Bridge Building and Foraging Efficiency in the Army Ant *Eciton burchellii*

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Abstract

Efficiency in food transport is vital for all organisms. Eusocial insects are efficient because of decentralized colony control, caste specialization, and unique behaviors. Bridge building in the army ant *Eciton burchellii* has been widely studied as a mechanism that augments prey transport efficiency. Little data exist on why bridges confer an advantage and how their dimensions facilitate rapid food delivery. It is also less well studied how efficiency on a bridge compares to the average efficiency of ant traffic on transport pathways that do not have ant bridges. Bridge lengths and widths were recorded and patterns were looked for between bridge dimensions and ant velocity, traffic density, and collision rate as proxies of food transport efficiency. Bridges were also compared to non-bridge sites and velocity, traffic density, and collision rates were compared between sites. Bridge dimensions were found to correlate with an increase in all three parameters. Non-bridge sites had significantly higher velocities and fewer collisions, and thus were more efficient. Larger bridges confer more efficiency up to the point where too many ants in bridges reduces the potential number of foragers. Areas without bridges were far more efficient than sites with bridges. This is possibly explained by the use of bridges only in uneven terrain; when compared to uneven terrain with no bridge, efficiency may be increased.

Resumen

La eficiencia en transporte de comida es vital para todos los organismos. Insectos eusociales son eficientes por algunas razones como control descentralizado de la colonia, especialización de las castas, y comportamientos únicos. Han estudiando bastante construyendo puentes en la hormiga arriera *Eciton burchellii* como un mecanismo de aumentación del transporte de la presa. Pocos datos existen por las razones que los puentes son ventajas por la colonia y como lo dimensiones del puente permiten que la comida esté movida más rápido al nido. Tampoco está estudiado como la eficiencia en un puente compara a la eficiencia en una columna normal sin puente. Los largos y anchos de los puentes estaban medidos y miraba patrones entre los dimensiones del puente y la velocidad de las hormigas, densidad del tráfico de las hormigas, y colisiones entre hormigas como ejemplos de eficiencia de transporte de comida. También, los puentes estaban comparados a sitios sin puentes, comparando velocidad, densidad de tráfico, y colisiones. Las dimensiones de los puentes mostraron una correlación positivamente con los tres parámetros. Los sitios sin puentes tenían velocidades más altas con menos colisiones, y por estas razones eran más eficientes. Los puentes más largos son más eficientes hasta el punto donde hay bastantes hormigas en el puente que reduzca el número potencial de hormigas forrajeando. Zonas sin puentes eran más eficientes que sitios con puentes. Una explicación es que los puentes están usados solamente en terrenos desiguales; si hacemos una comparación a terreno desigual sin puentes, es posible que eficiencia pueda ser aumentado.
Introduction

Efficiency is the keystone of a successful species. Optimizing energy use is important across all taxa and plays a central role in natural selection. It is thus both a driving force and a result of specialization and evolution. Suboptimal resource use reduces fitness and lowers competitive ability against other species and conspecifics. Food harvesting is one of the most fundamental actions that all organisms do; the behavior of food energy intake should be specialized to be as efficient as possible, gaining the most amount of food energy for the least amount of time spent foraging (Pyke et al. 1977). This is known as optimal foraging theory.

Eusocial insect colony interactions are fundamentally complex with emergent properties that arise from selective pressure to act efficiently, both for overall specialization and optimal foraging in general. There is a correlation between behavioral specialization and colony size, as well as intra-colonial conflict and colony size (Anderson and McShea 2001), and colonies with fewer conflicts should be more efficient at foraging. Fewer conflicts allow for more individuality in the actions of the workers. Simple individual interactions happening at the same time is one of the characteristics of complex insect societies, where control becomes decentralized. For example, different large-scale patterns in movement can be driven by the same individual actions (Deneubourg and Goss 1989). Allelomimesis, or imitating a neighboring conspecific, is a self-perpetuating process that raises the decision of one individual to a colony-sized reaction (Deneubourg and Goss 1989). If there is a strong trend in individual reactions, the entire group will quickly be galvanized to one task. Ants, for example, must constantly forage in order to sustain their colony, and random food searching leads on a greater scale to directional hunting (Couzin and Franks 2003), which increases the success of finding food due to higher recruitment. Foraging efficiency is important to ants because their bodies are not as derived for movement as more recently evolved taxa. Hurlbert et al. (2008) calculated that ants run slower than expected for their size; compared to small mammals, they have less efficient locomotion, so to support an entire colony they must find other ways to be efficient foragers than just selecting for speed.

One of the most widely studied predatory ant species that uses highly specialized foraging behaviors is the army ant Eciton burchellii (Formicidae: Ecitoninae). Eciton burchellii is an obligate nomadic predator with central foraging tendencies (i.e. they bring all prey back to the bivouac instead of eating it immediately) that hunts in a straight line from the bivouac in a swarm often over 5 m wide between dawn and dusk, bringing in about 30,000 prey items from up to 105 m away on an average raid (Franks 1982). Their life cycle consists of a 20-day stationary period, where they hunt in a radial pattern from the bivouac, and a 15-day nomadic phase, where the bivouac moves in the direction of the day’s raid (Franks and Fletcher 1983). Each swarm uses about one third of the colony (Franks and Fletcher 1983), with an average colony consisting of up to 700,000 workers (Franks 1985; Powell and Franks 2006). Food is brought back from the swarm to the bivouac via a single pathway, or column, which always links the swarm to the bivouac (Powell and Franks 2007). When a worker has brought foot back to the bivouac, it returns to the swarm front to continue hunting. Each facet of their hunting behavior requires extreme energy input and organization; efficiency is vital for the success of their lifestyle. E. burchellii has many different specialized behaviors to increase the efficiency of food transport.
One adaptation specific to *E. burchellii* is building bridges made of living ants over uneven terrain to smooth prey delivery (Powell and Franks 2007). Bridges are thought to be set up in areas of high terrain variability in order to smooth out the column or bypass obstacles more efficiently (Powell and Franks 2007). Bridging has been shown to effectively increase food intake by the colony, up to a 31 percent net gain in prey (Powell and Franks 2007). There is very little information, however, for how bridge structures increase colony efficiency. In this investigation I will study how *E. burchellii* bridge structure influences ant foraging efficiency and efficiency of bridges and non bridge sites. The dimensions of the bridges may have an impact on the ease of movement of workers, making them more efficient at foraging and directly influencing the fitness of the colony.

I predict that longer and wider bridges will allow ants to more efficiently transport food to the bivouac. Because both ants returning from the swarm and ants leaving the bivouac use the main column, inbound and outgoing ants collide with each other while trying to get to their destination, and bridge dimensions may influence how often this happens. Efficiency can best be estimated by measuring the velocity of the ants moving over the bridge, the number of collisions they have with other ants, and the rate of ants crossing the bridge. Bridges that are longer and wider should increase the velocity and traffic and reduce the number collisions. Because the bridges are created to increase foraging efficiency, there should also be a distinct difference in efficiency between bridges and non-bridge sites along the column.

**Methods**

This study was carried out at the University of Georgia Research Station in the San Luís Valley, Costa Rica (10° 18′ N, 84° 32′ W, 1000 meters above sea level) from April 12-May 5, 2011. The research station comprises 62 hectares, 60 percent of which is protected premontane moist forest. An estimated five *E. burchellii* colonies maximum were observed. I measured the length and width of 35 bridges and recorded ant velocity (measured as the bridge length divided by the time taken to cross the bridge for four ants per bridge), traffic density (number of ants crossing the bridge in 30 sec), and collision rate (the number of ant collisions on each bridge in 30 sec, collision defined as an interaction between two ants which slowed down or altered the course of one or both ants), on each bridge. These data were also collected for ten non-bridge locations from the main column.

**Additional Observations**

Many ants stopped at the edge of a bridge momentarily before they crossed. Traffic density was variable along the non-bridge column and ants often moved in groups, regardless of whether they were carrying food. Not all collisions had the same impact: some collisions stopped one ant while other times both ants were interrupted, and larger ants frequently crawled directly over smaller ants without any hindrance to either; these interactions were not counted as collisions. It was common for one ant to collide with multiple ants heading the other way or stalling many ants that followed behind.
Results

Bridge Structure and Efficiency

Bridge dimensions significantly affected velocity, number of collisions, and traffic density. Length was positively correlated with velocity ($N = 33, R^2 = 0.183, P = 0.01$; Fig. 1a) and traffic density ($N = 33, R^2 = 0.1699, P = 0.0139$; Fig. 1b), whereas width was positively correlated with collision rate ($N = 33, R^2 = 0.197, P = 0.0076$; Fig. 1c) and traffic density ($N = 33, R^2 = 0.3377, P < 0.0005$; Fig. 1d). There was also a positive correlation between length and width ($N = 33, R^2 = 0.25, P = 0.0076$).

Bridge and Control Sites

Non-bridge sites had lower collision rates (Welch’s $t$ test $= 2.4077$, df $= 43$, $P = 0.02042$; Fig. 2a) and higher ant velocity (Welch’s $t$ test $= -9.986$, df $= 52.245$, $P < 0.0001$; Fig. 2b) and lower collision rates (Fig. 2). Ants were over three times faster in non-bridge sites (mean +/- SD = 42.58 +/- 17.79 versus 12.36 +/- 7.03 mm/sec), and experienced half as many collisions (0.67 +/- 0.56 versus 1.3 +/- 0.73 collisions/sec). Width and traffic density did not differ between bridge and non-bridge sites (width: Welch’s $t$ test $= -0.4774$, df $= 43$, $P = 0.6355$, and traffic density: Welch’s $t$ test $= 0.7592$, df $= 43$, $P = 0.4519$).

FIGURE 1. The relationship between bridge dimensions and food transport efficiency in *Eciton burchellii*. Relationships are shown between a) ant velocity and length, b) traffic density and length, c) traffic density and width, and d) collision rate and width. All correlations shown are statistically significant.
FIGURE 2. Comparison of bridge and non-bridge traffic efficiency in *Eciton burchellii*. Means +/- SE are shown for bridge and non-bridge measurements of a) collision rate and b) velocity.

**Discussion**

**Bridge Structure and Efficiency**

Bridge length positively correlates with increased velocity and traffic flow, both of which increase the rate of food returning to the bivouac and therefore foraging efficiency. A longer bridge means that more uneven ground is made of ant bodies. This result supports the theory that ants build bridges in order to reduce time spent climbing over other obstacles. Increased velocity can also account for the increased traffic density because a faster bridge should allow ants to cross more often.

Increased bridge width was correlated with increased traffic density and increased collision rates. At first this might sound paradoxical, because a higher traffic flow indicates a more efficient bridge while more collisions signify a less efficient structure. However, width is 1.7 times more strongly correlated with traffic density than collisions ($R^2 = 0.337$ versus 0.197) and the slope of the regression for traffic density and width is 3.35 compared to 1.41 for collision rate and width. In other words, traffic density increases faster than collision rate, and efficiency is conserved.

If bridge width increases efficiency, why not make bridges excessively wider than the main column, which is generally about 3 cm wide (Gotwald 1995)? The bridges must be built efficiently as well; ants in bridges are not contributing to food transportation, and if too many ants aren’t actively hunting, the colony suffers a net loss of prey compared to no bridges. Powell and Franks (2007) calculated that a 23 percent daily net loss in prey would result if ten percent of potential foragers were in bridges, compared to a 27 percent daily net gain in prey with only one percent of potential foragers in bridges, assuming each worker in a bridge could have brought back one extra prey item. Bridge width is thus most efficient when conforming to the size of the main column.
The correlation between the length and width of the bridges is not surprising: as the bridge length increases, it makes sense that a corresponding increase in width might help stabilize the bridge by giving support to the minims that construct it.

**Bridge and Control Sites**

Ants were much more efficient were bridges were not necessary. *Eciton burchellii* moved at both a faster velocity and there were fewer collisions. Because bridges can be placed anywhere there is uneven terrain, the bridge may constitute a choke point that leaves it more susceptible to collisions. This may lead one to question why there are bridges in the first place if they do not contribute more efficient food transport compared to uncovered terrain, but it is important to remember the underlying theory that efficiency dictates bridge-building, but bridge building does not dictate efficiency. Compared to a column with no obstacles in its way, ants crossing a bridge in uneven terrain may take longer to cross; compared to the uneven terrain with no bridge, however, ants may be less efficient than if there were a bridge. Bridges are built whenever an area of the column is slowed down by the terrain and suffers from increased traffic congestion.

**Additional Observations**

Ants that stopped momentarily before a bridge may have needed to figure out the placement of the bridge; bridges may have to cover unconventional terrain that the ants crossing the bridge need to assess because a temporary halt along the path is far less detrimental to the survival of the colony than an ant completely losing the path of the colony.

Ants moving in clusters have been shown to increase overall transport efficiency in *Atta colombica* (Dussutour *et al.* 2009). Because ants leaving the nest will give way to ants heading back with food, including in *E. burchellii* (Couzin and Franks 2003), unladen ants heading to the bivouac will often choose to follow a slower, burdened ant than try to go around it. Mathematical models have shown that the decrease in speed required to follow an ant carrying prey is less wasteful than the average number of collisions an ant would sustain otherwise (Dussutour *et al.* 2009). Moving in clusters is beneficial for teams of ants that are carrying food, for teams of ants that have dropped off food at the bivouac and are returning to the swarm, and for reducing overall collisions.

Bridges are a well-studied but poorly understood method of efficient prey transport in *Eciton burchellii*. Increasing the length and width of a bridge can augment traffic density and velocity at the expense of a higher collision rate. Bridges are implemented when there is uneven terrain that may hinder individual ants from crossing quickly. Otherwise, bridges are not built because they render the colony slower, with more collisions, and are overall less efficient, in the sense of transportation efficiency.

Even within a bridge there are still many other efficiency-oriented behaviors such as spatial distribution of traffic flow. Couzin and Franks (2003) show that local traffic rules and pheromone trails collectively partition lanes of inbound and outgoing lanes of movement which also reduce the number of collisions on any particular section of trail.

This is a prime example of how even the smallest caste, the minim, cannot bring food to the bivouac very fast, but it still fulfills an essential role in helping sustain the entire group. Because the smallest caste is slowest and cannot carry as much food (Franks 1985), they are less
efficient at food transport. However, minims constitute 51 percent of all ants in bridges and 40 percent of minim behavior is spent in bridges (Nell 2010). Ants fill gaps based on their size and will work together to fill larger holes (Powell and Franks 2007). Minims can fill smaller holes without wasting a larger (and therefore faster) caste, increasing colony efficiency.

Further study of this particular mechanism should focus on the benefit of a given ant bridge compared to the same location without a bridge. This may shed light onto strategies by which ants choose to make a bridge in the first place, how they decide to place it, and when building bridges can be more of a hindrance than a benefit. On a broad spectrum this investigation shows that efficiency mechanisms are often implemented on an individual or miniscule level that has repercussions on a much larger scale that can not only affect individual survival but also long term fitness of an entire species.

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Literature Cited


