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A founder-controlled, social wasp assemblage, and a recent severe fall in numbers

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Abstract

The 35 species of social wasps surveyed in an 8 ha plot in the Cabeça de Veado valley near Brasilia (1979 and 1997) averaged 17.9 species per survey. From 1/3 to 1/2 of the species disappeared between consecutive surveys and only two were present in every survey. On average, 43% of the 40 species known to inhabit the valley were recorded on each survey. This high rate of turn-over demonstrates that the wasps comprised a "founder-controlled" assemblage. On two more surveys, nine species were recorded in 2010 and ten in 2015; numbers which reflect recent reports on the global trend of losses of social wasps.

Introduction

The study began as a simple survey of the species of social wasps encountered at a convenient place. When it transpired that there were large differences in the species composition between the initial surveys, the investigation was continued.

The high species richness of social wasps in the Neotropics is well-known (Richards, 1978). In the Federal District of Brasília 56 species have been recorded (Raw, 2016). Although they are predators, neotropical species often occur at relatively high densities (Raw, 1998a, 1998b; Silveira, 2002; Elpino-Campos et al., 2007; Souza et al., 2014a; Souza et al., 2014b). Neotropical social wasps have preferences for particular habitats (Raw, 1992, 1998b) and the study site was selected because it includes the three common natural vegetation forms of the region, and a garden.

The wasps possess characteristics that make them suitable subjects for surveys of this nature. They fly slowly and almost all are diurnal so they are easily seen and collected. They are social and philopatric, and an encounter with an individual is proof of the presence of a colony nearby. They occupy a nest continuously often for lengthy periods. Their generation turn-over is fast enough for sufficient individuals to be available to recolonise sites. Each colony can be regarded as a subpopulation of a metapopulation and the death of a colony as the extinction of that subpopulation but, when there are colonies of several species close by, a vacated site can be recolonised.

Social wasps initiate new colonies by two processes. The members of *Polistes* and *Mischocyttarus* are independent founders in which a lone female begins a nest and her daughters remain to enlarge the colony. The colony lasts a few months and the largest ones comprise a few dozen adult females (pers. obs). In the second group (Tribe Epiponini) a swarm of dozens to hundreds of wasps leaves the natal nest and may fly a kilometre to find a new nest site (pers. obs). A mature colony is active for a few months to several years and comprises hundreds to thousands of wasps (pers. obs).

Evidence is emerging, some of it anecdotal, of dramatic losses of social wasps in many parts of the world, including

the Neotropics; in French Guiana (Dejean et al., 2010; Dejean et al., 2011), Trinidad (C. K. Starr pers. com.), São Paulo State, Brazil (E. Giannotti pers. com.) and Paraguay (B. R. Garcete-Barrett pers. com). While these losses might be reported as good news in the popular press, the consequences will be detrimental for farming and forestry. Social wasps are important predators of innumerable insect pests (Rabb & Lawson, 1957; Nakasuji et al., 1976; Dowell & Johnson, 1986; Raw, 1988). The recent reports of losses prompted me to publish these results.

Study Area and Methods

The study area comprises 8 hectares in the Cabeça de Veado valley (15° 52' S; 47°52' W), 12 km south of the centre of Brasília. The area is described in detail in a previous study (Raw, 1998a). Three hectares of evergreen forest line a permanent stream, four are cerrado (see Eiten, 1972), one hectare is forest margin and a ½ hectare garden lies next to a house. The area was subject to very little disturbance, except maintenance of the garden, and sometimes parts of the cerrado were burnt. The study area outside the garden is part of the Brasília Botanical Garden, an area of 4,518 hectares, almost all under natural vegetation.

The area was searched visually for wasps and their nests during ten surveys. Baits and traps were not used. Eight surveys were from 1979 to 1997 and two were in 2010 and 2015. In the first two (1979 and 1981) the area was searched for 60 and 40 hours. However, all the species recorded had been encountered during 16 and 18 hours so, thereafter, the area was searched for 20 hours each survey. These were conducted between 20 Jan and 16 March which is towards the end of summer when social wasp populations are at their highest (pers. obs). It is often difficult to locate the wasps' nests in dense vegetation and in tree tops, but many wasps hunt at ground level where they are easily encountered so the presence or absence of the adults was recorded and searches were not made specifically for the nests. However, colonies attached to the house were recorded during each survey. The results of each survey were compared with the next one using Jaccard's similarity indices calculated from the total number of species per survey (after Real, 1999).

Results

Species composition

A total of 37 species of social wasps were collected during the ten surveys. Several of them were encountered elsewhere in the valley when they were not found in the study area. I found three additional species, but not in the study area during the survey period. *Polistes occipitalis* Ducke was collected in the study area in 1977, before the investigation began. *Polybia dimidiata* (Olivier) and *Mischocyttarus latior* (Fox) were collected in forest 250 m and 450 m away, but were never seen in the study area. Thus, a total of 40 species are known to have inhabited the valley.

By 2010, the numbers had dropped severely, with only ten species in 2010 and nine in 2015 (Table 1). Of the 14 recorded in these two surveys, *M. cassununga*, *M. cerberus* and *Polybia ignobilis* had been found in all or almost all the previous surveys, but two other frequent species, *P. occidentalis* and *P. sericea*, were not seen in 2015. *Agelaia pallipes* and *Polybia ruficeps* had not been recorded previously in the study area, but both were present in 2010 and *A. pallipes* also in 2015.

Nests and habitats

The wasps occupied three types of natural habitat. Two-thirds of the species (24 of 37) were restricted to one habitat in their nesting and foraging. These were 2 to forest, 16 to the forest margin and 6 to the open cerrado. None nested or hunted in all three habitats.

The wasps nested in several places. Most suspended their nests from branches and twigs (29 of 37). *Synoeca surinama* and *Parachartergus fraternus* attach their nests to tree trunks and thick boughs. *Agelaia pallipe*s, *Polybia flavifrons* and *P. ignobilis* nest in cavities. Seven species attached their nests to the undersides of leaves, but none was restricted to that surface. Active colonies of 27 species were discovered. Five (*P. ignobilis, P. liliacea, P. rejecta, E. tatua* and *S. surinama*) nested outside the study area and hunted within it.

The longevity of individual colonies encountered during this investigation was not recorded, but it varies greatly among species, from three to six months in *Polistes, Mischocyttarus* and *Polybia occidentalis* to more than ten years in *Epipona tatua* (pers. obs). Some of the species encountered on every survey had short-lived colonies that were continually replaced.

The numbers of colonies of the three species which nested on the house increased and decreased together between 1979 and 1997 (Figure 1). However, in 2010, the numbers had plummeted, though *M. cerberus* returned strongly in 2015. *Polistes satan* was present in all the surveys except that of 2015.

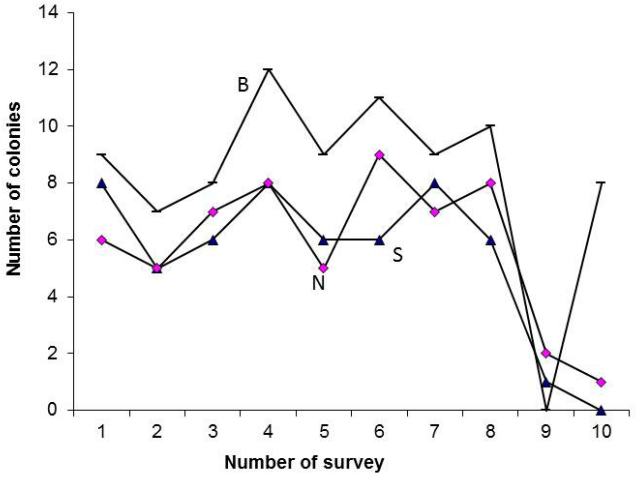

Fig 1. Numbers of colonies of Mischocyttarus cerberus (B), M. cassununga (N) and Polistes satan (S) attached to the house in the study area.

Table 1. Presence of workers (W) and colonies (C) of social wasps in eight surveys in 8 hectares near Brasilia.

Year recorded	1979	1981	1984	1987	1989	1991	1994	1997	2010	2015	Number of occurrences
Loners											
Mischocyttarus cassununga (von Ihering)	C	C	C	C	C	C	C	C	C	C	10
Mischocyttarus cerberus Ducke	C	C	C	C	C	C	C	C	C	C	10
Mischocyttarus drewseni de Saussure			W		C	C		W			4
Mischocyttarus goyanus Zikán	C	C		C							3
Mischocyttarus lecointei (Ducke)					C						1
Mischocyttarus marginatus (Fox)	C	C			C	C		W			5
Mischocyttarus mattogrossoensis Zikán			W		C	C		W			4
Mischocyttarus rotundicollis (Cameron)			W			W		W			3
Polistes billardieri F	W	W	W	W	W	W		W			7
Polistes cinerascens de Saussure	W	W	W		W		W				5
Polistes davillae Richards			W		W						2
Polistes geminatus Fox		W			W	W	W	W			5
Polistes satan Bequaert	C	C	C	C	C	C	C	C	C		9
Polistes subsericeus de Saussure	W			W	W	W					4
Swarmers											
Agelaia pallipes (Olivier)									W	W	2
Apoica pallens (F)	W	C		W		W		W		C	6
Apoica thoracica du Buysson	W										1
Brachygastra augusti (de Saussure)				C							1
Brachygastra lecheguana (Latreille)	W		C				W				3
Chartergellus communis Richards					C	C		W			3
Epipona tatua (Cuvier)	W			W							2
Parachartergus fraternus (Gribodo)		W	C	C	W		W	C			6
Polybia chrysothorax (Lichtenstein)					C	C					2
Polybia emaciata Lucas	C						C			C	3
Polybia fastidiosuscula de Saussure		W		C			C	W		C	5
Polybia flavifrons Smith			W		C						2
Polybia ignobilis (Haliday)	W		W	W		W	W	W	W	W	8
Polybia liliacea (F)					W		W	W			3
Polybia occidentalis (Olivier)	C	W	C	C	W	C	C	C	W		9
Polybia paulista von Ihering	W	C		C		C	C		W		6
Polybia rejecta (F)		W									1
Polybia ruficeps Schrottky									C		1
Polybia sericea (Olivier)	W	W	W	C	W	W	W	W	W		9
Protonectarina sylveirae (de Saussure)	C	C					W				3
Protopolybia exigua (de Saussure)	C	W			C		C	C	C	W	7
Pseudopolybia vespiceps (de Saussure)				C			W				2
Synoeca surinama (L)			W	W				W		W	4
Total species per survey	**19**	**17**	**16**	**17**	**20**	**17**	**17**	**19**	**10**	**9**	
Jaccard's similarity index		0.69	0.58	0.63	0.60	0.69	0.59	0.66	0.63	0.61	
Species present on previous survey		13	8	9	8	13	8	11	7	5	
% similarity between consecutive surveys		0,68	0,47	0,56	0,47	0,65	0,47	0,65	0,37	0,50	

Turnover

The numbers of species per survey of the first eight surveys (1979-1997) were similar (16 to 20; mean 17.9 (SD 1.4)) (Table 1) so they were analysed without the surveys of 2010 and 2015. On average, 43% of the 40 species known to inhabit the valley were recorded on each survey.

The proportion of the species recorded in a survey which had been present in the previous one varied from 37% to 65%, while the values of Jaccard's similarity indices calculated for all the species in the surveys ranged from 0.58 to 0.69 (Table 1).

Of the 30 species which were not present on all eight surveys, some missed an occasional survey, but others were absent for longer periods. *Protonectarina sylveirae* and *Polybia emaciata* were not recorded for 12 years. Similarly, *Brachygastra lecheguana* and *Synoeca surinama* were not recorded for ten years. *Agelaia pallipes* had been recorded 1½ km outside the study area in 1987 and 1989, but was not seen again in the valley until 2010. Only two species were recorded on all ten surveys (Table 1).

The 14 independent-founder species were recorded more regularly than the 23 swarming species. Indices of Jaccard's similarity were calculated for the two groups. Those for the independent founders ranged from 0.58 to 0.69 (mean 0.50), while those for the swarmers ranged from 0.19 to 0.43 (mean 0.32).

Discussion

Species composition

The total number of species recorded was substantial (71% of the total recorded for the Federal District (Raw, 2016)) so it is considered unlikely that species had been overlooked. Furthermore, independent founders with their small, scattered colonies were recorded more regularly than the swarmers.

Variable factors

No direct competition between any pair of species was detected, that is to say, the presence of one species did not coincide with the absence of another. Indeed, there are examples to the contrary. Two species of the nocturnal genus *Apoica* were present in the same survey, and absent from most. Nor was any successional tendency detected in the disappearance and appearance of species. Nest sites might be a limiting factor for the three cavity nesters, but it is doubtfully so for the other species.

A species might have disappeared and reappeared between consecutive surveys. Conversely, a species might have been present only between surveys so would not be recorded. However, these possibilities would increase the rate of turn-over which is already considered to be high. The index of similarity of species between consecutive surveys ranged from ½ to 2/3. All the values of the similarity indices of Jaccard were low (< 0.7) indicating a strong turnover.

Founder-controlled assemblage

Less than half of the species known to inhabit the valley were recorded on any survey. All the species had patchy dispersions and the locations of these patches continually change. This disappearance and reappearance of colonies is a major influence on the species composition at this site. Swarms rarely travel more than a kilometre (pers. obs.) so all these species were likely present somewhere in the Cabeça de Veado valley during the periods when the wasps were not recorded.

These findings demonstrate that it is an open system with attributes typical of a founder-controlled assemblage (after Yodzis, 1978). The species occupy gaps as they become available and apparently almost any one may occupy any gap regardless of which species had vacated it and no species is dominant. The high diversity of species is maintained in a "competitive lottery" (Sale, 1977) and the assemblage is maintained through the continuing births and deaths of colonies. Hence, the number of species per survey was relatively constant, though the species composition changed markedly.

Recent losses of species

Presumably, many of these species continue to exist in the valley, but their numbers have dropped. Ten species were recorded only in the earlier surveys, but it is not known if they had become locally extinct. All are widely dispersed in the region's forests and open cerrado. Conversely, *Chartergellus communis* and *Polybia liliacea* were present in three of the last four surveys and were not seen before that. Both have established themselves in several parts of the Federal District in the last 20 years (pers. obs).

The numbers of the three species nesting on the house increased and decreased together between 1979 and 1997 so it is thought that they did not compete and that the environmental factors regulating their numbers affected all three similarly. Absences are considered to be real disappearances as the nests are easily seen under the eaves. Conversely, it is not known why the number of colonies of *Mischocyttarus cerberus* recuperated so well.

It is difficult to suggest an explanation for these losses. The whole of the surrounding land is a protected area and not subject to the use of agricultural chemicals. All the species involved range into regions with cooler or warmer climates than Brasília so it is doubtful that the losses are related directly to a change of climate. Increased predation was not seen. It might be the availability of prey. It could not have been a dearth of nest sites.

Practical implications

The results of this study have two practical implications. First, when conducting surveys to investigate the real losses of species it is important to distinguish between temporary and prolonged absences and that requires long-term studies (though maybe not for twenty or thirty years).

Secondly, the planning and management of areas for conservation should take into account that the survival of an assemblage depends on the protection of neighbouring habitats harbouring sub-populations. A founder-controlled assemblage can exist only when the reservoir of species in the surrounding area is high enough to facilitate recolonization (Sale & Douglas, 1984; Lima et al., 1996). Even with insects, these patchy dispersions can be large. The Cabeça de Veado valley is a triangle 6 km long and 5 km wide. It is likely that all the 40 species are involved in the lottery of a founder-controlled assemblage throughout the valley.

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