

## ECOLOGY, BEHAVIOR AND BIONOMICS

### Foraging Patterns in a Nocturnal Swarm-Founding Wasp, *Apoica flavissima* van der Vecht (Hymenoptera: Vespidae)

FABIO S. NASCIMENTO E IVELIZE C. TANNURE-NASCIMENTO

Depto. Biologia, Ecologia e Evolução. FFCLRP, USP, 14040-901, Ribeirão Preto, SP, fsnascim@usp.br

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#### Padrões de Forrageamento na Vespa Noturna *Apoica flavissima* van der Vecht (Hymenoptera: Vespidae)

**RESUMO** - O comportamento de forragear é fundamental para o desenvolvimento das colônias de insetos sociais, pois permite que as colônias sejam supridas de alimento, água e materiais utilizados para a construção dos ninhos. Vespas sociais do gênero *Apoica* Lepeletier (Hymenoptera: Vespidae) têm comportamento de forrageamento noturno como uma de suas principais características, porém estudos sobre aspectos abióticos que influenciam esse comportamento são ainda escassos. Este estudo mostra que a frequência de forrageamento foi maior em noites de luas cheia e crescente. Além disso, as saídas e retornos ao ninho correlacionaram-se positivamente com o período da noite e a temperatura. Os resultados sugerem que a luminosidade é um componente importante nas atividades gerais das colônias do gênero.

**PALAVRAS-CHAVE:** Insecta, Polistinae, inseto social, Epiponini, bionomia

**ABSTRACT** - Foraging behaviour has a remarkable significance to colonies of social insects since it is directly related to the supply of food, water, and pulp. Social wasps of the genus *Apoica* Lepeletier are primarily nocturnal, but studies concerning the general aspects related to this habit are still scarce. This study showed that the rates of foraging flights were higher during the full moon and last quarter moon phases. Frequencies of arrival and departure were correlated with time and temperature at night. The results suggest that the moonlight is an important component to general activities in this genus.

**KEY WORDS:** Insecta, Polistinae, social insect, Epiponini, bionomics

The repertory of foraging strategies and the division of labour in social insects are diverse and sophisticated (Wilson 1971, Oster & Wilson 1978). Extrinsic contingences such as predation, availability of food resources, and weather conditions affect the usual course of the colonial development. Thus, the individuals should be sensitive to these changes and alter their behaviour accordingly (Jeanne 1986, O'Donnell & Jeanne 1992).

The swarm-founding polistines [Tribe Epiponini (Carpenter 1997)] are complex societies, in which worker age polyethism, complex tasks, and an elaborated communication network have evolved (Jeanne 1980, 1991a). Although foraging in social wasps does not involve recruitment as observed in other social insects (Wilson 1971, Jeanne *et al.* 1995), it plays an important role concerning the division of labour among workers in colonies of Epiponini (Jeanne 1991b).

The genus *Apoica* Lepeletier is unusual among social wasps because its nests lack an envelope covering the single brood comb, and it has evolved nocturnality as a primary

behaviour. In comparison to other genera, studies on the life history and behaviour of *Apoica* are still scarce. These include observations of the swarm emigration (Ducke 1905, Schremmer 1972, Hunt *et al.* 1995, Howard *et al.* 2003), nesting behaviour (Vecht 1972), caste differentiation (Shima *et al.* 1994, Jeanne 1995, Nascimento *et al.* 2003), and life history (Hunt *et al.* 1995).

Hunt *et al.* (1995) observed the colony composition, nesting sites, nightly and diurnal activities of *Apoica pallens* (F.). They noted that the foraging and activities in *A. pallens* may be influenced by the phases of moon, although they did not statistically compare it. This report shows the effects of the moon on the foraging patterns in *Apoica flavissima* van der Vecht.

#### Material and Methods

Observations of foraging activities by one colony of *A. flavissima* were carried out in Tocantins municipality, MG, Brazil (21°10'S, 43°01'W) between May and August, 1997.

The colony was in ergonomic phase of development: 1332 cells with 180 eggs, 50 larvae, and 227 pupae. After collection, 731 workers and 69 queens were dissected and stored in alcohol 70% for posterior analysis. Recordings of the number of arrivals and departures of wasps for the first 15 minutes of each hour were made between 18:00h and 22:00h. The nest was illuminated with lanterns covered with pieces of red plastic. Hand counters and a video-camcorder were used to number the foraging wasps. Temperature and sky conditions were registered for each period of observation.

The experiment was designed to test whether the frequency of wasps arriving and departing at the nest was influenced by the phases of the moon, the weather conditions, and the time of day. Replicates were grouped according to each phase of the moon at night: May 22, June 20 and July 18 as full moon nights; May 29, June 26 and July 25 as first quarter moon nights; June 6, July 4 and August 1 as new moon nights; and June 13, July 11 and August 8 as last quarter moon nights.

Analysis of variance (ANOVA) on log-normal-transformed data was used to test the null hypothesis that the number of foraging wasps arriving and departing at the nest during different phases of the moon did not vary. If differences among activities were confirmed, a Tukey test was used to test the effects of phases of the moon in each period of observation. Also, the Wilcoxon matched pair test was utilized to verify differences of foraging activities summed. All analyses were made with the program Statistica for Windows 5.0.

## Results

**General Aspects of Nocturnal Activities.** Until the sunset, the wasps remained in a symmetrical, motionless and massive pattern of bodies facing the margin of the nest. During the day, such array changed quickly when the nest was disturbed by mechanical touches in the supporting branch as imitating a predator, and then wasps covered entirely the top of the comb taking a typical defensive position. After few minutes they slowly returned to the original resting position. Wasps started intensively to move between 17:45h and 18:00h, and the movement culminated with most of wasps flying close to the nest and backing after some seconds (Fig. 1). This explosive departure of wasps, as described by Hunt *et al.* (1995), and their rapid return occurred in almost nights, except on June 06 and 13, and July 18 and 25, which was probably related to the cloudy sky and/or the rain.

**Patterns of Colony Foraging.** Analysis of variance showed that the phases of the moon associated with the time had an effect on the foraging activities of *A. flavissima* (Table 1). Analyzed as independent data, at most of time, frequencies of departures were significantly higher or close to higher during the last quarter and full moon than during other moon nights (Fig. 2). However, frequencies of arrivals only were significant at 18:00h and marginally significant at 22:00h. In such periods,



Figure 1. Explosive departure of wasps prior the onset of activities at night.

foraging wasps arrived significantly more at the nest during nights of last quarter moon than during other periods (Fig. 2A).

The patterns of foraging activities were affected by different phases of the moon (Table 2). When the summed data were dependent-treated, the results showed that both the frequency of departing and arriving of wasps were significantly higher during the full and last quarter moon than during the other moon nights (Table 2). Moreover, there were no differences between foraging activities performed during the full and last quarter moon, and during the new and first moon nights.

During the period of study the temperature decreased at about 4°C ( $3.8 \pm 1.5^\circ\text{C}$ ) from the onset to the end of the time of observation, and the rate of foraging flights dropped in response to this decreasing (Spearman rank correlation:  $r = 0.67$ ;  $P < 0.05$ ;  $N = 12$ ).

**Partitioning of Materials Foraged.** Video recordings provided additional information about the quality and number of loads transferred from foraging workers to nest workers (Table 3). Although foraging workers with prey were recognized during analyses, workers bringing water and nectar loads were not distinguished, so the resources were classified as liquid loads. Material-handling sequences were similar between solid and liquid loads. A total of 116 observations related to the material transference were recorded. Most of the materials were partitioned to two nestmates that used to feed larvae and other adults.

## Discussion

The presented data support the hypothesis that foraging activities in *A. flavissima* is affected by the phases of the moon. Preliminary preceding study indicated a similar pattern in *A. pallens* (Hunt *et al.* 1995). However, the present study documents a complete

Table 1. Results of the analysis of variance for departures and arrivals of *A. flavissima* workers during different times of the night.

Time	Sum of squared Effect	Mean squared Effect	Sum of squared Error	Mean squared Error	F-ratio	p-level
<b>Departures</b>						
18:00	0.98	0.33	0.64	0.08	4.05	0.050
19:00	1.02	0.34	0.72	0.09	3.78	0.059
20:00	1.52	0.51	0.56	0.07	7.30	0.011
21:00	2.72	0.91	1.06	0.13	6.83	0.013
22:00	1.29	0.43	0.85	0.11	4.05	0.050
<b>Arrivals</b>						
18:00	1.27	0.42	1.19	0.15	2.85	0.105
19:00	0.77	0.26	0.98	0.12	2.09	0.180
20:00	0.32	0.11	0.12	0.01	7.42	0.011
21:00	0.99	0.33	0.85	0.11	3.12	0.088
22:00	0.72	0.24	0.50	0.06	3.83	0.057

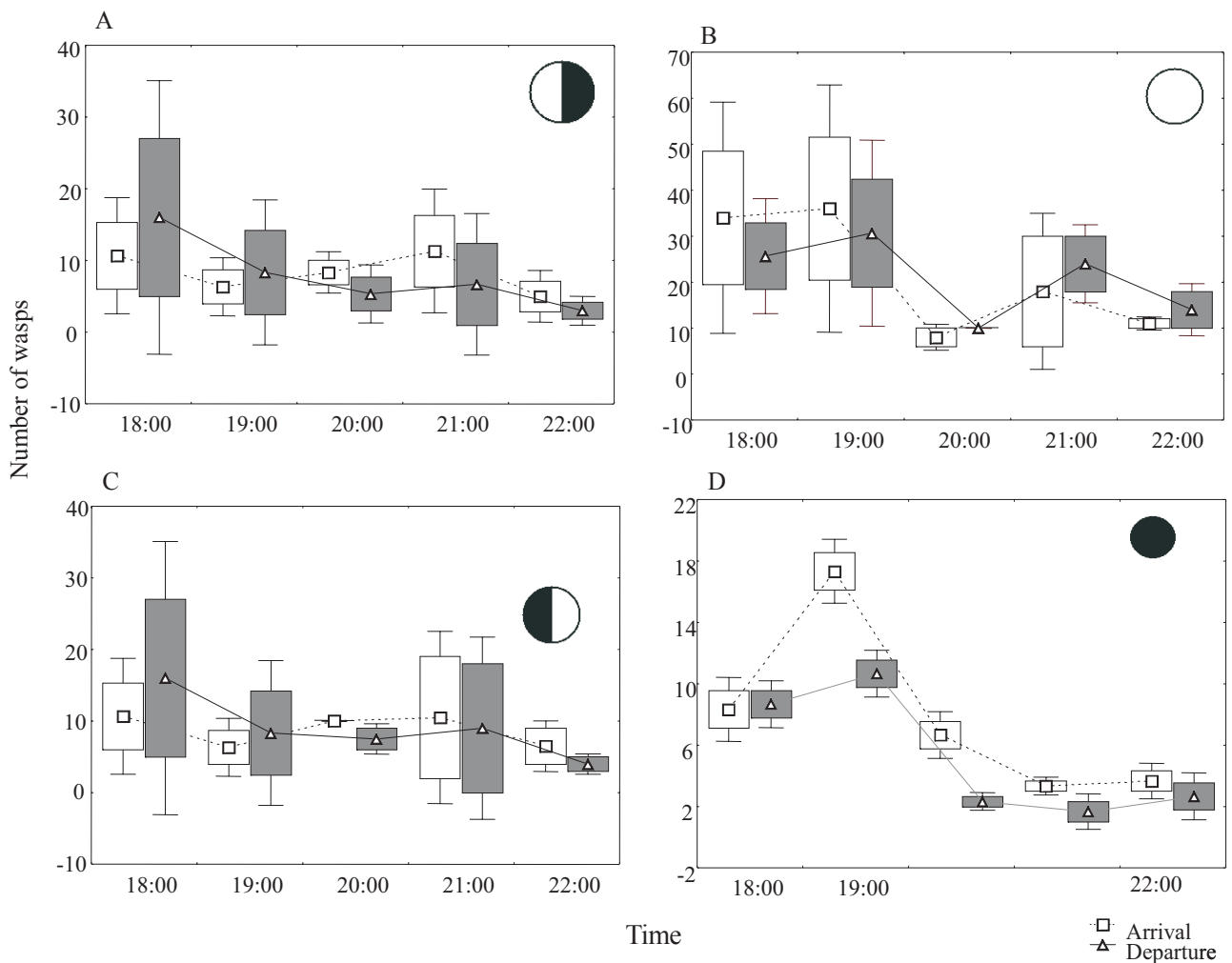


Figure 2. Rates of arrival and departure of *A. flavissima* foragers according to the phases of the moon. A – last quarter moon; B – full moon; C – first quarter moon; D – New moon. Squares = means, boxes = standard errors, and whiskers = standard deviations

Table 2. Matched comparisons of the data summed for foraging activities of *A. flavissima* workers between different phases of the moon (n=12).

Phases of the moon	Departures		Arrivals	
	Z	p-level	Z	p-level
Full x first quarter	3.41	0.001	2.95	0.003
Full x new	3.41	0.001	2.56	0.011
Full x last quarter	0.40	0.691	0.06	0.950
First quarter x new	0.52	0.600	0.41	0.683
Last quarter x first quarter	3.07	0.002	2.73	0.006
Last quarter x new	3.24	0.001	2.67	0.008

feature of such influence. The frequencies of foraging wasps arriving and departing from the nest were significantly higher during the full and last quarter moon. The presence of enlarged ocelli is evidently associated with nocturnal habits, but these results combined with previous ones suggest that the presence of light is an important factor during nocturnal activities in *Apoica*. In fact, recent study showed that swarm emigrations in *A. pallens* occurred at sunset, as the sky was not completely dark (Howard *et al.* 2003). In contrast to diurnal species, the frequency of departures of workers was often higher during the hotter periods of the night.

A number of studies on foraging activities in Epiponini noticed that both qualitative and quantitative rates of foraging are seasonally affected along the period of colony development (Gobbi & Machado 1985, 1986, Gobbi *et al.* 1984, Lima & Prezoto 2003, Paula *et al.* 2003). Although these variables were not analyzed in the present study, the influence of season and colonial development on the foraging patterns is not ruled out and remains to be verified in *Apoica*.

The results also support the existence of the explosive departure at the sunset in *A. flavissima*, which seems to be a common behavioural feature to the genus. Only under adverse weather conditions this kind of departure did not occur. Hunt *et al.* (1995) verified that the explosive departure is not a response to physiological needs (e.g. drinking water or defecating), which was also supported by this study, but instead this behaviour seems to stimulate the start of other activities of the colony including the foraging.

Table 3. Material partitioning from foragers to nest workers of *A. flavissima*.

Number of receiving nestmates	% Prey	% Liquid	Number of observations
1	0.25	0.11	20
2	0.43	0.67	64
3	0.08	0.17	16
4	0.12	0.05	10
5	0.12	0	6

Although *Apoica* is a basal genus within the tribe Epiponini, the task partitioning among *A. flavissima* workers was similar to different materials foraged. As other species studied so far (reviewed in Jeanne 1991b), food resources were completely distributed by foragers to nestmates. In conclusion, the present paper provides additional information on the life history of this interesting genus, and may contribute to understand the biology of the Neotropical swarm-founding wasp.

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