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Temporary prey storage along swarm columns of army ants: an adaptive strategy for

successful raiding?

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Abstract

While pillaging the brood of other ant colonies, *Eciton* army ants accumulate prey in piles, or caches, along their foraging trails. Widely documented, these structures have historically been considered as byproducts of heavy traffic or aborted relocations of the ants' temporary nest, or bivouac. However, we recently observed that caches of the hook-jawed army ant, *Eciton hamatum*, appeared independently from heavy traffic or bivouac relocations. In addition, the flow of prey through caches varied based on the quantity of prey items workers transported. As this suggested a potential adaptive function, we developed agent-based simulations to compare raids of caching and non-caching virtual army ants. We found that caches increased the amount of prey that relatively low numbers of raiders were able to retrieve. However, this advantage became less conspicuous - and generally disappeared - as the number of raiders increased. Based on these results, we hypothesize that caches maximize the amount of prey that limited amounts of raiders can retrieve, especially as prey colonies coordinately evacuate their brood. In principle, caches also allow workers to safely collect multiple prey items and efficiently transport them to the bivouac. Further field observations are needed to test this and other hypotheses emerging from our study.

Background

In army ants, foraging occurs through the formation of huge columns of workers roaming

forest floors and raiding other social insect colonies [1,2]. During raids, colonies of the hook-

jawed army ant, *Eciton hamatum*, accumulate brood prey in caches along their columns (Figure

1A). Pioneer army ant scientists attributed this behavior to traffic management inefficiencies.

Schneirla, for example, noticed that numerous workers swarming from the bivouac towards the

foraging fronts prevented prey-carrying foragers from returning, 'virtually forcing' them 'to

deposit their burdens in piles that form near the places of greatest confusion' [3]. Rettenmeyer

later suggested that caches emerge as prey-carrying workers gather in 'areas of greater booty

odor', eventually leading to the formation of new bivouacs if caches become especially large [4].

His observations implied that caches are by-products of bivouac regular relocation.

Observing the foraging activity of *E. hamatum*, we noticed that caches appeared regularly

even at low traffic intensities and at times of the day in which colonies do not usually relocate,

raising doubts about the hypothesis that caches exclusively emerge as byproducts. This idea was

corroborated by other experimental work on *Atta* leaf-cutting ants, which also transport huge

food quantities along long trails, showing that leaf fragment caches emerge at nest entrances

when food inflow exceeds processing rates, and reduce the costs of vertical transport [5,6]. As

Atta workers maximize food collection via unloading at caches and rapidly resuming foraging,

we hypothesized that *E. hamatum* caches may similarly serve to maximize prey retrieval.

Therefore, after measuring ant traffic and prey transport through caches in natural conditions, we

explored this hypothesis using agent-based simulations, aiming to determine whether and how

caches provide a selective advantage.

Results and discussion

Prior to field observations, we defined caches as structures including stacked prey brood, stationary *E. hamatum* workers (Figure 1A, B, C, video S1) and approaching/leaving individuals. Then, following foraging columns, we found ten caches, six of which included 116±130.56 prey items (total=697; min=18; max=296; all ants, mainly *Pheidole* and *Linepithema*; Figure S1, Tables S1, S2; Supplementary Material text). We found no bivouacs in the surrounding 10m radius. As we conducted observations between 8:00 am and 4:30 pm, we concluded that the observed caches did not originate from traffic bottlenecks or aborted bivouacs, which instead emerge immediately before sunset [3].

Analyzing videos of ant traffic through caches (Figure 1D), we counted 189.8±117.4 workers going from the bivouac to the foraging fronts and 226.1±116.3 workers in the opposite direction, transporting 75±71.9 prey items. We found no significant differences between the numbers of workers in the video frame portion including the stretch between the foraging front and the cache (FC), and that between the cache and the bivouac (CB), for individuals traveling from the foraging front to the bivouac (t=16, p=0.24), in the opposite direction (t=27, p=0.95) and in both directions pooled (U= 33.50, p=0.21). At caches, we recorded more prey loads passing through FC than CB (t= 6.0; p = 0.05, Figure 1E) and more workers carrying single-item prey loads in FC than CB (57.2±63.2 vs. 35.6±54.5; t=8.0; n=10, p=0.04, Figure 1F). The numbers of workers carrying multiple-item prey loads did not differ significantly (FC: 8.9±8.8; BC: 7.6±10.9; t=13.5; p=0.52, Figure 1G). This indicated that, at caches, ants accumulated single-prey loads, whereas multiple-prey loads, although arriving at caches in significantly lower numbers (8.9±8.8 compared to 57.2±63.2 single-prey loads, U = 75.5, p < 0.05), flowed relatively regularly. We found no differences between the numbers of unloaded workers in FC and BC (151.4±161.9 vs.

116.5±120.8; t=11; p=0.09, Figure 1H). If caches only emerged as by-products, we would not

expect prey accumulation/transport to depend on load size. We therefore suspected that, similar

to the caches of leaf cutting ants [5,6], *E. hamatum*'s caches may serve to optimize colony-level

foraging investments. We hypothesized that caches may emerge as raiders returning from

foraging fronts drop single-prey loads in safe locations, and rapidly return to foraging fronts.

From a colony-level perspective, short sequential trips between caches and foraging fronts would

maximize prey yields at limited numbers of raiders, especially because prey colonies

coordinately evacuate their brood [7,8]. In addition, in the chaos of raids, rapidly retrieving

single prey items may be safer and more convenient than sequentially collecting multiple prey

items. On the other hand, workers at caches could invest time in loading multiple items in a

significantly safer microenvironment, minimizing the distance walked per retrieved food mass on

their way to the bivouac.

To explore such hypotheses, and investigate whether and in which conditions caches would

increase prey retrieval, we developed Netlogo agent-based simulations (Video S2, Table S3,

Supplementary Material text) [9]. Our virtual ants formed columns via releasing/following a trail

pheromone, encountering prey item piles simulating the brood of prey colonies. As ants began

raiding, uncollected prey items started disappearing, simulating brood evacuation. Raiders

collected prey items and cached them with a probability increasing with nestmate density,

simulating the scenario we observed in nature. Other workers recovered up to two cached prey

items and transported them to a densely populated "safe area" simulating a trail bifurcation or the

bivouac itself. When loaded raiders or cache recoverers reached the safe area, prey items

disappeared and were counted as retrieved. We compared caching colonies to non-caching

colonies in which raiders transported prey items directly to the safe area.

Overall, the quantity of retrieved prey increased with the number of raiders, but decreased as

brood evacuation speeds and probability to cache/collect cached food increased (Table 1, Model

1). Interestingly, caches allowed ants to retrieve significantly more prey at low numbers of

raiders (50, 100), but this effect became generally less conspicuous - and disappeared - as raider

numbers increased (300, 500, 700; Figure 2, Table 1, Models 2-5). Brood evacuation speed

reduced the amount of prey ants collected at foraging fronts, in turn reducing the amount of time

ants spent retrieving it. Excluding the 700-raider condition, the time ants spent retrieving prey

decreased at increasing raider numbers, whereas the probability of caching/collecting cached

prey did not produce any effect (Table 1, Model 6). Hardly any combination of settings revealed

significant effects of caches on prey retrieval time (Table S4, Figure S2), indicating that,

everything else being equal, caching ants retrieved food at the same speed of non-caching ones.

At very high raider numbers, however, the high individual density occasionally resulted in

persisting 'death circles', decelerating prey retrieval. Allowing cache recoverers to keep caching

their loads after collection rarely produced significant effects on the amount of retrieved prey

(Table S5, Figure S3), but increased prey retrieval time at very low and very high numbers of

raiders (Table S6, Figure S4). This likely occurred because raiders in 50-100-individual groups

encountered cached food items relatively rarely, whereas 500-700-raider groups kept

encountering high densities of individuals, caching food very often. This suggested that

excessive caching may slow down prey retrieval, and accordingly, our field observations

revealed a relatively stable flow of multiple-item prey loads through caches (Figure 1G).

Therefore, we hypothesize that, for cache recoverers transporting multiple prey items, it may be

advantageous to unload only at the bivouac and not in other caches.

Overall, our findings are in line with the hypothesis that *E. hamatum* caches do not only

emerge as heavy traffic byproducts or as aborted bivouacs, but also increase prey collection

efficiency. They may maximize prey retrieval at limited raider numbers - suggesting raider

availability as a factor limiting prey collection at foraging fronts - and when attacked prey

colonies coordinate to evacuate their brood. Importantly, caches may rule out the need to recruit

large numbers of workers, crucially saving the time prey colonies need to evacuate their brood.

Further potential research questions concern caching from proximal and individual

perspectives. Experience affects ant behavioral ontogeny and task partitioning [10], but we

ignore its impact in large, complex societies. For example, do *Eciton* foragers specialize in

raiding at foraging fronts or in commuting between caches and the bivouac? Similarly, short-

term experience at foraging fronts (e.g., nest/prey features, prey colony defenses) or at caches

(e.g., number/type of prey items [7,8]) may affect individual foraging decisions. Caches may

allow transfer of information about prey colonies [11,12] and traffic intensity, reducing time-

consuming, risky, unnecessary travel. We also ignore whether returning raiders stop at caches or

proceed depending on prey load size. A potential proximal cause of this would be the stimulus

originating from the extension of the mandibles, greater extension meaning heavier and more

cumbersome loads. Another possibility is experience or age-dependent polyethism relegating

younger workers to traveling between foraging fronts and prey caches, with older individuals

specializing in raiding in a classic task partitioning paradigm [13]. Whatever the mechanism, an

ultimate cause explanation is that individuals carrying multiple prey items should proceed

straight to the bivouac, saving the unloading time and the time for other workers to further

load/unload multiple prey items. The relatively stable flow of multiple-item prey loads we

observed at caches supports this hypothesis.

Prey individual/colony size and specific defense strategies also potentially affect cache

emergence. In our study, small-sized *Pheidole* and *Linepithema* ant brood dominated cached

prey composition, possibly because caching single prey items and transporting them to the

bivouac in multiple-item loads is more efficient for tiny than large-sized prey. Future long-term

sampling across habitats/seasons can reveal whether *E. hamatum* iteratively adjusts its raiding

strategies at a local scale in a prey-dependent fashion. Finally, caches may contribute to safely

storing prey when returning directly to the bivouac is risky. For example, in case of rain,

stocking prey under the leaf litter may increase chances to successfully transport it to the bivouac

at a later time.

Conclusions

Food caches related to traffic partitioning emerge across distant ant taxa (i.e *Atta,*

Camponotus and *Eciton* [2,5,6,14–18], usually in societies where thousands of individuals

transport large amounts of food through long distances [19–21]. These must carefully balance

foraging investments in terms of energy and time [22–24]. In this study, we suggest that caches

improve prey collection and transport in *E. hamatum*. While our hypotheses need to be tested

through extensive work in the field, they raise novel questions integrating the growing

knowledge of foraging and migration in army ants.

Methods

We carried out observations in a 220 ha Amazonian primary forest fragment (Terra Firme, coordinates: -1.034113, -46.766017) in the Bragança city area, state of Pará, Brazil. To locate caches, we followed foraging columns across multiple sessions (July 2019-January 2020) between 8:00 am and 4:30 pm, when *E. hamatum* forages [25]. To minimize resampling, we did not collect caches closer than 50 meters. For each cache, we inspected the surrounding 10-meter radius for prey nests or bivouacs, noting whether: it appeared at a multiple-trail junction; it was exposed or covered by leaf litter/fallen tree branches; it was at the side of, or crossed by, trails. We collected all prey from six caches, immediately placing it in 700 ml plastic containers and then storing it sorted by developmental stages (larva, pupa, adult) in 70% ethanol. We later identified prey at the subfamily/genus level using keys for neotropical adult ants [26] and larvae [27], and measured their length.

Field observations and simulations

We filmed caches for 5 minutes from ~30 cm of height (30 fps, 1920 x 1080px). The frame included individuals arriving from the foraging front and leaving towards the bivouac, as well as individuals passing at the side of caches. We assumed that *E. hamatum* only transported prey from foraging fronts to caches to the bivouac (and not the opposite), and that multiple-prey loads always included only two prey items. We analyzed videos using Boris [28] and developed simulations in Netlogo.

Statistical analyses

Using STATISTICA v.10, we compared numbers of workers walking in the same direction through CB and FC, considering these as paired data, with Wilcoxon signed-rank tests. For workers walking in both directions, and one- vs. multiple-prey arriving/departing loads, we

considered data as unpaired, using Mann Whitney U tests. We analyzed data from simulations

using General Linear Models (GLM) in the R [29] package lme4 [30] (Table S7), generating all

graphs via ggplot2 [31] and gridExtra [32].

Data accessibility

All data are provided in the Supplementary Materials.

Authors' contributions

HPDL and RLCDL conceived the study, conducted fieldwork, analyzed fieldwork data and

edited the manuscript. NC conceived and supervised the study and wrote the manuscript. ST

conceived the study, developed the simulations, analyzed the simulation data and wrote the

manuscript. RSFC conceived the study and edited the manuscript. All authors approved the final

version of the manuscript and agreed to be held accountable for the content therein.

Competing interests

Authors have no competing interests.

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Figures

Figure 1. A. *Eciton hamatum* cache. **B.** Worker carrying two prey items. **C.** Worker carrying one

prey item. **D.** Scheme of field observations. **E**. Flow of all prey-carrying workers. **F.** Workers

carrying one prey item. **G**. Workers carrying multiple prey items. **H.** Workers without prey. In

whisker plots, central lines, boxes, whiskers and dots respectively show median, quartiles,

max/min and outliers. ***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$; NS: no significance.

Figure 2. Simulation results. Amount of retrieved prey. In whisker plots (each representing 25 simulations), central lines, boxes, whiskers and dots respectively show median, quartiles, max/min and outliers. ***: p < 0.001, **: p < 0.01, *: p < 0.05; NS: no significance.

230 **Table 1. Models' outputs.**

Model 1 - Prey retrieval	Estimate	Std. error	t value	p
Intercept	3.987343	0.01107	360.197	< 0.001
brood evacuation speed 2	-0.061278	0.008446	-7.255	< 0.001
brood evacuation speed 3	-0.17475	0.008704	-20.078	< 0.001
brood evacuation speed 4	-0.402512	0.009289	-43.333	< 0.001
brood evacuation speed 5	-1.311772	0.012765	-102.764	< 0.001
Probability to cache/collect cached food: 50%	0.033392	0.008616	3.875	< 0.001
Probability to cache/collect cached food: 75%	0.040408	0.008601	4.698	< 0.001
Probability to cache/collect cached food: 100%	-0.016747	0.008724	-1.92	0.054
100 raiders	0.280664	0.010991	25.535	< 0.001
300 raiders	0.550067	0.010418	52.8	< 0.001
500 raiders	0.516625	0.010482	49.285	< 0.001
700 raiders	0.511538	0.010492	48.753	< 0.001

Model 2 - Probability to cache/collect cached food: 25%				
Contrast: caches vs. no caches	Estimate	Std. error	t value	p
brood evacuation speed 1; 50 raiders	0.711218	0.049514	14.364	< 0.001
brood evacuation speed 2; 50 raiders	0.6913	0.050795	13.61	< 0.001
brood evacuation speed 3; 50 raiders	0.658218	0.052418	12.557	< 0.001
brood evacuation speed 4; 50 raiders	0.55878	0.056673	9.86	< 0.001
brood evacuation speed 5; 50 raiders	0.055024	0.074133	0.742	0.45809
brood evacuation speed 1; 100 raiders	0.361802	0.040311	8.975	< 0.001
brood evacuation speed 2; 100 raiders	0.281021	0.041745	6.75	< 0.001
brood evacuation speed 3; 100 raiders	0.302281	0.044256	6.83	< 0.001
brood evacuation speed 4; 100 raiders	0.336472	0.049444	6.805	< 0.001
brood evacuation speed 5; 100 raiders	-0.005753	0.073211	-0.079	0.93738
brood evacuation speed 1; 300 raiders	0.079757	0.03531	2.259	< 0.05
brood evacuation speed 2; 300 raiders	0.030299	0.035037	0.865	0.38734
brood evacuation speed 3; 300 raiders	-0.017608	0.038048	-0.463	0.6436
brood evacuation speed 4; 300 raiders	-0.018053	0.042454	-0.425	0.67073
brood evacuation speed 5; 300 raiders	-0.033483	0.070191	-0.477	0.63343
brood evacuation speed 1; 500 raiders	0.009605	0.034167	0.281	0.77866
brood evacuation speed 2; 500 raiders	-0.008272	0.035841	-0.231	0.81751
brood evacuation speed 3; 500 raiders	0.007149	0.039206	0.182	0.85535
brood evacuation speed 4; 500 raiders	0.052944	0.043291	1.223	0.22158
brood evacuation speed 5; 500 raiders	-0.001837	0.071648	-0.026	0.97955
brood evacuation speed 1; 700 raiders	0.041415	0.034551	1.199	0.2309
brood evacuation speed 2; 700 raiders	0.089328	0.036468	2.45	< 0.05
brood evacuation speed 3; 700 raiders	0.151532	0.038557	3.93	< 0.001
brood evacuation speed 4; 700 raiders	-0.013553	0.042473	-0.319	0.74971
brood evacuation speed 5; 700 raiders	0.00367	0.071615	0.051	0.95914

Model 3 - Probability to cache/collect cached food: 50%				
Contrast: caches vs. no caches	Estimate	Std. error	t value	p
brood evacuation speed 1; 50 raiders	0.77319	0.051412	15.039	< 0.001
brood evacuation speed 2; 50 raiders	0.732796	0.052618	13.927	< 0.001
brood evacuation speed 3; 50 raiders	0.683021	0.054988	12.421	< 0.001
brood evacuation speed 4; 50 raiders	0.628035	0.059201	10.609	< 0.001
brood evacuation speed 5; 50 raiders	0.113474	0.078415	1.447	0.148129
brood evacuation speed 1; 100 raiders	0.412915	0.042449	9.727	< 0.001
brood evacuation speed 2; 100 raiders	0.392355	0.043975	8.922	< 0.001
brood evacuation speed 3; 100 raiders	0.394055	0.046522	8.47	< 0.001
brood evacuation speed 4; 100 raiders	0.300105	0.050705	5.919	< 0.001
brood evacuation speed 5; 100 raiders	0.04437	0.07681	0.578	0.563606
brood evacuation speed 1; 300 raiders	0.050905	0.036643	1.389	0.165026
brood evacuation speed 2; 300 raiders	0.029921	0.038033	0.787	0.431606
brood evacuation speed 3; 300 raiders	0.079926	0.039451	2.026	< 0.05
brood evacuation speed 4; 300 raiders	-0.125964	0.044119	-2.855	< 0.01
brood evacuation speed 5; 300 raiders	-0.049219	0.0749	-0.657	0.511226
brood evacuation speed 1; 500 raiders	0.117118	0.037242	3.145	< 0.01
brood evacuation speed 2; 500 raiders	0.041114	0.037763	1.089	0.276494
brood evacuation speed 3; 500 raiders	-0.007391	0.039648	-0.186	0.852149
brood evacuation speed 4; 500 raiders	0.030813	0.046231	0.667	0.505218
brood evacuation speed 5; 500 raiders	0.012647	0.075921	0.167	0.867727
brood evacuation speed 1; 700 raiders	0.072964	0.036487	2	< 0.05
brood evacuation speed 2; 700 raiders	0.09985	0.038613	2.586	< 0.01
brood evacuation speed 3; 700 raiders	0.1072	0.04049	2.648	< 0.01
brood evacuation speed 4; 700 raiders	0.035396	0.046163	0.767	0.443374
brood evacuation speed 5; 700 raiders	-0.05311	0.075169	-0.707	0.47999

Model 4 - Probability to cache/collect cached food: 75%				
Contrast: caches vs. no caches	Estimate	Std. error	t value	p
brood evacuation speed 1; 50 raiders	0.770862	0.049487	15.577	< 0.001
brood evacuation speed 2; 50 raiders	0.741026	0.050432	14.694	< 0.001
brood evacuation speed 3; 50 raiders	0.687471	0.052173	13.177	< 0.001
brood evacuation speed 4; 50 raiders	0.621586	0.055291	11.242	< 0.001
brood evacuation speed 5; 50 raiders	0.145016	0.074259	1.953	0.051071
brood evacuation speed 1; 100 raiders	0.399499	0.039875	10.019	< 0.001
brood evacuation speed 2; 100 raiders	0.442905	0.041127	10.769	< 0.001
brood evacuation speed 3; 100 raiders	0.451911	0.043948	10.283	< 0.001
brood evacuation speed 4; 100 raiders	0.479421	0.049855	9.616	< 0.001
brood evacuation speed 5; 100 raiders	0.035221	0.073073	0.482	0.629892
brood evacuation speed 1; 300 raiders	0.144982	0.035261	4.112	< 0.001
brood evacuation speed 2; 300 raiders	0.001654	0.034511	0.048	0.961777
brood evacuation speed 3; 300 raiders	0.030548	0.037371	0.817	0.413856
brood evacuation speed 4; 300 raiders	0.028298	0.043039	0.657	0.510995
brood evacuation speed 5; 300 raiders	0.003534	0.071331	0.05	0.960499
brood evacuation speed 1; 500 raiders	0.071459	0.034605	2.065	< 0.05
brood evacuation speed 2; 500 raiders	0.094334	0.035824	2.633	< 0.01
brood evacuation speed 3; 500 raiders	0.14346	0.038073	3.768	< 0.001
brood evacuation speed 4; 500 raiders	0.106547	0.043697	2.438	< 0.05
brood evacuation speed 5; 500 raiders	-0.040678	0.071377	-0.57	0.568856
brood evacuation speed 1; 700 raiders	0.070488	0.034984	2.015	< 0.05
brood evacuation speed 2; 700 raiders	0.06809	0.03605	1.889	0.059165
brood evacuation speed 3; 700 raiders	0.100394	0.038637	2.598	< 0.01
brood evacuation speed 4; 700 raiders	0.322321	0.045115	7.144	< 0.001
brood evacuation speed 5; 700 raiders	0.050945	0.069947	0.728	0.466552

Model 5 - Probability to cache/collect cached food: 100%				
Contrast: caches vs. no caches	Estimate	Std. error	t value	p
brood evacuation speed 1; 50 raiders	0.392413	0.056245	6.977	< 0.001
brood evacuation speed 2; 50 raiders	0.360376	0.058843	6.124	< 0.001
brood evacuation speed 3; 50 raiders	0.329286	0.058897	5.591	< 0.001
brood evacuation speed 4; 50 raiders	0.341534	0.062102	5.5	< 0.001
brood evacuation speed 5; 50 raiders	0.025872	0.081051	0.319	0.749625
brood evacuation speed 1; 100 raiders	0.232182	0.043803	5.301	< 0.001
brood evacuation speed 2; 100 raiders	0.303544	0.045658	6.648	< 0.001
brood evacuation speed 3; 100 raiders	0.320526	0.049065	6.533	< 0.001
brood evacuation speed 4; 100 raiders	0.360469	0.054386	6.628	< 0.001
brood evacuation speed 5; 100 raiders	-0.001899	0.079176	-0.024	0.980865
brood evacuation speed 1; 300 raiders	0.099653	0.037684	2.644	< 0.01
brood evacuation speed 2; 300 raiders	0.062745	0.038473	1.631	0.10318
brood evacuation speed 3; 300 raiders	-0.077686	0.039927	-1.946	0.051925
brood evacuation speed 4; 300 raiders	-0.025494	0.043733	-0.583	0.560037
brood evacuation speed 5; 300 raiders	0.003704	0.07818	0.047	0.962223
brood evacuation speed 1; 500 raiders	0.074805	0.037579	1.991	< 0.05
brood evacuation speed 2; 500 raiders	0.032652	0.039241	0.832	0.405518
brood evacuation speed 3; 500 raiders	0.091788	0.041756	2.198	< 0.05
brood evacuation speed 4; 500 raiders	0.119578	0.048966	2.442	< 0.05
brood evacuation speed 5; 500 raiders	0.056123	0.077321	0.726	0.468071
brood evacuation speed 1; 700 raiders	0.17942	0.038247	4.691	< 0.001
brood evacuation speed 2; 700 raiders	0.161147	0.039754	4.054	< 0.001
brood evacuation speed 3; 700 raiders	0.13893	0.041664	3.335	< 0.001
brood evacuation speed 4; 700 raiders	0.030691	0.046428	0.661	0.508709
brood evacuation speed 5; 700 raiders	0.003559	0.076634	0.046	0.962969

Model 6 - Time spent retrieving prey	Estimate	Std. error	t value	p
Intercept	4.18616	0.03136	133.483	< 0.001
brood evacuation speed 2	-0.03542	0.02786	-1.272	0.203595
brood evacuation speed 3	-0.06278	0.02805	-2.238	< 0.05
brood evacuation speed 4	-0.09426	0.02828	-3.332	< 0.001
brood evacuation speed 5	-0.34247	0.0303	-11.303	< 0.001
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700 raiders	0.42363	0.02707	15.648	< 0.001

References

1. Gottwald HW. 1995 Army ants: the biology of social predators.

2. Kronauer DJC. 2020 *Army Ants: Nature's Ultimate Social Hunters*. Harvard University Press.

3. Schneirla TC. 1934 Raiding and Other Outstanding Phenomena in the Behavior of Army Ants. *Proc. Natl. Acad. Sci. U. S. A.* **20**, 316–321.

4. Rettenmeyer C w. 1953 ARTHROPODS ASSOCIATED WITH NEOTROPICAL ARMY ANTS WITH A REVIEW OF THE BEHAVIOR OF THESE ANTS (ARTHROPODA; FORMICIDAE: DORYLINAE). Doctor of Philosophy, Swarthmore College.

5. Hart AG, Ratnieks FLW. 2001 Leaf caching in the leafcutting ant Atta colombica: organizational shift, task partitioning and making the best of a bad job. *Anim. Behav.* **62**, 227–234.

6. Hart AG, Ratnieks FL. 2000 Leaf caching in Atta leafcutting ants: discrete cache formation through positive feedback. *Anim. Behav.* **59**, 587–591.

7. Topoff H, Mirenda J, Droual R, Herrick S. 1980 Behavioural ecology of mass recruitment in the army ant Neivamyrmex nigrescens. *Anim. Behav.* **28**, 779–789.

8. Droual R. 1983 The organization of nest evacuation in Pheidole desertorum wheeler and P. hyatti emery (Hymenoptera: Formicidae). *Behav. Ecol. Sociobiol.* **12**, 203–208.

9. In press. NetLogo Home Page. See http://ccl.northwestern.edu/netlogo/ (accessed on 10 August 2021).

10. Ravary F, Lecoutey E, Kaminski G, Châline N, Jaisson P. 2007 Individual experience alone can generate lasting division of labor in ants. *Curr. Biol.* **17**, 1308–1312.

11. Dussutour A, Fourcassié V, Helbing D, Deneubourg J-L. 2004 Optimal traffic organization in ants under crowded conditions. *Nature* **428**, 70–73.

12. Dussutour A, Beshers S, Deneubourg J-L, Fourcassié V. 2007 Crowding increases foraging efficiency in the leaf-cutting ant Atta colombica. *Insectes Soc.* **54**, 158–165.

13. Ratnieks FLW, Anderson C. 1999 Task partitioning in insect societies. *Insectes Soc.* **46**, 95–108.

14. Hoenle PO, Blüthgen N, Brückner A, Kronauer DJC, Fiala B, Donoso DA, Smith MA, Ospina Jara B, von Beeren C. 2019 Species-level predation network uncovers high prey specificity in a Neotropical army ant community. *Mol. Ecol.* **28**, 2423–2440.

15. Manubay JA, Powell S. 2020 Detection of prey odours underpins dietary specialization in a Neotropical top-predator: How army ants find their ant prey. *J. Anim. Ecol.* **89**, 1165–1174.

16. Anderson C, Boomsma JJ, Bartholdi, III, J. J. 2002 Task partitioning in insect societies: bucket brigades. *Insectes Soc.* **49**, 171–180.

17. Jeanne RL. 1986 THE EVOLUTION OF THE ORGANIZATION OF WORK IN SOCIAL INSECTS. *Monitore Zoologico Italiano - Italian Journal of Zoology* **20**, 119–133.

18. Wang Q, Song W, Zhang J, Lo S. 2018 Bi-directional movement characteristics of Camponotus japonicus ants during nest relocation. *J. Exp. Biol.* **221**. (doi:10.1242/jeb.181669)

19. Couzin ID, Franks NR. 2003 Self-organized lane formation and optimized traffic flow in army ants. *Proc.*
Biol. Sci. **270**, 139–146.

20. Fowler HG, Robinson SW. 1979 Foraging by Atta sexdens (Formicidae: Attini): seasonal patterns, caste
and efficiency. *Ecol. Entomol.* **4**, 239–247.

21. Losos JB. 2011 Convergence, adaptation, and constraint. *Evolution*

22. Bartholomew GA, Lighton JRB, Feener DH. 1988 Energetics of Trail Running, Load Carriage, and
Emigration in the Column-Raiding Army Ant Eciton hamatum. *Physiological Zoology*. **61**, 57–68.
(doi:10.1086/physzool.61.1.30163737)

23. MacArthur RH, Pianka ER. 1966 On Optimal Use of a Patchy Environment. *The American Naturalist*. **100**,
603–609. (doi:10.1086/282454)

24. Pyke GH. 1984 OPTIMAL FORAGING THEORY: A CRITICAL REVIEW. *Annu. Rev. Ecol. Syst.* **15**,
523–575.

25. Powell S, Baker B. 2008 Os grandes predadores dos neotrópicos: comportamento, dieta e impacto das
formigas de correição (Ecitoninae). *Insetos sociais: da biologia à aplicação* , 18–37.

26. Baccaro FB, Feitosa RM, Fernandez F, Fernandes IO, Izzo TJ, Souza LP, Solar R. 2015 Guia para gêneros
de formigas no Brasil. *Editora Inpa, Manaus, 382p*

27. Wheeler GC, Wheeler J, Others. 1976 Ant larvae: review and synthesis.

28. Friard O, Gamba M. 2016 BORIS : a free, versatile open-source event-logging software for video/audio
coding and live observations. *Methods in Ecology and Evolution*. **7**, 1325–1330. (doi:10.1111/2041-
210x.12584)

29. R Core Team. 2020 R: A language and environment for statistical computing. R Foundation for Statistical
Computing, Vienna, Austria.

30. Bates D, Mächler M, Bolker B, Walker S. 2015 Fitting Linear Mixed-Effects Models Usinglme4. *Journal*
of Statistical Software. **67**. (doi:10.18637/jss.v067.i01)

31. Wickham H. 2016 *ggplot2: Elegant Graphics for Data Analysis*. Springer.

32. Auguie B. 2017 Miscellaneous Functions for 'Grid' Graphics [R package gridExtra version 2.3].

A

B

C

D

CB   FC

Bivouac   Cache   Prey nest

Foraging front

E Flow - All Prey Loads

Workers/minute

FC   CB

F Flow - One-Prey Loads

Workers/minute

G Flow - Multiple-Prey Loads

Prey items/minute

FC

H Flow - Without Prey

Workers/minute

CB

Model 1 - Prey retrieval	Estimate	Std. error	t value	p
Intercept	3.987343	0.01107	360.197	< 0.001
brood evacuation speed 2	-0.061278	0.008446	-7.255	< 0.001
brood evacuation speed 3	-0.17475	0.008704	-20.078	< 0.001
brood evacuation speed 4	-0.402512	0.009289	-43.333	< 0.001
brood evacuation speed 5	-1.311772	0.012765	-102.764	< 0.001
Probability to cache/collect cached food: 50%	0.033392	0.008616	3.875	< 0.001
Probability to cache/collect cached food: 75%	0.040408	0.008601	4.698	< 0.001
Probability to cache/collect cached food: 100%	-0.016747	0.008724	-1.92	0.054
100 raiders	0.280664	0.010991	25.535	< 0.001
300 raiders	0.550067	0.010418	52.8	< 0.001
500 raiders	0.516625	0.010482	49.285	< 0.001
700 raiders	0.511538	0.010492	48.753	< 0.001

Model 2 - Probability to cache/collect cached food: 25%				
Contrast: caches vs. no caches	Estimate	Std. error	t value	p
brood evacuation speed 1; 50 raiders	0.711218	0.049514	14.364	< 0.001
brood evacuation speed 2; 50 raiders	0.6913	0.050795	13.61	< 0.001
brood evacuation speed 3; 50 raiders	0.658218	0.052418	12.557	< 0.001
brood evacuation speed 4; 50 raiders	0.55878	0.056673	9.86	< 0.001
brood evacuation speed 5; 50 raiders	0.055024	0.074133	0.742	0.45809
brood evacuation speed 1; 100 raiders	0.361802	0.040311	8.975	< 0.001
brood evacuation speed 2; 100 raiders	0.281801	0.041745	6.75	< 0.001
brood evacuation speed 3; 100 raiders	0.302281	0.044256	6.83	< 0.001
brood evacuation speed 4; 100 raiders	0.336472	0.049444	6.805	< 0.001
brood evacuation speed 5; 100 raiders	-0.005753	0.073211	-0.079	0.93738
brood evacuation speed 1; 300 raiders	0.079757	0.03531	2.259	< 0.05
brood evacuation speed 2; 300 raiders	0.030299	0.035037	0.865	0.38734
brood evacuation speed 3; 300 raiders	-0.017608	0.038048	-0.463	0.6436
brood evacuation speed 4; 300 raiders	-0.018053	0.042454	-0.425	0.67073
brood evacuation speed 5; 300 raiders	-0.033483	0.070191	-0.477	0.63343
brood evacuation speed 1; 500 raiders	0.009605	0.034167	0.281	0.77866
brood evacuation speed 2; 500 raiders	-0.008272	0.035841	-0.231	0.81751
brood evacuation speed 3; 500 raiders	0.007149	0.039206	0.182	0.85535
brood evacuation speed 4; 500 raiders	0.052944	0.043291	1.223	0.22158
brood evacuation speed 5; 500 raiders	-0.001837	0.071648	-0.026	0.97955
brood evacuation speed 1; 700 raiders	0.041415	0.034551	1.199	0.2309
brood evacuation speed 2; 700 raiders	0.089328	0.036468	2.45	< 0.05
brood evacuation speed 3; 700 raiders	0.151532	0.038557	3.93	< 0.001
brood evacuation speed 4; 700 raiders	-0.013553	0.042473	-0.319	0.74971
brood evacuation speed 5; 700 raiders	0.00367	0.071615	0.051	0.95914

Model 3 - Probability to cache/collect cached food: 50%				
Contrast: caches vs. no caches	Estimate	Std. error	t value	p
brood evacuation speed 1; 50 raiders	0.77319	0.051412	15.039	< 0.001
brood evacuation speed 2; 50 raiders	0.732796	0.052618	13.927	< 0.001
brood evacuation speed 3; 50 raiders	0.683021	0.054988	12.421	< 0.001
brood evacuation speed 4; 50 raiders	0.628035	0.059201	10.609	< 0.001
brood evacuation speed 5; 50 raiders	0.113474	0.078415	1.447	0.148129
brood evacuation speed 1; 100 raiders	0.412915	0.042449	9.727	< 0.001
brood evacuation speed 2; 100 raiders	0.392355	0.043975	8.922	< 0.001
brood evacuation speed 3; 100 raiders	0.394055	0.046522	8.47	< 0.001
brood evacuation speed 4; 100 raiders	0.300105	0.050705	5.919	< 0.001
brood evacuation speed 5; 100 raiders	0.04437	0.07681	0.578	0.563606
brood evacuation speed 1; 300 raiders	0.050905	0.036643	1.389	0.165026
brood evacuation speed 2; 300 raiders	0.029921	0.038033	0.787	0.431606
brood evacuation speed 3; 300 raiders	0.079926	0.039451	2.026	< 0.05
brood evacuation speed 4; 300 raiders	-0.125964	0.044119	-2.855	< 0.01
brood evacuation speed 5; 300 raiders	-0.049219	0.0749	-0.657	0.511226
brood evacuation speed 1; 500 raiders	0.117118	0.037242	3.145	< 0.01
brood evacuation speed 2; 500 raiders	0.041114	0.037763	1.089	0.276494
brood evacuation speed 3; 500 raiders	-0.007391	0.039648	-0.186	0.852149
brood evacuation speed 4; 500 raiders	0.030813	0.046231	0.667	0.505218
brood evacuation speed 5; 500 raiders	0.012647	0.075921	0.167	0.867727
brood evacuation speed 1; 700 raiders	0.072964	0.036487	2	< 0.05
brood evacuation speed 2; 700 raiders	0.09985	0.038613	2.586	< 0.01
brood evacuation speed 3; 700 raiders	0.1072	0.04049	2.648	< 0.01
brood evacuation speed 4; 700 raiders	0.035396	0.046163	0.767	0.443374
brood evacuation speed 5; 700 raiders	-0.05311	0.075169	-0.707	0.47999

Model 4 - Probability to cache/collect cached food: 75%				
Contrast: caches vs. no caches	Estimate	Std. error	t value	p
brood evacuation speed 1; 50 raiders	0.770862	0.049487	15.577	< 0.001
brood evacuation speed 2; 50 raiders	0.741026	0.050432	14.694	< 0.001
brood evacuation speed 3; 50 raiders	0.687471	0.052173	13.177	< 0.001
brood evacuation speed 4; 50 raiders	0.621586	0.055291	11.242	< 0.001
brood evacuation speed 5; 50 raiders	0.145016	0.074259	1.953	0.051071
brood evacuation speed 1; 100 raiders	0.399499	0.039875	10.019	< 0.001
brood evacuation speed 2; 100 raiders	0.442905	0.041127	10.769	< 0.001
brood evacuation speed 3; 100 raiders	0.451911	0.043948	10.283	< 0.001
brood evacuation speed 4; 100 raiders	0.479421	0.049855	9.616	< 0.001
brood evacuation speed 5; 100 raiders	0.035221	0.073073	0.482	0.629892
brood evacuation speed 1; 300 raiders	0.144982	0.035261	4.112	< 0.001
brood evacuation speed 2; 300 raiders	0.001654	0.034511	0.048	0.961777
brood evacuation speed 3; 300 raiders	0.030548	0.037371	0.817	0.413856
brood evacuation speed 4; 300 raiders	0.028298	0.043039	0.657	0.510995
brood evacuation speed 5; 300 raiders	0.003534	0.071331	0.05	0.960499
brood evacuation speed 1; 500 raiders	0.071459	0.034605	2.065	< 0.05
brood evacuation speed 2; 500 raiders	0.094334	0.035824	2.633	< 0.01
brood evacuation speed 3; 500 raiders	0.14346	0.038073	3.768	< 0.001
brood evacuation speed 4; 500 raiders	0.106547	0.043697	2.438	< 0.05
brood evacuation speed 5; 500 raiders	-0.040678	0.071377	-0.57	0.568856
brood evacuation speed 1; 700 raiders	0.070488	0.034984	2.015	< 0.05
brood evacuation speed 2; 700 raiders	0.06809	0.03605	1.889	0.059165
brood evacuation speed 3; 700 raiders	0.100394	0.038637	2.598	< 0.01
brood evacuation speed 4; 700 raiders	0.322321	0.045115	7.144	< 0.001
brood evacuation speed 5; 700 raiders	0.050945	0.069947	0.728	0.466552

Model 5 - Probability to cache/collect cached food: 100%				
Contrast: caches vs. no caches	Estimate	Std. error	t value	p
brood evacuation speed 1; 50 raiders	0.392413	0.056245	6.977	< 0.001
brood evacuation speed 2; 50 raiders	0.360376	0.058843	6.124	< 0.001
brood evacuation speed 3; 50 raiders	0.329286	0.058897	5.591	< 0.001
brood evacuation speed 4; 50 raiders	0.341534	0.062102	5.5	< 0.001
brood evacuation speed 5; 50 raiders	0.025872	0.081051	0.319	0.749625
brood evacuation speed 1; 100 raiders	0.232182	0.043803	5.301	< 0.001
brood evacuation speed 2; 100 raiders	0.303544	0.045658	6.648	< 0.001
brood evacuation speed 3; 100 raiders	0.320526	0.049065	6.533	< 0.001
brood evacuation speed 4; 100 raiders	0.360469	0.054386	6.628	< 0.001
brood evacuation speed 5; 100 raiders	-0.001899	0.079176	-0.024	0.980865
brood evacuation speed 1; 300 raiders	0.099653	0.037684	2.644	< 0.01
brood evacuation speed 2; 300 raiders	0.062745	0.038473	1.631	0.10318
brood evacuation speed 3; 300 raiders	-0.077686	0.039927	-1.946	0.051925
brood evacuation speed 4; 300 raiders	-0.025494	0.043733	-0.583	0.560037
brood evacuation speed 5; 300 raiders	0.003704	0.07818	0.047	0.962223
brood evacuation speed 1; 500 raiders	0.074805	0.037579	1.991	< 0.05
brood evacuation speed 2; 500 raiders	0.032652	0.039241	0.832	0.405518
brood evacuation speed 3; 500 raiders	0.091788	0.041756	2.198	< 0.05
brood evacuation speed 4; 500 raiders	0.119578	0.048966	2.442	< 0.05
brood evacuation speed 5; 500 raiders	0.056123	0.077321	0.726	0.468071
brood evacuation speed 1; 700 raiders	0.17942	0.038247	4.691	< 0.001
brood evacuation speed 2; 700 raiders	0.161147	0.039754	4.054	< 0.001
brood evacuation speed 3; 700 raiders	0.13893	0.041664	3.335	< 0.001
brood evacuation speed 4; 700 raiders	0.030691	0.046428	0.661	0.508709
brood evacuation speed 5; 700 raiders	0.003559	0.076634	0.046	0.962969

Model 6 - Time spent retrieving prey	Estimate	Std. error	t value	p
Intercept	4.18616	0.03136	133.483	< 0.001
brood evacuation speed 2	-0.03542	0.02786	-1.272	0.203595
brood evacuation speed 3	-0.06278	0.02805	-2.238	< 0.05
brood evacuation speed 4	-0.09426	0.02828	-3.332	< 0.001
brood evacuation speed 5	-0.34247	0.0303	-11.303	< 0.001
Probability to cache/collect cached food: 50%	-0.02138	0.02575	-0.831	0.406268
Probability to cache/collect cached food: 75%	-0.06035	0.026	-2.321	< 0.05
Probability to cache/collect cached food: 100%	-0.02857	0.02579	-1.108	0.268129
100 raiders	-0.05383	0.03017	-1.784	0.074455
300 raiders	-0.09955	0.03053	-3.26	< 0.01
500 raiders	-0.13098	0.03079	-4.254	< 0.001
700 raiders	0.42363	0.02707	15.648	< 0.001