Vol. 141, No. 1 The American Naturalist January 1993

SINGLE-SEX BROODS AND THE EVOLUTION OF NONSIBLICIDAL PARASITOID WASPS

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Submitted May 31, 1991; Revised December 26, 1991; Accepted January 6, 1992

Abstract.—Obligate siblicide as observed in many parasitoid wasps may commonly be a manifestation of parent-offspring conflict over clutch size. Genetic models have revealed that very stringent conditions may be required for a nonsiblicidal allele to successfully invade a siblicidal population. The parasitoid studied here, *Argochrysis armilla* Bohart (Hymenoptera: Chrysididae), appears to have undergone a transition from siblicidal to nonsiblicidal behavior during its recent evolutionary history. The appearance of nonsiblicide in *A. armilla* is paradoxical, because factors facilitating the evolution of nonsiblicidal behavior (costs of producing the fighting apparatus, female-biased sex ratios) appear to be absent, while factors favoring siblicidal behavior (superparasitism, mobile parasitoid larvae) appear to be present. *Argochrysis armilla* does, however, produce a preponderance of single-sex broods. I construct genetic models to demonstrate that single-sex broods can substantially relax the conditions under which a nonsiblicidal allele can invade a siblicidal population and simultaneously make more stringent the conditions under which a siblicidal allele can invade a nonsiblicidal population. The production of single-sex broods may be common during the evolutionary transition from siblicidal to nonsiblicidal behavior and could therefore play an important role in facilitating the evolution of nonsiblicidal behavior.

Much effort has recently been devoted to developing a theoretical understanding of clutch size determination in parasitic insects. Models have been constructed on the assumption that optimal clutch sizes are those that maximize some currency related to the parent's fitness gain (Iwasa et al. 1984; Parker and Courtney 1984; Skinner 1985; Begon and Parker 1986; Godfray 1986; Mangel 1987, 1989; Charnov and Stephens 1988; Godfray and Ives 1988; Ives 1989). However, as initially recognized by Trivers (1974) and further developed by Macnair and Parker (1978, 1979) and Parker and Macnair (1978, 1979), the level of parental investment in offspring that maximizes the parent's fitness may commonly differ from the level of parental investment that maximizes the fitness of individual offspring. Thus, parent-offspring conflict may frequently exist over clutch size decisions (Stinson 1979; Dickins and Clark 1987; Godfray 1987; Parker and Mock 1987; Godfray and Harper 1990; Anderson 1990*a*). Because most parasitic insects deposit a clutch of eggs on a given host resource and have no further contact with developing offspring (i.e., they practice mass provisioning), there is generally no opportunity for parents to suppress selfish behavior in offspring. We might therefore frequently expect to see an "offspring wins" resolution to parent-offspring conflict over clutch size in insects.

Am. Nat. 1993. Vol. 141, pp. 90–104.

Obligate sibilicide, observed in some birds (Anderson 1990*b*) and many insect parasitoids (Salt 1961), may commonly be a manifestation of parent-offspring conflict over clutch size. Genetic models of diploid populations (for avian systems) suggest that strikingly stringent conditions are required for a nonsiblicidal allele to invade a siblicidal population whenever broods lack an obvious runt (Stinson 1979; Dickins and Clark 1987; Anderson 1990*a;* Godfray and Harper 1990).

Godfray (1987) was the first to model evolutionary transitions between siblicide and nonsiblicide in haplodiploid parasitoid wasps. Parasitoids may be divided into two groups: "solitary" and "gregarious" species. In solitary species only a single parasitoid larva per host develops successfully, and multiple larvae placed on a single host engage in physical combat or physiological suppression resulting in the death of supernumerary larvae. In gregarious species multiple parasitoid larvae per host may develop successfully without physical or physiological aggression. The key results of Godfray's (1987) model were expressed in terms of $f(c)$, the fitness of individual offspring developing in clutches of size c. Godfray (1987) concluded from his simplest model that (1) siblicidal alleles can invade populations when parasitoids produce clutches of fewer than three or four eggs, (2) only under the very stringent condition that $f(2) > f(1)$ can a nonsiblicidal allele invade (i.e., the fitness of a parasitoid that shares the host resource with another developing larva must exceed the fitness of a parasitoid that develops on the host resource alone), and therefore (3) the solitary fighting condition is a locally absorbing state.

We are left with the task of reconciling these conclusions with the observed distribution of solitary and gregarious species within the parasitic Hymenoptera. Transitions between siblicidal and nonsiblicidal behavior have occurred in a number of lineages; 20 of the 24 major families contain both solitary and gregarious species (table 1), and it is common to find both solitary and gregarious species in the same genus (Blackburn 1990). For example, Shaw and Huddleston (1991) describe 14 genera in the family Braconidae that contain both solitary species and gregarious species. Although the phylogeny of the Hymenoptera is generally too poorly known to definitively infer the direction of evolution (solitary to gregarious or the reverse), in at least some groups solitary development is clearly the ancestral condition (e.g., Braconidae [Shaw and Huddleston 1991] and Chrysididae [Kimsey and Bohart 1991]; see below). Furthermore, the observation that gregarious development is widely distributed but mostly uncommon (i.e., gregarious development is generally a minority condition in polymorphic taxa) suggests that it may frequently be the derived state (Waage 1986). Thus, in at least some taxa the incidence of siblicide appears to be evolutionarily labile.

Modeling studies have identified several factors that can modify the conditions for the spread of a nonsiblicidal allele (table 2). Of these factors only two, costs associated with fighting (including both the energetic costs of producing the large, piercing mandibles used in combat and the risk of both fighters' dying as a result of combat) and female-biased sex ratios, appear to be potentially significant in facilitating the evolution of gregarious parasitoids. However, evidence supporting substantial costs of fighting is scant, and we would expect to find female-biased

TABLE 1

Distribution of Solitary and Gregarious Larval Development among the Major Families (families with more than 350 species described worldwide) of the Parasitoid Hymenoptera

Family	Reference
Families with only solitary development:	
Eucoilidae	Clausen 1940; Gauld and Bolton 1
Gasteruptiidae	Iwata 1976
Tiphiidae	Gauld and Bolton 1988
Mutillidae	Clausen 1940; Gauld and Bolton 1
Families with both solitary and gregarious development:	
Braconidae	Iwata 1976
Ichneumonidae	Iwata 1976
Mymaridae	Iwata 1976
Trichogrammatidae	Iwata 1976
Eulophidae	Iwata 1976
Encyrtidae	Iwata 1976
Aphelinidae	Clausen 1940
Eupelmidae	Iwata 1976
Torymidae	Gauld and Bolton 1988
Pteromalidae	Gauld and Bolton 1988
Eurytomidae	Iwata 1976
Chalcididae	Iwata 1976
Diapriidae	Iwata 1976
Scelionidae	Gauld and Bolton 1988
Platygasteridae	Iwata 1976
Ceraphronidae	L. Masner, personal communication
Megaspilidae	L. Masner, personal communication
Chrysididae	Kimsey and Bohart 1991; this study
Bethylidae	Iwata 1976
Dryinidae	Clausen 1940

sex ratios during the transition to a gregarious habit only in species exhibiting the rare form of sexual dimorphism in which males are larger than females, or in species in which sibmating is likely despite the fact that sibs develop in different hosts (e.g., egg parasitoids whose hosts deposit eggs in clusters; Waage 1982). Multipaternity within broods and especially the possibility that more than one parasitoid may oviposit on the same host ("superparasitism") will potentially counterbalance the influence of costs of fighting and female-biased sex ratios by strengthening selection against the spread of nonsiblicidal alleles. Are there then other biological features of parasitoid wasps that could complement costs of fighting and female-biased sex ratios in promoting the evolution of nonsiblicidal behavior?

Here I describe relevant aspects of the biology of a parasitoid, *Argochrysis armilla* Bohart (Hymenoptera: Chrysididae), that appears to have undergone a transition from solitary to gregarious development during its recent evolutionary history. I then extend Godfray's (1987) model to incorporate a feature of this

TABLE 2

FACTORS THAT CAN MODULATE THE CONDITIONS UNDER WHICH A RARE NONSIBLICIDAL ALLELE CAN SUCCESSFULLY INVADE A SIBLICIDAL POPULATION

Factor	Reference
Factors facilitating the spread of a nonsiblicidal allele:	
Costs of fighting	Godfray 1987
Female-biased sex ratio	Godfray 1987
Finite population size*	Macnair and Parker 1978; Stinson 1979; Godfray 1987
Size asymmetries among sibs†	Dickins and Clark 1987; Godfray and Harper 1990
Factors operating against the spread of a nonsiblicidal allele:	
Recessive nonsiblicidal allele	Godfray 1987
Superparasitism	Godfray 1987
Male-biased sex ratio	Godfray 1987
Incomplete penetrance of the nonsiblicidal allele	Godfray 1987
<100% Probability of producing a clutch of two eggs; superparasitism present	Godfray 1987
Multipaternity within broods	Macnair and Parker 1978, 1979
Direct benefits of fighting (e.g., cannibalism)	Parker and Mock 1987
Factors having no effect on the spread of a nonsiblicidal allele:	
Haplodiploidy vs. diploidy	Godfray 1987
<100% Probability of producing a clutch of two eggs; superparasitism absent	Godfray 1987

* Magnitude of this effect is extremely small for parasitoids (Godfray 1987).

† For size asymmetries to be significant, "runts" that are phenotypically nonsiblicidal even when bearing a siblicidal genotype must be present. There is no evidence for such runts in parasitoid broods.

parasitoid's biology, the prevalence of single-sex broods, to investigate the potential influence of this form of sex allocation on the evolution of nonsiblicidal behavior. Results of the model are compared with predictions made by kin selection theory. Finally, conditions under which single-sex broods might be expected to occur during the evolution of nonsiblicidal parasitoids are explored.

BIOLOGY OF *ARGOCHRYSIS ARMILLA*

Argochrysis armilla is a gregarious parasitoid of solitary ground-nesting wasps in the genus *Ammophila* (Hymenoptera: Sphecidae). I studied interactions of *A. armilla* with its hosts in 1982–1988 in the Sierra Nevada at the Sagehen Creek Field Station, Nevada County, California. *Ammophila* construct simple, unicellular nests, which they provision with caterpillar prey. *Argochrysis armilla* enters *Ammophila* nests, often during nest provisioning, and lays eggs on the ceiling or walls of the cell or directly on the caterpillar provisions. From one to eight larvae may develop successfully in a single cell by feeding indiscriminately on both the host larva and the caterpillar provisions (Rosenheim 1987*a*, 1987*b;* J. A. Rosenheim, unpublished data).

Argochrysis armilla is exceptional in being the only species in the large family Chrysididae (approximately 3,000 species described worldwide) that is known to develop gregariously (Kimsey and Bohart 1991). This is despite the fact that the family is exclusively parasitic and shows a great deal of ecological diversification. Detailed cladistic analyses of morphological traits suggest that the genus *Argochrysis* emerges as a relatively distal clade within the Chrysididae (Kimsey and Bohart 1991). On the basis of a single rearing record and the size of the parasite relative to its known hosts (*Ammophila* spp.), it appears that the only other species within the genus for which the biology is known, *Argochrysis mesillae* (Cockerell), is a solitary parasitoid (Kimsey and Bohart 1991; R. M. Bohart, personal communication). Thus, *A. armilla* is a candidate for a lineage that has undergone the transition from solitary to gregarious development during its recent evolutionary history.

The appearance of gregarious development in *A. armilla* is for several reasons particularly paradoxical under Godfray's (1987) model. First, strong piercing mandibles are required to feed externally on the host larva and the caterpillar provisions whether fighting occurs or not; thus, a potential cost associated with fighting, the energetic cost of producing large, piercing mandibles, will be attenuated. Second, *A. armilla* does not exhibit a female-biased sex ratio; 60 broods collected from the field in 1982–1986 and reared (176 sexable offspring) yielded an overall secondary sex ratio of 0.523 (proportion males). Third, substantial superparasitism occurs in at least some populations; direct observations of *A. armilla* parasitizing nests in aggregations of *Ammophila dysmica* Menke during 1983–1988 revealed that at least 12 of 32 (37.5%) parasitized nests were superparasitized; the mean number of parasitoids ovipositing per parasitized nest was 1.72 ± 1.57 (SD) (Rosenheim 1989; J. A. Rosenheim, unpublished data). Finally, perhaps because of their need to locate food within the cell on hatching, first instar larvae of *A. armilla* are highly mobile (J. A. Rosenheim, unpublished data); siblicide is therefore not likely to be prevented by constraints on intersib contact, as has been suggested for other ectoparasitoids (Godfray 1987). In sum, factors facilitating the evolution of nonsiblicidal behavior (costs of fighting, female-biased sex ratios) appear to be absent, while factors favoring siblicidal behavior (superparasitism, mobile parasitoid larvae) appear to be present.

Although *A. armilla* does not exhibit a female-biased sex ratio, it does display another sort of divergence from random sex allocation: most broods (32 of 43, or 74.4%) are composed of larvae of a single sex (table 3). Preliminary observations suggest that most, if not all, of the mixed-sex broods resulted from superparasitism of nests. The remainder of this article examines the potential influence of single-sex broods on the evolution of nonsiblicidal behavior.

INVASION BY A NONSIBLICIDAL ALLELE

Godfray's (1987) model can readily be extended to examine the influence of single-sex broods on the conditions under which a rare nonsiblicidal allele will invade a siblicidal parasitoid population (see Parker and Macnair 1978; Stinson 1979; Dickins and Clark 1987; Anderson 1990*a;* and Godfray and Harper 1990 for

TABLE 3

SEX ALLOCATION BY THE GREGARIOUS PARASITOID, *ARGOCHRYSIS ARMILLA*

Clutch Size*	Single-Sex Broods	Mixed-Sex Broods	*P*†
2	8	1	.020
3	10	2	<.0001
4	7	4	<.001
5	6	2	<.00001
6	0	1	NS
7	0	1	NS
8	1	0	.0083

* Number of sexable offspring (mature pupae or adults) reared per brood. Parasitoid broods were collected in the field from nests of *Ammophila* spp. as overwintering prepupae in cocoons and reared in the laboratory.

† Binomial probabilities of observing a number of single-sex broods equal to or greater than that observed; NS, nonsignificant.

similar explicitly genetic models). I retain the assumptions of the simplest case model: (1) parasitoids are never egg limited; thus, clutch size has no effect on the lifetime total number of broods produced; (2) only one offspring survives in broods with one or more siblicidal larvae, and nonsiblicidal larvae are always killed in broods with siblicidal members; (3) there are no costs associated with fighting; (4) there is no superparasitism; (5) females mate only once; (6) population size is infinite; (7) mate choice is random; and (8) larval fighting behavior is controlled by two alleles at a single locus: *K*, a dominant allele resulting in nonsiblicidal larvae, and *k*, a recessive allele resulting in siblicidal larvae. (The effects of relaxing some of these assumptions are summarized in table 2.) I further assume that there is some probability, p_2, that females deposit two eggs per host rather than one, and that the probability of clutch sizes greater than two is zero. (Conditions under which solitary parasitoids might deposit clutches of more than one egg are examined under Discussion.) In the absence of superparasitism the conditions for the spread of a nonsiblicidal allele can be shown to be independent of p_2, for $p_2 > 0$ (Godfray 1987); to simplify the analysis, I have set $p_2 = 1$.

When *K* is rare, we need only consider the dynamics of *Kk* females and *K* males to understand the conditions under which *K* will spread; the frequency of *KK* females will be negligible. Let the frequency of *K* among males be x and the frequency of *Kk* among females be y. Whether *K* is selected for or against will be determined by the production of nonsiblicidal offspring from the two mating types shown in table 4; the frequency of all other mating types involving *K* alleles will be negligible. Table 4 is identical to Godfray's (1987) table 1 except that the distribution of initial broods produced is influenced by the incidence of single-sex broods, s. (Throughout this article I assume that single-sex broods are equally likely to be all male or all female.) Under binomial sex allocation with even sex ratios (i.e., the number of males per brood is a binomial random variable with a probability distribution parameter, p, of 0.5) and clutches of size two, $s = 0.5$, and table 4 becomes identical to Godfray's (1987) table 1.

TABLE 4

BROODS PRODUCED BY PARENTS BEARING A RARE NONSIBLICIDAL ALLELE, K

Initial Brood	Brood after Fighting	Probability	Fitness of Each Offspring*
$kk \times K$ Matings (frequency $\simeq x$):			
$Kk + Kk$	$Kk + Kk$	$s/2$	$f(2)$
$Kk + k$	k	$(1 - s)$	1
$k + k$	k	$s/2$	1
$Kk \times k$ Matings (frequency $\simeq y$):			
$Kk + Kk$	$Kk + Kk$	$s/8$	$f(2)$
$Kk + kk$	kk	$s/4$	1
$kk + kk$	kk	$s/8$	1
$Kk + k$	k	$(1 - s)/4$	1
$Kk + K$	$Kk + K$	$(1 - s)/4$	$f(2)$
$kk + k$	kk or k	$(1 - s)/4$	1
$kk + K$	kk	$(1 - s)/4$	1
$K + K$	$K + K$	$s/8$	$f(2)$
$K + k$	k	$s/4$	1
$k + k$	k	$s/8$	1

* Letting $f(1) = 1$.

From table 4 the frequency of Kk females produced is $sf(2)x + (1/4)f(2)y$ and the frequency of K males is $(1/4)f(2)y$. To convert these frequencies into the frequencies of Kk females and K males in the next generation (y' and x', respectively), we need to divide by the mean number of female and male offspring in a single brood from a $kk \times k$ mating (0.5 and 0.5, respectively). The dynamics of the nonsiblicidal allele can now be described by two recurrence equations; in matrix form,

$$\begin{pmatrix} x' \\ y' \end{pmatrix} = \begin{pmatrix} 0 & 0.5f(2) \\ 2sf(2) & 0.5f(2) \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} . \tag{1}$$

For K to spread, the dominant eigenvalue of equation (1) must be greater than 1; the critical condition is

$$f(2) > \frac{1}{1/4 + \sqrt{1/16 + s}} , \tag{2}$$

as plotted in figure 1. The conditions under which the nonsiblicidal allele will invade successfully are relaxed as the proportion of single-sex broods increases. When $s = 1$, a nonsiblicidal allele will be favored when $f(2) > 0.78$.

INVASION BY A SIBLICIDAL ALLELE

We can now consider the influence of single-sex broods on the evolutionary stability of nonsiblicidal behavior; under what conditions will a rare mutant siblicidal allele successfully invade a nonsiblicidal population? The assumptions of

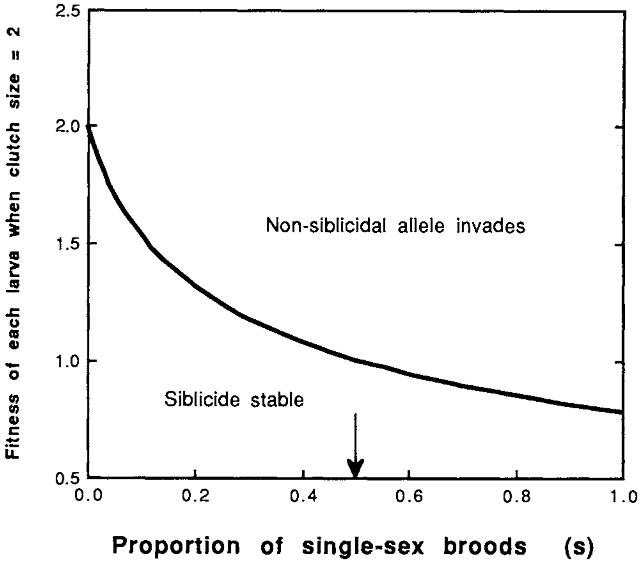

FIG. 1.—Influence of single-sex brood production on the minimum fitness value of a parasitoid developing in clutches of size two ($f(2)$) required for a rare nonsiblicidal allele to invade a siblicidal population. The *arrow* marks the proportion of single-sex broods produced under binomial (random) sex allocation (0.5), where the critical value of $f(2)$ is 1.

the previous model are retained with one modification: the allele for siblicide, G, is now assumed to be dominant with respect to the nonsiblicidal allele, g. Let the frequency of G among males be u and the frequency of Gg among females be w. When G is rare, we again need only consider $gg \times G$ and $Gg \times g$ matings. Matings of the type $gg \times G$ (frequency $\simeq u$) produce broods of two compositions: broods of all-male, nonsiblicidal offspring (probability $= s/2$) and broods with at least one siblicidal female offspring (probability $= 1 - [s/2]$). Matings of the type $Gg \times g$ (frequency $\simeq w$) produce six kinds of broods: (1) broods of all-male, nonsiblicidal offspring (probability $= [s/2][1/2]^c$, where c is the clutch size); (2) all-male broods with at least one siblicidal offspring (probability $= [s/2][1 - (1/2)^c]$); (3) broods of all-female, nonsiblicidal offspring (probability $= [s/2][1/2]^c$); (4) all-female broods with at least one siblicidal offspring (probability $= [s/2][1 - (1/2)^c]$); (5) mixed-sex broods, all nonsiblicidal (probability $= [1 - s][1/2]^c$); and (6) mixed-sex broods with at least one siblicidal offspring (probability $= [1 - s][1 - (1/2)^c]$). The surviving offspring from brood type 6 will be equally likely to be Gg females or G males.

As before, to calculate u' and w' (the frequencies of G among males and Gg among females in the next generation) we need to sum the probabilities of generating siblicidal offspring from the just-described matings and divide by the mean number of offspring in a single brood from a $gg \times g$ mating that are female ($0.5cf(c)$) and male ($0.5cf(c)$). (Note that for broods containing at least one siblicidal offspring, $cf(c) = (1)(1) = 1$.) The dynamics of the siblicidal allele can be described by the recurrence equations

$$\begin{pmatrix} u' \\ w' \end{pmatrix} = \begin{pmatrix} 0 & F \\ \dfrac{2-s}{cf(c)} & F \end{pmatrix} \begin{pmatrix} u \\ w \end{pmatrix}, \tag{3}$$

where $F = [1 - (1/2)^c]/[cf(c)]$. Allele G will spread if the dominant eigenvalue of equation (3) is greater than one; the critical condition is

$$0.5F + 0.5\sqrt{F^2 + \frac{4F(2-s)}{cf(c)}} > 1 . \tag{4}$$

To evaluate this inequality we need to specify both the form of the function $f(c)$ and the clutch size deposited by parasitoids in the nonsiblicidal population. Again following the simplest case model developed by Godfray (1987), assume (1) that $f(c) = j\exp(-hc)$, where h measures the degree to which fitness declines with increasing clutch size and j is a constant defined such that $f(1) = 1$, and (2) that parasitoids always deposit the "Lack clutch size," that is, the clutch size that maximizes the fitness gain from the host being parasitized. (The latter assumption is equivalent to assuming that parasitoids are host limited.) The Lack clutch size gives $f(c) = \exp((1/c) - 1)$; substituting this for $f(c)$ in equation (4) and numerically solving the resulting equation as an equality yields a relationship between the proportion of single-sex broods and the critical clutch size value below which the siblicidal allele will successfully invade (fig. 2). Increasing the proportion of single-sex broods narrows the conditions under which siblicidal alleles can invade. When $s = 1$, a siblicidal allele will invade only if parasitoids produce clutches of fewer than 2.69 eggs. Under binomial (random) sex allocation only 13% of broods will be single sex when clutch size is near the critical value (3.94 eggs). Thus, further decreases in single-sex brood production toward 0% (i.e., "precise sex ratios"; Green et al. 1982) will only slightly facilitate the spread of a siblicidal allele (fig. 2).

DISCUSSION

This investigation of the influence of single-sex broods on the evolution of nonsiblicidal parasitoid larvae was motivated by the discovery of a gregarious parasitoid, *Argochrysis armilla,* in a family of parasitoids that is otherwise exclusively solitary. *Argochrysis armilla* exhibits two key attributes thought to act against the evolution of nonsiblicidal behavior, high larval mobility and a potentially high incidence of superparasitism, and fails to exhibit two key attributes thought to facilitate the evolution of nonsiblicide, costs associated with producing the fighting apparatus and a female-biased sex ratio. *Argochrysis armilla* does, however, produce a preponderance of single-sex broods. Incorporating this factor into explicitly genetic models demonstrated that single-sex broods can substantially relax the conditions under which a nonsiblicidal allele can invade a siblicidal population and simultaneously make more stringent the conditions under which

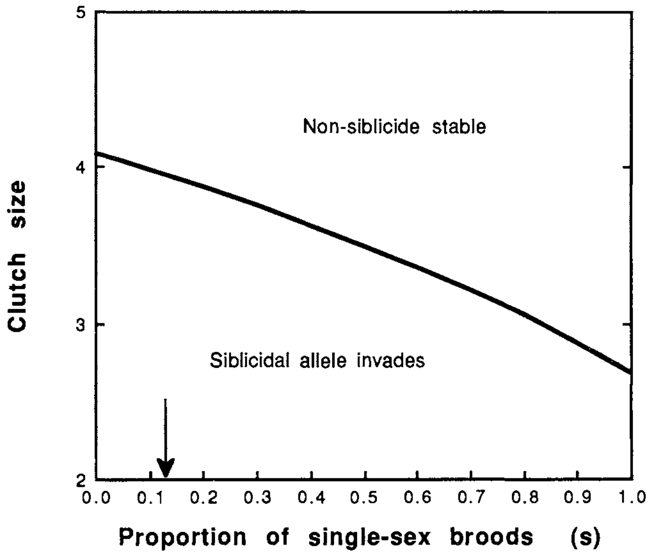

FIG. 2.—Influence of single-sex brood production on the critical clutch size below which a rare siblicidal allele can invade a nonsiblicidal population, assuming that $f(c) = j\exp(-hc)$ and that parasitoids always deposit the Lack clutch size. The *arrow* marks the proportion of single-sex broods produced under binomial (random) sex allocation (0.13) at the critical clutch size of 3.94.

a siblicidal allele can invade a nonsiblicidal population. Single-sex broods may therefore be important in enabling populations to make the evolutionary transition from siblicidal to nonsiblicidal behavior.

What is the mechanism by which single-sex broods exert this effect? The evolutionary dynamics of a rare nonsiblicidal allele are essentially the product of two opposing forces: selection operating against nonsiblicidal larvae when they are present in broods with at least one siblicidal larva (selection operating via mortality of nonsiblicidal larvae) and selection operating in favor of nonsiblicidal larvae when they are the sole members of gregarious broods (selection operating via the ability to successfully produce broods of more than one offspring). Single-sex broods facilitate the evolution of nonsiblicidal behavior simply by increasing the likelihood that nonsiblicidal larvae will be found together in broods rather than mixed with siblicidal larvae. This effect is generated exclusively by the $kk \times K$ matings analyzed in table 4. Observe that the three initial brood types produced correspond to all-female broods ($Kk + Kk$), mixed-sex broods ($Kk + k$), and all-male broods ($k + k$). Nonsiblicidal offspring develop successfully only in the first brood type, comprising two female, nonsiblicidal larvae. By producing an increasing proportion of single-sex broods, parasitoids produce an increasing proportion of these all-female, nonsiblicidal broods at the expense of a decreased production of mixed-sex, siblicidal-plus-nonsiblicidal broods; both of these effects facilitate the spread of the nonsiblicidal allele. Exactly analogous effects make it more difficult for a rare siblicidal gene to spread; single-sex broods increase the likelihood that siblicidal larvae will be placed together in broods in which all but one will die, rather than in broods with nonsiblicidal larvae, which represent easy victims.

Single-sex broods might be especially important in facilitating the spread of a nonsiblicidal allele if normally solitary parasitoids making the evolutionary transition to gregarious development sometimes deposited clutches of more than two eggs, for example, during a host range expansion to include a new, much larger host. In this case, the fitness gained from clutches of size c would not generally increase more than linearly with c, whereas the probability of obtaining broods without a single siblicidal individual would decrease exponentially with c. Single-sex broods can maintain a high probability of producing purely nonsiblicidal broods for any value of c for one of the two critical mating types outlined in table 4 ($kk \times K$ matings). The question of whether evolutionary transitions to nonsiblicidal behavior frequently coincide with host range expansions has not yet been addressed and represents a potentially important area for further empirical and theoretical investigation.

Kin Selection Theory

I have not thus far appealed to kin selection theory to explain the observed influence of single-sex broods on the evolution of nonsiblicidal behavior. Although inclusive fitness arguments have been used to investigate siblicide (e.g., O'Connor 1978), Godfray and Harper (1990) have clearly demonstrated that predictions of kin selection models frequently diverge from those of explicitly genetic models. The disagreement stems from the failure of models of siblicide to satisfy a key requirement for applying Hamilton's rule (Hamilton 1964), the requirement of weak selection (Michod 1982; Grafen 1984; Godfray 1987; Godfray and Harper 1990). Nevertheless, inclusive fitness theory can help provide an intuitive understanding of why single-sex broods should facilitate the evolution of nonsiblicidal behavior. Haplodiploidy creates relatedness asymmetries among sibs; females are more closely related to their sisters (r, the relatedness coefficient, is 3/4) than to their brothers ($r = 1/4$), while males are equally related to their brothers and sisters ($r = 1/2$). The net effect of this is that the mean within-brood relatedness of single-sex broods ($r = 0.625$) is greater than the mean within-brood relatedness of mixed-sex broods ($r = 0.375$ when broods contain an equal number of male and female sibs; Pickering 1980). Hamilton's rule predicts that selection will favor the expression of altruistic behavior whenever the costs of performing the behavior are less than the product of the benefits reaped by the recipient(s) and the relatedness of the donor and recipient(s). The conditions under which an altruistic behavior, such as nonsiblicide, is favored are therefore broadened as the production of single-sex broods increases.

Incidence of Single-Sex Broods

Although the simple models developed here demonstrate that single-sex broods can facilitate the evolution of nonsiblicidal behavior, the question remains as to how widespread a phenomenon this may be within the Hymenoptera. The production of primarily single-sex broods has been recorded from only a very few parasitoid genera (Askew and Ruse 1974; Bryan 1983; Godfray and Shaw 1987; reviewed in Hardy 1991); thus, if one were to judge the importance of single-sex broods by its prevalence among extant gregarious species, one might infer at most a minor role for this factor. However, might single-sex broods be more common during the critical period of evolutionary transition to nonsiblicidal behavior?

To address this question, we need first to ask why a solitary parasitoid (i.e., a parasitoid with siblicidal offspring) would deposit more than one egg during a single encounter with a host, given that at most one offspring can develop successfully per host (''self-superparasitism''). Five hypotheses have been proposed, suggesting that a second egg might be deposited (1) accidentally (Godfray 1987), (2) as an ''insurance egg'' in response to some risk that the first egg or larva dies because of an immune response by the host insect (encapsulation) or any other source of developmental failure (Parker and Courtney 1984; Godfray 1987), (3) to increase the probability that one of the eggs is the winner in competitive interactions among larvae deposited by different parasitoids in superparasitized hosts (Parker and Mock 1987; van Alphen and Visser 1990), (4) to discourage oviposition by additional conspecific parasitoids when these parasitoids can ''count'' the number of eggs already present (van Alphen and Visser 1990), and (5) to overwhelm the host's encapsulation response and thereby allow one of the offspring to survive (Blumberg and Luck 1990; van Alphen and Visser 1990). Self-superparasitism has been documented for some solitary parasitoids (Linsley and MacSwain 1955; Schlinger and Hall 1961; Shaw 1983; Mollema 1988; Blumberg and Luck 1990; van Alphen and Visser 1990; J. Nelson, personal communication). Because superparasitism in solitary parasitoids has, until very recently, generally been viewed as aberrant, nonadaptive behavior (van Alphen and Visser 1990), self-superparasitism may be more common than the current literature would indicate.

What sort of within-brood sex allocation patterns would we expect to observe in these cases of self-superparasitism? Unfortunately, the relevant empirical studies (i.e., studies in which the two eggs are sexed directly or in which one of the two eggs is transferred to another host so that both can develop successfully and be sexed as pupae or adults) have not been performed. It may be possible, however, to suggest some likely sex allocation strategies.

Sex allocation patterns are difficult to predict under hypothesis 1 above (accidental self-superparasitism). Females that lay two eggs when attempting to lay a single male egg will probably produce two male eggs because no sperm will be released from the spermatheca; however, females that are attempting to lay a female egg might produce two female eggs or one female and one male, depending on the number of sperm released and the precise position in the reproductive tract of the accidentally deposited egg when the first egg is fertilized. The events surrounding egg fertilization in the Hymenoptera are too poorly understood to carefully evaluate the likelihood of producing all-female broods by accident. For the few well-studied species, accidental fertilization of two eggs seems unlikely (see, e.g., Wilkes 1965).

Under hypotheses 2–5, however, it seems likely that parasitoids that for any reason are selected to assign sex to particular hosts in a nonrandom fashion will also be selected to produce single-sex broods when engaging in self-superparasitism. This is because the ovipositing parasitoid will generally be unable to predict which of the offspring will survive, and therefore should assign whatever sex is appropriate for the host being parasitized to each of the deposited eggs. Furthermore, nonrandom sex allocation is very common in solitary parasitoids, often as a response to host size or quality (Charnov 1982; King 1987).

Thus, single-sex brood production may be a frequent component of self-superparasitism among solitary parasitoids and could therefore play an important role in facilitating the evolution of nonsiblicidal behavior. Once gregarious development has been established, however, selection will favor not only a shift to mixed-sex brood production (due to selection operating within spatially structured parasitoid populations; see review in Charnov 1982) but even perhaps a shift to "precise" sex ratios, whereby the production of single-sex broods is less than that expected under binomial sex allocation (Green et al. 1982). Thus, of the two effects of single-sex broods identified by the models developed here, facilitating the spread of a nonsiblicidal allele and making it more difficult for a siblicidal allele to invade, the former is probably the more significant.

ACKNOWLEDGMENTS

I thank L. K. Bailey-Segal, M. Berman, J. Hesse, T. Meade, and I. G. Powch for assistance in the field, and J. P. Thornton, M. P. Yoder-Williams, and the staff and directorship of the Sagehen Creek Field Station (University of California) for greatly facilitating the field research. For kindly sharing unpublished results I thank R. M. Bohart (biology of *Argochrysis mesillae*), L. Masner (biology of the Proctotrupoidea), and J. Nelson (self-superparasitism in *Opius dimidiatus*). I gratefully acknowledge critical reviews of the manuscript by H. C. J. Godfray, I. C. W. Hardy, G. E. Heimpel, K. M. Heinz, R. G. Lalonde, M. Mangel, and M. J. Pitcairn. Work was supported under a National Science Foundation graduate fellowship and grants from the Graduate Division, University of California, Berkeley; University of Hawaii; and University of California, Davis.

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Associate Editor: Geoffrey A. Parker