Factors affecting female-biased sex ratio in a trap-nesting wasp, *Trypoxylon malaisei*

Abstract We examined the female-biased sex ratio of a trap-nesting wasp *Trypoxylon malaisei* considering the following factors: (1) local mate competition (LMC), (2) resource quality, (3) partial bivoltinism, and (4) presence of constrained females. The sex ratio (expressed as male ratio) at emergence was strongly female biased, i.e., 0.30 and 0.19, in terms of the number and investment, respectively. To evaluate the primary sex ratio, we analyzed the data from nests where all the offspring successfully emerged, excluding nests composed of single-sex offspring. The primary sex ratio was also female biased, at 0.33 and 0.21, in terms of the number and investment, respectively. LMC was highly responsible for the female-biased sex ratio because both the nonrandom oviposition sequence [females at inner cells and male(s) at outer cells] and earlier emergence of males allowed sib-matings to occur. In contrast, the other three factors little affected the female-biased sex ratio: the sex ratio was fairly constant when resource quality (nest size) varied, partial bivoltinism was extremely rare or absent, and constrained females were absent or did not reproduce at all.

Key words Constrained female · Local mate competition · Partial bivoltinism · Resource quality · *Trypoxylon malaisei*
factors lead to female-biased sex ratios. Considerable efforts have been devoted to analyze these factors separately, but not comprehensively (but see King 1996).

The life history of trap-nesting wasps provides interesting information to discuss the sex ratio phenomena from an evolutionary point of view: a mating group is highly structured spatially, at least in some species (Cowan 1979, 1981; Chapman and Stewart 1996), resource availability for mothers varies considerably (Krombein 1967), constrained females may exist, and partial bivoltinism sometimes occurs (Brockmann and Grafen 1992). Thus, all four hypotheses just described would be possible. We examined the sex ratios in a trap-nesting wasp, *Trypoxylon malaisei*, and tested the validity of these four hypotheses in this species.

**Materials and methods**

**Study area**

The study area, extending over approximately 10 km north to south and 3 km east to west, was located along the eastern hillside of Kyoto City, Western Japan. Within the study area we chose 12 study sites: site 1, sites 4–9, and sites 11–15 (Fig. 1). All the study sites were chosen among places that were facing a secondary forest, mainly consisting of oak (*Quercus serrata*), Japanese red pine (*Pinus densiflora*), and Japanese cedar (*Cryptomeria japonica*), and the nests were protected from rainfall by wooden buildings such as a shrine or barn, because the wasp preferentially constructed nests in such places (Itino, personal communication). The study was done for 5 consecutive years, 1992–1996, but we sometimes chose different study sites in different years (see Methods).

**Methods**

Bamboo shoots (3–12 mm in diameter and 200–400 mm in length) sectioned below each node were used for trap-nests. Each trap-nest was placed into a lattice hole of a plastic latticework piece (250 × 400 × 150 mm) with 50 lattice holes. This method allowed us to remove and replace trap-nests freely without changing the nest position. Each trap-nest was split longitudinally into two pieces, which were then precisely stuck together with adhesive tape to repeatedly monitor nest contents without causing severe damage.

Four latticework pieces, each equipped with 50 trap-nests, were set up at site 8 in early June 1992. These trap-nests were left in natural conditions without observation until the following August, when we started to observe and census the nesting activities of each trap-nest at least 1 h daily. To confirm the nesting activity of the observed trap-nests, we opened them every day to check the number of brood cells. If no nesting activity was observed at the trap-nest for more than 2 days, we regarded it as the end of nesting activity and then brought the nests into the laboratory to record and measure the following items: nest length, species composition and fresh weight of provisioned spiders per cell, and clutch size. These nests were placed again at the same position in the same study site and were left in natural conditions for 2 weeks to allow the larvae to develop to the pupal stage.

Two weeks after replacement, the trap-nests were again collected. All the pupae found in each brood cell were put into a vinyl tube (9 mm in diameter, 40 mm in length), both ends of which were stuffed with cotton, and were reared in the laboratory under 25°C and 16L:8D. Sex, emergence date, and cell position within a trap-nest were recorded for all the adult wasps emerged. Here, emergence date refers to the day when a wasp emerged from a cocoon, although trypoxylonid wasps often stay in a cocoon for several days after eclosion (Nambu 1966). Emerged adults were then released at the natal site to minimize disturbance caused by research activities. The same research was conducted at site 8, in 1995 and at site 4, in 1996, except that trap-nests were promptly brought to the laboratory after confirming the end of nesting activities and were left under 25°C 16L:8D conditions until adult emergence.

During early June 1993 and 1994, 100 unworked trap-nests were placed at each of the 11 study sites (sites 1, 4–8, 11–15) in 1993 and 10 study sites (sites 1, 4–8, 11, 13–15) in 1994. Thereafter, nesting activities were monitored every 7

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**Fig. 1.** Locations of the study sites