Abdominal Tip Movements during Oviposition by Two Parasitoids (Hymenoptera: Ichneumonidae) as an Index of Predicting the Sex of Depositing Eggs¹

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Many parasitoid wasps reproduce arrhenotokously and can control offspring sex ratios by regulating sperm access to eggs (FLANDERS, 1939, 1956; CHARNOV, 1982; KING, 1987). In most sex ratio studies of parasitoid wasps, offspring sex ratios have been measured at the time of wasp emergence. However, under certain circumstances, one sex may suffer higher mortality during the immature stages in or on the host (CHARNOV, 1982; KING, 1987). When this phenomenon, called differential mortality, occurs, sex ratios at the time of wasp emergence can differ from sex ratios at the time of oviposition, i.e., primary sex ratios. In parasitoid wasps, 1) egg transfer experiments (e.g., SANDLAN, 1979), 2) application of models predicting primary sex ratios (WELLINGS et al., 1986), 3) comparison of offspring mortality of mated females with that of unmated females (SANDLAN, 1979), and 4) use of cytological methods to observe chromosomes to directly determine primary sex ratios (VAN DIJKEN, 1991) have been made to estimate the effect of differential mortality on sex ratios upon wasp emergence.

GERBER and KLOSTERMEYER (1970) first reported that in the alfalfa leaf-cutter bee *Megachile rotundata* (F.), females showed two types of abdominal movement during oviposition which reflected their fertilization act, and hence the sex of an egg that she deposited could be predicted. Similarly, differential movements during oviposition were observed in some parasitoid species and were shown to be useful for determining primary sex ratios (COLE, 1981; SUZUKI et al., 1984; VAN DIJKEN and WAAGE, 1987; STRAND,

1989; UENO, unpublished).

Pimpla nipponica UCHIDA and *Itopectis naranyae* ASHMEAD are polyphagous solitary ichneumonid parasitoids that attack lepidopterous pupae (UENO and TANAKA, 1994; UENO, unpublished). Here, I report differential movements during oviposition by *P. nipponica* and *I. naranyae*, which can be used as an

Fig. 1. A female of *Pimpla nipponica* ovipositing in a host. A female wasp, after thrusting a host with her ovipositor, becomes almost motionless with the ovipositor inserted (a, b). At this stage, her abdominal tip and ovipositor show rhythmical contractions. After a brief period, an egg is seen passing through the base of the ovipositor (indicated by an arrow) (c), and thus oviposition is readily confirmed.

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Table 1. Sexes of offspring wasps of *Pimpla nipponica* and *Itopectis naranyae* in relation to abdominal tip movements during oviposition

Movements	Total no.	No. of female offspring	No. of male offspring	No. that died as larva	% of female offspring
<i>P. nipponica</i> /mated					
Continuous	31	0	26	5	0
Interrupted	66	48	10	8	82.8
<i>P. nipponica</i> /unmated					
Continuous	48	0	41	7	0
Interrupted	65	0	56	9	0
<i>I. naranyae</i> /mated					
Continuous	47	0	40	7	0
Interrupted	55	44	5	6	89.8
<i>I. naranyae</i> /unmated					
Continuous	25	0	23	2	0
Interrupted	41	0	35	6	0

index for predicting primary sex ratios.

MATERIALS AND METHODS

Parasitoids were reared on a laboratory host, *Galleria mellonella* (L.), at $25 \pm 0.5^\circ\text{C}$, 60–70% R.H. under 16L–8D. Mated or unmated female parasitoids were placed individually in plastic cups (10 cm dia. $\times$ 4.5 cm ht.) and provided with a honey solution every two days and host cocoons for 2 h every day after wasp emergence. Individual host cocoons were offered to 5–10 day old females and abdominal tip movements during oviposition were observed under a binocular microscope. Parasitized hosts were individually placed in plastic cups (4.5 cm dia. $\times$ 3 cm ht.) and maintained at $25 \pm 0.5^\circ\text{C}$, 60–70% R.H., under 16L–8D for wasp emergence. Twelve mated and 14 unmated *P. nipponica* and 13 mated and 8 unmated *I. naranyae* females were used for experiments.

RESULTS AND DISCUSSION

Both mated and unmated females of the two parasitoid species showed two distinct abdominal tip movements during oviposition: interrupted and continuous movements (Table 1). A female, after thrusting her ovipositor into a host, stood motionless on it with the ovipositor inserted (Fig. 1a). At this stage, her abdominal tip showed rhythmical contractions, probably an action which propelled an egg from the lateral oviduct where eggs are stored. In some cases, abdominal contractions showed a brief pause, usually for 1–2 s (interrupted movements), but in other cases, contractions were completed without a pause (con-

tinuous movements). Then an egg was seen passing through the base of the ovipositor (Fig. 1b, c), and after a brief period, the female withdrew her ovipositor and ended oviposition. Since egg deposition was readily observed, oviposition was easily confirmed. No difference in oviposition behavior was found between mated and unmated females.

Hosts parasitized by mated females that showed continuous movements always yielded male offspring wasps (Table 1). Thus, deposition of male offspring can be estimated with a 100% accuracy when a female shows continuous movements. Hosts parasitized by females with interrupted movements yielded both male and female offspring, but the majority of offspring were females (82.8% in *P. nipponica*, $N=58$ and 89.8% in *I. naranyae*, $N=49$, Table 1). In *P. nipponica*, one female wasp produced 5 male and 2 female offspring despite interrupted movements. Therefore, in both parasitoid species, movements during oviposition are good indicators for predicting the sex of the eggs deposited, although the accuracy can vary among individual wasps.

In some heteronomous hyperparasitoids, in which female larvae develop as primary parasitoids while males develop as hyperparasitoids of the same or other related species, unmated females oviposit selectively on hosts that are suitable for development of male offspring and hence appear to recognize their unmatedness (FLANDERS, 1959). Similarly, GERBER and KLOSTERMEYER (1970) suggested that *M. rotundata* females were aware of their unmatedness. However, unmated *P. nipponica* and *I. naranyae* females, like

mated females, showed two distinct movements during oviposition, although they produced exclusively male offspring wasps (Table 1). Therefore, females of both parasitoid species appear to be unable to recognize their unmatedness.

Although abdominal tip movements are useful for predicting primary sex ratios, some females produce male offspring even when they show interrupted movements (Table 1). This suggests that mated females can be constrained to produce male offspring, regardless of their decisions to lay female eggs. It is not known what factors result in the sex allocation constraint. One possible explanation for this constraint is physiological constraints such as sperm depletion. Although there are many known biotic factors that influence offspring sex ratios of parasitoid wasps (e.g. KING, 1987; GODFRAY, 1994), few studies have focussed on the distinction between the mother wasp's decisions and physiological constraints. For example, it was frequently found that older females produced more male-biased sex ratios (KING, 1987). This may be due to physiological constraints such as sperm depletion or to sex allocation adjustment by females. These distinctions can be made by comparing female's decisions reflected through abdominal movements with offspring wasp sex ratios with increasing female age. Thus, differential abdominal movements during oviposition are useful for sex ratio research.

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