RATES OF ATTACK AND CONTROL
OF THE OFFSPRING SEX RATIO IN THE PARASITIC WASP
LARIOPHAGUS DISTINGUENDUS IN AN ENVIRONMENT
WHERE HOST QUALITY VARIES

by

G. SIMBOLOTTI¹), F. A. PUTTERS and J. VAN DEN ASSEM²)
(Zoological Laboratory, Division Ethology, University of Leiden,
P.O. Box 9516, 2300 RA Leiden, The Netherlands)

(With 11 Figures)
(Acc. 1-III-1986)

Introduction

Problems of sex allocation have played an important role in theorizing
about the factors which direct evolution (CHARNOV, 1978, 1979, 1982;
STUBBLEFIELD, 1980), and they continue to do so. Indeed, sex allocation
represents one of the most fruitful blends of theory and observation in all
of evolutionary biology (LEIGH et al., 1985), although, no doubt,
empirical data lag behind, considering the recent flourish of theories.
This paper is a contribution to the collection of empirical data in the first
place; we will address a sex-allocation problem in the form of decisions
on the ratio of male to female offspring by a parasitic wasp.

The theory of natural selection predicts that animals behave in such a
way as to maximize reproductive success. This implies the ability to
make the most profitable decisions at the appropriate times. Because
trade-offs are always involved, optimization procedures have to be
employed for attaining maximum profits. The behavioural machinery
underlying such efforts is a topic of interest in this paper; we agree with
CHEVERTON et al. (1985) that the construction of optimality models
involves a knowledge of mechanisms controlling behaviour (TINBERGEN,
1963).

¹) Present address: Università degli Studi dell’Aquila, Dipartimento di Scienze
Ambientali, Settore Zoologico, Piazza Regina Margherita 7, 67100 L’Aquila, Italia.
²) We acknowledge financial support given to the first author during her stay in the
Netherlands by the Dr J. L. Dobberke Stichting voor Vergelijkende Psychologie
(Amsterdam). The authors thank Professor J. J. A. van IERSEL for criticising a manu-
script draft and for discussions, and for many valuable suggestions.
More specifically, our paper is dealing with oviposition behaviour and sex-ratio decisions by the parasitic wasp *Lariophagus distinguendus*. Upon finding a potentially suitable host, a *Lariophagus* female has to make a twofold decision: accept or reject; produce a son or a daughter. (The haplodiploid sex-determination system of the Hymenoptera provides a potential for the control of the sex of an offspring). Variations in host size and host-size frequencies, in terms of frequencies of encounters, play a role in the parasite's decision-making. In this respect, two aspects of *Lariophagus*’ life-history are particularly relevant. First, parasitized hosts (larval instars of weevils, which may vary considerably in size) are permanently paralyzed. Hence, the amount of food which is available for use by a parasite offspring (*Lariophagus* lays one egg per host) varies, and eventually this results in size differences among a wasp's progeny. Secondly, reproductive prospects of small and large males (sons) differ less from one another than those of small and large females (daughters): for a female it is far more important to grow as large as possible than for a male (Charnov et al., 1981).

Rules for maximizing reproductive profits when offspring fitness varies with body size were formulated by Charnov (1979, 1982). Green (1982) extended these rules to account for the effects of host density; Werren (1984) combined host-size and host-density effects. The experiments to be described below deal with the impact of differences in host size and host density on parasitisation decisions; some of the results will be discussed in relation to these rules.

Females of several species of parasitic wasps (among them *L. distinguendus*) discriminate between hosts of different size (e.g. Chewyrevu, 1913; Kishi, 1970; van den Assem, 1971; Sandlan, 1979; Charnov et al., 1981; Jones, 1982; van den Assem et al., 1984): small hosts are preferably used for male offspring, large hosts for female offspring. This implies the ability to measure hosts somehow. *Lariophagus* females have been shown to react to host-size differences of .2 mm or less, and moreover, to discriminate between hosts in a relative sense, *i.e.* a given host is judged as "small" or "large" relative to the size of other hosts present in the population; when relatively small it receives more males than when relatively large (Charnov et al., 1981). How females manage to assess host size is an open question; sense organs located on the tip of the ovipositor seem to be involved in the process. Possibly, with weevil larvae for hosts, the dimensions of the tunnel, which is excavated in a grain by a larva during feeding, are used as cues (van den Assem, 1971).