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Parasitoid clutch size and irreversible evolution

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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.

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The siblicidal behaviour of the larvae of some parasitoid species has received widespread attention in the evolutionary and ecological literature. This interest largely stems from a theoretical paper by Godfray (1987), who showed that killing other larvae in the same brood could evolve as an adaptive strategy. In accordance with kin selection theory, such behaviour was more likely to evolve when the number and relatedness of brood mates was low, reducing inclusive fitness costs. Because in siblicidal broods only one larva can generally survive (e.g. Salt 1961), mothers of siblicidal larvae should be selected to lay only a solitary egg in each host. If siblicidal behaviour and solitary development are widespread it becomes difficult for nonsiblicidal behaviour and gregarious development to spread, because nonsiblicidal larvae would die at the mandibles of their siblicidal broodmates. This situation is thus an example of irreversible evolution, or an "evolutionary black hole" (Harvey & Partridge 1987).

Some intriguing comparative data (le Masurier 1987) provide support for Godfray's model. In the braconid genus *Apanteles* (now recognized to be a polyphyletic assemblage of closely related lineages, and partly revised into 28 genera), the distribution of brood sizes is bimodal, with a distinct absence of broods of 2–12 offspring. In addition, single egg broods are laid even on very large hosts that provide enough resources for several offspring. Such data suggest that small multiple-egg broods are unstable and that solitary larval development has taken their place, just as Godfray's model predicts. Similar accounts are given in several widely read texts (e.g. Clutton-Brock 1991; Clutton-Brock & Godfray 1991; Harvey & Pagel 1991; Mock & Parker 1997).

In his original paper, Godfray (1987) took considerable care to investigate a range of biological parameters, and their effect on the evolution of siblicide. He found that different natural histories could promote the spread of either siblicide or nonsiblicide, suggesting that the simple story presented above might not always hold. Recent studies show this to have been good foresight. First, attention has been drawn to the fact that, unlike *Apanteles*, several parasitoid taxa consistently develop in small gregarious broods (Rosenheim 1993; Mayhew 1998a, b; Mayhew & Hardy 1998). Thus, siblicide may not ubiquitously and rapidly evolve when brood size is small. Second, the phylogenetic distribution of solitary and gregarious development strongly suggests that solitary development was ancestral, and that, far from being irreversible, gregarious development has evolved on numerous 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 inbreed. 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 intermediate 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–and nonsiblicidal–parasitoids is far from complete.

REFERENCES

Clutton-Brock, T.H. (1991). *The Evolution of Parental Care.* Princeton: Princeton University Press.

Clutton-Brock, T.H. & Godfray, H.C.J. (1991). Parental investment. In *Behavioural Ecology*, 3rd edn, ed. Krebs J.R., Davies N.B. Oxford: Blackwell Scientific, pp. 234–262.

Godfray, H.C.J. (1987). The evolution of clutch size in parasitic wasps. *Am. Nat.*, 129, 221–233.

Harvey, P.H. & Pagel, M. (1991). *The Comparative Method in Evolutionary Biology.* Oxford: Oxford University Press.

Harvey, P.H. & Partridge, L. (1987). Murderous mandibles and black holes in hymenopteran wasps. *Nature*, 326, 128–129.

Hobbs, G.A. & Krunic, M.D. (1971). Comparative behavior of three chalcidoid (Hymenoptera) parasites of the alfalfa leafcutter bee, *Megachile rotunda*, in the laboratory. *Can. Entomol.*, 103, 674–685.

le Masurier, A.D. (1987). A comparative study of the relationship between host size and brood size in *Apanteles* spp. (Hymenoptera: Braconidae). *Ecol. Entomol.*, 12, 383–393.

Mayhew, P.J. (1998a). The evolution of gregariousness in parasitoid wasps. *Proc. R. Soc. Lond. B*, 265, 383–389.

Mayhew, P.J. (1998b). The life histories of parasitoid wasps developing in small gregarious broods. *Neth. J. Zool.*, 48, 225–240.

Mayhew, P.J. & Hardy, I.C.W. (1998). Non-siblicidal behavior and the evolution of clutch size in bethylid wasps. *Am. Nat.*, 151, 409–424.

Mock, D.W. & Parker, G.A. (1997). *The Evolution of Sibling Rivalry.* Oxford: Oxford University Press.

Ode, P.J. & Rosenheim, J.A. (1998). Sex allocation and the evolutionary transition between solitary and gregarious parasitoid development. *Am. Nat.*, 152, 757–761.

Rosenheim, J.A. (1993). Single-sex broods and the evolution of nonsiblicidal parasitoid wasps. *Am. Nat.*, 141, 90–104.

Rosenheim, J.A. & Hongkham, D. (1996). Clutch size in an obligately siblicidal parasitoid wasp. *Anim. Behav.*, 51, 841–852.

Salt, G. (1961). Competition among insect parasitoids. *Symp. Soc. Exp. Biol.*, 15, 96–119.

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