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SEX RATIOS AND MULTIFACETED PARENTAL INVESTMENT

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Abstract.—Although theories of parental investment and sex ratio generally assume that a single resource limits reproduction, many organisms invest two or more qualitatively different types of resources in the production of offspring. We examine the consequences of multifaceted parental investment for offspring provisioning and sex allocation, building our argument around a study of the nest-building Hymenoptera (wasps, bees, and ants). We review empirical studies that demonstrate that lifetime reproductive success may be constrained not only by resources used to provision offspring but also by the supply of mature oocytes or, in some cases, by the availability of space within nest sites or the time required to defend nests. Under multifaceted parental investment, the factor limiting parental fitness determines the currency of the optimization problem; parents are predicted to adjust reproductive behavior to maximize fitness returns per unit of the limiting resource. We develop simple models that predict that a greater availability of resources used for provisions will lead to an increase in the amount provisioned per offspring and an increase in the numerical or biomass proportion of females produced. These predictions explain widely observed patterns of variation in offspring provisioning and sex allocation in the nest-building Hymenoptera.

Frank (1990) highlighted the problem of ascertaining an appropriate currency for parental investment: Although theories of sex allocation and parental investment typically assume a unidimensional limiting resource, real organisms often invest qualitatively different types of resources in the production of offspring. For example, parental investment in birds may comprise nutrients allocated to eggs, egg incubation, the feeding of altricial young, nest defense, and the sharing of foraging territories with fledged young. Many mammals invest heavily in the developing fetus, lactation, and the postweaning feeding and protection of young. Some colonial invertebrates allocate both nutrients and limited free space on a stable substrate to reproductive zooids of different sexes. Plants may allocate many different nutrients to seeds. Frank (1990) raised the question of whether theories that reduce multiple-component parental investment to a single limiting resource are robust. Indeed, the few studies that have addressed multiple-component parental investment, including those examining the trade-off between

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seed size and number (McGinley and Charnov 1988), sex allocation in hermaphroditic plants (Charnov et al. 1976; Geber and Charnov 1986; Lloyd and Venable 1992), and invertebrates that brood their young in a pouch with limited space (Lloyd and Venable 1992) do suggest that single- and multicomponent models produce substantially different predictions. Frank (1990, p. 33) concluded that "both the major theoretical questions about multidimensionality and the problems of relating theory to observation remain unsolved."

In this article, we follow Frank in arguing that our understanding of sex allocation can be deepened by recognizing the potentially multifaceted nature of parental investment. We build our argument around a study of the nest-building Hymenoptera (wasps, bees, and ants). Because this group demonstrates extensive sexual size dimorphism and has maternal control of primary sex ratio, we can examine directly the consequences of multicomponent investment for predicted patterns of offspring provisioning and sex ratio.

THE NEST-BUILDING HYMENOPTERA

Haplodiploidy affords the Hymenoptera maternal control of sex allocation. The resulting diversity of sex allocation patterns has made ants, bees, and wasps especially valuable for developing and testing sex allocation theory (Charnov 1982; Wrensch and Ebbert 1993). In particular, sex investment ratios in nest-building Hymenoptera have played central roles in the development of theory for evolutionary conflicts within colonies of eusocial species (Trivers and Hare 1976; Alexander and Sherman 1977; Noonan 1978; Nonacs 1986*a;* Mueller 1991) and between mates (Brockmann and Grafen 1989), local resource enhancement (Schwarz 1988; Stark 1992), local resource competition (Visscher and Danforth 1993), local mate competition (Cowan 1991), and the evolution of sociality (Seger 1983; Brockmann and Grafen 1992).

Many nest-building Hymenoptera are also sexually size dimorphic (females generally larger than males). As such, they have provided some of the clearest support for Fisher's (1930) basic prediction that numerical sex ratios will evolve to produce a larger number of the less expensive sex (males), such that population-wide investment in the production of males and females is equal (Noonan 1978; Torchio and Tepedino 1980; Charnov 1982; Frohlich and Tepedino 1986; Visscher and Danforth 1993; Helms 1994).

Recent studies of ants (Boomsma 1989) and solitary and social wasps and bees (Helms 1994) have, however, revealed consistent patterns of deviation from Fisherian sex ratios: female/male sex investment ratios increase with increasing female/male size dimorphism. Parental investment in these and other studies of nest-building Hymenoptera has been defined narrowly by the costs of providing food to offspring (Noonan 1978; Torchio and Tepedino 1980; Cowan 1981; Strickler 1982; Boomsma and Isaaks 1985; Frohlich and Tepedino 1986; Tepedino and Parker 1988; Sugiura and Maeta 1989; Field 1992*a;* Stark 1992; Boomsma and Eickwort 1993). Thus, attempts to explain deviations from Fisherian sex ratios have focused on the choice between a variety of indices to quantify the investment in offspring provisions (e.g., foraging time, provision wet or dry weight, provision energy content, offspring wet or dry weight, cell volume) (Boomsma 1989; Danforth 1990; Crozier and Pamilo 1993; Visscher and Danforth 1993; Helms 1994).

THE THESIS

Here we argue that lifetime reproductive success in the nest-building Hymenoptera can be limited not only by the availability of food provisions for offspring but also by the availability of mature oocytes, the availability of space in suitable nest sites, and the time required to defend the nest. Limited availability of oocytes is likely to be a general phenomenon because of two common trade-offs: first, the trade-off between allocation of resources to egg production versus somatic maintenance; second, the trade-off between the number versus the size of oocytes. Evolutionary optima are reached under these trade-offs when a fraction of the population is egg limited (Rosenheim, in press). Comparative evidence from the Hymenoptera suggests that increased oocyte size has been favored evolutionarily until the trade-off between oocyte size and oocyte number leads to some risk of oocyte shortage. Because parental investment includes any component of parental care that decreases the parent's ability to produce additional offspring in the future, parental investment is multifaceted.

To make predictions under Fisher's (1930) theory of sex allocation, it is therefore necessary to consider more than just the costs of providing food to offspring. We propose that the relative importance of the different components of parental investment is shaped by ecological conditions and will thus vary in space and time. Fluctuating environmental conditions create variation in the optimal amount of food provisioned per offspring. Fluctuating environmental conditions can also change the optimal numerical sex ratio whenever male and female offspring require different relative amounts of the various resources that comprise parental investment. For example, when food for offspring is the sole limiting factor, Fisherian sex allocation entails the production of a larger number of the sex requiring fewer provisions (males). However, when oocytes are the sole limiting factor, Fisherian sex allocation predicts production of an equal number of sons and daughters, regardless of the relative amounts of food provided to each. It is therefore very difficult to make precise, quantitative, population-level predictions of the relative biomass or numerical investment in the sexes for natural populations of sexually size-dimorphic Hymenoptera. Nevertheless, we can make novel predictions for shifts in provision masses and numerical sex ratios as functions of ecological conditions. We predict that a greater availability of resources used for provisions will lead to (1) an increase in the amount provisioned per offspring and thus an increase in offspring size and (2) an increase in the proportion of females produced (for solitary species) or the ratio of total female/male biomass (for solitary and especially social species).

We begin by summarizing evidence that the nest-building Hymenoptera demonstrate several discrete components of parental investment. We then explore the consequences of multifaceted parental investment with simple analytical arguments and dynamic state variable modeling. Dynamic modeling allows us to examine the simultaneous influences of different components of parental investment (each of which can be measured in its own appropriate units) on realized lifetime reproductive success; we can thus understand the evolution of parental behavior (Mangel and Clark 1988; Mangel and Ludwig 1992). We then examine the substantial body of empirical work conducted with wasps, bees, and ants to assess the extent to which variation in sex allocation can be understood as a functional response to fluctuations in the relative importance of different components of parental investment.

MULTIFACETED PARENTAL INVESTMENT

Some definitions will be useful in our discussion. First, *parental care* is defined as any form of parental behavior that increases offspring fitness, without regard to the cost of the behavior (Clutton-Brock 1991). *Parental investment,* in contrast, is defined as only those components of parental care that decrease the parent's residual reproductive value—that is, the ability to produce additional offspring in the future (Clutton-Brock 1991). The sex investment ratio considered by Fisher (1930) is the product of the numerical sex ratio and the magnitude of parental investment in each sex.

Dissection of a typical hymenopteran nest reveals a variety of parental contributions to offspring fitness. First, there is the nest itself, which provides protection from both harsh abiotic conditions and natural enemies; nests may be excavated in the earth, wood, or pithy plant stems, constructed as free-standing structures, or placed in preexisting cavities (often insect-produced galleries in dead wood). Second, offspring are completely dependent on their parents for food, which may take the form of animal prey, pollen or nectar, or parental secretions of various sorts. Third, eggs are often large and heavily yolked. Fourth, parents may actively defend offspring against parasitoids and predators.

Which of these components of parental care contribute to parental investment? The answer to this question hinges on which of the factors limit lifetime reproductive success (Evans 1990). We now review evidence that lifetime reproductive success in nest-building Hymenoptera can commonly be limited by at least three of the components of parental investment: nest sites, resources for offspring provisions, and oocytes or brood. A fourth factor, the time devoted to guarding offspring, may also limit reproductive success (e.g., Brockmann and Grafen 1989; Field 1992*c*). However, we are not aware of any studies that have quantified the relative costs of guarding female versus male offspring, so we will not consider guarding costs further.

Nest Site Availability

Nest site availability may limit reproductive success in those species that have narrowly defined requirements for nest locations (e.g., broken stems of pithy plants) and particularly in species that adopt preexisting insect galleries in wood. When the availability of nest sites is limiting, the volume of space within an acquired nest site that is devoted to the production of a single male or female offspring may become an important component of parental investment for that offspring. The volumes of male- and female-producing cells often differ (Krombein 1967; Cowan 1991; Helms 1994); thus, the "space costs" of sons and daughters may be unequal. Danks (1971) suggested that nest sites limited densities of several species of tube-dwelling solitary bees and wasps. This suggestion is supported by studies demonstrating that populations of tube-nesting species can be augmented by providing artificial nest sites (see references in Danks 1971). In a similar vein, Michener (1971) suggested that the limited volume of the hollow stems used as nest sites by social allodapine bees might limit the size of colonies.

Nest site limitation in cavity-nesting wasps and bees is also suggested by widespread observations of intra- and interspecific usurpation of nests after complete removal of the cells and cell contents produced by the previous owner (Field 1992*b*). In at least some species, nest site usurpation appears to be conditional on a lack of unoccupied nest sites and may involve fights between females (Cowan 1981; Barthell and Thorp 1995). When multiple females of the solitary wasp *Euodynerus foraminatus* nest simultaneously in adjacent nest sites, they adjust their provision masses to produce larger daughters, apparently a response to enable their larger daughters to compete more successfully for limiting nest sites. An ecologically similar co-occurring species that uses more abundant nest sites does not show this response (Cowan 1981).

Reproduction by cavity-nesting social species, like honey bees, may also be limited by the availability of nest sites and the size of an acquired nest site (Winston 1987). The volume requirements of drone comb and worker comb (workers are needed for successful swarming of queens) may then influence the sex investment ratio.

Resource Availability for Provisions

It is widely assumed that resources used to feed offspring can limit the reproductive success of solitary and social nest-building Hymenoptera. However, few studies have actually combined independent measures of resource availability with realized lifetime reproductive success. For solitary species, the first demonstration of a correlation between resource availability and mean reproductive success was provided by Minckley et al. (1994), who observed that a population of bees, *Dieunomia triangulifera,* completed a larger than average number of cells per nest in years of high pollen availability. Minckley et al. (1994) concluded, however, that while resource availability may be an important influence on reproductive success, it may not be the sole or even the primary regulatory factor (see *Oocyte Production*). Clearly, field experiments manipulating resources available to solitary species are needed.

Ants tend to blanket their habitats in exclusive and expensively maintained territories, which leads researchers to conclude that the overall productivity of ant colonies must be closely tied to available food resources (Hölldobler and Wilson 1990). The total production of sexuals has been observed to be greater in "good" habitats than in "poor" ones (Brian et al. 1967; Brian 1979; Herbers 1990) or to be greater in larger colonies than in smaller ones (Brian et al. 1967; Elmes and Wardlaw 1982; Bourke et al. 1988). Most important, experimental food supplementation has been shown to increase total sexual production in ants (Buschinger and Pfieffer 1988; Backus and Herbers 1992; Backus 1995).

Finally, experimental food supplementation also increased colony productivity in the eusocial paper wasp *Polistes metricus* (Rossi and Hunt 1988).

Oocyte Production

Oocyte production can limit lifetime reproductive success in two ways. First, egg production may entail a physiological cost. Although we know of no studies that have quantified the physiological cost of reproduction in the Hymenoptera, egg production in other insects may produce long-term increases in rates of age-specific mortality (Kirkwood and Rose 1991; Lessells 1991; Tatar et al. 1993 and references therein) or a magnification of the negative effects of maternal age on egg size and offspring larval performance (M. Tatar, personal communication). Thus, eggs are unlikely ever to be truly cost free. Second, absolute constraints may exist in the ability to mature oocytes; oviposition then entails an "opportunity cost" in that it depletes a finite resource of mature oocytes. Opportunity costs exist because a deposited egg cannot be used later to garner reproductive success in a subsequent reproductive event. We now review evidence that egg availability can constrain reproductive success.

Solitary species.—Despite the abundant literature on the nesting biology of the Hymenoptera, empirical studies assessing the extent to which lifetime reproductive success is limited by the ability to produce eggs are rare. Bohart and Youssef (1976) concluded that reproduction by the solitary bee *Evylaeus galpinsiae* was constrained by oocyte production rather than the availability of pollen provisions for offspring. Although no ovarian dissections were conducted, circumstantial evidence supports this view. Bees were able to collect sufficient pollen to provision four cells during just one of the two daily foraging periods. Experimental excavations of nests after bees had completed a period of sustained foraging often revealed one to two completed provisions that lacked eggs. Bees generally undertook minimal foraging during the next 1–2 d, which Bohart and Youssef (1976) interpreted as the period necessary for egg production to "catch up." Occasional observations of fully provisioned cells lacking an egg have been made in other studies of solitary bees and wasps, and they may similarly reflect females who were constrained by a complete lack of mature oocytes (Frohlich and Tepedino 1986; Hager and Kurczewski 1986), although other interpretations are also possible.

Similar circumstantial evidence supports the same interpretation of reproduction being constrained by oocyte production in the solitary bee *Dieunomia triangulifera*. Minckley et al. (1994) observed that during periods suitable for foraging, approximately 25% of all bees did not forage on any given day, only to resume foraging later. For bees that did forage, the total number of foraging trips completed per day was highly variable (zero to eight), which again suggests submaximal foraging activity for some females. Although no dissections were performed, Minckley et al. (1994) hypothesized that these bees may be able to mature no more than one egg every 2–3 d, while during periods of peak pollen availability, approximately one cell could be fully provisioned per day.

In an observational field study of the facultatively communal bee *Perdita coreopsidis,* Danforth (1989) found that two factors influenced the ability of bees to complete a second offspring cell per day. The first factor was the availability of resources for nest provisions: as the mean duration of pollen-collecting trips decreased seasonally (apparently as a result of greater availability of flowers), the proportion of bees completing a second cell each day increased. The second factor was the availability of a mature oocyte: bees provisioning a cell carried a mature oocyte, whereas bees that chose to feed themselves rather than initiate the provisioning of a second cell generally did not carry a mature oocyte.

Useful insights may also be obtained from a close outgroup to the nest-building Hymenoptera, the parasitoid wasps (Dowton and Austin 1994). The biology of many parasitoids differs from that of the solitary nest-building wasps only in the absence of the nest; they still hunt for ''provisions'' (i.e., hosts) on or into which they lay one or more eggs (Askew 1971). Field studies with four species of parasitoid wasps—*Bracon hebetor* (Braconidae) (Ode 1994), *Anagrus epos* (Mymaridae) (Cronin 1991), *Leptopilina clavipes* (Eucoilidae) (Driessen and Hemerik 1992), and *Aphytis aonidiae* (Aphelinidae) (Heimpel 1995)—have consistently revealed that small to moderate proportions of the population were constrained by either transient or permanent exhaustion of their egg supply. Theory developed for oviposition behavior of insects that may face egg limitation predicts that the opportunity cost of depositing an egg will influence host acceptance and clutch size (Iwasa et al. 1984; Mangel 1987). Manipulative tests employing parasitoids have confirmed these predictions (Rosenheim and Rosen 1991; Minkenberg et al. 1992; Fletcher et al. 1994; Heimpel and Rosenheim 1995), which suggests that egg limitation has been sufficiently important to shape the evolution of parasitoid reproductive behavior.

For both parasitoid and nest-building Hymenoptera, the number of eggs produced is likely to respond over evolutionary time to the range of reproductive opportunities encountered (Michener 1971; Price 1973; Charnov and Skinner 1988). Species that rarely become egg limited will often benefit by reallocating resources from ''excess'' oocytes to other uses that make contributions to fitness (Rosenheim, in press). At least two trade-offs are particularly relevant to many insects in this regard. First, several insects may experience a trade-off between allocation of resources to reproduction (oocyte production) and somatic maintenance (Kirkwood and Rose 1991; Lessells 1991; Tatar et al. 1993). Under this trade-off, resources reallocated from excess oocytes to somatic maintenance may contribute to longevity and hence to reproductive success. Evolutionary optima occur with allocations that balance an intermediate risk of egg limitation against an intermediate risk of dying with large stores of unused oocytes (Rosenheim, in press). Second, insects generally face a trade-off between the number and size of eggs produced (Price 1973; Berrigan 1991). Species that are rarely egg limited will often benefit by producing a smaller number of larger eggs, because larger eggs provide a range of advantages related to offspring survivorship, rate of growth, final size, and reproduction (Tauber et al. 1991; Fox 1993 and references therein). Egg size is predicted to increase until egg limitation becomes sufficiently common to oppose further evolutionary increases (Rosenheim, in press). The solitary nest-building Hymenoptera generally have a smaller number of larger eggs compared to the parasitoid wasps, which are often highly fecund (Clausen

1940; Iwata 1964). Many nest-building species have at most one to two mature oocytes stored in the ovaries at one time, modest maximum fecundities, and possibly extremely large eggs (Iwata 1964; Michener 1971; Maeta 1978; Alexander and Rozen 1987; Sugiura and Maeta 1989). The most spectacular example of "egg giantism" is recorded from solitary carpenter bees in the genus *Xylocopa,* which produce eggs 12.5–16.5 mm in length, which may be more than 50% of the mother's total body length (Iwata 1964). Evolutionary trade-offs between egg size and number are also evident in parasitic bee lineages, in which egg size has decreased and egg number increased, apparently in response to selection for the ability to oviposit in rapid succession (Alexander and Rozen 1987).

Social species.—Primitively social bees and wasps may also experience egg limitation. Colonies of three *Lasioglossum* species may experience shortfalls of egg production late in the season, when the number of workers foraging for pollen and nectar is high; thus, the rate of cell provisioning outstrips the rate of egg maturation by egg layers (Batra 1964, 1966, and references therein). This interpretation is supported for one species by the observation of increases in the ratio of pollen balls lacking eggs to pollen balls with eggs (Batra 1966). West-Eberhard (1987) suggested that females of the primitively social wasp *Zethus miniatus* are constrained by the lack of mature oocytes immediately following oviposition or late in life. Under these conditions, they are more likely to adopt orphaned larvae present in multifemale nests.

Studies on egg limitation in the eusocial bees and wasps are rare and have not been aimed directly at whether egg limitation exists. Forsyth (1978) found that when queen-to-worker ratios were low in *Metapolybia azteca,* the number of empty cells in the colony increased. It seems that the ability to produce cells in such colonies exceeds the queens' capacity to oviposit in them. Boomsma and Eickwort (1993), noting the large size of halictid eggs, also hypothesized that colonies of the eusocial halictid *Halictus ligatus* may become egg limited when worker number is high.

Ant colonies are probably much less likely to be egg limited than are solitary species or many social species with an annual colony cycle. Some ant queens are among the most fecund individuals in the insect world. For example, it has been estimated that an army ant queen may lay more than 6 million eggs in a 6-yr life span (Franks 1989). Nevertheless, egg limitation may exist in some cases, such as for *Rhytidoponera* species, in which queens have been replaced by mated workers (gamergates). Colonies often have only one egg-laying gamergate, and her egg production is on the order of one to two eggs per day (Peeters 1991).

The egg-laying capabilities of most ant queens lie between these two extremes, and eggs are not likely to be limiting for many species. Brian (1951) estimated that only one-third of the eggs produced by a queen survive to adulthood. Brood cannibalism may be routine even in colonies not under food stress (Nonacs 1991). Finally, the use of eggs as food for larvae (i.e., trophic eggs) is widespread and well documented (Hölldobler and Wilson 1990). All these factors combine to suggest that an egg is not a particularly precious commodity in a large ant colony.

Although eggs may not be limiting for some ants, sex ratios can still be constrained by brood dynamics. Most species of ants have a particular and restricted time of year in which sexuals are released from the colony to mate and initiate new colonies (Hölldobler and Wilson 1990). The production of sexuals is an extended process, which can take from several months to over a year. For example, in *Myrmica,* reproductive females that mature in the late spring and early summer come from eggs laid early in the previous summer (Elmes 1991). Eggs laid later in the previous year or early in the current year cannot be "sped up" to become sexuals—their fate is to become workers. Similar extended maturation periods have been found for leptothoracines (Franks et al. 1990) and formicines (Rosengren et al. 1993).

Therefore, an ant colony, much like a solitary wasp, may find itself in a transient resource bonanza that cannot be exploited by simply producing a larger number of sexuals. More eggs can be laid, but they cannot be reared in time for the mating season. Thus, one might find a variation of the egg limitation hypothesis in the social Hymenoptera—that is, a brood limitation hypothesis. Still, the implications for how to measure parental investment would be the same as for solitary Hymenoptera. Note, however, that while many bees and wasps can respond to changing ecological conditions by modulating the numerical sex ratio, ant colonies are often constrained by the existing brood, which impose a numerical sex ratio that is fixed in the short term. Ants can still adjust the allocation of provisions to maturing sons and daughters, however. Thus, when discussing ants later, our focus will often be on the biomass ratio (the ratio of total female/male biomass).

In sum, we suggest that lifetime reproductive success of nest-building Hymenoptera may be constrained by their ability to mature eggs (or, equivalently, for some social species, the ability to produce sufficiently mature brood before the mating season). Egg or brood limitation is most likely to occur at times or places of great resource abundance (i.e., abundant nest sites and abundant sources of food for offspring). Thus, we hypothesize that, at times of resource abundance, the cost of egg production becomes the more important component in selection on parental investment.

PROVISION MASS AND FISHERIAN NUMERICAL SEX RATIO

How might the multifaceted nature of parental investment influence the optimal amount of food to be provided to each offspring and the evolutionarily stable sex ratio in a sexually size-dimorphic nest-building hymenopteran? To make our basic hypothesis as clear as possible, we will examine two simple scenarios for a hypothetical solitary wasp. Also for the sake of simplicity, we assume in all cases that excess nest sites are available and that there is no inbreeding or local mate competition. More realistic (and complex) cases of optimal provisioning are considered subsequently with dynamic modeling.

We will also invoke Fisherian sex allocation, a simplifying assumption whose acceptance in the literature on the nest-building Hymenoptera has perhaps been too uncritical. Fisher's theory (1930) rests on the assumption of linear fitness returns to the parent from investment in each sex during each "investment period." Offspring are defined as being produced in separate investment periods when resources acquired by the parent during one investment period cannot be allocated to subsequent investment periods. Because fitness returns from a *single offspring* are generally not a linear function of investment (i.e., we expect diminishing returns), linear fitness return curves occur only if the parent provisions a series of offspring per investment period. The larger the number of offspring provisioned is, the closer the total returns approximate linearity and the more robust the predictions of Fisherian allocation are (Frank 1987*a*, 1990). This point raises an important question: What is the investment period for the nest-building Hymenoptera? Frank and Crespi (1989) have discussed cases in which the investment period is best defined by the time required to produce a single offspring; this condition applies in particular if offspring provisioning must be completed at the close of each day's activity. In this case, population sex allocation is predicted to be sensitive to both the distribution of resources among individuals and the details of fitness return curves per offspring, and population-wide equal allocation is not expected whenever male and female fitness return curves are unequal (Frank 1995). In other cases, in which the completion of cells is not dictated by daily cycles, the investment period may be the complete lifetime of the parent, and Fisherian allocation is a reasonable expectation as long as a modest number of cells is completed per female per lifetime. This is the case we analyze below. However, we recognize that it may be precisely the multifaceted nature of parental investment that makes the problem of defining the investment period particularly difficult for the nest-building Hymenoptera. Thus, we analyze sex allocation only under the simplest of conditions, where investment is defined by different components, considered one at a time. We reserve for future treatments the problem of defining the investment period and the evolutionarily stable sex allocation ratio when investment is defined by a combination of resources.

Scenario 1: Fitness Limited by Resources for Feeding Offspring

When the rate of egg production is sufficiently high that surplus eggs are always available, reproductive success is completely determined by the ability to collect food for offspring. Under these conditions, mothers are faced with the classic trade-off between the size and number of offspring: as more is invested in each individual, fewer total offspring can be raised. In such situations, Smith and Fretwell (1974) predicted that (1) there is an optimal size of offspring that maximizes the parents' fitness, and (2) offspring number should be varied in response to changes in resource level rather than offspring size (fig. 1). Under Fisherian sex allocation, the total investment in females must equal the total investment in males; thus, half of all food resources goes to the production of each sex, and Smith-Fretwell optima are obtained independently for each sex. Because parental investment under this scenario is completely defined by the provisions provided to each daughter (p_d) and son (p_s), the evolutionarily stable strategy (ESS) Fisherian proportion of males (r) to be produced is determined by

$$\text{investment in daughters} = \text{investment in sons};$$

$$p_d(1 - r) = p_s r; \tag{1}$$

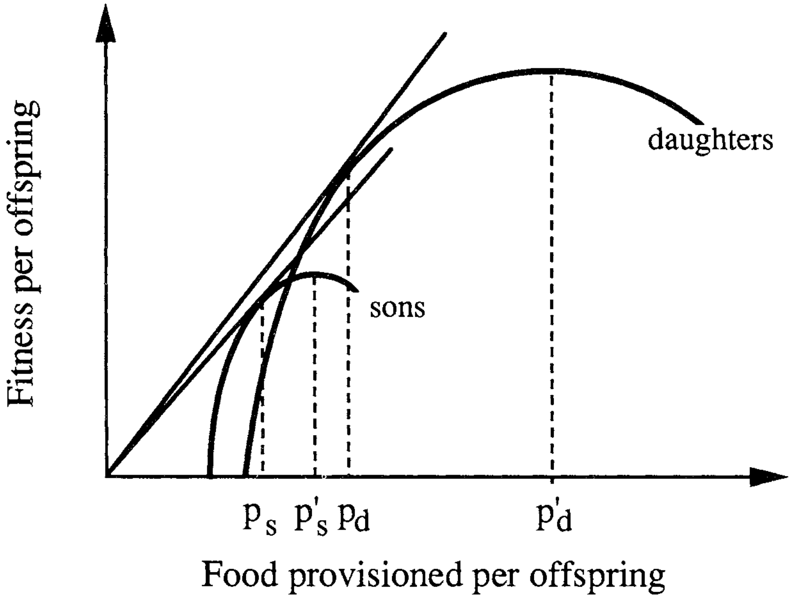

FIG. 1.—Optimal amount of food to provide per offspring in a species with multifaceted parental investment. When parental reproductive success is limited entirely by the availability of resources used to provision nests, optimal parental investment for each daughter (p_d) and son (p_s) is obtained following Smith and Fretwell (1974). When parental reproductive success is limited entirely by the ability to produce eggs, the optimal food to provide each offspring is that which maximizes the fitness of each daughter (p'_d) and son (p'_s). (We postulate offspring fitness curves that are domed rather than reaching an asymptote because excess provisions that remain uneaten may foul the nest as they decay, promote the growth of potentially pathogenic microorganisms, or attract parasites or predators.)

$$r = p_d/(p_d + p_s)\,.$$

Thus, at the ESS a larger number of the "cheaper" sex is produced. If we assume that the efficiency of converting provisions into adult biomass is independent of sex or amount of provisions consumed (which is untrue for many species; see Boomsma 1989 and Helms 1994), then the sexual size dimorphism ratio (female/male) is simply p_d/p_s, and the total biomass ratio (females/males) is $p_d(1 - r)/p_s r$, which equals 1.0 under Fisherian sex allocation.

Scenario 2: Fitness Limited by Egg Production Ability

When the rate at which nest provisions can be collected is sufficiently high that surplus provisions are always available, reproductive success is completely determined by the ability to mature eggs. The optimal amount of food to provide each daughter (p'_d) and son (p'_s) is now simply the quantity that maximizes the fitness of each offspring (fig. 1). Because parental investment under this scenario is completely defined by the cost of producing an egg for a daughter (e_d) or a son (e_s), the ESS Fisherian proportion of males to be produced (r') is

$$\text{investment in daughters} = \text{investment in sons};$$

$$e_d(1 - r') = e_s r'; \tag{2}$$

$$r' = e_d/(e_d + e_s).$$

The sexual size dimorphism ratio is p'_d/p'_s, and the total biomass ratio is $p'_d(1 - r')/p'_s r' = p'_d e_s/p'_s e_d$, which may differ from 1.0 (fig. 1).

By comparing these two scenarios, we obtain two basic results. Both results are tied fundamentally to the notion that under multifaceted parental care, the factor limiting parental fitness determines the "currency" of the optimization problem, and parents are predicted to "make the most" of the limiting resource. First, the optimal amount of food to provide each offspring depends on which factor is limiting parental reproductive success. When food resources are limiting, parents should maximize their fitness returns per unit of food provided; when eggs are limiting, parents should maximize their fitness returns per egg. Thus, as resource availability increases and egg limitation becomes more likely, the amount of food to be provided to each offspring will increase (see also the dynamic model described below).

Second, the ESS Fisherian sex ratio also depends on which factor is limiting parental reproduction. The factor that limits parental fitness is the factor that defines parental investment; in so doing, it also defines the appropriate currency for calculating the relative costs of producing daughters and sons. Our key observation is that the quantitative cost ratios calculated in the different currencies are likely to be unequal. This result occurs because sons and daughters require different relative amounts of the two components of parental investment (eggs and provisions). Consider, for example, the population of the solitary wasp *Euodynerus schwarzi* studied by Krombein (1967), in which daughters were observed to receive 2.29 times as much food as sons. Assume for the sake of argument that $p_d/p_s = p'_d/p'_s = 2.29$ (this assumption is made only to simplify the argument; without additional ecological information about the factors constraining reproduction in this wasp population, we cannot say whether 2.29 is an estimate of p_d/p_s, p'_d/p'_s, or some other value appropriate for intermediate levels of egg limitation). Although no estimates are available for e_d/e_s, for most Hymenoptera the only difference between male and female eggs is fertilization just before oviposition, and so e_d/e_s is generally 1.0 (Maeta and Sugiura 1990; for exceptions, see Levin 1966; Beig 1972; Jayasingh 1980). Thus, the ESS proportion of males is 0.696 under food limitation (scenario 1) and 0.500 under egg limitation (scenario 2). The ESS biomass ratio (females/males) is 1/1 under food limitation (scenario 1) and 2.29/1 under egg limitation (scenario 2). Thus, as resource availability increases and egg limitation becomes more likely, the proportion and biomass of females produced will increase.

In these simplest-case scenarios, we have ignored within-population variation in which factor(s) constrain reproductive success of individual females; our calculations concern sex allocation at the population level. We have also assumed that a single factor completely limits reproductive success; thus, parental investment is defined by that factor alone, and other components of parental care make no contribution to parental investment. For example, under strict egg limitation, the ESS proportion of males produced is 0.5 regardless of the degree of sexual size dimorphism or differential feeding requirements of daughters and sons. Resources are sufficiently abundant that the time required to collect provisions does not decrease residual reproductive value. These scenarios are extreme cases; it is likely that real populations of nest-building Hymenoptera fall somewhere between these extremes, with multiple factors playing complementary roles in shaping parental investment. For example, even if resources for provisions are very abundant and eggs become limiting, it is unlikely that provisions will become completely free of cost, because of the possibilities of enhanced risk of predation while foraging, enhanced metabolic costs associated with foraging, and enhanced risks of nest parasitism while the mother is away from the nest foraging. However, previous analyses of sex investment ratios in the Hymenoptera have examined only the first extreme scenario (fitness limited by resources for provisions). Indeed, only by accepting this extreme case do we obtain static, quantitative predictions of numerical sex ratios like those proposed by Trivers and Hare (1976).

A DYNAMIC MODEL OF OFFSPRING PROVISIONING

Here we develop a simple dynamic state variable model (Mangel and Clark 1988) for parental provisioning by a solitary ground-nesting wasp under dual-component investment: mothers invest both eggs and provisions in offspring production. This model illustrates one of our main points concerning the multifaceted nature of parental investment. To keep the model simple, we consider only a single kind of offspring (i.e., we avoid the issue of sex allocation and sexual size dimorphism, and we assume that egg size is fixed).

We envision that if a mother provides f provisions to an egg, then the expected reproductive success of that offspring is $g(f)$. The function $g(f)$ also represents the gain in the mother's lifetime fitness by providing f provisions to that egg. We use

$$g(f) = A - B(f - f_0)^2 \quad \text{for } f > 0 \tag{3}$$

and $g(f) = 0$ otherwise. In this equation, A, B, and f_0 are parameters; f_0 determines the optimal level of provisions, B determines the steepness of the fitness function as the amount provisioned deviates from optimality, and A is a scaling constant (fig. 2). We never expect provisions to be larger than f_0, so that the range of interest is $1 \leq f \leq f_0$.

The state of the mother is characterized by a single variable $X(t)$ that represents the egg complement at the start of period t. Eggs are matured at a constant rate Δ, so that if a mother does not lay an egg during period t,

$$X(t + 1) = X(t) + \Delta\,; \tag{4}$$

whereas if she does lay an egg,

$$X(t + 1) = X(t) + \Delta - 1\,. \tag{5}$$

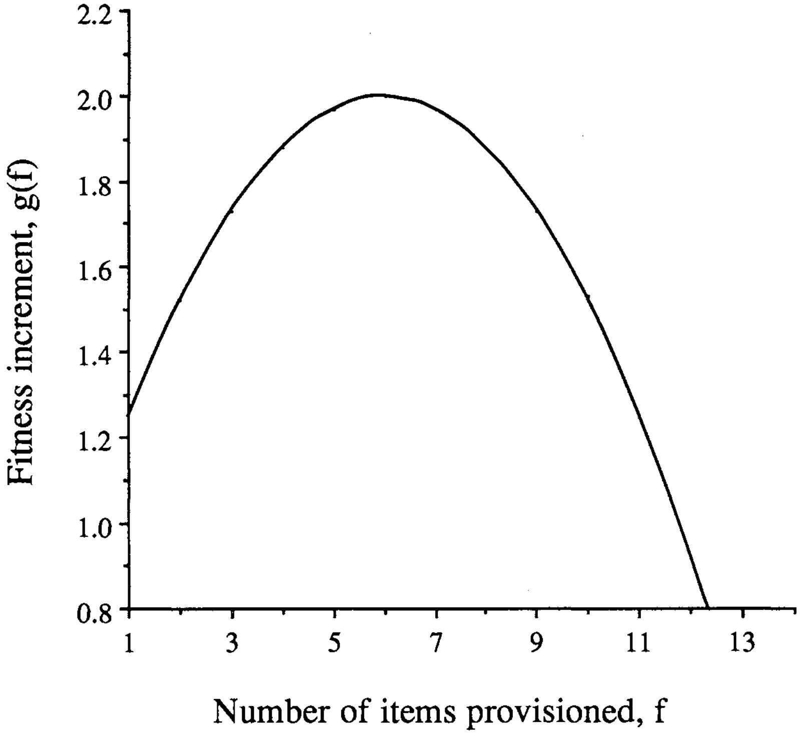

FIG. 2.—The fitness increment to a mother from providing *f* provisions to a cell that she has already dug and in which she will oviposit.

The dynamics (4) are constrained so that $X(t + 1)$ cannot exceed a maximum egg complement $x_{\max}$.

At the start of nesting activity, each mother can choose between resting ("re") or digging ("d") a new cell. If she digs, then following nest construction she will initiate nest provisioning ("pr") and must provide one or more units of provisions (e.g., arthropod prey). Following the completion of provisioning, females return to the resting state. Each activity has a potentially different per unit time mortality (m_{re}, m_{d}, or m_{pr}).

We measure fitness to the provisioning mother in terms of total number of grandchildren and let

$F_{\mathrm{re}}(x, t, T)$ = maximum expected accumulated fitness between t and T for an individual who is currently resting, given that $X(t) = x$,

and

$$F_{\mathrm{d}}(x, t, T) = \text{maximum expected accumulated fitness between } t \text{ and } T \text{ for an individual who has just finished digging a cell, given that } X(t) = x. \tag{6}$$

The maximum is taken over behaviors (rest, dig, and how much to provision). Here T denotes the end of the season.

We derive the dynamic iteration equations for these fitness functions by considering the fitnesses of different options available to individuals. It is easiest to begin with an individual who is currently resting. She may continue to rest, in which case her egg complement increases from x to $x + \Delta$, and she survives to period $t + 1$ with probability $1 - m_{\mathrm{re}}$. Alternatively, she may dig a new cell, which requires τ time units. At the end of this time, she is in the "digging" state with new egg complement $x + \tau\Delta$. Note that we make the simplifying assumption that the rate of egg maturation is the same regardless of the activity. The chance that she survives to the end of the digging is $(1 - m_{\mathrm{d}})^{\tau}$. Comparing the fitness associated with these two behaviors gives

$$\begin{aligned} F_{\mathrm{re}}(x, t, T) = \max[&(1 - m_{\mathrm{re}})F_{\mathrm{re}}(x + \Delta, t + 1, T); \\ &(1 - m_{\mathrm{d}})^{\tau}F_{\mathrm{d}}(x + \tau\Delta, t + \tau, T)]\,. \end{aligned} \tag{7}$$

We assume that upon completing the digging, the female decides how many units of provisions (f) to collect for the offspring and does not oviposit until cell provisioning is completed. Suppose that she can find at most one unit of provisions per time period and that p is the probability that she finds a food item in a single period. We must compute

$$\rho(s|f) = \text{probability that it takes } s \text{ periods to find } f \text{ provisions}\,. \tag{8}$$

It must be true that $s \geq f$. For the mother to find f provisions in s periods, she must find $f - 1$ provisions in the first $s - 1$ periods and one provision in the last period. Consequently,

$$\rho(s|f) = \left(\binom{s-1}{f-1}p^{f-1}(1-p)^{s-f}\right)p = \binom{s-1}{f-1}p^{f}(1-p)^{s-f}\,. \tag{9}$$

Equation (9) is a negative binomial distribution (Feller 1968; Hilborn and Mangel 1996), and the terms can be evaluated by an iterative scheme (Mangel and Clark 1988). First note that

$$\rho(f|f) = p^{f} \tag{10}$$

since the mother can only find the f provisions in f periods if she searches successfully in each period. Subsequent values are computed according to

$$\rho(s + 1|f) = \frac{s}{s - f + 1}(1 - p)\rho(s|f)\,. \tag{11}$$

If a mother takes s periods to find the provisions, she survives the provisioning activity with probability $(1 - m_{\mathrm{pr}})^{s}$. The fitness associated with digging and provisioning a cell is thus

$$F_{\mathrm{d}}(x, t, T) = \max_{f} \sum_{s=f}^{\infty} \rho(s|f)(1 - m_{\mathrm{pr}})^{s}[g(f) + F_{\mathrm{re}}(x - 1 + s\Delta, t + s, T)]\,. \tag{12}$$

Given these assumptions, what is the optimal level of provisioning, f^*? The dynamic model, with parameters as described in the appendix, predicts that f^* is a function of egg complement x and egg maturation rate Δ (physiological variables) and the probability p of finding food in a single period (an ecological variable). We find that as egg complement or egg maturation rate increases, the optimal level of provisions decreases (fig. 3). Conversely, as the probability of finding food increases, the optimal level of provisioning increases. These results can be understood by reference to figure 2. The first provision provides an increment of about 1.2 units of fitness, and the next five provisions combined (leading to f_0) give an additional 0.8 units of fitness. Thus, it is the first provision that provides the bulk of the fitness gain. When egg complement is low or egg maturation rate is low, it pays the female to provide additional provisions because while she is provisioning, she continues to mature eggs. Under these conditions, eggs are relatively limiting, and females move toward maximizing fitness returns per egg (which occurs when offspring are provided six units of provisions). In many cases, females continue to add provisions to cells even though their egg complement is two or more (fig. 3). At high egg complement or fast rates of egg maturation, however, the greater payoff comes from providing a single provision and then moving on to dig the next cell. As the probability of finding food decreases, the optimal level of provisions decreases because it takes longer for the mother to find those provisions, and at the end of the provisioning period she has additional eggs. Under these conditions, resources for feeding offspring are limiting, and females move toward maximizing fitness returns per unit of provisions (which occurs when offspring are provided just one unit of provisions). Thus, our results demonstrate the importance of the multifaceted nature of provisioning. The optimal level of provisioning changes as female lifetime reproductive success shifts between the constraints of egg production and the limited availability of resources for feeding offspring.

PREDICTED AND OBSERVED PROVISIONING AND SEX RATIO PATTERNS

Multifaceted parental investment leads to the general prediction that numerical sex ratio and/or total biomass ratios will, under strict Fisherian conditions (i.e., panmixis, Mendelian segregation of sex alleles, additive offspring costs), be sensitive to environmental conditions (see also Longair 1981; Tepedino and Torchio 1982*a;* Danks 1983; Clutton-Brock 1991; Brockmann and Grafen 1992). If parental investment reflects costs of eggs, provisions, space within nest sites, defense, and perhaps other factors, then overall reproductive costs and hence sex investment ratios will be sensitive to changes in the relative availability of these different resources. This general prediction can be decomposed into a family of more specific hypotheses.

Solitary Hymenoptera

We can make two simple and readily testable hypotheses for solitary, sexually size-dimorphic species. First, an increase in the availability of resources for provisioning offspring will favor increased provision masses per offspring. Second, for

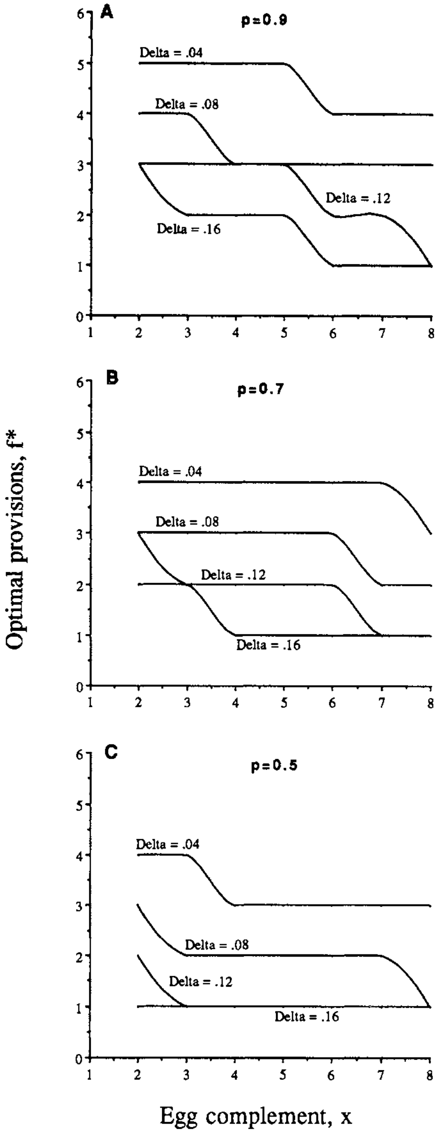

FIG. 3.—The optimal number of provisions to provide to each offspring when parental investment is made up of both food provisions for offspring and nutrients invested in eggs. Optimal parental behavior is plotted as a function of the number of mature eggs available in the ovaries (x) and the rate of egg maturation (*delta*). Solutions are shown for three levels of availability of food used to provision offspring (p, the probability of finding food in a single time period): A, $p = 0.9$; B, $p = 0.7$; C, $p = 0.5$. All results are stationary solutions of equation (12); that is, behavior is examined for individuals that are sufficiently young that behavior does not change across adjacent time steps. The optimal number of provisions is high when food is abundant (compare panels A, B, and C) or when current egg availability (x) is low and the ability to replenish supplies is limited (delta is small).

sexually size-dimorphic species in which females receive more provisions than males, an increase in the availability of resources for offspring provisions will lead to a less male-biased numerical sex ratio. (Analogously, for species in which males receive more provisions than females, an increase in the availability of resources for offspring provisions will lead to a less female-biased numerical sex ratio.) In the limiting case of superabundant resources, the ESS proportion of sons approaches 0.5 regardless of the relative feeding requirements of males and females. What evidence exists for such resource-driven shifts in provision masses and numerical sex ratios?

A series of observational and experimental studies of sexually size-dimorphic solitary bees and wasps has documented shifts in provision masses, offspring sizes, and numerical sex ratios under conditions of varying resource availability (table 1). Positive relationships generally have been observed between resource availability and (1) the amount of food provisioned per offspring, or offspring size (seven of 10 studies, with the remaining three studies showing no relationship), and (2) the proportion of female offspring produced (11 of 11 studies). These results are consistent with the predictions of the multifaceted parental investment model.

Social Hymenoptera

Our predictions for an increase in provision masses and the proportion of female offspring in response to an increase in resource availability can be extended directly to those social Hymenoptera that are not subject to brood limitation. However, when numbers of brood are fixed, Smith and Fretwell's (1974) solution of increasing offspring number in response to increasing resources is no longer possible. In this case, the optimal amount of food provided to males and females should increase to the point where if they were any larger, they would actually start to lose fitness (p'_s and p'_d in fig. 1, respectively). If male and female fitnesses increase at different rates, excess resources should be allocated to the two sexes so as to gain an equal return per unit of resource in either sex. However, there is no intrinsic reason that this allocation should have a particular ratio; it may not be that resources are divided equally across the sexes or in the 3:1 ratio of investment predicted by Trivers and Hare.

We would argue that for most ant species (for which sex ratio shifts have been most intensively studied and for which brood limitation may be common), the greatest fitness increments will be realized when excess food resources are allocated to females. Size is probably much more closely affiliated with fitness in females than it is in males. For a male to be successful, he must find and mate with a female. Males of most species of ants are not known to engage in any type of competition for females other than a scramble competition, and large male size has not been observed to be a consistent advantage in scrambles (Hölldobler and Wilson 1990). On the other hand, females not only must survive the mating flight, but in many species they must also raise the first brood of workers solely from their stored energy reserves. This demand appears highly stressful for females, and many colonies fail at this stage (review in Rissing and Pollock 1988). Thus, it is probably fair to assume that in most species male fitness reaches its maximum more rapidly with increasing size than does female fitness. For example, Keller and Passera (1989), in a cross-species comparison, showed that female size closely predicted whether species exhibited independent colony founding or whether queens needed assistance from their parental colony. Male size is less variable across species (J. J. Boomsma, L. Keller, and M. G. Nielsen, unpublished manuscript) and within species across populations (Sundström 1995*a*), which suggests narrower size optima for male reproductive strategies.

Thus, as presented in figure 1, we predict that when resources are unlimited, individual daughters will get a proportionally greater share of provisions compared to individual sons ($p'_d/p'_s > p_d/p_s$). At an individual colony level, this would predict an increasing female bias with increased food resources. At a population level, this would predict a positive correlation between female bias and total amount of sexual production (the latter variable reflecting the overall availability of resources). Our predictions for brood limitation in social species are therefore parallel to our predictions for egg limitation in solitary and social species: in both cases, increasing resource availability is predicted to lead to increased investment in females. Conversely, resource-stressed colonies should tend to produce more male-biased sex investment ratios.

In a study controlling for worker number, a significant positive relationship was found between the amount colonies invest in sexuals and the proportional female investment across a sample of 24 ant species (Nonacs 1986*b*). Besides this cross-species comparison, there have been a number of correlative studies of individual species under field conditions and several experimental manipulations of resource levels in both the laboratory and the field (table 2). In 10 of 12 studies of ants, proportional investment in females increased with more resources. In two studies of ants in which data were available, the size of sexuals was also larger in habitats with putatively higher food abundance. Two studies of primitively social bees in the genus *Lasioglossum* have also shown that the mass of pollen balls provisioned increases as resource availability increases because of an increased ratio of foraging to ovipositing bees. These results are consistent with the predictions of the multifaceted parental investment model.

DISCUSSION

Tests of Fisher's (1930) theory of equal investment in the production of each sex in a panmictic population hinge on measurements of both the numerical sex ratio and the cost of producing individual female and male offspring. Theoretical and empirical analyses of sex investment ratios in the nest-building Hymenoptera have assumed that parental investment could be quantified by measuring the cost of feeding the developing young. Our analysis of the biology of solitary and social nest-building Hymenoptera suggests, however, that parental investment is fundamentally multifaceted, including not only the cost of provisions but also the cost of the nest, the egg, and possibly the defense of offspring. Egg costs in particular appear to be a very general component of parental investment. Because the relative importance of each component of parental investment is a function of the availability of resources in the environment, the relative costs of producing female and male offspring will vary with changing ecological conditions. Sex

TABLE 1

STUDIES OF SOLITARY NEST-BUILDING WASPS AND BEES EXAMINING THE RELATIONSHIP BETWEEN RESOURCE AVAILABILITY AND PARENTAL PROVISIONING OF OFFSPRING AND SEX ALLOCATION

SPECIES	TYPE OF STUDY	CAUSE(S) OF CHANGE IN RESOURCE AVAILABILITY	RELATIONSHIP BETWEEN RESOURCE AVAILABILITY AND: Food per Offspring or Offspring Size	RELATIONSHIP BETWEEN RESOURCE AVAILABILITY AND: Proportion Females	REFERENCE
Osmia lignaria propinqua (Megachilidae)	Observational, field	Decreasing flowers and bee aging within one generation	+	+	Torchio and Tepedino 1980
Osmia lignaria propinqua (Megachilidae)	Observational, greenhouse	Bee aging within one generation decreases foraging efficiency	+	+	Tepedino and Torchio 1982*b*
Osmia bruneri (Megachilidae)	Observational, greenhouse	Bee aging within one generation decreases foraging efficiency	0	+	Frohlich and Tepedino 1986
Osmia cornifrons (Megachilidae)	Observational, laboratory	Bee aging within one generation decreases foraging efficiency	+	+	Sugiura and Maeta 1989
	Experimental, laboratory	Manipulations of provisions masses; larger bees were less likely to be resource limited	+	+	
	Semiexperimental, laboratory	Accidental transient shortage of flowers	0	+	

Osmia taurus (Megachilidae)	Semiexperimental, laboratory	Bees caged with minimal floral resources	ND	+	Maeta 1978
Osmia cornifrons (Megachilidae)	Semiexperimental, laboratory	Bees caged with minimal floral resources	ND	+	Maeta 1978
Hoplitis anthocopoides (Megachilidae)	Observational, field	Decreasing flowers	0	ND	Strickler 1982
Dieunomia triangulifera (Halictidae)	Observational, field	Between-year variation in flower availability	ND	+	Minckley et al. 1994
Cerceris arenaria (Sphecidae)	Observational, field	Between-year variation in prey availability	+	ND	Field and Foster 1995
Trypoxylon politum (Sphecidae)	Observational, field	Between-generation variation in prey availability	+	+	Brockmann and Grafen 1992
Trypoxylon politum (Sphecidae)	Observational, field	Presence of male guards increases female foraging efficiency	+	+	Brockmann and Grafen 1989

NOTE.—Females are larger than males for all species studied. ND, No data; 0, no relationship; +, positive relationship.

TABLE 2

STUDIES OF ANTS AND SOCIAL NEST-BUILDING BEES EXAMINING THE RELATIONSHIP BETWEEN RESOURCE AVAILABILITY AND SIZE OF OFFSPRING AND SEX ALLOCATION

SPECIES	TYPE OF STUDY	CAUSE(S) OF CHANGE IN RESOURCE AVAILABILITY	RELATIONSHIP BETWEEN RESOURCE AVAILABILITY AND:		REFERENCE
			Food per Offspring or Offspring Size	Proportion Females	
Lasioglossum duplex (Halictidae)	Observational, field	Variation in the number of foragers relative to the number of egg layers	+	ND	Sakagami and Hayashida 1960
Lasioglossum zephyrum (Halictidae)	Observational, laboratory and field	Variation in the number of foragers relative to the number of egg layers	+	ND	Batra 1964, 1966
Formica aquilonia (Formicidae)	Observational, field comparison across populations	Differences in habitat quality	ND	+	Rosengren and Pamilo 1986
Formica podzolica (Formicidae)	Observational, field comparison across colonies	Colony size: large colonies have more resources available for production of sexuals	ND	+	R. Savolainen and R. J. Deslippe, unpublished data
	Experimental, field comparison across colonies	Colonies receive food supplementation	ND	+	Deslippe and Savolainen 1995
Formica rufa (Formicidae)	Observational, field comparison across populations	Differences in habitat quality	ND	+	Rosengren and Pamilo 1986

Harpagoxenus sublaevis (Formicidae)	Observational, lab comparison across colonies	Differences in slave (= worker) number, resulting in differences in productivity	ND	0	Bourke et al. 1988
Lasius alienus (Formicidae)	Observational, field comparison across populations	Differences in habitat quality	ND	+	Brian 1979
Lasius niger (Formicidae)	Observational, field comparison across populations	Differences in habitat quality due to presence of competing species *Lasius flavus*	ND	+	Boomsma et al. 1982
Leptothorax acervorum (Formicidae)	Experimental, lab comparison across colonies	Colonies given access to differing levels of protein	ND	+	Buschinger and Pfieffer 1988
Leptothorax longispinosus (Formicidae)	Observational, field comparison across populations	Differences in resource stress across habitats	+	+	Herbers 1990; Backus 1993
Leptothorax longispinosus (Formicidae)	Experimental, lab and field comparison across colonies	Colonies food-supplemented with dead flies	ND	–	Backus and Herbers 1992
Myrmica punctiventris (Formicidae)	Observational, field comparison across populations	Differences in habitat quality	+	+	Banschbach and Herbers 1996*a*, 1996*b*
Tetramorium caespitum (Formicidae)	Observational, field comparison across populations	Differences in habitat quality	ND	+	Brian 1979

NOTE.—In the case of the observational field studies, the causes for changes in resource availability were inferred and not measured by the authors. ND, No data; 0, no relationship; +, positive relationship; –, negative relationship.

allocation will then change to maximize fitness returns per unit of the limiting resource (whether it be provisions, eggs, or space for cell construction).

Our multifaceted model of parental investment predicts increases in the amount of food per offspring and a shift in sex ratio toward the production of more females (or a greater relative biomass of females for some ants) as the availability of resources for feeding offspring increases. Although critical field experiments manipulating resource levels are rare, a large body of observational studies conducted with a diverse array of species has documented the behavior patterns predicted by our model.

Resource Availability and Parental Investment

How do the predictions of our multifaceted parental investment theory compare with predictions of other models for parental investment and sex allocation as functions of resource availability? Here we attempt to relate our model to other general theories that have been used to explain resource-mediated variation in sex investment.

Solitary species.—A number of authors have explained seasonal shifts in sex ratios by arguing that when resources become more limiting, a greater proportion of the less expensive sex (males) is produced (Maeta 1978; Frohlich and Tepedino 1986; Danforth and Visscher 1993). Although such a behavioral response may seem intuitively reasonable, we cannot find a basis in theory for a *general* prediction of a sex ratio response to resource availability under a single-component model of parental investment. If parental investment is comprised solely of provisions for offspring (as has been assumed), the ESS Fisherian sex ratios are simply a function of the *relative* costs of providing provisions to females and males (eq. [1]). The level of resource availability influences only the average *absolute* costs of provisions, not the relative costs, and thus will have no influence on sex ratio. A single-component model of parental investment likewise does not predict that the mean quantity of food provisioned for offspring will change in response to changing resource availability.

In some animals, including many birds and mammals, parental survival during or immediately after the period of parental care may be an inverse function of the rate of parental investment. In this case, the optimal parental investment strategy must consider parental condition, with the result that the optimal amount of food to provide offspring may decrease during periods of resource scarcity. Indeed, parents may even choose to reduce brood size through infanticide or simply abandon broods altogether (Clutton-Brock 1991). When such species have sexually size-dimorphic young, they may also be selected to adjust sex ratios with changing resource availability. In the Hymenoptera, however, these sorts of considerations do not generally apply. Unlike the case for many birds or mammals that use an entire breeding season to provide care for a single group of offspring, solitary hymenopterans generally complete many cycles of offspring provisioning within a single season. Thus, the parent is not choosing a rate of outlay of parental investment but rather how to divide investment between successively produced young (e.g., when to cap one cell and initiate the next). A single-faceted model of parental investment predicts an optimal amount of food for each offspring (Smith and Fretwell 1974), again independent of the level of resource availability. Changing resource availability results in changes in the number of offspring produced, not the per-offspring level of investment. For the same reason, models of conditional sex allocation (Trivers and Willard 1973; Charnov 1982) do not predict shifts in sex ratio with changing resources for the nest-building Hymenoptera.

When the lifetime fecundity of nest-building hymenopterans is very low (as may occur for some solitary species during years of very limited resources), or if resources cannot be redistributed among offspring, the conditional sex allocation theories of Trivers and Willard (1973) and Charnov (1982) may become applicable. These conditions may occur because of the possibility that returns from investment in a given sex become functionally nonlinear (Frank 1987*a*, 1990, 1995). Nonlinearity can create deviations from Fisherian sex allocation whose magnitude increases as total fecundity drops and as the differences between the fitness return curves of individual males and females become greater (Frank 1987*a*). Population sex allocation may be biased toward either sex (Frank 1987*a;* Frank and Swingland 1988). Frank (1995) has shown how nonlinear fitness return curves can produce associations between the degree of sexual size dimorphism and the population sex allocation ratio, when parental investment is defined by the amount of food provided to offspring. Additional work is needed to examine the simultaneous effects of multifaceted parental investment and nonlinear fitness returns.

Increases in provision masses and enhanced production of females by hymenopterans have also been predicted in response to the enhanced availability of resources made possible by male guards (Brockmann and Grafen 1989) or workers at the nest (Frank and Crespi 1989; see later discussion also). These theories emphasize the adaptive significance of changes in parental investment to the male guards and workers, both of which benefit through enhanced relatedness to female versus male offspring. These hypotheses are entirely complementary to those that we propose here: what our model shows is that the egg layer also benefits from exactly these same shifts in sex allocation. In addition, the proximate mechanisms, or ''rules of thumb,'' by which Brockmann and Grafen (1989) and Frank and Crespi (1989) envision that sex investment responses may be achieved are quite reasonable models for proximate rules by which the predictions of our multifaceted parental investment model might be implemented. Male guards and workers may simply be exploiting a conditional strategy of maternal investment that is made optimal by the need to balance the costs of multicomponent parental care.

Although we can find no general theory that explains the resource-mediated skews in sex investment in the solitary nest-building Hymenoptera, a number of hypotheses have been erected that seek explanations in *species-specific* aspects of selective forces influencing parental investment. For example, parental investment may vary with the parent's risk of mortality during cell provisioning (Torchio and Tepedino 1980), when offspring size affects overwintering survivorship (Torchio and Tepedino 1980; Tepedino and Torchio 1982*b*), with variation in the risk of parasitism (Alcock et al. 1977; Torchio and Tepedino 1980; Danforth and

Visscher 1993), or seasonally in partially bivoltine species (Seger 1983; Brockmann and Grafen 1992). These ideas complement our theory.

Social species.—The social Hymenoptera, particularly ants, have been a popular focal group for studying sex investment ratios. Trivers and Hare (1976) first suggested that social species should show a female bias because of kin-selected conflict between queens and workers. Their data and those of subsequent authors have demonstrated that a population-wide female bias does appear to exist (Nonacs 1986*a;* Boomsma 1989; Pamilo 1991), although in most species individual colonies tend to produce highly male- or female-biased sex ratios (Nonacs 1986*b*).

Such sexual specialization is consistent with our hypothesis of multifaceted parental investment but may also result from other processes. Boomsma (1993) formulated a hypothesis for sexual specialization in which the multiple facets of investment are different components of the offspring provisions. If the production of females and males requires different combinations of essential nutrients, then mothers (or colonies) could favor specializing in the sex that is better suited to the locally available resources. Although no species' sex ratios are known to be influenced in this manner, Boomsma suggested that ant colonies tending aphids may produce more females because of their increased access to carbohydrates.

Boomsma and Grafen (1990, 1991) proposed that sexual specialization could also arise in species with variable social systems that produce different relative relatedness asymmetries (RRAs) between males and females across colony types. In such species it is very unlikely that any single population sex ratio will be stable for all colonies; therefore, some (or all) colonies will be selectively favored to specialize in the sex that is rare from their point of view.

Although the RRA model and the multifaceted parental investment model both predict the observed sex specialization in colony-level reproduction, they differ in their underlying mechanisms. The RRA model predicts a causative relationship between a colony's social structure and the sex ratio it produces and makes no predictions for influences of the amount of food available on sexual reproduction. Our model proposes that resource availability will be an important predictor of the sex ratio any given colony will produce and makes no predictions for the effects of relatedness asymmetries.

Some species fit the pattern predicted by RRA. Colonies in which the workers have a relatedness asymmetry between female and male sibs produce more female-biased broods than do colonies in which relatedness asymmetry is reduced or absent (Mueller 1991; Sundström 1994, 1995*b;* Evans 1995). However, other species exhibit split sex ratios that do not match the underlying RRAs (Pamilo and Seppä 1994) or have split sex ratios where no variance in social systems exists (e.g., fire ants; L. Keller, personal communication).

Consistent with the multifaceted parental investment hypothesis is the observed association between resources and sex ratios across a wide range of species (table 2; Nonacs 1986*b*). A similar pattern would be predicted by the RRA model only if resource-stressed colonies also have fundamentally different social systems than well-fed colonies.

If resource environments are more variable in time than are colonies' social environments, then the RRA model predicts more temporal stability in colony sex investment ratios than does the multifaceted investment model. The detailed, long-term studies needed to test this prediction are both difficult and time-consuming, so, not surprisingly, they are rare. Herbers (1979) followed 18 colonies of *Formica obscuripes* for 3 yr, found extreme between-colony and year-to-year variation in sex ratios, and could not predict colony-level investment patterns. Although Herbers had no measures for either relatedness or resource availability, it seems unlikely that relatedness asymmetries could have fluctuated rapidly enough to produce such a pattern.

The RRA models and our model certainly are not mutually exclusive. Social insect colonies may alter sex ratios in response to both their social and foraging environments (see Sundström 1995*b*), and it remains to be seen to what degree both operate as general principles. Besides the RRA models and the multifaceted parental investment model, there are two other recent attempts to explain the sex specialist phenomenon. However, both of these hypotheses may be more applicable as species-specific rather than general explanations.

Frank (1987*b*) predicted that because of local mate competition (LMC), a pattern of sexually specialized colonies would develop even when the effects of LMC were not measurable at a population level. One prediction was that colonies should invest a constant amount in males, independent of resources. This would positively correlate female investment and total investment in that once the constant level of investment in males was achieved, all further investment should be channeled into females. When specifically tested for, such a pattern of investment has been observed in *Messor aciculatus* (Hasegawa and Yamaguchi 1995) but not in *Leptothorax longispinosus* (Herbers 1990). The converse of the constant male hypothesis is the constant female hypothesis, which states that if daughter colonies are in resource competition, excess resources should be biased toward males (Pamilo 1991). Evidence exists for such an outcome in *Leptothorax acervorum* (Chan and Bourke 1994) and polygynous colonies of *Formica truncorum* (Sundström 1995*b*), and it may be a more common effect in polygynous, fissioning species than previously realized (A. F. G. Bourke, personal communication).

Crozier and Pamilo (1993) suggested that colonies with few resources to invest in sexuals should invest them in males because they are smaller per capita. Thus, if a colony experiences a shortage in food, a male can be abandoned without losing as much invested resource capital. However, this explanation is likely to affect colonies with very little to invest and therefore unlikely to affect the population sex ratio appreciably (except in the very unlikely case that most colonies in an area are extremely stressed). Therefore, one would not necessarily predict the observed pattern of extreme female bias in the most productive colonies (Nonacs 1986*a*).

In sum, sex ratio theory as applied to social insects over the last 20 yr has provided viable explanations for a variety of phenomena, but it still has not convincingly explained why food resource level should affect sex investment ratio. The ideas presented here that parental investment has several components and that at times, owing to ecological conditions, the components should vary in their strength of effect go far in providing a mechanistic explanation of the observed patterns. This is not to say that female-biased sex ratios as predicted by

Trivers and Hare (1976) are actually ecological artifacts. Ultimately, the observed population-level sex ratio should reflect the kin-selective optima of the competing interests in the social colonies. However, what an individual colony may do may be as much influenced by its immediate environment as by its social dynamics.

Multifaceted Parental Investment: Beyond the Nest-Building Hymenoptera

Our model highlights the difficulty of estimating the relative costs of producing a male or female offspring when parental investment is comprised of more than one component. Clutton-Brock (1991) discusses an analogous situation for red deer, in which preweaning costs of males are greater than those of females, but males disperse before females, and additional costs are incurred by mothers caring for their philopatric daughters (Clutton-Brock et al. 1982). Depending on the magnitude of postweaning costs of females, the overall costs of producing a son may be greater than, equal to, or less than that of producing a daughter. Multidimensional investment also occurs in an unusual group of insect parasitoids, the heteronomous hyperparasitoids, in which male and female offspring develop in different types of hosts that may vary in availability. Some heteronomous hyperparasitoids invest two types of resources in offspring production: eggs and time to locate hosts. In a manner similar to that discussed here for nest-building Hymenoptera, changing ecological conditions may change which resource (eggs or time) is limiting, with sex allocation predicted to change accordingly (Godfray and Waage 1990; Godfray and Hunter 1992; Hunter and Godfray 1995).

Geber and Charnov (1986) examined reproduction in hermaphroditic plants when resources are not equally substitutable between the two sex functions. They predicted that total allocation to female function (ovules and ovary, seeds, and fruit) may be greater than total allocation to male function (pollen) when reproduction is constrained by resource availability early during reproduction, when pollen and ovules are produced. Our prediction of female-biased biomass ratios in the Hymenoptera when mothers are egg limited is directly analogous to this result for hermaphroditic plants.

The theory developed here for changes in optimal parental investment with shifting resource availability is most similar to the multiple resource pool model of seed provisioning developed by McGinley and Charnov (1988). McGinley and Charnov (1988) and we predict that the optimal amount of resources to provision per offspring will change in response to changing resource availability, in contrast to the static predictions made by the single resource pool model of Smith and Fretwell (1974). Empirical studies of seed provisioning have, however, largely failed to support McGinley and Charnov's predictions (Lalonde 1988; Dawson and Ehleringer 1991; see also Tessier and Consolatti 1991 for a similar result in a study of *Daphnia pulicaria*). A possible explanation for these discrepancies again lies in the difficulties of quantifying investment; although the McGinley and Charnov model recognizes the distinction between carbon and nitrogen allocations, other nutrients may also be important (e.g., phosphorous) (Lalonde 1988). Seed provisioning may prove to be more complex than what we have described in the insect cases here.

Throughout our analysis of parental investment in the Hymenoptera, we have implicitly assumed that food provided for offspring can be considered a unidimensional resource. Although this assumption may be appropriate for wasps that provide arthropod prey to their offspring, bees that provision both pollen and nectar (and potentially other types of food, e.g., floral lipids) (Roubik 1989) may have functionally multifaceted parental investment even if their lifetime reproductive success is limited solely by the availability of resources for feeding offspring. (Boomsma [1993] has proposed a similar hypothesis for ants, as discussed above.) If, for example, pollen and nectar availability vary at least partially independently (e.g., Harbo 1986), then the optimal amount of food to provide each offspring may vary with resource availability, as predicted by McGinley and Charnov (1988). Sex allocation would not be influenced unless male and female offspring received different nectar-to-pollen ratios.

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APPENDIX

TABLE A1

Parameters and Their Values for Computations in the Dynamic Model of Offspring Provisioning

Parameter	Definition	Value
A	Constant in offspring payoff	2
B	Steepness of deviations in fitness from optimality	.03
f_0	Number of provisions at which offspring fitness is maximized	6
$x_{\max}$	Maximum egg complement	8
Δ	Egg maturation rate	Varies, but <1
m_{re}	Probability of mortality in one unit of time while resting	.001
m_{d}	Probability of mortality in one unit of time while digging	.002
m_{pr}	Probability of mortality in one unit of time while provisioning	.003
T	End of the season, at which time fitness is assessed	800
τ	Time to dig a cell	4
p	Probability of finding a food item in a single period	Varies

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