"Egg dumping" in lace bugs
(*Gargaphia solani,* Hemiptera: Tingidae)*

Douglas W. Tallamy
Department of Entomology and Applied Ecology, University of Delaware, Newark, Delaware 19717-1303, USA

Summary. Data are presented which document that females of the subsocial lace bug, *Gargaphia solani* lay eggs in the nests of conspecifics whenever the opportunity arises. Because of an inverse relationship between time invested in maternal care and fecundity, maternal behavior in *G. solani* is an ecologically expensive trait that is adaptive only in the face of heavy predation on eggs and nymphs. By facultatively utilizing the maternal defensive behavior of conspecifics, it is possible for egg donors to protect their progeny from predators without limiting fecundity. Whenever possible, females oviposit in recently established egg masses of conspecifics. While guarding their own eggs, egg recipients inadvertently protect the eggs of egg donors. Egg donors need not establish and guard their own masses as long as there are females with egg masses in the vicinity. Instead, egg donors are free to lay as many eggs as physiologically possible by avoiding long periods of maternal care.

Introduction

"Egg Dumping" describes the behavior of female birds that regularly or occassionaly lay their eggs in the nests of conspecifics. Such behavior has been labeled intraspecific brood parasitism (Brown 1984; Dhindsa 1981; Nudds 1980; Sugden 1980; Weatherhead and Robertson 1978; Weller 1959; Yom-Tov 1980), though it has not been clearly demonstrated that egg donors enjoy greater fitness than egg recipients. Similar behavior is also common in certain solitary Hymenoptera (Custer and Hicks 1927; Eickwort 1973, 1975; Fabre 1914; Matthews 1965; Raw 1972), but has yet to be reported in other insect orders. Here I describe facultative egg dumping in the subsocial lace bug. *Gargaphia solani* Heidemann and hypothesize as to its adaptive significance.

G. solani is an iteroparous lace bug with large clutches and short generations, completing as many as eight generations a year in Virginia (Bailey 1951). This species is common on horsenettle (*Solanum carolinense* L.; Solanaceae) in the middle Atlantic States and ranges as far west as Iowa (Drake and Ruhoff 1965). Both adults and nymphs feed by extracting the contents of parenchymal cell tissues. Females cement their eggs in discrete masses to the undersurface of horsenettle leaves over a period of two to three days. As the mass is completed, females undergo a physiological suppression of egg production and begin to exhibit maternal behavior (Tallamy and Denno 1981; Kearns and Yamamoto 1981). Mothers remain with and aggressively defend their eggs and gregarious nymphs from predators throughout all five nymphal stadia. As the young mature and disperse, females produce a second egg mass and resume their maternal duties. Two to three clutches are reared before death.

Methods

Egg mass size distribution produced by natural populations of *G. solani* was estimated by recording the size of every egg mass ($n=214$) within a pasture during July 1982. To establish the relationship between lace bug density and egg mass size, absolute density of lace bugs and the size of each egg mass was recorded within 75 discrete horsenettle patches throughout the breeding season of 1983.

Oviposition patterns of interacting females were quantified in the lab by confining groups of 2, 3, 4, 5, 7 and 13 gravid females with horsenettle leaves in containers ($15 \times 30 \times 10$ cm) such that there was one leaf/female. Females were left until oviposition was complete (24–36 h) whereupon the number and size of the resulting egg masses was recorded.

Oviposition patterns were also quantified under less controlled conditions. Groups of 5, 25, 50 and 100 gravid females were placed on 10 potted horsenettle plants in 1.8 m³ screen field cages and left to oviposit. The number and size of the resulting egg masses was subsequently recorded.

Specific interactions between females during oviposition (2–3 days) and egg guarding (6 days at 27° C) were quantified in the following way. Pairs of females gravid with their first clutch were isolated on potted horsenettle plants with at least 6 mature leaves to ensure sufficient oviposition sites for both females. At 15 min intervals from 8 am to 5 pm the position and behavior of each female was observed and recorded. Records were kept until no interactions between females were observed for 9 consecutive h.

Results

Laboratory and field data alike support the contention that *G. solani* egg masses are commonly formed by more than one female. Young females isolated from other females deposit $\bar{x}=110$ eggs ($n=191$) in their first clutch and each subsequent clutch ($\bar{x}=90$: $n=117$, and 67: $n=14$ eggs respectively) is significantly smaller ($F_{2,317}=29.38$; $P<0.00001$). Field surveys, however, reveal much variation in the size of discrete egg masses, ranging from 31 to 800 eggs per mass. Greater than 46% of all of the masses found in a particular field during July 1982 were over one standard deviation larger than the mean egg mass size produced by isolated females (Fig. 1).

Several types of data suggest that the formation of multiple egg masses is a density dependent phenomenon that is unrelated to host plant availability. When varying numbers of gravid females are left to oviposit in a container with host leaves such that host resources increase proportionally with female density, the number of egg masses that result is not in one to one correspondence with female density (Fig. 2a), and there is a positive, highly significant relationship ($r^2=0.59$; $P<0.0001$) between female number and the size of the largest egg mass (Fig. 2b). For example, 13 gravid females only create $\bar{x}=3.25$ distinct egg masses, but the largest mass contains $\bar{x}=633.25$ eggs. Not only do most females seek out the same leaf for
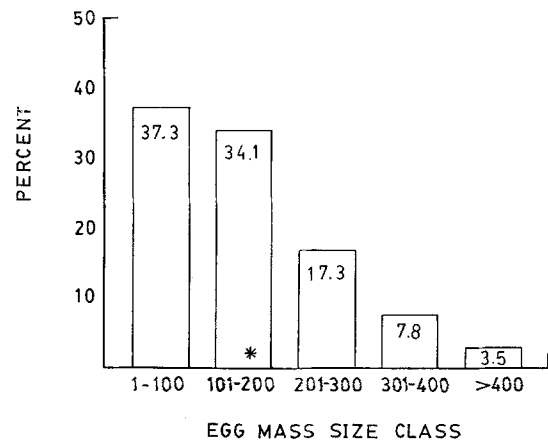

Fig. 1. Egg numbers found in egg masses of a field population of *Gargaphia solani*. ($n=255$ egg masses) $*=\bar{x}$ egg mass size created by isolated females
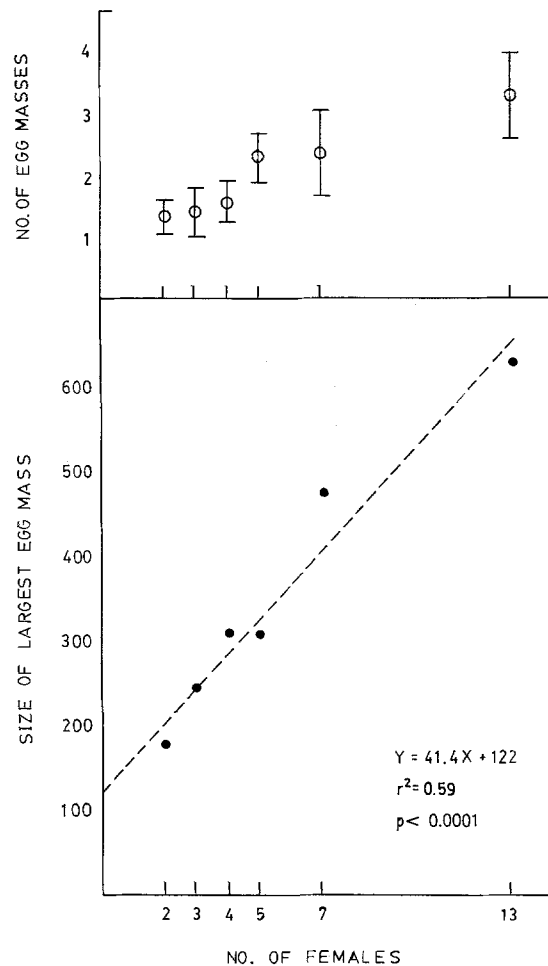

Fig. 2. The effect of female density on number of egg masses (above; $\bar{x}$ with SD) and maximum egg mass size (below) when gravid *Gargaphia solani* females were confined in lab containers through first oviposition. Host plant availability increased proportionally with female density. From left to right $N=14$, 12, 10, 8, 7, 8 replicates respectively

Table 1. $\bar{x}$ and SD of egg numbers in egg masses produced by *Gargaphia solani* females confined at increasing densities (females per 10 host plants)

Female density	$\bar{x}$	SD	n
1	110[a]	28	191
5	105[a]	51	10
25	257[b]	200	15
50	313[b,c]	25	32
100	368[c]	234	30

[a,b,c] Means with different letters are significantly different (Duncan's Multiple Range: $P < 0.05$)

oviposition, but they confine their eggs to a single, discrete mass.

Similar results were derived from field cage manipulations in which host resources were plentiful but did not increase with female density. When 5 gravid females were placed in 1.8 m³ field cages, each containing 10 horsenettle plants, the resulting egg masses produced were not significantly larger than egg masses produced by isolated females (Table 1). However, egg masses resulting from groups of 25, 50 and 100 females cage were each significantly larger than those from isolated females ($F_{4,273} = 43.46$; $P < 0.0001$). Furthermore, the size of the largest egg mass created by each group increased significantly with increasing group size ($r^2 = 0.60$; $P < 0.0025$) (Fig. 3).

Additional evidence for density dependence in egg dumping behavior comes from field surveys of lace bug populations. There is no relationship between horsenettle patch size (from 1–18 plants) and lace bug density (from 1–30 bugs) ($r^2 = 0.06$; $P > 0.05$), suggesting that even small patches contain ample resources for small lace bug populations. The data do reveal a positive asymptotic relationship between lace bug density within discrete horsenettle patches and size of the largest egg mass within those patches (Fig. 4). Egg mass size increases with increasing lace bug density only until there are ca. 9 lace bugs in a patch. Higher densities do not create larger egg masses, suggesting that there may be a critical maximum size, beyond which egg masses are no longer attractive to egg donors.

The most convincing evidence for egg dumping comes from long term laboratory observations of gravid females. Interactions often include several females but the principal behaviors involved are best exemplified by the simplest case of two interacting lace bugs. Approximately two days after mating the first of two gravid females. ♀ A,
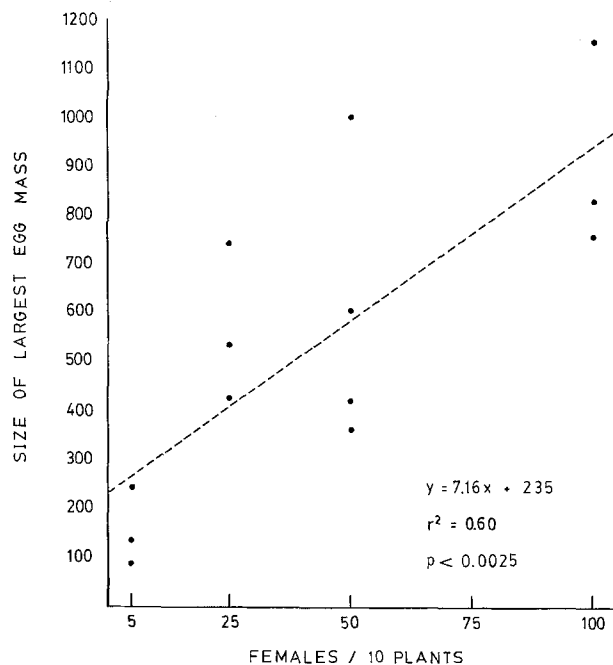

Fig. 3. The effect of female density on egg mass size when gravid *Gargaphia solani* females were confined within 1.8 m³ field cages through first oviposition. Host plant availability remained constant over increasing female densities (N = 3)

physiologically reaches the stage of egg maturation when she must begin to oviposit. One option is to locate a female with eggs and attempt to lay at least some eggs in that egg mass. If there are no females with eggs in the vicinity, she initiates her own mass. As soon as she does this she is subject to "dumping" from the other gravid female, B. While ovipositing and egg guarding, A periodically moves $\bar{x} = 6.2$ cm ($n = 161$) from her mass and feeds for $\bar{x} = 9.3$ min ($n = 161$). In so doing she does not deplete the parenchymal tissues adjacent to the eggs that are essential to the survival of eclosing nymphs. While she is gone, B approaches the egg mass and cements her own eggs among those of A. When A returns to continue ovipositing, B either leaves temporarily to feed or remains and continues ovipositing. Both females alternate possession of the mass for 2–3 days until B abandons the site permanently, presumably to lay additional eggs in another location. A then guards the egg mass and subsequent nymphal aggregation until the young reach maturity.

Of the 96 paired females observed, 80% exhibited the sequence of behaviors described above. Surprisingly, only 3% of the females aggressively defended their egg masses from intruding females.
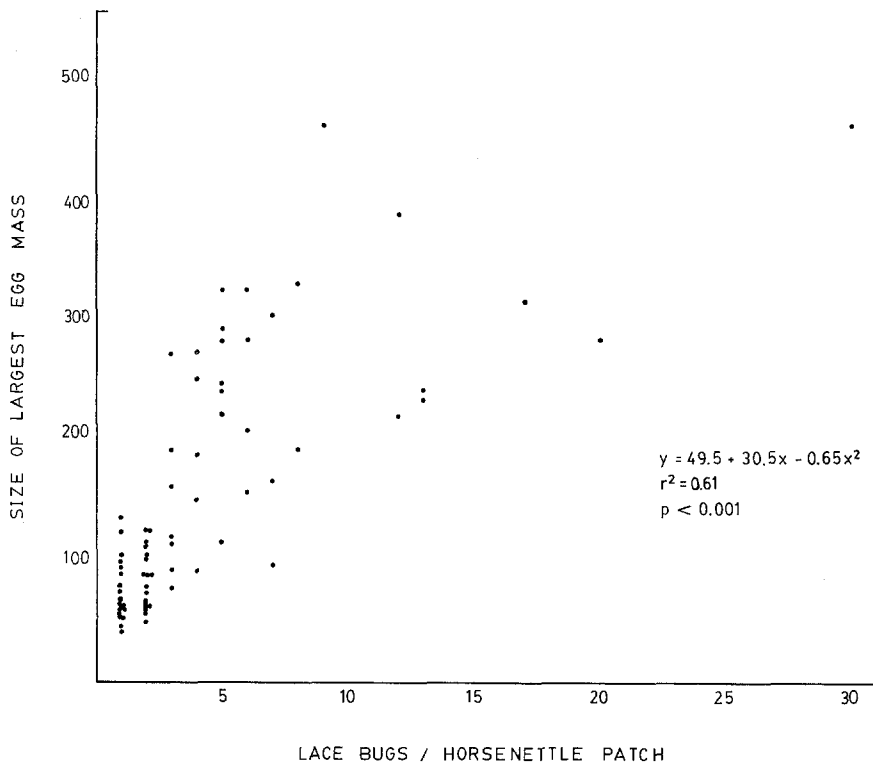
Fig. 4. The effect of lace bug density on egg mass size in field populations of *Gargaphia solani* inhabiting discrete patches of horsenettle, *Solanum carolinense*

The plot shows:

$$y = 49.5 + 30.5x - 0.65x^2$$
$$r^2 = 0.61$$
$$p < 0.001$$

Y-axis: SIZE OF LARGEST EGG MASS (100, 200, 300, 400, 500)

X-axis: LACE BUGS / HORSENETTLE PATCH (5, 10, 15, 20, 25, 30)

Discussion

The results unequivocally demonstrate that under natural and contrived conditions *G. solani* females oviposit in the egg masses of conspecifics. Egg donors abandon their eggs to the care of females that originate egg masses. Such "egg dumping" behavior is most common when populations of lace bugs with synchronized life histories are locally high. The data also suggest that egg dumping is a facultative behavior that is expressed only when one or more egg masses are developing within the immediate perception of gravid females, i.e. within the same patch of horsenettle. In the absence of susceptible egg masses, gravid females must initiate and guard their own egg masses, or face serious losses to predators.

The adaptive significance of egg dumping can not be interpreted without detailed information on the associated advantages and disadvantages for egg donors and egg recipients. Though most of these data are as yet unavailable some advantages to egg donors are presently clear. Maternal care is an effective but ecologically expensive solution to the predation problem facing *G. solani* (Tallamy and Denno 1981; Tallamy and Denno 1982). In addition to the physical risks associated with protecting offspring from predators (Tallamy 1982), there is a costly inverse relationship between

time invested in maternal behavior and fecundity (Tallamy and Denno 1982). To guard a clutch of young through all five nymphal stadia requires a maternal time inverstment of about 19 days, nearly one-half of an adult female's life span. Since egg production is suppressed throughout this period, maternal care significantly reduces fecundity. In fact, females which consistently abandon their eggs lay more than twice as many eggs as females that guard, and more importantly, lay most of their eggs much earlier in life (Tallamy and Denno 1982).

In light of this trade-off, maternal behavior in *G. solani* seems balanced between two powerful selection pressures (Tallamy 1984). On the one hand, there is pressure to protect young from adverse environmental conditions, for without protection offspring survival is often negligible. On the other hand, there is selection against maternal care because of the reduction in fecundity that is associated with such behavior.

Egg dumping is a behavioral compromise in *G. solani* that satisfies both of these opposing forces. By facultatively utilizing the maternal defensive behavior of conspecifics, it is possible for a female to have her young protected without limiting fecundity. Egg donors need not establish and guard their own egg masses as long as there are conspecific females with egg masses in the vicinity.

Instead, egg donors are free to lay as many eggs as physiologically possible by avoiding long periods of maternal care. In essence, egg dumping effectively circumvents the ecological costs of parental behavior, conveying a powerful advantage to egg donors that is not shared by egg recipients.

Though *G. solani* oviposition behavior is remarkably similar to what has been termed brood parasitism in birds, (Hamilton and Orians 1965; Lack 1968) labeling it as such would be premature. There may in fact be a mutulistic relationship between egg donors and egg recipients. In view of Hamilton's (1971) selfish herd effect it may be advantageous to guard egg masses containing eggs from other individuals (Bertram 1979). As in bird flocks (Galton 1871; Vine 1971), schools of fish (Pitcher 1973; Williams 1966) and mammal herds (Darling 1937; Treisman 1975), being in an egg mass or nymphal aggregation produced by more than one female may be advantageous to individual eggs and nymphs if the probability of any one individual being killed by predators decreases when there are more individuals in the aggregation. Furthermore the degree of relatedness among simultaneously gravid females in local lace bug populations may have both proximate and ultimate effects on the social interactions of *G. solani* females (Crozier 1979; Hamilton 1964, 1972; Holmes and Sherman 1983; Michod 1982; Oster and Wilson 1978). If egg recipients are closely related to egg donors the disadvantages of receiving eggs may be balanced by the benefits of heightened inclusive fitness. Recognition of a kinship component in the ovipositional behavior of *G. solani* would provide important insight into the low levels of intraspecific aggression thus far observed at oviposition sites.

Countering the possible benefits of egg dumping are several factors that may negatively affect either egg recipients, egg donors, or both. A large egg mass and subsequent nymphal aggregation resulting from egg dumping may be more apparent and/or attractive to predators (Hassell 1978), thereby increasing risks for the defender and decreasing the probability of offspring survival for both females involved. Oviposition damage from the deposition of a large number of eggs can also seriously injure the leaf on which the mass is layed. If tissue injury is extensive, the leaf will drop from the plant, causing total mortality to all eggs. In the event that a large communal egg mass hatches, the resulting nymphal aggregation is more apt to deplete the resources of a small or moderately sized horsenettle host leading to the starvation of the entire aggregation. It is also possible that a nymp-

hal aggregation resulting from egg dumping may be too large to be effectively guarded by a single lace bug mother. These disadvantages are likely to be compounded every time an additional female adds her eggs to an egg mass. Thus, as the data from field surveys suggest, there may be selection for gravid females to avoid contributing to egg masses that have reached some critical size and for females to abandon their masses if they become too large.

References

Bailey NS (1951) The Tingoides of New England and their biology. Entomol Am 31:1–140

Bertram BCR (1979) Ostriches recognise their own eggs and discard others. Anim Behav 28:278–286

Brown CR (1984) Laying eggs in a neighbor's nest: benefit and cost of colonial nesting in swallows. Science 224:518–519

Crozier R (1979) Genetics of sociality. In: Hermann HR (ed) Social insects, vol I. Academic, New York, pp 223–286

Custer CP, Hicks CH (1927) Nesting habits of some anthidiine bees. Biol Bull 52:258–277

Darling FF (1937) A herd of red deer. Oxford University Press, Oxford

Dhindsa MS (1981) Intraspecific nest parasitism in two species of Indian weaverbirds *Ploceus benghalensis* and *P. manyar.* Ibis 125:243–245

Drake CJ, Ruhoff FA (1965) Lacebugs of the world: a catalog (Hemiptera: Tingidae). Smithsonian Institution, US Nat Mus Bull 243, Washington, DC

Eickwort GC (1973) The biology of the European mason bee, *Hoplitis anthocopoides* (Hymenoptera: Megachilidae), in New York State. Search (Cornell Univ Agricult Exp Sta) 3

Eickwort GC (1975) Gregarious nesting of the mason bee, *Hoplitis anthocopoides* and the evolution of parasitism and sociality among megachilid bees. Evolution 29:142–150

Fabre JH (1914) The mason-bees. Translation by deMattos AT. Hodder and Stoughton, London

Galton F (1871) Gregariousness in cattle and men. Macmillan's Magazine, London 23:353

Hamilton WD (1964) The genetic evolution of social behavior, I and II. J Theor Biol 7:1–52

Hamilton WD (1971) Geometry for the selfish herd. J Theor Biol 31:295–311

Hamilton WD (1972) Altruism and related phenomena, mainly in social insects. Annu Rev Ecol Syst 3:193–232

Hamilton WD, Orians GH (1965) Evolution of brood parasitism in altricial birds. Condor 67:361–382

Hassell MP (1978) The dynamics of arthropod predator – prey systems. Princeton University Press, Princeton

Holmes WG, Sherman PW (1983) Kin recognition in animals. Am Sci 71:46–51

Kearns RS, Yamamoto RY (1981) Maternal behavior and alarm response in the eggplant lace bug. *Gargaphia solani* Heidemann (Tingidae: Heteroptera). Psyche 88:215–230

Lack D (1968) Ecological adaptations for breeding in birds. Methuen, London

Matthews RW (1965) The biology of *Heriades carinata* Cresson (Hymenoptera, Megachilidae). Contrib Am Entomol Inst 1, 3, 33

Michod RE (1982) The theory of kin selection. Annu Rev Ecol Syst 13:23–55

Nudds TD (1980) Canvasback tolerance of redhead parasitism: an observation and an hypothesis. Wilson Bull 92:414

Oster GF, Wilson EO (1978) Caste and ecology in the social insects. Princeton University Press, Princeton

Pitcher TJ (1973) The three-dimensional structure of schools in the minnow *Phoxinus phoxinus* (L.). Anim Behav 21:673–686

Raw A (1972) The biology of the solitary bee *Osmia rufa* (L.) (Megachilidae). Trans R Entomol Soc (Lond) 124:213–229

Sugden LG (1980) Parasitism of canvasback nests by redheads. J Field Ornithol 51:361–364

Tallamy DW (1982) Age specific maternal defense in *Gargaphia solani* (Hemiptera: Tingidae). Behav Ecol Sociobiol 11:7–11

Tallamy DW (1984) The ecology of insect parental care. Bioscience 34:20–24

Tallamy DW, Denno RF (1981) Maternal care in *Gargaphia solani* (Hemiptera: Tingidae): Anim Behav 29:771–778

Tallamy DW, Denno RF (1982) Life history trade-offs in *Gargaphia solani:* the cost of reproduction. Ecology 63:616–620

Treisman M (1975) Predation and the evolution of gregariousness II, an economic model for predator-prey interaction. Anim Behav 23:801; 825

Vine I (1971) Risk of visual detection and pursuit by a predator and the selective advantage of flocking behavior. J Theor Biol 30:405–422

Weatherhead PJ, Robertson RJ (1978) Intraspecific nest parasitism in the savannah sparrow. Auk 95:744

Weller MW (1959) Parasitic egg laying in the redhead (*Aythya americana*) and other North American Anatidae. Ecol Monogr 29:333–365

Williams CG (1966) Adaptation and natural selection. Princeton University Press, Princeton

Wilson EO (1975) Sociobiology: the new synthesis. Harvard University Press, Cambridge

Yom-Tov Y (1980) Intraspecific nest parasitism in birds. Biol Rev 55:93–108