Ecological Entomology

Ecological Entomology (2015), **40**, 483–485 DOI: 10.1111/een.12194

SHORT COMMUNICATION

The effect of body size on oviposition success of a minute parasitoid in nature

MICHAL SEGOLI[1,2] and JAY A. ROSENHEIM[2] [1]Mitrani Department of Desert Ecology, The Swiss Institute for Dryland Environmental and Energy Research, The Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Midreshet Ben-Gurion, Israel and [2]Department of Entomology and Nematology, University of California, Davis, California, U.S.A.

Abstract. 1. Individual fitness is often assumed to be positively correlated with body size, but this has rarely been explored under realistic field conditions. This assumption was tested in a minute parasitoid foraging for planthopper eggs in saltmarsh habitats.

2. We used a novel sampling technique that captures females as they naturally die and fall off the vegetation, and estimated their oviposition success according to the number of eggs remaining in their bodies.

3. Our results support a positive relationship between oviposition success and body size of female parasitoids.

4. Only a single female had exhausted her eggs before she died suggesting that the larger body size advantage is not realised primarily via increased fecundity, but instead via increased longevity or foraging-efficiency.

Key words. Fecundity, longevity, proovigenic parasitoids, size-fitness relationship.

Introduction

Parasitoids have long been used to address basic questions in ecology and evolution. In his landmark book, Godfray (1994) concluded that a key gap in our understanding of parasitoid ecology was our understanding of how body size influenced expected fitness. As a result, assumptions of many classic life-history models remain untested. Under laboratory conditions, parasitoid body size has been shown to increase egg production, longevity, and oviposition rate (Bezemer & Mills, 2003; Saeki & Crowley, 2013). However, this does not necessarily translate into higher success in the field. For example, if females rarely deplete their eggs in the field, a positive effect of body size on egg production is unlikely to affect realised fitness. Similarly, a positive effect of body size on longevity may be of small importance if predation sharply depresses survival in the field. Hence, it is crucial to study these relationships under realistic natural conditions.

Several release–recapture field studies demonstrated that the average size of female parasitoids finding a host-patch is significantly larger than the average size of all emerging females (Kazmer & Luck, 1995; Ellers *et al.*, 1998). However, this approach does not provide a direct measurement of fitness. Another approach was to examine the relationship between body size and egg loads of field-collected females, assuming that females with fewer eggs have laid more eggs (Visser, 1994; Ellers *et al.*, 1998). However, these data are scarce and difficult to interpret, because females might have had the opportunity to lay more eggs if not captured. In addition, most parasitoid species are synovigenic, i.e. females continue to mature eggs throughout their life (Papaj, 2000).

We studied a proovigenic species, in which adult females emerge with their full egg load. In addition, we used a novel technique to collect females soon after they died naturally in the field. This allowed us to estimate realised fitness as the number of eggs laid by individual females during their lifetime. A similar approach was taken previously to measure the fitness of female parasitoids foraging in agricultural vineyards (Segoli & Rosenheim, 2013). Here we took a further step to explore body size–fitness relationships for a parasitoid foraging in a natural salt marsh habitat.

Materials and methods

Anagrus sophiae Trjapitzin, 1995 is a proovigenic minute wasp (< 1 mm) that parasitises the eggs of planthoppers in saltmarshes. Populations along Pacific coasts are

Correspondence: Michal Segoli, Mitrani Department of Desert Ecology, Ben-Gurion University, Midreshet Ben-Gurion, 8499000, Israel. E-mail: msegoli@bgu.ac.il

Table 1. Relationships between initial egg load (= egg load at emergence) and hind tibia length (μm) of *Anagrus sophiae* females emerging from *Spartina* leaves.

Population	N	Equation	R^2	P
Chula Vista, SD Bay	50	$y = 0.45x - 45.88$	0.25	< 0.001
Petaluma River, SF Bay	33	$y = 0.36x - 25.66$	0.25	0.003
Sonoma Creek, SF Bay	59	$y = 0.20x - 5.48$	0.10	0.013

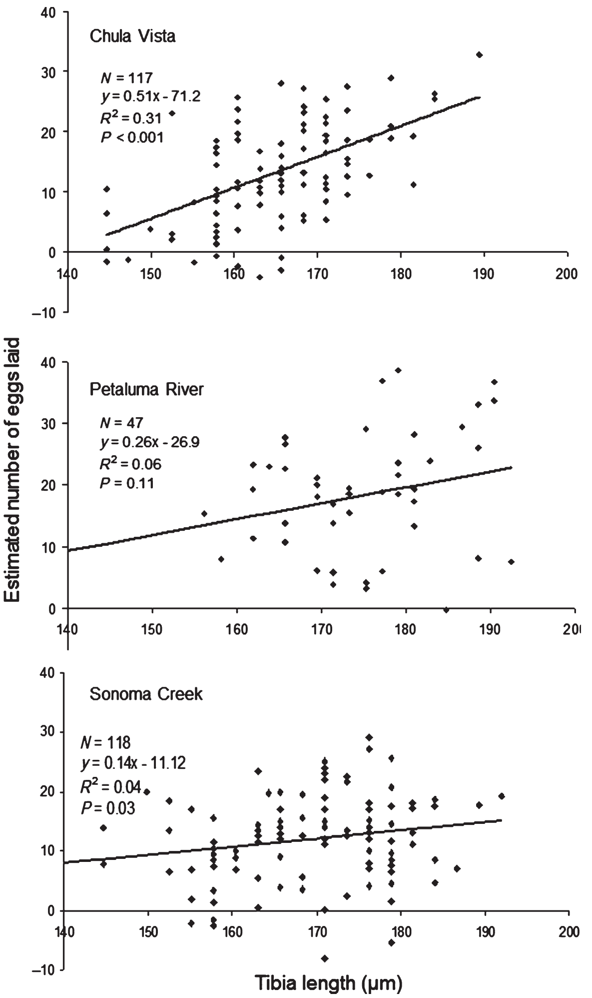

Fig. 1. Relationships between realised fitness (estimated number of eggs laid by females during their lifetimes) and body size (hind tibia length, μm) for three *A. sophiae* populations.

almost entirely female, probably because they carry a *Wolbachia* strain that induces parthenogenesis (Segoli *et al.*, 2013). We sampled parasitoids from one population near San Diego: Chula Vista (GPS: 32.639262, −117.113357), July 2011; and two populations in northern San Francisco Bay: Petaluma River (GPS: 38.116315, −122.504581), August–September 2010; and Sonoma Creek (GPS: 38.155655, −122.409121), July–August 2011.

To characterise the relationship between parasitoid size and initial egg load for each population, we collected *Spartina* leaves harbouring planthopper eggs from the field and placed them in emergence cages. Emerging parasitoid females were dissected in a drop of water, their eggs counted, and a hind tibia measured. Although the relationships between hind tibia length and initial egg load were significant in all populations (Table 1), R^2 values were low. This increased the noise in our estimates of realised fitness; we compensated for this by gathering larger samples of parasitoids for our analyses. In a separate collection, we estimated the realised fitness of females. *Anagrus sophiae* Trjapitzin, 1995 forage on *Spartina* foliage for planthopper eggs, and upon death, fall out of the plant canopy. We collected these dead wasps using modified collection trays, where they were retained using a system of baffles. Trays were left in the field for 24 h with the aid of a flotation system that prevented them from being inundated during high tides. Females were dissected, and their oviposition success was estimated as their egg load at emergence (estimated based on the relationship between body size and initial egg load in each population) minus their actual egg load upon death.

Results and Discussion

Body size can potentially enhance fitness through increasing fecundity, longevity or foraging efficiency. We found a positive relationship between body size and realised fitness in the field [Fig. 1; generalised linear model (GLM): $F_{1,276} = 32.9$, $P < 0.001$ for tibia length; $F_{2,276} = 7.58$, $P < 0.001$ for field site; and $F_{2,276} = 6.67$, $P = 0.002$ for the interaction]. The slopes of these functions were not significantly different from those of the potential fitness functions (*t*-test, $P =$ NS for all three populations), indicating that the realised body size advantage was similar to the potential body size advantage. However, only a single female ($N = 282$) from our field collection trays had entirely exhausted her egg supply before she died, suggesting that the larger body size advantage is not realised primarily via increased egg load at emergence. Instead, the observed size-fitness association is more likely to be mediated via increased longevity or oviposition rate in the field. In particular, *A. sophiae* females have been observed to spread their eggs among host patches (Cronin & Strong, 1993). Hence, larger females may have a substantial advantage if they survive longer or have better foraging efficiency, allowing them to visit more host patches during their lifetimes. Another interesting possibility is that females might still be limited to some extent by their egg supply, but exhibit decelerating oviposition rates as they approach egg limitation (Casas *et al.*, 2000), thereby avoiding egg depletion.

Our results suggest inter-population variation in the shape of the size-fitness relationship. This may be explained by variation in local conditions among field sites. Food availability, host density, and climatic conditions may all affect parasitoid fitness, and the magnitude of these effects may differ between small and large females. To further explore hypotheses regarding the relative importance of different factors in determining the shape of the size-fitness relationship, it is necessary to obtain fitness estimates for a larger number of populations and at different timings along the season. Our findings and the general applicability of our methods may provide an important stepping stone for such future work.

Acknowledgements

We thank Collin Edwards, Cory Fernandez, Timothy Fong, Tobias Glik, Tierra Groff, Orly Oren, Michael Park, Paul Rugman-Jones, Moran Segoli, Corinne Stouthamer, Richard Stouthamer, Ian Taff, and Lucinda Ye for technical support, fruitful discussions, and comments on the manuscript. We thank Jen McBroom, Leonard Liu, Chris Chamberlain, Giselle Block, Brian Swedberg, and Brian Collins for aid in obtaining permits and access to study sites. This study was partially funded by grants from the Israel Science Foundation (ISF), the Bi-national Agricultural Research and Development (BARD), and the United States National Science Foundation (NSF: DMS-1022639).

References

Bezemer, T.M. & Mills, N.J. (2003) Clutch size decisions of a gregarious parasitoid under laboratory and field conditions. *Animal Behaviour*, **66**, 1119–1128.

Casas, J., Nisbet, R.M., Swarbrick, S. & Murdoch, W.W. (2000) Eggload dynamics and oviposition rate in a wild population of a parasitic wasp. *Journal of Animal Ecology*, **69**, 185–193.

Cronin, J.T. & Strong, D.R. (1993) Substantially submaximal oviposition rates by a mymarid egg parasitoid in the laboratory and field. *Ecology*, **74**, 1813–1825.

Ellers, J., van Alphen, J.J.M. & Sevenster, J.G. (1998) A field study of size-fitness relationships in the parasitoid *Asobara tabida*. *Journal of Animal Ecology*, **67**, 318–324.

Godfray, H.C.J. (1994) *Parasitoids: Behavioral and Evolutionary Ecology*. Princeton University Press, Princeton, New Jersey.

Kazmer, D.J. & Luck, R.F. (1995) Field tests of the size-fitness hypothesis in the egg parasitoid *Trichogramma pretiosum*. *Ecology*, **76**, 412–425.

Papaj, D.R. (2000) Ovarian dynamics and host use. *Annual Review of Entomology*, **45**, 423–448.

Saeki, Y. & Crowley, P.H. (2013) The size-number trade-off and components of fitness in clonal parasitoid broods. *Entomologia Experimentalis et Applicata*, **149**, 241–249.

Segoli, M. & Rosenheim, J.A. (2013) Limits to the reproductive success of two insect parasitoid species in the field. *Ecology*, **94**, 2498–2504.

Segoli, M., Stouthamer, R., Stouthamer, C.M., Rugman-Jones, P. & Rosenheim, J.A. (2013) The effect of *Wolbachia* on the lifetime reproductive success of its insect host in the field. *Journal of Evolutionary Biology*, **26**, 2716–2720.

Visser, M.E. (1994) The importance of being large – the relationship between size and fitness in females of the parasitoid *Aphaereta minuta* (Hymenoptera, Braconidae). *Journal of Animal Ecology*, **63**, 963–978.

Accepted 26 January 2015
First published online 10 March 2015