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Ecologia comportamental e diversidade em um sistema hospedeiro-parasitóide: Vespas parasitóides de *Schismatodiplosis lantanae* Rübsaamen, 1916 (Cecidomyiidae) em *Lantana camara* L. (Verbenaceae)

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Porto Alegre, Abril de 2012

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Resumo

Este estudo investigou a ecologia de vespas parasitóides ocorrentes em galhadores *Schismatodiplosis lantanae* Rübsaamen, 1916 (Cecidomyiidae) em folhas de *Lantana camara* L. (Verbenaceae). Dessa forma, o primeiro artigo trata da ecologia comportamental da vespa parasitóide *Torymus* sp. (Torymidae, Hymenoptera), onde foi avaliado como as fêmeas dessa espécie defendem seu recurso de oviposição no hospedeiro. Foi analisado mudanças no comportamento devido à presença de outra fêmea coespecífica no local, ser residente do recurso, tamanho das vespas e número e tamanho das galhas através de filmagens dos experimentos realizados em laboratório. Com esse trabalho observou-se que fêmeas mudam seu comportamento quando estão na presença de um competidor em um território com hospedeiros. A estratégia de ataque foi através da ameaça, na qual suas antenas e asas são levantadas para expulsar o competidor do local. A probabilidade de haver ataques a fêmeas coespecíficas depende do tempo prévio de exploração da galha e da permanência na folha. O interesse no hospedeiro pelas invasoras foi a principal causa de conflitos com a residente. O segundo artigo trata da diversidade de vespas parasitóides e de um ciclo parasita-hospedeiro observado no período de um ano no sistema de *L. camara*. Foram encontradas nove espécies de vespas parasitóides, divididas em quatro famílias. Ocorreu um ciclo no parasitismo das espécies de vespas sobre seu hospedeiro no ano amostrado, podendo ser observado que são mais elevadas nos meses de Julho a Janeiro e a sobrevivência do hospedeiro foi maior nos meses de Fevereiro a Maio. As estratégias comportamentais de fêmeas de uma vespa parasitóide em relação a seus hospedeiros foram analisadas, bem como um sistema composto de diversas espécies parasitóides e sua variação no tempo. Estas observações podem contribuir para um melhor entendimento da ecologia comportamental e do padrão temporal das vespas parasitoides, e também para futuros programas de controle biológico mais eficientes.

Palavras-chaves: comportamento; conflitos; galhas; ciclo parasita-hospedeiro.

Abstract

We investigated the ecology of parasitoid wasps attacking *Schismatodiplosis lantanae* Rübsaamen, 1916 (Cecidomyiidae) galls on leaves of *Lantana camara* L. (Verbenaceae). The first article discusses the behavioral ecology of the parasitoid wasp *Torymus* sp. (Torymidae, Hymenoptera), reporting how their females defend oviposition resources on the hosts, changing their behavior due to the presence of a conspecific female in the patch. The identity of the wasp (resident or intruder) on the resource, female size and number and size of galls in the patch were factors studied through analysis of the behaviors revealed by video recordings of the laboratory experiments. Females change their behavior in the presence of a competitor in a territory with hosts. The strategy was to threat, raising their antennae and wings to expel the competitor of the patch. The probability of an attack on a conspecific females depended on the host exploitation time and time spent on the galled leaf. Interest in host by intruders was the main cause for conflicts. The second article reports the diversity of parasitoid wasps and a host-parasite cycle during one year period in the *L. camara* leaf galls system. Nine parasitoid wasp species were found, divided in four families. A cycle between parasitism and host survival was found during the sampling period. Wasp species are more abundant from July to January and host survival higher from February to May. Behavioral strategies of parasitoid wasp females toward their hosts and conspecifics have been elucidated, with the system composed of different parasitoid wasp species apparently going through an annual cycle of parasitism rate. These observations may contribute to a better understanding of parasitoid behavioral ecology and host-parasitoid dynamics, enabling more efficient future biological control programs.

Keywords: behavior; conflicts; galls; host-parasitoid cycle.

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Introdução Geral

Os indivíduos de uma mesma espécie têm necessidades muitos semelhantes para sobreviver, crescer e se reproduzir. Para isso, há uma demanda de recursos que pode exceder a sua oferta no ambiente. Assim os indivíduos podem competir pelo recurso, e na maioria das vezes, alguns ficam privados dele. Quando ocorre uma interferência ativa entre indivíduos em uma mesma área, reconhecida como um território, ela é defendida de intrusos através de um padrão de comportamento reconhecível, conhecido como conflito (Begon et al., 2006).

Esses conflitos representam o meio através do qual os indivíduos procuram excluir os intrusos do recurso (Riechert, 1998). Estudos teóricos que utilizam a teoria dos jogos e estratégias evolutivamente estáveis como modelo (ESS no original em inglês, Maynard-Smith, 1982; Hammerstein, 1998) sugerem que há uma série de fatores que influenciam o desfecho final desses conflitos. Em um primeiro modelo, a diferença de habilidades entre os competidores, conhecida como “poder de apropriação do recurso” (*resource-holding power* - RHP, Alcock, 2009), implica que o combatente reconheça o tamanho, força ou habilidade de luta do oponente, o que pode proporcionar uma desistência do embate. Um segundo modelo considera a importância que o recurso presente no território representa para o indivíduo, conhecido como “valor do recurso” (RV, Maynard-Smith & Parker, 1976; Hammerstein, 1981). Neste caso entram fatores avaliados pelo residente do território como o tamanho, número e qualidade de recursos existentes. Portanto, os ganhadores dos conflitos podem ser previstos como sendo os indivíduos detendo altos níveis de RHP e/ou RV. Entretanto, resultados diferentes já foram encontrados na natureza (Alcock, 2009), colocando dúvidas sobre a validade desses modelos.

Em um território maior, apesar de fornecer mais recursos para o residente, a frequência de intrusos poderá ser maior e o esforço para a defesa aumentará (Begon et al., 2006). Nestes casos, a territorialidade só é favorecida pela seleção natural se os custos energéticos dos embates forem menores do que os benefícios do recurso e se for apresentada uma compensação reprodutiva do recurso defendido (Alcock, 2009).

Esse tipo de competição por território e por recursos pode ser observado em diversas espécies, sendo que entre insetos parasitóides esse aspecto ainda é pouco estudado. Os parasitóides constituem cerca de 20-25% da diversidade das espécies encontrada na ordem Insecta. Parasitóides, geralmente vespas ou moscas, possuem larvas que se desenvolvem alimentando-se de outros insetos, os hospedeiros. Dependendo da espécie, os parasitóides podem atacar os diferentes estágios de desenvolvimento do hospedeiro, tanto o ovo, a larva, a pupa ou o adulto. A larva do parasitóide emerge do ovo depositado e consome o hospedeiro até sua morte (Godfray, 1994).

A fêmea parasitóide em geral precisa encontrar um hospedeiro específico e para isso, ela analisa com suas antenas e seu ovipositor se o hospedeiro é ideal para o desenvolvimento da prole. Um problema enfrentado pelos insetos parasitóides é que após atacarem o hospedeiro, este fica vulnerável a ataques de outros indivíduos da mesma ou de diferentes espécies de parasitóides, não garantindo que a prole do primeiro realmente irá sobreviver (van Alphen et al., 2003). Fêmeas coespecíficas podem competir por hospedeiros depositando seus ovos em hospedeiros já parasitados (superparasitismo), como encontrado em Field et al. (1997), ou através de uma forma de proteção do local onde foi colocado a maioria de seus ovos, comportamento encarado como cuidado maternal por Goubault et al. (2007).

Portanto, algumas fêmeas de parasitóides defendem seus hospedeiros, ou o local contendo o hospedeiro, de competidores coespecíficos. Se duas fêmeas se encontram em um mesmo hospedeiro, elas poderão exibir um comportamento ritualístico ou até mesmo um combate corporal (Godfray, 1994). Quando fêmeas se encontram várias interações comportamentais são observadas: (1) se encontram e apontam suas antenas na direção da fêmea oponente (“detecção coespecífica”); (2) fazem contato através das antenas não agressivamente (“contato não agressivo”); (3) atacam uma a outra através de batidas com as antenas (“contato agressivo”); ou (4) evitam o contato (“evitação coespecífica”) (Goubault et al., 2005). Outros comportamentos observados são o batimento de asas ou levantamento das asas para cima, a fim de intimidar o oponente; e perseguição, mordidas e picadas (Petersen & Hardy, 1996; Stokkebo & Hardy, 2000).

Os parasitóides são considerados os principais inimigos naturais dos insetos galhadores. É muito comum encontrar internamente na galha, ao invés do inseto indutor, outros organismos vivendo como inquilinos, predadores ou parasitóides. Galhas são estruturas formadas nas plantas a partir do crescimento anormal dos tecidos devido a uma atividade parasita, podendo ser encontrados em diferentes locais no corpo das plantas e induzidos por diferentes organismos, tais como insetos, ácaros, nematódeos, bactérias, vírus e fungos (Stone & Schonrogge, 2003). As galhas proporcionam à larva dos insetos nutrição e abrigo de condições ambientais adversas e inimigos naturais (Price et al. 1987). É sugerido que a evolução dos insetos galhadores pode se dar como uma resposta aos ataques dos parasitóides, visto que o tecido vegetal serve como uma proteção física (Price et al., 1986, 1987).

As galhas, por conterem os hospedeiros dos ovos das vespas parasitóides, são motivo de competição. O resultado da competição entre fêmeas de parasitóides pode variar de acordo com fatores como a fêmea já ter ovipositado, tamanho e idade do adversário, capacidade de avaliar os custos da competição, habilidade de luta e o valor do recurso disputado (Field & Calbert, 1999; Petersen & Hardy, 1996; Stokkebo & Hardy, 2000; Humphries et al., 2006). Conflitos agressivos ocorrem entre fêmeas de várias espécies de vespas parasitóides, como por exemplo, no estudo de Field e Calbert (1999), que apresentou um ciclo de comportamento agressivo entre fêmeas parasitóides colocadas aos pares para competir. Porém, poucos estudos examinaram o mecanismo de como estes conflitos são resolvidos e como os fatores presentes podem influenciar no desfecho final.

Comunidades centradas em insetos galhadores e parasitóides são ideais para os estudos de interações, pois, além de apresentarem uma grande diversidade, as galhas são um recurso estático de fácil acesso, contagem e observação (Godfray & Shimada, 1999; Stone & Schonrogge, 2003) e os parasitóides são extremamente eficientes em utilizar os recursos limitados dos hospedeiros, mostrando que as espécies são intimamente ligadas (Godfray, 1994; Craig et al., 1990; Harvey et al., 2009).

O objetivo deste trabalho foi avaliar a maneira como fêmeas de vespas parasitóides defendem seu recurso de oviposição, e os efeitos sobre o comportamento devido à presença de outra fêmea coespecífica no local, tamanho das vespas e número e tamanho das galhas. Para isso foram utilizadas fêmeas da vespa parasitóide *Torymus* sp. (Torymidae, Hymenoptera), que utiliza larvas do galhador *Schismatodiplosis lantanae* Rübsaamen, 1916 (Cecidomyiidae) como hospedeiro, que, por sua vez é galhador em folhas de *Lantana camara* L. (Verbenaceae) (Gagné, 1994) (Figura 1a, 1b e 1c). Esta espécie de vespa foi o parasitóide mais abundante neste sistema. A maioria das vespas do gênero *Torymus* são ectoparasitóides solitários (Figura 1d e 1e) e parasitam larvas e pupas de Diptera, em sua maioria cecidomídeos galhadores (Hanson, 2006).

Várias hipóteses e previsões podem ser elencadas relativas a diferentes fatores: as fêmeas devem comportar-se diferentemente na presença de um competidor no recurso (Visser et al., 1992; Goubault et al., 2005); devem defender galhas já parasitadas por elas pelo grande valor reprodutivo que representam (Field & Calbert, 1999); devem defender recursos mais ricos em hospedeiros, como um local com maior número de galhas (Humphries et al., 2006; Goubault et al., 2007); e fêmeas maiores devem ganhar conflitos mais frequentemente que fêmeas menores (Petersen & Hardy, 1996; Stokkebo & Hardy, 2000; Humphries et al., 2006).

Outro objetivo do trabalho foi registrar a diversidade de espécies de parasitóides e a variação na taxa de parasitismo dos galhadores imposta pelas vespas parasitóides associadas a esse sistema. Com estas variações, podemos prever flutuações nas populações causadas pelas interações parasita-hospedeiro. Esses ciclos foram descritos por Lotka-Volterra (Begon et al. 2006) e preveem uma coexistência estável entre os competidores em situações na qual a competição interespecífica, para ambas as espécies, é menor que a intraespecífica. O modelo é muito simples e útil, porém não inclui as complexidades que a competição pode trazer (Begon et al. 2006). Estudos prévios mostram que eventos nos ciclos de vida do hospedeiro podem ter efeito direto na dinâmica de população de seus parasitóides (May et al. 1981, Godfray & Hassell 1989, Gordon et al. 1991), ou o hospedeiro sozinho pode gerar ciclos na qual a dinâmica dos parasitoides é sincronizada (Begon et al. 1995).

O arbusto *L. camara* é uma planta comum no sul do Brasil. Geralmente ocorre em locais abertos e ensolarados, como terrenos baldios, clareiras, beiras de mata, vassourais, áreas em recuperação e áreas urbanas. É uma planta tóxica e tem sido agressiva e invasora em diversos países ao redor do mundo. É um grande problema na criação de gado pelo envenenamento dos animais. A grande distribuição de *L. camara* é um reflexo da sua alta tolerância ecológica (Sharma et al., 2005). Apesar de apresentar vários estudos que abordam *L. camara* como uma planta invasora, não existe nenhum registro sobre os parasitoides de seus galhadores e seus ciclos de vida.

Dessa forma, este estudo procurou investigar a ecologia comportamental de vespas parasitóides, através de uma pesquisa empírica, com a manipulação de díades (invasora-residente) em ambiente de laboratório (Figura 1f). Além disso, foi observada a diversidade e a variação na taxa de parasitismo, através da identificação de vespas parasitóides em galhas de arbustos de *L. camara*.

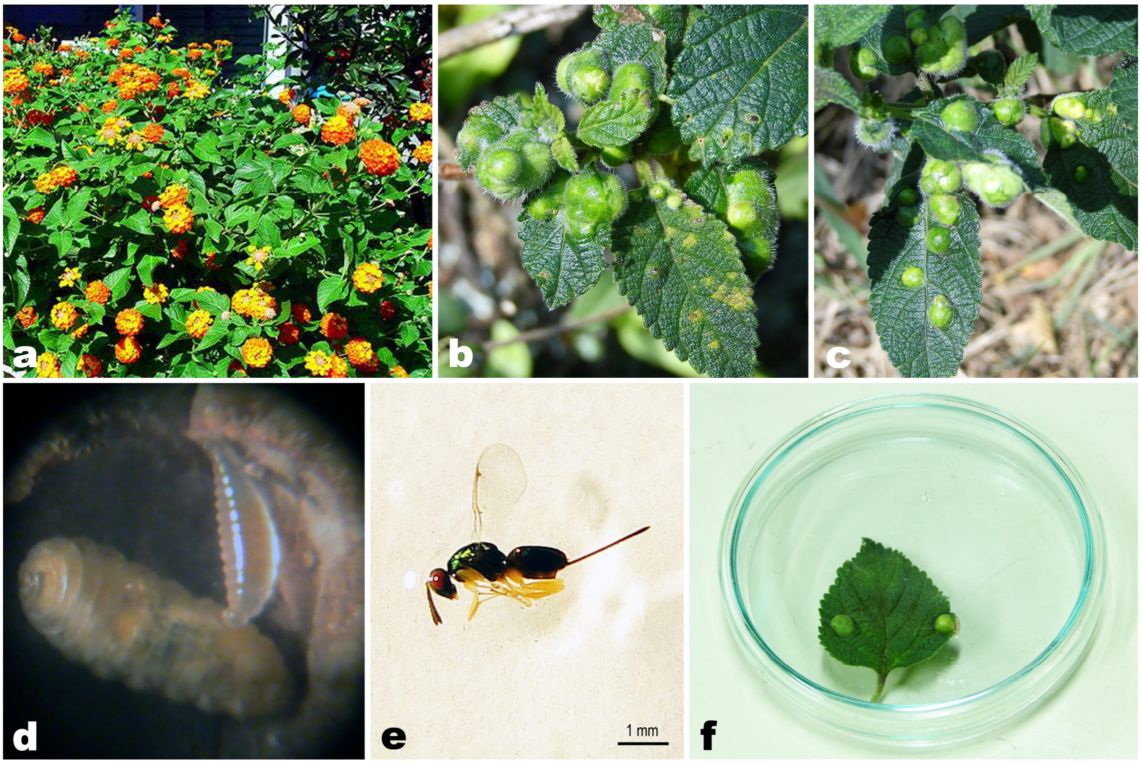

Figura 1. Arbusto de *Lantana camara* (a). Galhas de *Schismatodiplosis lantanae* em folhas de *L. camara* (b e c). Larva de vespa parasitóide em *S. lantanae* internamente na galha (d). Vespa parasitóide *Torymus* sp. (e). Folha galhada em Placa de petri (Ø 9 cm) utilizada em experimento (f).

Artigo 1.

Galls as a disputed resource for female parasitoid wasps contests[1]

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Abstract

In parasitoid wasps, adult females can compete for hosts against conspecifics engaging in aggressive contests for patch ownership. Within these patches their offspring develop and the consequences of these competitive interactions can have a direct influence on the wasp's fitness. The aim of this study was to investigate how the parasitoid *Torymus* sp. (Hymenoptera: Torymidae) attacking galls of *Schismatodiplosis lantanae* Rübsaamen, 1916 (Diptera: Cecidomyiidae) on *Lantana camara* behaves in the presence of a conspecific female competitor in the patch. The interest was on how these female wasps defend their oviposition resource and whether factors considered crucial such as number and size of galls in the patch and female size interfere with behavior. The presence of a competitor greatly changed resident exploitation behavior. The wasps alone spent more time in gall exploitation behaviors (*walk-antennate* and *probe*) and in post-oviposition behaviors (*stationary* and *groom*), and when the residents were with a competitor present they spent more time in *walking*. The attack strategy was trough threatening, raising wings and pointing the antennae towards the opponent. Different from theoretical expectations, residents were not always the attacker. Number of galls in the patch and female wasp size did not affect contest outcomes. Gall exploitation time and time on the host plant leaf were significant factors for the probability of having attacks. Intruder interest in the host was the main cause of contests. Female parasitoids are behaviorally plastic when dealing with their host, acting differently depending on

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[1] Este trabalho será submetido à revista Ethology.

the situation with behavioral patterns differing whether a conspecific is present or not. Neither the resource-holding power nor the resource value models fitted the system adequately.

Introduction

Individuals of a same species demand similar needs for survival, growth and reproduction that may be in a limited supply, leading to competition between them. Direct competition occurs when individuals interact while exploiting the same resource. Among a variety of results that could ensue, resource items or patches can be defended through agonistic contests. These contests represent the means by which individuals exclude others from resources (Riechert 1998). Theoretical studies using game theory and looking for evolutionary stable strategies (ESS, Maynard-Smith 1982; Hammerstein 1998) suggest that there are distinct factors influencing the results of such conflicts. First, there might be differences in the competitive abilities of the contestants, known as resource-holding power (RHP, Alcock 2009) such as body size, strength or fighting ability which could provide a physical benefit for the territory holder. Second, the importance the conflicting individual place in the resource being defended, known as resource value (RV, Maynard-Smith & Parker 1976; Hammerstein 1981) such as resource size, number and quality. Thus, the intensity of contests can be predicted by contestants with the highest RHP and/or through RV characteristics, although different results have been found in natural settings (Alcock 2009).

These theoretical studies on resource competition have been applied to several animal species; however, for insect parasitoids this aspect has not been fully studied. Adult parasitoid females can compete for hosts from which their offspring develop and the consequences of this competition have a direct influence in their fitness (van Baalen & Hemerik 2008). One problem faced by them is that after attacking the host, it becomes vulnerable to an attack by another individual of the same or different species of parasitoid, which does not guarantee that the first parasitoid offspring will actually survive (van Alphen et al. 2003). Conspecific females frequently exploit simultaneously the same host patch (Godfray 1994). Thus, eggs can be deposited in already parasitized hosts (superparasitism) (van Alphen & Visser 1990; Field et al. 1997), and females can show a form of protection toward the oviposition site, in a form of maternal care behavior (Hardy & Blackburn 1991; Goubault et al. 2007a). Therefore, some parasitoid females can compete by defending their hosts, or its location, from conspecific competitors, sometimes engaging in aggressive contests for possession of the patch. These contests may consist of repeated interactions between the same individuals, where female wasps can also interfere with each other indirectly by modifying their host exploitation strategies (Visser et al. 1992; Goubault et al. 2005).

In the context of animal contests, many researchers reported aggressive behavior from a variety of parasitoid species, mainly focused on Bethylid, Pteromalid and Scelionid wasps, which use insect eggs masses, larvae or pupa as the oviposition resource. These studies explore specific aspects of wasp contests, such as Petersen & Hardy (1996) investigating size-fitness relationships in which larger females tended to win contests; Field & Calbert (1999) observed that patch defense was mainly caused by residents; Humphries et al. (2006) concluded that female weight and age interact to influence contests outcomes; and Stokkebo & Hardy (2000) reported that when asymmetries were absent in contests, egg load is a important factor. Galling insects, when hosting parasitic wasps, are also a target for competition between ovipositing females (Godfray 1994), and agonistic conflicts can arise with single galls or whole plant organs acting as resource patches. So, the aim of the present study was to investigate female ecology behavior and how these factors can influence contest outcome in a parasitoid wasp that uses galls as oviposition resource.

It was used a solitary parasitoid wasp of a gall-forming cecidomyiid (Diptera), *Torymus* sp. (Hymenoptera: Torymidae) as a model. This is a unique report both in terms of the target species and the nature of the disputed resource, a gall-inducer inside a singular spatial unit, the gall. The purpose was first, to describe how they behave in the absence and in the presence of a conspecific female competitor in the patch and agonistic interactions displayed during contests, and second, to test contest theory predictions about the effect of ownership status, number of hosts in patch, galls size, female size and some behaviors lengths in contests occurrences.

Material and Methods

Study system

Torymus sp. (Hymenoptera: Torymidae) is a metallic green small wasp with females approximately 2.7 mm (±0.1 mm) long without the ovipositor. This solitary parasitoid wasp attacks a gall-forming midge, *Schismatodiplosis lantanae* Rübsaamen, 1916 (Diptera: Cecidomyiidae). The galler induces green round monothalamous galls on leaves of *Lantana camara* (Verbenaceae) (Gagné 1994), a common and native shrub in south Brazil. Galls diameter is about 7.4 mm (± 0.3 mm) when fully developed (Moura et al. 2008). The wasp uses its long and thin ovipositor to lay one egg inside each gall, reaching the solitary insect in the gall chamber. The oviposition process leaves a small round scar on the gall which is identifiable under stereomicroscope. A single parasitoid larva develops per host, consuming it in 15 to 20 days in laboratory conditions.

Wasp rearing

The galler host plants occur in forest borders and open spaces and were collected in specific tracks in Morro Santana, located in Campus do Vale of the Federal University of Rio Grande do Sul (UFRGS), Porto Alegre, RS, Brazil (30°04'S 51°07'W, 90m altitude) during spring and summer of 2010/2011. Galled leaves were collected and taken to the lab where they were stored in Petri dishes until the emergence of adult parasitoid wasps. The wasps produce a small hole in the gall wall, leaving an easily identifiable exit hole. After the wasps emerge, they were removed from the Petri dish and kept isolated in glass containers before used in the experiments. A honey and distilled water solution (1:3) droplet was used for feeding the wasps in each container. Both female wasps used in the experiments were of the same age (emerging from galls at same day, and from 2-6 days old) with no previous oviposition experience and not fertilized (parthenogenetic parasitoid wasps). Each wasp was used only on a single experiment.

Experimental procedures

Behaviors were observed in the laboratory by releasing females in a Petri dish (Ø 9 cm) containing one fresh leaf of *L. camara* with non-parasitized galls. Before the experiments, galls were observed in a stereomicroscope and checked for parasitoid wasp oviposition marks to ensure galls were not previously parasitized. To explore the mechanisms of contest resolution, we varied the number of galls on the leaf (1 to 8), size of the galls (2.5 to 12 mm) and size of the female wasps (1.55 to 2.60 mm wing length). The experiments were performed at the laboratory ambient temperature (20-25ºC) and were recorded using a digital camera (JVC camcorder, GZ-MG630RU).

The behavior of 20 pairs of females was observed. Experiments were divided in three steps. First, the behavior of a single wasp on a galled leaf was observed for 30 min, in order to reveal the standard behavioral responses, such as patch exploration and host exploitation. Recording started the moment the wasp was released in the Petri dish. Second, after 24 h of the wasp release in the dish, it was considered a resident; a second wasp was then introduced in the experiment. Recording started the moment the intruder wasp was released in the Petri dish and lasted for 1 h. Third, the resident wasp was removed from the Petri dish, leaving the intruder alone with a host already parasitized but in the absence of the resident, in order to observe the behavior of the intruder. Again, recording started the moment the resident wasp was removed and lasted for 30 min.

After the experiments, the females had the length of their tibia of the second pair of legs and the first pairs of wings measured. These measures were highly correlated (r=0.88), and thus wing length was used as a measure of body size since *Torymus* sp. raise the wings in the conflicts (see below).

Data analysis

The digital videos were analyzed using event-recording open software and its R-package (CowLog: Hänninen & Pastell 2009) for the continuous time records of each behavioral category. All analyses were carried out in the R 2.10.1 environment (R Development Core Team 2011). The data were not normally distributed thus nonparametric tests were used to analyze the behavioral categories. *U*-tests (Mann-Whitney) were used to compare the duration times between wasps alone, residents, intruders and intruders alone behaviors. Behavior categories were further grouped in two different groups: gall exploitation (*walk-antennate* and *probe*) and patch exploitation (*walking*, *stationary* and *groom*). The leaf and the Petri dish were considered the "patch" for the wasps. The *threat* and *retreat* behaviors were reported by frequency only since they occur too fast and have thus very short durations.

We analyzed the effect of behavior duration, female size, galls size and host numbers on the probability of contests occurrence (a binary variable: 1 = conflict or 0 = no conflict). The explanatory variables were calculated as the difference in wings size (mm) between contestants (resident – intruder), number of hosts in the patch (galls per leaf) and time spent in host exploitation and spent in leaf (min). Logistic regressions analyses were employed, as they are commonly used to test the influences of factors and duration in behaviors on contests outcomes (Hardy & Field 1998). To compare significant differences in wings size (mm) in terms of attack (attacker – retreater) a two tailed *t* test was used. To relate patch ownership and the occurrence of threat behavior to the previous occurrence of *probe* behavior a chi-square test was used.

Ethograms were constructed to illustrate the relationships between the different behaviors and their associated frequencies for the period wasps remained together. The frequency in which a behavior was followed by another was calculated on the basis of the total number of instances the preceding behavioral act was observed, dividing the number of times it was succeeded by another given act. Sequences below 1% were not included.

Results

Behavioral categories

Detailed behavioral categories were established for the particular species used in this study (Table 1). Some categories listed were composed of more than one behavioral element, not distinguished for practical observations. In *probe* behavior, direct observation of egg deposition was impossible because the host is concealed. No behavioral sequences could be found that distinguished successful from unsuccessful probes into the gall.

Table 1: Behavioral categories and definitions of *Torymus* sp.

Category	Definition
walk	walking on the surrounding substrate, exploring the patch, moving the antennae and/or making small jumps and flights.
stationary	remaining motionless, antennal movements may be present.
groom	cleaning body parts, such as wings and antennae, using legs and/or mandibles.
feed	consuming the honey/water solution.
walk-antennate	host examination, walking in circles on top of the gall, drumming the gall with the antennae.
probe	probing the gall, inserting the ovipositor, examining its content and/or releasing an egg, moving the head, antennae and whole body.
threat	running or flying directly toward the other female with wings raised.
retreat	withdrawing temporarily from the patch after being threatened.

Although sequences and respective durations of observed behaviors vary among individuals, general behavior patterns are similar (Table 2). The *stationary* behavior normally was subsequent to host exploitation, when females usually walk away from the host and rest, and by this time, all the hosts were usually already probed. Wasps may remain motionless for extensive periods of time, moving their antennae and grooming. Thus, *stationary* and *groom* were considered post-gall exploitation behaviors.

Wasps when alone differed in behavior durations from resident wasps with intruder presence (Table 3). Wasps alone spent more time in *stationary*, *groom*, *walk-antennate* and *probe* behaviors than when with the intruder. They also remained on or near the host throughout the experiment, with short periods of absence, thus they spent more time in gall exploitation behaviors than when with the intruder present and spent more time on the leaf than off. After a detection of a conspecific female, residents frequently interrupted their gall exploitation behavior sequences. They could either attack the opponent or simply leave the leaf (Fig. 1). Most of behavioral patterns of the intruder with the resident did not differ from the intruder when alone, only the post-gall exploitation behaviors (*stationary* and *groom*) differ significantly.

From the ethograms (Fig. 1 and 2) two main behaviors cycles are characterized: patch exploitation, consisting of *walking*, *stationary* and *groom*, and gall exploitation with *walk-antennate* and *probe*. *Walking* is the behavior from which more complex sequences originate. Although residents and intruders have similar behaviors change points, some distinct shifts can be seen in relation to before and after agonistic behaviors, *threat* or *retreat*. For residents, behaviors were more associated with several cycles of patch exploitation; but if a resident encountered an intruder while walking it usually attacked it and then went back to walking or exploiting the host through probing. For intruders, behaviors were more associated with repeated cycles of gall exploitation and every time an intruder was attacked it was during the gall exploitation cycle.

Table 2: Percentage of time spent in each behavior for wasps released alone in the patch, with two conspecifics in the patch (resident and intruder) and for intruder alone. Behaviors are presented individually, grouped in patch and gall exploitation categories and in terms of wasp position relative to the patch (on or off the leaf).

Behaviors	Wasp alone	Conspecifics in patch		Intruder alone
		Resident	Intruder	
walk	59.75	83.15	71.55	82.17
stationary	23.18	11.06	19.94	7.80
groom	5.69	3.03	2.78	5.64
feed	0.20	0.57	0.00	0.21
walk-antennate	6.45	1.60	4.15	2.78
probe	4.73	0.59	1.58	1.40
gall exploitation	11.17	2.18	5.73	4.17
patch exploitation	88.83	97.82	94.27	95.83
on the leaf	33.10	13.78	19.15	21.66
off the leaf	66.90	86.22	80.85	78.34

Table 3: *U*-test values (significant differences in bold, α=0.05) for wasp alone, resident, intruder and intruder alone. Behaviors are presented individually, grouped in patch and gall exploitation categories and in terms of wasp position relative to the patch (on or off the leaf).

Behaviors	Wasp alone x Resident	Intruder alone x Intruder	Resident x Intruder
walk	**0.009**	0.165	0.097
stationary	**0.007**	**0.003**	0.070
groom	**0.004**	**0.023**	0.560
feed	1.000	0.371	1.000
walk-antennate	**0.005**	0.556	0.149
probe	**0.005**	0.684	0.162
gall exploitation	**0.005**	0.666	0.117
patch exploitation	0.430	0.277	0.155
on the leaf	**0.015**	0.408	0.268
off the leaf	0.114	0.812	0.312

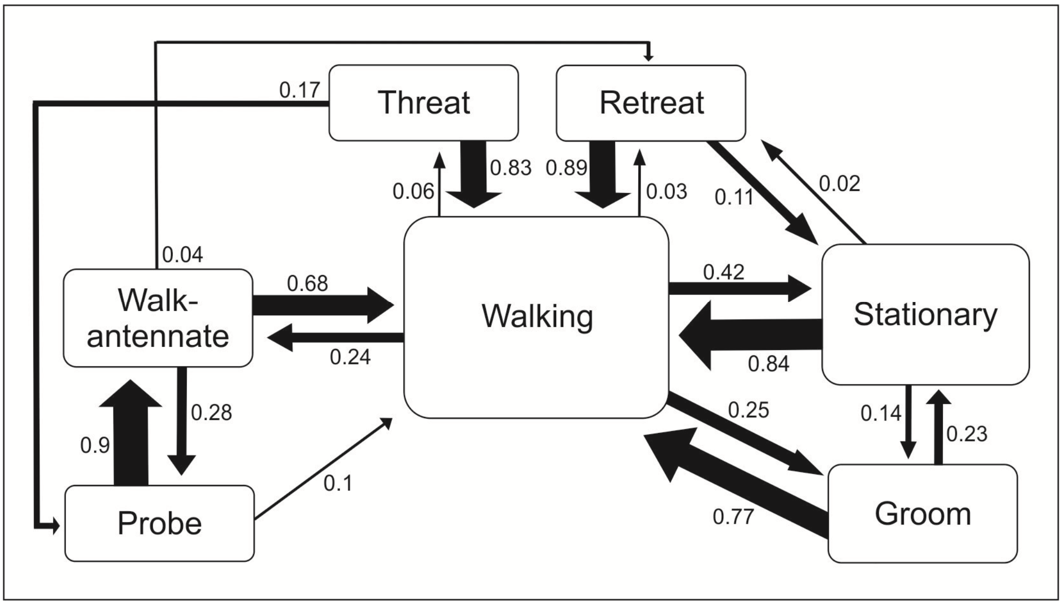

Fig. 1: Ethogram for resident females with intruder under experimental conditions in the 20 replicas. Arrows connect sequential behaviors. Numbers and width of the arrows represent behavioral sequence's proportions.

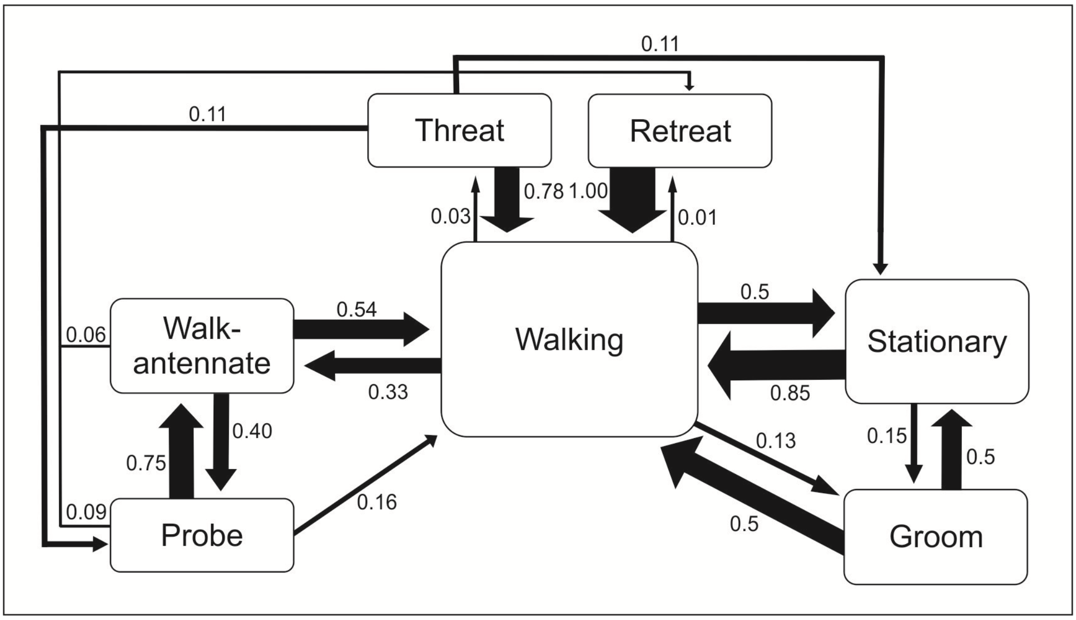

Fig. 2: Ethogram for intruder females with resident under experimental conditions in the 20 replicas. Arrows connect sequential behaviors. Numbers and width of the arrows represent behavioral sequence's proportions.

Resident-intruder contests

There was one type of encounter between females at one level of agonistic behavior: threats. The threats consisted of one individual attacking and the other retreating without retaliation. The attacker raised its wings and pointed its antennae in the direction of the opponent as an intimidation. Since the opponent suffered no apparent injuries this can be classified as “non-aggressive” attack or “ritualized” attack, with extreme close proximity and not resulting in fights or chases. Threats occurred in 10 of the 20 replicates. The retreater wasp temporarily flees from the patch, and begins the stationary behavior, then later returns and attempts to continue searching. Meanwhile, the attacker remains on the patch, walking and/or probing. As there were no retaliations, the threatening wasp won the patch and was able to probe the gall. It was always a clear winner, since the attacker wasp always got to explore the host patch; however the retreater wasp sometimes returned to the gall and probed it without being detected by the other wasp.

Most of the time, both females tolerated one another’s presence and continued exploiting the patch. Some wasps showed no interest for hosts: 7 residents and 10 intruder wasps left the patch without probing them, with a total of 5 experiments with no gall probing by either female. Owners did not tended to attack more than intruders: 11 threat events were by residents and 9 by intruders ($\chi^2_{1;19} = 0.2$, $p = 0.65$). The mean time to have the first contact with the gall was 8 min (± 2.5 min) for wasps when alone, 19 min (± 3.8 min) resident with the intruder, 8 min (± 4.4 min) for intruders and 9 min (± 3.5 min) for intruders when alone.

Logistic regression analysis showed that the probability of contests occurrence was not determined by differences in size between resident and intruders (G_1=2.12, N=20, P=0.16), size of the galls (G_1=1.53, N=60, P=0.21) and number of galls in the leaf (G_1=0.11, N=20, P=0.75). Neither by differences in body size between the attacker and retreater wasp were not significant (t=1.27, d.f.=14.4, p=0.22), or by any interaction between the variables.

Probability of contest occurrence showed a positive relationship with time spent by the attacking female in host exploitation (G_1=4.65, N=40, P=0.04, Fig. 3) and time in the leaf (G_1=8.25, N=40, P=0.01, Fig. 4). Correlation between the occurrence of threats and the manifestation of the *probe* behavior by the intruder was high (r=0.81). Threat occurrence due the presence of *probe* behavior was statistically significant for the intruder ($\chi^2_{1;19}$=13.3, p<0.001) but not for the resident ($\chi^2_{1;19}$=0.20, p=0.65).

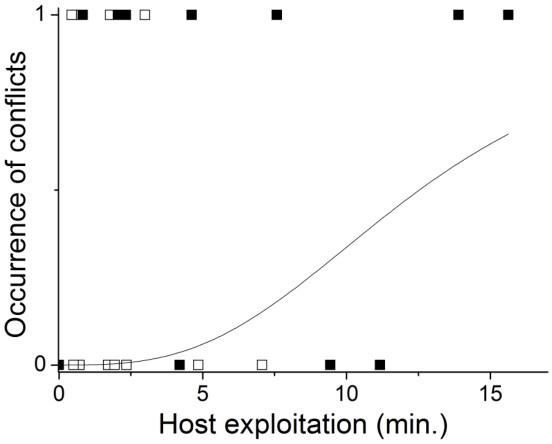

Fig. 3: Predicted probability of conflicts occurring (1) or not occurring (0) in relation to gall exploitation behavior duration (min.) (*p*=0.04). Resident wasps: open squares. Intruder wasps: filled squares.

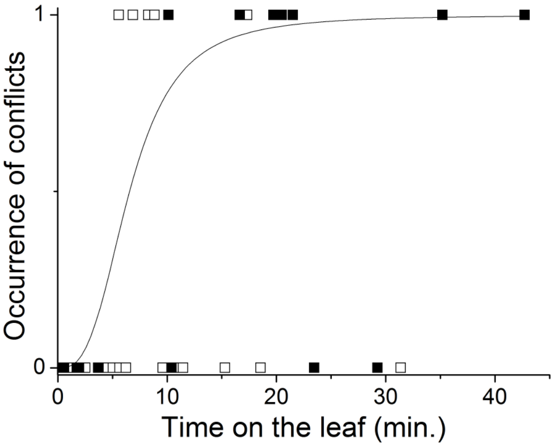

Fig. 4: Predicted probability of conflicts occurring (1) or not occurring (0) in relation to time spent on the leaf (min) (*p*=0.01). Resident wasps: open squares. Intruder wasps: filled squares.

Discussion

In this study, we reported for the first time *Torymus* sp. females displaying agonistic behaviors towards conspecific competitors. The experiments allowed us to identify differences in behavior sequences and duration when female co-occur with conspecifics in a resource patch. Behavioral categories found for this particular species were similar to previous authors that described aspects of host and patch exploitation behaviors for different parasitoid wasp species (Field 1998; Field et al. 1998), agonistic behaviors in other parasitoid wasp conflicts (Petersen & Hardy 1996; Stokkebo & Hardy 2000; Goubault et al. 2005) and similar behavior sequences in host exploitation for a Bethylid parasitoid wasp (Lauzière et al. 2000).

The presence of a competitor greatly changed both resident and intruder exploitation behaviors. The residents alone spend more time in gall exploitation and post-oviposition behaviors. After detecting conspecific females, they clearly changed their behavior sequences, spending more time in patch exploitation. This probably indicates that females are avoiding losing time in an already explored host and investing this time searching for a better patch. Patterns in gall exploitation behavior were already observed in other *Torymus* wasp, *Torymus capite* (Weis 1983), who failures to parasitize all hosts in discovered galls in the patch and the possible explanations for this include a 'fixed-time' foraging strategy shown by the wasp.

The temporarily escape from the patch by the retreater wasps and the subsequent return to continue searching has been described as a “waiting game” by Field et al. (1998). Although the retreater wasp also had the option of leaving the patch, if it chose to stay its key decision was how often to return to the patch and check whether it was unoccupied, and therefore suitable for oviposition. Agonistic behaviors were linked to cycles of host exploitation behaviors, which highlight the trade-off wasps experienced between continuing to explore the patch and excluding their opponent from the patch (Field & Calbert 1999). In Goubault et al. (2005) females tended to avoid contests by leaving the patch early.

Wasp behavior when together did not differ significantly from one another. The residents tolerated the intruders and this reinforces a potential resource denial of the already explored and oviposited hosts. Tolerating some intrusion while exploiting a patch might be relevant in the field, where it is possible that more than a single intruder may arrive on a patch (Field et al. 1998). In addition, Goubault et al. (2007b) found that females successfully protected their host against intruders during host exploitation behavior and not after oviposition.

Not all experiments showed conflicts for hosts and there might be two possible explanations: recognition by intruder of the first wasp having arrived previously and respected residency and/or there was no advantage of defending unparasitized hosts, since some of them were not probed by any wasp. Residents tend to take care of the host and threaten the intruder only when the intruder appears to positively evaluate the host by trying probe it. However, female wasps did not show complete respect for ownership, as it would be expected from previous researches (Field & Calbert 1999; Bentley et al. 2009). Intruders were not totally blocked from probing galls by residents and were able to initiate conflicts as well. Field & Calbert (1999) observed that once a female started a conflict and win, she continued to do so behaving like an owner, regardless of whether the asymmetries in patch were small or large.

In general, residents are expected to have a better estimate of RV than intruders, which would lead to patch defense and would affect female aggressiveness (Leimar & Enquist 1984; Mohamad et al. 2010). However, number and size of galls did not affect contests occurrences and did not appear to be an important factor for residents. Humphries et al. (2006) used host weight as a source for RV asymmetry and found significant influences in contests outcomes. The type of resource used here does not enable us to distinguish resource value asymmetry in terms of host size, quality and development stage previous to an experiment. The host is enclosed inside the gall making it difficult to measure, galls would have to be damaged to observe the insect inside. Host quality has an important role (Bentley et al. 2009), and this might be the reason why some of the wasps left the patch without probing the galls.

Female wasp size did not influence the probability of conflict occurrence. Thus, asymmetries in wing size did not confer an advantage or a better contest ability. In other studies on parasitoid wasp contests, such as Petersen & Hardy (1996), female size influenced the conflicts outcome for host resources, since being larger was an important feature and conferred a competitive advantage and a higher fitness.

It appears that females were not completely able to recognize the asymmetry in resident status, resource value and competitor size difference or to react to it through conflicts. Although there are several differences in resident behavior, contest occurrence was elicited only by intruder interest in the host, and not just patch invasion. Thus, neither the RHP nor the RV models fitted the system adequately.

Although the best strategy for short-lived insects may be not wasting time in conflicts but searching for more resources, the evolution of such agonistic behavior can be justified because levels of competition and superparasitism in the field can be high (Field et al. 1997; Plantegenest et al. 2004; van Alphen & Visser 1990). There are more species of parasitoids wasps that use *S. lantanae* as host (Chapter 2). Thus, other parasitoid wasp species that share the same host might have different competitive strategies to allow their coexistence, as was shown by Mohamad et al. (2011). Also, in order to protect their offspring from other parasitoids, these species might have developed other forms of defense than female agonistic conflicts, such as larval competition inside the gall.

The current theories on contest and contest resolution may not be applicable when finding other patches is not a limiting factor or female-female contests are costly in time and energy (Goubault et al. 2005). Accordingly, other behavioral strategies may prove useful to solve contests occurrences. Further research in this system, for example employing more complex arenas or comparing the different parasitoid species attacking the galling host can help to refine our knowledge of the species involved. Wasp behavior responses and the fact that a gall holds a host inside but is a motionless, plant-based structure, occurring on a plant organ, are important to further understanding of parasitoid wasp behavioral ecology and its evolution.

Acknowledgments

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Artigo 2.

Parasitoid wasps of *Schismatodiplosis lantanae* (Cecidomyiidae), a galler on *Lantana camara* L. (Verbenaceae)[2]

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ABSTRACT. Parasitoid wasps of *Schismatodiplosis lantanae* (Cecidomyiidae), a galler on *Lantana camara* L. (Verbenaceae). Host-parasitoid systems include ecological interactions between at least one host and one parasitoid which consume the entire host biomass to conclude its development. Parasitoids are considered the main natural enemy of galling insects. The aim of this study was to report species richness of parasitic wasps in association with spherical galls induced by *Schismatodiplosis lantanae* (Diptera: Cecidomyiidae) on *Lantana camara* (Verbenaceae) leaves and the temporal pattern of parasitism rate. This is the first report on the ecology of this parasite-host system. Nine different species of parasitic wasps were found from galls of *S. lantanae*, belonging to four different families, and most species are as yet undescribed. A cycle in parasitoid attacking rate and host survival was found along the year. Wasp species are more abundant from July to January while the host midge is more abundant from February to May. Gall diameter differences as well as presence of *L. camara* bushes in several patches may contribute to the richness of parasitoids wasps since their possible limited dispersal would decrease competition and result in species co-existence. The observation of yearly cycles in host survival and mortality rates such as reported here highlights the importance of temporal patterns and may contribute to a better understanding of the population ecology of parasitoid wasps and to the development of efficient biological control programs.

KEYWORDS. galls; host-parasitoid cycle; parasitoid richness; population fluctuation.

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[2] Este trabalho será submetido à revista Brasileira de Entomologia.

RESUMO. Vespas parasitóides de *Schismatodiplosis lantanae* (Cecidomyiidae), galhador de *Lantana camara* L. (Verbenaceae). Sistemas hospedeiro-parasitoides incluem interações ecológicas entre pelo menos um hospedeiro e um parasitóide, o qual consome inteiramente a massa do hospedeiro para concluir seu desenvolvimento. Por isso, os parasitóides são considerados os principais inimigos naturais dos insetos galhadores. O objetivo deste estudo foi descrever a riqueza de vespas parasitóides em associação com galhas esféricas causadas pelo *Schismatodiplosis lantanae* (Diptera: Cecidomyiidae) em folhas de *Lantana camara* L. (Verbenaceae) e o seu padrão temporal na taxa de parasitismo. Este é o primeiro trabalho sobre taxas de parasitismo nesse sistema. Nove espécies de vespas parasitoides foram encontradas nas galhas de *S. lantanae*, pertencendo a quatro famílias, sendo a maioria ainda não descrita. Um ciclo nas taxas de incidência de parasitoides e sobrevivência do hospedeiro foi encontrado durante o ano de coleta. As espécies de vespas foram mais abundantes durante os meses de Julho a Janeiro, enquanto o hospedeiro galhador o foi de Fevereiro a Maio. Diferenças no tamanho do diâmetro das galhas assim como a presença de arbustos de *L. camara* distribuídos em diversas manchas podem ter contribuído para a riqueza de vespas parasitoides, pois sua possível dispersão limitada pode diminuir a competição e resultar na coocorrência das espécies. Essas observações durante o ciclo de um ano das taxas de sobrevivência e mortalidade do hospedeiro ressaltam a necessidade do entendimento de padrões temporais nas interações e podem contribuir para um melhor entendimento da ecologia populacional das vespas parasitoides e para o desenvolvimento de programas de controle biológico eficientes.

PALAVRAS-CHAVE. ciclo parasita-hospedeiro, flutuação populacional, galhas, riqueza de parasitoides.

INTRODUCTION

Parasitoidism is an ecological interaction between a victim, the host, and an exploiter, the parasitoid, which consumes the host’s entire biomass during its developmental process. Adult female parasitoids forage actively for hosts and oviposit in or near host individuals. After hatching, the larvae begin feeding on host tissues and complete its development either in or on the host (Godfray 1994).

Parasitoids are considered the main natural enemy of galling insects (Godfray 1994). It is very common to find inside the gall, instead of the inducing insect, other organisms living as inhabitants, predators or parasitoids. Galls are structures composed of plant tissue within which the gall former feeds, and can be present in different plant body parts induced by different organisms such as insects, mites, nematodes, bacteria, viruses and fungi (Stone & Schonrogge 2003). It is suggested that the evolution of galling insects may be a response to parasitoid attack, since plant tissue serves as physical protection (Price *et al.* 1986, 1987). Parasitoids are extremely efficient in using their limited resources, suggesting that the species are intimately related with their hosts (Craig *et al.* 1990; Harvey *et al.* 2009).

Communities centered on galling insects and associate parasitoids are ideal for ecological interactions studies, due to the great diversity of species involved and because galls are a static and identifiable resource sometimes within easy reach, allowing counting and observation (Godfray & Shimada 1999; Stone & Schonrogge 2003).

The tritrophic system formed by parasitoid wasps in association with the galling insect *Schismatodiplosis lantanae* Rübsaamen, 1916 (Diptera: Cecidomyiidae) on *Lantana camara* L. (Verbenaceae) (Gagné 1994) has not been study yet. The midge *S. lantanae* induces spherical, green pocket galls with a unique larval chamber mostly prominent on the abaxial leaf side (Moura et al. 2008). The shrub *L. camara* is native in southern Brazil, but it is an aggressive invasive plant in several other countries. As a toxic weed, it has been a problem in cattle raising in many countries (*e.g.* Australia). The broad geographic distribution and diverse set of habitats occupied by *L. camara* is a reflection of its wide ecological tolerance (Sharma *et al.* 2005). Although many studies approach *L. camara* as an invasive plant, there is no record of its galler parasitoids and their life cycles.

Beyond that, this system allows us to predict cyclic fluctuations of animal populations caused by host-parasite interactions. These cycles have long been predicted by Lotka-Volterra type models (Begon *et al.* 2006). The model predicts the stable coexistence of competitors in situations which interspecific competition is, for both species, less significant than intraspecific competition. The model is very simple and useful but, for instance, it does not account the complexities of competition in the real world (Begon *et al.* 2006). Previous studies showed that events in the host life cycle can have an effect on the parasitic population dynamics (May *et al.* 1981, Godfray &

Hassell 1989, Gordon *et al.* 1991), or host alone can generate cycles, to which the dynamics of the parasitoid are synchronized (Begon *et al.* 1995).

The aim of this study was to report species richness of parasitic wasps in association with the galler *S. lantanae* on *L. camara* and the temporal pattern of parasitism in this host-multi-parasitoid system. This study is the first report of a temporal pattern of this host-parasitoid system.

MATERIAL AND METHODS

This study was conducted in Morro Santana, Vale Campus of Federal University of Rio Grande do Sul (UFRGS), Porto Alegre, RS, Brazil. The shrub *L. camara* generally grows in open, un-shaded conditions such as wastelands, rain forests edges, beachfronts, shrub lands, urban areas, wetlands and forests recovering from fire or logging. It does not invade intact rain forests, but is found on their margins (Sharma *et al.* 2005). *L. camara* leaves were collected in bush patches in forest borders and open spaces in specific tracks and taken to the laboratory.

Sampling occurred monthly over a period of one year, from June/2010 to June/2011. Samples consisted of at least eight galled leaves from four different bush patches. During spring/summer these numbers were higher due to the abundance of galled leaves in the field; thus, the sampling regime mirrored the availability of the galls. Galled leaves were stored in Petri dishes under controlled conditions (16 hrs light/day, RH 80%, 25±1°C,) until the emergence of adult parasitoid wasps. The wasp uses its long and thin ovipositor to lay one egg inside each gall, reaching the solitary insect in the gall chamber, so the oviposition process by wasps leaves a small round scar in the gall wall which is easily identifiable under a stereomicroscope. After obtaining the adult wasp, they were counted and fixed in 70% alcohol. Body length (from head to the tip of the abdomen, excluding the ovipositor if present) of some wasps from each species was measured under a stereomicroscope. A subset of the galls was opened under a stereomicroscope to determine parasitoid feeding behavior.

The mean number of galls, parasitoids and midges per leaf were based on the total number of leafs collected per month. Wasp identification was provided by the Laboratório de Controle Biológico and deposited (voucher 432) in the Entomophagous Insects “Oscar Monte” Collection (IB-CBE), both at Centro Experimental Central of Instituto Biológico, Campinas, SP, Brazil.

RESULTS

In a period of one year 2422 galls were brought to the lab, with 1064 of them resulting in the midge *S. lantanae* (44%), 805 in parasitoid wasps (33%) and 553 in empty or predated galls (23%). The mean gall diameter is about 7.4 mm (± 0.3 mm) when fully developed (Moura *et al.* 2008) with mean number of galls per leaf at 4.8 (± 0.2). A single parasitoid larva develops per host, consuming it completely in about 15 to 20 days in laboratory conditions, with smaller wasps emerging sooner than larger ones. The window of opportunity for gall attack is apparently wide with galls of varied sizes being oviposited in and also because galls are present all year round.

Nine different species of parasitic wasps were found from galls of *S. lantanae*. These belonged to four different families, and most species are as yet undescribed (V. Costa, IB, Campinas, pers. comm.). Observations revealed that some species feed internally in the host (endoparasitoids) while others externally (ectoparasitoids). Female wasp body length varied considerably among species (Table 1).

A cycle of parasitoid wasps and midge survival is apparent during the sampling period (Figure 1). Wasp species are more abundant in the months from July to January and the midge host from February to May, and the number of galls per leaf reached a peak in April.

Table 1. Parasitoid wasp species found in *Schismatodiplosis lantanae* on *Lantana camara* leaves, with information on parasitoid feeding mode and mean adult body length (mm) ± standard error. Monthly samples are from June 2010 to June 2011 in Morro Santana, Porto Alegre, RS, Brazil.

Parasitoids wasps	Feeding mode	Mean size
Torymidae		
Torymus sp. 1	ecto	2.71 ± 0.11
Torymus sp. 2	ecto	2.17 ± 0.12
Torymoides sp. 1	ecto	1.94 ± 0.09
Eulophidae		
Galeopsomyia sp. 1	ecto	2.25 ± 0.12
Galeopsomyia sp. 2	ecto	1.05 ± 0.01
Platygastridae		
Platygastridae sp. 1	endo	1.16 ± 0.03
Platygastridae sp. 2	endo	1.15 ± 0.01
Platygastridae sp. 3	endo	1.05 ± 0.02
Proctotrupidae		
Proctotrupidae sp. 1	endo	0.75 ± 0.01

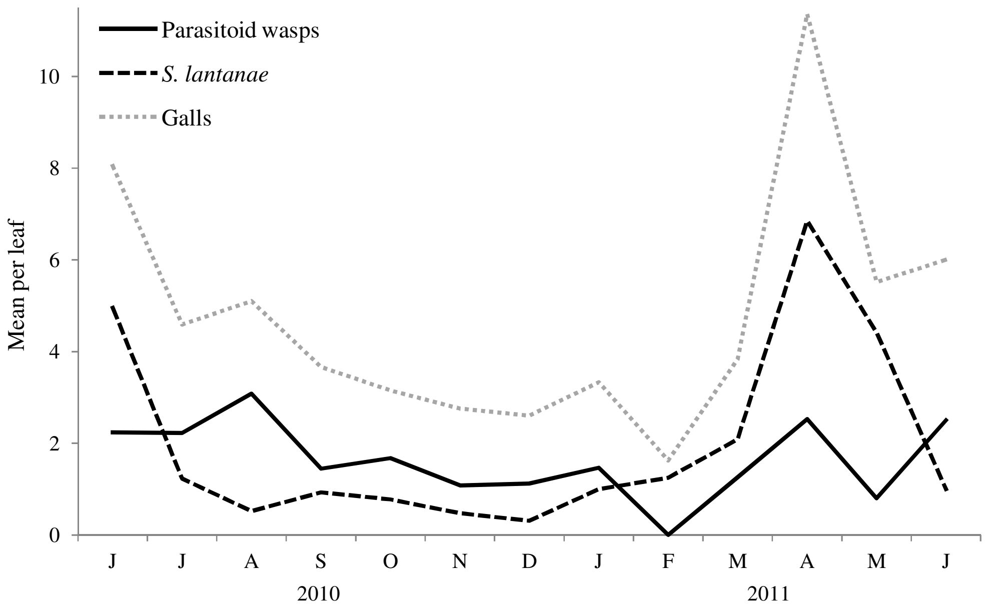

Figure 1. Mean number of galls per leaf, number of midge hosts (*Schismatodiplosis lantanae*) and number of parasitoid wasps emerging (all species combined) across the sampling months (June 2010 to June 2011) in Morro Santana, Porto Alegre, RS, Brazil.

DISCUSSION

In this study, the diversity of parasitoids and a host-parasitoid cycle were described. Nine different species were found from four wasp families, extending the knowledge of parasitoid wasps associated with *S. lantanae*, which was restricted to four species recorded in Rio de Janeiro State, Brazil (Maia & Azevedo 2009). Three wasp families are common to both studies. There are few studies on micro-hymenoptera diversity in galling insect systems for Brazil, and records are usually restricted to the family or genus level, demonstrating the lack of knowledge on the Neotropical fauna.

Studies have shown that limited dispersal abilities of individuals have the potential to both stabilize host-parasitoid interactions and promote strategies of co-existence in competing parasitoid species (Comins & Hassell 1996; Briggs & Latto 2000; van Nouhuys & Punju 2010). Briggs & Latto (2000) noticed that a Platygastrid parasitoid wasp was frequently observed in the field searching meticulously for hosts in *Baccharis pilularis* (Asteraceae) bush. It is likely that this wasp has very limited dispersal in the field and it may spend its entire life on a single bush. Thus, the presence of *L. camara* bushes in several patches may contribute to parasitoid wasp diversity since their possible limited dispersal would decrease competition and result in species co-existence.

In another study, van Nouhuys & Punju (2010) found that the co-occurrence of two parasitoid wasps in a host was due not only to an absence of a superior competitor or more dispersive species, but to differences in timing among wasp species. As *S. lantanae* galls occurred all year round, it is possible that parasitoid species have distinct seasonality patterns, providing the opportunity for co-occurrence.

The wasp species have large differences in size and consequently differences in their ovipositor length. Gall diameter had some influence in the diversity of the parasitoid-host system studied by Price & Clancy (1986). Thus, difference in gall diameter and especially in gall wall thickness across gall development, responding through hyperplasy and hypertrophy and generating a spongy parenchyma wall (Moura *et al.* 2008), could selected parasitoid wasp species across time. Thus, wasps with a longer ovipositor may face little competition over mature galls, whilst smaller wasps or wasps with smaller ovipositors may thrive only on earlier stages of gall development.

The host-parasitoid interaction exhibited rounds of host overexploitation and crash, followed by parasitoid decline and host recovery, as in other host-parasitoid cycles found in Ferraz & Monteiro (2003) and Begon *et al.* (1995). According to Anderson & May (1978), parasite species with cycling populations may in certain circumstances play an important role in regulating or controlling the growth of their host population. In such cases, the parasite will play an analogous role to a predator which suppresses the growth of its prey population. However, *S. lantanae* galls occurring all year round could provide another type of refuge that allows population persistence even under periods of high parasitoids densities.

In a tritrophic system study, parasitoids can enhance plant fitness. In a guild of three Eulophid parasitoids, all of them oviposit directly into the weevil larvae that consume plant seeds (Gómez & Zamora 1994). The presence of parasitoids in this system greatly decreases the success of the weevil larvae and, as a result of this indirect facilitation of host plant protection, both plant and parasitoids benefit from this interaction. In *L. camara* system, parasitoids and the galler seem not to have visible effect on plant fitness since they do not attack reproductive plant organs, although it could cause stress affecting plant phenology and reproductive output, for example. An interesting research development to this report would be to analyze whether parasitoid attack can serve the plant in any way to lessen the damage induced by the insect.

The control of *L. camara* as an invasive shrub has not been successful. None of the over 40 biocontrol agents released in 32 countries have been successful in controlling the weed effectively (Sharma *et al.* 2005). Many of the leaf feeding insects are unable to maintain high enough populations to cause significant damage to *Lantana*, since leaves fall in extended periods of drought. Nevertheless, the study of parasitoid species and their relations with hosts might be of importance for future biological control programs, for example those combining multiple enemies of the plant.

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Considerações Finais

Neste estudo com vespas parasitóides de *Schismatodiplosis lantanae* em *Lantana camara*, a ecologia comportamental das fêmeas de *Torymus* sp. foi estudada através de experimentação, bem como a diversidade do sistema e seu ciclo hospedeiro-parasitóide foi descrita.

No primeiro artigo, foram encontradas diferenças comportamentais e presença de conflitos entre fêmeas da vespa parasitóide *Torymus* sp. através das assimetrias experimentalmente criadas como diferenças no tamanho das vespas, número de galhas na folha e tempo de chegada no local. Este trabalho é o primeiro a relatar comportamentos para vespas deste gênero. Ao contrário do esperado, essas assimetrias não influenciaram a ocorrência dos conflitos, porém a presença de um competidor no local provocou mudanças de comportamento na vespa residente. Fêmeas que passaram mais tempo presentes na folha ou dedicando seu tempo em exploração da galha tiveram mais probabilidade de apresentar conflitos, e consequentemente tiveram a oportunidade de possivelmente ovipositar no hospedeiro. Outro fator significativo foi o interesse da invasora pelo hospedeiro, que em todas às vezes resultou em conflitos, seja por parte da invasora ou pela residente.

Os vídeos resultaram em informações qualitativas e quantitativas valiosas para caracterizar o comportamento de *Torymus* sp. e suas relações com o hospedeiro. Em condições naturais, o comportamento das fêmeas parasitóides não poderia ser diretamente observado devido ao tamanho muito pequeno do animal e a habilidade de explorar uma diversidade de microhabitats. Como os parasitóides são difíceis de observar, experimentos em laboratório aproximam do que pode ocorrer em seus ambientes naturais. Portanto, estes experimentos são válidos em estudos de comportamento e os resultados podem ser extrapolados para o que ocorre na natureza dentro de certos limites.

As competições entre as fêmeas de vespas parasitóides podem ter sido influenciadas por outros atributos que podem estar presentes nesta espécie de *Torymus*, como, por exemplo, competição larval. O resultado da competição entre larvas de parasitóides dependem de sua morfologia (se apresentam mandíbulas para a luta ou não), interações fisiológicas com o hospedeiro, mobilidade dentro da galha, assim como taxas de desenvolvimento e parasitismo simultâneas (Van Nouhuys & Punju, 2010.).

Outro atributo que pode ter influenciado as competições é o fato das vespas poderem ser geneticamente próximas. Apesar das vespas terem sido coletadas em manchas diferentes, algumas emergiram da mesma folha ou da mesma planta, nas quais podem ter sido parasitadas por uma única fêmea de vespa parasitóide. De acordo com Lizé et al. (2012), comportamentos agonísticos podem ser menos violentos quando competidores são mais relacionados geneticamente e também quando são desenvolvidos no mesmo hospedeiro.

No segundo artigo, foi descrita a diversidade de vespas parasitóides encontradas nas galhas de Cecidomyiidae em *L. camara*. Foram encontradas nove espécies, as quais provavelmente não foram ainda descritas, visto a falta de trabalhos referentes a este tipo de sistema e o grau de especificidade destes organismos. O fato de galhas de *S. lantanae* estarem presentes o ano inteiro, apresentarem variados tamanhos e arbustos de *L. camara* se distribuírem em manchas relativamente isoladas entre si podem ser fatores importantes para manter a diversidade de vespas parasitóides encontrada. O ciclo de taxas de parasitismo apresentado mostrou um equilíbrio anual muito dinâmico entre o hospedeiro e seus parasitoides. Para trabalhos futuros, o interessante seria investigar os ciclos anuais de cada espécie de parasitóide individualmente, revelando quais parasitóides realmente competem entre si pelo único hospedeiro em questão, *S. lantanae*.

Ambos os artigos mostraram características da interação planta, hospedeiro e parasitóides, porém, muito deste sistema ainda precisa ser estudado. A observação desses ciclos populacionais e ecologia comportamental de vespas parasitóides podem ser importantes para contribuir para um melhor entendimento do sistema e no desenvolvimento de programas de controle biológico eficientes.

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