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Siblicide and life-history evolution in parasitoids

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Parasitoid wasps exhibit a stark dichotomy in larval behavior and developmental mode. In gregarious species, siblings developing together tolerate each other; hence more than one individual can successfully complete development. In contrast, solitary species have intolerant larvae that will engage in siblicide, leading to only one individual successfully completing development. Previous theoretical and empirical work has suggested that females from species with intolerant larvae should reduce their relative investment in reproduction. We tested this prediction by measuring investment in survival and reproduction in a pair of sister species from the genus *Aphaereta* (Hymenoptera: Braconidae). With increasing body size, divergent patterns of investment exist in the two species. Females of the solitary *A. genevensis* allocate additional resources almost exclusively toward greater fat reserves, resulting in enhanced longevity. Females of the gregarious *A. pallipes* invest relatively more in reproduction and hence have lower fat reserves, reduced longevity, and greater egg loads than *A. genevensis.* These differences reflect a trend toward greater investment in survival relative to reproduction in the solitary species, as predicted. We discuss the implications of these findings for the development of sibling rivalry and life-history theory. *Key words:* Alysiinae, *Callosobruchus,* fecundity, optimal investment, parasitoids, resource allocation, trade-offs. *[Behav Ecol 13:690–695 (2002)]*

The behavior of siblings toward each other, and the effects on parents, is a topic of enduring interest for evolutionary biologists (Cheplick, 1992; Elgar and Crespi, 1992; Mock and Parker, 1997). The behavior of family members toward each other may include conflict between offspring (Mock and Parker, 1997) and conflict between parents and offspring (Godfray, 1995; Trivers, 1974). Previously the main challenge has been to determine the conditions that facilitate either cooperation or conflict between relatives. In this article, our focus is on the consequences of parent–offspring conflict and sibling rivalry on the evolution of life-history traits.

Parasitoids are insects that develop by feeding on the bodies of other arthropods. The completion of feeding inevitably kills the host. The adult parasitoid is free-living, and the main task of females is finding new hosts for the next generation (Godfray, 1994; Quicke, 1997).

Parasitoids are classic examples of nursery species, in which siblings are required to share a limited space and set of resources. Sibling rivalry and parent–offspring conflict is particularly acute in many species of parasitoids. Parasitoids can be solitary, with only one larva developing successfully from an individual host, or they can be gregarious if several individuals successfully develop together (Mayhew et al., 1998). The majority of parasitoids develop solitarily, although gregarious development is taxonomically widespread and is probably the derived state (Mayhew, 1998). The larvae of solitary species engage in lethal fighting or physiological suppression until only one individual remains to consume the host (Godfray, 1994; Salt, 1961). This behavior has been described as ''ultrasiblicide'' (Mock and Parker, 1997). The siblicidal behavior of developing wasps is an extreme example of parent–offspring conflict over clutch size and implicitly the level of parental investment received, with the offspring determining the outcome. In this article, we examine the life-history consequences of siblicide that feed back to adult parasitoids. Predictions come from both general life-history theory and from more specific work on parasitoids, which we review briefly below.

The general theoretical framework and empirical evidence suggest that sibling rivalry should have direct consequences on the allocation of resources to survival and reproduction in adults. Optimal investment models (e.g., Roff, 1992; Smith, 1991; Stearns, 1992; Young, 1990) predict that reduced instantaneous investment in reproduction and greater investment in survival will be favored by any factor that increases the value of adults over juveniles. These factors include increases in the mean and variance in juvenile mortality, which devalues reproduction relative to adult survival. Siblicide is a cause of juvenile mortality, and so should select for greater investment in survival (Smith, 1991).

Comparisons between populations and species of bruchid beetles from the genus *Callosobruchus* are consistent with the above prediction. As in parasitoids, juveniles of these beetles share a limiting resource during development (a seed), and populations differ in their larval behavior with tolerant and intolerant larvae, giving rise to scramble and contest competition, respectively. Species with fighting larvae may suffer high juvenile mortality relative to those with tolerant larvae. Beetles with tolerant larvae also have higher numbers of eggs on eclosion and reduced longevity compared to strains and species with contest competition (Giga and Smith, 1983; Thanthianga and Mitchell, 1990; Smith, 1991).

Research on investment in survival and reproduction in parasitoids has focused on the effects of internal (physiological) state or of habitat characteristics, such as the distribution and abundance of hosts (see Ellers et al., 2000, and references therein), and the likelihood of host survival during the development of juveniles (Price, 1974).

Price's (1974) balanced mortality hypothesis is a potential framework for understanding patterns of investment in reproduction and survival observed in parasitoids. It is based on the empirical observation that potential fecundity in some parasitoid assemblages is positively correlated with host abundance and the risk of extrinsic environmental mortality for hosts (see Price, 1974: Figure 1). Parasitoid species attacking hosts during an early life-stage (when the host is abundant, but it experiences low survivorship rates) compensate for the resultant high level of juvenile mortality by producing more

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eggs and attacking more hosts. In contrast, those species attacking hosts at a later life-stage have reduced potential fecundity. The balance thus is shifted away from investment in reproduction when juvenile mortality is low. However, Price's hypothesis is not directly supported by explicit theory and gives predictions in relation to juvenile mortality that are at odds with general life-history models (see above). An alternative interpretation of the data, which is not at odds with theory, is that it is not juvenile mortality but host density that controls investment in this case and that would select for increasing adult survival when hosts are old but rare (see below). We return to these two alternative selection pressures in the Discussion.

Recent parasitoid models, and some empirical data, do in fact suggest that increasing host-patch density and quality will favor investment in reproduction rather than survival (Ellers et al., 2000). Studies of the alysiine parasitoid *Asobara tabida* have compared populations from different geographic locations. Those from northern Europe allocate relatively more resources toward survival than those from southern Europe, as predicted from the properties of the habitats in those two regions (Ellers and van Alphen, 1997). In this article we provide a similar but contrasting study, comparing two sister species taken from the same geographic location. Differences in allocation cannot then be due to geographical characteristics and instead represent different intrinsic properties of the species. We use these species to assess for the first time relative instantaneous investment in reproduction and survival as a likely function of parent–offspring conflict in parasitoids.

Our study species, the sister species *Aphaereta genevensis* and *Aphaereta pallipes* (Hymenoptera: Braconidae: Alysiinae) are close relatives of *A. tabida* and are extremely similar to each other: They can both use the same host species, are almost indistinguishable morphologically, and have similar developmental periods and trajectories. The species both use hosts (such as *Drosophila* spp.) which congregate on discrete, empheral patches such as rotten fruit. These patches represent not only a set of reproductive opportunities but the substrate also represents a potential source of food for adults. During dispersal females must in all likelihood survive periods without food and use energy in flight. *A. genevensis* larvae display siblicidal behavior and develop solitarily, whereas the larvae of *A. pallipes* are tolerant of each other and develop gregariously (Mayhew and van Alphen, 1999). Here we test the hypothesis that the two species also have contrasting strategies with respect to relative investment in survival and reproduction at adult eclosion that reflect the difference in the resolution of parent–offspring conflict. We predict that the solitary species invests relatively more resources to survival, as predicted by ecological theory (see Roff, 1992; Smith, 1991; Stearns, 1992; Young, 1990).

METHODS

Cultures

We used laboratory populations of *A. genevensis* and *A. pallipes* in this study. The cultures were collected in New York state, USA, during 1995 and 1996, in a region where the species are sympatric (see Mayhew and van Alphen, 1999). Since 1997, both species have been reared on *Drosophila virilis*. The hosts were reared in glass bottles on standard yeast-based medium. Wasps were reared in 5-cm diam glass jars with foam stoppers. A 2-cm layer of nutrient agar was poured into the base of a jar and allowed to set. Several 5- to 8-day-old *D. virilis* larvae were added along with a dab of viscous yeast medium. Groups of mated females (2–5 females) with no prior experience of hosts were introduced to the jars and left until death. We placed jars in secure plastic boxes to ensure that both species were kept separate within a single culturing room. The cultures were maintained at 20°C under constant light and ambient humidity. All experiments described in this study were also performed under these environmental conditions. All experiments and observations were performed simultaneously with respect to both species over the course of the year 2000.

Longevity experiments

To test our hypothesis of differential survival in these species, we observed female longevity in both species with and without food (representing survival in favorable and unfavorable conditions). Pupae containing developing wasps were gently washed out from culture jars with lukewarm water and placed into specimen tubes to ensure no feeding before experimental treatments. We checked these rearing tubes every 24 h for newly emerged females.

Upon emergence, females of both species were randomly assigned to one of two treatments: with food or without food. Females were individually placed into 75 × 25 mm specimen tubes. Tubes in the feeding treatment contained a cotton-wool ball moistened with a 35% sucrose solution. Tubes in the control (nonfeeding) treatment contained a cotton-wool ball moistened with distilled water. We checked tubes every 24 h and recorded longevity for each female. The food or water resources were refreshed every 1–2 days, as needed, to ensure a constant supply of sugar solution or water. Upon death, we recorded hind tibia length. Specimens were then dried continuously at 70°C for 4 days and weighed.

Fat reserves upon emergence

We investigated the likely mechanistic basis for any differences in longevity between the species by quantifying investment in survival as measured by fat reserves upon eclosion. Pupae containing developing wasps were placed into rearing tubes as in the longevity experiment, except that a cotton-wool ball moistened with 35% sucrose solution was placed in the rearing tube to ensure no decrease in fat reserves due to starvation. Previous work in the closely related species *A. tabida* has shown that feeding on sugar does not increase fat reserves but can significantly slow their rate of decrease (Ellers, 1996). We checked the tubes every hour during the working day and immediately upon the start of the next working day. This ensured that the oldest wasps were at most only 12 h old. Females were killed upon emergence by placement in a freezer at −20°C. We measured hind tibia length after death had occurred.

We measured fat content using ether extraction. Specimens were dried at 70°C for 4 days and then weighed. Whole females were placed into sealed vials with 3 ml of diethyl ether [$(C_2H_5)_2O$, water content $< 0.001\%$] and left in a fume cupboard. After 24 h the ether was removed and replaced with 3 ml of fresh ether. This was repeated for 3 days, after which specimens were dried again for 4 days at 70°C and weighed. We calculated the size of the fat reserves by subtracting the dry weight after ether extraction from the dry weight before ether extraction.

Egg number and size upon emergence

Pupae were placed into rearing tubes as above and killed in the same manner upon emergence. After hind tibia length had been recorded, we carefully dissected the eggs out from females placed into a drop of Ringer's solution on a glass slide under a light microscope. A coverslip was placed over the droplet, and eggs were then counted using a compound microscope (480× magnification). We measured the maximum length and width of the first five individual eggs found using an eyepiece graticule. Because egg width showed little observable variation (the eggs are elongated), we used the mean egg length as a measure of egg size.

Statistical analysis

We analyzed the longevity results by fitting a Weibull distribution to the data in the GLIM statistical package. The Weibull distribution is two-parameter model with the exponential as a special case. The two parameters are α and λ, the shape of the hazard function and the rate parameter, respectively. If $\alpha = 1$ (the exponential distribution), then the hazard (risk of death) is constant. If $\alpha > 1$, the hazard increases with age, and for $\alpha < 1$ the hazard declines with age. The rate parameter is a linear combination of explanatory variables (Crawley, 1993). In the case of a Weibull distribution, a chi-square approximation is used to assess whether the removal of variables from the model significantly increases the deviance. We analyzed the fat reserve data and the egg load/egg size data using standard techniques within SPSS.

RESULTS

Longevity

Average (± SE) female life span from eclosion in *A. genevensis* was 16.94 ± 1.12 days ($n = 36$) with food and 12.5 ± 0.88 days ($n = 36$) without food. In *A. pallipes* average female life span from eclosion was 16.64 ± 1.06 days ($n = 33$) with food and 5.8 ± 0.43 days ($n = 40$) without food. In addition, dry weight upon death was reduced in both feeding treatments compared to the dry weights of newly emergent females (ANOVA; *A. genevensis,* $F_{2,103} = 49.54$, $p < .001$; *A. pallipes,* $F_{2,107} = 34.03$, $p < .001$). Post-host tests (Student-Newman-Keuls) indicated that dry weight in all three groups (feeding, nonfeeding, and newly emerged females) were significantly different from each other within both species ($p < 0.05$ in all comparisons), a trend consistent with previous findings in *Asobara tabida* that feeding reduced the rate of fat loss (Ellers, 1996). This is a problem because it means that dry weight upon death does not accurately reflect size at emergence, which is the most objective way to estimate total resources available to wasps that have just completed development. Regressions were therefore performed to calculate what the dry weights of females of both species in the longevity treatments would have been if those individuals had been newly emergent (*A. genevensis*: dry weight [mg] = 0.853 × hind tibia [mm] − 0.445, $R^2 = .77$; *A. pallipes*: dry weight [mg] = 0.563 × hind tibia [mm] − 0.258, $R^2 = .86$). These calculated dry weight measurements ("size" in the GLIM analysis) allowed for genuine comparisons of the influence of dry weight on longevity.

Using the Weibull distribution was justified in all the models because it significantly improved each of the model's explanatory power. The shape parameter was > 1 for all models, indicating that the risk of death increased over time (Figure 1). Fed wasps lived significantly longer than unfed wasps in both species (*A. genevensis,* $\chi^2_1 = 10.63$, $p < .01$; *A. pallipes,* $\chi^2_1 = 69.38$, $p < .001$). Size also significantly increased longevity in both species (Figure 2; *A. genevensis,* $\chi^2_1 = 38.6$, $p < .001$; *A. pallipes,* $\chi^2_1 = 8.91$, $p < .005$). In the no-food treatment, there was a significant interaction between species and size, indicating that longevity (under unfavorable conditions) in the two species responded differently to increases in size, with *A. genevensis* living longer than *A. pallipes* of the same size (Figure 2; $\chi^2_1 = 6.92$, $p < .01$).

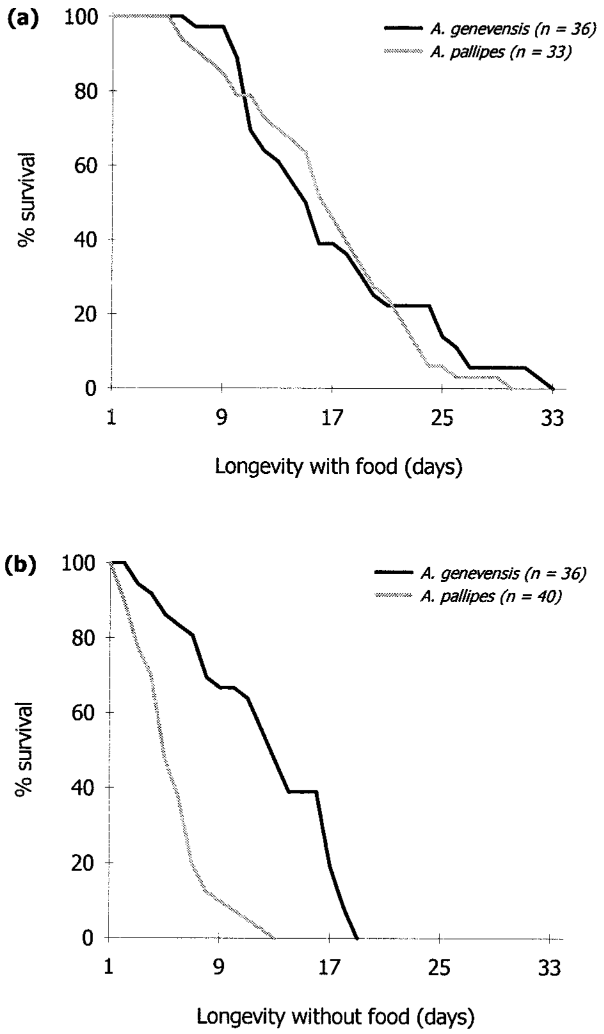

Figure 1
Survival over time of female *A. genevensis* and *A. pallipes* (a) with food (35% sucrose solution), (b) without food (water only).

Fat reserves upon emergence

Fat reserves increased with total dry weight upon emergence ($F_{1,68} = 635.77$, $p < .001$), and there was a significant interaction between dry weight and species, with *A. genevensis* having more fat for a given body size than *A. pallipes.* The difference increased at larger body sizes (Figure 3; $F_{1,68} = 48.23$, $p < .001$).

Egg number and egg size upon emergence

Egg number (upon eclosion) increased with size ($F_{1,56} = 107.86$, $p < .001$), and there was a significant interaction between size and species, indicating that the rate of increase in egg number (upon eclosion) with size differed between species, with *A. pallipes* having more eggs than *A. genevensis* of the same size, the difference being greatest at large body sizes (Figure 4; $F_{1,56} = 71.31$, $p < .001$). Egg size increased with body size ($F_{1,56} = 84.11$, $p < .001$), but there was no significant effect of species on egg size and no significant interaction of body size and species ($F_{1,56} = 2.98$, 1.68, respectively). Egg size was positively associated with egg number across all individuals ($F_{1,56} = 13.12$, $p < .01$). There was no evidence for a negative egg size/egg number trade-off in either species.

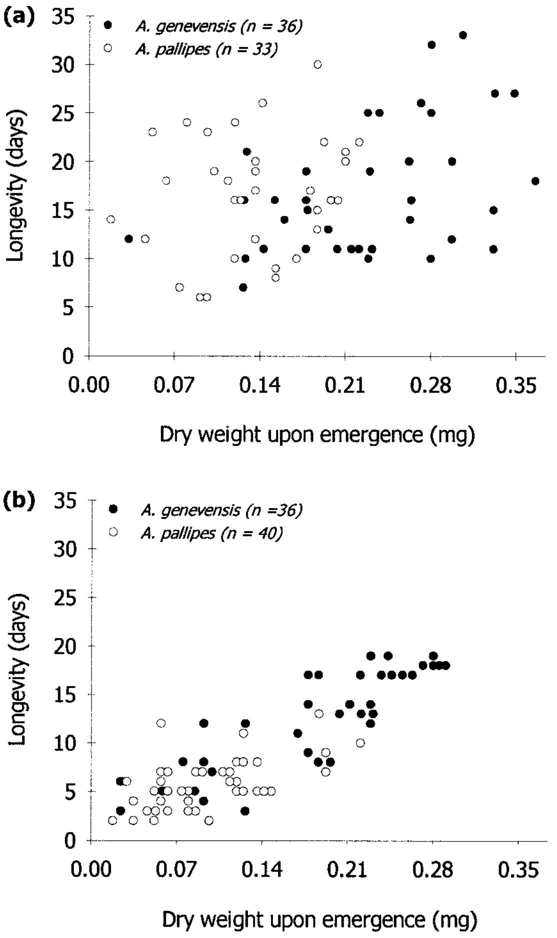

Figure 2

Longevity and dry weight upon emergence in female *A. genevensis* and *A. pallipes* (a) with food (35% sucrose solution), (b) without food (water only).

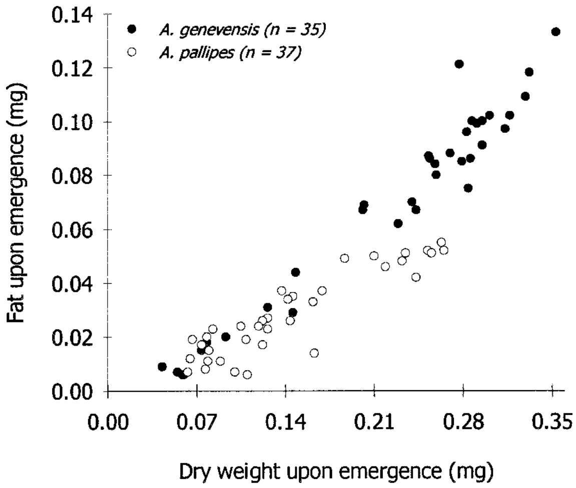

Figure 3

Fat reserves upon emergence in female *A. genevensis* and *A. pallipes*.

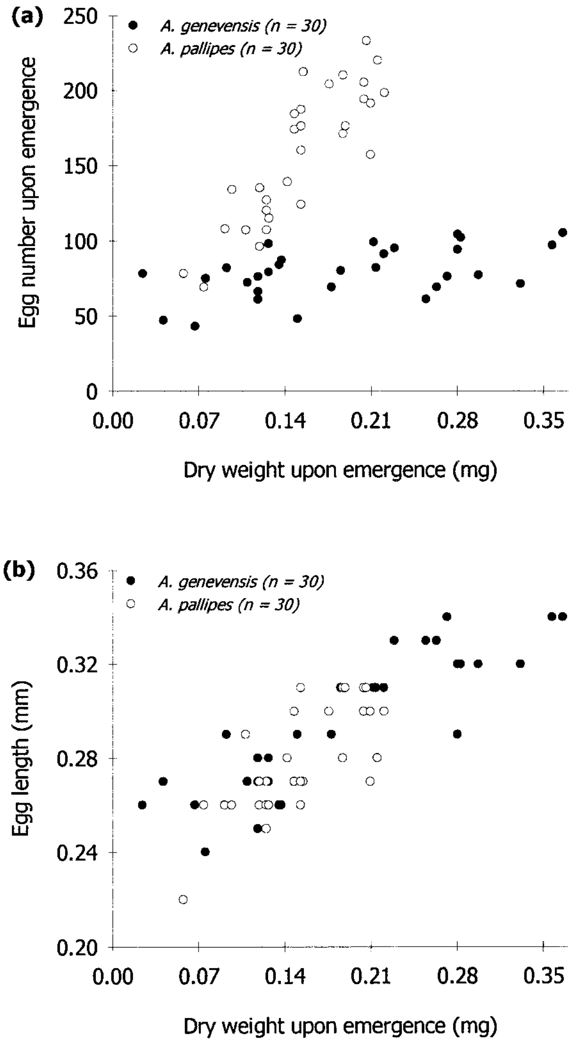

Figure 4

(a) Egg number upon emergence in female *A. genevensis* and *A. pallipes* and (b) egg size upon emergence in female *A. genevensis* and *A. pallipes*.

DISCUSSION

The primary finding of this study is that female *A. genevensis* and *A. pallipes* exhibit contrasting investment patterns in survival and reproduction at adult eclosion, as would be expected from life-history theory. Small-bodied individuals of both species display similar allocation. With increasing body size, the solitary *A. genevensis* invests relatively more in fat and relatively less in eggs than the gregarious *A. pallipes*. Upon emergence *A. pallipes* has consistently more eggs and has much less fat than *A. genevensis*. These differences in fat are reflected in differences in longevity; in the absence of food *A. pallipes* live for only a few days, whereas *A. genevensis* live for a much longer period. Thus, *A. genevensis* invests considerably more resources at eclosion in survival relative to reproduction compared to its sister species *A. pallipes,* as predicted by theory.

In this study, we used a pair of sister species to test the prediction that solitary species should allocate more resources to survival than gregarious species. Our data are consistent with this hypothesis and contribute to previous comparative evidence in bruchid beetles (Smith, 1991), demonstrating that sibling rivalry and lethal fighting between developing larvae are associated with increased allocation to survival. In comparative terms, our data represent a single independent contrast (Harvey and Pagel, 1991) and cannot alone confirm or reject the hypothesis, but together with other studies on similar systems will eventually make possible a broader test. Thus, our study should be viewed as one step toward this long-term strategic goal. As with most comparative studies, we can say nothing firm about the actual causes of the differences we observe in a single comparison. However, we speculate below on exactly which intrinsic properties may have been influential.

Causes of differences in investment

In previous work on bruchid beetles, differences in allocation between populations were attributed to differences in juvenile mortality caused by different types of larval competition (Smith, 1991). In the present study, differences in juvenile mortality may also play a direct role, but we urge caution. One reason for caution is that the extent of juvenile mortality is also determined by clutch size. In solitary species, small clutches are generally laid that minimize wastage of investment in offspring that inevitably fail to complete development (Mayhew and Glaizot, 2001; Skinner, 1985; Waage and Godfray, 1985). *A. genevensis* generally lays only one egg per clutch, and in fact only suffers higher juvenile mortality than *A. pallipes* when several females oviposit in the same host (superparasitism) or if a single female lays a multiple clutch (Mayhew and van Alphen, 1999). The extent of superparasitism in the field is currently unknown. It is at least possible that juvenile mortality does not directly contribute to the present observations. However, the reduction in clutch size seen in solitary parasitoids will be to a large extent a consequence of parent–offspring conflict; therefore the possibility of juvenile mortality indirectly influences the differences in allocation. We mention here two other possible differences between the species that might be responsible for the differences in allocation to reproduction and survival. These differences may have evolved in response to differences in larval behavior.

The first such factor is clutch size. The effect of clutch size on the degree of investment in reproduction and survival across parasitoid populations has not, to our knowledge, been investigated theoretically, but intuitively we would expect larger clutch sizes to result in reduced allocation to survival. Previous parasitoid investment theory has shown that increasing patch quality selects for reduced investment in survival (Ellers et al., 2000). Producing many offspring per host is equivalent, in some respects, to experiencing greater patch quality because more offspring can be produced within a patch. Hence, we expect increasing clutch size to lead to increased allocation to reproduction at the expense of survival.

The second possible factor may be the degree of host specialization. Allocation models in parasitoids have suggested that as host availability increases, species should invest more in reproduction and less in survival. Hence, our results might be explained if *A. pallipes* is more generalist and thus experiences an environment rich in reproductive opportunities. Anecdotal evidence suggests that this is indeed the case. Little is known about the range of host species of *A. genevensis*. However, 20 different species of North American Diptera have been recorded as being parasitized by *A. pallipes* (Whistlecraft et al., 1984), which for an alysiine is a relatively large range of host species (Wharton, 1984). Large numbers of host species may also be a general feature of gregarious alysiines (Shaw and Huddleston, 1991). Decreased oviposition specificity is also found in bruchid beetles with tolerant larvae (Smith, 1991).

The reasons for the apparent decrease in host specialization in gregarious species have not been addressed in earnest. We suggest two potential reasons for decrease in host specialization. First, systematically laying large clutches of eggs may make previously unsuitable hosts suitable, perhaps by overwhelming a host's immune response or allowing larger-bodied hosts to be fully consumed, examples of Allee effects. Effects of this type have been reported in parasitoids (Ode and Rosenheim, 1998; Streams, 1971). Second, reduced oviposition selectivity is predicted if expected life span is short (e.g., Fletcher et al., 1994; Mangel and Clark, 1988; Roitberg et al., 1992, 1993; Sirot et al., 1997). If true for this system, the degree of oviposition-site selectivity and investment in survival and reproduction may feed back positively on each other, enhancing the difference in allocation.

Conclusions

Finally, we consider briefly the wider implications of our data. The fact that *A. genevensis* invests relatively more in fat reserves (resulting in enhanced survival) suggests that it hardly ever runs out of eggs and hence that it is severely time limited. In contrast, *A. pallipes* invests in both time and eggs; hence, given extra life span, it is more likely to run out of eggs (egg limited). Though the idea requires more specific testing, we suggest that intraspecific allometric variation in investment strategy may indicate whether a species is relatively time or egg limited.

The present, although still somewhat limited, picture of insects with a parasitoid-like life history is one in which the degree of sibling rivalry is correlated with, and has likely affected, several other traits. Some of these traits are expected to feed back on each other, enhancing the observable variation. This raises the possibility that in other systems where siblicide has evolved, such as many birds, carnivores, and ovipositing invertebrates, siblicide may account for a large fraction of the variation in life-history parameters. Such systems would seem ripe for investigation of this type.

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