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

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Abstract

While pillaging brood of other social insects, *Eciton* army ants often accumulate prey in piles (or caches) along their foraging trails. Descriptions scattered throughout the past 100 years link this behavior to foraging-related migration. However, no empirical work has yet investigated its adaptive value. Here we asked whether caches facilitate prey flow from foraging fronts to temporary nests (or bivouacs) in the hook-jawed army ant, *Eciton hamatum*. We counted workers arriving at caches with prey from foraging fronts and departing caches towards the bivouac, quantifying their prey loads. While more workers carrying single-item prey loads arrived at rather than left caches towards the bivouac, ants carrying multiple-item prey loads arrived at and departed at the same rate. This probably resulted from raiders depositing prey in safe locations and rapidly returning to the foraging front, while other workers safely transported prey to the bivouac in multiple-item loads. This cache-mediated traffic partitioning probably allows maximizing the prey collection rate, and may be a counter-adaptation to the strategies prey colonies deploy to defend their brood from army ants.

Background

In some army ants, cohorts of simultaneously developing larvae require high quantities of protein intake, resulting in bursts of intense foraging activity [1]. Columns of foraging *Eciton* workers roam neotropical forests in search of prey, often mass-attacking social insect colonies to feed captured brood to their own larvae [2–4]. Insect colonies include large amounts of potential prey, but also adaptively deploy specific defenses against army ant attacks (e.g., coordinated evacuation). This limits the access to prey to relatively short time windows after the beginning of raids [5–14]. Therefore, to maximize prey collection, *Eciton* raids involve huge numbers of individuals transporting brood from pillaged colonies to their temporary nest (the bivouac) [15]. As many raiding workers travel in both directions along narrow columns, adaptations have emerged that fluidify traffic and minimize risks of bottleneck and traffic congestions. These include multiple-lane trails averting collisions between workers walking opposite directions [16] and ‘living bridges’ of ant bodies over gaps along trails [17].

Despite the presence of traffic-optimizing adaptations, naturalists have frequently observed piles of brood prey (or caches) along the raiding columns of the hook-jawed army ant, *E. hamatum*. Authors initially suggested that these emerged due to traffic management inefficiencies, as workers going towards the foraging front prevented prey-carrying returning foragers from advancing. According to Schneirla, this ‘virtually forces’ returning raiders ‘to deposit their burdens in piles that form near the places of greatest confusion’ [18]. In the 1950-60’s, Rettenmeyer linked the emergence of caches to the collective dynamics underlying the formation of bivouacs. He suggested that caches form and grow as prey-carrying workers gather in ‘areas of greater booty odor’, eventually leading to the formation of new bivouacs when these reach especially large sizes [19]. Although Rettenmeyer does not explicitly mention it, his observations imply that caches emerge as a result of workers simply depositing prey loads in presence of groups of nestmates with stacked prey. Following this argument, caches were considered as by-products of the same collective dynamics underlying the relocation of bivouacs across novel, potentially prey-rich territories.

Nevertheless, our preliminary work on *E. hamatum* revealed that prey caches appear regularly at low traffic intensities and at times of the day in which bivouacs are not necessarily relocating. This raises doubts about the hypothesis that prey caches exclusively emerge as a byproduct of bivouac relocation dynamics. In addition, experimental evidence from *Atta* leaf-cutting ants, which also transport huge quantities of food along long trails, shows that food caches emerge at nest entrances when the inflow of leaf fragments significantly exceeds its processing rate [20,21]. By freeing themselves from their loads, *Atta* workers readily return to the foraging grounds, maximizing foraging efficiency. This corroborates the idea that food caches can have an adaptive function in *E. hamatum*. We therefore hypothesized that caches allow optimizing the transport of prey from the foraging fronts to the bivouac. To test this hypothesis, we measured the traffic of workers approaching caches from the foraging front and returning to the bivouac, assessing the quantity of prey each worker transported.

Methods

Cache collection and prey characterization

We carried out the research in a 220 ha area of an Amazonian primary forest fragment (Terra Firme, coordinates: -1.034113, -46.766017) in the Bragança city area, state of Pará, Brazil. To locate *E. hamatum* caches, we searched for and followed foraging columns across multiple experimental sessions (July 2019-January 2020) between 8:00 am and 4:30 pm, when *E. hamatum* forages [22]. We identified caches as structures including stacked prey brood and stationary *E. hamatum* workers (Figure 1A), as well as workers approaching and leaving the area. To minimize the likelihood of resampling the same colony, we did not collect caches in predation events closer than 50 meters. For each cache, we first inspected the surrounding 10-meter radius for prey nests or bivouacs; then, we noted whether caches appeared at multiple-trail junctions, whether they were exposed or covered by leaf litter/fallen tree branches and if they were at the side of - or crossed by - trails. Finally, we assessed if debris or other structures slowed down the worker flow in the respective trails. Where possible, we collected all prey from easily accessible caches in a single quick move. We immediately placed collected caches in 700 ml plastic containers, storing ant prey 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 [23] and larvae [24] , and measured their length.

Worker flow

We filmed caches for 5 minutes from approximately 30 cm of height at 30 fps and 1920 x 1080px. The frame included portions of worker columns, with individuals arriving from the foraging front to the cache and leaving towards the bivouac, as well as individuals passing at the side of the cache, that were considered part of the same trail. Assuming that *E. hamatum* workers only transport prey from the foraging front to the cache to the bivouac, and not the contrary, we established a region between the foraging front and the cache (RFC), and a region between the cache and the bivouac (RCB) (Figure 1D). We counted workers passing through the cache via RFC and RCB, in both directions, noting if they carried one, multiple or no prey items (Figure 1B, C). We visually analyzed each video using the software Boris [25].

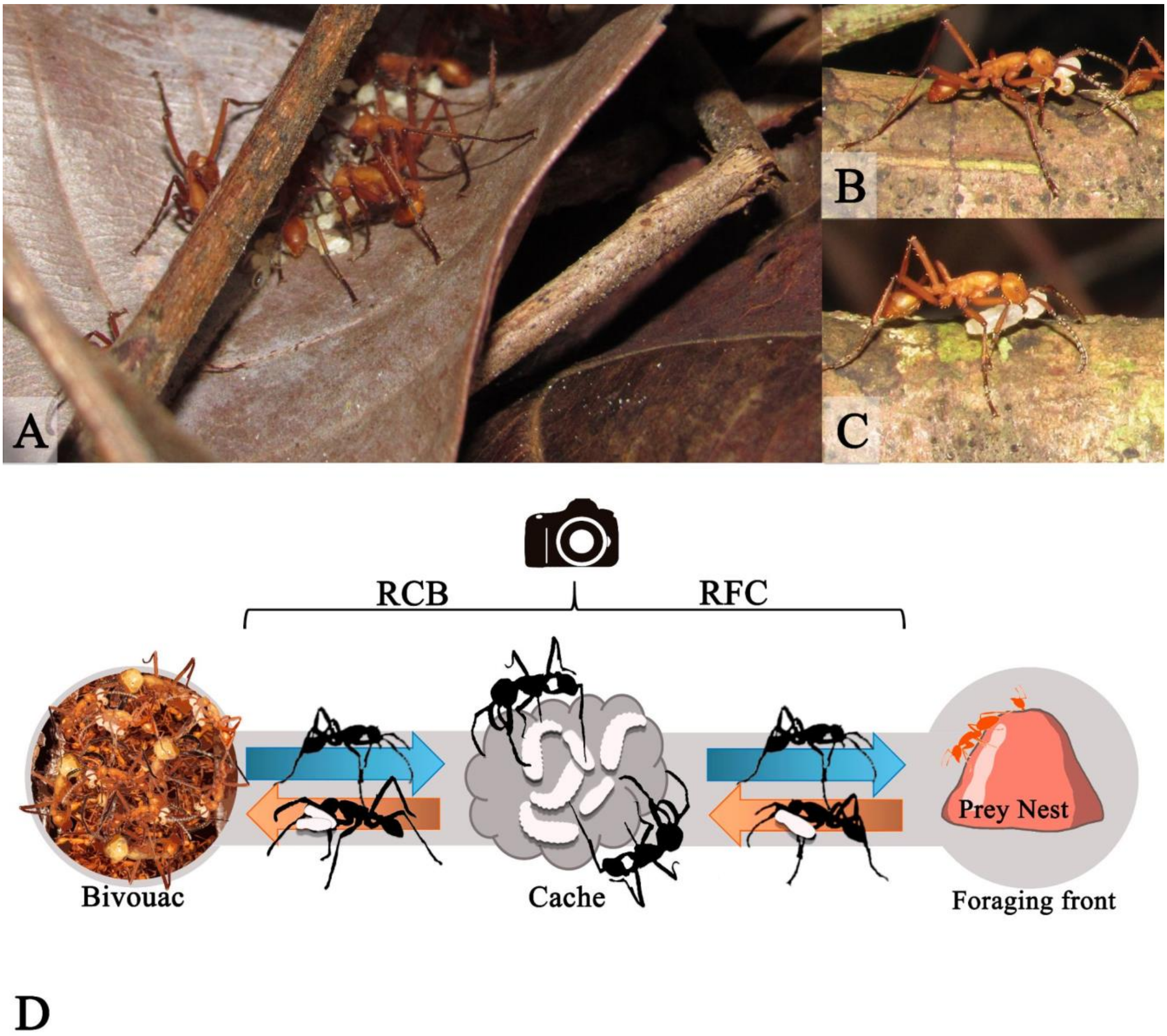

Figure 1. A. *Eciton hamatum* cache on a dry leaf (primary rainforest floor, Bragança, Pará, Brazil). **B.** Worker carrying two prey items. **C.** Worker carrying a single prey item. **D.** The flow of ants passing through caches. RFC: region between the foraging front and the cache; RCB: region between the cache and the bivouac. Foraging workers travel along two lanes with opposite directions.

Statistics

We compared numbers of workers walking in the same direction going through RCB and RFC, considering these as paired data, with Wilcoxon signed-rank tests. We conducted separate tests for workers carrying one, multiple or no prey items. For analyses of workers walking in both directions, we considered data as unpaired, and used the Mann Whitney U test. Since quantifying prey items in multiple-item loads was not always possible, we assumed multiple-prey loads to include two prey items. We performed tests using STATISTICA v.10 and generated graphs with R 4.0.4 [26].

Results

Cache characterization and prey diversity

We found ten caches, nine of which in potential bottleneck locations (three after trail junctions and six near logs, fallen branches or roots obstructing the trails). Five caches were located at the side of foraging trails, whereas the other five were crossed by foraging trails (Table 1). Four caches were partially exposed (we could see workers manipulating prey or, in a single cache, feeding on it), while six were hidden in the leaf litter or under logs. We found no prey nests or bivouacs in the 10m radius around caches. Our six collected caches included 116±130.56 prey ants (total=697; min=18; max=296). We identified 624 of these specimens (277 larvae, 334 pupae, 86 adults of which 42 males and 5 gynes) as from the ant subfamilies Myrmicinae (530), Dolichoderinae (91) and Formicinae (3). Among those, we assigned 362 specimens to the genera *Pheidole* (304), *Linepithema* (55) and *Camponotus* (3). Substantial damage to prey items (probably caused by *E. hamatum* workers) prevented us from identifying 73 specimens. Prey size ranged from 0.5 to 5.5 mm (2.34±0.74 mm), with gynes of *Camponotus* (3) and Myrmicinae (2) as the largest specimens (respectively, 5.5 and 4 mm) (Figure 2E). Interestingly, two caches included prey of multiple ant subfamilies (Formicinae and Myrmicinae; Dolichoderinae, Formicinae and Myrmicinae, respectively).

Table 1. *Eciton hamatum* cache characteristics (leaf litter in primary rainforest floor, Bragança, Pará, Brazil)

Cache ID	**Cache Date**	**Cache Time**	**Cache Position**	**Cache Area**	**Cache Situation**
Cache 1	01/07/2020	11h04 am	Side of the trail	Near a Trunk, Branch or Root	Sheltered
Cache 2	07/09/2019	10h48 am	Side of the trail	Near a Trunk, Branch or Root	Sheltered
Cache 3	07/09/2019	10h35 am	Side of the trail	Near a Trunk, Branch or Root	Sheltered
Cache 4	01/07/2020	10h56 am	Side of the trail	Near a Trunk, Branch or Root	Sheltered
Cache 5	12/17/2019	02h41 pm	Side of the trail	Two trails merge	Sheltered
Cache 6	12/17/2019	04h17 pm	Crossed by foraging trails	Two trails merge	Partially Exposed
Cache 7	12/20/2019	02h52 pm	Crossed by foraging trails	Near a Trunk, Branch or Root	Partially Exposed
Cache 8	10/22/2019	09h10 am	Crossed by foraging trails	No obstacles or trail merge visible	Partially Exposed
Cache 9	10/22/2019	09h53 am	Crossed by foraging trails	Two trails merge	Partially Exposed
Cache 10	10/31/2019	04h47 pm	Crossed by foraging trails	Near a Trunk, Branch or Root	Sheltered

Worker flow

We counted 189.8±117.4 workers going from the bivouac to the foraging front and 226.1±116.3 workers going from the foraging front to the bivouac. Workers transported 75±71.9 prey items to the bivouac. We found no significant differences in the numbers of workers in RFC and RCB, going from the foraging fronts to the bivouac (t=16, p=0.24), from the bivouac to the foraging fronts (t=27, p=0.95) and in both directions pooled (U= 33.50, p=0.21). At caches, we recorded more prey loads in RFC rather than in RCB (t= 6.0; p = 0.050, Figure 2A). However, worker flow through caches varied according to the number of carried items. More workers carrying single-item prey loads were found in RFC compared to RCB (respectively, 57.2±63.2 vs. 35.6±54.5; t=8.0; n=10, p=0.04, Figure 2B). Conversely, the numbers of workers in RFC and RBC carrying multiple-item prey loads did not differ significantly (RFC: 8.9±8.8; RBC: 7.6±10.9; t=13.5; p=0.52, Figure 2C). Similarly, we found no differences between workers in RFC and RBC without prey (RFC: 151.4±161.9; RBC: 116.5±120.8; t=11; p=0.09, Figure 2D).

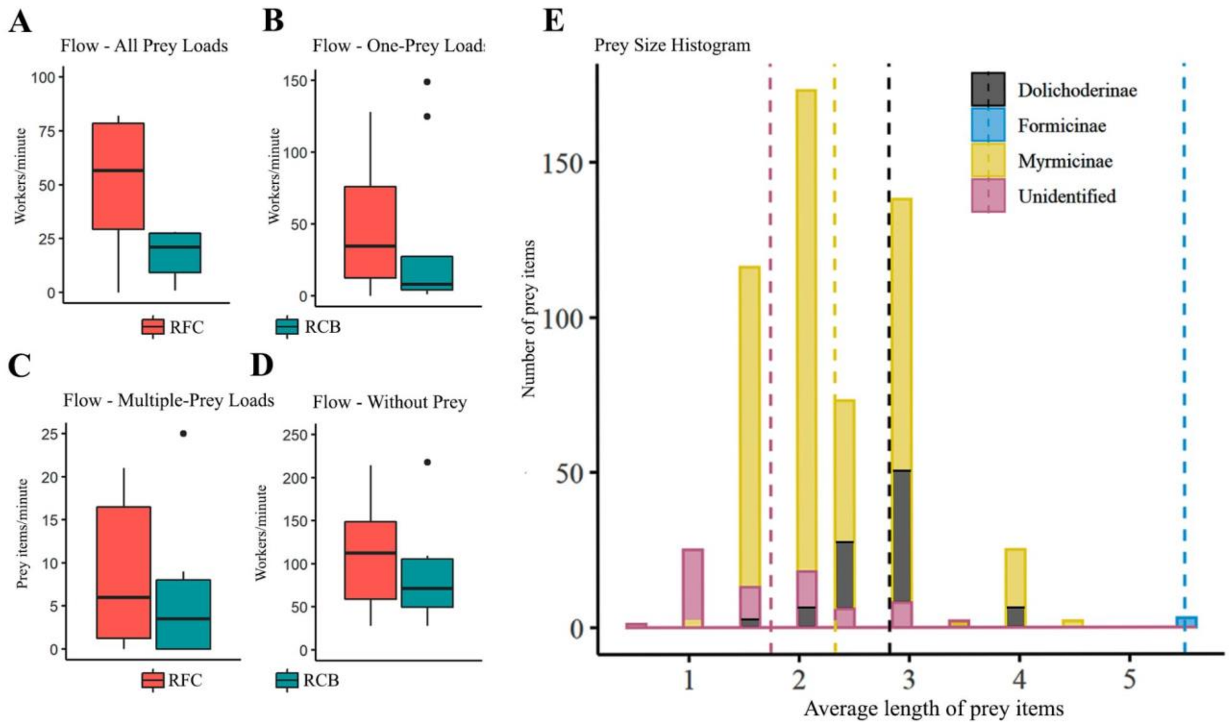

Figure 2. A. Flow of all workers carrying prey to the bivouac, in the region between front and cache (RFC) and region between cache and bivouac (RCB). **B**. Workers carrying one prey item between RFC and RCB. **C**. Workers carrying multiple prey items between RFC and RCB. **D**. Workers without prey between RFC and RCB. For B, C and D, black dots represent outliers. **E**. Length distribution of prey items in collected caches, by subfamily. Dotted lines represent the mean value for each subfamily.

Discussion

In this study, we show that *E. hamatum* caches emerge independently of the congestion resulting from clashing flows of workers walking in opposite directions [18]. While such bottlenecks typically occur immediately before sunset, when *E. hamatum* colonies gather large amounts of prey and/or bivouacs are relocated [18], we conducted our observations mainly between late morning and early afternoon. Therefore, the small, traffic-independent caches we describe are probably different from the large caches forming before sunset. In addition, as we observed raiders in the act of piling prey in caches, we exclude that these were vestiges of larger caches remaining from the previous day. Finally, we show that while ants carrying single-item prey loads mainly deposited these in caches, workers carrying multiple prey items appeared in equal numbers in RFC and RCB, indicating that prey transport varies depending on numbers of prey items in loads. We would not expect this to occur if caches only emerged as by-products of traffic bottlenecks.

Why do caches emerge? At caches, we found an accumulation of single-prey loads and a stable flow of multiple-prey loads, which suggests two non-mutually exclusive scenarios. The first is that workers carrying single prey items deposit their loads at caches and return to the foraging fronts (Video S1), while multiple-prey item carriers continue through the cache towards the bivouac. The second scenario is that caches interface two different transport networks: one consisting of raiders commuting between foraging fronts and prey caches, dropping single-prey loads and returning to the foraging front; the other comprising workers travelling between bivouac and caches, bringing multiple-item prey loads back to the bivouac. One hypothesis is that such task partitioning, reminiscent of that found in *Atta* leaf-cutting ants [20], emerged because attacked social insect colonies defend themselves or escape with the brood [27,28], restricting prey availability to short time windows. As a consequence, *E. hamatum* has probably been selected to maximize prey collection, which depends on prey retrieval rate and the turnover of operational raiders at foraging fronts. During raids, rapidly retrieving single prey items probably pays more than sequentially accumulating items to maximal carrying capacity, especially if the turnover or raiding workers is high. Therefore, as our results also suggest, raiders would tend to retrieve single prey items of any size, safely cache them in locations inaccessible to workers from the prey colony and rapidly return to foraging fronts. This not only maintains high prey retrieval rates, but also maximizes the speed at which the foraging front advances, increasing probabilities to find novel food sources. It also implies that prey traits such as individual/colony size and specific defense strategies affect cache formation. In our study, small-sized *Pheidol*e and *Linepithema* brood dominated cached prey composition, probably because transporting prey to the bivouac in multiple-item rather than individual loads is more efficient for tiny than for large-sized prey which needs to be handled separately. Further long-term sampling across habitats and seasons would reveal whether *E. hamatum* iteratively adjusts its raiding strategies at a local scale in a prey-dependent fashion. Finally, establishing caches also allows safely storing prey when returning directly to the bivouac is risky. For example, in case of rain, temporarily stocking prey under the leaf litter may increase chances to safely transport it to the bivouac at a later time.

Traffic partitioning and caches emerge across relatively distant ant taxa (i.e *Atta*, *Camponotus* and *Eciton* [4,20,21,29–33]), possibly as a result of convergent evolution in large ant societies with thousands of individuals transporting large amounts of food through long distances [16,34,35]. Such huge societies must maximize foraging efficiency and compensate for the energy spent in collecting and transporting food [36–38]. In both cache-forming *Atta* leaf-cutting ants and *E. hamatum*, caching seems to prioritize novel trips to the foraging areas over bringing food items directly to the nest.

How did *Eciton* caches evolve? *Eciton* workers are strongly attracted by prey nest material, prey workers or recruiting pheromones [30], which may become especially concentrated at trail junctions or other places that hinder workers' flow. We hypothesize that, originally, prey caches exclusively emerged as by-products of intense traffic at such bottleneck sites. As raiders started dropping their loads and returning to foraging fronts, prey retrieval rate increased and traffic diminished, incidentally increasing the foraging success of colonies and thus selecting for caching behavior.

A set of potential research questions concerns caching from an individual perspective. Individual experience affects behavioral ontogeny and task partitioning in ants [39], but we ignore its impact in large and 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 the foraging fronts (e.g., nest/prey features, prey colony defenses) or at caches (e.g., number/type of stored prey items [27,28]) may also affect individual foraging decisions. Caches may allow information transfer about prey colonies [40,41] and traffic intensity, reducing time-consuming, risky, unnecessary travel. Finally, we 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 an age-dependent polyethism relegating younger workers to travel between foraging fronts and prey caches, with older individuals specializing in the raiding itself in a classic task partitioning paradigm [42]. Whatever the mechanism, an ultimate cause explanation is that individuals carrying multiple prey items should proceed straight to the bivouac, avoiding the unloading time and the time for another worker to load/unload the multiple prey items again. Future experiments are needed to determine how single workers behave at caches.

In this study, we suggest that caches improve prey collection and transport in *E. hamatum*, complementing the current knowledge of foraging and migration in neotropical army ants. Caching prey may be especially beneficial for ants living in large societies, foraging through long trails and relying on patchily distributed food sources.

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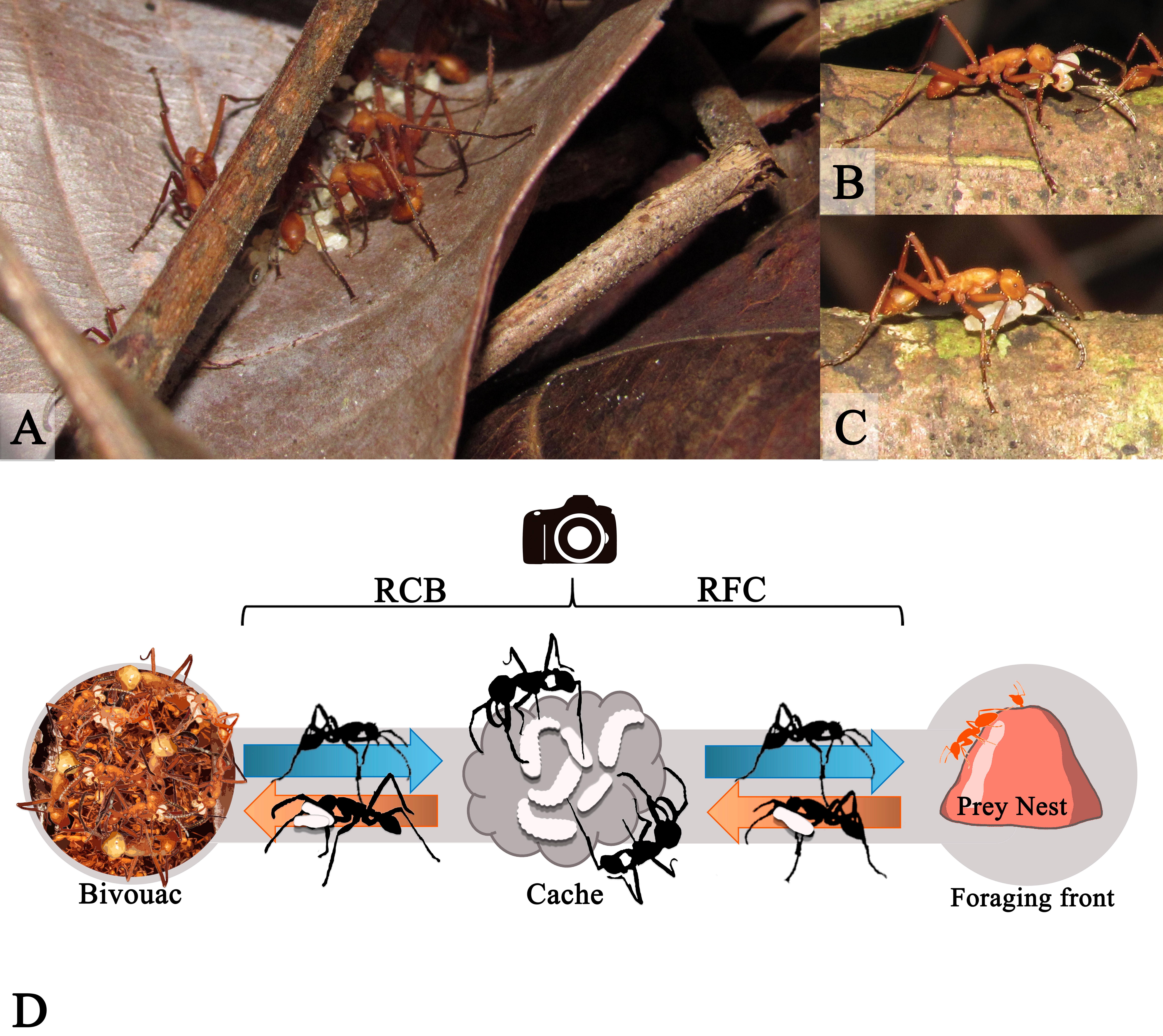
A
B
C
RCB
RFC
Bivouac
Cache
Prey Nest
Foraging front
D

A
Flow - All Prey Loads
Workers/minute
100
75
50
25
0
B
Flow - One-Prey Load
Workers/minute
150
100
50
0
RFC
RCB
C
Flow - Multiple-Prey Loads
Prey items/minute
25
20
15
10
5
0
D
Flow - Without Prey
Workers/minute
250
200
150
100
50
0
RFC
RCB
E
Prey Size Histogram
Number of prey items
150
100
50
0
1
2
3
4
5
Average length of prey items
Dolichoderinae
Formicinae
Myrmicinae
Unidentified