Foraging seed-harvester ants run slower when carrying cargo

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Foragers make decisions about the types of foods to gather from among many potential types of food that are available in the environment. One basis for such decisions is the profitability of a food item, which is defined as the net potential energy contained in a food item relative to the time it takes to obtain that energy. Net potential energy reflects energy contained in indigestible material, and the energetic costs of pursuing, capturing, handling, transporting, eating, and processing a particular food item, which are deducted from the total potential energy contained in the food item. Animals attempt to maximize their rate of energy intake while foraging; they have many other demands on their time, so time spent gathering a particular type of food determines the profitability of that type of food.

Time required to gather food items is particularly important for central place foragers. Because such foragers return food items to a central location (territory, burrow, colony, hive, etc), their outward-bound trip adds to the time required to gather each item. Therefore the decisions made by central place foragers take into consideration both the energetic costs and benefits of choice of a particular food item and the costs and benefits with respect to time required to obtain that food item. Central place foragers must strike a balance between energetic costs and benefits and time costs and benefits, to maximize energy gains while foraging.

The purposes of this investigation were to assess velocity of a common central place forager, the seed harvester ant (*Pogonomyrmex barbatus*), running away from the colony without cargo and toward the colony with cargo, and to quantify mass of ant and mass of cargo as a way to test hypotheses about the relationship between ant mass, cargo mass, and running velocity. Cargo mass is an indirect measure of energetic value of cargo, and running velocity is an indirect measure of time costs.

Methods:

We conducted this study on September 29, 2009, between 2 and 4 pm, on the property of Alan Kainrad, which is just north of Austin College's Sneed Environmental Research Area, on Keyes Rd., about 15 km west of Sherman, Grayson Co., TX. The weather was sunny, about 80^{o} F, low humidity, with a light northerly breeze. The Kainrad property is gently rolling, with a transitional soil that is sandy clay. Herbaceous vegetation included ragweed, sneezeweed, bitterweed, Texas nightshade, snow-on-the-prairie, prickly pear, silver bluestem, Bermuda grass, and buffalo grass. The very sparse woody vegetation included mesquite, bois d'arc, hackberry, and honey locust. The vegetation in general was low-growing and sparse because of heavy grazing by cattle. Cow pies littered the ground surface.

The Kainrad property is home to several mature colonies of *Pogonomyrmex barbatus*, each of which may contain up to 30,000 workers. *Pogonomyrmex barbatus* colonies are perennial and may have a life span of 20 yr or more. A colony's location is marked by a large, conical crater that may be a meter or more in diameter and 25-30 cm tall; the crater is composed of small bits of rock and soil brought out of the tunnels of the colony by the workers. The worker ants forage for seeds and small insects using trunk trails to travel outward from the colony. Trunk trails are cleared of vegetation and are marked by trail pheromones. After traveling several meters along a trunk trail, the workers fan out into the habitat, select a food item, then return to the colony along the trunk trail. Trunk trails are persistent features of the habitat around seed harvester ant colonies; they may exist for months or years, and may be tens of meters in length. Seed harvester ants are found primarily in relatively dry, short-grass prairie and desert areas of the western US, although populations occur in the southeastern US including Florida and Georgia, and as far north as the Great Basin desert in Washington and far southern Canada.

We collected data on workers of several seed harvester ant colonies. We timed both unladen ants running away from the colony (N = 116) and laden ants running toward the colony (N = 114), using a standard 10 cm distance. Once we had timed a laden ant, we attempted to capture the ant with its cargo. We preserved ants and cargoes that we successfully captured in 70% ethanol (N = 75); we later weighed ants and cargoes to the nearest 0.1 mg.

Results:

Ants running toward the colony with cargo were significantly slower than ants running away from the colony without cargo (toward mean = 3.51 ± 2.45 sec; away mean = 2.17 ± 1.13 sec; $t = 5.30$, $P < 0.001$). These running times translate to 2.85 cm/sec and 4.6 cm/sec, respectively.

Average ant mass was 14.8 mg ($s = 1.91$). Average cargo mass was 7.70 mg ($s = 11.0$); this is 52% of average ant mass. The range of cargo masses was 0.1 mg – 68.8 mg; the heaviest cargo was 465% of average ant mass. Median cargo mass was 4.90 mg; this is 33% of average ant mass. Ants carrying cargoes at or below the median cargo mass were significantly slower than unladen ants (mean = 2.83 ± 1.22, $N = 36$; $t = 2.88$, $P = 0.006$), but were significantly faster than all laden ants ($t = 2.20$, $P = 0.03$).

There was no correlation between ant mass and cargo mass ($r = 0.013$, $P = 0.915$). There was no correlation between ant mass and running time ($r = 0.000$, $P = 0.997$). There was a significant positive correlation between cargo mass and running time ($r = 0.457$, $P < 0.001$)

Discussion:

Ants ran significantly faster going away from the colony without cargo than going toward the colony with cargo. This result is not surprising: burdened ants would be expected to slow down. The average cargo mass was 52% of average ant mass, but this average is inflated by a few ants carrying very massive cargoes. The median cargo mass was 33% of average ant mass, so half of the ants were carrying cargoes one-third or less of their body mass. Even ants that were carrying relatively light cargoes ran slower than unladen ants. Cargo mass is positively correlated with running time, which means the larger the cargo, the slower an ant runs. This result is also not surprising – more heavily burdened ants run slower that less heavily burdened ants.

Seed-harvester worker are monomorphic – there is relatively little variation in ant mass. There is extreme variation in cargo mass, but that variation is not related to worker mass; larger ants do not carry larger cargoes. Also, ant mass is unrelated to running time – larger ants do not run faster than smaller ants, or vice versa.

As central place foragers, seed-harvester ants make a round-trip to gather each food item. This round trip may be several meters each way, so the time to run the round trip has the potential to be a substantial part of the time available for foraging. Ants must make decisions about the size of cargo they will carry relative to the distance they will run. One possibility is that ants run relatively short distances and carry relatively small cargoes. This might provide the greatest rate of energetic return per unit time foraging because of the short time necessary for each round trip. An alternative is that ants may run farther and bring back larger cargoes, which would take longer but would deliver more energy. Which of these or other alternatives is pursued by ants is unknown. Their choices may be affected by a variety of environmental factors, such as seed (or other prey) availability, presence of predators, soil temperature (which affects running velocity), and needs of the colony for energy and other important nutrients.

Another consideration in the ants' decisions is the energetic cost of running, both with and without cargo. Because ants are small animals with an exoskeleton, as opposed to large animals with an endoskeleton, and because they are hexapods, the energetic costs of running and of carrying cargoes may be minimized. The force required to deform the exoskeleton is directly proportional to its thickness, and inversely proportional to the cross-sectional area of the body. Considerable force is required to deform the exoskeleton of a small animal with a relatively thick exoskeleton, such as an ant. The flexible but resilient exoskeleton provides support for carrying cargo, and also antagonizes muscle contractions that deform the exoskeleton from within. The musculature of the thorax provides power for the legs, and the antagonism by the exoskeleton may increase the power that can be delivered. Bristles that subtend the mandibles are used to carry cargo, and contribute to the ability of the ants to carry large cargoes. The morphological characteristics of the seed harvester ant may contribute to their ability to carry massive objects, even ones that are several times the body mass of the ant.

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