Parasitoid clutch size and irreversible evolution

Abstract

Previously, theoretical and empirical studies suggested that parasitoids developing in small multiple-egg broods would evolve siblicidal behaviour, making such brood sizes rare and single-egg broods an evolutionary absorbing state. Recent evidence, however, suggests that small gregarious broods are relatively stable in many parasitoid taxa, and that gregarious development has evolved many times from solitary development. This suggests that new research is needed to assess how nonsiblicidal behaviour can spread and become stable. We discuss some potentially rewarding possibilities.

Keywords

Clutch size, Hymenoptera, irreversible evolution, life histories, parasitoid, parent–offspring conflict, sibling rivalry.
numeros occasions (Rosenheim 1993; Mayhew 1998a).
The question is now whether and how these observations
can be explained within the present theoretical framework.

One likely solution to the problem of the stability of
nonsiblicidal behaviour in small broods is that relatedness
between broodmates is often very high, raising the
inclusive fitness costs of siblicide (Godfray 1987;
Rosenheim 1993). Because the haplodiploid inheritance
of many parasitoid species means that females are more
related to their sisters than to their brothers, one way in
which this can come about is when broods consist only of
a single sex (Rosenheim 1993), as seen in several species
developing in small gregarious broods (Rosenheim 1993;
Mayhew 1998b). Another way might be if broods are laid
by a single mother, and offspring habitually inbred. This
is notably true of one large family of parasitoids with
small gregarious broods, the Bethylidae (Mayhew &
Hardy 1998). However, these two mechanisms are
unlikely to account for all small gregarious broods,
which occur in many taxa with diverse natural histories,
making alternative stabilizing factors likely or necessary
(Mayhew 1998b).

How gregarious development arose in the first place is
a very different problem. There are two possible routes
from a siblicidal solitary development to a nonsiblicidal
gregarious one: (i) lose the siblicidal behaviour and then
increase the brood size, or (ii) first increase the brood size
and then lose the siblicidal behaviour. The second of these
possibilities arises from studies on the encyrtid Comperiella
bifasciata, a parasitoid of scale insects. In C. bifasciata only
one offspring ever survives from each host, but more than
one egg is frequently laid in each (Rosenheim &
Hongkham 1996). This strategy of laying “insurance eggs” appears to be more widespread amongst parasitoids
than was previously thought (Rosenheim & Hongkham 1996), and may be selected for if there is a risk that single-
egg clutches will die before completing development
(Rosenheim 1993; Rosenheim & Hongkham 1996). Once
multiple egg clutches are routinely produced, an inclusive
fitness cost is added to siblicide, and should this cost be
large, siblicide itself may then be lost. In C. bifasciata,
multiple-egg clutches are sexually segregated and the
population sex ratio is female-biased, a combination that
leads to high relatedness between broodmates (Ode &
Rosenheim 1998). This species may thus present an
example of the transitional stage between solitary and
gregarious development, where brood size increases
before the loss of siblicide.

These recent studies show that solitary parasitoid
development is, in many cases, far from irreversible, and
that small gregarious broods are, in many cases, far from
unstable. To develop and test theoretical explanations
further, research is needed in several key areas. First, we
need a better understanding of the mechanisms of brood
reduction and the genetics underlying this behaviour.
Second, estimates are required of selection pressures such
as relatedness amongst brood members, and the costs and
benefits of brood reduction. Third, comparative studies of
parasitoid genera within which multiple evolutionary
transitions between solitary and gregarious development
have occurred may be particularly rewarding. By mapping
behavioural and developmental traits onto well-supported
phylogenies, we may be able to establish the polarity of
the evolutionary transitions and distinguish between the
two pathways to the evolution of gregarious development
described above. Studies of species exhibiting intermedi-
ate characteristics, and in particular facultatively siblicidal
parasitoids (e.g. Hobbs & Krunic 1971), may also provide
important insights. Whatever future research shows, it is
clear that thinking based on a simple and elegant model is
being replaced by consideration of more complex
scenarios. The story of the siblicidal—nonsiblicidal—
parasitoids is far from complete.

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evolutionary transition between solitary and gregarious

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Manuscript received 5 August 1998
First decision made 17 August 1998
Manuscript accepted 8 September 1998

**BIOSKETCH**

Peter J. Mayhew’s research interests include evolutionary and behavioural ecology, insect reproductive strategies, life history strategies, sex allocation, biology of parasitoid Hymenoptera, and evolution of sibling rivalry.