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Research News

Immobility: the key to family harmony?

John J. Pexton and Peter J. Mayhew

The lethal fighting of larvae in many parasitoid species is a striking example of sibling rivalry. Theory has suggested that such fighting, and subsequent solitary development, might be irreversible, but phylogenetic evidence suggests otherwise. New empirical work now shows that the loss of mobility in parasitoid larvae, with the retention of fighting behaviour, is one way to escape the trap of solitary development.

Competition for resources is a major influence on ecological and evolutionary processes¹. One striking outcome of such competition is the evolution of rivalry between siblings². Sibling rivalry has long held a fascination for heuristic reasons, one of which is the potential for irreversibility, or directionally biased, evolution³. In particular, once strife between siblings has arisen, rare peaceful offspring might find success more difficult in the competitive world of their uncompromisingly aggressive sibs. This irreversibility, or rather its lack, is the subject of a new paper by Boivin and van Baaren that suggests a novel mechanism to escape the evolutionary trap of disagreeable families in parasitoid wasps⁴.

Parasitoid wasps lay eggs in or on the bodies of other arthropods. The young parasitoids feed on the still-living body of the host, eventually killing it. Parasitoids can develop either solitarily or gregariously on a host. In solitary species, offspring kill broodmates until only one individual is left to use the host's resources fully. Rivals are eliminated by physical attack (with hardened

mandibles) or by physiological suppression⁵. Gregarious species are generally not siblicidal and more than one individual develops per host⁶. Parasitoids thus provide examples of species in which family strife is common and of species in which siblings appear to be more tolerant of each other.

Population-genetics models^{7,8} have shown that the conditions for a nonsiblicidal allele to invade a population of siblicidal individuals are very stringent (Fig. 1), suggesting that the evolution of the solitary state might be irreversible, dubbed an ‘evolutionary black hole’⁹. However, the phylogenetic distribution of solitary and gregarious behaviour suggests strongly that solitary development is ancestral, with gregarious development having arisen independently at least 43 times in 26 different families of Hymenoptera¹⁰. Solitary and gregarious development are frequently found in the same genus. The recent challenge has been to demonstrate mechanisms by which solitary development might have been lost. Boivin and van Baaren provide experimental evidence for a new proximal mechanism in the transition between solitary and gregarious behaviour, and hence a route through which species could avoid the evolutionary trap of family strife.

In the standard population-genetics model of the evolution of solitary and gregarious development, an individual with tolerant behaviour will lose any competitive encounter with an intolerant individual occupying the same host. Boivin and van Baaren investigated this assumption in two closely related species

of parasitoids. The mymarid wasps *Anaphes victus* Huber and *Anaphes listronoti* Huber are endoparasitic egg

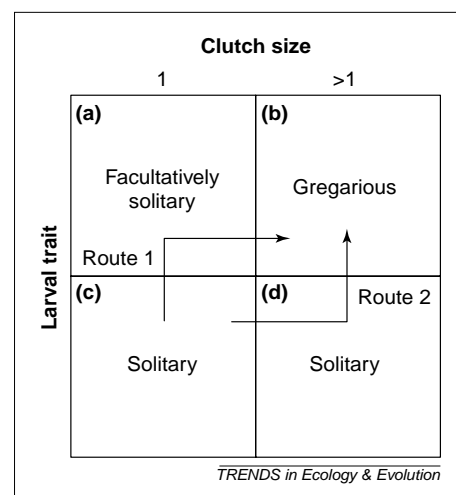


Fig. 1. The evolution of gregariousness. Larvae in the top row (a,b) show either tolerance (in the traditional model of gregariousness) or immobility (in the model suggested by Boivin and van Baaren⁴) and can evolve towards gregarious development if clutch size increases (a to b). Larvae in the bottom row (c,d) are mobile, intolerant and develop solitarily. For gregarious development to appear, there must exist both a clutch size of more than one and tolerance or immobility (b). In the traditional model, a species can become gregarious by either the gain of tolerance and a subsequent increase in clutch size (Route 1) or by an increase in clutch size and the subsequent gain of tolerance (Route 2). Route 1 allows tolerance to spread more easily because tolerant individuals are isolated. However, a subsequent increase in clutch size makes the species susceptible to reinvasion by an intolerant allele. Route 2 involves laying ‘insurance’ eggs and some mechanism for increasing the relatedness of broodmates to allow tolerant individuals to survive. In the model suggested by Boivin and van Baaren, individuals are essentially intolerant but siblicide can be restricted by immobility. Each route then becomes much more plausible because the ability of immobile larvae to retaliate makes them less vulnerable to elimination by mobile individuals.

parasitoids of the weevil *Listronotus oregonensis* (Le Conte) in north-eastern North America. These parasitoids are sympatric and are frequently found together in the field¹¹. *Anaphes victus* is solitary and *A. listronoti* is gregarious, and the first instar larvae of both species have highly developed mandibles.

The gregarious or solitary status of each species was confirmed in a series of superparasitism experiments in which several eggs from the same species are laid per host; only one offspring per host developed successfully in *Anaphes victus* but several could complete development in *A. listronoti*. The fighting ability of larvae was then examined under conditions of multiparasitism, in which eggs from both species were laid into a single host. Under the standard model assumptions, only a single larva from the solitary species should remain.

However, the results showed that each species had an equal probability of surviving encounters, with a 50:50 ratio of adults emerging from hosts containing one larva from each species. In addition, if more than one gregarious larva was present then the probability of the solitary larva surviving was dramatically reduced. Dissected hosts contained larvae with visible scars and these scars were seen in both species. This suggests that fighting is still the key to success in larval competition but that the larvae of the gregarious species are able at least to retaliate and win in the presence of aggressive broodmates. In hosts containing many gregarious larvae, some brood reduction was also observed, presumably because crowding makes larval encounters inevitable.

In vitro observations of parasitoid larvae showed that the degree of mobility in first instar larvae was significantly different for the two species. Twisting (lateral torsion) and folding (vertical bending) were recorded, with the solitary *A. victus* showing significantly more movement than the gregarious *A. listronoti*. In these species, Boivin and van Baaren suggest that the phenotypic changes involved in the transition from solitary to gregarious development involve not loss of aggression *per se* but rather loss of the mobility and searching behaviour that allows intolerant sibs to find and kill each other. This mechanism is intuitively attractive because it seems to allow much greater freedom for the

spread of gregarious development than the traditional model: rare immobile mutants will still be able to defend themselves in the presence of their mobile broodmates and should more easily gain a foothold in the population. If this mechanism is widespread, it offers a solution to the paradox of the phylogenetic distribution of gregarious development (Fig. 1).

At least one previous study suggests that loss of mobility is not the only mechanism involved in the evolution of gregarious development. *Argochrysis armilla* Bohart is a gregarious wasp from the family Chrysididae (the only confirmed gregarious species of 3000 described species from this family) but has first instar larvae that are highly mobile and have powerful mandibles⁸. In this species, the spread of tolerant behaviour (rather than immobility) is thought to have allowed gregarious development to evolve. Tolerant behaviour might be able to spread because most broods consisted of only one sex. Single sex broods change the potential inclusive fitness costs involved in siblicide because sisters are, on average, much more closely related to each other than to brothers in the Hymenoptera. This means that rare tolerant individuals have a good chance of sharing hosts occupied by other tolerant individuals, allowing them to establish in the population.

In other cases, it is still unknown whether larval intolerance or larval mobility has changed. The braconid genus *Aphaereta* parasitizes fly larvae of several genera including *Drosophila* and contains both solitary and gregarious species. Although larval fighting is observed in solitary species but not gregarious ones¹², it is currently unknown whether the phenotypic changes involved support the mechanism suggested by Boivin and van Baaren, the traditional mechanism or some alternative. Multiparasitism experiments such as those described above would help to resolve this situation, although many of these species are so similar morphologically that behavioural or genetic markers are necessary to identify individual survivors reliably.

Boivin and van Baaren have intriguingly shown that more than one kind of phenotypic change seems to be available as a route out of solitary development. One mechanism is the loss

of aggression while retaining mobility and the other is the retention of aggression but with reduced mobility. Their study forces us to reassess the ecological interactions and evolutionary forces that can result in the evolution of gregariousness. One interesting question that is now raised is which factors might promote one mechanism over another in the evolution away from solitary behaviour. Immobility with aggression might be adaptive for conditions in which multiparasitism occurs frequently or if superparasitism rates are high, by allowing some post-oviposition regulation of brood size.

We expect that Boivin and van Baaren's results will stimulate more experimental studies of multiparasitism to determine the outcome of competitive interactions within or on hosts. A thoughtful reassessment of the theoretical basis of the subject is probably required in the light of their study. In particular, their findings suggest a whole new range of potential larval behavioural strategies, from conditional retaliatory behaviour to a continuum of mobility or searching strategies. The theoretical implications of these possibilities can now be investigated in earnest. The evolutionary resolution of family strife is still an open question in parasitoids but it seems that the 'black hole' of solitary development is a little less dark when the light of empirical investigation illuminates our view.

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Research News

What's bugging brood parasites?

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Brown-headed cowbirds (*Molothrus ater*) might reduce populations of the songbird species they parasitize, including endangered species. Data are therefore needed on the frequency with which cowbirds use different species of foster parents. Hahn *et al.* propose a clever new approach by which the identity of foster parents can be inferred from host-specific lice the cowbirds acquire as nestlings. We discuss the feasibility of this method and underlying assumptions.

'Tell me what company thou keepest,
and I'll tell thee what thou art.' –

Cervantes

Brown-headed cowbirds (*Molothrus ater*) are obligate brood parasites, which lay their eggs in the nests of other species of birds. Nestling cowbirds reduce the reproductive success of their hosts because cowbird nestlings outcompete host nestlings for food. Their negative impact on host species has been implicated in the decline of endangered species, such as the Kirtland's warbler (*Dendroica kirtlandii*)¹. Monitoring the influence of cowbirds, which parasitize a variety of passerine species, requires reliable data regarding which host species are used by cowbirds. Obtaining such data is difficult because it requires considerable time and money, and enough personnel who are capable of finding large numbers of nests. Indeed, the time taken to understand the extent to which cowbirds affect other species could be significantly reduced if a strategy facilitating identification of cowbird hosts could be found.

A new paper by Hahn *et al.*² describes such a potential shortcut. They propose an approach in which host-specific chewing lice (Phthiraptera) are used as natural markers to identify the foster parents of cowbirds. As such, their study is the first in-depth assessment of infestations of

chewing lice on cowbirds. Chewing lice are relatively host-specific 'permanent' ectoparasites that pass their entire life cycle on the body of the host. They move onto new hosts mainly during periods of direct contact between host individuals, such as between parent birds and their offspring in the nest³. Assuming that cowbird nestlings get lice from their foster parents, it should be possible to identify the foster species simply by determining which species of lice fledgling cowbirds have.

To test the feasibility of this idea, Hahn *et al.*² trapped and fumigated 244 recently fledged cowbirds. Lice were removed from the cowbirds and identified. Next, lice were collected from 320 birds representing most of the possible foster species at the study site ($n = 30$). Lice from cowbirds were compared with those from potential foster species to see how many cowbirds could be linked to a particular host species. Although interesting, the results were not quite as satisfying as one might have hoped. Only 44 (18%) of the fledgling cowbirds and 45 (14%) of their potential fosters yielded lice. Of the cowbirds yielding lice, only 11 (4.5%) could be assigned unambiguously to a single foster species.

Several factors contributed to the low proportion of cowbirds that could be matched with foster species. The most obvious problem was that so few birds had lice. This low prevalence contrasts with an earlier study of cowbirds in which lice were recovered from 71 of 155 (46%) of the birds sampled⁴. Hahn *et al.*'s low returns reflect their sampling of lice from live birds; the earlier studies had sampled dead birds. Lice were removed by exposing live birds to ethyl acetate fumes in a glass fumigation chamber, while keeping the head of the bird outside the chamber. Unfortunately, in addition to missing lice on the head, up to two-thirds of the lice on the body of the bird can also be missed by this method⁵.

Another problem discussed by Hahn *et al.*² was that several of the lice they collected were not specific for any one particular host. The worst offender by far, was *Menacanthus eurysternus*, a louse known from more than 150 species of passerines⁶. Conversely, eight species of lice collected from cowbirds were not found on any species of host², although several of these lice were already known to parasitize some of the sampled foster species⁶. It is possible that some of the eight species of lice recovered only from cowbirds are host-specific parasites of cowbirds, although further sampling is needed to confirm this specificity.

The existence of cowbird-specific lice would raise an interesting paradox about lice and other vertically transmitted parasites of brood parasites. Because lice depend largely on direct contact between hosts for transmission, and because no contact occurs between brood-parasitic nestlings and their biological parents, how would young brood parasites acquire their own specific lice? Two possibilities exist:

(1) lice from adult brood parasites are deposited in the nest and move onto the young after they hatch; and (2) lice are transmitted from adult to juvenile cowbirds once they leave the nest. The first possibility is unlikely because without association with a host, the survival of lice is severely limited. If cowbird-specific lice exist, therefore, they must presumably transfer during periods of contact between juvenile and adult cowbirds.

This conundrum is the subject of two recent papers concerning another renowned group of brood parasites, the Old World cuckoos. Cuckoos are a much older group of brood parasites than are cowbirds^{7,8}; a fact which is reflected by the existence of two genera of cuckoo-specific lice (*Cuculoeacus* and *Cuculicola*). The transmission paradox described above is