1982), and all other species in the same subgenus, *Trypargilum* (Peckham & Peckham 1895, 1898; Rau & Rau 1916; Rau 1928; Hartman 1944; Kurczewski 1963; Lin 1969; Cross et al. 1975; Coville 1979, 1981, 1982; Coville & Coville 1980; Coville & Griswold 1983, 1984; Hook 1984), and in a few other species of sphecid wasps (Tsuneki 1970; Peckham et al. 1973; Eberhard 1974; Peckham 1977; Alcock et al. 1978; Kimsey 1978) males are long lived, nearly as large as the females and they guard the females' nests for extended periods of time, copulating repeatedly with the same individual. In addition, in pipe-organ mud-daubing wasps, we have observed some intriguing behavioural patterns which suggest that this evolutionary conflict may be translated into direct aggression between the sexes. Do males that expend effort in guarding the females' nests influence the sex of the offspring laid, or can males preferentially choose to guard female brood?

BACKGROUND, STUDY LOCATIONS AND METHODS

Female *T. politum* work alone to construct their tubular mud nests, gathering the mud, carrying it to the nest site in their mandibles and applying it to a smooth, vertical surface (Cross et al. 1975; Brockmann 1980). Over the next 1–2 days, the female provisions the nest with several araneid spiders which she captures and paralyzes with her sting. After stinging, she often feeds for a few minutes on fluids from the mouth of the spider (malaxating; see also Steiner 1982) before carrying it to the nest and packing it into the top of the brood cell (away from the nest entrance). Spider-packing involves pushing on and vibrating the provisions with the mandibles and has the effect of keeping the spiders firmly in place. Although the wasps are normally solitary with one male and one female occupying the nest during provisioning, there are frequent nest usurpations by both sexes, occasional joint occupations by more than one female and even some intraspecific brood parasitism (Brockmann 1980). Females also maraud the nests of other females, removing and malaxating the spiders. After the provisioning of a brood cell is complete, the female copulates with the male, lays a single egg on the accumulated spiders, and constructs a partition which separates this brood cell from the next one down in the nest. The duration of the pre-oviposition period is defined from the moment the female brings in the last spider to the point at which she leaves to collect mud for the partition. In about 2 days, the egg hatches into a larva which consumes the provided food in about 10 days and then spins a cocoon (Cross et al. 1975; personal observation). The larva may then pupate immediately and emerge later in the same summer (direct development) or, alternatively, it may enter diapause (delayed development), remain as a larva in a cocoon (prepupa) over the winter, and then pupate in the following spring (Seger & Brockmann 1987). Adults do not live for more than about 5 weeks and all adults die by the end of the summer (i.e. these wasps overwinter only as prepupae).

T. politum were observed in natural nesting aggregations under bridges in Alachua County near Gainesville, Florida. With the help of field assistants, we observed the nest-related activities of wasps through four nesting seasons (June–September 1979–1982). During the course of a summer, several hundred wasps nest at the two principal sites, Hatchet Creek ('HC', County Road 225) and Rocky Creek ('RC', County Road 121), with fewer at a bridge 500 m from HC ('NF', County Road NE 30B). A second bridge over Rocky Creek ('AB', County Road NW 18C; 1 km from RC) was used for censusing and collecting eggs for a study on wasp development in 1981 and 1982.

Observations and Measurements

Each nest was marked individually and each brood cell was indicated with colour-coded, paper tags glued to the surface. A wasp was captured when it first appeared at the nesting area either by letting it back out of its nest into a test-tube (females) or by chasing it into the tube with a small stick inserted into the nest (males). We measured each individual with a caliper while holding it in a restraining device. In 1981 and 1982, size was measured as thorax width across the tegulae at their widest point. In 1979, size was measured as body length and in 1980, adults were not measured in the field. Each wasp was marked uniquely with dots of enamel paint on the thorax (males) or tiny numbered tags glued to the thorax (females). Wasps filled in observation holes that we poked in their nests, but when they were working on the last brood cell in a nest, they often hung outside where it was possible to observe them closely. Once we

were familiar with their behaviour, we could identify the actions of adults while inside the nest.

Reproductive success was assessed by opening each brood cell in a nest, removing the cocoon (with its larva or prepupa inside), measuring the length of the brood cell (measured from the bottom of the plug of the preceding brood cell to the top of the plug for this brood cell) and the length of the cocoon along its longitudinal axis. It was then stored in a test-tube which was kept in an outdoor environment similar to that under a bridge. In the spring the larvae pupated and the adult wasps emerged in their test-tubes during May. Each adult was measured, sexed, and released at its natal site within a few hours of emergence. During the first 3 years of this study, we only measured the reproductive success of overwintering wasps, since we opened brood cells during the spring (March and April; at the time we did not know that there was a second generation), but in the summer of 1982, we gathered data on reproductive success from both the overwintering and summer generations. We did this by removing each cocoon 3 weeks after the brood cell had been closed by the female. In this way we then knew the size and sex of all wasps hatching from the nests we had observed the previous summer (or whether the brood cell had been parasitized).

Adult weight was difficult to measure since we tried to spend as little time as possible handling the animals. Since adult weight was well correlated with thorax width (1980: $r=0{\cdot}64$, $N=135$; 1981: $r=0{\cdot}75$, $N=130$; 1982: $r=0{\cdot}81$, $N=590$; $P<0{\cdot}0001$ for each year), we used the latter as a measure of adult size. Similarly, since the length of the pupal case was well correlated with its weight (1980: $r=0{\cdot}72$, $N=183$; 1981: $r=0{\cdot}83$, $N=1287$; 1982: $r=0{\cdot}86$, $N=871$; $P<0{\cdot}0001$ for each year) and with the thorax width of the emerging adult (1980: $r=0{\cdot}57$, $N=135$; 1981: $r=0{\cdot}74$, $N=124$; 1982: $r=0{\cdot}79$, $N=594$; $P<0{\cdot}0001$ for each year), this provided a useful measure for the size of the offspring.

To measure the relationship between maternal provisioning and offspring size and sex, we opened sealed brood cells just after the egg had been laid (conducted at site AB in 1982) and removed and weighed the spider provisions. The delicate egg and the spider to which it was attached were placed in an enclosed plastic dish until the larva had moulted into the second instar. Each larva was then placed in a mud nest and reared with the provisions it had been given by its mother at 27° C (in constant dark) in a laboratory environmental chamber. It proved necessary to rear the larvae in *T. politum* mud nests (which had been removed from the field and cleaned out) because the larvae incorporated mud from the lining of the brood cell into their cocoons. After a larva had spun its cocoon, we weighed any remaining food, measured the length of the prepupal cocoon and stored it in the same outdoor environment as the cocoons collected in the field. When the adults emerged in the following spring, they were weighed, measured and sexed.

Three kinds of observations form the basis of this study. (1) If the last partition in a nest were more than 2 cm from the nest entrance, then wasps were likely to use that nest (i.e. it is 'available' for use), so it was censused twice daily. Census records gave us the day each brood cell was initiated, the day of completion and often the male and female most closely associated with the nest. (2) Each day some nests were chosen opportunistically and observed carefully. These observations gave us the time that each brood cell was initiated and closed, most of the occupants and visitors associated with the nest, in short, whatever happened at the nest. (3) Some brood cells were the subject of experimental manipulations and were observed intensively (described below). All behavioural observations were recorded in the field as running-commentary notes (in 1980, copulation and fight sequences were recorded on tape) which were coded, entered into the computer, checked for accuracy and sorted. This meant that we had biographies on individual wasps and histories of particular brood cells. Because of the large numbers of wasps and nests involved, the data are somewhat spotty, i.e. we might have an intensive record on a wasp for two brood cells and then only occasional citings thereafter, or we might have intensive observations on brood cells 1 and 3 but only a brief note for cell 2.

Experimental Manipulations

Three field experiments were conducted to examine the effect of males and provisioning rates on female behaviour and sex-allocation decisions. In each experiment, brood cells that had been altered by experimental and control treatments were compared.

(1) Experimental removal of the male during pre-oviposition period. To examine the effect of the male on the pre-oviposition behaviour of the