SEXUAL SIZE DIMORPHISM AND SEX RATIOS IN BEES AND WASPS

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Abstract.—When parental investment is estimated from the body weight of offspring, the sex investment ratio increases with increasing sexual size dimorphism across species of bees and wasps. This relationship was recently found in ants and was hypothesized to be artifactual and occur because body weight overestimates parental investment in the larger sex (females) proportional to the degree they are larger than the smaller sex (males). Analyses using an apparently unbiased alternative to body weight in estimating parental investment in solitary wasps support this hypothesis. The analyses also show, however, that increase in the sex investment ratio with increasing sexual size dimorphism may not be entirely artifactual. In solitary wasps, it is hypothesized that actual covariance between sexual size dimorphism and the sex investment ratio will occur if mothers produce small males when those males compete primarily with brothers for access to mates.

Estimates of parental investment in the sexes in aculeate Hymenoptera (ants, bees, and wasps) have provided important support for theories on sex ratio evolution. Aculeates provide all resources required to produce adult offspring, and theory predicts natural selection acts on the offspring sex ratio according to parental resources invested (Fisher 1930). For example, if individual females require twice the amount of parental resources to produce as individual males and equal investment in the sexes is expected, male offspring should be twice as numerous as female offspring within a population (Fisher 1930; Charnov 1982). Study of aculeates has supported this general prediction (Trivers and Hare 1976; Torchio and Tepedino 1980; Charnov 1982; Tepedino and Torchio 1982; Frohlich and Tepedino 1986).

In nature, aculeate populations may commonly produce unequal offspring sex investment ratios. Male-biased sex investment ratios have been hypothesized to result from local resource competition (Clark 1978), and female-biased sex investment ratios have been hypothesized to result from local resource enhancement (Schwarz 1988), local mate competition, and/or inbreeding (Hamilton 1967; Alexander and Sherman 1977; Cowan 1981; Pamilo and Rosengren 1983; Herre 1985; Schwarz 1988; Danforth 1990; Cowan 1991).

In addition, eusocial aculeates may invest in the sexes according to relatedness asymmetries within colonies that result from haplodiploid sex determination (Trivers and Hare 1976). In colonies with a single, outbred queen mated with a single male, sterile workers are three times more closely related to females than

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males and would optimize fitness by investing three times as much in reproductive females as males. The queen is equally related to male and female offspring and would optimize fitness with equal investment in the reproductive sexes (Trivers and Hare 1976; Craig 1980; Pamilo 1982). Many authors have suggested that workers control investment at the expense of the queen (e.g., Trivers and Hare [1976]; Ward [1983]; Nonacs [1986]; Suzuki [1986]; Van der Have et al. [1988]; Boomsma [1989]; Boomsma and Grafen [1990]).

The strength of aculeate tests of sex ratio theory may often depend on how well they estimate any difference in the amount of parental resources invested in female and male offspring. Trivers and Hare (1976) proposed that differences in investment can sometimes be measured in the amount of food the sexes receive. They and other researchers also recognized that the amount of food provided could underestimate or overestimate parental investment in either sex (Hölldobler and Bartz 1985; Boomsma 1989; Brockmann and Grafen 1989; Danforth 1990). At present, no evidence is available indicating whether such error is substantial across the majority of aculeate taxa, but it would likely be substantial in those social species in which workers adopt newly mated sisters (Trivers and Hare 1976) or when colonies reproduce by budding (Macevicz 1979; Pamilo 1991).

Data on the amount of food provided for the sexes are rare in aculeates, and Trivers and Hare (1976) proposed offspring weight as a readily measured estimate of the amount of food provided. In the majority of their analyses, investment in females was estimated as the total weight of reproductive female offspring produced and investment in males as the total weight of male offspring produced (Trivers and Hare 1976). Trivers and Hare (1976) also outlined how weight of the sexes may generally overestimate the amount of food provided for reproductive females. While acknowledging this problem (and others) in estimating parental investment, authors of most subsequent studies have used weight of the sexes as a measurement of their cost in estimating aculeate sex investment ratios (e.g., Noonan [1978]; Owen et al. [1980]; Torchio and Tepedino [1980]; Pamilo and Rosengren [1983]; Nonacs [1986]; Suzuki [1986]; Ross and Matthews [1989]).

In an analysis of ants, Boomsma (1989) questioned whether using weight of the sexes to estimate parental investment will result in even approximately valid sex investment ratios when sexual size dimorphism is substantial. Like Trivers and Hare (1976), Boomsma (1989) hypothesized that the amount of food provided for reproductive females is often overestimated in ants but also that overestimation increases with increasing female divided by male (i.e., F/M) body size (i.e., F/M weight ratio). Support for Boomsma's (1989) hypothesis comes largely from a relationship between the degree of sexual size dimorphism and the sex investment ratio. As estimated by weight of the sexes produced, the F/M sex investment ratio increases with increasing F/M weight ratio across ant species (Boomsma 1989). Based on energetics studies, Boomsma (1989) proposed that the relationship results from decreasing energetic cost of respiration per unit body weight with increasing body size, a phenomenon perhaps amplified by accumulation of nonmetabolizing fat reserves in females. If so, weight of the sexes would increasingly overestimate the amount of food required to produce the larger sex (females) with increasing sexual size dimorphism. The F/M sex investment ratio would

only appear to increase with increasing F/M sexual size dimorphism (Boomsma 1989).

Boomsma (1989) also discussed whether the F/M sex investment ratio might actually increase with increasing sexual size dimorphism. If so, increasing F/M size should be associated with increased importance of phenomena hypothesized to result in the evolution of increased F/M sex investment ratios. In ants, increasing F/M size could be associated with either (or some combination of) increased local mate competition (Hamilton 1967), increased worker control over investment, decreased polyandry, decreased polygyny, or decreased worker reproduction (Boomsma 1989). No such associations were apparent, although the available information was limited (Boomsma 1989).

The relationship between the sex investment ratio estimated by weight and sexual size dimorphism found by Boomsma (1989) has not been examined for any other group of organisms. This article shows that the relationship is common and substantial within bees and wasps, even though sexual size dimorphism is slight when compared to ants. Indirect information on food provided for the sexes is available for a group of solitary wasps. These data are used to test whether covariance between the sex investment ratio and sexual size dimorphism is artifactual and results in important error and, alternatively, whether the relationship demonstrates a true phenomenon.

METHODS

I will use *female* to refer only to reproductive female offspring (i.e., gynes, virgin queens); all males are reproductive. I obtained or derived F/M weight ratios (W), F/M numerical sex ratios (S), F/M brood cell volume ratios (CV), and F/M provision amount ratios (PR) from published studies. Since data came from a number of independent sources, and in many cases I present them differently than they were by the original authors, data and references are listed in Appendixes A and B. The F/M weight ratio (W) is estimated by $W = W_F \div W_M$, where W_F is the mean weight of females measured and W_M is the mean weight of males measured. Female and male weights were most often given by authors as wet (or live) weight in studies of social wasps and as dry weight for other aculeate groups. Exceptions are noted in the appendixes. The F/M numerical sex ratio (S) is estimated by $S = N_F \div N_M$, where N_F is the number of female offspring censused and N_M is the number of male offspring censused.

As discussed previously, the sex investment ratio is often estimated from the total weight of female and male offspring produced. I refer to the sex investment ratio derived by this method as the F/M sex investment ratio estimated by weight (I_W), which is estimated by $I_W = W \cdot S$. The F/M cell volume ratio (CV) in trap-nesting solitary wasps is estimated by $CV = CV_F \div CV_M$, where CV_F is the mean cell volume of female brood cells measured, and CV_M is the mean cell volume of male brood cells measured (Trivers and Hare 1976). All measurements of CV were taken directly from table 5 in Trivers and Hare (1976). The brood cells of trap-nesting wasps may often be stuffed full of prey (Trivers and Hare 1976); the F/M sex investment ratio was also estimated by cell volume (I_{CV}),

where $I_{CV} = CV \cdot S$. The F/M provision amount ratio (PR) is estimated by $PR = PR_F \div PR_M$, where PR_F is the mean amount of food provisioned in female brood cells and PR_M is the mean amount of food provisioned in male brood cells (Trivers and Hare 1976).

Sex ratios in trap-nesting solitary aculeates can be artificially biased if the range and frequency of cavity sizes available in trap nests do not match those used by the species in nature (Krombein 1967; Charnov et al. 1981; Cowan 1981). Solitary aculeates collected from trap nests were analyzed separately from those from natural nests unless evidence from the authors suggested trap-nest cavities presented would result in valid sex ratios for the population studied. Those cases are noted in Appendix A. Potential biases in trap-nest data are addressed in greater detail in following sections of this article.

Distributions of many dependent variables in my regression analyses (I_W, I_{CV}, S, CV) were skewed to the left and were almost significantly nonnormal (Kolmogorov-Smirnov goodness-of-fit test, $P < 0.10$). To correct for this, all dependent variables were natural-log transformed (following Boomsma 1989), which resulted in distributions that were not significantly different from normal ($P > 0.35$ in all cases). Independent variables were also natural-log transformed to result in one-to-one correspondence with values of the dependent variables.

A common problem in regression analysis is that values of independent variables are often measured and subject to some inherent error (Chatterjee and Price 1991). If measurement errors are independent among values of an independent variable, tests of the hypothesis that a linear regression slope is equal to zero remain valid, although the slope will be biased toward zero (Fuller 1987). In a regression analysis of sexual size dimorphism and sex ratios in ants, measurement errors were found to have a minor effect (Boomsma 1989). However, information is not available to evaluate the effect of measurement errors in the analyses presented on bees and wasps. As a result, the magnitude of functional relationships between variables revealed by regression slopes should be treated as approximations and subject to some measurement error.

RESULTS AND DISCUSSION

Sexual Size Dimorphism and the Sex Ratio

As was found in ants (Boomsma 1989), the F/M sex investment ratio estimated by weight (I_W) increases with increasing F/M weight ratio (W) in bees and wasps. Regressions of I_W on W result in slopes significantly greater than zero in analyses of social wasps, solitary bees from natural nests, and solitary wasps from both natural and trap nests. The slope of the regression was marginally significant in bumblebees ($.05 < P < .10$) and not significant in solitary bees from trap nests (fig. 1). However, estimates of I_W are not independent of W ($I_W = W \cdot S$). Lack of independence between variables is corrected by regressing the F/M numerical sex ratio (S) on W. If there is either increasing error in estimating the amount of food provided for the sexes with increasing W or actual increase in the F/M sex investment ratio with increase in W, slopes of the regressions should be greater than -1 (Boomsma 1989). Consistent with this prediction, regression slopes are
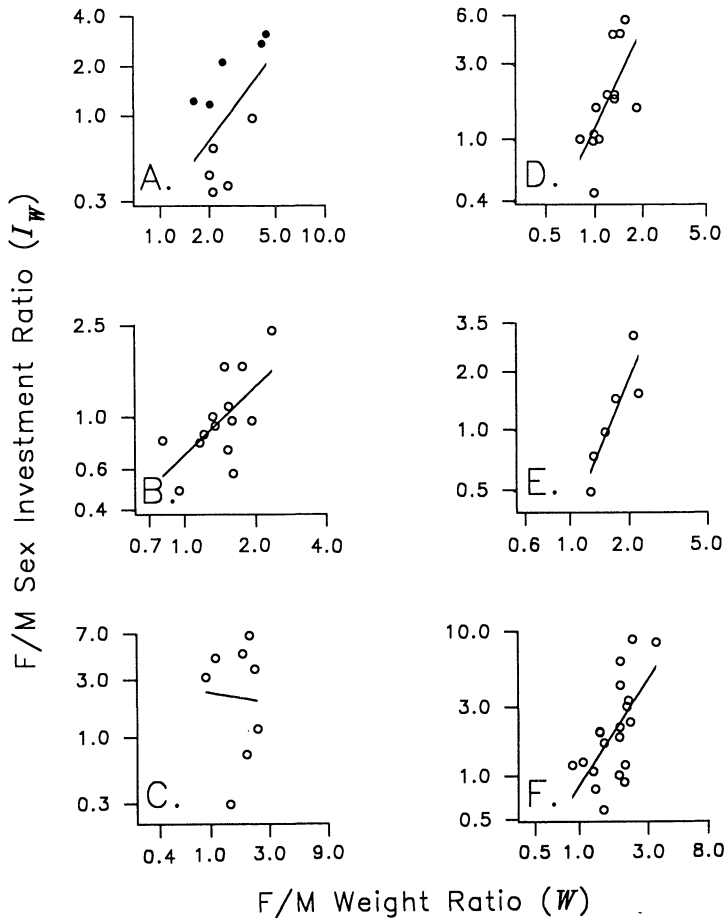
FIG. 1.—The F/M sex investment ratio estimated by weight (I_W) as a function of F/M weight ratio (W) for social and solitary bees and wasps. A, Bumblebees (data for *solid circles* from study in Webb 1961 that may have overestimated investment in females due to sampling procedure [Owen et al. 1980]; data for *open circles* from more recent studies): b = 1.346, r^2 = 0.321, P < .10. B, Solitary bees from natural nests: b = 0.956, r^2 = 0.396, P < .02. C, Solitary bees from trap nests: b = −0.186, r^2 = 0.003, P > .80. D, Social wasps: b = 2.128, r^2 = 0.443, P < .02. E, Solitary wasps from natural nests: b = 1.973, r^2 = 0.763, P < .05. F, Solitary wasps from trap nests: b = 1.550, r^2 = 0.398, P < .005. Probability values (P) are from tests of the hypothesis that β = 0.

significantly greater than −1 in social wasps, solitary bees from natural nests, and solitary wasps from both natural and trap nests. The slope of the regression was marginally greater than −1 for bumblebees (.05 < P < .10) and not significantly different than −1 for solitary bees from trap nests (fig. 2).

Systematic Error or Actual Relationship? A Test with Trap-nesting Solitary Wasps

Trap-nesting solitary wasps are those wasps that normally nest in hollow twigs or vacant insect borings. They will also nest in holes bored in wood (trap nests)
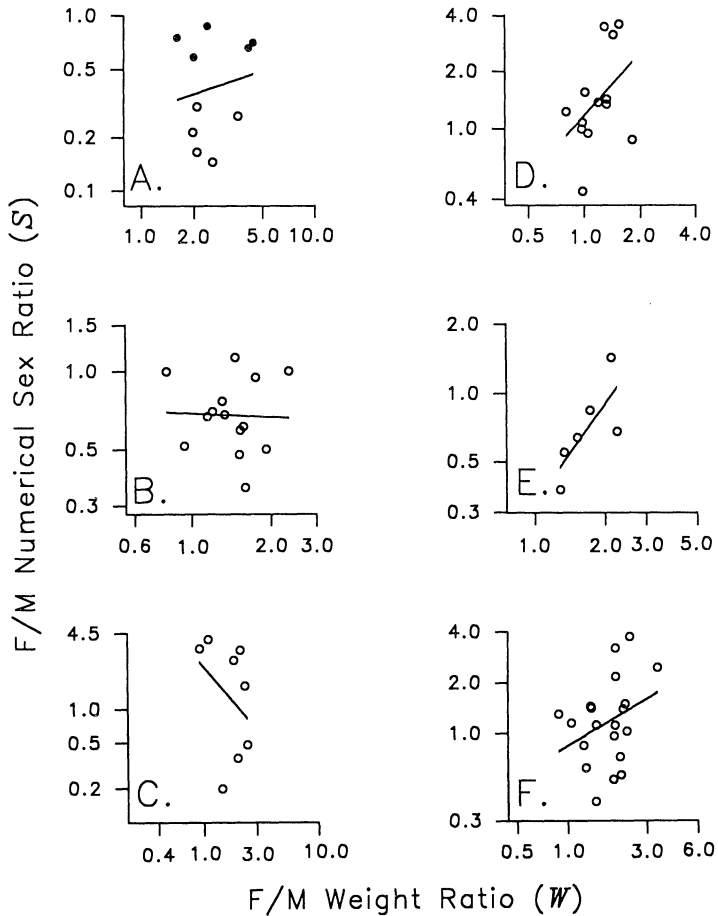
FIG. 2.—The F/M numerical sex ratio (S) as a function of F/M weight ratio (W) for social and solitary bees and wasps. A, Bumblebees (data for *solid circles* from study in Webb 1961 that may have overestimated investment in females due to sampling procedure [Owen et al. 1980]; data for *open circles* from more recent studies): $b = 0.343$, $r^2 = 0.030$, $P < .10$. B, Solitary bees collected from natural nests: $b = -0.045$, $r^2 = 0.001$, $P < .02$. C, Solitary bees collected from trap nests: $b = -1.168$, $r^2 = 0.123$, $P > .90$. D, Social wasps: $b = 1.128$, $r^2 = 0.182$, $P < .02$. E, Solitary wasps collected from natural nests: $b = 0.968$, $r^2 = 0.437$, $P < .02$. F, Solitary wasps collected from trap nests: $b = 0.551$, $r^2 = 0.077$, $P < .01$. Probability values (P) are from tests of the hypothesis that $\beta = -1.0$.

placed in the field by researchers (see, e.g., Krombein 1967). Mother wasps construct brood cells within trap-nest borings in a linear (end-to-end) sequence. The mother oviposits within a cell cavity and provisions it with paralyzed prey. Brood cells are separated from one another and the nest exterior by partitions or plugs constructed of mud or other materials. Cells are provisioned prior to hatching of the egg; when the sexes differ substantially in body size, sex of the egg can sometimes be reliably inferred from size of the cell, and amount of food provisioned for the sexes can be measured.

Using the trap-nest data collected by Krombein (1967), Trivers and Hare (1976)

TABLE 1

PARENTAL INVESTMENT IN INDIVIDUALS OF THE SEXES IN SOLITARY WASPS COLLECTED FROM TRAP NESTS
ESTIMATED BY F/M WEIGHT RATIO (W), F/M AMOUNT OF FOOD PROVISIONED (PR), AND F/M CELL
VOLUME RATIO (CV)

Taxa	W	PR	CV
Vespidae:			
Ancistrocerus adiabatus*	1.95†	1.61‡	. . .
Ancistrocerus antilope antilope§	1.90†	1.21‖	1.48
Euodynerus foraminatus*	1.72†	1.57‡	. . .
Euodynerus foraminatus apokensis§	2.07†	1.75‖	1.69
Euodynerus megaera§	2.22†	1.76‖	1.74
Euodynerus schwarzi§	. . .	2.29‖	2.37
Monobia quadridens§	1.93†	1.38‖	1.39

NOTE.—W is significantly different from PR for taxa in which both W and PR were measured
(paired comparisons by the sign test, P < .05). CV is not significantly different from PR for taxa in
which both CV and PR were measured (paired comparisons by the sign test).
  * Data from Cowan (1981).
  † Based on dry weights.
  ‡ Based on wet weights of prey items.
  § Data from Krombein (1967) and Trivers and Hare (1976).
  ‖ Based on number of prey items.

estimated the F/M ratio of amount of food provisioned (PR), the F/M cell volume
ratio (CV), and the F/M body weight ratio (W) for a limited number of species.
They also estimated CV and W for a greater number of additional species. The
results of Trivers and Hare (1976) and Cowan (1981) show that W consistently
overestimates PR, while CV fairly closely approximates and appears to neither
systematically underestimate nor overestimate PR (table 1). However, cell vol-
ume ratio may be a biased estimate of provision amount in at least one wasp in
the data set (App. B). The vespid wasp Stenodynerus saecularis often constructs
unusually long terminal cells that often house male offspring (Krombein 1967).
These cells presumably contain substantial empty space, and F/M cell volume
probably underestimates F/M provision amount in this species. Tentatively as-
suming that cell volume is not biased in the same direction across other species
of trap-nesting wasps, values of CV can be substituted for values of W as esti-
mates of the amount of food provided for the sexes.

Using cell volume ratios as substitutes for weight ratios, a number of analyses
can be performed to address the potential causes of covariance between the sex
investment ratio and sexual size dimorphism found in trap-nesting wasps (figs.
1F, 2F). First, we can see if F/M weight ratios are valid estimates of F/M provi-
sion amounts across species. If so, substituting CV for W in the regression analy-
ses illustrated in figures 1F and 2F should result in similar regression slopes to
those originally found.

Substituting the F/M cell volume ratio (CV) for the F/M weight ratio (W) in
estimating the sex investment ratio (I_{CV}) and regressing I_{CV} on CV results in a
slope very near and not significantly different from zero ($b = -0.013$; fig. 3A).
Correcting for lack of independence between variables ($I_{CV} = CV \cdot S$), regression
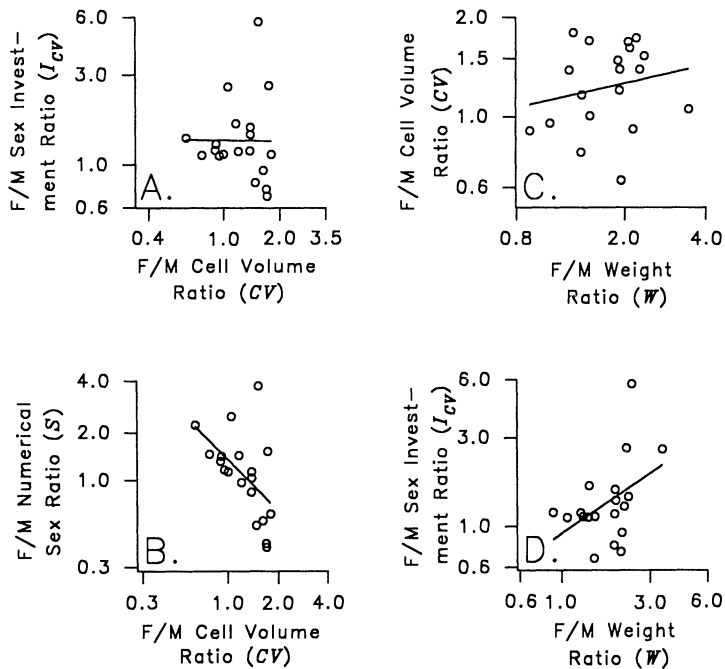of the F/M numerical sex ratio (S) on CV results in a slope very near and not

FIG. 3.—Sex ratios and estimates of parental investment in trap-nesting solitary wasps. A, The F/M sex investment ratio estimated by cell volume (I_{CV}) as a function of F/M cell volume ratio (CV) ($b = -0.013$, $r^2 = 0.000$, $P > .90$). B, The F/M numerical sex ratio (S) as a function of F/M cell volume ratio (CV) ($b = -1.014$, $r^2 = 0.274$, $P > .90$). C, The F/M cell volume ratio as a function of F/M weight ratio (W) ($b = 0.188$, $r^2 = 0.040$, $P < .01$). D, The F/M sex investment ratio estimated by cell volume (I_{CV}) as a function of the F/M weight ratio (W) ($b = 0.678$, $r^2 = 0.189$, $P < .10$). Probability values (P) are from tests of the hypothesis that $\beta = 0$ (A, D), $\beta = -1$ (B), and $\beta = 1$ (C).

significantly different from -1 ($b = -1.014$; fig. 3B). These results suggest that the F/M sex investment ratio does not actually increase as the F/M cost ratio increases, as was suggested by regressions of I_W on W and S on W (figs. 1F, 2F). If so, W is a substantially biased estimate of F/M provision amount across species of trap-nesting wasps.

While suggesting substantial error in estimating F/M cost from weight ratios, the preceding analysis does not address whether that error results from increasing overestimation of F/M cost with increasing F/M weight ratio (W; sensu Boomsma 1989). If such overestimation occurs, the F/M amount of food provisioned should not increase one-to-one with W across species of trap-nesting wasps. Regression of CV on W results in a slope significantly less than one (fig. 3C), which suggests that F/M cost may indeed be increasingly overestimated with increasing W in these wasps. However, the magnitude of error might be greater than that proposed by Boomsma (1989). In ants, F/M cost was hypothesized to increase with increasing W across ant species but more slowly than W, according to the function F/M cost $= W^{0.7}$ (Boomsma 1989). The function predicts that the slope of the

regression of CV on W should not differ from 0.7. In my data (fig. 3C), the slope of the regression of CV on W was significantly less than 0.7 ($P < .05$) and not significantly different from zero ($P > .40$). If F/M cost increases with increasing F/M size across these species of trap-nesting wasps, it appears to do so at a lesser rate than hypothesized for ants, which suggests greater systematic error.

The preceding analyses provide no information on whether the F/M sex investment ratio may actually increase with increasing F/M size dimorphism. An alternative analysis suggests such a relationship may occur; regression of the F/M sex investment ratio estimated by cell volume (I_{CV}) on the F/M weight ratio (W) results in a marginally significant positive slope ($.05 < P < .10$; fig. 3D). An actual increase in the F/M sex investment ratio with increase in W in these wasps may explain why deviation of the regression slope of the F/M numerical sex ratio (S) on W from -1 is so substantial (fig. 2F). If F/M cost does not increase with increasing F/M size (fig. 3C), the slope of the regression of S on W should be near zero. A positive regression slope would only be predicted if either F/M cost actually decreases with increasing F/M size or the effect of error on the regression slope is amplified by actual increase in the sex investment ratio with increasing F/M size. While not significantly different from zero ($P > .20$), slope of the regression of S on W in trap-nesting wasps was greater than zero ($b = 0.551$; fig. 2F).

Regressions of S on W for three of the remaining five groups of bees and wasps analyzed also exhibit slopes greater than, but not significantly different from, zero (fig. 2A, D, E). In monogynous ants, the slope of the regression was approximately -0.7, with the difference between -0.7 and -1.0 attributable to error resulting from the use of weight ratios (Boomsma 1989). Either error is tremendously greater in bees and wasps than in ants, or actual increase in F/M sex investment ratios with increasing F/M size commonly occurs across species of bees and wasps. It seems likely that some of the regression slopes in figures 1 and 2 reflect both systematic error and actual increase in the sex investment ratio with increasing sexual size dimorphism.

GENERAL DISCUSSION

Error in estimating differences in the amount of food provided for the sexes using differences in body weights could be very substantial within bees and wasps. Such errors may be minor when sexual size dimorphism is slight and great when sexual size dimorphism is substantial (Boomsma 1989). Among species of trap-nesting wasps, the geometric mean sex investment ratio estimated by cell volume (I_{CV}) is 1.33, while that estimated by weight (I_W) is 2.00. Similar error was proposed to occur over a greater range of sexual size dimorphism for monogynous ants. In monogynous ants, I_W was 2.81 while the sex investment ratio estimated from energetic cost was 1.82 (Boomsma 1989).

The estimate of a F/M sex investment ratio of 1.33 among trap-nesting wasps is useful in estimating the magnitude of error across species resulting from the use of weight ratios, but it might not be an accurate estimation of the sex investment ratio among those wasps in nature. One reason is that many of the trap-

nesting wasps in the data set may be partially bivoltine (Krombein 1967). The sex investment ratios in summer generations are predicted to be female biased, and the sex investment ratios in overwintering generations are predicted to be male biased (Seger 1983). If one generation were oversampled, sex ratios could be artificially biased. In addition, many of the bivoltine species were collected at multiple locations with potential differing durations of the summer generation (Krombein 1967). Biased sex investment ratios among trap-nesting wasps would not affect the validity of the analyses in figures 1F, 2F, or 3, unless one sex is increasingly oversampled with increasing sexual size dimorphism. This might occur if sexual size dimorphism were either greater or less in bivoltine species than in those remaining in the data set. This is not the case; there is no significant difference between F/M weight ratios in species with bivoltine populations ($N = 12$) and those species where populations have either one or more than two generations per year (Mann-Whitney U-test, $U = 43$, $N = 7$; Krombein 1967).

An additional source of bias in the sex ratio data on trap-nesting wasps can occur because mothers often preferentially produce the larger sex in large-diameter borings and the smaller sex in small-diameter borings (Krombein 1967; Charnov et al. 1981; Cowan 1981). If the diameter of trap-nest borings available are either larger or smaller than the mean cell diameter a wasp uses in nature, trap-nest data may result in oversampling one of the sexes when they differ substantially in body size. As long as cell diameters available are not consistently larger or smaller than the mean size used across species, the effect would be increased sex ratio variance among species with increasing sexual size dimorphism and not systematically biased sex ratios across species (Trivers and Hare 1976).

Avoiding errors resulting from the use of weight ratios in estimating food provided for the sexes may not be difficult for most solitary aculeates. Cell volume ratio did not appear systematically biased in Krombein's (1967) data on cavity-nesting solitary wasps from trap nests (Trivers and Hare 1976; table 1). Cell volume ratio is not very useful in estimating parental investment in a number of other solitary aculeates, however. Many solitary bees and wasps construct complete nests rather than use preformed cavities. If offspring brood cells are completed prior to cell provisioning, and the sex of offspring produced depends on success in acquiring provisions (see, e.g., Brockmann and Grafen 1989), there may be no difference in cell volumes, even though one sex might be provided with more food. Fortunately, actual amount of food provisioned by solitary aculeates can often be measured and reliably assigned to sex (Krombein 1967; Cowan 1981; Danforth 1990).

Accurate measurement of amount of food provided for the sexes is more difficult for the minority of solitary aculeates with progressive provisioning, as well as the eusocial aculeates. Reproductive offspring are fed at intervals, either throughout their stay in the nest or during some portion of the period they occupy the nest. Estimation of amount of food offspring consume may require energetics studies such as those by Boomsma and Isaaks (1985) and MacKay (1985). Alternatively, weight ratios in ants could be measured and then corrected with the power function proposed by Boomsma (1989), $C = W^{0.7}$, where C is the estimated F/M energetic cost of the sexes. However, Boomsma's (1989) formula might not result

in correction of weight ratios in bees and wasps. In any case, the correction must be used with caution, since it predicts an average correction for F/M weight ratios (W) for the group from which it was derived, and it may not result in accurate correction for any given species or population.

While amount of food provided for the sexes may not be systematically biased in estimating difference in parental investment across species in some aculeate groups, it could result in inaccuracy within any given species or population. For example, female offspring could be provisioned with more food than males, while males require more time to provision (Brockmann and Grafen 1989, 1992). In social species, one sex could differentially contribute to colony productivity prior to leaving the nest (Hölldobler and Bartz 1985).

The best approach to estimating difference in parental investment in the sexes may be to identify potential offspring costs (and benefits), measure as many meaningful alternatives as possible, and evaluate those measurements against one another (see, e.g., Danforth 1990; Brockmann and Grafen 1992). In addition, there are indirect methods that estimate cost of the sexes by analysis of the trade-off between family size and family sex ratio (Bull and Pease 1988; K. R. Helms and G. B. Pollock, unpublished data). These methods have limitations but may provide additional information in evaluating cost of the sexes.

Sexual Size Dimorphism and Local Mate Competition in Solitary Wasps

It appears that increase in the F/M sex investment ratio with increased F/M weight ratio in bees and wasps may not be entirely attributable to error resulting from the use of weight ratios. Circumstantial evidence from solitary wasps suggests actual covariance between sex investment ratios and sexual size dimorphism could result from an association between sexual size dimorphism and the importance of competition between related males for mates, local mate competition (LMC; Hamilton 1967). Solitary wasp populations can be structured such that competition between sibling males is common, and, as predicted by LMC theory (Hamilton 1967), female-biased sex investment ratios occur (Cowan 1981; Cowan 1991). In addition, large males often appear more successful than smaller males in acquiring mates in solitary wasps (Cowan 1981; O'Neill 1983; Evans and O'Neill 1988; Cowan 1991). Success by males in competition with their brothers has no clear positive effect on the fitness of the mother (Hamilton 1967). Even though large male size might be advantageous to males under LMC, mothers apparently exert strong control over offspring body size by the amount of food provisioned (O'Neill 1985; Evans and O'Neill 1988) and could produce small male offspring in circumstances in which those males will compete primarily with brothers. In populations in which male offspring will compete largely with unrelated males, success by male offspring in competition for mates has a strong effect on a mother's fitness. Mothers might produce larger males in populations in which competition between males occurs primarily among unrelated individuals. The effect of LMC on the sex investment ratio in such populations should be weak (Hamilton 1967). Analyses of solitary wasp populations that differ in the importance of LMC could reveal a general trend of increase in F/M size with increase in the F/M sex investment ratio.

The reasons for actual covariance between the sex investment ratio and sexual size dimorphism could vary among, and even within, aculeate groups. Local mate competition is but one possible explanation. The identification of alternative explanations and tests requires additional information on aculeate population structure and social biology. In addition, such tests may require accurate estimation of parental investment in the sexes. Weight ratios may often be erroneous in making such estimations. Alternative estimates of parental investment such as amount, energetic, and nutritional content of food provided, amount and energetic cost of providing nest materials, energetic cost of parental time expended, and potential returns from reproductive offspring helping behavior, should, when applicable and possible, be estimated and evaluated.

TABLE A1

SAMPLE SIZE (N), F/M NUMERICAL SEX RATIO (S), AND F/M WEIGHT RATIO (W) FROM STUDIES OF
BUMBLEBEES, SOCIAL WASPS, SOLITARY BEES, AND SOLITARY WASPS FROM NATURAL NESTS

Taxa	N^*	S	W	Reference
Bumblebees:				
Bombus affinis†	22	.264	3.63‡	Fisher 1987
Bombus americanorum	25	.657	4.17	Trivers and Hare 1976
Bombus auricomus	12	.876	2.42	Trivers and Hare 1976
Bombus fraternus	4	.752	1.62	Trivers and Hare 1976
Bombus griseocollis	20	.581	2.02	Trivers and Hare 1976
Bombus impatiens	5	.704	4.44	Trivers and Hare 1976
Bombus melanopygus	17	.144	2.58‡	Owen and Plowright 1982
Bombus ruderatus	5	.213	2§	Pomeroy 1979
Bombus terrestris‖	26	.300	2.11	Duchateau and Velthuis 1988
Bombus terricola	32	.164	2.10	Owen et al. 1980
Social wasps:				
Sphecidae:				
Microstigmus comes	102	1.338	1.33#	Ross and Matthews 1989
Vespidae:				
Mischocyttarus drewseni	8	.451	.99	Jeanne 1972
Mischocyttarus flavitarsis	7	1.543	1.02**	Little 1979
Parapolybia indica††	18	14.786‡‡	2.00	Suzuki 1986
Polistes chinensis	12	.860‡‡	1.83	Suzuki 1986
Polistes exclamans	19.75§§	1.516§§	1.20	Strassmann 1984
Polistes fuscatus	17	.932	1.06	Noonan 1978
Polistes jadwigae	8	.981‡‡	.98	Suzuki 1986
Polistes japonicus	8	3.174‡‡	1.45	Suzuki 1986
Polistes mandarinus	3	1.417‡‡	1.33	Suzuki 1986
Polistes metricus	228	1.216‡‡	.81	Metcalf 1980
Polistes snelleni	12	3.602‡‡	1.56	Suzuki 1986
Polistes variatus	48	1.065‡‡	.99	Metcalf 1980
Polistes sp.‖	. . .	3.500	1.30	Yamane 1980 in Suzuki 1986
Solitary bees (natural nests):				
Andrenidae:				
Calliopsis persimilis	274	1.124	1.47	Danforth 1990
Anthophoridae:				
Anthophora abrupta	169	.610	1.58	Trivers and Hare 1976
Anthophora edwardsii	225	.679	1.34	Trivers and Hare 1976
Anthophora flexipes	200	.667	1.15	Trivers and Hare 1976
Anthrophora occidentalis	241	.944	1.76	Trivers and Hare 1976
Anthophora peritomae	70	1.000	2.36	Trivers and Hare 1976
Apidae:				
Euplusia surinamensis	297	.697	1.20	Trivers and Hare 1976
Colletidae:				
Chilicola ashmeadi	84	.355	1.60	Trivers and Hare 1976
Halictidae:				
Agapostemon nasutus	87	.475	1.52	Trivers and Hare 1976
Nomia melanderi	500	.992	.80	Trivers and Hare 1976
Megachilidae:				
Hoplitus anthocopoides	351	.513	.94	Trivers and Hare 1976
Osmia bruneri##	291	.764	1.31‡	Frohlich and Tepedino 1986
Osmia excavata	2,820	.592	1.53	Trivers and Hare 1976
Osmia lignaria propinqua##	1,123	.499	1.93	Torchio and Tepedino 1980

Taxa	N^*	S	W	Reference
Solitary bees (trap nests):				
Megachilidae:				
Anthidium maculosum	78	3.333	.93	Trivers and Hare 1976
Ashmeadiella meliloti	136	1.566	2.31	Trivers and Hare 1976
Ashmeadiella occipitalis	845	3.225	2.10	Trivers and Hare 1976
Megachile gentilis	290	.198	1.46	Trivers and Hare 1976
Megachile mendica	208	.368	1.99	Trivers and Hare 1976
Osmia lignaria lignaria	732	.482	2.42	Trivers and Hare 1976
Osmia pumila	315	2.621	1.84	Trivers and Hare 1976
Prochelostoma philadelphi	85	4.000	1.11	Trivers and Hare 1976
Solitary wasps (natural nests):				
Sphecidae:				
Chalybion bengalense	183	.679	2.25	Trivers and Hare 1976
Ectemnius paucimaculatus	169	.550	1.33	Trivers and Hare 1976
Passaloecus eremita	114	1.426	2.13	Trivers and Hare 1976
Trypoxylon politum***	7,049†††	.608	1.28‡‡‡	Brockman and Grafen 1992
Vespidae:				
Antodynerus flavescens	200	.639	1.52	Trivers and Hare 1976
Euodynerus foraminatus##	1,331	.838	1.72	Cowan 1981

NOTE.—Data attributed to Trivers and Hare (1976) were taken or derived from their tables; the original sources are cited in that article.

* Sample size refers to number of colonies censused in bumblebees and social wasps and to number of offspring censused in solitary bees and wasps.

† Data from colonies not parasitized by Psithyrus.

‡ Based on wet weight.

§ Pomeroy (1979) gives no specific quantitative data on weight ratio but states that females are twice as large as males.

‖ Duchateau and Velthuis (1988) present data for 21 colonies of Bombus terrestris terrestris (662 females, 2,514 males) and five colonies of Bombus terrestris sassaricus (142 females, 170 males). As only a single estimate of W was given, data from the two subspecies were combined.

Head and thorax weight.

** Based on wing length. This ratio may be similar to wet weight ratios in social wasps (Strassmann 1984).

†† Transformed data on dependent variables (S and I_w) for P. indica were significant outliers (Grubb's test for outliers, $P < .05$) and excluded from regression analyses. Since W in P. indica was only slightly greater than in other social wasps, while S was extremely female biased, their exclusion results in a more conservative test of whether the F/M sex investment ratio increases with increasing F/M size dimorphism in social wasps.

‡‡ Based on number of the sexes produced by an average nest.

§§ Mean values over a 4-yr period.

‖‖ Undescribed species called Polistes biglumis in Yamane (1980) (Suzuki 1986).

Trap-nest data included in analyses of natural nests (see Methods).

*** Data from the Florida study.

††† Data collected over an 8-yr period.

‡‡‡ Based on wet weights of overwintering pupae.

APPENDIX B

TABLE B1

NUMBER OF OFFSPRING CENSUSED (N), F/M NUMERICAL SEX RATIO (S), F/M WEIGHT RATIO (W), AND
F/M CELL VOLUME RATIO (CV) FOR SOLITARY WASPS FROM TRAP NESTS

Taxa	N	S	W	CV
Pompilidae:				
Dipogon sayi	107	2.452	3.46	1.05
Sphecidae:				
Trypargilum clavatum	314	1.122	1.50	1.00
Trypargilum johannis	72	.846	1.26	1.38
Trypargilum striatum	349	.623	1.30	1.80
Trypargilum tridentatum tridentatum	332	1.306	.90	.90
Trypoxylon frigidum	82	1.412	1.40	1.16
Vespidae:				
Ancistrocerus adiabatus*	1,202	3.203	1.95	. . .
Ancistrocerus antilope antilope	375	.531	1.90	1.48
Ancistrocerus campestris	83	.566	2.10	1.62
Ancistrocerus catskill	189	1.032	2.28	1.39
Ancistrocerus tigris	114	3.750	2.37	1.53
Euodynerus foraminatus apopkensis	1,551	.435	2.07	1.69
Euodynerus foraminatus foraminatus	96	.391	1.49	1.70
Euodynerus megaera	240	1.500	2.22	1.74
Monobia quadridens	227	1.121	1.93	1.39
Pachodynerus erynnis	240	1.400	2.16	.91
Stenodynerus krombeini	69	1.156	1.07	.95
Stenodynerus lineatifrons	92	2.172	1.95	.63
Stenodynerus saecularis	149	1.443	1.39	.77
Symmorphus cristatus	114	.966	1.92	1.20

NOTE.—Unless noted, all data were taken or derived from table 5 in Trivers and Hare (1976).
* Data from Cowan (1981).

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