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General News

Why Biocontrol Practitioners Should Be More Interested in Parasitoid Sex Ratios

The use of parasitoid wasps in biological pest control pivots around a crucial event: a female wasp finding and attacking a target host. Females have to be able to find hosts, successfully parasitize them and, ideally, their offspring need to survive to maturity to sustain the process into future generations; but first there have to be females. Most species of parasitoid wasps are sexual, i.e. there are both males and females, but it is only the females that attack hosts, via parasitization and/or feeding. Males are required for mating, otherwise females will not be able to produce daughters, but since one male can generally inseminate many females, a few males can suffice. From a pragmatic perspective, female biased sex ratios are desirable to both maximize the production of female parasitoids for field release from mass-rearing facilities and for enhancing parasitoid establishment rates and the degree of pest suppression in the field.

The above points appear to be both obvious and widely known. What is also widely known, at least among evolutionary ecologists, is that there is a very good understanding of the selective factors that influence sex ratios and also that some of the most studied organisms in this respect are parasitoid wasps. There is, however, a problem: while the interconnection between what might be called 'pure' and 'applied' studies of parasitoid sex ratios has clear, and moreover long-discussed, potential to be hugely beneficial, there are hardly any instances of this potential being achieved. Our motivation is thus to bring this issue to the attention of biocontrol practitioners and outline the ways in which we think progress could most readily be made. Here we provide a distillate: a much longer treatment of this topic, in which full details and references can be found, will shortly be available elsewhere[1].

The Intricacies of Sex Ratio Theory

The evolutionarily-based study of sex ratios constitutes a large, longstanding and quite complex field of research encompassing genetic mechanisms of sex determination, game-theoretic approaches to optimal sex allocation and empirical work on a huge diversity of organisms, including many parasitoid wasps. The study of sex ratios is claimed to be one of the most successful areas of evolutionary ecology due to its refined theoretical achievements being closely and reciprocally coupled with empirical testing. Sex ratio studies can be taken right to the heart of philosophical debate about the study of evolutionary adaptation and the value of the optimality approach and also used to explore the putative existence of fundamentally important though controversial behaviours such as spite. While these research areas are deeply fascinating, they may seem esoteric to a pragmatist. The study of sex ratio also has a more directly applicable side and it is on that facet that we focus here. Applications of an understanding of sex ratios include improving the effectiveness of epidemiology and conservation ecology, as well as pest biocontrol, which is our present concern. In the following sections we briefly outline the main areas of parasitoid sex ratio research that should be of interest to biocontrol practitioners and try to avoid the 'esoteric intricacies' by describing theory on a 'need-to-know' basis.

The Simplicities of Parasitoid Sex Ratios

Sex ratio theory started historically with a 'natural selection' explanation for why most animal species have unbiased sex ratios. The core idea is that in sexually reproducing populations that happen to have a sex ratio bias, individuals belonging to the rarer sex will be more reproductively successful than those belonging to the more common sex (e.g. if males are rare, males will usually have many mates, but if males are common, males will on average have less than one mate; in both cases females will generally average one mate). In such populations parents that tend to produce the rarer gender among their progeny will thus have more grandchildren (≈evolutionary fitness) than those that do not. Such frequency dependent selection thus tends to return population sex ratios to, and retain them at, equality. The evidence for the operation of frequency dependent selection for sex ratio equality is surprisingly scant, and we know of no strong evidence from parasitoids. Nonetheless, many parasitoid species do exhibit approximately even sex ratios and sex ratio equality provides a baseline expectation for biocontrol practitioners who aim to mass-rear or deploy parasitoids as biocontrol agents. Further, the theory outlined above relies on a number of crucial assumptions, two of which are that individuals find mates from throughout a large population and that parental investment of resources into individual male and female offspring generates identical returns in terms of offspring future success. Examining cases where these assumptions do not hold has been a major endeavour in 'pure' sex ratio research and is also the key to the potential application of sex ratio studies to biocontrol because both scenarios can lead to a greater production of females.

Achieving Female Bias Using Population Sub-division

If the pool of potential mates is restricted to subgroups (each lasting one generation) within larger populations (a scenario called 'local mate competition') mothers are selected to adjust their progeny sex ratios in response to the number of other mothers producing offspring within the local group. When the number of mothers is small, the optimal sex ratio for each mother to produce is female biased because mothers achieve more evolutionary fitness via their

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daughters than via their sons. Consider the extreme, but not unknown among parasitoids, situation of a mother reproducing alone in a sub-group or 'patch'. If one male can mate with many females, then to maximize the number of mated daughters that will develop in and then disperse from the patch to eventually produce grandchildren the mother should produce very few sons and as many daughters as possible. The theory behind this summary has been extremely well known within evolutionary ecology for 40 years and the evidence for its operation in parasitoid wasps is strong. Given that the result of population sub-division is strong female bias, and that female biased sex ratios will enhance mass-rearing efficiency and are thought favourable to post-release pest–parasitoid population dynamics, the benefits to biocontrol practice seem obvious (indeed, such potential benefits were explicitly pointed out in the applied biology literature some 25 years ago). What is of concern, and only a little encouragement, is that we can only find one example of the explicit usage of this theory to manipulate parasitoid sex ratios in order to benefit biocontrol programmes. The example involves the mass-rearing of three species of *Gonatocerus* (Mymaridae), which are egg parasitoids of the glassy-winged sharpshooter (*Homalodisca coagulata*), a hemipteran pest of numerous crop plants. All three species have female biased sex ratios, which are dependent, in a manner consistent with theoretical predictions, on the number of mothers searching for hosts in a patch. By simply minimizing contact between females that are searching for hosts the production cost of a female parasitoid can be reduced to a third of the cost under less efficient conditions. Furthermore, females only need to be isolated while host searching as experience of other females prior to presentation with hosts does not adversely affect sex ratios. Therefore, females can conveniently be held together in insectary cages or during transport to the field for release, provided they are separated or held at very low density once in the presence of hosts. These findings have been published only recently and seem ripe to be adopted commercially.

Achieving Female Bias Using Host Quality

Insects of a given species can vary greatly in their size. Larger hosts provide developing parasitoid offspring with more food and can generally be considered to be better quality. Sex ratio theory makes predictions as to whether a mother finding a host of a given quality should use it to support male or female offspring. The decision is non-neutral if the fitness (future success) of male and female offspring is not equivalently affected by variation in host quality. In parasitoids, larger offspring emerge from large hosts and in general female fitness is thought (with reasonable evidence) to be more sensitive to body size variation than is male fitness. As therefore predicted, parasitoids tend to produce male offspring on small hosts and female offspring on large hosts. This body of theory and evidence has been well known to evolutionary ecologists for 25 years. There have also been some applications of host-quality dependent sex ratios within biocontrol practice. For instance, biological control of cassava mealybug (*Phenacoccus manihoti*) can be enhanced by improved soil quality: better soil leads to stronger plants bearing larger mealybugs which, when parasitized by *Apoanagyrus lopezi* (an encyrtid with host-size dependent sex ratios), give rise to an enhanced proportion of female parasitoids in the subsequent generation and improved biocontrol. While this example is very pleasing, our concern is that it is one of only a very small number of such applications of the understanding of host-quality dependent sex ratio behaviour to biocontrol in the field: given the time eclipsed since the theory and sufficient empirical evidence have been widely known there could have been so many more.

We turn now to a further, and more refined, way in which sex ratio responses to host-quality can be used by biocontrol practitioners to improve mass-rearing efficiency. This is based on two further predictions of sex ratio theory: that there is a threshold to host size above which only daughters are laid and that the threshold is relative rather than absolute. Thus, a mother may lay a son in a medium-sized host that is encountered among a batch of large hosts, but would lay a daughter in a medium-sized host found among small-sized hosts. Females are expected to update their estimations of the distributions of host sizes as they encounter a succession of hosts during their lives. Several studies, on *Catolaccus grandis*, a parasitoid of boll weevils (*Anthonomus grandis*), and *Diglyphus isaea*, which attacks agromyzid leafminers, have now shown that increasing the size of hosts presented to females over several days leads to a greater production of female offspring than does presenting similar host sizes each day, and presenting smaller and smaller hosts leads to male biased sex ratios. The technique works not just with females held in isolation (which would be labour intensive in a mass-rearing facility) but also when hosts are presented to groups of parasitoids. Under simulated mass-rearing conditions the production costs of females can be cut by as much as a half. The first of these studies was published ten years ago, yet it seems that no commercial insectary has adopted such modified rearing techniques.

Further Considerations

In the sections above we have implicitly assumed that female parasitoids are in full control of the sexes of their progeny. The assumption is acceptable to a reasonably close approximation for a large number of species, yet there are many ways in which sex ratios can be brought out from under complete maternal control. These include that limited mating opportunities or the genetic basis of sex determination may constrain the sex ratios mothers are able to produce, often adversely from the biocontrol practitioner's point of view, since male bias is a common result. Parasitoids may also be infected by a variety of genetic and bacterial sex ratio distorters, some of which may disrupt biocontrol while others may actually be beneficial via the promotion of female production. In addition, the understanding of the interplay between all of the influences on parasitoid sex ratios that we have discussed or mentioned and of pest–parasitoid population dynamics, from both theoretical and the applied perspectives, is still in its infancy, despite many years of population-biology research focusing on parasitoid wasps as model organisms.

Conclusion

We wish to provoke action from both 'pure' and 'applied' parasitoid biologists, preferably in the form of collaboration. The most obvious benefits of such cross-disciplinary research are, however, already on offer: simple and practicable manipulations of parasitoid rearing conditions can greatly enhance efficiency by promoting female bias. Practitioners who are trained more in 'applied entomology' than in 'evolutionary ecology' may take solace in the fact that there should be no need to delve very deeply into the fascinating, yet huge and dauntingly complex, literature on sex ratio evolution: the essential assumptions and predictions of the theory, as outlined above (and given in more detail in ref. [1]), are relatively straightforward.

[1]Ode, P.J. & Hardy, I.C.W. (2008) Parasitoid sex ratios and biological control. In: Wajnberg, E., Bernstein, C. & van Alphen, J.J.M. (eds) *Behavioral ecology of insect parasitoids: from theoretical approaches to field applications.* Blackwell, Oxford, UK. pp. 253–291. [In press]

By: Ian C. W. Hardy[a] & Paul J. Ode[b]

[a]School of Biosciences, University of Nottingham, Sutton Bonington Campus, Loughborough, Leicestershire LE12 5RD, UK.
Email: ian.hardy@nottingham.ac.uk
Fax: +44 115 9516060

[b]Department of Entomology, North Dakota State University, 270 Hultz Hall, 1300 Albrecht Blvd., Fargo ND 58105, USA.
Email: paul.ode@ndsu.edu
Fax: +1 701 231 8557