



ELSEVIER

Contents lists available at ScienceDirect

## Biological Control

journal homepage: [www.elsevier.com/locate/ybcon](http://www.elsevier.com/locate/ybcon)

# Trapping success and flight behavior of two parasitoid species of the woodwasp *Sirex noctilio*

Andrés S. Martínez<sup>a,\*</sup>, Deborah Fischbein<sup>a</sup>, José M. Villacide<sup>a</sup>, Juan C. Corley<sup>a,b</sup>

<sup>a</sup> Grupo de Ecología de Poblaciones, Instituto de Investigaciones Forestales y Agropecuarias Bariloche, 8400 Bariloche, Argentina

<sup>b</sup> Departamento de Ecología, Centro Regional Universitario Bariloche, Universidad Nacional del Comahue, 8400 Bariloche, Rio Negro, Argentina

## ARTICLE INFO

## Keywords:

*Ibalia leucospoides*  
Integrated pest management  
*Megarhyssa nortoni*  
Monitoring  
Natural flight path  
Semiochemical

## ABSTRACT

Classical biological control relies on the deliberate introduction of natural enemies to reduce pest populations below damage thresholds. Knowledge on key aspects of the behavior of antagonists and their population densities through time can be important to increase the efficiency of control programs. The woodwasp *Sirex noctilio* is a global threat to pine forests and biological control can be based, among other agents on two parasitoids, *Ibalia leucospoides* and *Megarhyssa nortoni*, with variable success. Currently no sensitive and standardized monitoring method exists for these control agents and little is known on their behavior, such as their vertical flight-distribution. Our aims were: firstly, assess the efficiency in capturing the parasitoids of four methods (two passive traps based on flight-path interception or caging previously-attacked trees to retain emerging insects, and two active traps baited with pine volatiles), and secondly establish the parasitoids vertical flight distribution. *Ibalia leucospoides* (females) was captured by all methods but intercept panel traps registered the highest captured individuals when accounting for effort. Conversely *M. nortoni* did not respond to baited traps, and low numbers were recorded in passive traps. Males of both species flew higher than females of *I. leucospoides*. Intercept traps baited with pine volatiles could be used to monitor *I. leucospoides*, but *M. nortoni* is not captured in these traps. We suggest that both species could be monitored by passively trapping insects at the moment of emergence from previously-infested trees. Further research is needed, especially on the chemical ecology of both species, to further develop inexpensive and standardized monitoring methods.

## 1. Introduction

Classical biological control is often implemented as part of integrated pest management (IPM) programs to help prevent economic losses caused by non-native pests (Orr, 2009). The method relies on the deliberate introduction of natural enemies, collected from the area of origin of the pest, into the new habitats in which the pest has established, with the aim of persistently reducing its population below a damaging threshold (Bale et al., 2008). Since local conditions can affect natural enemy performance, a critical component of any biological control program should be post-release monitoring and evaluation of natural enemy establishment, prevalence and impact on the pest. In addition, it is important to assess the degree of dispersal from release sites as both high and low dispersal rates can affect the establishment and suppression capacity of natural enemies (Kidd and Jervis, 2007; Heimpel and Asplen, 2011). Information on local population densities through time can guide re-inoculation practices, the prevention of genetic bottlenecks, negative impacts from Allee effects, ultimately

facilitating the adaptation of IPM programs to local conditions for increased chances of success (Hopper and Roush, 1993).

The woodwasp *Sirex noctilio* Fabricius (Hymenoptera: Siricidae) constitutes a major threat to cultivated pine forests throughout the world, being the only species of the Siricidae family capable of killing healthy trees (Spradbery, 1973). Native to Europe and Northern Africa, the woodwasp has invaded in the past century Oceania, South Africa, South America and more recently North America (Boissin et al., 2012). Tree death occurs when females lay eggs into pine stems (normally stressed trees are preferred, but vigorous individuals can occasionally be attacked (Haavik et al., 2018), together with a venom and mycelia of a symbiotic fungus that weaken and eventually kill the tree. In South America, the woodwasp was first detected in the early 80 and since then it has spread considerably being found in most regions with cultivated pines, causing severe damage throughout the years (Martinson et al., 2018).

In response to *S. noctilio* spread and impact, IPM programs have been implemented with varying degrees of success (Slippers et al.,

\* Corresponding author.

E-mail address: [andmarv77@gmail.com](mailto:andmarv77@gmail.com) (A.S. Martínez).

<https://doi.org/10.1016/j.biocontrol.2019.04.008>

Received 4 February 2019; Received in revised form 5 April 2019; Accepted 15 April 2019

Available online 19 April 2019

1049-9644/ © 2019 Elsevier Inc. All rights reserved.

2012). These programs include, among other actions, silvicultural practices aimed at minimizing the proportion of susceptible trees within a stand and the use of specific natural enemies (Corley et al., 2018). In addition to the parasitic nematode *Deladenus siricidicola*, a number of parasitoid species originating from Europe, Asia, North Africa and North America were initially introduced as biocontrol agents in many of the affected regions (Taylor, 1976; Bain et al., 2012; Cameron, 2012). Two of these parasitoid species, *Ibalia leucospoides* (Hochenwarth) (Hymenoptera: Ibalidae) and *Megarhyssa nortoni* (Cresson) (Hymenoptera: Ichneumonidae) are considered among the most effective biocontrol agents and in some occasions, are reared for introduction, redistribution or augmentative biological control purposes (Corley et al., 2018; Cameron, 2012). Despite the variety of measures applied, the pest continues to be a significant threat and is still causing severe economic losses to pine plantations in many invaded regions. For instance, in Argentina despite the presence of the nematode and parasitoids, *S. noctilio* continues to be widespread and outbreaks associated with drought events are observed (Corley et al., 2018).

Often, the parasitoids used in *Sirex noctilio* biological control plans are reared off-site, using different effort-intensive methods such as locating and felling trees that have been naturally-attacked by the *Sirex* woodwasp and antagonists. Alternatively billets are obtained from artificially-weakened trees (i.e., “trap trees”, Neumann et al., 1982; Neumann and Morey, 1984) that have attracted *S. noctilio* and the parasitoids. These same methods are used to monitor parasitoid establishment in new regions and to obtain a crude estimate of their impact on the pest population (i.e., number of parasitoids/total number of emergences). These protocols are labour-intensive and costly, and more importantly, results are difficult to compare across sites and regions. These limitations highlight the absence of a standardized and cost-effective method to assess antagonist population levels over time used in *S. noctilio* biocontrol programs.

Although occasional parasitoid captures have been reported in studies aimed at assessing *S. noctilio* trap/lure effectiveness (Bashford, 2008; Barnes et al., 2014), none of the studies have addressed this subject specifically. Furthermore, studies focused on understanding the behavior of *S. noctilio* parasitoids to improve capture methods are scarce. The objective of the present study was twofold: (i) to evaluate the capture rates of different approaches to retain *I. leucospoides* and *M. nortoni*, two of the most widely used parasitoid species in biocontrol programs of *S. noctilio*, and (ii) to assess their natural flight paths (i.e., vertical distribution patterns) in order to gain further insights that could improve trapping protocols, such as trap placement.

## 2. Material and methods

### 2.1. Study sites and trapping methods

The study was conducted in three pine plantations, each between 10 and 14 ha in size, located in northern Patagonia, separated by at least 20 km. Plantations consisted of *Pinus contorta* and *Pinus ponderosa* of a similar age (25–30 years) and height (13–16 m), infested by *Sirex noctilio* and both parasitoids. Between 5 and 15 % of trees had evidence of recent attack (e.g. resin beads), in addition to having established populations of both *I. leucospoides* and *M. nortoni* (J. Villacide pers. obs.). Average tree density was  $970 \pm 90$  trees/ha (mean  $\pm$  standard error (se)), and diameter at breast height was  $23 \pm 4$  cm (mean  $\pm$  se,  $n = 100$  trees/site). Two types of passive traps (sticky and sheath traps) and two types of active devices (baited intercept panel and Lindgren multifunnel traps) were installed in the field during the *S. noctilio* and parasitoid flight period, for 2 months between February and April 2013.

#### 2.1.1. Sticky traps

A total of 28 unbaited sticky traps (i.e. 28 replicates) were placed in the three sites mentioned above (site a: 10 traps, site b: 9 traps, and site c: 9 traps). Traps consisted of a black plastic netting (mesh size: 1 cm)

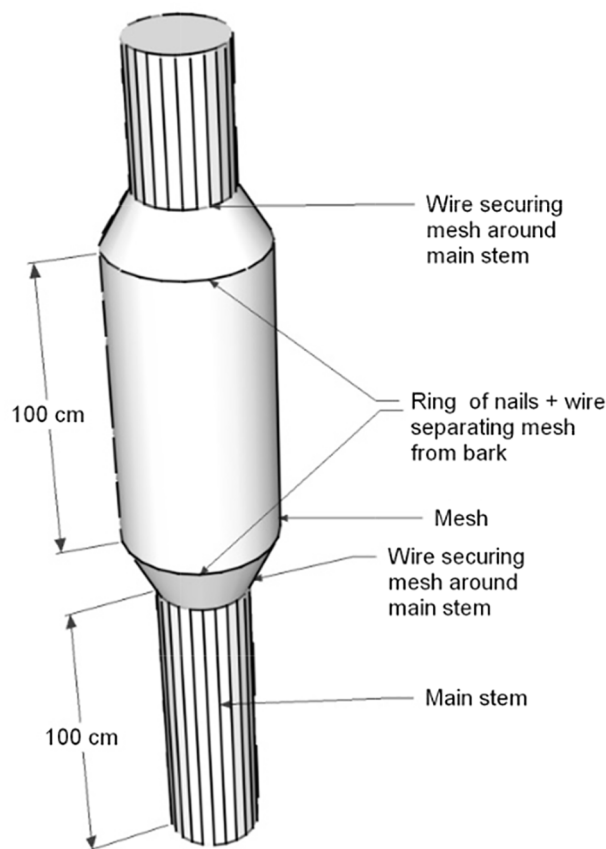


Fig. 1. The “sheath trap”. Capture method used to retain emerging *S. noctilio*, *I. leucospoides* and *M. nortoni* adults from previously naturally-infested trees. The trap consists of a plastic mesh, secured around a 1 m portion of the main stem.

covered with sticky material (Tute gel, Tute S.A. Argentina) and were distributed within each plantation separated by a minimum distance of 20 m between traps and 20 m from the plantation edge. Each trap was 0.4 m wide  $\times$  6 m high (intercept surface accounting both sides = 4.8 m<sup>2</sup>) and the top edge of each trap was hung at 6 m high from two trees separated by ca. 2 m edge (see Martínez et al., 2014 for more trap details). All facing branches within the 6 m vertical section of the main stems were removed so that traps hung freely. To reduce movement due to wind, traps were secured to tree bases with ropes. A pulley was secured on each tree so the trap could be lowered and checked for captured insects and then raised again. The stickiness of the material was such that wasps remained in the initial position where the interception occurred. Insect collections were carried out every-two weeks.

#### 2.1.2. Sheath traps

A second type of passive trap was placed in the field (Fig. 1), thirty trees with previous-year attack symptoms (i.e., with presence of fresh resin beads as indicators of *S. noctilio* oviposition) were located throughout the plantations (10 infested trees/site at least 20 m from other traps) and branches removed in a section a section between 1 and 2.5 m above ground. This cleared portion of the main stem was surrounded with a 1.2 m wide plastic net (mesh 2 mm) separated 8 cm from the main stem with a ring of nails and thin wire joining them. In this way, a 1 m section of the trunk was “sealed” and any wasps emerging from the tree were retained between the trunk and the mesh (surface considering the circumference = 1 m<sup>2</sup>). Insect collections were carried out every 2 weeks.

### 2.1.3. Intercept and Lindgren funnel traps

Two types of baited traps were installed in the three sites. Intercept panel traps and eight-unit Lindgren funnel traps (0.25 m wide × 0.72 m high, intercept surface = 0.7 m<sup>2</sup>) baited with volatile compounds normally emitted by stressed pine trees, these compounds are commonly used in monitoring *S. noctilio* (Bashford and Madden, 2012). We mixed (-)- $\alpha$ -pinene and (-)- $\beta$ -pinene in a ratio of 70:30 respectively (99%, Aldrich Inc. UK), and 5 ml of the blend were introduced in a 5 × 5 cm Ziploc® bag. Fifteen traps of each model were placed *per* site (45 intercept and 45 funnel replicates in total). Traps were located at least 20 m away from each other/other traps and the same distance from the plantation edges. Trap collections and bait renewal were done every 15 days.

### 2.2. Data collection and analysis

Number, species and sex of each captured individual of *S. noctilio*, *I. leucospoides* and *M. nortoni* was recorded for each of the traps. For parasitoids retained in sticky traps, the height of capture (cm from the ground) was also recorded. To evaluate the efficiency of trapping methods within species and sex, data was analyzed with zero-inflated Poisson (ZIP) models. Count data (i.e., captured individuals) presented more zero observations than expected by the Poisson model, hence, zero-inflated models that account for the excess of zeros were fitted with the zeroinfl function from the pscl package (Zeilis et al., 2008) for R (version 3.5.1; R Foundation for Statistical Computing, Vienna, Austria). Zero inflated Poisson models are divided into two parts: first, a Poisson count model predicts the number of individuals captured by traps accounting for true zeros (i.e., those traps that did not capture individuals of a given species or sex because the trap did not work for them) and second, a logistic regression model that predicts the excess zeros (for instance, those traps that did not capture individuals because the trap is inefficient or captures are lower than that expected for the given population densities). For the first part of the model, a significant result denotes differences in capture levels between treatments (i.e., trapping methods). For the latter model, the null hypothesis is that the predictor (trap type) has no effect on the zero-inflation component of the model, hence, if  $p < 0.05$  then the predictor does significantly contribute with excess zeros. An important point to mention here, is that due to the fact that trapping effort differed considerably between some methods, captures were adjusted to a common scale considering the surface of the trap (number of insects captured per trap replicate/m<sup>2</sup> of trap). This correction was accounted for in the ZIP model as an offset variable to fit the expected number of captured individuals per square meter of trap. It is important to mention that the working principle of the sheath trap is based on locating infested trees and preventing emerging insects to disperse, whereas the other models are based on the interception of flying insects. Despite this difference, we consider that using the surface of the trap is an acceptable measure of “trapping effort” and a suitable way to normalize across methods.

Because height-of-flight data did not fit the normality assumption, data was analyzed using non-parametric statistics with contrasts between sexes within species by using Mann-Whitney-Wilcoxon (one way test with chi-square approximation). Data was analyzed with R programme, version 3.5.1; R Foundation for Statistical Computing, Vienna, Austria.

## 3. Results

### 3.1. Captures

A total of 433 individuals of the three species were captured (Table 1). Most captured insects were *S. noctilio* (345 individuals) followed by *I. leucospoides* (68 individuals), while the least captured species was *M. nortoni* (20 individuals). *Sirex noctilio* and *I. leucospoides* were captured at all sites (*S. noctilio*: site a = 207 individuals, site

**Table 1**

Total captures of two parasitoid species, *Ibalia leucospoides* and *Megarhyssa nortoni*, and their host, *Sirex noctilio* with two passive and two active trapping methods.

Trap type	<i>Ibalia leucospoides</i>			<i>Megarhyssa nortoni</i>			<i>Sirex noctilio</i>		
	♀	♂	Total	♀	♂	Total	♀	♂	Total
Sticky	30	22	52	0	13	13	184	11	195
Sheath	2	4	6	5	2	7	22	39	61
Panel	7	0	7	0	0	0	64	0	64
Funnel	3	0	3	0	0	0	25	0	25
Total	42	26	68	5	15	20	295	50	345

b = 49 individuals and site c = 89 individuals; *I. leucospoides*: site a = 27 individuals, site b = 10 individuals and site c = 31 individuals) while *M. nortoni* was only captured at two sites (site a = 12 individuals, site b = 8 individuals).

### 3.2. Captures

With trap surface (i.e. trapping effort) accounted for, baited panel traps captured significantly more *I. leucospoides* females in comparison with all other methods (Fig. 2, Table 2). Additionally, more *I. leucospoides* males were captured in sheath traps than sticky traps, while baited traps did not capture males of this species. *Megarhyssa nortoni* females were only captured in sheath traps while there was no statistical difference in captures/m<sup>2</sup> of *M. nortoni* males between sticky traps and sheath traps. More *S. noctilio* females were captured per m<sup>2</sup> in panel traps than in sticky and funnel traps while in equal amounts vs sheath traps. Furthermore, sticky traps captured significantly fewer individuals per m<sup>2</sup> of trap than funnel or sheath traps. Except for sticky traps, both funnel and sheath traps had no false zero effects. For *S. noctilio* males, sheath traps captured more individuals per m<sup>2</sup> than sticky traps.

### 3.3. Parasitoid vertical flight path

*Ibalia leucospoides* males were found at higher altitudes than females (male median height = 405 cm, n = 22; female median height = 180 cm, n = 30;  $\chi^2 = 27.4$ ,  $P < 0.0001$ ). In turn, only males of *M. nortoni* were captured in sticky traps, at a median height of 495 cm (n = 13) from the ground (Fig. 3).

## 4. Discussion

We evaluated different methods to capture *I. leucospoides* and *M. nortoni*, two parasitoid species frequently used in biological control programs of the pest *S. noctilio*. We additionally assessed their vertical flight-paths in order to gain further insights that could improve trapping protocols. The study involved four types of traps with different capture principles: two passive traps based either on flight-path interception or via partially caging previously-attacked trees to retain emerging adults, and two types of traps baited with pine volatile compounds, normally used to capture and monitor forest insects, such as *S. noctilio* (Haavik et al., 2014; Allison and Redak, 2017).

Our results indicate that the number of individuals of each species caught, varied according to the method used. In terms of absolute captures, unsurprisingly the most captured species was *S. noctilio*, given that selected sites were affected by the pest. Nevertheless, parasitoids were also captured, albeit in lower numbers. Both sexes of *I. leucospoides* were captured on passive traps, with most individuals found on sticky traps. Conversely, baited traps only captured females of *I. leucospoides*, with panel traps retaining most individuals. The least caught parasitoid species was *M. nortoni*, as only males were reported on sticky traps and both sexes on sheath traps. No individuals of this species were captured in the baited traps.

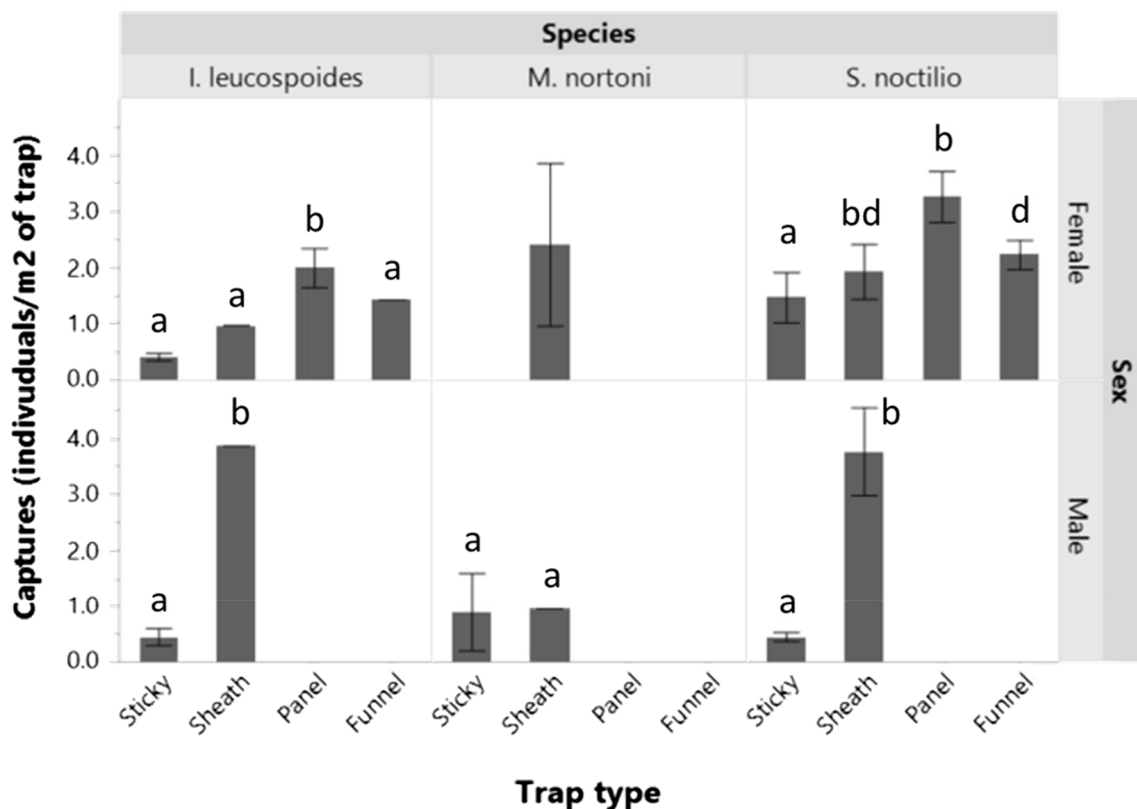


Fig. 2. Captures of *Ibalia leucospoides* and *Megarhyssa nortoni*, two parasitoid species used in biocontrol programs of *Sirex noctilio*, using four different trapping methods. Because the trapping effort was different between methods, the number of captured individuals was statistically compared by normalizing data using each trap's intercept surface (individuals/m<sup>2</sup> of trap). Traps that did not capture individuals are not included in the figure, but were included in the statistical analysis. Statistical comparisons were done within each species/sex. The top of bars indicate the mean value and error bars the standard error. Different letters above the box plots denote statistical differences in captures between trap types within species/sex (zero inflated data analysis with trap surface as offset variable,  $p < 0.05$ ).

Generally, sticky traps captured most the individuals, due to the relatively larger sampling effort (note that a single sticky trap had an intercept surface of 4.8 m<sup>2</sup>, while each panel/multifunnel trap consisted of 0.7 m<sup>2</sup>). With these size differences accounted for, panel traps showed a higher efficiency at capturing *I. leucospoides* females than sticky traps. This suggests the attractiveness of the terpene blend as bait for *I. leucospoides* females. Interestingly, funnel traps did not work as efficiently as panel traps, even though the same volatile blend was used. Lower capture rates were registered not only for *I. leucospoides* but

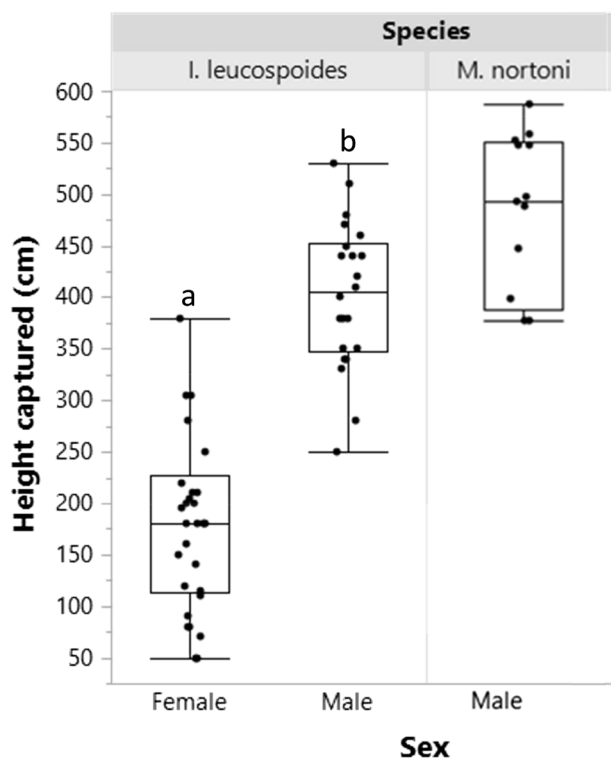
also for *S. noctilio* females in this type of trap. These lower capture rates observed in funnel traps vs panel traps are similar to those previously reported for Siricids (Bashford, 2008; Allison and Redak, 2017). Nevertheless other studies have reported equal number of captures of *S. noctilio* and *S. nigricornis* between these two trap types (Haavik et al., 2014). There is no certainty as to why these differences were registered in this study, but since the same volatile compounds were used, it is likely that construction and/or material differences between traps could have affected factors such as the odor plume, visual attraction and/or

Table 2

Results of the Zero-inflated Poisson (ZIP) analysis to assess the effect of trap-type on the number of captured individuals within each sex of each species. An offset variable was included in the ZIP model to account for different trapping effort, allowing comparison across methods. Regression coefficients (B), standard errors (SE), statistics (Z) and p-values (P) are shown for the count model on the left of the “/”, while the zero-inflated part of the model on the right. Il = *Ibalia leucospoides*, Mn = *Megarhyssa nortoni*, Sn = *Sirex noctilio*. St = Sticky, Sh = Sheath, P = Panel and F = Funnel. Asterisks following p-values denote significant differences (\*\*\* =  $P < 0.001$ , \*\* =  $P < 0.01$ , \* =  $P < 0.05$ ).

Species	Sex	Trap type	B	SE	Z	p-value		
Il	♀	P vs F	2.37/8.08	0.89/92.65	2.65/−0.07	0.0078 **/0.930		
		Sh vs F	−0.33/−3.19	0.92/567.53	−0.37/−0.006	0.713/0.996		
		St vs F	−0.92/6.08	0.63/92.65	−1.46/0.06	0.142/0.948		
		P vs St	3.29/1.99	0.71/1.00	4.624/1.98	< 0.0001***/0.046*		
		Sh vs St	0.59/−7.38	0.75/217.73	0.788/−0.03	0.431/0.972		
		P vs Sh	2.71/8.93	0.98/173.57	2.76/0.05	0.005 **/0.959		
		St vs Sh	−4.51/−3.04	0.58/1.12	−7.73/−2.71	< 0.0001***/0.007**		
		St vs Sh	0.39/8.74	0.77/104.54	0.51/0.08	0.61/0.933		
		Mn	♂	P vs F	0.70/−0.67	0.35/0.78	2.03/−0.85	0.042*/0.393
				Sh vs F	0.16/0.45	0.42/0.80	0.38/0.56	0.702/0.575
St vs F	−2.11/−2.28			0.32/0.98	−6.57/−2.33	< 0.0001***/0.019*		
P vs St	2.82/1.61			0.16/0.87	16.71/1.85	< 0.0001***/0.063		
Sn	♀	Sh vs St	2.27/2.73	0.28/0.88	7.94/3.07	< 0.0001***/0.002**		
		Sh vs St	−4.48/0.65	0.41/0.66	−10.98/0.98	< 0.0001***/0.325		
		♂	St vs F	−2.11/−2.28	0.32/0.98	−6.57/−2.33	< 0.0001***/0.019*	
			P vs St	2.82/1.61	0.16/0.87	16.71/1.85	< 0.0001***/0.063	





**Fig. 3.** Average height flight of *Ibalia leucospoides* and *Megarhyssa nortoni*, captured in sticky traps. No *M. nortoni* females were captured. The top and bottom of the box indicate the interquartile range. The line across the middle indicates the median value. Filled circles indicate individuals captured. Vertical lines indicate spread of data. Different letters above the box plots denote statistical differences (Wilcoxon rank sums test,  $p < 0,0001$ ).

insect retention capacity.

As indicated by previous studies, terpene-baited traps attract and retain *S. noctilio* females, (Simpson, 1976; Simpson and McQuilkin, 1976; Bashford and Madden, 2012), in addition to *I. leucospoides* females. Captures of parasitoids via traps aimed at capturing Siricids, have been reported on several occasions. Allison et al. (2011) assessed the effect of lubricant sprays (e.g., fluon and silicone) in the capture efficiency of panel and funnel traps baited with commercial lures known to attract multiple genera and families of forest insects. Among the 22 species captured in their study, *I. leucospoides* was captured in addition to 2 species of Siricids. Interestingly, lubricant-treated traps did not increase the capture of Siricids, but did increase those for *I. leucospoides*. Barnes et al. (2014) tested the efficiency of different capture methods (i.e., “trap trees” and baited intercept/multi-funnel traps) for North American native Siricids and their parasitoids, reporting low captures (2 individuals) of *I. leucospoides* in baited traps, while significant captures were recorded in trap trees (486 individuals).

The semiochemicals used in the above studies, and in our study, consist of a combination of terpenes (mainly  $\alpha$  and  $\beta$  pinene) that simulate some of the compounds released by stressed and *S. noctilio*-attacked trees. These compounds have been proven successful in attracting *S. noctilio* and frequently are used in monitoring programs in some parts of the world (Corley et al., 2018; Bashford and Madden, 2012). Although the role of the terpenes functioning as a kairomone is well-established in *S. noctilio* females, knowledge on the relevance of these pine volatile-emissions in *I. leucospoides* is scarce. Previous studies have established that females of *S. noctilio* rely on specific volatiles produced by the hosts fungal symbiont, *Amylostereum areolatum*, to locate oviposition sites (Spradbery, 1974; Martinez et al., 2006) and to assess larval age and suitability while searching for eggs and early-instar larvae (Jofré et al., 2016). In addition to these specific cues, current

results also confirm that  $\alpha$  and  $\beta$  pinene are of relevance during the host-location process in this parasitoid species. As such, future *S. noctilio* monitoring programs that rely on baited traps, could incorporate recording captures of *I. leucospoides*, with little additional effort.

Interestingly, relatively few *M. nortoni* individuals were captured. No individuals of this species were found on terpene-baited traps. This negative result, could have been affected by trap design: the size of the opening of the collecting jar in both trap models could have been too small affecting specimen retention for this species, since females can measure up to 15 cm in body length (including the ovipositor). In addition to this, our results suggest that the blend of terpenes used, could not have been attractive to this species. Recall that females of *M. nortoni* parasitize late-instar larvae and pupae, stages that occur considerably later in the season and consequently it is likely that relevant volatiles involved in the attraction of females could be others than those associated with *S. noctilio* recent attacks. Previous studies have shown that the quantity and quality of the tree volatile profile changes as the Sirex woodwasp attack develops with time (Böröczky et al., 2012). Even though there is scant information on the cues used by this species during the host location process, one study indicates that semiochemicals emitted by the fungal symbiont could be of relevance (Fischbein et al., 2018). Using baited traps to monitor *M. nortoni* populations seems a limited possibility today, and research aimed at understanding the chemical ecology of the species could in the long run help guide the development of a semiochemical-based capture method for the species.

Flight path data indicate that male and female *I. leucospoides* have contrasting flight-paths, with males flying at significantly higher altitudes than females. A previous study (Martínez et al., 2014) recorded a similar pattern for *S. noctilio*, with males flying higher than females. In the case of *S. noctilio*, this was explained by the species mating behavior, where males form mating leks in the higher branches of trees after emerging (Madden, 1988), and remain at high altitudes. Conversely, female *S. noctilio* after copulating, perform horizontal flights at lower altitudes, searching for suitable trees where to oviposit. In the case of *I. leucospoides*, the mating behavior has not been studied in detail, therefore, there is room for speculation: Males could respond positively to sun-light, and tend to move upwards, while females perform host-searching flights at lower altitudes. *Megarhyssa nortoni* natural flight path was only established for males, and found to be at the higher end of the measured range. Interestingly no females of the species were captured in this type of trap. The reason for the lack of female captures remains unknown, with a possible explanation being that females could have actively avoided sticky traps (e.g., volatiles from sticky substance could have repelled them).

When designing sampling protocols to monitor insects of economic importance, trap attributes such as sensitivity, ease of installation, portability, weight and ease of insect collection are sought. The baited traps used in our study have all these attributes, but regrettably only captured one of the parasitoid species. Our study indicates that current *S. noctilio* monitoring programs have the potential to incorporate tracking *I. leucospoides* populations with no additional effort or cost. On the other hand, unbaited traps had higher success at capturing both targeted insects (Table 3), albeit in lower numbers. Sticky traps, even though require a higher installation and revision effort, have the advantage of retaining the host while capturing both parasitoid species (but no *M. nortoni* females). Installation of these traps can be labour-intensive, since trees need to be pruned, with a ladder. Sheath traps have the added advantage of capturing individuals of both sexes of the three species, and installation can be straight forward, especially if trees are weakened using herbicides (Neumann et al., 1982) at pre-defined accessible locations ahead of the flight season (i.e. spring) and sheaths set up in autumn. Once installed, revisions are straightforward and results comparable across regions once calibration and validation trials are made (e.g. correlation of host/parasitoid trap catches with actual population levels; required densities of trap trees).

**Table 3**

Comparison of trap attributes between the different capture methods evaluated for two species of *S. noctilio* parasitoids. Il = *Ibalia leucospoides*, Mn = *Megarhyssa nortoni*, Sn = *Sirex noctilio*. “+” denote the relative amount of insects captured. “–” denotes no captured individuals.

Trap type	Cost	Installation & revision effort	Degree of standardization across regions	Monitoring efficiency					
				Il		Mn		Sn	
				♀	♂	♀	♂	♀	♂
Sticky	High	High	High	+	+	–	++	+	+
Sheath	Low	Medium	High	+	++	+	+	++	++
Panel	Low	Low	High	+++	–	–	–	+++	–
Funnel	Medium	Low	High	+	–	–	–	++	–

Although many aspects of the biology and ecology of *S. noctilio* parasitoids used in biological control programs are well-known, we believe further knowledge on specific aspects of parasitoid behavior, specifically their chemical ecology, are warranted. The implementation of active traps to monitor both species of *S. noctilio* parasitoids is critical to determine establishment of introduction and quantify population level for sustainable biological control. Further studies are needed to offer improvements of the protocols that look at pest natural enemies, including specific monitoring through baited traps, in addition to complementary strategies such as push–pull protocols designed to retain parasitoids within desired areas (Cook et al., 2007; Rodriguez-Saona and Stelinski, 2009; Rodriguez-Saona et al., 2012).

#### Author contribution statement

ASM and JMV conceived, designed and conducted research. ASM and DF analyzed data. All authors discussed ideas, wrote, read, corrected and approved the manuscript.

#### Acknowledgements

We would like to thank Alejandro Fernandez Ajó, Maria Victoria Lantschner, Sharon Martinson and Ana Julia Pereira for helping out with field work. Estancia Fortín Chacabuco, Estancia El Mirador and Estancia Mallín Chacay kindly allowed access to study sites.

#### Funding

Funding: This work was financed by grants provided by SAFO109 (Unidad para el Cambio Rural, Argentina), PICT-2011-1775 and PICT 2015-3864 (Agencia Nacional para la Promoción Científica y Tecnológica, Argentina) and PIP 0730/14 (Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina).

#### References

Allison, J.D., Johnson, C.W., Meeker, J.R., Strom, B.L., Butler, S.M., 2011. Effect of aerosol surface lubricants on the abundance and richness of selected forest insects captured in multiple-funnel and panel traps. *J. Econ. Entomol.* 104, 1258–1264.

Allison, J.D., Redak, R.A., 2017. The impact of trap type and design features on survey and detection of bark and woodboring beetles and their associates: a review and meta-analysis. *Annu. Rev. Entomol.* 62, 127–146.

Bain, J., Sopow, S.L., Bulman, L.S., 2012. The siren woodwasp in New Zealand: history and current status. In: Slippers, Bernard, de Groot, Peter, Wingfield, Michael John (Eds.), *The Sirex Woodwasp and Its Fungal Symbiont: Research and Management of a Worldwide Invasive Pest*. Springer, Dordrecht, pp. 167–173.

Bale, J.S., van Lenteren, J.C., Bigler, F., 2008. Biological control and sustainable food production. *Philos. Trans. R Soc. Lond. B Biol. Sci.*

Barnes, B.F., Meeker, J.R., Johnson, W., Miller, D.R., Gandhi, K.J.K., Asaro, C., 2014. Trapping Techniques for Siricids and their Parasitoids (Hymenoptera: Siricidae and Ibalidae) in the Southeastern United States Trapping Techniques for Siricids and their Parasitoids (Hymenoptera: Siricidae and Ibalidae) in the Southeastern United. *Ann. Entomol. Soc. Am.* 107, 119–127.

Bashford, R., 2008. The development of static trapping systems to monitor for wood-boring insects in forestry plantations. *Aust. For.* 71, 236–241.

Bashford, R., Madden, J.L., 2012. The use of kairomone lures for the detection of *Sirex noctilio* in susceptible *Pinus radiata* plantations in Australia. In: Slippers, B., de Groot, P., Wingfield, M.J. (Eds.), *The Sirex Woodwasp and Its Fungal Symbiont*. Springer, Dordrecht, The Netherlands, pp. 159–166.

Boissin, E., Hurler, B., Wingfield, M.J., Vasaitis, R., Stenlid, J., Davis, C., de Groot, P., Ahumada, R., Carnegie, A., Goldarazena, A., Klaser, P., Wermelinger, B., Slippers, B., 2012. Retracing the routes of introduction of invasive species: the case of the *Sirex noctilio* woodwasp. *Mol. Ecol.* 21, 5728–5744.

Böröczky, K., Zylstra, K.E., McCartney, N.B., Mastro, V.C., Tumlinson, J.H., 2012. Volatile profile differences and the associated *sirex noctilio* activity in two host tree species in the northeastern united states. *J. Chem. Ecol.* 38, 213–221.

Cameron, E.A., 2012. Parasitoids in the management of *Sirex noctilio*: looking back and looking ahead. In: Slippers, B., de Groot, P., Wingfield, M.J. (Eds.), *The Sirex Woodwasp and Its Fungal Symbiont: Research and Management of a Worldwide Invasive Pest*. Springer, Dordrecht, Netherlands, pp. 103–117.

Cook, S.M., Khan, Z.R., Pickett, J.A., 2007. The use of push-pull strategies in integrated pest management. *Annu. Rev. Entomol.* 52, 375–400.

Corley, J., Lantschner, M.V., Martínez, A.S., Fischbein, D., Villacide, J.M., 2018. Management of *Sirex noctilio* populations in exotic pine plantations: critical issues explaining invasion success and damage levels in South America. *J. Pest. Sci.* 1–12.

Fischbein, D., Villacide, J.M., Lopez, B., Colrey, J.C., Martinez, A.S., 2018. Host-related volatile cues used by a parasitoid wasp during foraging for its woodboring host. *Entomol. Exp. Appl.* 166, 907–913.

Haavik, L.J., Batista, E., Dodds, K.J., Johnson, W., Meeker, J.R., Scarr, T.A., Allison, J.D., 2014. Type of intercept trap not important for capturing female *Sirex noctilio* and *S. nigricornis* (Hymenoptera: Siricidae) in North America. *J. Econ. Entomol.* 107, 1295–1298.

Haavik, L.J., Dodds, K.J., Allison, J.D., 2018. *Sirex noctilio* (Hymenoptera: Siricidae) in Ontario (Canada) pine forests: observations over five years. *Can. Entomol.* 150, 347–360.

Heimpel, G.E., Asplen, M.K., 2011. A ‘Goldilocks’ hypothesis for dispersal of biological control agents. *Biocontrol* 54, 441–450.

Hopper, K.R., Roush, R.T., 1993. Mate finding, dispersal, number released, and the success of biological control introductions. *Ecol. Entomol.* 18 (321), 331.

Jofré, N., Pildain, M.B., Cirigliano, A.M., Cabrera, G.M., Corley, J.C., Martínez, A.S., 2016. Host selection by *Ibalia leucospoides* based on temporal variations of volatiles from the hosts’ fungal symbiont. *J. Appl. Entomol.* 140, 736–743.

Kidd, N.A.C., Jervis, M.A., 2007. Population dynamics. In: Jervis, M.A. (Ed.), *Insects As Natural Enemies: A Practical Perspective*. Springer, pp. 504–518.

Madden, J.L., 1988. *Sirex* in Australasia. In: Berryman, A. (Ed.), *Dynamics of Forest Insect Populations: Patterns, Causes, Implications*. Springer, New York, NY, pp. 407–429.

Martinez, A.S., Fernandez-Arhev, V., Corley, J.C., 2006. Chemical information from the fungus *Amylostereum areolatum* and host-foraging behaviour in the parasitoid *Ibalia leucospoides*. *Physiol. Entomol.* 31, 336–340.

Martinez, A.S., Villacide, J., Fernández Ajó, A., Martinson, S.J., Corley, J.C., 2014. *Sirex noctilio* flight behavior: toward improving current monitoring techniques. *Entomol. Exp. Appl.* 152, 135–140.

Martinson, S.J., Fernández Ajó, A.A., Martínez, A.S., Krivak-Tetley, F.E., Villacide, J.M., Ayres, M.P., Corley, J.C., 2018. Attack rates of *Sirex noctilio* and patterns of pine tree defenses and mortality in northern Patagonia. *Bull. Entomol. Res.*

Neumann, F.G., Harris, J.A., Kassaby, F.Y., Minko, G., 1982. An improved technique for early detection and control of *Sirex* wood wasp in radiata pine plantations. *Aust. For.* 45, 117–124.

Neumann, F.G., Morey, J.L., 1984. Influence of natural enemies on the *sirex* wood wasp in herbicide-treated trap trees of radiata pine in north-eastern victoria. *Aust. For.* 47, 218–224.

Orr, D., 2009. Biological control and integrated pest management. In: *Integrated Pest Management: Innovation-Development Process*. Springer, Dordrecht, pp. 207–239.

Rodriguez-Saona, C., Blaauw, B.R., Isaacs, R., 2012. Manipulation of natural enemies in agroecosystems: habitat and semiochemicals for sustainable insect pest control. In: Laramendy, M.L., Soloneski, S. (Eds.), *Integrated Pest Management and Pest Control – Current and Future Tactics*. InTech, Rijeka, Croatia, pp. 89–126.

Rodriguez-Saona, C., Stelinski, L., 2009. IPM, behaviour-modifying strategies in IPM: theory and practice. In: Peshin, R., Dhanan, A.K. (Eds.), *Integrated Pest Management: Innovation-Development Process Vol. 1*. Springer, pp. 689.

- Simpson, R.F., 1976. Bioassay of pine oil components as attractants for *Sirex noctilio* (Hymenoptera: Siricidae) using electroantennogram techniques. *Entomol. Exp. Appl.* 19, 11–18.
- Simpson, R., Mcquilkin, R., 1976. Identification of volatiles from felled *Pinus radiata* and the electroantennograms they elicit from *Sirex noctilio*. *Entomol. Exp. Appl.* 19, 205–213.
- Slippers, B., De Groot, P., Wingfield, M.J., 2012. *The Sirex Woodwasp and its Fungal Symbiont*. Springer, Dordrecht.
- Spradbery, J.P., 1973. A comparative study of the phytotoxic effects of siricid woodwasps on conifers. *Ann. Appl. Biol.* 75, 309–320.
- Spradbery, J.P., 1974. The responses of *Ibalia* species (Hymenoptera: Ibalidae) to the fungal symbionts of siricid woodwasp hosts. *J. Entomol.* 48, 217–222.
- Taylor, K.L., 1976. The introduction and establishment of insect parasitoids to control *Sirex noctilio* in Australia. *Entomophaga* 21, 429–440.
- Zeileis, A., Kleiber, C., Jackman, S., 2008. Regression models for count data in R. *J. Stat. Softw.* 27.