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Bait and Habitat Preferences, and Temporal Variability of Social Wasps (Hymenoptera: Vespidae) Attracted to Vertebrate Carrion

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ABSTRACT In addition to feeding on carrion tissues and fluids, social wasps can also prey on immature and adult carrion flies, thereby reducing their populations and retarding the decomposition process of carcasses. In this study, we report on the occurrence and behavior of social wasps attracted to vertebrate carrion. The collections were made monthly from September 2006 to October 2007 in three environments (rural, urban, and forest) in six municipalities of southeast Brazil, using baited bottle traps. We collected *Agelaia pallipes* (Olivier, 1791) ($n = 143$), *Agelaia vicina* (Saussure, 1854) ($n = 106$), *Agelaia multipicta* (Haliday, 1836) ($n = 18$), and *Polybia paulista* Ihering, 1896 ($n = 3$). The wasps were observed feeding directly on the baits and preying on adult insects collected in the traps. Bait and habitat associations, temporal variability of social wasps, and possible forensic implications of their actions are discussed.

KEY WORDS *Agelaia*, Epiponini, forensic entomology, necrophagy, *Polybia*

Neotropical social wasps belong to the subfamily Polistinae, a group that encompasses >900 species in 25 genera, and are most abundant and diverse in the tropics and subtropics (Gomes and Noll 2009). The subfamily is divided into four tribes, of which three occur in Brazil, as follows: Polistini, Mischocyttarini, and Epiponini (Silva and Silveira 2009). In the last group, *Agelaia* Lepeletier, 1836; *Angiopolybia* Araujo, 1946; and some species of *Polybia* Lepeletier, 1836 are commonly recorded as consumers of vertebrate carcasses (Gomes and Noll 2009, O'Donnell 1995).

Although the literature on feeding habits of social wasps is sparse and anecdotal (Hunt 1991), it is well known that carrion may play an important role in the nourishment of these insects (Silveira et al. 2005). Nonetheless, few studies on insects associated with vertebrate carcasses in Brazil have dealt with social wasps (but see, e.g., Gomes et al. 2007a, 2007b; Moretti et al. 2008; Noll and Gomes 2009), and, with the exception of Silveira et al. (2005), almost no extensive surveys have dealt specifically with carrion wasps.

Ecologically, social wasps using vertebrate carrion function as both predators and necrophages. As predators, adults feed their larvae immatures and adults of carrion flies (mainly blow flies and flesh flies), and deplete their populations. This may retard the decomposition process (Wells and Greenberg 1994). As necrophages, social wasps not only feed their larvae the carcass tissue itself, but also may produce holes or abrasions that can attract other kinds of necrophagous insects, accelerating the decomposition process. Moreover, social wasps, as ants (Campobasso et al. 2009), can produce postmortem artifacts that can be interpreted as premortem mutilations or injuries, possibly leading to errors in forensic evaluations.

The current study aims to report the occurrence, behavior, and annual variation in abundance of social wasps attracted to three types of vertebrate carrion (fish, chicken gizzards, and beef liver) in different environments of São Paulo state, southeast Brazil.

Materials and Methods

Study Sites. The collections were carried out in rural, urban, and forest environments in the following six municipalities: Artur Nogueira, Campinas, Cosmópolis, Jundiaí, Mogi Guaçu, and Paulínia (Fig. 1). The rural sites in these municipalities are characterized by moderate agricultural activity and livestock farming, with a few scattered houses; their urban sites have little commercial activity; and the forest sites are mainly woodland remnant patches with similar phytophysiognomic features, with the exception of Campinas, where the forest area is a 250-ha mesophilic semideciduous Atlantic Forest fragment (Morellato and Leitão Filho 1995) surrounded by human dwellings.

All of these cities have the same type of weather according to the Köppen climate classification, Cwa-

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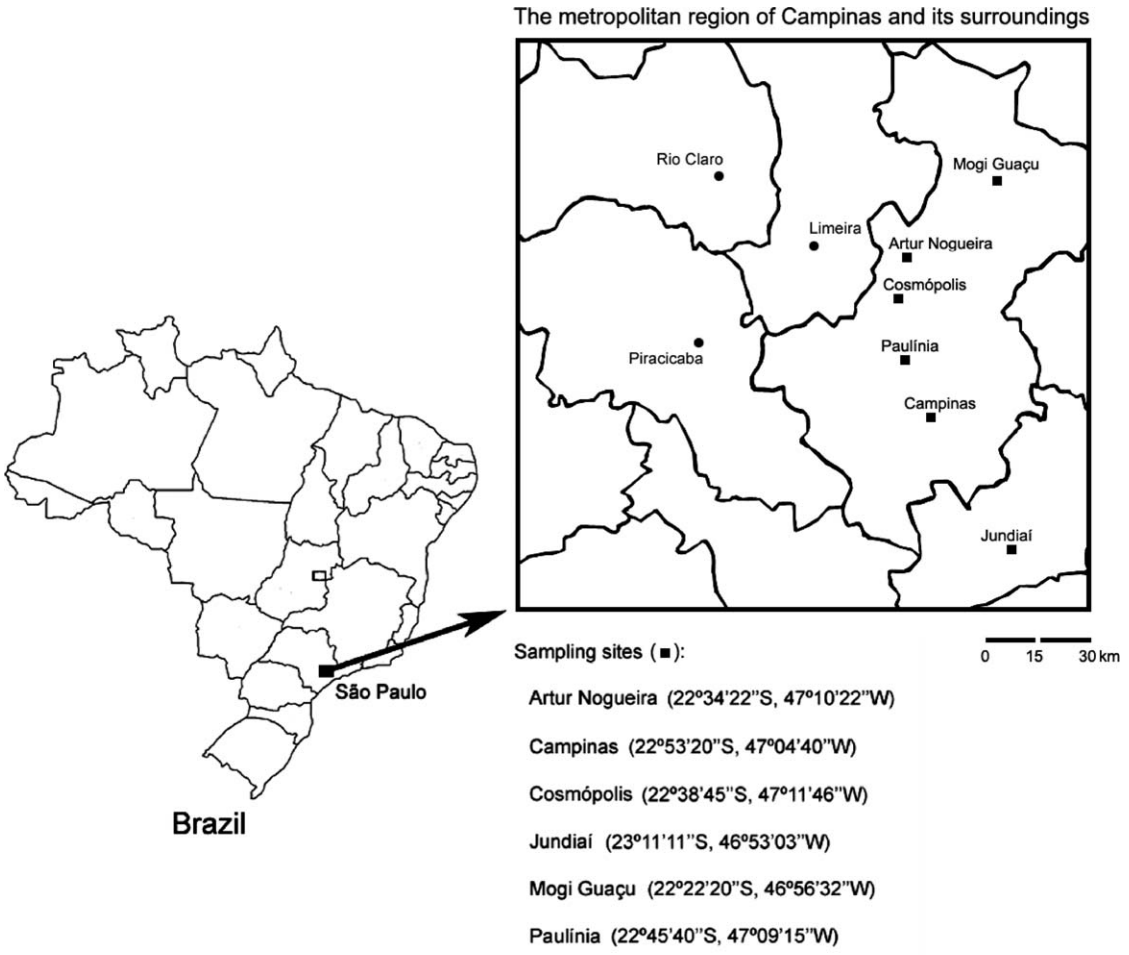

Fig. 1. Map showing the study sites.

subtropical climate, with cool, dry winters (temperatures below 18°C) and hot, humid summers (with the mean temperature in the hottest month above 22°C), as generally occurs in the state of São Paulo, mainly in the central and eastern regions, at altitudes between 500 and 700 m (Setzer 1966).

On-Site and Laboratory Procedures. The collections were made monthly from September 2006 to October 2007. Each of the environments in each municipality was monitored using six traps per month, two for each kind of bait, totaling 18 traps per municipality/mo and 1,512 sample units during the study. Baits composed of 12 g of fish (sardines), beef liver, or chicken gizzards were employed. Carrion traps, similar to those used to collect muscoid flies by several authors (Ferreira 1978, Linhares 1981a, Erzinçlioglu 1996, Hwang and Turner 2005, Silveira et al. 2005), were installed ≈15 m apart at the collection sites. Each trap (Fig. 2) was made of two 2.0-L plastic soft-drink bottles, each ≈35 cm in height and 8 cm in diameter. The bottoms of both bottles were removed to allow one to fit into another and to permit the entrance of insects through the bottom opening of the lower bottle, which was painted black. The cap of the lower bottle was also removed, so its top end was open. Each bait was placed at the top end of the lower bottle with a small metal hook and was replaced in the traps every 24 h.

As recorded by Hwang and Turner (2005), this type of bottle trap is low priced and easy to make and to transport to and from the field. Each trap was suspended with a cord from a tree branch, ≈180 cm above the ground. Each trap remained exposed at the study site for a period of 72 h, after which any wasp trapped in the top bottle was collected, taken to the laboratory, and killed by freezing at −20°C, until later identification. After identification, the specimens were stored in a freezer. Any nonwasp arthropods collected in the traps were excluded from the analyses. Meteorological data were obtained from AGRITEMPO (2011).

Voucher specimens have been deposited in the Escola Superior de Agricultura Luiz de Queiroz Entomological Museum (Department of Entomology and Acarology, Escola Superior de Agricultura Luiz de

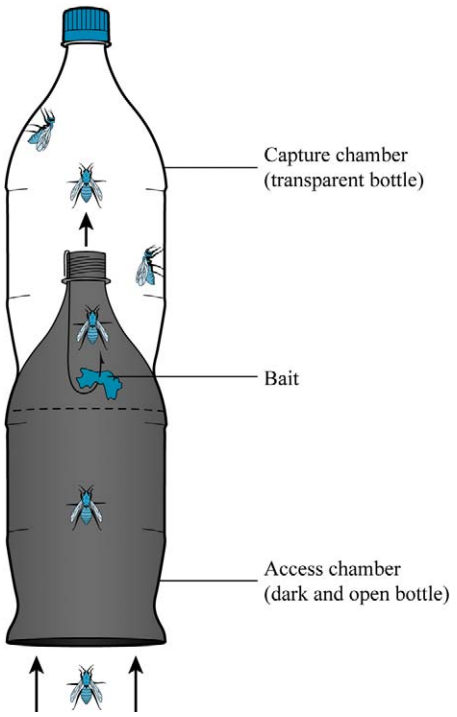

Fig. 2. Carrion trap used to collect social wasps in southeast Brazil (adapted from Moretti et al. 2009). (Online figure in color.)

Queiroz/University of São Paulo, Piracicaba, São Paulo, Brazil).

Statistical Analyses. A one-way analysis of variance (Gotelli and Ellison 2004) (independent variables: municipality, environment, and bait; dependent variable: abundance) was employed to compare the differences in abundance for the two most abundant species, *Agelaia pallipes* (Olivier, 1791) and *Agelaia vicina* (Saussure, 1854).

The χ^2 test (Beiguelman 2002) was used to verify the possible preference of *A. pallipes* and *A. vicina* for type of environment (rural, urban, and forest) and bait (fish, beef liver, or chicken gizzards).

Results

We collected 270 adult specimens of four social wasp species: three of *Agelaia* Lepeletier, including *A. pallipes* (Olivier, 1791) (52.96%), *A. vicina* (Saussure, 1854) (39.26%), and *Agelaia multipicta* (Haliday, 1836) (6.67%); and one of *Polybia* Lepeletier, *Polybia paulista* Ihering, 1896 (1.11%) (Table 1). Most wasps were attracted to fish (47.78%), followed by chicken gizzards (28.15%) and beef liver (24.07%) (Table 1). Regarding the collection environment, most specimens were collected in the forest (71.48%), followed by the rural (22.96%) and the urban environments (5.56%) (Table 1). The municipality ($F = 0.012$, $P = 0.99$), environment ($F = 0.23$, $P = 0.63$), and type of bait ($F = 5.67$, $P = 0.15$) did not affect the abundance of *A. pallipes* throughout the study. Similarly, these same factors (municipality, $F = 0.94$, $P = 0.41$; environment, $F = 0.58$, $P = 0.57$; type of bait, $F = 0.067$, $P = 0.93$) showed no correlation with the abundance of *A. vicina.*

The χ^2 test showed that the only significant difference was for the bait preference of *A. vicina*, which prefers fish ($\chi^2 = 52.8$, df = 4). For the other analyses (*A. vicina*/environment, *A. pallipes*/bait, and *A. pallipes*/environment), no significant preference was identified ($P > 0.05$).

Table 2 compares the species compositions found in the current study with assemblages found in three other studies on social wasps associated with vertebrate carrion in Brazil: Silveira et al. (2005), Gomes et al. (2007b), and Noll and Gomes (2009). *A. pallipes* was the only species common to all of these studies. Fig. 3 shows the annual variation in abundance of *A. pallipes* and *A. vicina* (the two species with the highest abundance throughout the study) in relation to rainfall (mm). The annual variation in abundance of *A. pallipes* and *A. vicina* in relation to temperature (°C) is shown in Fig. 4. For *A. vicina*, three clear abundance peaks were observed: one in November 2006, another in August 2007, and finally one in September 2007. For *A. pallipes*, there was only one pronounced peak in September 2007. The abundance peaks for both species occurred when the precipitation levels were low and the temperature rose.

The wasps were observed feeding directly on the baits and preying on adult insects collected in the traps (flies, moths, butterflies, ground crickets, coneheaded katydids, grasshoppers, common lacewings, and earwigs). When feeding on carcasses, foragers of epiponine wasps, similarly to their behavior with arthropod prey, their major protein source for the larvae, were observed cutting the carrion into a small

Table 1. Social wasps collected in southeast Brazil: bait and environment preferences

Species	Bait/Environment								
	Fish (47.78%)[a]			Beef liver (24.07%)[a]			Chicken gizzard (28.15%)[a]		
	R	U	F	R	U	F	R	U	F
Agelaia pallipes ($n = 143$)	20	–	38	12	–	33	20	–	20
Agelaia vicina ($n = 106$)	1	6	52	–	3	11	–	5	28
Agelaia multipicta ($n = 18$)	6	1	5	–	–	4	–	–	2
Polybia paulista ($n = 3$)	–	–	–	2	–	–	1	–	–

n, Total abundance of each species collected during the study. F, forest; R, rural; U, urban.
[a] Percentage of wasps attracted to each type of bait.

Table 2. Comparison of species composition among the present study and other surveys of carrion wasps in Brazil

Species	Surveys			
	Silveira et al. (2005)[a]	Gomes et al. (2007b)[b]	Noll and Gomes (2009)[c]	Present study (2011)[d]
Angiopolybia pallens (Lepeletier, 1836)	x			
Angiopolybia paraensis (Spinosa, 1851)	x			
Agelaia fulvofasciata (Degeer, 1773)	x			
Agelaia angulata (Fabricius, 1804)	x			
Agelaia pallipes (Olivier, 1791)	x	x	x	x
Agelaia cajennensis (Fabricius, 1798)	x			
Agelaia vicina (Saussure, 1854)		x	x	x
Agelaia multipicta (Haliday, 1836)				x
Polybia paulista Ihering, 1896		x		x
Polybia ignobilis (Haliday, 1836)		x		

[a] Ferreira Penna Research Station (ECFPn), "Floresta Nacional de Caxiuanã," Amazon Rainforest, municipality of Melgaço, state of Pará, Brazil (1:32′S, 51:20′W/1:50′S, 51:41′W).
[b] Open field area on the campus of the Universidade Estadual Paulista, municipality of Rio Claro, state of São Paulo, Brazil (22° 23′5″S, 47° 32′32.28″W).
[c] A fragment of semideciduous seasonal forest, municipality of Paulo de Faria, state of São Paulo, Brazil (19° 58′S, 49° 31′W/19° 55′S, 49° 30′W).
[d] See *Materials and Methods* section (study sites).

piece, molding each piece into a ball with the mandibles and forelegs, and then transporting it to the nest (O'Donnell 1995).

Some of these predated insects gained access to the trap by crawling down the hanging cord. Frequently, only fragments of these insects, which proved insufficient to allow their identification to species level, were found in the traps from which wasps were collected, demonstrating that predation by wasps had taken place.

Discussion

A. pallipes was the only species in common among previous studies conducted by Silveira et al. (2005), Gomes et al. (2007b), Noll and Gomes (2009), and the current study (Table 2). Also, *A. vicina* appeared in three of the four studies. More species in common might have been found if all the studies had used the same method to attract wasps. Silveira et al. (2005) used carrion traps baited with 50-g pieces of beef lung, whereas Noll and Gomes (2009) used 15-cm pieces of beef muscle. Gomes et al. (2007b) used pig carcasses weighing ≈10 kg and a hand net to collect the wasps. A whole carcass provides more flesh and available niches for wasps compared with small pieces of carrion; therefore, higher abundance and species diversity would likely occur in whole carcasses than in baits. Although these studies used different baits, we believe that they are comparable because, as pointed out by Bourel et al. (1999), most necrophilous insects are not specifically attracted to a particular type of carrion. The stage of decomposition is probably more important than the type of

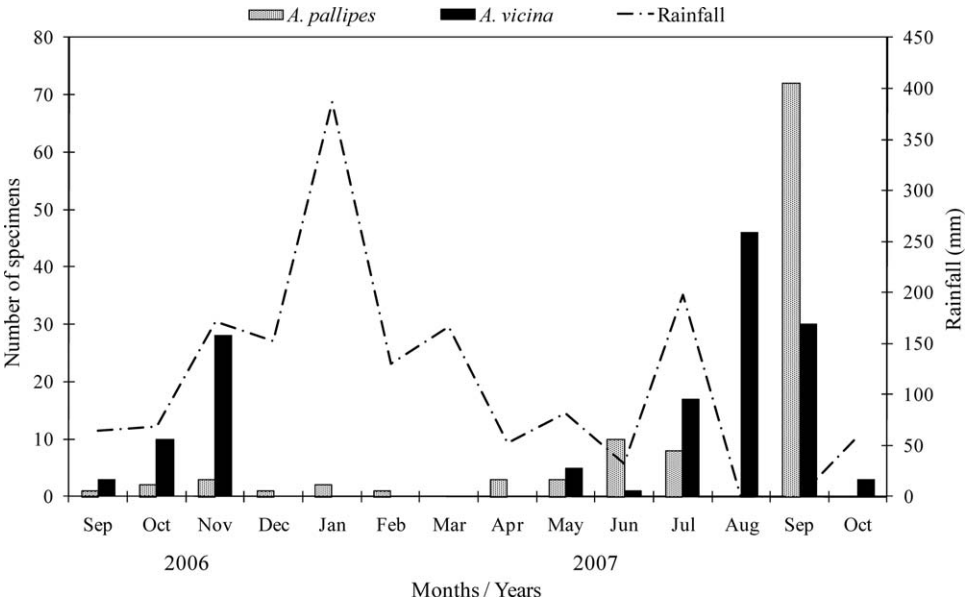

Fig. 3. Annual variation in abundance of *A. pallipes* and *A. vicina* in relation to rainfall (mm).

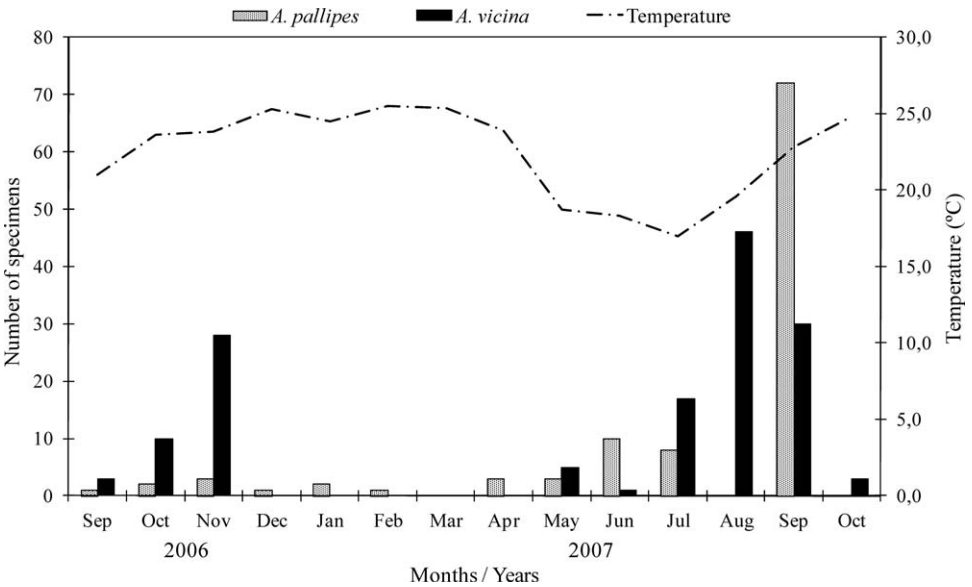

Fig. 4. Annual variation in abundance of *A. pallipes* and *A. vicina* in relation to temperature (°C).

carrion in attracting a specific group of necrophagous insects (Early and Goff 1986).

The variation in species abundance and composition we found may be related to habitat features or other site differences (see Table 2). The collection method may also explain the relatively low diversity of species of social wasps found in the current study. Silveira (2002) stated that traps would be efficient only for sampling the most abundant species of a given site, because this method is strongly dependent on the abundance, size of colonies, and season. Thus, bait trapping limits the number of species more than whole carcasses, which may affect forensic determinations.

Another reason for our observed low species diversity is the high degree of degradation in the forest environments at our study sites (Noll and Gomes 2009). A well-preserved forest would probably host many more species of *Agelaia*, for example. Other possible causes for the low species number are the availability of food resources, nesting sites, and season of the year (Santos et al. 2009).

Our study provides some evidence that the physical dimensions and perhaps placement of baits can greatly affect the outcome of monitoring. Our traps were installed 180 cm above the ground. D'Adamo and Lozada (2007) found that the higher a visual clue is placed, the easier it will be detected by wasps and bees. The height of the traps also most likely affected which wasp species were collected.

Although the *Agelaia* species occurred in all three types of environments and the statistical test showed no significant difference among areas, the wasp species seemed to be most attracted to forest sites. Silva and Silveira (2009) found similar results. This result may be related to the occurrence of larger numbers of decomposing animals and available habitat for nest construction in the forest, compared with the urban/rural sites.

Species of *Agelaia* have large colonies (Zucchi et al. 1995), which would allow them to be collected frequently throughout the year. *Agelaia* foragers regularly feed on vertebrate carrion, and are commonly more numerous locally than those of other Epiponini (Hunt et al. 2001). Occasionally, the abundance of *Agelaia* is surpassed by that of *Polybia*, which often live in smaller, but more numerous colonies (O'Donnell 1995). Because foragers of these two genera are usually abundant on carcasses, similar numbers of collected specimens should be expected. The predominance of specimens of *Agelaia* over *Polybia* in our collections is therefore most likely caused by other factors, for instance, the distance between the nests and the baits. We collected a large number of *A. vicina* in the forest sites. This species requires large spaces to build its nests, such as holes in large trees (Zucchi et al. 1995), which are found in the forest environments of all the municipalities where the collections took place. According to Santos et al. (2009), vegetation has a direct (by providing nesting sites and food resources) and indirect (by causing variations in temperature, air humidity, and shade levels) influence on the communities of social wasps in a given locality.

With respect to bait preferences, we collected more wasps attracted to the fish. This finding is not entirely new, because some *Agelaia* species are strongly attracted to fish carcasses (O'Donnell 1995). This preference is probably related to the adaptation of wasps to the easily available fish carcasses in the study area, which contains several rivers belonging to three main hydrographic basins, as follows: Piracicaba, Capivari, and Jundiaí. Because of this preference, *Agelaia fulvofasciata* is known in Brazil as "caba de peixe" (fish wasp) (Ducke 1910). However, to our knowledge, *Agelaia* does not necessarily or preferably nest in riparian areas. The utilization of antibiotics in poultry production, mainly as growth promoters (Edens

2003), may have affected the attraction of wasps to chicken gizzards, because these substances remain in their carcasses.

Although food preferences exist in social wasps, the broad range of protein and carbohydrate sources used by foragers would overcome the potential difficulties arising from the reduction in the availability of a preferred food item (Spradbery 1973). Because the baits were replaced in the traps after 24 h of exposure, relatively fresh baits were available throughout the study. The choice of a food item by social wasps depends on the stage of decomposition of a vertebrate carcass. An animal dead for a long time or already infested with fly maggots does not offer the same nutritional quality as a freshly dead carcass, and will be avoided by foragers (O'Donnell 1995). Alternatively, in poorly diversified communities of arthropod prey types, the carcass may be an important alternative for the wasps. Future studies using stable isotope analysis (Ikeda et al. 2006, Tooker and Hanks 2004) could determine whether wasps are feeding on vertebrate carrion and confirm which arthropod species present in the carcass are being consumed by them. We believe that wasps most likely have a greater effect on the decomposition process than we realize.

The peaks of abundance of social wasps tended to occur in months with low levels of precipitation in the study area (Fig. 3). During the dry and cold season, carcasses tend to remain preserved for longer periods, and may then attract more wasps. Water availability is a key factor for the survivorship rates of social wasps, because of the depletion of nectar and insects. In this scenario, the carrion in the traps becomes a viable alternative source of sugar, water, and proteins (Elpino-Campos et al. 2007). In contrast, carcasses may become waterlogged and unattractive to wasps because of excessive rainfall (Archer 2004). Figs. 3 and 4 also demonstrate a clear mutual avoidance between *A. pallipes* and *A. vicina* throughout the collection period, possibly because the two species have similar niches. Displacements of one wasp species by others are common (O'Donnell 1995). When more than one wasp species is foraging at a carcass, competition for arthropod prey is likely to occur. Species that are less efficient in capturing prey (e.g., have a long handling time) may use the carcass as a protein source. To our knowledge, there are no published records of interactions between *A. pallipes* and *A. vicina.* Studies focusing on overlapping niches may clarify the true extent of interaction between these species.

A notable aspect of these findings is that the quantity and diversity of forensically important insects (mainly blow flies and flesh flies) may be underestimated. This is a possible practical implication of the usual finding of only insect fragments in the bottle traps, because of the predation of wasps on these flies. When extrapolating this circumstance to real forensic cases, the postmortem interval may be inaccurately estimated, when its inferences are based on insect succession. Therefore, caution is recommended in this regard, because surveys of flies of forensic importance that use the methodology employed in the current study are widespread (e.g., Ferreira 1978, 1983; Linhares 1981a, 1981b). However, caution must be exercised because the confined space of the trap may have artificially increased the degree of predation compared with that on actual carcasses, because the probability of predator/prey encounters was increased (Hampton 2004).

Self-Critique. The sampling method used in the current study has potentially strong biases, as opposed to netting on a natural carcass. This issue was previously raised by Hwang and Turner (2005) for blow flies. According to these authors, the attractiveness of baited traps may be affected, among other factors, by different reactions to the trap stimulus among different species, weather aspects, height, and position of traps. However, because our experimental design used 1,512 sample units, it would have been difficult, in terms of logistics and fieldwork, to use pig carcasses (currently considered the best model to reproduce the decomposition of a human body; see Michaud and Moreau 2009) in the current study. Moreover, our sampling method has the following advantages: 1) no pigs are killed, avoiding problems with ethical norms of animal experimentation; 2) traps can be distributed in a wider range of localities/municipalities; 3) sampling errors are minimized, because it is unnecessary to compare weights of pig carcasses.

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