



Lessons from the multitudes: insights from polyembryonic wasps for behavioral ecology

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Even for parasitic Hymenoptera, polyembryonic wasps are unusual creatures. Two features in particular, allow for novel exploration of major questions in behavioral ecology: the production of multiple offspring per egg and, in some species, the production of a soldier caste. Because final brood sizes of polyembryonic species are not constrained by trade-offs between current and future parental reproductive effort, we can clearly examine the selective forces at play that drive the balance between the number of offspring and their body size. Polyembryony also provides excellent opportunities to compare the performance of identical genotypes under different environmental conditions. Finally, polyembryonic species can provide unique tests of how genetic conflicts at multiple levels are resolved.

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Introduction

Polyembryony is a developmental mode whereby a single egg gives rise to multiple, genetically-identical offspring. Sporadic polyembryony is a very widespread phenomenon across all animal groups including humans. Obligate polyembryony is far more restricted in distribution; in the insects, it occurs only in two orders: the Hymenoptera (in four parasitoid families: Dryinidae, Encyrtidae, Braconidae, and Platygasteridae) and the parasitic Strepsiptera [1,2]. Polyembryony involves the production of yolk-poor eggs that undergo complex genetic [3,4], endocrine [1], and developmental [2,5,6] processes, many of which are unique to these species. With few exceptions (e.g. [7,8]),

nearly all developmental studies have involved the encyrtid wasp *Copidosoma floridanum*.

Polyembryony provides several selective advantages for parasitoids. First, polyembryonic development may provide a way for ovipositing females to overcome egg limitation. In other words, the cloning of embryos allows higher reproductive output without laying additional eggs. Second, it may alleviate conflict and aggression (which often lead to mortality) between genetically-identical larvae that develop within the same host. Finally, because all polyembryonic parasitoids are koinobionts, females may not be able to accurately predict the future quality of the host for their developing offspring at the time of oviposition. By dynamically adjusting the number of clonal divisions to the size of the growing host, brood size can be fitted to the carrying capacity of the host when that final carrying capacity cannot be foreseen by the parents [9,10].

The reasons for the rarity of polyembryony in parasitoids are far from clear. Craig *et al.* [9,11] suggested that polyembryony is costly because it clones an unproven genotype (different from that of the parent) at the expense of genetic diversity within a brood. However, this cost may be relatively small, because each mother produces several, genetically-distinct clones through regular sexual reproduction. Thus, polyembryony leads to a loss of within-clone genetic variation, but might not affect the overall population-level genetic diversity [12].

Two features of polyembryony permit unique tests of several important aspects of behavioral ecology [13]. First, as discussed below (see ‘Clutch versus brood-size’), polyembryony typically results in offspring brood sizes and sex ratios that are very different from the number and sex of eggs laid by the mother. This feature allows for unusually straightforward tests of the size–number trade-off problem as well as the role of sibling conflict in driving offspring sex ratio patterns. Second, some species within the Encyrtidae have evolved a larval caste system, where soldier larvae defend their clone-mates from intra-specific and inter-specific competitors (see ‘Soldiers, sex ratios, and sociality’, below). This raises the possibility of using these polyembryonic species to explore aspects of sociality as well as to study genetic conflict phenomena such as sibling rivalry and parent–offspring conflict. In addition, polyembryonic species can be excellent systems to differentiate between genetic and environmental effects on phenotype because it is easy to compare the effects of

different environments on different individuals of the same genotype [14,15*].

Clutch versus brood size

One of the most remarkable qualities of polyembryony is the apparent disconnect between maternal decisions — both clutch size (number of eggs laid per host) and sex allocation — and the resulting brood phenotype (total number of wasps emerging from a host and offspring sex ratios). While clutches often comprise only 1–2 eggs, several polyembryonic encyrtids produce broods that exceed 1000 offspring; in *C. floridanum* as many as 3400 offspring can arise from a single egg [2,16]. As a result, the investment in any one clutch is not expected to greatly constrain future reproductive effort, a confounding issue when trying to study clutch size decisions in monoembryonic species. When all brood-mates are genetically identical, parent–offspring and sibling conflict are also absent. These features permit exceptionally clean tests of classic questions in behavioral ecology including clutch size decisions and trade-offs between individual body size and the number of offspring per brood. As described below, such tests have received some attention to date in polyembryonic species.

Within the genus *Copidosoma*, ovipositing females typically lay clutches of either one or two eggs per host, which clonally divide to produce single-sex broods (all-male or all-female) or mixed-sex broods (originating from one male and one female egg). Whether one or more eggs are laid per host depends in part on host encounter rate, with low encounter rates resulting in a higher proportion of mixed-sex broods whereas high encounter rates result in a higher proportion of single-sex broods [17,18]. This maternal clutch size and sex allocation pattern has been interpreted in the context of mating opportunities for adult offspring (see ‘Soldiers, sex ratios, and sociality’ and ‘Future directions’ sections, below).

In species that produce broods of multiple offspring, there is a continuum of ways to partition limited resources among offspring ranging from producing few, relatively large body-sized progeny to producing many, relatively small body-sized progeny. The optimal balance point between individual body size and brood number is the one that maximizes the product of brood number and per capita offspring fitness [19–21]. Body size has been repeatedly shown to influence life history traits (i.e. survivorship, fecundity, and age at maturity) that are related to other traits linked to fitness such as dispersal, mating ability, and competitive ability [22,23], implying that selection acts on both number of individuals per brood and body size. Virtually all empirical studies of the size–number trade-off have shown that observed clutches comprise fewer individuals than the predicted optimum [20,21,24]. The most widely accepted explanation for this discrepancy is that other trade-offs such as those between

present and future reproductive effort [23,25,26], parent–offspring conflict, or sibling rivalry obscure the size–number trade-off [20,27]. These trade-offs are largely absent in polyembryonic species, permitting examination of the role of mating systems as selective forces on the body size–brood number trade-off. Furthermore, the influence of sibling rivalry on the size–number trade-off can be studied in the absence of present vs. future reproductive effort trade-offs. A second, less appreciated, reason for the discrepancy noted above is the fact that environmental conditions determining the optimal trade-off point often fluctuate spatially and temporally. Variation in such environmental conditions that affect reproductive success across generations can select for a phenomenon known as ‘bet-hedging’ [28]. Key to understanding how bet-hedging can be advantageous is recognizing that selection acts on the geometric mean rather than the arithmetic mean of a fitness related trait. Decreasing variance of fitness across generations can increase the geometric mean even if the arithmetic mean is reduced [28]. Therefore, a clutch size that is smaller than the predicted optimum (based on within-generation conditions) may be selected for if this reduces across generation variation in this trait. Thus, both bet-hedging and current vs. future reproductive effort trade-offs predict lower clutch sizes compared to the theoretical prediction; polyembryonic species permit the study of the role of bet-hedging in the absence of current vs. future reproductive effort trade-offs [29,30*].

A handful of studies of *Copidosoma* species suggest that all-male and all-female broods have different trade-off optima, possibly reflecting different selective pressures experienced by males and females as adults. In a study of *Copidosoma bakeri* that explicitly examined differences in the optima between all-male and all-female broods [31,32*], all-female broods comprised fewer, larger body-sized individuals compared to all-male broods. *Copidosoma sosares* [33,34] exhibits a similar pattern where all-female broods contain fewer, larger-bodied individuals. In the case of the univoltine *C. sosares*, females emerge, mate, and overwinter before they are able to mature eggs and locate hosts the following spring. Immediately after emerging, males (from both mixed-sex and single-sex broods) mate locally with females from nearby all-female and mixed-sex broods (multiple broods synchronously emerge within the same host plant). Unlike females, males die within a few days. Given these life history differences between the sexes, there is a premium placed on large body-sized females compared to males, as larger females are more likely to successfully overwinter and find hosts the following spring (at the cost of fewer females per brood) [33]. In contrast, all-male broods of *C. floridanum* and *Copidosoma koehleri* contain fewer, larger-bodied individuals compared to all-female broods [16,35–37]. It is tempting to infer that such differences between male and female broods in the trade-off optima

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