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Source: *Ecology*, Vol. 64, No. 4 (Aug., 1983), pp. 688-695

Published by: Ecological Society of America

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SELECTIVE PRESSURES ON CLUTCH SIZE IN THE GALL MAKER *ASTEROMYIA CARBONIFERA*¹

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Abstract. The insect *Asteromyia carbonifera* (Diptera; Cecidomyiidae) has a life history that entails larval development in a gall with several sibs, maturation of a single batch of gametes during pupal development, and an ephemeral adult existence that includes many ovipositional events, each of which results in formation of a gall. Ecological factors acting on both the adult and larval stages were evaluated to determine the selective pressure they exert on the number of eggs deposited per ovipositional site (i.e., clutch size).

Optimal clutch size is determined by a balance between the fitness per offspring, which is dependent on clutch size, and the number of clutches mothers can deposit in their brief life-span. As clutch size increased, so did sibling competition, with the result of smaller size and lower fecundity for larvae developing in large clutches. Larval survivorship was lower in small clutches because of differential attack by parasitoids. From the offspring's viewpoint, benefits of small clutch size outweighed the deficits, since those deposited in clutches of one enjoyed the greatest potential fitness. A model was constructed indicating that when mothers experience no risk of mortality, optimal clutch size from their viewpoint is also one. However as the risk of mortality between ovipositional events increases, females are unlikely to survive to deposit all their eggs. When fewer clutches can be formed, females will be selected to deposit several eggs per clutch, since this results in the development of many moderately fecund offspring whose aggregate fitness is greater than that of the few highly fecund offspring that would result if one egg were deposited per site.

Key words: *Asteromyia*; *Cecidomyiidae*; clutch size; gall makers; parasitoids; reproductive tactics; semelparity; sibling competition; *Solidago*.

INTRODUCTION

Like all heritable traits, reproductive patterns are subject to the forces of natural selection (Fisher 1930). Variations in physiological and behavioral characters which, on average, increase the reproductive success of the individuals that express them will supplant less productive variants. The goal of life history theory has been to understand how traits involved in reproduction will evolve under particular conditions (Stearns 1976). A basic step in achieving this goal is an examination of the selective pressures which may act upon the different types of species in the evolution of their reproductive patterns. The present report examines the structure of the selective regime that potentially acts upon the semelparous, gall-making insect, *Asteromyia carbonifera* (O.S.; Diptera: Cecidomyiidae).

The effect of semelparity (reproducing once before death) vs. iteroparity (repeated reproduction) on reproductive rate, and thereby on fitness, was first ex-

amined theoretically by Cole (1954). In a further development of that model, Charnov and Schaffer (1973) predicted semelparity would be favored by selection when the yearly adult survival rate of adults is low compared to that of juveniles. Iteroparity would be favored when juvenile survivorship is low. Further refinements of this model were made by Young (1981).

Given that it is adaptive for individuals of a particular species to reproduce only once, the question of how reproductive effort is apportioned to various activities remains. Little attention has been paid to questions about the structure of the reproductive tactics employed by semelparous organisms, perhaps because the familiar examples of semelparity are organisms with very simple reproductive patterns, such as salmon, bamboo, and agave. The single, suicidal reproductive bout of these species has been termed the "big-bang" strategy by Gadgil and Bossert (1970). It could be inferred from their paper that the "big bang" is synonymous with semelparity, but this is not the case. The extreme in semelparity would be when reproductive effort is devoted solely to propagule production, i.e., the "big bang," but in cases where activities such as parental care constitute a substantial proportion of reproductive effort, more complex tactics can result. Fritz et al. (1982) point out that in many insect species

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the full complement of gametes is produced during pupal development, thus making them semelparous, but that upon adulthood eggs are deposited singly or in a series of small clutches. This group includes gall makers and parasitoids (Hassell and Southwood 1978) in which the female deposits eggs at sites that hold all the resources needed for development of the sessile larval stage. The acts of searching and oviposition in these species are a form of parental care, because by transporting their offspring to sites that hold needed resources, mothers "influence the expectation of success of the young before the genotypes of the young begin to exert their effects . . ." (Brockelman 1975: 679). Price (1972, 1974) showed how a number of morphological and physiological traits among parasitoids of the family Ichneumonidae are adapted to the particular situations in which they search for hosts; it is revealing that these traits were considered as adaptations for reproduction as opposed to foraging.

Within this particular reproductive facies, selection will, over evolutionary time, determine the number of eggs deposited at each ovipositional site, i.e., clutch size. We examined three ecological factors that may act as selective forces upon *A. carbonifera* in this regard. The first is differential growth performance and survivorship of offspring due to competition among siblings within the gall; as clutch size increases, each sib receives a smaller share of the resources available at an ovipositional site. Second is the dependence of vulnerability to natural enemies on clutch size. Third is the probability of adult survival between deposition of one clutch and the next. The first and second factors affect the productivity (Lack 1947) of each clutch, in terms of quantity and quality of offspring. The importance of offspring quality in structuring reproductive tactics has been emphasized by Smith and Fretwell (1974) and Crossner (1977). Chances of adult survival between clutches affect the total number of clutches that can be produced over the adult lifespan. An important feature of this type of insect life history is that for a given level of fecundity, the number of clutches a mother makes is inversely proportional to clutch size, e.g., a female with 100 eggs will form 100 clutches if the clutch size is 1, but only 1 clutch if clutch size is 100. Thus when clutches are small the mother is exposed to various mortality factors during each of the many flights between ovipositional sites and hence has a lower probability of surviving long enough to deposit all eggs than when a few large clutches are produced.

BIOLOGY OF *ASTEROMYIA CARBONIFERA*

In Illinois, larvae of the gall-midge *A. carbonifera* induce ellipsoid, biconvex, blister-like galls on the leaves of *Solidago canadensis* L. (Compositae). Photographs of the gall can be seen in Gagne (1968). The eggs are found in small clutches, glued to the underside of the leaf. First instars bore into the leaf lamina, thereby initiating gall development. All individuals in

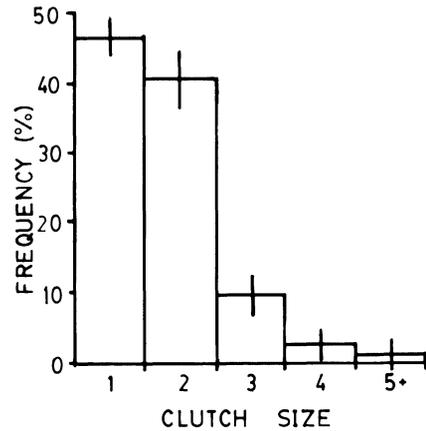


FIG. 1. Frequency distribution of clutch sizes produced by *Asteromyia carbonifera*; means and standard deviations (vertical lines) of three generations are represented.

a clutch reside in a single central chamber, covered by a flattened dome of deformed leaf epidermis. There the second and third instars feed by sucking plant fluids (Gagne 1968). Also inhabiting the gall is the fungus *Sclerotium asteris* (Mycilia Sterilia) (Batra 1964) which is vectored by the female midge at oviposition. Larvae do not feed directly upon the fungus, but it may be involved in their nutrition by altering the composition of the plant fluid (L. R. Batra, *personal communication*). When the third and final instar finishes feeding, *S. asteris* undergoes a period of rapid proliferation within the gall, thereby filling the central chamber and enclosing each midge larva in an individual pupation chamber (Gagne 1968).

In central Illinois the egg-to-adult development time is ≈ 4 wk. Three generations are completed per year; the first appears in early June and the last in August. The full-grown larvae of the last generation pass the winter in the gall.

From 1 to 5 larvae usually reside in each gall, although as many as 12 have been found on occasion; the mean clutch size is 1.88 (Fig. 1). All larvae within a gall are the offspring of a single mother, as can be deduced from their sex. Many members of the family Cecidomyiidae produce unisexual families, i.e., throughout her lifetime a mother produces either all sons or all daughters (Barnes 1946). An account of the sex determination system of this family is given in White (1973). If each larva came from a different mother, 50% of all multilarva galls would contain both sexes, but only 2 of the 858 galls examined in this study contained both sexes, and in these cases the galls may have been produced when two galls developing on the same leaf coalesced to form a single, larger-than-average gall.

This study focuses on galls occurring on *S. canadensis*, although *Asteromyia*-type galls also occur on *S. juncea* in this study area. Galls on the latter always

contain a single larva (Gagne 1968). There is reason to believe that the *S. juncea* galls are produced by a sibling species of *A. carbonifera* (Gagne 1968). In addition to the constant clutch size of one, galls on *S. juncea* differ in phenology from those on *S. canadensis*, and in some fields where the two plants co-occur, galls are virtually absent from *S. juncea* (A. E. Weis, *personal observation*). Experiments to determine whether the difference in clutch size on the two host plants is due to different behavioral responses to plant identity by a single midge species or due to innate behaviors of two host-specific, sibling midge species have not met with success (Gagne 1968, A. E. Weis, *personal observation*) because of the failure of the midge to mate and oviposit under controlled conditions.

MATERIALS AND METHODS

This study was conducted in a 20-ha, restored, tall-grass prairie, located in Robert Allerton Park Nature Reserve (Piatt County, Illinois, USA). The dominant forb of the community was *S. canadensis*. The prairie is burned on a 3-yr cycle, with the last burning prior to the study occurring in spring 1977. This study started in June 1978, ran 18 mo, and examined four midge generations.

To determine the effect of sibling competition on survivorship, we used a method of periodic, destructive sampling of age-cohorts of naturally occurring galls. At the beginning of a host generation we marked 300–400 newly formed galls (<2.0 mm in diameter), by tying flagging tape around the base of the affected leaf. The marking process never extended more than two consecutive days so that the galls were as close in age as possible. We immediately collected a random sample of 50 galls from the cohort and determined the frequency distribution of clutch size by dissection. Subsequent weekly samples were collected and examined in the same manner. The last sample of the generation was handled differently; when the cohort neared pupation all remaining galls were collected and the contents reared by placing them individually in labeled 16-mL (four-dram) vials, stoppered with moist cotton, and storing them in an incubator set at 24°C and a 25L:9D photoperiod. Midges were collected daily from the vials and saved for further study. All galls were subsequently dissected in search of unemerged individuals and clutch size determined by counting the number of pupation cells per gall. An increase in the relative frequency of small clutches (i.e., sizes 1 and 2) and a commensurate decrease in large clutches (>3) with the passage of a generation would be expected if within-clutch mortality increases with clutch size. The frequency distributions of clutch size in successive samples were tested for a downward shift with time, using Ghent's (1976) adaptation of Kendall's tau statistic for use with contingency tables.

Sibling competition during the larval stage may be responsible for nonlethal effects that reduce offspring

fitness during adulthood. Among these effects can be decreased longevity, smaller size, and lower fecundity in adults emerging from large clutches. We measured these three variables for adults from age-cohorts from separate generations and compared the values for individuals emerging from different-sized clutches. Size was characterized by biomass. Newly emerged specimens were dried at 80°C for at least 48 h, and weighed on a Cahn Electrobalance (Model G) to the nearest 10^{-6} g. To measure longevity in the adult stage, we aspirated newly emerged adults individually into labeled, plastic "Drosophila vials" which were equipped with a nylon mesh vent in the cap. Midges were kept in an incubator under conditions described above and checked daily to record the length of life. Fecundity was measured by dissecting out the ovaries, teasing the eggs from their ovariole sheaths, photographing the dissections through a dissecting microscope, and counting the number of eggs per female from the photograph print. Given the small size of the midge (2.5 mm), the dissection required a delicate touch and many specimens were spoiled. Adults of the family Cecidomyiidae emerge from the pupal stage with their full complement of ova matured and ready for oviposition and live 2–5 d (Barnes 1946); thus, the egg count on the day of emergence represents the upper limit on lifetime fecundity. We used linear regression to determine the effect of clutch size on these variables, adopting the .05 level of significance.

Five species of hymenopterous parasitoids attacked *A. carbonifera* in the study area (Weis 1982). All five species emerge from the host after the gall fully matures. Data on parasitism were obtained from the last sample of the age-cohorts in each generation. The number and identity of the parasitoids to emerge from each gall were recorded. Percent parasitism by clutch size-class was obtained by dividing the total number of midge larvae in that class into the number killed by parasitoids. The mean percent parasitism measurements for four midge generations were regressed over clutch size. The angular transformation (Sokal and Rohlf 1969) was performed to normalize percentages.

Attempts to measure mortality and to construct a time budget for adult females were unsuccessful, as several features of the adult biology conspired against efforts to get these data. The small size and nocturnal flight of these insects made observation under natural conditions impossible. We tried observing females in the laboratory in cages stocked with potted goldenrods and illuminated by red light, but midges did not oviposit in any of the three cage designs used. Three more cage designs were used in the field, but no oviposition was observed, either directly or indirectly through the appearance of new galls.

RESULTS

The larval mortality rate due to causes other than parasitism did not differ significantly across the range of clutch sizes made by *A. carbonifera* in nature. Ta-

TABLE 1. Frequency distribution of clutch size in galls of marked cohorts periodically sampled. Downward shifts in the distribution over time would indicate that larvae in large clutches are suffering disproportionately greater mortality because of the effects of sibling competition within the gall. No such shifts were found when tested with Ghent's (1976) adaptation of Kendall's tau for contingency tables. Frequencies displayed as percentages.

	Clutch size						\bar{x}	N	P
	0	1	2	3	4	5+			
Generation I, 1978									
17 June	0.0	47.2	40.0	9.1	0.0	3.6	1.72	55	
23 June	5.0	37.5	27.5	20.0	5.0	0.0	1.83	40	
7 July	8.0	38.0	34.0	20.0	0.0	0.0	1.66	50	
12 July	7.3	47.7	33.0	9.2	2.8	0.9	1.58	109	>.10
Generation II, 1978									
18 July	1.1	43.5	44.5	6.5	3.3	1.1	1.71	92	
25 July	5.7	45.7	31.4	17.1	0.0	0.0	1.60	35	
1 August	4.1	38.7	40.8	10.2	6.1	0.0	1.75	49	
8 August	7.5	35.0	57.5	7.5	0.0	0.0	1.62	42	
11 August	3.8	37.7	45.5	11.5	1.5	0.0	1.69	162	>.10
Generation III, 1978									
17 August	4.2	47.2	36.1	12.5	4.2	0.0	1.73	72	
24 August	2.1	46.8	31.9	10.6	8.5	0.0	1.68	47	
30 August	6.7	51.1	31.1	11.1	0.0	0.0	1.46	45	
10 September	4.7	49.6	34.6	10.2	0.8	0.0	1.52	127	>.10

ble 1 shows no shift toward smaller clutch sizes with the developmental progress in the three generations produced during 1978. There is a somewhat consistent decrease in average clutch size with time in each generation, but this would be expected even if within-clutch mortality was the same for all sizes. Galls in which no larvae were recovered were present in almost every sample (Table 1). These were probably due to early death of the larva or larvae they contained, as judged by the small size of the galls. Cadavers were rarely found in inhabited galls, which suggests that, except for parasitoid attack, the larvae of *A. carbonifera* suffer little mortality. In some instances where dead larvae were found in a gall, death was probably the result of the feeding of the adult parasitoid *Torymus capite* (Weis 1982). Females of this species pierce the body of the gallmaker and imbibe haemolymph through a "feeding tube" (Askew 1971). No egg is laid on the exsanguinated larva; thus, they are found dead, but not parasitized, in the gall.

Perhaps a more-desirable method for assessing the effect of sibling competition would involve manipulating clutch size, as did Perrins (1965) with the Great Tit, and Crossner (1977) with the European Starling. However, such a method is logistically impossible in this system: to add larvae to a clutch artificially would require opening the galls, which would cause the gall, and the larvae within, to desiccate.

Longevity of adult midges was not significantly affected by sibling competition, as is shown in Fig. 2, although a weak trend might have emerged if more individuals from clutches of four or greater were available. Males and females did not differ in longevity, so the sexes were combined in the analysis. These data represent longevity under the conditions of constant temperature and humidity, in cages with restricted

room for movement, and therefore may differ considerably from life expectancy in nature. The data indicate that the reserves of energy and nutrition that the adults bear at time of eclosion provide equally for adult basal metabolic requirements across the spectrum of sibling competition. The level of reserves is of the utmost importance to this species because adults do not feed; when presented with honey water, they did not drink, and when they were kept in cages supplied with honey water, longevity was not significantly different from that of controls kept with only water (A. E. Weis, *personal observation*). Feeding in the adult stage is rare in the Cecidomyiidae (Barnes 1946) as reflected by poorly developed mouthparts in the family (Mamaev 1975).

Mass of adults is negatively related to the level of

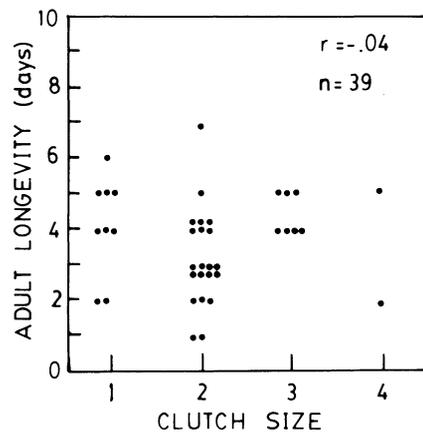


FIG. 2. Relation of adult longevity to the size of the clutch in which the individuals developed. Increasing levels of sibling competition had no negative effect on subsequent adult lifespan under laboratory conditions.

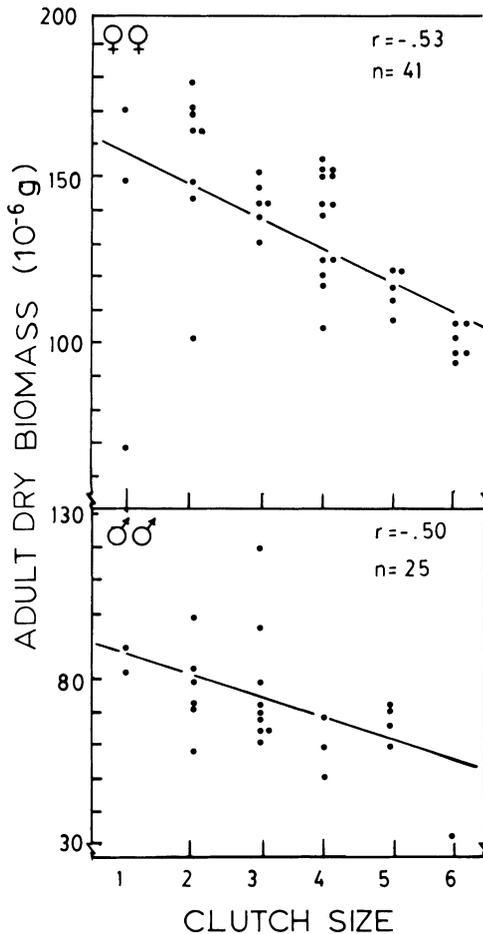


FIG. 3. Regression of adult dry mass over the size of the clutch in which the individuals developed. Regression line for females: $y = 167.6 - 9.2x$; $F = 15.5$; $P < .005$. Regression line for males: $y = 96.4 - 7.0x$; $F = 8.07$; $P < .01$. Increasing levels of sibling competition resulted in decrease in mass at eclosion.

sibling competition experienced in the larval stage (Fig. 3). The contribution of mass to fitness is due in part to the associated increase in gamete production. The negative relationship between fecundity and competition is shown in Fig. 4. A female emerging from a clutch of four bears only 57% as many eggs as does a female emerging from a clutch of one. With this measure of lifetime fecundity, the productivity of various clutch sizes can be evaluated by not only the number of offspring produced, but by the potential number of grandchildren as well. The effect of larval sibling competition on mass and fecundity might act as a selective pressure that favors the wide dispersion of eggs, i.e., one egg per ovipositional site. This behavior could produce the maximum number of grandchildren for the ovipositing mother, all other things being equal.

However, the effects of parasitism mitigate those of sibling competition with respect to offspring fitness.

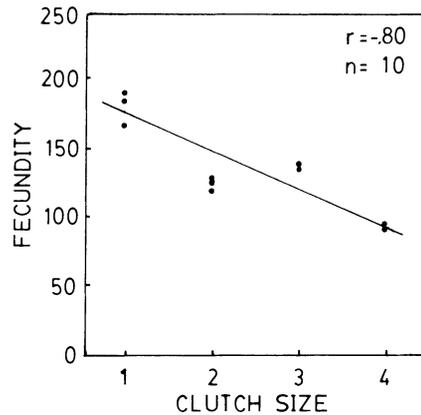


FIG. 4. Regression of fecundity over the size of the clutch in which the individuals developed. Regression line: $y = 196.5 - 24.7x$; $F = 14.66$; $P < .005$. Increasing levels of sibling competition resulted in decrease in fecundity at eclosion. Cecidomyiids produce all gametes during the pupal stage; hence, these data represent lifetime fecundity.

Mortality due to this cause decreases with clutch size (Fig. 5). A midge larva that shared a gall with four sibs was 58% as likely to be killed by parasitoids as one that developed alone. In this case, natural enemies affect clutch size productivity in a direction opposite to that which has been argued for birds. Large clutches of chirping birds are probably more easily discovered by predators than are small ones (Perrins 1965) and thus may suffer greater mortality. Of course, gall-making insect larvae do not chirp, but the gall they produce acts as a searching cue to natural enemies, specifically parasitoids (Askew 1961). Commonly, gall size is proportional to the number of larvae within (Chen 1973, Brewer and Johnson 1977) as is the case with *A. caribonifera* (Weis 1981). However, the variation in gall

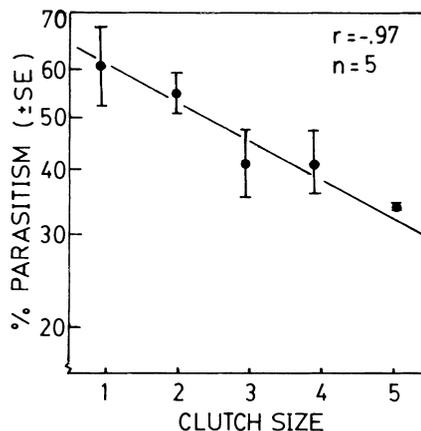


FIG. 5. Regression of percent parasitism over clutch size; means and standard errors (vertical line) for four generations are plotted. Regression line: $\arcsin \sqrt{y} = 45.33 - 3.77x$; $F = 16.4$; $P = .05$. Parasitoids usually failed to kill all midge larvae when attacking galls with clutch size greater than one.

TABLE 2. Fitness components for female offspring developing in clutches of different sizes. Fecundity per daughter, m_c , calculated from regression line in Fig. 4 and probability of surviving parasitism, l_c , from the regression line in Fig. 5. Expected fitness is the product of these two components.

	Clutch size					
	1	2	3	4	5	6
Fecundity (m_c)	173	147	122	97	73	49
Survivorship (l_c)	0.40	0.46	0.53	0.59	0.65	0.72
Expected fitness ($l_c m_c$)	69.2	67.6	64.7	57.2	47.5	35.3

size in this species is not sufficiently great to make large clutches more easily discovered (Weis 1981). Large clutches suffer less parasitism because of the tendency for parasitoids to leave a discovered gall before all the hosts within have been killed (Weis 1981, 1982).

The potential fitness of *A. carbonifera* offspring decreases with increase in clutch size. This is especially true for female offspring, which experience a loss of fecundity, but may also be true for male offspring if large body size is beneficial in locating and inseminating mates. Table 2 shows the clutch size-dependent rates of survival from egg to adult, and fecundity at eclosion, for females of *A. carbonifera*. A comparison of daughters developing in clutches of one and six illustrates the relative contributions of these two factors to offspring fitness. While a daughter developing in a clutch of six enjoys an 80% greater probability of surviving to adulthood than one developing alone, her expected fecundity is only 28% that of a daughter emerging from a clutch of one. Thus females developing alone have a potential fitness twice that of females sharing a gall with five sisters.

Female-producing mothers can maximize the fitness of each daughter by placing them in clutches of one, but by doing so mothers will not necessarily maximize their own fitness because of the risk of mortality incurred while moving between ovipositional sites. A female with a given number of eggs has to fly to six times as many ovipositional sites if she leaves one egg per site, than if she deposits six per site. During each move the mother is exposed to possible mortality factors, which include spider predation and the danger of being swept from the habitat on wind currents. Barnes (1946) stated that members of the family Cecidomyiidae are frequently collected in high-altitude, aerial plankton nets. Given the influence of adult survival, an optimal clutch size from the mother's point of view would be one for which the product of the expected fitness per offspring and the number of offspring deposited is maximized. This follows from the argument developed by Smith and Fretwell (1974) that parental fitness is maximized when a given amount of effort (of which risk is a component) is devoted to many moderately fit offspring rather than a few highly fit ones.

A model was developed to evaluate the magnitude of the effect of adult risk-taking on optimal clutch size

within the type of life history shown by *A. carbonifera*. In this model we estimated the expected fitness (measured as the potential number of grandchildren) of female-producing mothers that deposited their eggs in a series of clutches of fixed size. For simplicity it was assumed that mothers laid their eggs in clutches of the same size as the clutch into which they themselves were oviposited. Because of this assumption, each mother had a supply of eggs determined by the amount of competition she experienced during her larval development. The model is expressed in the equation:

$$W_c = \sum_{i=1}^{(m_c/c)} p^{i-1} l_c m_c,$$

where W_c is the expected fitness of the female when all her eggs are deposited in the clutches of size c , p^{i-1} is the probability of female survival to produce the i^{th} clutch (p is the probability of surviving the move from one ovipositional site to the next and will be referred to as the "between-site" survival probability; it is assumed to be the same throughout the adult life-span), l_c is the probability of egg-to-adult survival of daughters in clutches of size c , and m_c is the expected fecundity of daughters developing in clutches of size c . The term (m_c/c) is the mother's fecundity divided by the size of the clutches into which she deposits her eggs; this represents the maximum number of clutches a mother can produce in her lifetime. The term $c(l_c m_c)$ represents the contribution to the mother's fitness made by each clutch produced. Values for these two terms were set by values observed for *A. carbonifera* and are listed in Table 3.

When females lived to deposit all eggs (between-site survival probability equal to 1.00), their expected fitness equaled the maximum number of clutches they could produce times the fitness contribution per clutch. Under this condition, the females placing their eggs singly at oviposition sites realized a level of fitness 20% greater than those females depositing eggs in clutches of two, and nearly a sevenfold advantage over those producing clutches of six (Fig. 6). However, as the between-site survival probability decreased, optimal clutch size increased (Fig. 6). Even when between-site survivorship was as high as 99%, the optimal clutch size shifted up to two. Females emerging from and producing clutches of two are likely to sur-

TABLE 3. Maximum potential fitness attainable for mothers emerging from, and depositing eggs in, clutches of a given, fixed size. The maximum number of clutches deposited (m_c/c) is equal to the expected fecundity of a female emerging from a clutch of a given size divided by the size of the clutches into which these eggs are deposited. Fitness contributions to mother per clutch deposited ($c[l, m_c]$) calculated as fitness per offspring multiplied by the number of offspring in the clutch. Maximum potential fitness per mother is the product of these two components.

	Clutch size					
	1	2	3	4	5	6
Maximum number of clutches deposited (m_c/c)	173	73.5	40.7	24.3	14.6	8.2
Fitness contributions per clutch deposited ($c[l, m_c]$)	69.2	135.2	194.1	228.8	237.5	211.8
Maximum fitness attainable	11 971.6	9940.1	7899.9	5559.8	3467.5	1736.8

vive to deposit several clutches containing two moderately fit daughters, while females emerging from and producing clutches of one form a similar number of clutches containing a single, very fit daughter. The aggregate fitness of the daughters of the former mother exceeds that of the latter. With between-site survivorships of 95 and 90%, optimal clutch size rises to three and four, respectively. At these levels of survivorship, females producing clutches of one enjoy the lowest level of fitness.

DISCUSSION

A conflict in the interests of parent and offspring (Trivers 1974) exists in the reproductive patterns of *A. carbonifera*. The interests of each offspring would be best served (i.e., fitness maximized) if they were deposited alone at ovipositional sites. On the other hand, a mother that disperses her eggs in clutches of one is more likely to die before all eggs are deposited than a mother that deposits several per clutch. Selection will act favorably upon mothers that strike an optimal bal-

ance between the number of offspring oviposited and the fitness per offspring.

The model is presented to illustrate the interactions of sibling competition, parasitism, and adult risk of mortality on the potential fitness of ovipositing females. It indicates that for a clutch size of 1.88 (the population average) to be optimal, between-oviposition survivorship must be near 99%; whether this is indeed the case, we cannot say. The particular solutions obtained are influenced by underlying assumptions about parental and larval mortality schedules; by changing these assumptions, the optimal solution will also be changed.

Several mortality factors not included in the model may bias its outcome. Clutch size-independent mortality of offspring was not included, although some does occur (Table 1). Underestimating density-independent mortality would inflate the absolute fitness as predicted by the model, but relative fitness is unchanged.

The estimated relative fitness of mothers forming small clutches would be increased if density-dependent predation of eggs occurred. Under this condition the expected fitness of offspring in small clutches increases relative to those in large ones.

Another assumption of the model is that of no adult mortality at the ovipositional site. A. E. Weis has seen hunting spiders capture newly emerged adults perched on leaves of the host plant; mothers may be subject to attack while laying eggs. If the time spent at a site increases with the number of eggs laid, then mothers laying a single egg per site may survive to make it to more sites. This would select for smaller clutch size.

Selection will favor small clutches if large body size enhances adult survivorship. Females emerging from clutches of one will be at an advantage because of the inverse relationship between sibling competition and adult size (Fig. 3). Although differential mortality was not found under laboratory conditions, in nature large body size could increase resistance to mortality factors such as desiccation (by a reduced surface to volume ratio), predation, and the action of wind currents.

The model was structured with the assumption of no phenotypic plasticity in the ovipositional behavior of the mother; her clutches are of equal size. This con-

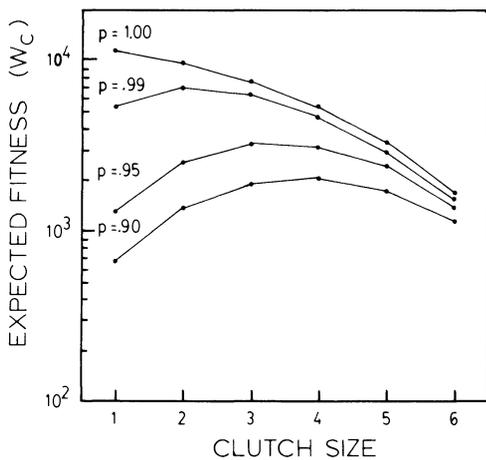


FIG. 6. Expected fitness of mothers emerging from, and depositing eggs in, clutches of a given size in relation to the probability of surviving the flight from one ovipositional site to the next. As between-site survivorship falls, the relative fitness of mothers depositing large clutches increases. W_c is the expected fitness, measured in potential grandchildren; p is the probability of survival from the deposition of one clutch to the next. Calculations are based on the model in the text.

dition probably does not hold. The related gall midge *Mayetiola destructor* shows some individual variation in clutch size (A. E. Weis, *personal observation*). Similar variation has been recorded for parasitoids (Roth and Willis 1954, Podoler et al. 1978), although the additional complication of variation in host size may influence oviposition behavior in these cases. The question can be raised, is there any selective pressure on *A. carbonifera* to change the size of clutch produced during the brief adult life-span? The model indicates a selective advantage if clutch size can be modified according to probability of adult survival. Females able to monitor environmental conditions and their physiological state would be selected if they adjusted clutch size downward when chances of survival were good and upward when they were unlikely to make it to the next site.

The data and hypotheses offered in this paper indicate that organisms with life histories like those of gall makers and parasitoids have reproductive tactics molded by a considerably more-complex selective regime than the one that operates on more-familiar semelparous species. The extension of parental care, in the form of oviposition at widely dispersed sites, can lead to a tradeoff between the number and quality of offspring beyond tradeoffs in gamete size and number. Additional work, using similar organisms that are more easily manipulable, will allow further development and verification of life history theory presented here.

ACKNOWLEDGMENTS

We thank Steven Fox, Carl Bouton, and Audrey Kapelinski for assistance in the field. Thanks are also due to Ron Greek and Philip Marcus for mathematical advice and to Arthur Ghent for statistical help. Funding was provided by the Research Board of the University of Illinois and National Science Foundation Grants DEB78-16152 and DEB80-21754 to P. W. Price. Research in this paper was submitted by the senior author in partial fulfillment for the Doctor of Philosophy degree from the University of Illinois at Urbana-Champaign.

LITERATURE CITED

- Askew, R. R. 1961. A study of the biology of species of the genus *Mesopolobus* Westwood (Hymenoptera: Pteromalidae) associated with cynipid galls on oak. *Transactions of the Royal Entomological Society of London* **113**: 155-173.
- . 1971. *Parasitic insects*. Heinemann Educational Books, London, England.
- Barnes, H. F. 1946. *Gall midges of economic importance*. Volumes I-VII. Cosby Lockwood and Sons, London, England.
- Batra, L. R. 1964. Insect-fungus blister galls on *Solidago* and *Aster*. *Journal of the Kansas Entomological Society* **37**:227-234.
- Brewer, J. W., and P. R. Johnson. 1977. Biology and parasitoids of *Contarinia coloradensis* Felt, a gall midge on ponderosa pine. *Marcellia* **39**:391-398.
- Brockelman, W. Y. 1975. Competition, the fitness of offspring, and optimal clutch size. *American Naturalist* **109**: 677-699.
- Charnov, E. L., and W. M. Schaffer. 1973. Life history consequences of natural selection: Cole's result revisited. *American Naturalist* **107**:791-793.
- Chen, C. N. 1973. Bionimics of the cypress twig gall-midge, *Taxodiomyia cupressianassa* (O.S.) (Diptera: Cecidomyiidae) in central Illinois. Dissertation. University of Illinois, Urbana, Illinois, USA.
- Cole, L. C. 1954. The population consequences of life history phenomena. *Quarterly Review of Biology* **29**:103-137.
- Crossner, K. A. 1977. Natural selection and clutch size in the European starling. *Ecology* **58**:885-892.
- Fisher, R. A. 1930. *The genetical theory of natural selection*. Dover Publications, New York, New York, USA.
- Fritz, R. S., N. E. Stamp, and T. G. Halverson. 1982. Iteroparity and semelparity in insects. *American Naturalist* **120**:264-268.
- Gadgil, M., and W. H. Bossert. 1970. Life historical consequences of natural selection. *American Naturalist* **104**: 1-24.
- Gagne, R. J. 1968. Taxonomic revision of the genus *Asteromyia* (Diptera: Cecidomyiidae). *Miscellaneous Publications of the Entomological Society of America* **6**:1-40.
- Ghent, A. W. 1976. Theory and application of some non-parametric statistics. V. *Tau*, *Gamma*, and "W" as measures of rank order correlation in contingency tables and multiple rankings. *The Biologist* **58**:41-60.
- Hassell, M. P., and R. E. Southwood. 1978. Foraging strategies of insects. *Annual Review of Ecology and Systematics* **9**:75-98.
- Lack, D. L. 1957. The significance of clutch size: I and II. *Ibis* **89**:302-352.
- Mamaev, B. M. 1975. *Evolution of gall forming insects; gall-midges*. British Library Lending Division, Wetherby, Yorkshire, England.
- Perrins, C. M. 1965. Population fluctuations and clutch-size in the Great Tit, *Parus major*. *Journal of Animal Ecology* **34**:601-647.
- Podoler, H., D. Rosen, and M. Sharoni. 1978. Ovipositional response to host density in *Aphytis holoxanthus* (Hymenoptera: Aphelinidae), an efficient gregarious parasite. *Ecological Entomology* **3**:305-311.
- Price, R. W. 1972. Parasitoids utilizing the same host: adaptive nature of differences in size and form. *Ecology* **53**:190-195.
- . 1974. Energy allocation in ephemeral adult insects. *Ohio Journal of Science* **74**:380-387.
- Roth, L. M., and E. R. Willis. 1954. The biology of the cockroach egg parasite *Tetrastichus hegenowii*. *Transactions of the American Entomological Society* **80**:53-74.
- Smith, C., and S. D. Fretwell. 1974. The optimal balance between size and number of offspring. *American Naturalist* **108**:499-506.
- Sokal, R. R., and F. J. Rohlf. 1969. *Biometry*. W. H. Freeman, San Francisco, California, USA.
- Stearns, S. C. 1976. Life history tactics: a review of the ideas. *Quarterly Review of Biology* **51**:3-47.
- Trivers, R. L. 1974. Parent-offspring conflict. *American Zoologist* **14**:249-264.
- Weis, A. E. 1981. *Ecological and evolutionary consequences of variation in clutch size in Asteromyia carbonifera* (O.S.) (Diptera: Cecidomyiidae). Dissertation. University of Illinois, Urbana, Illinois, USA.
- . 1982. Resource utilization patterns in a community of gall-attacking parasitoids. *Environmental Entomology* **11**:908-915.
- White, M. J. D. 1973. *Animal cytology and evolution*. Third edition. Cambridge University Press, London, England.
- Young, T. P. 1981. A general model of comparative fecundity for semelparous and iteroparous life histories. *American Naturalist* **118**:27-36.