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Employing evolutionary theory to improve biological pest control: Causes of non-adaptive sex allocation behavior in parasitoid wasps and implications

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Abstract

Models based on sex allocation theory predict that when the fitness gains from larger size differ between male and female offspring, mothers should produce the sex that will offer the greatest investment return. Behavioral studies on parasitoid wasps have confirmed predictions of models, which additionally have practical implications because of their relevance in biological control. We investigated how a parasitoid attacking a scale insect matches theoretical model predictions in a 2-year field study. As predicted by Charnov's host quality model, mothers laid female eggs in hosts above a threshold size. This threshold was absolute, i.e. independent of the host size distribution, independently of the sampling site and date. Further laboratory assays confirmed field results for at least one parasitoid generation and, moreover, excluded the possibility that the observed behavior was a consequence of immature mortality. By comparing the characteristics of our system with others, we hypothesize that this short-term absolute threshold might be favored in polyphagous parasitoids that attack multivoltine hosts. We propose three measures to mitigate the negative implications of this sex allocation behavior in classical and augmentative biological control programs.

Zusammenfassung

Modelle, die auf der Geschlechter-Allokation basieren, sagen voraus, dass, wenn die Fitnessgewinne aus höherer Körpergröße zwischen Männchen und Weibchen unterschiedlich sind, die Mutter das Geschlecht produzieren sollte, welches die höchste Rendite erbringt. Verhaltensstudien an parasitischen Wespen haben die Vorhersagen der Modelle bestätigt, die zusätzlich praktische Bedeutung wegen ihrer Relevanz für die biologische Schädlingsbekämpfung haben. Wir untersuchten in einer zweijährigen Freilandstudie, wie ein Parasitoid, der Schildläuse angreift, mit den theoretischen Modellvorhersagen übereinstimmt. Wie von Charnovs Wirtsqualitäts-Modell vorhergesagt legten die Mütter weibliche Eier in Wirte oberhalb einer Schwellengröße. Diese Schwellengröße war absolut, d.h., unabhängig von der Verteilung der Wirtsgrößen und unabhängig von Versuchsfläche und Probedatum. Weitere Laborstudien bestätigten die Ergebnisse aus dem Freiland für wenigstens eine Parasitoidengeneration und eliminierten überdies die Möglichkeit, dass das beobachtete Verhalten eine Konsequenz von Mortalität unter den immaturen

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Stadien war. Indem wir die Eigenschaften unseres Systems mit denen anderer Systeme vergleichen, nehmen wir an, dass dieser kurzfristige, absolute Schwellenwert von polyphagen Parasitoiden bevorzugt werden sollte, die plurivoltine Wirte befallen. Wir schlagen drei Maßnahmen vor, um die negativen Effekte dieser Geschlechter-Allokation in klassischen und ergänzenden Programmen der biologischen Schädlingsbekämpfung abzumildern.

Keywords: Sex ratio theory; Coccoidea; Encyrtidae; Behavioral ecology

Introduction

Models based on sex allocation theory predict that when the fitness gains from larger size differ between male and female offspring, mothers should produce the sex that will offer the greatest investment return (Trivers & Willard 1973; West 2009). It has long been observed that some parasitoid Hymenoptera species respond to varying host size (i.e., host quality) by producing female offspring in large-sized (high-quality) hosts and males in small-sized (lower quality) hosts (Chewyreuv 1913; Clausen 1939). Charnov, Los-den Hartogh, Jones, and van den Assem (1981) presented a model in order to explain the available data according to which: (i) female wasps should respond to varying host size, by allocating male eggs in small hosts, and daughters in the larger hosts; (ii) there is a threshold in host size above which only female eggs should be laid; and that (iii) this threshold is not absolute but relative, specifically, it depends on the distribution of host sizes available. The two first predictions of the model are remarkably accurate for parasitoids that paralyze their hosts and eventually stop host growth at oviposition (idiobionts) (Waage & Hassell 1982; Werren 1984; King 1990; Godfray 1994; West & Sheldon 2002). On the other hand, there are rather few studies testing the third prediction and, moreover, the results reported are rather contradictory. There are parasitoids which can adjust their sex allocation behavior in response to the host sizes available in one or several generations (relative threshold) and other species which cannot shift immediately (e.g., in one generation time) their sex allocation decisions according to available host sizes (short-term absolute threshold) (see Appendix A: Table S1). The latter studies are based on either field studies or laboratory experiments with only one parasitoid generation. Therefore, these female parasitoids may exhibit inflexible sex allocation responses to absolute thresholds during one generation (short-term), yet still match Charnov et al.'s third prediction because sex ratio shifts over time (long term; i.e., several generations) are expected, if the sex ratio is a heritable character (Charnov et al. 1981; Jones 1982).

Whether the oviposition threshold of a parasitoid species is relative or absolute (either short-term or long-term) is relevant for its evolutionary fitness, population dynamics and any resulting biological control services (Godfray 1994; Luck & Nunney 1999). For example, a parasitoid species with an absolute oviposition threshold will not be able to respond immediately to changes in host size distribution. In the field, hosts vary in size temporarily or spatially, and in many cases, hosts larger than the threshold size desired to lay female eggs are scarce or even unavailable during certain periods of the year (Luck & Nunney 1999; Pekas, Aguilar, Tena, & Garcia-Marí 2010; Beltrà, Soto, & Tena 2011). Under these circumstances, female parasitoids with an absolute threshold will not be able to produce female offspring and, consequently, fail to build up populations. Besides that, a sparse and strongly male biased population is unfavorable for biological control given that female parasitoids are the ones which kill host pests through oviposition and host-feeding (Godfray 1994).

The main aim of the present study is to investigate the match between predictions made by Charnov's host quality model and the observed sex ratio of the endoparasitoid *Metaphycus helvolus* (Compere) (Hymenoptera: Encyrtidae), and moreover, how this affects biological control services provided by the parasitoid. Specifically, we first analyzed two years of field data and afterwards, we carried out several laboratory assays to corroborate that the oviposition threshold observed in the field was due to the females' decision and not due to immature mortality in small hosts. Finally, we compare the characteristics of our parasitoid-host system and propose solutions to improve classical as well as augmentative biological control programs in which parasitoids with a similar oviposition pattern are used.

Materials and methods

Study system

Our study system includes *M. helvolus* a facultative gregarious endoparasitoid attacking various soft scales. It is native to South Africa and was introduced in the Mediterranean Basin for the control of black scale *Saissetia oleae* Olivier and brown soft scale *Coccus hesperidum* L. (Hemiptera: Coccidae) during the 1960s and 1970s (Guerrieri & Noyes 2000). The host of our system is the pyriform scale *Protopulvinaria pyriformis* (Cockerell) (Hemiptera: Coccidae). It is native to South America and was first recorded in the Mediterranean attacking avocado in 1948 (Gómez-Menor 1948). Despite their different geographic origins *M. helvolus* and *P. pyriformis* are in close association in the Mediterranean; *M.*