Sociobiology
An international journal on social insects

RESEARCH ARTICLE - WASPS

Effect of the Habitat Alteration by Human Activity on Colony Productivity of the Social Wasp *Polistes versicolor* (Olivier) (Hymenoptera: Vespidae)

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Article History
Edited by
Fernando Noll, UNESP, Brazil
Received 14 October 2013
Initial acceptance 12 November 2013
Final acceptance 28 November 2013

Keywords
Nest, Independent foundation, Polistinae, Reutilization of cells, Synanthropy

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Abstract

Currently, the main impacts on biodiversity are generated by human activities in natural environments. Monitoring the number of species of social wasps nesting attached to buildings is important to evaluate the effect of this activity on colony productivity. This study evaluated the effect of habitat alteration, particularly by human activity on the productivity of colonies of the wasp *Polistes versicolor.* We evaluated 20 abandoned nests and compared the productivity parameters: number of cells constructed, number of adults produced, nest dry mass, proportion of productive cells, number of generations, and diameter of the petiole. Most of these parameters showed higher values in the colonies nesting in the habitat less altered by human activity. Therefore, productivity was significantly higher in this habitat. In the nests, regardless of the site, the cells that were central and closer to the petiole were the most productive. Colonies in the two habitats used different strategies: in the habitat more altered by human activity, the wasps invested more in reusing cells than in enlarging the nest. However, the species continues to nest in the urban area, probably because of decreased interspecific competition, predation, and interference from climate variations.

Introduction

Eusocial wasps are represented by 29 genera in the Neotropical region, 22 of which are recorded in Brazil (Carpenter & Marques, 2001). These wasps occupy many kinds of habitats, primarily associated with human constructions (Lima et al., 2000; Prezoto et al., 2007), i.e., show a high degree of synanthropy (Fowler, 1983).

Among the numerous factors that contribute to the success of social wasps, the colony productivity stands out. Productivity depends on ecological factors including changes in temperature, prey availability, and number of founders, among others (Gamboa et al., 2005; Inagawa et al., 2001). According to Gamboa (1978), for example, colonies of *Polistes metricus* (Say) founded by association are more productive than those initiated by a single female. Tibbetts & Reeve (2003) found that *Polistes dominula* (Christ) colonies initiated by association better defend their colonies from predators and/or conspecific wasps, and this cooperation increases the colony productivity.

Environmental factors may also be related to colony success and productivity, for example, the nesting site, as evidenced by Inagawa et al. (2001) and Nadeau & Stamp (2003) in *Polistes snelleni* (Saussure) and *Polistes fuscatus* (Fabricius), respectively. These studies showed that colonies founded in locations with higher mean temperatures had higher productivity.

For colonies under the same environmental conditions, Giannotti (1997) noted that the productivity can be influenced by intrinsic factors such as the number of cells, reuse of cells, duration of immature stages, and the mortality of the immatures in the different stages. As observed by Montagna et al. (2010), the productivity can vary within the comb; the central cells of the combs of *Mischocyttarus consimilis* (Zikán) are more productive than the peripheral cells.

Santos & Gobbi (1998), Inagawa et al. (2001) and Gamboa et al. (2005) evaluated the effect of habitat on the colony productivity of the social wasps, while others such as Penna et al. (2007), Montagna et al. (2010), Oliveira et al. (2010) and Sinzato et al. (2011) evaluated the productivity in urban environments. However, only Michelutti et al. (2013) compared the productivity of colonies between environments with high and low degrees of human interference, in *M. consimilis*.

According to Samways (2005, 2007), disturbances caused by humans in natural environments are the main factors acting to reduce biodiversity in the tropics. The human presence alters habitat quality (Raupp et al., 2010; Schowalter, 2012). The expansion of ranching and other agricultural activities as well as urbanization are the main factors modifying the natural habitats (Abensperg-Traun & Smith, 2000; New, 2005; Raupp et al., 2010) and often have forced wasps to search for new nesting environments. It is common to find wasps nesting on or in human constructions (Clapperton, 2000; Mead & Pratte, 2002). This can be explained by the abundance and quality of available sites, and the reduced interspecific competition and predation by vertebrates in these environments.

Among the Polistinae, several species of *Polistes* use human constructs as nesting substrates (Fowler, 1983; Butignol, 1992; Giannotti & Mansur, 1993). However, Gould & Jeanne (1984) and Michelutti et al. (2013) suggested that the urban environment negatively affects the productivity and development of the colonies, since it offers fewer resources than do preserved environments.

Polistes versicolor (Olivier, 1791) builds nests formed by a single, uncovered comb attached to the substratum by a single petiole (Richards, 1978). This species is facultatively synanthropic, since it is associated with human constructions (Oliveira et al., 2010) and also occurs in natural environments. Studies of predation (Butignol, 1992; Prezoto et al., 2006) and productivity (Ramos & Diniz, 1993; Oliveira et al., 2010) have been performed with this species, but none has evaluated the alteration of habitat by human activity on this aspect. Therefore, this study evaluated the effect of the habitat alteration, particularly by human activity, on the productivity of *P. versicolor*.

Material and Methods

Data collection and field procedures

To evaluate the effects of human activity on colony development, we compared the final productivity of colonies of *P. versicolor* in two habitats in the municipality of Mundo Novo in the state of Mato Grosso do Sul, Brazil.

We collected 10 abandoned nests in each habitat during April 2012 to August 2012. All these colonies were monitored weekly to determine the end of the colony cycle. We used only nests that reached the decline stage as defined by Jeanne (1972), which showed widespread presence of empty cells in the comb and nest abandonment.

Following the parameters proposed by Michelutti et al. (2013), productivity was measured from the number of cells constructed, number of adults produced, and dry mass of the nest. We also measured the diameter of the petiole, proportion of productive cells and number of generations in each cell for estimated productivity of the central and peripheral cells.

By counting the number of layers of meconium in each cell of the comb was estimated the number of adults produced. This meconium layer is formed on the floor of the cells that produced adults, since just before pupation, when the last-instar larva eliminates feces (Gobbi & Zucchi, 1985; Giannotti, 1999). Each cell of the comb was sectioned with the aid of tweezers to extract the meconium layer and for analysis of the nest dry mass, the nest was weighed on a precision balance according Michelutti et al. (2013).

Areas of study

We compared the degree of alteration of the environment by human activity, according to the parameters suggested by Michelutti et al. (2013).

Thus, the first area (23°93’77”S; 54°33’90”66W), categorized as habitat less altered by human activity, was located 8 km from the urban perimeter, and has little human activity. This area consists of rural properties with grassland, agricultural crops and forest fragments predominating, associated with rivers and streams.

The second area (23°93’79”S; 54°29’47”W), categorized as habitat more altered by human activity, contains numerous buildings of wood or brick, most of them inhabited. There is intense movement of people, and mainly areas of pavement and grass lawn adjacent to the buildings.

Statistical analyses

The t-test for independent samples was used to evaluate possible differences between the colony productivity parameters of the two populations. We applied a Pearson correlation analysis to compare the number of cells constructed with the number of adults produced, to evaluate possible differences in strategies of comb use between the two populations. We also estimated the correlation between the diameter of the petiole and the nest dry mass. For all analyses was used the Software Systat 11 and the variable was considered when the resulting regression coefficient was significant at the 0.05 level.

Results

In the habitat more altered by human activity, 60% of the nests occurred on human constructions and 40% on trees. In the habitat less altered by human activity, 100% of the nests were in trees, even if buildings were nearby.

For the 10 nests in the habitat less altered by human activity, the mean values (±SE, n=10) were: 411.30 ± 123.27

cells constructed, 493.90 ± 213.03 adults produced, nest dry mass of 9.50 ± 4.28 g, 90.20 ± 10.87% of cells were productive, 24.76 ± 14.90% of cells were reused, and 1.16 ± 0.26 adults produced per cell (Table 1). In this environment we found a significant positive correlation between the number of adults produced and the number of cells constructed (r = 0.86, p <0.01, n = 10) (Fig. 1). The correlation between the diameter of the petiole and the nest dry mass was also significantly positive (r = 0.75, P = 0.01, n = 10) (Fig. 2).

For the 10 nests in the habitat more altered by human activity, the mean values (±SE, n=10) were: 203.00 ± 44.79 cells constructed, 200.90 ± 65.69 adults produced, nest dry mass of 3.17 ± 0.99 g, 69.23 ± 17.18% of cells productive, 23.19 ± 15.95% of cells reused and 1.02 ± 0.34 adults produced per cell (Table 1). In this environment there was no significant correlation between the number of adults produced and the number of cells constructed (r = 0.30, p = 0.40, n = 10) (Fig. 1), or between the diameter of the petiole and the nest dry mass (r = 0.33, p = 0.36, n = 10) (Fig. 2).

The results of t-tests showed that the productivity in the habitat less altered was significantly higher than in the habitat more altered, with respect to the number of cells constructed (t = -5.02, df = 11.3, p <0.001), number of adults produced (t = -4.15; df = 10.7, p = 0.002), dry mass of nests (t = -5.98, df = 11.4, p <0.001) and proportion of productive cells (t = -3.29, df = 15.5, p = 0.005) (Table 1). However, the proportion of reused cells (t = -1.11, df = 17.6, p = 0.28) and the number of adults produced per cell (t = -0.62, df = 18, p = 0.53) did not differ significantly between the two habitats (Table 1).

Regarding the cell productivity in the habitat less altered, we observed that were older cells and therefore closest to the petiole produced more adults, up to 3 generations of adults (Fig. 3A), and the cells that were farther from the petiole, generally the younger cells, produced fewer individuals. In the habitat more altered a similar pattern was observed with cells producing up to 4 generations (Fig. 3B).

Discussion

In the habitat less altered, the colonies nested only on plants; whereas in the habitat more altered, most nests were sited on human constructions. This is probably related to the availability of the types of substrate in each environment, although sometimes in the habitat less altered, a few buildings were located near the nests.

Sinzato et al. (2011) found significant differences in the nesting sites of *P. versicolor*, in which 99% of the nests were located on human constructions and only 1% on vegetation. These authors found that the nests were located high on the buildings, which afforded greater protection from human interference, weather, and direct sunlight. Thus, there was a high degree of synanthropy. Butignol (1992) and Sinzato & Prezoto (2000) found similar results, demonstrating that the choice of the nesting site is based on the influence of physical climate factors such as temperature and luminosity (Butignol, 1992).

The number of cells constructed and the number of adults produced were larger in the habitat less altered (Table 1). Oliveira et al. (2010) found a positive correlation between the number of cells constructed and the total number of adults produced in colonies of *P. versicolor*; however, all these colonies were evaluated in an urban environment. These authors reported that the colonies produced on average 244 ± 89.5 cells and 171.67 ± 109.94 adults, values close to those found in this study for the habitat more altered.

The colony productivity was determined by the size of the nest in both habitats; larger nests are generally more productive. The results of t-tests (Table 1) showed that most of these parameters differed significantly between the two habitats, and nests in the habitat less altered were more productive. In the study of Michelutti et al. (2013) with *M. consimilis*, the results were similar, and nests in the habitat with less human interference are more productive; however, the proportion of productive cells showed no significant differences, as

Table 1. Comparison of the colony productivity of the social wasp *Polistes versicolor* nesting in two environments. 10 nests were used for each habitat.

Parameters	Habitat less altered by human activity		Habitat more altered by human activity				
	Mean	SE	Mean	SE	T	df	*P*
Cells constructed	411.30	123.27	203.00	44.79	- 5.02	11.3	<0.001
Adults produced	493.90	213.03	200.00	65.69	- 4.15	10.7	0.002
Nests dry mass (g)	9.50	4.28	3.17	0.99	- 5.98	11.4	<0.001
Productive cells (%)	90.20	10.87	69.23	17.18	- 3.29	15.5	0.005
Reused cells (%)	24.76	14.90	23.19	15.95	- 1.11	17.6	0.28
Adults produced/cell	1.16	0.26	1.02	0.34	- 0.62	18	0.53

observed in this study. Therefore, as previously suggested by Michelutti et al. (2013), colony productivity of the social wasps can be affected by the habitat quality, and negatively impacted by human activity.

The habitat more altered has a large concentration of buildings and predominantly grassy vegetation, which suggests a low availability of resources for the colonies. Anjos et al. (1986) and Zanuncio et al. (1991) emphasized that habitat quality contributes to lower productivity in degraded environments, which may have limited resources available during unfavorable periods, especially those used in feeding immatures, such as the larvae of other insects. Mead & Pratte (2002) demonstrated that populations of *P. dominula* in situations that differed in prey availability also differed in colony growth and in the rate of production of offspring.

However, Judd (1998) and McGlynn (2012) suggested that nesting on human buildings is advantageous to reduce interspecific competition and to protect against predation, especially by vertebrates, since these factors are less intense than in preserved natural environments. Moreover, human structures can provide greater protection against variations of climatic factors (Michelutti et al., 2013).

The proportion of productive cells was lower in the habitat more altered, and the maximum number of generations was higher (Figs. 1 and 2). Ramos & Diniz (1993) and Oliveira et al. (2010) analyzed the productivity of *P. versicolor* colonies and found cells producing 4 and 6 generations, respectively, values close to those observed here. However, the difference between the 3 or 4 generations produced by the two populations is probably due to different strategies for reuse of the comb, since colonies in the habitat more altered invest more in reusing cells, while in the habitat less altered the colony productivity is ensured by construction of new cells, resulting in large nests with a higher proportion of productive cells (Figs. 1 and 2).

The existence of different strategies in colonies in the two habitats is reinforced by the significant positive correlation between the number of cells constructed and the number of adults produced, and also between the diameter of the petiole and the nest dry mass (Figs. 2 and 3) in the habitat less altered, since in these colonies the population increases concomitantly with the size of the nest. Downing & Jeanne

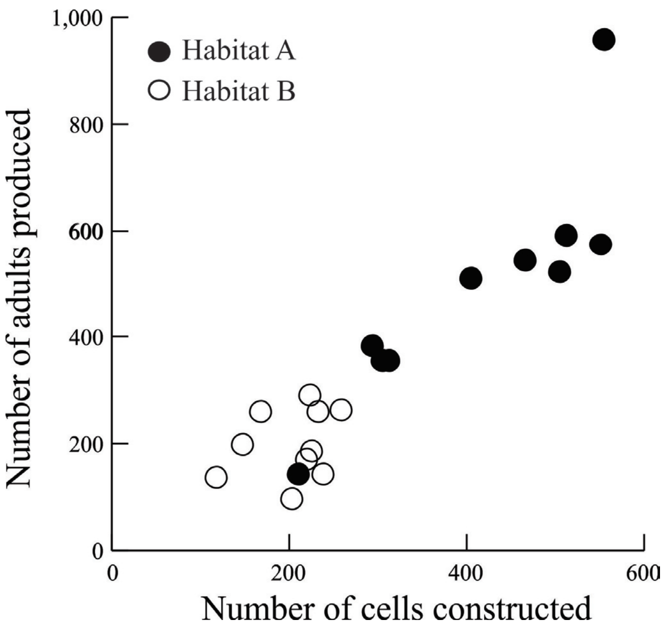

Figure 1. Linear correlation between the number of cells constructed and the number of adults produced in nests of *Polistes versicolor* in two habitats. Habitat A: less altered by human activity (r = 0.86, p <0.01, n = 10) and Habitat B: more altered by human activity (r = 0.30, p = 0.40, n = 10).

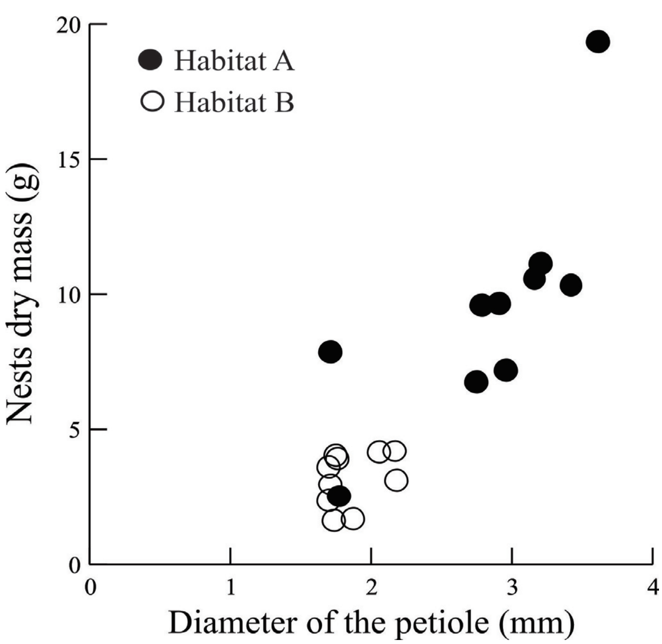

Figure 2. Linear correlation between the nest dry mass and the diameter of the petiole in nests of *Polistes versicolor* in two environments. Habitat A: less altered by human activity (r = 0.75, *P* <0.01, n = 10) and Habitat B: more altered by human activity (r = 0.33, p = 0.36, n = 10).

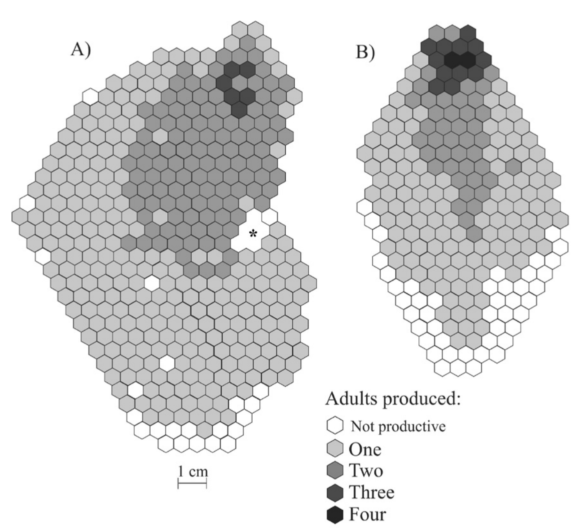

Figure 3. Productivity and number of adults produced per cell in nests of *Polistes versicolor* in two habitats. A) Habitat less altered by human activity. B) Habitat more altered by human activity. NOTE: The asterisk indicates an area of cells that were destroyed at the time of collection.

(1986) stated that in groups of independent foundation, the increase in the diameter of the petiole is associated with the construction of new cells, a relationship also observed by Montagna et al. (2010) for *M. consimilis*. According to Giannotti (1997), the petiole is reinforced with additional pulp and salivary secretions to support the weight of the nest. A nest with more cells can produce more adults.

A likely explanation for these different strategies is that in environments with more human activity, a larger nest may attract more attention and is therefore more likely to be eliminated. The insects may have adapted to this situation, preferring to reuse cells instead of increasing the size of the nest. However, Michelutti et al. (2013), comparing data for *M. consimillis* in environments with features similar to this study, did not observe differences in reuse of the comb cells, although the nests of this species in a forest environment were larger and more productive than those in an urban environment.

On the other hand, Fig. 3 shows a pattern of cell use in which the cells near the petiole are more productive, probably because these cells are older and therefore are used more often. Oliveira et al. (2010) found that cells that are central and closer to the petiole are more productive because they are older and better protected from the pressure of predators, parasites and reproductive conflicts, as also noted by Gobbi et al. (1993). Therefore, both the position and the age of the cells are important in determining the productivity of a cell.

According to Montagna et al. (2010), the central cells of the combs of *M. consimilis* are more productive than the peripheral cells, because they provide better physical conditions for the development of immature individuals; this region has a higher concentration of adults and is less exposed to attack by predators. However, in *M. consimilis* the petiole is central (Montagna et al. 2010), and therefore the more productive cells are also older.

Finally we conclude that colony productivity in *P. versicolor* is significantly higher in habitat less altered by human activity; and regardless of the habitat, the cells central and closer to the petiole are more productive. Furthermore, colonies in habitat more altered by human activity prefer to invest more in reuse of cells than to enlarge the nest structure, perhaps because a smaller nest is less conspicuous. The species probably continues to nest in this habitat because of reduced interspecific competition and greater protection against variations in climatic factors, as suggested by Michulleti et al. (2013).

Acknowledgments

The authors thank Orlando T. Silveira (Museu Paraense Emílio Goeldi) for the identification of the species, and Janet W. Reid (JWR Associates) for the revision of the English text. We are grateful to CAPES for a doctoral fellowship awarded to the second author. WFAJ acknowledges his research grants from CNPq.

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