SEX ALLOCATION IN SOLITARY BEES AND WASPS

Fisher's (1958) famous sex-ratio theory suggests that natural selection favors equal investment in each sex. Because of Fisher's theory, authors typically assume that biased population allocation requires spatial subdivision, such as local mate competition, or unusual genetics, such as cytoplasmic inheritance. However, I have shown previously that a biased population-level sex allocation occurs if individuals adjust the sex ratio of their offspring in response to resource availability or environmental cues (Frank 1987, 1990).

Recently, Boomsma (1989) and Helms (1994) have found a positive relation between female:male (F/M) size ratios and F/M population allocation ratios in some hymenopteran groups. In this note I apply the theory I developed previously to explain the association between size and allocation ratios. Before presenting my theory I will discuss two alternative explanations. First, the association between size ratios and allocation ratios may be an artifact of measurement (Trivers and Hare 1976; Boomsma 1989). Second, the association may be real and caused by a positive association between the intensity of local mate competition and F/M size ratios. I discuss these explanations in turn.

Both size and allocation have been measured by dry weight. Adult weight appears to be an accelerating function of the resources that parents invest in offspring. Thus, weight ratios overestimate investment in the larger sex, which, in Hymenoptera, is usually the female. This measurement problem, if not corrected, can lead to a spurious positive relation between F/M size ratio and F/M allocation ratio.

Helms (1994) used data from solitary wasps to analyze the measurement problem. These data provide information on the actual amount of parental investment and the size of resulting offspring. Helms concluded that using adult weight as a measure of investment does lead to an overestimate of the F/M population allocation ratio. Helms corrected for this bias and still found a positive association between F/M size ratio and F/M allocation ratio, although the sample sizes were not sufficient to draw a strong conclusion.

Both Boomsma (1989) and Helms (1994) considered local mate competition as an explanation for female-biased allocation ratios (Hamilton 1967). Local mate competition is the most commonly discussed hypothesis to explain female-biased allocation, perhaps because few other alternatives are believed to be widely applicable. There is no evidence to support local mate competition as a general explanation for the association between size ratios and allocation ratios in Hymenoptera (Boomsma 1989; Helms 1994).

I develop a simple theory that predicts an increasing F/M allocation ratio with increasing F/M size ratio. This theory applies to all species that meet the follow-

ing conditions. First, the sex of offspring is controlled according to available resources. Second, the resources that can be used for one offspring are (mostly) unavailable for other offspring. Third, the relation between investment and fitness is not strongly accelerating. These assumptions match many parasitoids very closely and probably apply to many solitary bees and wasps. I will consider these assumptions more carefully later.

THE MODEL

My derivation follows closely the approach in a previous article (Frank 1987, sec. 3). Let x be the amount of resource available to invest in a particular offspring. The probability distribution for x is $h(x)$. The relation between investment in males and male fitness follows the curve $f(x)$. The relation between investment in females and female fitness follows the curve $g(x)$.

I assume that female offspring are favored when resources are relatively abundant (high x) and male offspring are favored when resources are relatively scarce. This pattern is commonly observed in solitary Hymenoptera (Charnov 1982) and is explained by the Trivers-Willard theory (Trivers and Willard 1973) for conditional adjustment of sex ratio in response to parental resources. At equilibrium there is a value $\lambda = x$ where the switch from males to females occurs. This switch point is obtained by solving (Frank 1987)

$$\frac{f(\lambda)}{\int_0^\lambda f(y)h(y)dy} = \frac{g(\lambda)}{\int_\lambda^1 g(y)h(y)dy} .$$

This equation is based on the requirement that, at equilibrium, the value of a male at the switch, $f(\lambda)$, divided by the average value of all males in the population, must equal the value of a female at the switch, $g(\lambda)$, divided by the average value of all females in the population. The equation holds for any functional forms of $h(x)$, $f(x)$, and $g(x)$ whenever, at equilibrium, males are made below λ and females are made above λ.

To solve this equation specific assumptions are needed for $h(x)$, $f(x)$, and $g(x)$. I assume that the probability distribution for x is proportional to $h(x) = x^{a-1}(1 - x)^{a-1}$, where x varies between zero and one. The parameter a controls the shape of the distribution (see fig. 1). I chose this distribution because it has a variety of shapes to describe resource distribution and, because x is bounded between zero and one, the distribution is analytically compatible with allocation expressed as a fraction of the total resources devoted to a particular sex.

I assume that the relation between investment in males and male fitness follows the curve $f(x) = x^r$ and the relation for females follows the curve $g(x) = x^s$. The values of r and s determine the rate of returns for additional allocation to males and females, respectively. Some examples of how r controls the shape of the male return curve are shown in figure 2.

The equilibrium equation can be solved numerically for λ when given values for the three parameters, r, s, and a. For simplicity, I set $s = 1$, implying linear returns on female investment. My analyses suggest that it is the difference be-
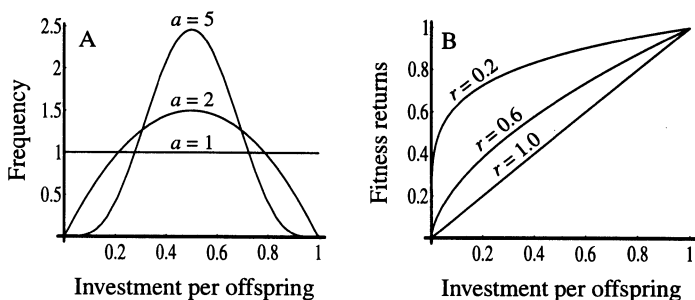
Fig. 1.—A, The distribution of resources available for investment in offspring. The curves show the beta distribution, $\{[\Gamma(a + b)]/[\Gamma(a)\Gamma(b)]\}x^{a-1}(1 - x)^{b-1}$, where $\Gamma(\ )$ is the gamma function and I have assumed that $a = b$. B, The shape of the relation between investment and fitness, where $f(x) = x^r$.
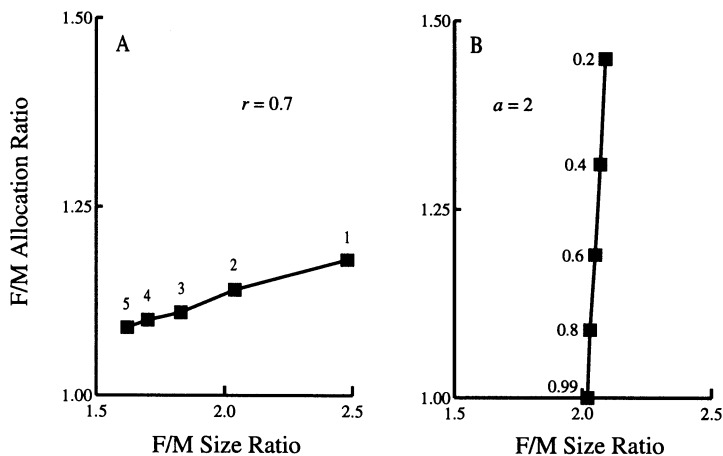

Fig. 2.—Predicted size ratio versus allocation ratio. A, Changes with different distributions of resources as the parameter a varies (see fig. 1A). The numbers above each point show different values of a. Returns are linear for females, $s = 1$, and diminishing for males with $r = 0.7$. B, Changes with different rates of diminishing returns for male investment. The numbers next to each point show different values of r (see fig. 1B). Returns are linear for females, $s = 1$, and the distribution of resources is constant with $a = 2$.

tween r and s that controls the patterns I describe below, subject to the constraint that $r < 1$ and that $r < s < C$, where C varies between one and approximately two depending on the value of r. For each value of r, the value of C can be determined by numerical analysis. The particular values of C are not important because s is unlikely to be greater than one, that is, returns on female investment are unlikely to be rapidly accelerating. The assumption that $r < s$ causes males to be favored when offspring will be small and females to be favored when offspring will be large.

I assume that the relation between investment and body size is x^k for both males and females. If $k = 1$, then investment and size are equivalent. Size dimor-

phisms become increasingly exaggerated as k increases from one, but k has no effect on the allocation ratio. Thus any trend between the F/M size ratio and the F/M allocation ratio can be seen clearly with $k = 1$. I present the following definitions with k present but assume that $k = 1$ in all numerical analyses.

With the definition

$$H(a, k, z) = \int_0^z y^k h(y)dy = \int_0^z y^k y^{a-1}(1 - y)^{a-1}dy ,$$

we can write the definitions for average size:

Female size = $[H(a, k, 1) - H(a, k, \lambda)]/[H(a, 0, 1) - H(a, 0, \lambda)]$
Male size = $H(a, k, \lambda)/H(a, 0, \lambda)$,

where the numerators are proportional to the total size of individuals and the denominators are proportional to the total number of individuals. Similarly, for allocation,

Female allocation = $[H(a, 1, 1) - H(a, 1, \lambda)]/H(a, 1, 1)$
Male allocation = $H(a,1,\lambda)/H(a, 1, 1)$.

Numerical analyses demonstrate the positive relation between size and allocation ratios. There are two parameters: a controls the shape of the distribution of resources (fig. 1A), and r controls the shape of returns on male investment (fig. 1B). I have assumed the returns on female investment are linear, $s = 1$, as is the relation between investment and size, $k = 1$.

Figure 2A shows that the distribution of resources, controlled by a, determines size ratios. As the variation in resources rises (decreasing a), the size ratio increases rapidly. The variation in the resource distribution has relatively little effect on the allocation ratio. Figure 2B shows that the relation between returns and investment, controlled by r, determines allocation ratios. As returns on male investment diminish more rapidly (smaller r), the allocation ratio becomes increasingly female biased. The rate of returns on investment has relatively little effect on size ratios. Changes in either the resource distribution or the rate of returns on investment cause a positive association between size ratios and allocation ratios.

I provide a brief intuitive explanation for the positive association between size and allocation ratios when there are changes in the rates of returns, $f(x)$ and $g(x)$, and a fixed resource distribution, $h(x)$. I then turn to the biological significance of the models.

Figure 2B shows that small increases in the F/M size ratio are associated with large increases in the F/M allocation ratio when the resource distribution is held constant. This pattern is explained in figure 3 for arbitrary functional forms of $h(x)$, $f(x)$, and $g(x)$. Initially, mothers produce a son whenever the resources available are less than λ and a daughter when resources are greater than λ. The total allocation to males is the proportion of the area under the resource curve below the point λ, weighted by resource level—that is, $\int_0^\lambda yh(y)dy/\int_0^1 yh(y)dy$. Total allocation to females is the proportion of the area under the resource curve above the point λ, weighted by resource level, $\int_\lambda^1 yh(y)dy/\int_0^1 yh(y)dy$. If sizes of
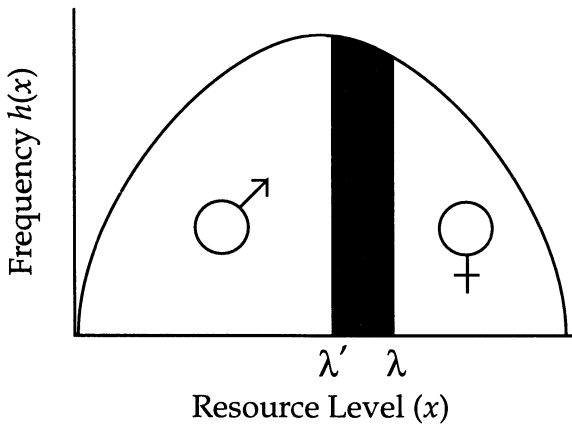
FIG. 3.—Change in switch point, λ, causes change in F/M allocation ratio and F/M size ratio.

offspring are proportional to resources available, then average male size is the average of the resources allocated to males, $\int_0^\lambda yh(y)dy/\int_0^\lambda h(y)dy$. Similarly, average female size is the average of the resources allocated to females, $\int_\lambda^1 yh(y)dy/\int_\lambda^1 h(y)dy$.

When the resource distribution $h(x)$ is fixed, an increase in female allocation occurs when smaller individuals are made into females, that is, the switch point λ is lowered to a new value λ'. The switch point changes for fixed resource distribution whenever there is a change in the male or female return curves, $f(x)$ or $g(x)$. The particular changes in these return curves are not important for understanding the qualitative pattern of association between size ratios and allocations ratios.

After a change in λ to λ', shown in figure 3, female allocation is the weighted area under the upper region of the curve, from λ to 1, plus the shaded region between λ' and λ. Male allocation is now the weighted area between 0 and λ', males having lost the resources between λ' and λ. The F/M allocation ratio increases rapidly as the size of the shaded region between λ' and λ increases.

The change from λ to λ' also affects the F/M size ratio. Females have added a relatively smaller class of individuals (*shaded region*) to their distribution, and males have lost a relatively larger class of individuals from their distribution. This difference in relative size occurs because females are larger than males, so the middle-sized individuals in the shaded region are either small females or large males.

The addition of relatively small females reduces the average size of females; the loss of relatively large males reduces the average size of males. The proportional reduction in male size is usually greater than the reduction in female size, since adding a relatively small size class typically has less effect on average size than losing a relatively large size class. A numerical example is shown in figure 4. In that figure there are five discrete patch types, each with resource level of 1, 2, 3,

Resource Level:	1	2	λ' 3	λ 4	5			

		M	F	F/M
Switch at λ { Allocation	0.4	0.6	1.50
Size	2	4.5	2.25
Switch at λ' { Allocation	0.2	0.8	4.00
Size	1.5	4	2.67

FIG. 4.—Numerical example illustrating the positive association between F/M size ratio and F/M allocation ratio when the resource distribution is held constant and the switch point λ changes.

4, or 5. The five patch types are equally frequent; that is, $h(x)$ is a discrete, uniform distribution.

Initially, the switch point λ is between 3 and 4, so that males are produced on patches with resource level 1, 2, or 3 and females are produced on patches with resource level 4 or 5. The proportions of resources allocated to males and females are 0.4 and 0.6, respectively, and sizes of males and females are 2 and 4.5, respectively. Now suppose that, because of changes in the return curves $f(x)$ or $g(x)$, the switch point changes to λ' between resource levels 2 and 3. The new allocations and sizes are shown in the bottom two rows. The F/M allocation ratio has jumped from 1.5 to 4, whereas the F/M size ratio has increased a relatively small amount from 2.25 to 2.67. This shows that a reduction in λ tends to cause a relatively rapid increase in F/M allocation ratios and a relatively slow increase in F/M size ratios.

A similar style of argument can be used to show why F/M size ratios change rapidly and F/M allocation ratios change slowly for changes in the resource distribution, $h(x)$, and fixed return curves, $f(x)$ and $g(x)$. The essential point is that the relative marginal returns on male and female investment are controlled mainly by the shapes of $f(x)$ and $g(x)$; thus, these curves strongly influence allocation ratios. By contrast, the resource distribution strongly influences the F/M size ratio by determining whether a fixed allocation is made to many relatively small individuals of a sex or to a few relatively large individuals of that sex.

DISCUSSION

There are three important assumptions that determine the species to which this model applies. First, the sex of offspring is adjusted according to available resources. This occurs when there is environmental sex determination (Bull 1983) or when parents control the sex of offspring according to available resources (Trivers and Willard 1973; Charnov et al. 1981). There is considerable evidence that parasitoids and solitary bees and wasps choose offspring sex according to the size of the host or the abundance of food for the offspring (Charnov 1982).

Second, the resources that can be used for one offspring are (mostly) unavailable for other offspring. The particular models here assumed that resources available must be used for the next offspring produced and cannot be saved for future offspring. That assumption is true for parasitoids that lay one offspring on each host. Solitary bees and wasps that mass provision often find or build a cell that will contain one offspring, add food, and then lay one egg. That cell cannot be used for another offspring. In many cases the size of the cell determines the size of the offspring, presumably because more food is provisioned into larger cells (Krombein 1967). In other cases it appears that the time and food used for one offspring could be used for other offspring. However, various constraints may prevent the parent from freely allocating resources among a set of offspring (Frank and Crespi 1989). The theory presented here could be extended to cases in which resources may be allocated among different offspring (Frank 1987).

Third, the relation between fitness and investment is not strongly accelerating. The sex allocation patterns depend on the shapes of the curves that relate investment to fitness for males and females (Frank 1987). The fact that, in most bees and wasps, small individuals are males and large individuals are females suggests that fitness increases more rapidly with size for females than for males (Charnov et al. 1981). In most species direct male-male competition is rare; thus, it is likely that male mating success increases at a diminishing rate with size (fig. 1A). Female fecundity probably does increase with size for many species, but the relation between parental investment and the fitness of female offspring is not known. It seems unlikely that female fitness increases at a strongly accelerating rate with size (see Frank 1987 for an analysis with an accelerating female fitness function).

Fisherian equal allocation is almost universally assumed as the default prediction for natural populations. Thus, when a population-level bias is observed, most authors are compelled to invoke competition among relatives or genetic asymmetries. However, a proper economic analysis of investment and return, in the spirit of Fisher's (1958) original theory, shows that selection acting on individual sex ratios often causes biases at the population level (Frank 1987, 1990).

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