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# Eciton burchellii : polymorphism of submajor caste and foraging efficiency

# *Eciton burchellii*: Polymorphism of Submajor Caste and Foraging Efficiency

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## ABSTRACT

Due to the link between efficiency and fitness, there should be selective pressure for morphology and behavior that promotes foraging efficiency. Among social insects, selective pressures act on individuals, shaping the physical castes of a colony. The highly polymorphic army ant, *Eciton burchellii*, has castes with morphological adaptations to allow task specialization. This study investigates what selective pressures are acting to shape the polymorphism of the submajor caste in *E. burchellii*. Ants were collected to find a relationship between ant caste and the prey's biomass, width, and length. Results show that prey width is the greatest pressure effecting transportation efficiency, and in turn, shaping the evolution of the specialized porter caste (*i.e.*, submajor). Results also indicate that of all the castes, submajors are found to be the most morphologically different and they carry the most different sized prey. Possible explanations to *Eciton*'s physically exaggerated submajor caste include their outstanding need of transport efficiency and unique prey preferences.

## RESUMEN

Debido a la unión entre eficiencia y éxito reproductivo, debe haber una presión selectiva por comportamiento y morfología que promueve la eficiencia en el forrjeo. Entre insectos sociales, las presiones selectivas actúan en individuos dando origen a diferentes castas en la colonia. La altamente polimórfica hormiga arriera, *Eciton burchelli*, posee castas con adaptaciones morfológicas que permiten estas especializaciones. Este estudio investiga que presiones selectivas actúan moldeando el polimorfismo de la casta submayor. Hormigas fueron colectadas para encontrar una relación entre la casta y la biomasa de la presa, ancho y largo. Los resultados muestran que el ancho de la presa es el mayor factor que ejerce una presión selectiva en la eficiencia de transporte, por lo tanto, moldeando la evolución de la casta. Los resultados también indican que todas las castas, submayores parecen ser las más diferentes morfológicamente y estas cargan presas de diversos tamaños. Posibles explicaciones para las castas exageradas de *Eciton* incluyen una necesidad sobresaliente de transporte y preferencia única de presas.

## INTRODUCTION

Fitness is increased when an animal maximizes foraging efficiency, which generally correlates to a faster handling time (Orians & Pearson 1979; Krebs & Davies 1993). For social insects, like army ants, greater foraging efficiency indicates an increase in colony growth rate, and a greater fitness of all members of a colony (Franks 1985a). Due to this relationship between efficiency and fitness, there should be selective pressure for morphology and behavior that promotes foraging efficiency.

Socialization among insects, and especially ants, has allowed for their incredible ecological success (Gotwald 1995; Powell & Franks 2005). Their success is expressed in the fact that while ants and termites make up only 2% of the earth's 900,000 known insect species, they constitute for more than half of the insect biomass (Wilson & Holldobler 2005). An aspect

of insect sociality allowing for this success is caste systems. The creation of worker castes is driven by the increasing efficiency of division of labor in a colony (Oster & Wilson 1978). This efficiency comes with specialized work forces with task-dependent adaptations. These adaptations can be expressed as morphological differences among castes. Army ants, a highly specialized group, have castes that are behaviorally as well as morphologically separated (Harvell 1994). While it is clear that these morphological and behavioral differences create efficiency among castes, the ecological pressures causing these differences are not yet clear. The circumstances needed for the evolution of specialized castes presents a key issue in the understanding of social species.

*Eciton burchellii,* a well-studied army ant species, has behavioral characteristics that may have great selective pressure on maximizing transportation efficiency. Their aboveground lifestyle puts them more at risk to kleptoparasites during prey retrieval than any other species of New World army ants, which typically spend life partly or exclusively subterranean (Rettenmeyer 1963; Powell & Franks 2005). This vulnerability may play a role in the fast tempo of *E. burchellii* (Rettenmeyer 1963). Lower transportation costs benefit *E. burchellii* by helping them to avoid kleptoparasitism. In addition, their strict raid-migration schedule, dependent on larval development, brings further time limitations on foraging time (Franks *et al.* 1999). *Eciton burchellii* caste evolution may be partly driven by this need to maximize foraging and transportation efficiency.

Morphology varies greatly among the workers of *E. burchellii;* corresponding to different behavioral roles, or castes, within the colony (Powell & Franks 2005, Franks 2005, Franks 1985b). A morphologically exaggerated submajor caste exists in *E. burchellii*. This caste is more distinct and exaggerated in *E. burchellii* than in any other army ant species known to have this caste (Powell & Franks 2005). Submajors are the second largest caste next to majors (*i.e.*, soldiers) and have disproportionately large legs, head, and grasping mandibles (Franks 1985b, Powell & Franks 2005). These characteristics make submajors better porters of prey (Franks 1985b; Gotwald 1995; Franks *et al.* 1999; Powell & Franks 2005). Because their legs are the longest in proportion to body size of all *E. burchellii* workers, they can run the fastest when not burdened with prey (Franks 1985a). This characteristic allows them to improve transport efficiency by returning to the raid quickly after depositing food within the bivouac (Franks 1985). Due to the large size of submajors, and because unit transportation costs decrease with increasing worker size, they are able to carry heavier and larger prey items in relation to their body weight than any other caste (Franks 1985a). Based on this species' overpowering need for efficient transport, the morphological characteristics of *E. burchellii* submajors, and their resulting specialty in carrying prey, it would appear that food transport is the ecological pressure causing the evolution of this caste.

FIGURE 1. Arrows represent head width measurement.

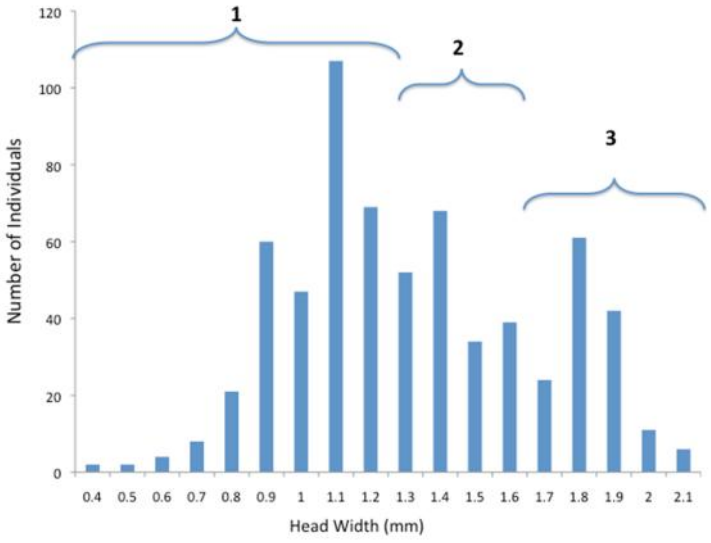
In this study, I explore prey transportation efficiency as an evolutionary pressure on *E. burchellii* submajor evolution. I plan to investigate the roles and importance of 1) prey biomass 2) prey width and 3) prey length on *E. burchellii*. I predict that prey biomass is driving the selection for the production of the submajor caste. Therefore, prey biomass will be the best indicator of caste differentiation in *E. burchellii.*

## METHODS

The study was conducted in San Luis, Costa Rica on the trails of the University of Georgia Ecolodge. All specimens were collected along the *Camino Real* trail and closely surrounding forest. Data collection occurred during afternoons from 13 April 2009 to 6 May 2009. Because all colonies studied were in the nomadic phase, where they were moving their colony every night to a new location, it is difficult to determine the exact number studied. A probable estimation is 3-6 different colonies.

For each data collection period I spent 2-3 hours collecting both individuals and groups of ants traveling with prey items along the column back to the bivouac. I concentrated my efforts on a 1-2 meter portion of the column and collected ants as they passed. Every 30 minutes, I did a 5-minute collection of individuals not carrying ant prey items along a one-meter portion of the column to determine caste distribution in *E. burchellii* colonies. I placed all specimens into 70% alcohol vials or bags. Before all calculations, specimens were briefly dried with a paper towel. I measured each individual's head width with a caliper and placed it into castes (N = 664). Head width was measured between the eyes (Fig. 1) and caste was determined using Franks' definition of caste distinctions by head width (Franks 1985a). I weighed individuals and groups of porters with a scale to the nearest 0.001 mg (N =174). The prey the porters had in tow was also weighed in the same manner (N =174). The maximum length and width of each prey item was measured with a caliper (N =236).

Relationships between prey measurements and caste were analyzed using one-way ANOVA. Differences between pairs of means were determined using a Tukey *post-hoc* test.




**F**IGURE 2**.** Head width distribution. Distinctions of casted individuals are bracketed 1) minor 2) media and 3) submajor.

## RESULTS

A trend of all head widths of all ants measured shows a greater morphological difference in submajors when compared to the rest of the castes (minors and medias) (Fig 2). Submajors carried the most different prey based on width (ANOVA, F ratio= 11.3661, P<0.001, df = 235; Fig. 3). Submajors carried the most different prey based on prey length (ANOVA, F = 6.8147, P

= 0.0013, df = 235; Fig. 4) and on prey biomass (ANOVA, F ratio= 3.2813, P=0.04, df = 173; Fig. 5). Overall, submajors carried the widest, longest, and heaviest prey items (Figs. 3, 4, and 5).

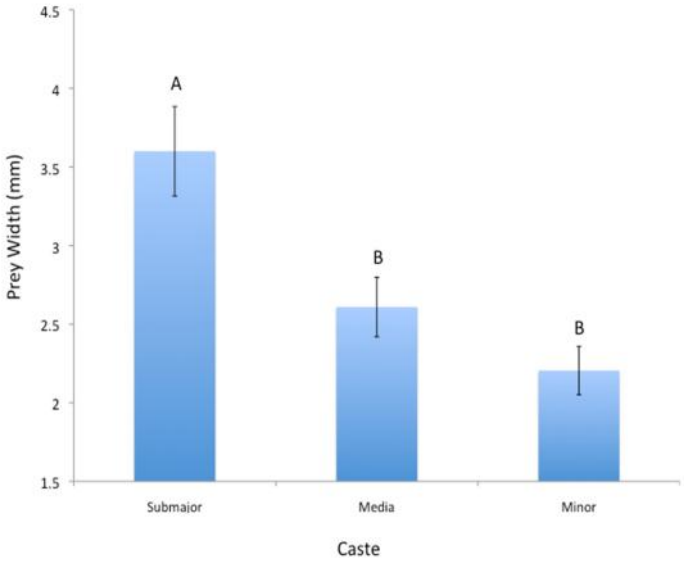



FIGURE 3. The mean prey width carried by each caste. Letters designate different means castes.

## DISCUSSION

In comparing the head width distributions of all ants measured, I found that submajors appear to be the most morphologically different from other worker castes (Fig. 2). A clear distinction is apparent between submajor headwidth and the headwidths of the other two castes. The distribution of the headwidths for media and minor are less distinguishable from each other and a smooth gradient exists. This difference in morphology shows submajors may be specialized for a specific task within the colony, a behaivoral role which medias and minors do not need to accomplish.

In constrast to my prediction, I found that prey biomass does not play the greatest role in predicting caste determination. In fact, I found that prey width best determines the caste of its carriers while prey length is the second best determinant and prey biomass is the last. For all three analysis, I found that submajors carried more varied prey than media and minor castes. Among the three castes observed and measured carrying prey, submajors are the most morphologically different and carry the most different sized prey. The morphological differences

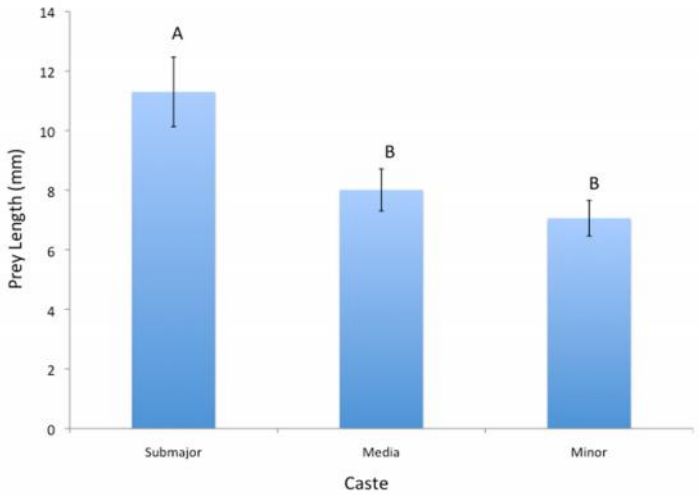



FIGURE 4. The mean prey length carried by each caste. Letters designate different caste means

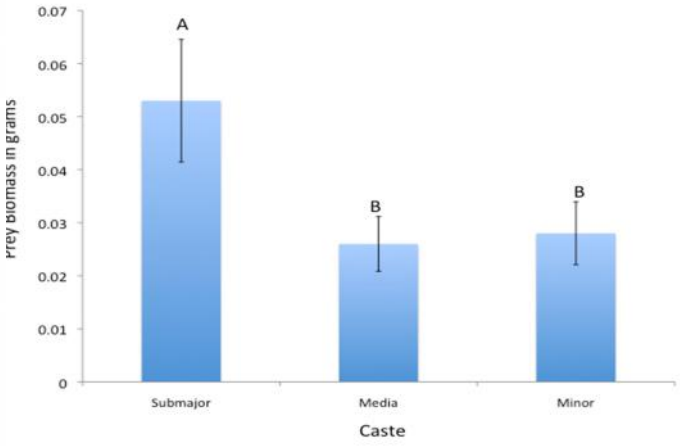



FIGURE 5. The mean prey biomass carried by each caste. Letters designate different caste means.

of submajors makes them better suited for wider prey. In comparison to minors and medias, submajors have the longest legs, largest head and largest mandibles.

Like all other army ants, *E. burchellii* individuals carry prey items slung beneath their bodies (Franks 1985b). This load-transport method is mechically efficient and adheres to *E. burchellii*'s time-limited lifestyle (Powell & Franks 2005). The submajor caste of *E. burchellii*'s is adapted to transport awkward prey loads: their longer legs increase ground clearance, while their large head and mandibles allow for a more powerful grip to hold the load well above the substrate (Paul 2001). The inefficiencies of under-body prey transport is typically noted with wider prey, not necessarily longer prey. Long legs may make carrying wider prey more efficient, where this morphological variation may not change the efficiency of carrying long prey items. Long prey can be tackled by groups of ants forming a line and carrying the item in tandum. Accordingly, my results indicate that prey width is more of a pressure on caste differentiation.

If all army ants carry prey slung below their bodies, what ecological pressures are at work that make *E. burchellii*'s submajor caste more exaggerated than other army ant species? Possibly, their diet preference appears to be a factor. *Eciton burchellii*'s diet is composed of approximately 50% social insect larvae and 50% large arthropods (Franks 1983). These large arthropod prey sources are captured and then dismembered into a multitude of different sized portions. *Eciton burchellii* is the only *Eciton* that is not a specialist on social insect larvae as prey (Powell & Franks 2005). The submajor caste has evolved as a specialized caste for awkward prey loads which typically differ greatly in width. Contrasting caste composition and diet of other species such as *E. mexicanum* proves this assertion. This species lacks a submajor caste and specializes on monomorphic poneroid ant larvae as prey (Rettenmeyer *et al. 1983)*. If *E. burchellii* had maintained a strict larvae only diet, transportation efficiency would be greater and submajors may not have evolved (Powell & Franks 2005).

Well-known theories of evolution explain how morphological characteristics often develop through ecological pressures and niche partitioning. However, little is known about the pressures that act to develop castes within social species. My results strongly suggest that prey size, in particular width, is the driving force behind the evolution of *E. burchellii*'s submajor caste. The specialization of the submajor caste in porting awkward loads may explain these results. In investigating the pressures that act on caste evolution, my results attribute to the overall understanding of social insects and their evolutionary history.

Future studies could delve deeper into the selective forces acting on the submajor and other castes. Due to submajor's extreme efficiency, one may expect to find greater numbers in caste distribution analysis. Future studies may want to focus on other selective forces for the submajor caste and attempt to find an answer to their relatively small proportions. In addition, measuring the velocity of carrying ants with prey in tote would offer a better explanation as to the efficiencies of different castes and may offer insight to the specialties of other castes.

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