Notes and Comments

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EFFECT OF FORAGING DISTANCE ON WATER CONTENT OF SUBSTRATES HARVESTED BY ATTA COLUMBICA (GUERIN)[1]

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Recent investigations into the foraging behavior of quasi-herbivorous leaf-cutting ants (*Atta* spp.) have failed to formulate a general theory of plant exploitation. Although several independent investigations have documented attine preference for plant tissues with a high water content (Cherrett and Seaforth 1968, Barrer and Cherrett 1972, Haines 1971, 1975, Rockwood 1972), the factors affecting this choice are unknown. Leaf-cutting ants prefer introduced (Beebe 1921) over native plant species and new leaves and flowers over mature leaves (Rockwood 1976), suggesting that these tropical ants minimize secondary compounds in fungus gardens by selecting plants that, for evolutionary or phenological reasons, are low in toxic anti-herbivorous substances. In effect, attine ants are ecological vicars for their mutualistic fungus and probably select substrates that maximize fungal growth. Independent evidence suggests that attine ants may simultaneously maximize water and minimize secondary compounds delivered to the fungus if certain plant substrates are selected. Feeny (1970) has shown that newly produced oak leaves are low in tannin content. These leaves, if they are like new leaves on tropical plants, have a high water content (Cherrett 1968). Moreover Cherrett (1968) and Rockwood (1972, 1976) have reported data indicating a higher proportion of water in leaves which are palatable to *Atta* species when compared to unpalatable leaves. Regardless of the causes, the effects are the same in that leaf-cutting ants harvest substrates with a relatively high water content. In fact, the trends are sufficient to suggest that sappiness could, a priori, be considered a key factor determining substrate palatability.

This present study tests the hypothesis that *Atta columbica* individuals select plant substrates partially on the basis of water content.

Methods

Three *Atta columbica* colonies on Barro Colorado Island, Canal Zone, Panama, were studied from 21 April to 12 May 1979, in what has previously been described as a lowland, tropical evergreen forest (Willis 1974). In contrast to earlier investigations into attine foraging, this study did not attempt to catalogue the species, or even parts of plants utilized. Instead, we were interested in the water content of harvested substrates and how this was related to distance from the main colony. Theoretically, we predicted that the greater the cost (in this case, distance from colony nest) in acquiring a substrate, the more selective the foraging behavior. Similar cost-benefit analysis has recently been successful in interpreting complex foraging behaviors (see Pyke et al. 1977 for a review).

Ant-harvested plant substrates were collected as close to the actual location of cutting as possible. Substrates were randomly selected by collecting the plant material carried by every fifth ant as it passed a given location and then immediately placing these substrates in airtight plastic vials. Forty plant substrates were collected from each cutting site. The distance between the cutting area and main colony was measured by running a tape alongside the foraging trail. In most cases this foraging distance was between 1.25 and 1.75 times the linear distance. When ants were harvesting in the forest canopy, the estimated vertical distance (an ocular estimate) was added to the horizontal distance to give a total foraging distance. Vials containing substrates were transferred to the laboratory of the Smithsonian Tropical Research Institute (within 2 km of all study sites) for further analysis. Leaves were taken from the vials one by one, their mass determined on a Mettler balance to the nearest microgram, and dried in an oven at 50° C for 24 h. Upon removal, the mass of leaves was determined immediately.

Results and Discussion

Over the 3-wk study period, 720 ant-harvested substrates were collected from 18 different cutting locations representing all cutting sites for the three colonies studied. These sites varied substantially in: (1) foraging distances from the main colonies and (2) average water content of harvested substrates. Fig. 1 shows the mean water content of harvested substrates as a function of distance from the nests of the three colonies. A Spearman rank correlation procedure confirmed the interdependence of water content of harvested substrates and distance from colony nests ($r = .72$, $P < .001$). The best fit line, a logarithmic function, predicts that ants harvest substrates of higher water content as distance from the colony nest

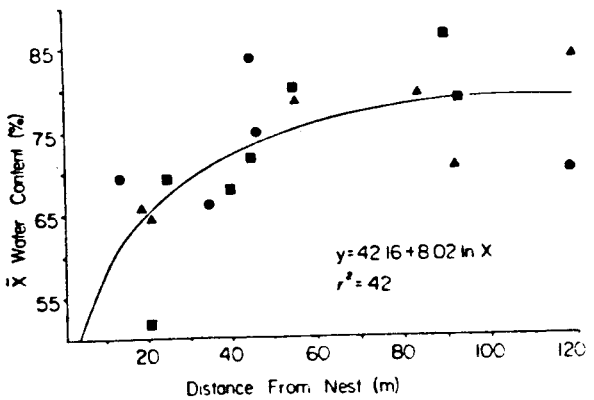

FIG. 1. Relationship between the average water content of harvested substrates (ordinate) and harvesting distance from three *Atta columbica* nests (abscissa). Squares, circles, and triangles represent all extant harvesting sites for the three colonies. The r^2 value was obtained from log-transformed data.

increases. This relationship is not linear and asymptotes at a water content of 80%, suggesting that attine ants are able to harvest substrates of maximum water content at distances of <85 m. In fact, the data suggest that the costs accrued through foraging long distances are compensated for, at least partially, by selecting substrates with a high water content. Thus, the hypothesis of water maximization cannot be rejected, even though more data are needed before confirmation. Moreover, the data suggest that *Atta columbica* differentially use their foraging area, exhibiting more generalized diets (substrates of relatively low water content) close to the colony nest relative to far away (but see Cherrett 1968, Rockwood 1976). Although in our study diets are expressed in terms of water content, we predict that distance-dependent palatability might also be manifested by the exploitation of plant species close to the colony nest, which are shunned at greater foraging distances. More work documenting the relation between distance and exploitation of plant species is needed to test this hypothesis.

Although a significant portion (42%) of the variation in water content of ant-collected plant substrates can be explained by harvesting distance from the colony nest, 58% remains unexplained. This unexplained variance probably has two main components: experimental error and selection of plant substrates for reasons other than water maximization (particularly, selection against certain biocides and/or for certain micronutrients). For example, Rockwood (1976) noted that *Atta columbica* and *Atta cephalotes* in Costa Rica regularly harvested a small amount of several plant species which collectively accounted for a very small proportion of the total plant biomass harvested. He suggested that these plant species may provide the fungus with a micronutrient beneficial to its growth but may also contain secondary compounds which are energetically expensive to detoxify. More data on the chemical makeup of palatable vs. unpalatable plant substrates are needed before such relationships can be elucidated.

Although our data show a clear pattern of water content influencing substrate palatability (for the fungus), at least one caveat is warranted. Specifically, our data set was collected at the end of the Panamanian dry season and the ants (and particularly the fungus gardens) may have been temporarily water stressed. Consequently, the logical result would be for the ants to maximize their intake of water with the constraint of minimizing biocide infusion. Rockwood (1972, 1975, 1976) has reported interseasonal differences in foraging patterns and in the species of plants harvested, suggesting that ants are sensitive to the needs of the fungus garden. More work in the rainy season is needed to determine if water maximization is a general characteristic of *Atta* foraging.

Regardless of the generality of water maximization through the seasons or even to other fungus-growing ants, the data presented reflect one of the few cases in which a herbivore has been shown to maximize some currency. In fact, we can think of no explanation, other than water maximization, to account for the data. Our simple methods, combined with the tractable concepts embodied in cost-benefit analysis, demonstrate that simple approaches to complex questions are still viable alternatives for modern ecologists.

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