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When attempts at robbing prey turn fatal

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Abstract Because group-hunting arboreal ants spread-eagle insect prey for a long time before retrieving them, these prey can be coveted by predatory flying insects. Yet, attempting to rob these prey is risky if the ant species is also an effective predator. Here, we show that trying to rob prey from *Azteca andreae* workers is a fatal error as 268 out of 276 potential cleptobionts (97.1 %) were captured in turn. The ant workers hunt in a group and use the "Velcro®" principle to cling firmly to the leaves of their host tree, permitting them to capture very large prey. Exceptions were one social wasp, plus some *Trigona* spp. workers and flies that landed directly on the prey and were able to take off immediately when attacked. We conclude that in this situation, previously captured prey attract potential cleptobionts that are captured in turn in most of the cases.

Keywords Ant predation · *Azteca andreae* · Cleptobiosis · Myrmecophyte · Social wasps · Stingless bees · Reduviidae · Flies and dung beetles

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Introduction

Cleptobiosis, well documented throughout the animal kingdom, was recently redefined as the robbing of food, nesting materials, or other items of value from members of either the same or a different species (Breed et al. 2012). Indeed, as foraging is time consuming and its success uncertain, robbing a resource from another species can be an alternative if an opportunity arises and can even in certain cases result in a kind of specialization. In social insects, robbing food or nesting material is relatively frequent (Hölldobler 1986; Sakagami et al. 1993; Corbara and Dejean 2002; Grasso et al. 2004; Richard et al. 2004; Breed et al. 2012; Dejean et al. 2012).

Prey robbing permits predatory species to save the time and energy necessary to search for and subdue prey and also to avoid the risk of being injured when the prey defends itself. Because many arboreal ant species hunt in a group and spread-eagle the captured insects for a long time before retrieving them, these insect prey can be coveted by predatory flying insects (see LaPierre et al. 2007). Yet, this is risky if the ant species is also a very efficacious predator, as

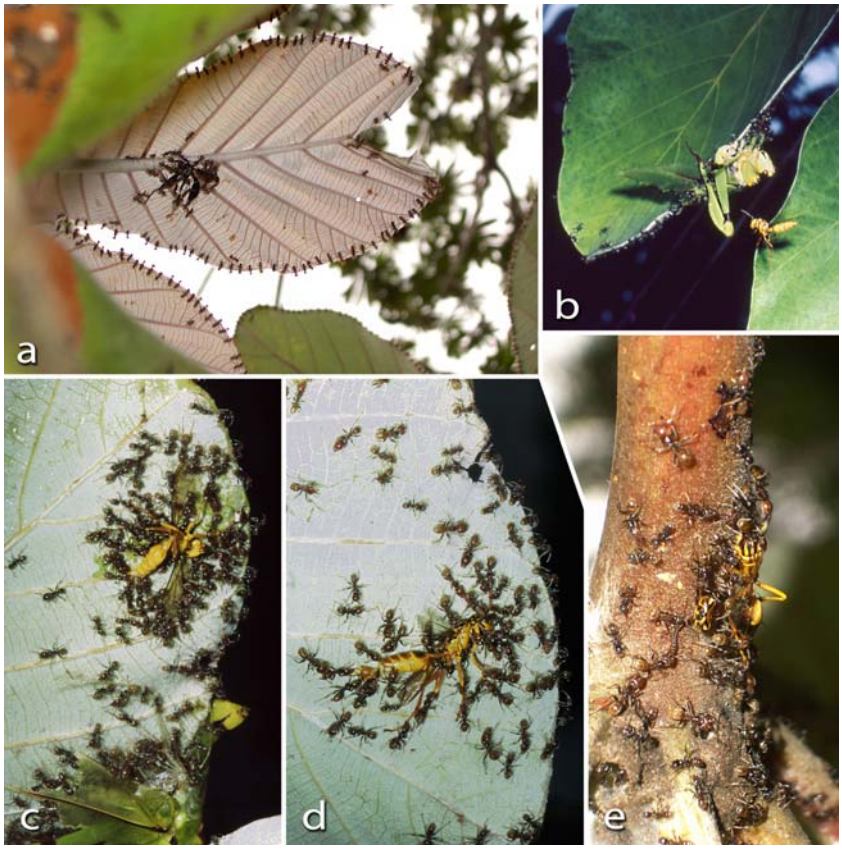

Fig. 1 Different social wasps trying to rob pieces of prey from hunting *A. andreae* workers. **a** A *Synoeca surinama* was captured on a young leaf. **b** An *Agelaia cajennensis* wasp approaching a grasshopper recently captured by *A. andreae* ants. **c** and **d** *A. cajennensis* wasps spread-eagled by *A. andreae* ants after they tried to rob pieces of prey. **e** *A. andreae* ants retrieving an *Agelaia pallipes*

was recently shown for several insect taxa trying to rob pieces of prey captured by workers of the plant ant species *Allomerus decemarticulatus* which build gallery-shaped traps on the stems of their associated myrmecophyte, *Hirtella physophora* (Dejean et al. 2012). Among the cleptobionts, social wasps and stingless bees of the genus *Trigona* were the most frequent.

In French Guiana, the myrmecophyte *Cecropia obtusa* is often associated with *Azteca andreae* whose colony foundation occurs at the expense of previously installed, mutualistic *Azteca ovaticeps* colonies that shelter in the hollow *C. obtusa* branches and feed mostly on the food bodies provided by this plant, although they also attend Hemiptera and can be predatory (Dejean et al. 2009, 2010b). *A. andreae* workers build their own carton nest and do not feed on the food bodies supplied by the host tree, but have instead developed a hunting strategy based on a very elaborate social predatory organization. They line up side by side beneath the leaf margins of the host tree and wait for prey to alight. These workers use the "Velcro®" principle to cling firmly to the host tree leaves and so can capture very large prey, i.e., up to 18.61 g or 13,350 times the mean weight of a single worker. Here, too, prey are spread-eagled for a long time before being retrieved whole or in pieces (Dejean et al. 2010a, b).

We hypothesized that an initial prey capture by the ants may attract a cleptobiont that risks being preyed upon in turn if it tries to rob the prey or pieces of the prey. We therefore investigated what flying insects attempt to rob entire prey or parts of prey from *A. andreae* workers and if these potential cleptobionts are successful or preyed upon in turn.

Material and methods

This study was conducted between June 2006 and December 2011 along the road leading to the Petit Saut dam, Sinnamary, French Guiana (5° 03′ 30.0″N; 52° 58′ 34.6″ W). We worked on 11 trees sheltering an *A. andreae* colony when the workers were hunting along the leaf margins (see Dejean et al. 2010a, b) and potential cleptobionts were active: in the morning between 7:30 and 9:30 and at the end of the afternoon between 17:30 and dusk. For each experiment, we furnished the hunting *A. andreae* ants with five 5- to 8-cm-long grasshoppers captured at a light trap (this size range, chosen after a preliminary study, permits the observation of enough cases of attempts at cleptobiosis to conduct comparisons); the latter were immediately seized and spread-eagled by the hunting *A. andreae* workers situated in the surroundings. Immediately afterwards, additional workers were recruited that took up the classical ambush position under the leaf margins, while still others stayed in the proximity of the spread-eagled prey. We then waited for

the arrival of cleptobionts and noted their behavior as well as that of the ants during ca. 200 h of observation (130 periods each 1.5 h long) and 650 grasshoppers tested.

Voucher specimens of the wasps were deposited in the American Museum of Natural History, New York.

Results and discussion

We noted a total of 276 attempts at cleptobiosis (42.46 % of the 650 grasshoppers furnished to the ants) by different insect taxa during 91 of the 130 periods of observation (70 %). The prey furnished to the hunting *A. andreae* workers mostly attracted social wasps (66.67 % of the 276 insects attracted; Fig. 1), which are very frequent along forest edges in the area (Corbara et al. 2009). Stingless bees (*Trigona* spp.) were in the second position (13.04 %), just before flies (12.68 %); dung beetles (4.35 %) and reduviids (3.26 %) were also noted (Table 1).

The rate of escape for potential cleptobionts was extremely low, whatever their size, when they tried to rob pieces of prey from hunting *A. andreae* workers. This is particularly true if we compare the present results with those obtained for *Allomerus* ants even though the latter build a trap to capture prey (Table 1). Exceptions concerned two *Trigona* individuals that avoided being seized by these ants as they landed directly on the prey; each of them was able to gather a piece of the prey's abdomen and then return to its nest. After less than 5 min, three and four recruited *Trigona*, respectively, arrived in turn, but all of them were seized and captured by the *A. andreae* workers. Only one social wasp individual (*Agelaia pallipes*) flew off safely just after landing on the prey even though one ant had seized the extremity of one of its hind legs, whereas all of the five flies that escaped lost one or several legs (Table 1).

By means of comparison, in a previous study on the cleptobiotic behavior directed towards the much smaller *Allomerus* ants (Dejean et al. 2012), we noted, first, a relatively high rate of escape that, in social wasps, is related to the worker's size. Second, *Trigona*, although of the same size as the smallest wasps, were comparatively good at escaping; nonetheless, 17.8 % of them were captured (Dejean et al. 2012; Table 1). Third, dung beetles, which were not recorded as trying to rob prey from *Allomerus* ants, can be attracted to flesh (see Ururahy-Rodrigues et al. 2008); only one species is predatory and is specialized in the capture of millipedes (Larsen et al. 2009).

Insects trying to rob prey or pieces of prey from hunting *A. andreae* workers hardly qualify as "cleptobionts" as they became prey in turn in the vast majority of the cases. The

Table 1 Insects noted attempting to rob pieces of prey (5-to-8-cm-long grasshoppers) captured by *A. andreae* workers

	Azteca andreae			*Allomerus decemarticulatus*[a]		
Potential cleptobionts	Mean±SD weight (mg)	No. of insects involved/ captured	% captured	No. of insects involved/ captured	% captured	Statist. compar.
Stingless bees (Apinae; Meliponini)						
Trigona spp.	16.1±0.3	36/34	94.4 %	264/47	17.8 %	$P<0.05$[c]
Social wasps (Polistinae)						
Angiopolybia pallens	15.8±0.5	51/51	100.0 %	157/59	37.6 %	$P<0.001$
Agelaia cajennensis	29.7±0.5	33/33	100.0 %	37/11	29.7 %	$P<0.001$
Agelaia pallipes	33.0±0.5	74/73	98.6 %	85/20	23.5 %	$P<0.001$
Agelaia fulvofasciata	50.1±0.1	–	–	10/0	00.0 %	–
Synoeca surinama[d]	93.5±0.8	26/26	100.0 %	–	–	$P<0.001$
Diptera						
Species1[b]	106.8±0.8	11/9	81.8 %	–	–	–
Species 2[b]	36.0±0.7	24/21	87.5 %	13/4	30.8 %	NS
Dung beetles (Scarabeinae)						
Deltochilus sp.	155.5±0.7	7/7	100.0 %	–	–	–
Coprophaenaeus sp.	353.2±1.9	5/5	100.0 %	–	–	–
Reduviidae	45.1±1.4	9/9	100.0 %	6/6	100.0 %	NS
Total		276/268	97.1 %	562/147	26.1 %	–

[a] See Dejean et al. (2012)

[b] All of the flies (Diptera) able to escape lost one or several legs

[c] One-sided Fisher's exact test (GraphPad Prism 4.03, Inc. software) was used for statistical comparison

[d] Comparison between *Agelaia fulvofasciata* and *S. surinama* using Fisher's exact test

hemolymph the prey loses when it is spread-eagled likely attracts flying predators, and as the prey begins to decay, dung beetles and flies. Consequently, the more prey hunting *A. andreae* ants catch, particularly large items (i.e., an 8-cm-long grasshopper) that they spread-eagle for up to 1 h, the more they attract new insects that they catch in turn, whereas they only very rarely lose pieces of prey. This self-sustaining process (i.e., not part of a strategy by the ants to use already-captured insects as bait to attract new items) favors the preying success of the hunting workers and likely has a slight positive impact on colony fitness.

In conclusion, when faced with a very efficacious predator like hunting *A. andreae* workers, potential cleptobionts have little or no chance to successfully rob prey or pieces of prey and are even more likely to become prey themselves.

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Ethical standards The experiments comply with the current laws of the country in which they were conducted. The authors declare that they have no conflict of interest.

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