

This article was downloaded by:[Usda Ars Mwa Ncaur]
[Usda Ars Mwa Ncaur]

On: 7 June 2007

Access Details: [subscription number 771007643]

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954

Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Biocontrol Science and Technology

Publication details, including instructions for authors and subscription information:

<http://www.informaworld.com/smpp/title~content=t713409232>

The functional response of **Ibalia leucospoides** (Hymenoptera: Ibalidae), a parasitoid of **Sirex noctilio** (Hymenoptera: Siricidae)

Valeria Fernández-Arhex; Juan C. Corley

To cite this Article: Fernández-Arhex, Valeria and Corley, Juan C. , 'The functional response of **Ibalia leucospoides** (Hymenoptera: Ibalidae), a parasitoid of **Sirex noctilio** (Hymenoptera: Siricidae)', *Biocontrol Science and Technology*, 15:2, 207 - 212

To link to this article: DOI: 10.1080/09583150400016084

URL: <http://dx.doi.org/10.1080/09583150400016084>

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.informaworld.com/terms-and-conditions-of-access.pdf>

This article maybe used for research, teaching and private study purposes. Any substantial or systematic reproduction, re-distribution, re-selling, loan or sub-licensing, systematic supply or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

© Taylor and Francis 2007

SHORT COMMUNICATION

The functional response of *Ibalia leucospoides* (Hymenoptera: Ibalidae), a parasitoid of *Sirex noctilio* (Hymenoptera: Siricidae)

VALERIA FERNÁNDEZ-ARHEX & JUAN C. CORLEY

CONICET, Laboratorio de Ecología de Insectos Forestales, Bariloche, Río Negro, Argentina

(Received 6 January 2004; accepted 14 June 2004)

Abstract

We experimentally studied the functional response of the parasitoid *Ibalia leucospoides* on its host, *Sirex noctilio*. Our results show a type III functional response, which we suggest is due to a changing probability, in host encounter. We discuss its relevance to the biological control of woodwasp populations in the field.

Keywords: Parasitoid–host interactions, biological control, behavioural response, logistic regression, host kairomones

The woodwasp *Sirex noctilio* Fabricius (Hymenoptera: Siricidae) is a primitive xylophagous insect that attacks pine trees. *S. noctilio* is native to Mediterranean Europe, but in the last century, has successfully invaded Australia, New Zealand, South Africa and South America (Madden 1988; Fritz 1993; Klasmer et al. 1997). In many of these areas, *S. noctilio* has become the economically most important pest of pine tree plantations (Iede et al. 1993).

Ibalia leucospoides Hochenwarth (Hymenoptera: Ibalidae), a solitary koinobiont parasitoid of *S. noctilio*, has been used in classical biological control of woodwasps in Australia and New Zealand. The parasitoid, is now found throughout most pine-tree plantations in the Southern hemisphere where there are woodwasps. This is because *I. leucospoides* has been distributed together with *S. noctilio* by transportation of infested wood (Corley 2001).

Ibalia leucospoides attacks eggs and first instar larvae of *S. noctilio*, and is endoparasitic until its third instar, a stage at which it becomes an ectoparasite. Its life cycle is closely related with the development of woodwasp larvae, usually lasting 1 year (but see Corley et al. 2004). In field conditions, *I. leucospoides* may parasitize up

Correspondence: Juan C. Corley, CONICET, Laboratorio de Ecología de Insectos Forestales INTA EEA Bariloche CC 277, Bariloche 8400, Río Negro, Argentina. Tel: +54-2944-422731. Fax: +54-2944-424991. E-mail: jcorley@bariloche.inta.gov.ar

to 40% of its hosts, although values are highly variable in space and time (Corley unpublished data). In spite of the fact that it is generally reported as a successful control agent of *S. noctilio* (e.g., Kidd & Jervis 1996), some studies suggest that under given environmental conditions, its regulatory role is secondary to that of other parasitoids (Taylor 1978). Indeed, most current woodwasp population control efforts are based on the augmentative releases of the parasitic nematode *Deladenus siricidicola* Bedding (Nematoda: Neotylenchidae), and intense silvicultural management (Bedding 1984). Because successful control of *S. noctilio* has been reported after the introduction of several natural enemies together with the implementation of forest management practices aimed to enhance forest health, the relative importance of *I. leucospoides* on *S. noctilio* population suppression, remains obscure. In addition, given that the pest is distributed in habitats with very different environmental characteristics, impact of control strategies are difficult to predict.

Research on this parasitoid, has focused largely on its host foraging behaviour (Chrystal 1930; Madden 1968; Spradbery 1970a,b). It has been shown that *I. leucospoides* uses olfactory cues to locate woodwasp eggs and larvae. The parasitoid is attracted to *Amylostereum aerolatum*, a fungus species which is in close association with *S. noctilio* (Madden 1968; Martínez et al. in prep.). Woodwasp females carry fungal spores which are placed close to eggs, burrowed 1.5 cm deep inside tree stems. Wood decomposed by fungal growth will be used as food by the developing woodwasp larvae (Madden 1968; Spradbery 1970a,b). On a larger spatial scale, parasitoids are attracted to stressed trees that liberate α - and β -terpenes (Madden 1968, 1988; Spradbery 1970a,b).

In this paper, we report on the functional response of *I. leucospoides* using *S. noctilio* as a host. We exposed single, recently emerged (<48 h) female parasitoids, to 0.5-m long pine tree billets (diameter varied between 9.5 and 11 cm) with host ovipositions. The experiments were carried out in a wire mesh cage ($1 \times 0.40 \text{ m}^2$) at a temperature of $26.2 \pm 0.2^\circ\text{C}$ and natural midday lighting. Parasitoids had been previously left to feed for 24–48 h on 30% sucrose solution and kept in small plastic cages (30 cm^3) in closed room conditions (natural lighting and a temperature of $24.4 \pm 0.4^\circ\text{C}$).

We obtained adult parasitoids (and hosts) from 1-m long lodgepole pine billets (*Pinus contorta* var. *latifolia*), collected in the field in the proximity of Bariloche ($41^\circ 08' \text{ S}$; $71^\circ 20' \text{ W}$; Argentina) by logging attacked trees. The logs were kept under ambient conditions in locker-type cages, and viewed on a daily basis during host and parasitoid emergence.

Host-rich logs were obtained by releasing one *S. noctilio* adult female on each log. However, successful host oviposition was difficult to ascertain because eggs are laid in tunnels within the wood, that branch out from a single hole (number of eggs per hole 0–3) (Madden 1974). Therefore, we considered only holes in which the woodwasp had inserted its ovipositor completely, because these contained at least one egg and fungus (see Madden 1968, 1974). We observed host females and marked each oviposition insertion with a white pen-eraser.

Host densities (treatments) were 2, 4, 6, 10 and 14 oviposition holes per log. Each treatment was replicated 10 times, in each case changing both parasitoids and logs. We continuously observed the parasitoid on logs and measured its searching time until it flew to cage walls and remained for 5 min (i.e., a variable time experiment). Our response-variables were the number of holes attacked and the total time on the patch per trial. Because we were unable to see eggs inside the log, we considered as

successful attacks on host holes in which the parasitoid spent more than 2 min (Spradbery 1970a).

Following Trexler et al. (1988) and Juliano (1993), we studied the proportion of parasitized hosts as a function of initial host density using logistic regression to distinguish between a type II and III response (SAS Institute Inc. 1999). The proportion of parasitized hosts declines monotonically with host density in a type II response, but is positively density-dependent over some region of host density in a type III response. The sign of the linear coefficient estimated by the logistic regression can be used to distinguish the shape of the functional response curve. We estimated functional response parameters by fitting a non-linear least squares regression to the number of hosts attacked versus the number of hosts available (Quasi-Newton estimation). We used the type III curve parasitoid equation (Hassell 1978) to obtain estimates for handling time (T_h) and attack rate (a). In this equation, $a = (d + bN_0) / (1 + cN_0)$, where b , c and d are constants and N_0 is the number of hosts available. For our data, c and d parameters were not significantly different from 0 (95% confidence intervals), $a = bN_0$. Thus, we used the following equation,

$$N_{at} = N_0 * \{1 - \exp[-(b * N_0) * T / (1 + (b * T_h * (N_0)^2))]\}, \tag{1}$$

where N_{at} and N_0 are the number of holes attacked and available, respectively, T_h is the handling time and T stands for the total length of the experiment.

Given that our experiment considered variable time (Walde & Murdoch 1988; Fernández-Arhex & Corley 2003, 2004), we estimated the parameters of the functional response by replacing total time (T) in Eq. (1) by the following function,

$$T = P_1 / (1 + P_2 * \exp(-P_3 * N_0)) + R_0, \tag{2}$$

where P_1 , P_2 and P_3 are constants (estimated by fitting a non-linear curve to the function), and R_0 is the mean parasitoid residence time on logs without hosts. In our case $P_1 = 6136 (\pm 247)$, $P_2 = 35 (\pm 21)$ and $P_3 = 0.75 (\pm 0.13)$ ($r^2 = 0.99$) and $R_0 = 14.08$ min.

I. leucospoides has a type III functional response (Table I; Figure 1). The mean searching time ranged from 32 min to 2 h, according to host density. The attack rate was a function of host density, with parameter b averaging 0.0001 (± 0.00008) and handling time, 12 (± 2) min ($r^2 = 0.57$).

A sigmoidal functional response (type III) suggests direct density-dependence up to some threshold host density, which may contribute to stability if average densities fall below this threshold (Hassell et al. 1977). Type III curves have been related, for example, to a decrease in time spent handling hosts or an increase in searching rates in response to increased host density. However, these curves have been observed in a limited number of parasitoid species (Fernández-Arhex & Corley 2003). In addition, in several of these studies, the density-dependence threshold values are low in relation

Table I. Results of the logistic regression of the proportion of *S. noctilio* oviposition holes attacked by *I. leucospoides* against the initial number offered

Parameter	Estimate	SE	χ^2	<i>P</i>
Constant	-1.2167	0.5953	4.18	0.041
Linear	0.3263	0.1503	4.71	0.0299
Quadratic	-0.0179	0.0082	4.74	0.0294

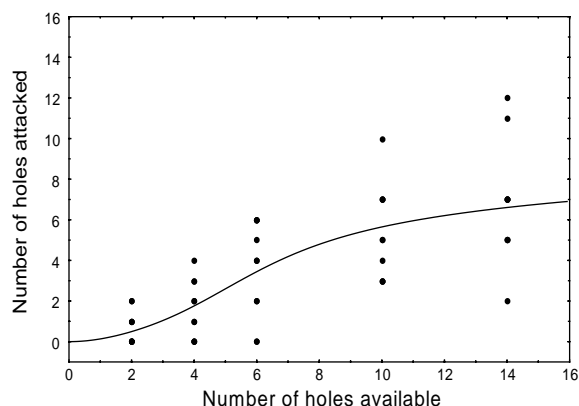


Figure 1. Functional response of the parasitoid *I. leucospoides*. A type III response curve was fitted by least squares, following Hassell's (1978) equation. Overlapping values are shown as a single dot, $n = 10$ for each density.

to both the offered densities and host density in the field (Hughes et al. 1992; van Steenis & El-Khawass 1995).

The type III functional response shown by *I. leucospoides* is probably a consequence of a variable host search success. In our experiment, the probability of a parasitoid not attacking hosts was higher at lower host densities ($n_2 = 0.5$, $n_4 = 0.3$, $n_6 = 0.2$, $n_{10} = 0$, $n_{14} = 0$) (Figure 1). The observed probability of not finding any hosts, estimated by maximum likelihood from the experimental data, differed significantly from an expected constant encounter probability ($P = 0.5^{N_0}$; $\chi^2_{19,0.05} = 39.47$; $P < 0.05$). Furthermore, change in the slope of the sigmoid curve occurs at densities below five host drills per billet (Figure 1). Consequently, the contribution of the type III response of *I. leucospoides* to *S. noctilio* population regulation is limited to low host density values.

I. leucospoides host foraging success is determined by its ability to detect odors derived from *A. aerolatum*. The parasitoid detects hosts in a log, determines host development and probably host abundance by fungal presence and growth (Madden 1968; Bettinelli 2001). The failure of some parasitoids to find hosts at low densities, may be due to a minimal threshold in concentration of chemicals, proportional to host abundance. Remember that host discovery in parasitoids, is typically influenced by the detection of a given intensity of some chemical associated with the host (kairomones) which is usually proportional to host density (Chiri & Legner 1982; Kumar et al. 1994; Vet et al. 1995, 2002).

Our findings are in line with recent *meta*-analysis results reported by us (Fernández-Arhex & Corley 2003) in which we suggest that Type II curves are more likely to be described for parasitoids under realistic conditions. While *I. leucospoides* displayed a type III response in our study, the curve shape is most probably a consequence of host discovery inefficiencies at low host densities. This, in turn may be explained by the limited response to host related chemical cues below some minimal threshold. In addition, the type III curve has its density dependent segment below five host holes per billet. Because hosts are highly aggregated in the field (i.e., > 5 holes per billet), the contribution of the type III response of *I. leucospoides* towards *S. noctilio*

population regulation, and hence to the biocontrol of woodwasps populations is probably minimal.

Acknowledgements

The authors acknowledge the encouragement and valuable comments received from C. Bernstein, C. Gittins, E. Gayone, J.M. Villacide, J. Gyenge, M. Lozada and two anonymous reviewers. We also thank I. Scivetti MECOM, Centro Atómico Bariloche. This work was carried out with financial support from grant CONICET-PIP 529/98, PIA 01/00 (SAGPyA) and the Ecos Sud Programme (A98B05).

References

- Bedding RA. 1984. Nematode parasites of Hymenoptera. In: Nickle WR, editor. Plant and Insect Nematodes. New York: Marcel Dekker Inc. pp 755–795.
- Bettinelli J. 2001. Mecanismos de elección y explotación de parches del parasitoide *Ibalia leucospoides* (Hymenoptera: Ibalidae). Graduate Dissertation Universidad Nacional del Comahue (UNC), Argentina. p 61.
- Chiri AA, Legner EF. 1982. Host searching kairomones alter behaviour of *Chelonus* sp. nr. *curvimaclatus*, a hymenopterous parasite of the pink bollworm *Pectinophora gossypiella* (Saunders). Environmental Entomology 11:452–455.
- Chrystal RN. 1930. Studies of the *Sirex* parasites. Oxford For Memories No 11. London: Oxford University Press. p 63.
- Corley JC. 2001. La diapausa prolongada y su papel en la dinámica poblacional de sistemas huésped – parasitoide. PhD Dissertation, FCEyN, U.B.A (Argentina).
- Corley JC, Capurro AF, Bernstein C. 2004. Prolonged diapause and the stability of host-parasitoid interaction. Theoretical Population Biology 65:193–203.
- Fernández-Arhex V, Corley JC. 2003. The functional response of parasitoids and its implications for biological control. Biocontrol Science and Technology 13:403–413.
- Fernández-Arhex V, Corley JC. 2004. La Respuesta Funcional: Una Revisión y Guía Experimental. Ecología Austral (in press).
- Fritz G. 1993. *Sirex noctilio*, su presencia en Dina Huapi y el impacto sobre el recurso forestal de la región. Informe Dirección General de Bosques y Fauna de Río Negro. p 8.
- Hassell MP. 1978. The Dynamics of Arthropod Predator-Prey Systems. Monographs in population biology. Princeton University Press, Princeton, New Jersey.
- Hassell MP, Lawton JH, Beddington JR. 1977. Sigmoid Functional Responses by invertebrate predators and parasitoids. Journal of Animal Ecology 46:249–262.
- Hughes RD, Woolcok LT, Hughes MA. 1992. Laboratory evaluation of parasitic Hymenoptera used in attempts to biologically control aphid pests of crops in Australia. Entomologia Experimentalis et Applicata 63:177–185.
- Iede ET, Pentead SRC, Gaiad DCM, Silva SMS. 1993. Panorama a nível mundial da ocorrência de *Sirex noctilio* F., 1793 (Hymenoptera: Siricidae), in Conferência Regional da Vespa da Madeira, *Sirex noctilio*, na América do Sul, (EMBRAPA), Colombo, PR, Brasil. pp 23–33.
- Juliano SA. 1993. Nonlinear curve fitting: Predation and functional response curves. In: Scheiner SM, Gurevitch J, editors. Design and Analysis of Ecological Experiments. New York: Chapman and Hall. pp 159–182.
- Klasmer P, Corley JC, Botto E. 1997. Presencia de la avispa barrenadora de los pinos *Sirex noctilio* F. (Hymenoptera: Siricidae) en la región andino – patagónica de Argentina. Estado actual de la investigaciones para su control biológico. Serie programa de Investigación y Desarrollo Ambiental # 20-Universidad de Belgrano.
- Kidd N, Jervis M. 1996. Populations dynamics. In: Kidd N, Jervis M, editors. Insect natural enemies. Practical approaches to their study and evaluation. UK: Chapman & Hall. pp 21–284.
- Kumar N, Kumar A, Tripathi CPM. 1994. Functional response of *Campoletis chloridae* Uchida (Hymenoptera: Ichneumonidae), a parasitoid of *Heliothis armigera* (Hübner) (Lepidoptera: Noctuidae) in an enclosed experimental system. Biological Agriculture and Horticulture 10:287–295.

- Madden JL. 1968. Behavioural responses of parasites to the symbiotic Fungus associated with *Sirex noctilio* F. *Nature* 218:189–190.
- Madden JL. 1974. Oviposition behaviour of the woodwasp, *Sirex noctilio* F. *Australian Journal of Zoology* 22:341–351.
- Madden JL. 1988. *Sirex* in Australasia. In: Berryman AA, editor. *Dynamics of forest insect populations: patterns, causes and implications*. Plenum Press. pp 407–427.
- SAS Institute Inc. 1999. SAS® System for Microsoft® Windows®, version 8.0 (TSMO), Cary, NC, USA.
- Spradbery JP. 1970a. Host finding by *Rhyssa persuasoria*, an ichneumonid parasite of siricid woodwasps. *Animal Behaviour* 18:103–114.
- Spradbery JP. 1970b. The biology of *Ibalia drewezensi* Borries, a parasite of siricid woodwasps. *Proceedings of the Entomological Society London B* 45:104–113.
- Taylor KL. 1978. Evaluation of the insects parasitoids of *Sirex noctilio* (Hymenoptera: Siricidae) in Tasmania. *Oecologia* 32:1–10.
- Trexler JC, McCulloch CE, Travis J. 1988. How can the functional response best be determined? *Oecologia* 76:206–214.
- Van Steenis MJ, El-Khawass KAMH. 1995. Behaviour of *Aphidius colemani* searching for *Aphis gossypii*: Functional Response and Reaction to previously searched aphid colonies. *Biocontrol Science and Technology* 5:339–347.
- Vet LEM, Lewis WJ, Cardé RT. 1995. Parasitoid foraging and learning. In: Carde RT, Bell WJ, editors. *Chemical Ecology of Insects*. 2nd ed. NY: Chapman & Hall.
- Vet LEM, Hemerik L, Visser ME, Wäkers FL. 2002. Flexibility in Host-search and Patch-use Strategies of Insect Parasites. In: Lewis EE, Campbell JF, Sukhdeo MVK, editors. *The Behavioural Ecology of parasites*. CAB International. pp 39–64.
- Walde SJ, Murdoch WW. 1988. Spatial density dependence in parasitoids. *Annual Review of Entomology* 33:441–466.