg}) + Q_c(\text{larva})]. \quad (4)$$

where P_c = survival rate (%) of clutch member in clutch size *c* and $Q_c(\text{egg})$ = mortality rate (%) of eggs at clutch size *c*. Similarly, expected fecundity per clutch member was estimated by the following equation, which was determined from the control treatment in the field experiment (Fig. 3b):

$$F_c = 54.4 - 2.7 \times D_c - 37.7 \times D_c^2. \quad (5)$$

where F_c = expected fecundity per clutch member at clutch size *c*. Then, fitness per clutch member, fitness per clutch, and maximum number of clutches throughout the lifetime of the female were estimated for each clutch size by the following equations:

Table 3. ANOVA tables of survival rate, body size, and relative fitness.

Factor	d.f.	SS	MS	F	P
<i>(a) Survival rate</i>					
Treatment	1	1.55	1.55	5.88	0.016
Density	4	4.93	1.23	4.67	0.001
Treatment × Density	4	2.08	0.52	1.97	0.098 NS
Residual	542	143.29	0.26		
<i>(b) Body size</i>					
Treatment	1	1.02	1.02	13.21	<0.001
Density	4	13.62	3.40	44.26	<0.001
Sex	1	2.11	2.11	27.41	<0.001
Treatment × Density	4	0.24	0.06	0.79	0.530 NS
Treatment × Sex	1	0.02	0.02	0.21	0.648 NS
Density × Sex	4	0.39	0.10	1.26	0.285 NS
Treatment × Density × Sex	4	0.20	0.05	0.66	0.623 NS
Residual	547	42.07	0.08		
<i>(c) Relative fitness</i>					
Treatment	1	305.22	305.22	1.34	0.248 NS
Density	4	9494.74	2373.69	10.42	<0.001
Treatment × Density	4	1655.74	416.44	1.83	0.122 NS
Residual	542	123468.70	227.80		

$$W_c(\text{member}) = P_c/100 \times F_c, \quad (6)$$

$$W_c(\text{clutch}) = W_c(\text{member}) \times c,$$

$$N_c = F_c/c,$$

where $W_c(\text{member})$ = expected fitness per clutch member at clutch size c , $W_c(\text{clutch})$ = expected fitness of mother per clutch of size c , and N_c = maximum number of clutches throughout the lifetime of the female at clutch size c .

Potential reproductive success of the female was estimated for each clutch size with different survival rates of the female between successive bouts of oviposition (p), using the following equation (Weis *et al.*, 1983):

$$W_c(\text{mother}) = \sum_{i=1}^{N_c} p^{i-1} W_c(\text{clutch}). \quad (7)$$

where $W_c(\text{mother})$ = expected reproductive success of the female at clutch size c , and p^{i-1} = survival rate of the female until the i th bout of oviposition.

Predictions of optimal clutch size

The model predicted that the clutch size maximising fitness of individual offspring is two (Fig. 4a), whereas clutch size to maximise fitness per clutch is four (Fig. 4b). Where female survival is high (>0.95), greatest reproductive success is obtained at clutch size of two (Fig. 4c). In contrast, reproductive success is highest for clutch sizes of three and four when the survival rate of the female decreases to 0.95 and 0.80 respectively.

Discussion

Offspring performance

Many studies have demonstrated that larval survival and/or body size of leaf miners decreased consistently with increasing larval density because of larval competition and leaf abscission (Stiling *et al.*, 1984; Auerbach & Alberts, 1992; Preszler & Price, 1993). The present study also showed that larval mortality due to premature leaf abscission increased while adult body size decreased with increasing larval density. Premature leaf abscission is thought to be an induced response of host plants to leaf-mining damage (Preszler & Price, 1993), and the reduced size of emerged adults results from exploitative competition for food resources during larval period (Murai, 1974; Stiling *et al.*, 1984). On the other hand, egg dropping from leaves in *L. sinuella* occurred at low egg densities. Egg dropping may be affected by clutch size directly, independent of leaf size, because large clutches with a greater adhesion surface area are likely to adhere to leaves more tightly than small clutches. In the field experiment, most of the small clutches (in particular, clutches containing only one egg) were assigned to low-density classes. These density-dependent factors, including leaf abscission, larval competition, and egg dropping, largely contributed to the highest fitness of individual offspring at intermediate densities (0.2–0.4 eggs cm⁻²). This indicates that the adjustment of clutch size by females in response to leaf size is for the benefit of offspring (Kagata & Ohgushi, 2002a).

In gregariously feeding insects, attack by natural enemies is affected by host insect's feeding group size (Godfray, 1986; Subinprasert & Svensson, 1988; Siemens & Johnson, 1992), and this may explain the evolution of gregarious

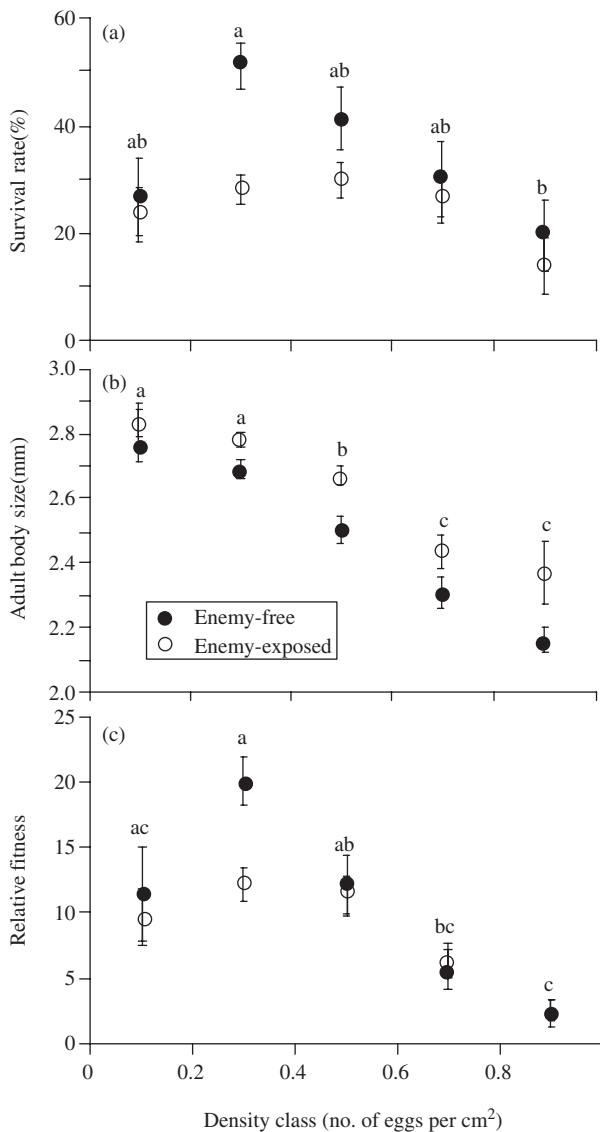


Fig. 2. (a) Survival rate, (b) adult body size, and (c) relative fitness at different density classes. Vertical bars show SE. ●, Enemy-free treatment; ○, enemy-exposed treatment. Different letters show significant differences among density classes (Scheffé test, $P < 0.05$), based on data pooled for the enemy-free treatment and the control (and sexes in adult body size) because there is no interaction among them.

feeding behaviour. On the other hand, larvae in a large feeding group may be at a disadvantage because they are more easily found by predators and parasitoids (Tsubaki, 1995; Hunter, 2000). In the present study, however, natural enemies did not act in a density-dependent manner, and parasitism was not affected by clutch size. In addition, there was no significant difference in offspring fitness between the enemy-exposed and enemy-free treatments because decreased survival due to predation or parasitism was compensated for by increased fecundity. Larger body

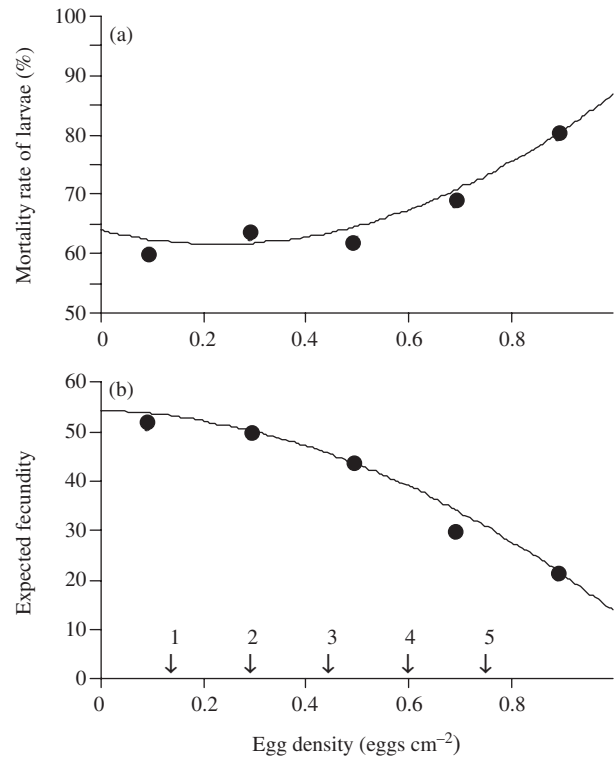


Fig. 3. (a) Mortality rate of larvae and (b) expected fecundity at different density classes, based on experimental data. $Y = 64.0 - 20.0X + 42.8 \times 2$, $r^2 = 0.95$, $P = 0.05$ for mortality rate, and $Y = 54.4 - 2.7X - 37.7 \times 2$, $r^2 = 0.98$, $P < 0.05$ for expected fecundity. Arrows show standardised density of each clutch size (see text).

size in the enemy-exposed treatment may be due to decreased larval competition by natural enemies that killed potential competitors in clutch members (Faeth & Simberloff, 1981). However, it is possible that the decreased body size in the enemy-free treatment results from the alteration of environmental conditions by bagging (e.g. light, temperature, humidity), which affects insect development directly and indirectly via changes in leaf quality (Sipura & Tahvanainen, 2000). In either case, the impact of natural enemies on offspring fitness was relatively small, compared to egg dropping, leaf abscission, and larval competition.

Optimal clutch size

The evolution of life-history characters should be discussed based on lifetime fitness (Ohgushi, 1991). In clutch size determination, natural selection should favour a female that deposits the clutch that maximises her reproductive success, which incorporates both offspring fitness and female oviposition efficiency. As a result, the optimal clutch size is not determined by offspring fitness alone. The optimal clutch size should be on the continuum between the clutch size that maximises the fitness of individual offspring

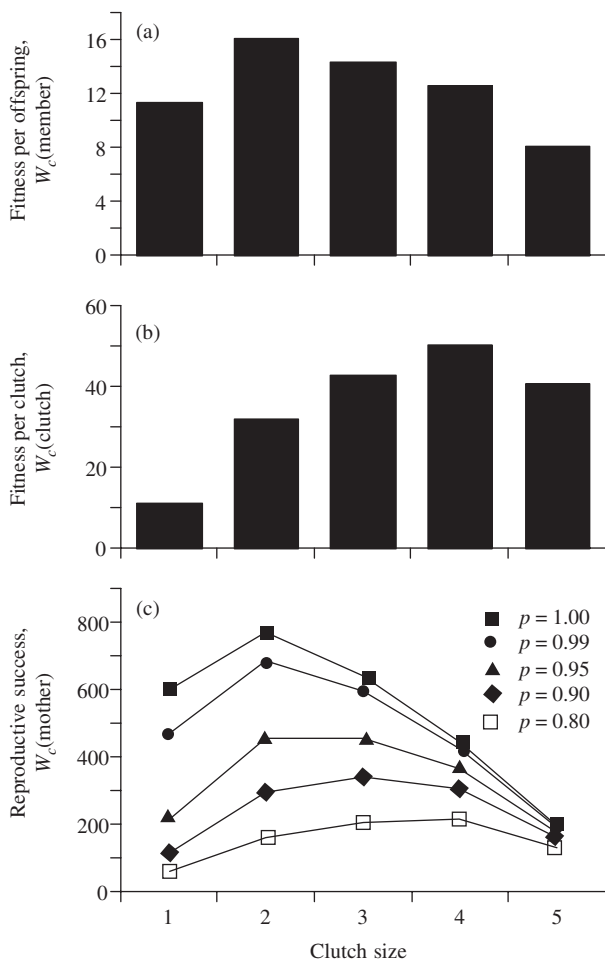


Fig. 4. (a) Fitness of individual offspring, (b) fitness of female per clutch, and (c) reproductive success of the female for differing clutch sizes and survival rates between oviposition events (p).

and that which maximises the fitness per clutch, depending on the oviposition efficiency of the female (Godfray, 1987).

Godfray (1986) demonstrated in a leaf-mining fly, *Pegomya nigritarsis*, that the clutch size that maximises fitness per individual offspring was identical to the clutch size to maximise fitness per clutch. Hence, an optimal clutch size that maximises reproductive success was predicted independent of oviposition efficiency of the female. However, the present study showed that the clutch size maximising the fitness of individual offspring differed from the clutch size to maximise fitness per clutch. Therefore, the model predicts that the reproductive success of females varies between a clutch size of two to four, depending on survival between oviposition events (Fig. 4c). The clutch size that maximises reproductive success of the female was identical to the clutch size that maximises fitness of individual offspring (two), but only if the female's survival rate between oviposition events was greater than 95%. When the survival rate was less than 95%, an ovipositing female should lay eggs in clutch sizes of

three or four to maximise reproductive success, even though this decreases offspring fitness.

The clutch size observed most frequently in the field in *L. sinuella* was two (Kagata & Ohgushi, 2002a), corresponding to the prediction of the model when the female's survival rate between oviposition events was high (95%). To verify this assumption, the survival rate of females between oviposition events was estimated in the leaf miner, using the method employed by Desouhant *et al.* (2000). The parameters that were needed for the estimation (i.e. female's daily survival rate and fecundity) were obtained in the present study and in oviposition tests in the laboratory (Kagata & Ohgushi, 2002c). The survival rate between oviposition events in the laboratory was estimated at 95%, corresponding to the rate that can explain the observed clutch size according to the model (i.e. >95%). However, the actual survival rate in the field should be much lower, because the laboratory condition did not include predation, unfavourable weather, failure to locate a host, and random mortality, all of which cause adult death in the field. The model predicted optimal clutch size of three or four when the survival rate is <95%. Thus, the most frequent clutch size of *L. sinuella* is smaller than that predicted by the model of Weis *et al.* (1983). Likewise, Desouhant *et al.* (2000) used this model to explain clutch size in the chestnut weevil *Curculio elephas*, and showed that the model is likely to overestimate optimal clutch size.

It is argued that Weis's model assumes only advantages of large clutch size for ovipositing females; however, some disadvantages of large clutches should be incorporated in the model to reduce the overestimation of optimal clutch size. For example, large adult body size may be advantageous. Large body size may enhance not only fecundity but also adult survival and mating success (Desouhant *et al.*, 2000; Andersen & McNeil, 2001). The large body size would result from small clutch size because of decreased competition for food resources. Taking this factor into account, the optimal clutch size is expected to decrease because small clutch size is more advantageous for female reproductive success. More information on adult performance, such as survival rate and oviposition efficiency, would lead to further understanding of the trade-off between mother and offspring in determining clutch size in herbivorous insects.

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