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Caste and Division of Labor in Leaf-Cutter Ants (Hymenoptera: Formicidae: *Atta*)

II. The Ergonomic Optimization of Leaf Cutting

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Summary. Leaf cutting was selected for an evaluation of ergonomic efficiency in the fungus-growing ant *Atta sexdens* because it is performed largely by medias (head width 1.8–2.8 mm), which attend to relatively few other functions and hence are less likely to be evolutionarily compromised by the demands of competing tasks (Fig. 1).

Three alternative a priori criteria of evolutionary optimization were envisioned that are consistent with natural selection theory: the reduction of predation by means of defense and evasion during foraging, the minimization of foraging time through skill and running velocity during foraging, and energetic efficiency, which must be evaluated with reference to both the energetic construction costs of new workers and the energetic cost of maintenance of the existing worker force.

In order to measure the performance of various size groups within the *A. sexdens* worker caste in isolation, I devised the 'pseudomutant' technique: in each experiment, groups of foraging workers were thinned out until only individuals of one size class were left outside the nest. Measurements were then made of the rate of attraction, initiative in cutting, and performance of each size group at head-width intervals of 0.4 mm (Figs. 2, 3, and 7). Other needed measurements were made in body weight, oxygen consumption, and running velocity (Figs. 5, 6, and 8).

The size-frequency distribution of leaf cutters in the *A. sexdens* conforms closely to the optimum predicted by the energetic efficiency criterion for harder forms of vegetation, such as rhododendron leaves. The distribution is optimum with reference to both construction and maintenance costs. The difference between the predicted and actual modal size groups specializing on leaf cutting is 10% or less of the total size range of the *sexdens* worker caste.

A model was next constructed in which attraction and initiative were allowed to 'evolve' genetically to uniform maximum levels. The theoretical maximum efficiency levels obtained by this means were found to reside in the head-width 2.6–2.8 mm size class, or 8% from the actual maximally efficiency class (head width 2.2–2.4 mm). In the activity of leaf cutting, *A. sexdens* can therefore be said to be not only at an adaptive optimum but also, within at most a relatively narrow margin of error, to have been optimized in the course of evolution.

Introduction

How well organized is an ant colony? This question is simple in tone but potentially profound in meaning. It can be translated into the following more operational form: is the colony as efficient in its basic operations as natural selection can make it, without some basic change in the ground plan of anatomy and behavior? The answer, deduced species by species, is of importance not only for sociobiology, but for general evolutionary theory (Oster and Wilson 1978). At stake may be our very understanding of the process of natural selection.

I have selected the *Atta* leaf-cutter ants for analysis of efficiency and optimization because they possess caste systems and patterns of division of labor that rank among the most complex found in ants (Wilson 1980). They provide an unusual number of opportunities to measure and evaluate performance. As understanding of the species increases, we can hope to understand better the forces that have set an upper limit on the social evolution of ants.

I have, for the moment, further narrowed the choice of tasks to leaf cutting, for two reasons. First, the work is performed by the ants outside the nest and is therefore experimentally more easily managed. Second, the great majority of leaf cutters fall within

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an intermediate size range of workers (head width 1.8–2.8 mm) that engage in few other tasks (Wilson 1980); the evolution of the workers within this size segment with reference to leaf cutting is consequently less likely to have been compromised by necessities imposed by other modes of specialization.

The ideal way in which to test the natural selection hypothesis and to estimate the degree of optimization is to first write a list of all conceivable optimization criteria, deduced a priori from a knowledge of the natural history of the species. The next step is to conduct experiments to determine which of the criteria has been most closely approached, and to what degree. Finally, with the results in hand, the theoretician can alter behavioral and anatomical parameters in simulations in order to judge whether the species is capable of still further optimization by genetic evolution. If the approach actually taken by the species cannot be significantly improved by the simulations, we are justified in concluding that the species has not only been shaped in this particular part of its repertory by natural selection, but that it is actually on top of an adaptive peak. In other words, it is both at an optimum and evolutionarily optimized; it is doing as well as its genotype permits, and the genotype cannot evolve over short distances to produce a better optimum. This is the sequence taken in the analysis of leaf cutting in *Atta*.

The Optimization Criteria

The criteria envisioned a priori were the following:

1) Evasion or Defense. If predation were an overwhelmingly important mortality factor and hence a principal cost item in the energy budget of the growing colony (see Oster and Wilson 1978 p 169), we could expect to see evidence that the foraging caste was molded so as to place an effective defensive technique ahead of other criteria. Thus the leaf cutters might be the smallest size class capable of cutting leaves, regardless of their degree of skill or energetic efficiency. The size of these workers would enable them to run in inconspicuous, even partially hidden columns – a method employed by many other ant species, such as *Solenopsis* fire ants and *Labidus* army ants. Or the leaf cutters might consist of very large, soldierlike forms capable of fending off most enemies. Alternatively, a mixed technique might be employed: small foragers guarded by a large soldier caste; this is in fact the method employed by some other ant species, including members of the genus *Pheidole*.

2) Skill and Running Velocity. Pure skill is the rate of cutting measured by the length of the cut or the weight of material cut, regardless of the degree of attraction, initiative, or energetic efficiency. Running velocity determines how quickly the foragers can retrieve the material. These criteria are expected to be dictated by natural selection if there is a premium on speed, due for example to predator pressure or shortness of time in which the vegetation can be harvested.

3) Energetic Efficiency. This is the criterion to be expected if the foragers are acting as a relatively untroubled economic system, attempting to maximize their net energetic yield in an environment not excessively dominated by predators and with a relatively plentiful food resource. Skill and running speed continue to matter a great deal, but attraction to the vegetation and initiative in cutting would be expected to be adjusted in evolution so as to enable workers to cut the maximum amount of vegetation per unit of energy expended. There exist in turn two categories of energy expenditure. The first is *construction cost*: the number of calories required to rear a worker of a given size class from egg to adult; this quantity is reasonably assumed to be a linear function of the dry weight of the adult. Construction cost can be expected to rise to the status of a major factor in the energy budget if mortality is high. Consider the extreme imaginable case in which every leaf-cutter worker dies following its first foraging trip; then a very large part of the cost of leaf cutting must come from the heavy construction costs of daily forager replacement. The second category of energy expenditure is *maintenance cost*: the rate of metabolic energy consumption by a worker ant. In the extreme imaginable case, in which foraging workers live for the life of the queen, maintenance cost would be paramount and construction cost minor. In the intermediate case, where active members of the leaf-cutting class survive for periods of weeks or months, maintenance will outweigh construction, but to a degree that has not been determined. The prudent course in evaluating energetic yield is to measure both categories of cost, that is, both construction and maintenance, and treat them as a mix.

In order to evaluate adherence to the three competing criteria of optimization, both in the real species and in potentially evolvable species, it is necessary to measure the following properties for each size class in turn: tendency to leave the nest on foraging expeditions, attraction to fresh vegetation, initiative, pure skill in leaf cutting, performance in leaf cutting, energetic efficiency by the two cost criteria (construction and maintenance), speed and cost of running back and forth between the nest and vegetation, and differential mortality. In the present study, all of these properties have been measured across the size range of *Atta sexdens* workers except for the last, differential mortality. I have not been able to estimate the death rate of workers under natural conditions. Nevertheless, I believe that it is a relatively minor factor, for the reason that foraging workers in the laboratory are long-lived and do not appear, at least under these special conditions, to vary significantly in mortality rate as a function of size. On the other hand, the role of other factors, particularly cutting skill, does vary so greatly with size as to outweigh greatly the effects of all but the most striking differential mortality.

Materials and Methods

The study was conducted with a colony of *Atta sexdens* (Linné) from Timehri, Guyana, about eight years of age and containing the original mother queen and approximately 7,000 workers. The colony was maintained in a closed series of clear plastic chambers 14 cm × 19 cm and 9 cm high. Foraging workers were allowed to leave the chambers through a 26-mm-wide plastic tube that opened onto the floor of a foraging platform. The platform, measuring 32 cm × 40 cm, was the bottom of an inverted enameled metal tray, which was set in turn in a larger, upright tray partly filled with water to provide a moat. During the routine maintenance of the colony, a wide variety of vegetable materials was given to the foraging workers, including the leaves and flowers of several plant species as well as wheat germ and other dry cereals. As the colony expanded, the ants filled one chamber after another with characteristic spongelike masses of degraded and processed vegetable material, through which the whitish symbiotic fungus (*Rozites*) grew abundantly. In the experiments of leaf cutting, petals of American roses (ForeverYours variety) were used to represent soft vegetation, while the thick, leathery leaves of overwintering ornamental rhododendron were used to represent hard vegetation. Most vegetation utilized by *A. sexdens* in the field falls between these two extremes. In order to standardize the conditions, the ants were offered ten 22-mm-wide circles of the petals or leaves freshly cut with a large cork borer. They were then observed during the ensuing period of 15 min.

The following measurements were taken. *Attraction* is the fraction of workers on the foraging table that are on or at least touching the vegetation sample; the figure is the average of three counts taken 2, 7, and 12 min, respectively, after the vegetation sample is placed on the table. *Initiative* is the number of cuts started per ant per minute by the ants attracted to the vegetation sample. More precisely, it was defined as the number of pieces of vegetation cut free by the ants divided by 15 times the average number of workers observed on the vegetable sample at 2, 7, and 12 min. *Skill* is the length of the cut made by one ant in mm/s, where the measurements apply only to the interval of time in which the ant was actually cutting. *Performance* is the rate of cutting in either mm of cut per ant per minute or mg of dry weight of vegetation cut per ant per minute, averaged over the 15-min interval following introduction of the vegetable sample and for all the workers in the foraging force, regardless of whether they were attracted to the sample or not. *Energetic efficiency by the first criterion* is the dry weight in mg of vegetation cut per mg of ant per minute during the first 15 min following introduction of the vegetable sample and for all workers in the foraging force, regardless of whether they were attracted to the sample or not. *Energetic efficiency by the second criterion* is the dry weight in mg of vegetation cut by the foraging force in the first 15 min, per μl of oxygen consumed by resting or slowly moving workers at 30° C/min. Note that the oxygen consumption was not taken while the ants were cutting the leaves, an activity that consumes only a tiny fraction of their time in nature, but while they were at rest or slowly moving about in a confined space.

Respiration was measured with Scholander manometers of a design modified by C.M. Williams and Edward Seling. Ants were placed singly or in groups of up to ten individuals of the same size in tubes 18 mm in diameter. A screen floor separated them from a layer of saturated KOH solution at the bottom of the tube, so that they had a cylindrical space 18 mm in diameter and 35 mm long in which to move. As they consumed oxygen, the reduction in volume was marked by an advancing column of dyed water drawn forward in a connecting tube by the reduced pressure. At the end of 24 h, the volume was restored by injecting oxygen with a syringe – until the column of dyed water reached the original level – and the volume of consumed oxygen was read off as the amount of advance by the plunger in the cylinder. To ensure that the apparatus was airtight, it was submerged in a beaker of water after the apparatus had been sealed. All tests were run at 30° ± 2° C.

The heart of the experimental procedure is the creation of what I have loosely called *pseudomutants*. These can be defined as colonies or fractions of colonies in which the age-sex ratios have been altered in chosen ways by differentially screening out members of various age-sex classes. Thus the foraging *A. sexdens* workers were all older individuals and mostly medias, in the head-width range 1.8–2.8 mm, accompanied by a few smaller and larger individuals. As this foraging force emerged onto the platform each morning, I removed all of the workers except those of the size class (say, head width 1.0–1.2 mm or head width 2.2–2.4 mm) whose performance I wished to study on that occasion. Thus it was possible to create a 'pseudomutant', a colony which for the moment fielded a worker force consisting exclusively of minors or medias of a narrowly restricted size range, as though its caste ratios had been altered by a genetic mutation. The performance of each size class could be evaluated separately, without the complicated interaction effects caused by the presence and activity of other size classes. Moreover, the same colony – and even part of the same set of foraging workers – was used throughout, minimizing variance due to overall colony size and health.

In the report to follow, the frequency distribution of the size classes is referred to as the *caste distribution function* (CDF), to align the experimental results with the models of Oster and Wilson (1978). The unmodified foraging force is then said to possess a natural CDF, while the 'pseudomutant' force altered by restriction is called a synthetic CDF. The size measurement used is the *head width* (HW) of ant systematics, defined as the greatest width of the head that can be obtained by measuring at right angles to the longitudinal axis of the head while the head is viewed full face.

Results

As illustrated by the data in Fig. 1, the population of *A. sexdens* workers that left the laboratory nest to forage has nearly the same size-frequency mode as the populations that cut various kinds of vegetation (HW 2.2–2.4 mm), although the range is slightly greater (HW 1.2–4.0 mm as opposed to 1.4–3.8 mm). However, both explorer and cutter samples were very

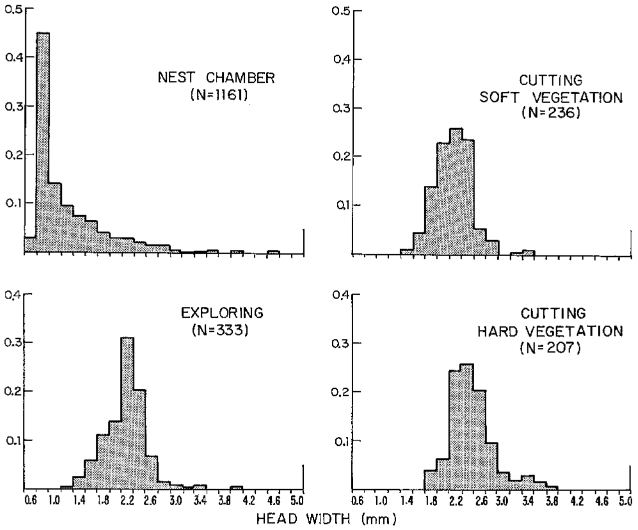

Fig. 1. The frequency distributions shown are of workers of the *A. sexdens* laboratory colony collected at random from a nest chamber during a period of nonforaging (hence representative of the colony as a whole), other workers sampled while exploring the foraging platform outside the nest, and still others sampled while cutting vegetation. Soft vegetation was represented by rose petals, hard vegetation by rhododendron leaves (see additional size-frequency data in Wilson 1980)

different from the overall colony population, which had a mode of 0.8 mm and proportionately few workers in the HW 2.2–2.4 mm range. The population cutting soft vegetation had a somewhat smaller overall head width than that cutting hard vegetation, but the modal difference is less than 10%; additional data on variation as a function of vegetation type are given in Wilson (1980). In general, workers in the exploring and foraging population are substantially larger in average size than those drawn randomly from the total nest population. They consist mostly of medias in the 1.8–2.8 mm range. The trait is probably a general one in this and closely related species. Authors who have observed *A. sexdens* and other *Atta* species in the wild refer consistently to medias as the leaf-cutter caste (references in Wilson 1980). In the film 'Millions of years ahead of man' (Taunus Film, GMBH, Wiesbaden, West Germany), workers of *A. sexdens* are shown foraging and cutting leaves in the field in Brazil; from the proportions of the head and body, I have subjectively estimated them to fall in the size range HW 1.8–2.8 mm. Samples of *A. sexdens* from Panama (Ancon Hill, Balboa, Gamboa) collected while cutting a wide variety of types of vegetation in the field also conform to the size distribution of *A. sexdens* leaf cutters in the laboratory. All of four samples had modes at HW 2.2 mm. Comparable but more variable results were obtained with ten colonies of *Atta cephalotes* sampled in the field at three localities in Ecuador. Cherrett has presented data on the size of foraging *A. cephalotes* workers in Guyana rain forest. With the aid of allometry curves, I have transformed his data, which are based on the length of the hind femur, into frequency curves based on the standard head-width measurement. The mode of workers collecting flower parts is HW 2.1 mm and that of workers collecting leaves is HW 2.4 mm, a result closely consistent with curves obtained in my own studies with both *A. cephalotes* and *A. sexdens*.

Using the 'pseudomutant' method, I tested all size groups in the HW 1.0–3.6 mm range at 0.4-mm intervals to determine the degree of their attraction to vegetation, initiative in cutting, cutting skill, and overall performance. As noted previously, two types of vegetation were chosen to represent different degrees of hardness: rose petals as a form of very soft vegetation, and the thick, tough evergreen leaves of ornamental rhododendron as a form of relatively hard vegetation. The results are presented in Figs. 2–4. A further estimate displayed in Figs. 2 and 3 is energetic efficiency measured by the criterion of construction costs; this measure is based on the dry weight of leaves cut in mg per mg of dry weight of the ants, taken as a function of worker size (HW). The conversion of the linear size measurement (HW) to dry weight of the entire ant, required for the estimate of energetic efficiency by the construction criterion, is given in Fig. 5. In Fig. 4, the energetic efficiency by the maintenance criterion is given. The measure used is the amount of dry-weight vegetation cut per μl oxygen consumed per mg dry weight of worker at rest in 30° C ambient air.

The oxygen consumption rate of workers used to evaluate maintenance cost is presented in Fig. 6. In this illustration, the curves are fitted to the power equation with reference to the standard linear measure (that is, head width), in order to facilitate estimates of energetic efficiency with reference to maintenance costs across the worker size range. However, to make the data more accessible to physiologists, the data can also be expressed in the more conventional form relating oxygen consumption to total body dry weight, as follows:

$$y = 3.52\, w^{0.79}$$

where y is O_2 consumption in μl per individual ant per hour at 30° C, and w is the total dry weight of the individual ant. These parameters are consistent with those obtained by Jensen and Nielsen (1975) for nine species of European ants. All of their combined data fit the following equation:

$$y = 1.95\, w^{1.01}$$

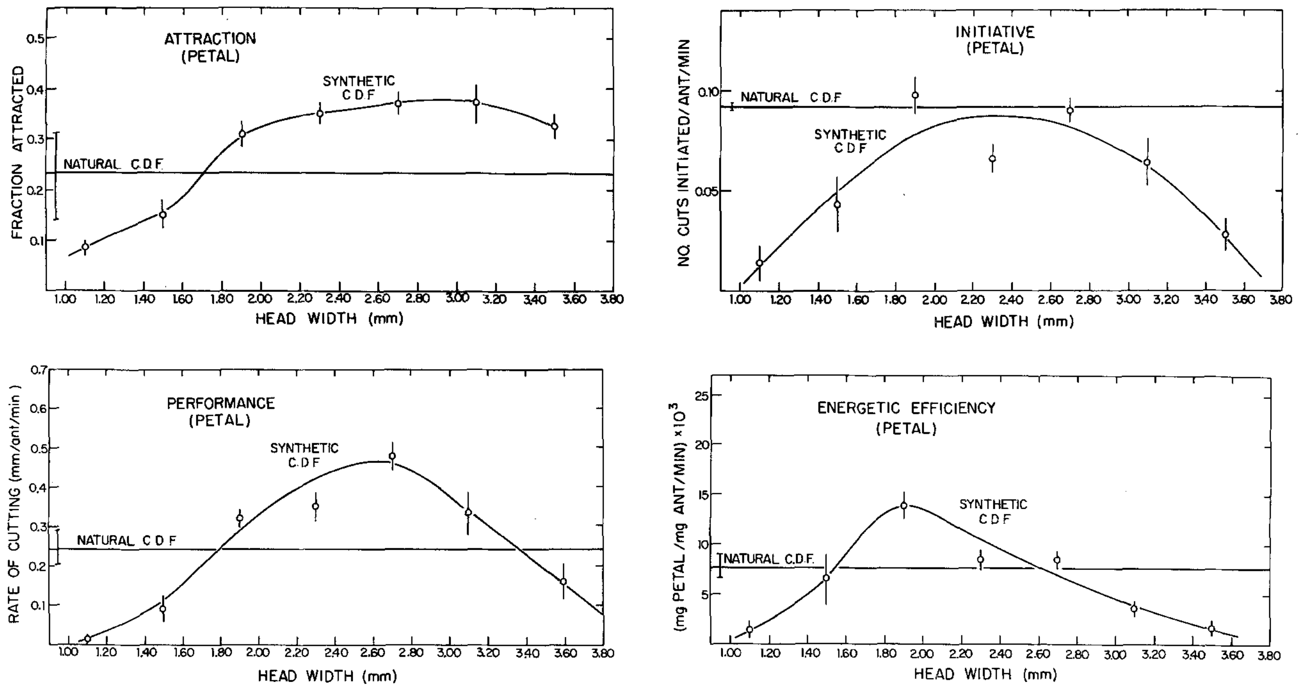

Fig. 2. The capabilities of isolated ensembles of *A. sexdens* workers of varying sizes in the handling of soft vegetation, represented by rose petals. Energetic efficiency shown here is based on the criterion of construction costs, estimated from the total dry body weight. The *natural CDF* (caste distribution function) is an unmodified group of foragers; the *synthetic CDFs* are the groups reduced to consist only of members of single size classes

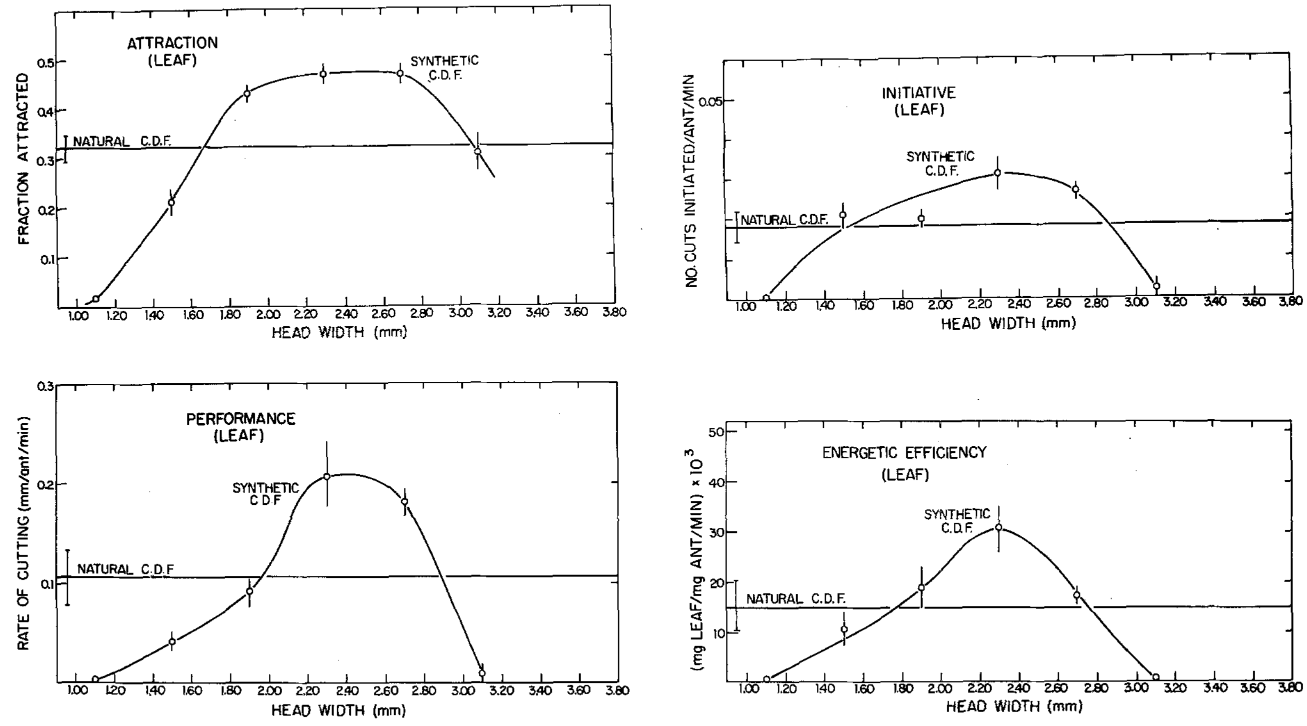

Fig. 3. The capabilities of isolated ensembles of *A. sexdens* foraging workers of varying sizes in the handling of hard vegetation, represented by overwintered rhododendron leaves. Energetic efficiency shown here is based on the criterion of construction costs, estimated from the total dry body weight

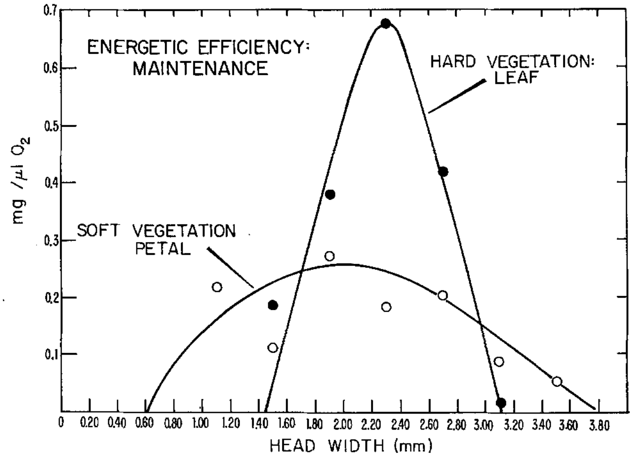

Fig. 4. Energetic efficiency estimated on the basis of maintenance. The measure used is the dry weight of vegetation cut per mg dry weight of worker per unit time, divided by the oxygen consumed by mg dry weight of resting workers in μl per unit time, at 30° C (oxygen consumption data are displayed in Fig. 6)

The *A. sexdens* values fall well within the total range of parameter values displayed among these European species, and the measurements obtained are also consistent with the response of the European species to the higher temperature employed (30° C). It is of interest that the power coefficient is significantly less than 1.0 in *A. sexdens*, so that maintenance cost falls off with an increase in size.

The skill of workers in cutting the two extreme forms of vegetation as a function of head width is illustrated in Fig. 7. These data reveal several notable features. First, the curves for petal cutting and leaf cutting are parallel, allowing the inference that the slope ($a=0.1$) is relatively invariant for all forms of vegetation. Second, the curves are linear or nearly so; as the head width increases by a given proportion, the cutting skill increases by an approximately equal proportion. The fact that skill so closely reflects linear dimensions, rather than area or volume of the head, may be of still wider significance. Skill might well depend primarily on the length of the mandibles, which is related to head width as follows:

$$y=0.11+0.34x$$

where y is length of the mandibular blade and x is head width (based on measurements of 23 workers in the range HW 0.6–3.8 mm).

Finally, and this is a feature of unusual importance in the ecology of *A. sexdens*, all size classes are at least theoretically capable of cutting the softest vegetation, although the smallest (HW 0.6–1.0 mm) have not been observed to do so, and even though their skill – estimated by an extrapolation of the curve – would be very low. On the other hand, rhododendron leaves can be cut only by ants with HW over 1.6 mm. By comparing the two skill curves, it is apparent that most fresh vegetation of moderate to very

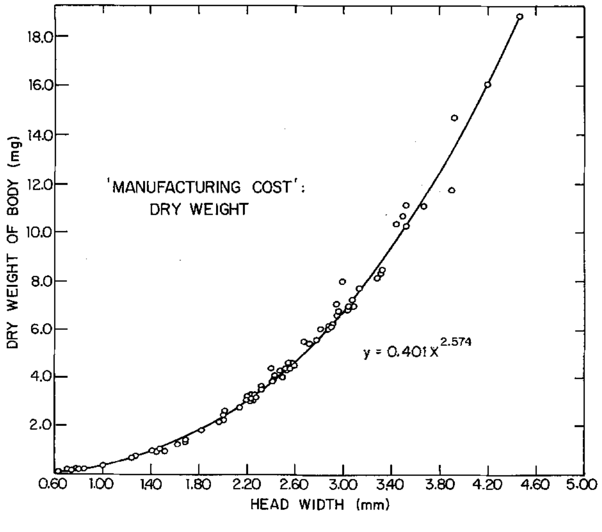

Fig. 5. The relation of head width to body dry weight in workers of *A. sexdens*, used in the analysis of energetic efficiency

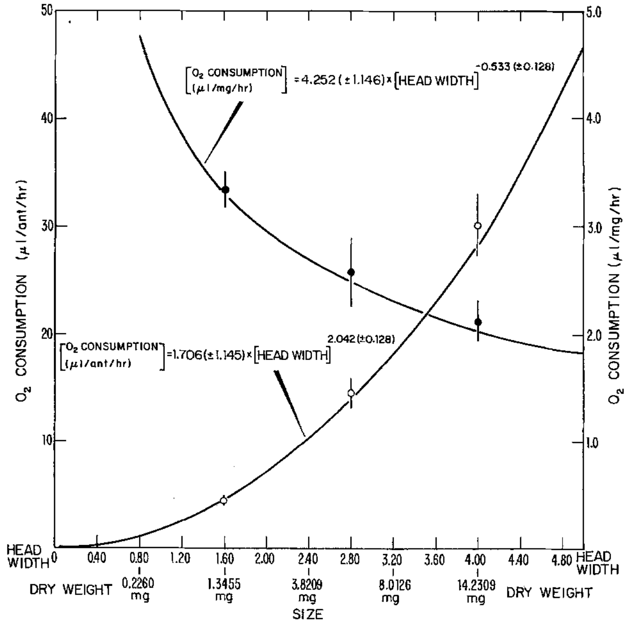

Fig. 6. Oxygen consumption rate of workers of varying sizes at 30° C, given as a function of both total body dry weight and per mg of dry weight

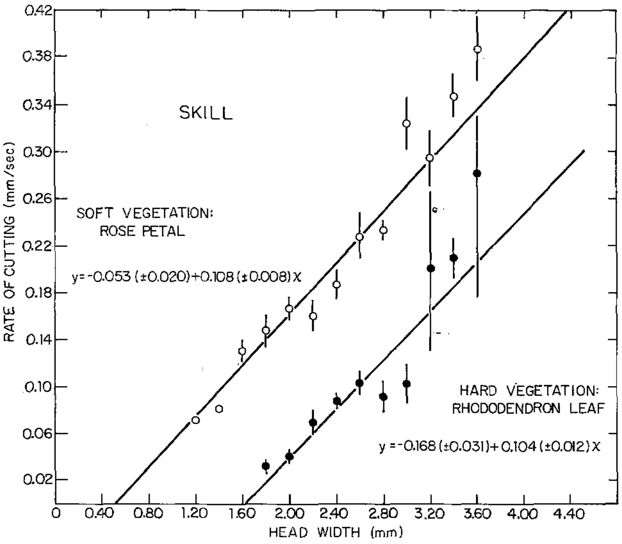

Fig. 7. Skill at cutting soft vegetation (rose petals) and hard vegetation (rhododendron leaves) as a function of head width

hard consistency could not be handled by workers with head widths less than a head width of about 1.4 mm. The inference is consistent with the fact that relatively few workers in the numerically dominant size class of head width 0.6–1.4 mm leave the nest on foraging expeditions.

Finally, the running speed of workers in the various linear size classes is evaluated in Fig. 8. It is an interesting fact that velocity changes very little over a wide range of size variation, and an even more remarkable fact that the *average* velocity of burdened and unburdened running changes not at all as a function of linear size. The result can be interpreted as an adaptation to maintain an even traffic flow in the foraging columns, so that workers of large size do not overtake and trip over their smaller nestmates. Without doubt this is a result of the uniform velocity; the smooth flow of the *A. sexdens* foraging column in both the laboratory and the field is an impressive sight. However, the data are also consistent with a more general, canonical rule (see, for example, Alexander 1971): because the work performed per unit time is a constant times body mass ($a \times M$), and the work done during running is equal to the kinetic energy expended, which is equal to another constant times the square of velocity, multiplied by the mass ($b \times M \times V^2$), it follows that

$$aM = bMV^2$$

$$V = \left(\frac{a}{b}\right)^{\frac{1}{2}}$$

In other words, velocity should be a constant independent of body size.

Discussion

The conclusions suggested by the data in this ergonomic study can be stated very simply. In its performance of leaf cutting, *Atta sexdens* does not depend upon an 'evasive' caste as part of a defensive strategy, the possibility suggested by the first a priori criterion. To be specific, it does not commit the smallest size class (HW 1.6 mm, see Fig. 9) capable of cutting most forms of vegetation. Similarly, colonies of the species do not depend upon their soldiers for leaf cutting, the possibility raised as an alternative defensive strategy. In fact these individuals, with HW exceeding about 3.4 mm, rarely cut leaves at all (see Fig. 1). Furthermore, *A. sexdens* has not utilized the workers with the greatest pure skill. These too would be the largest individuals (Fig. 7), which do little or no cutting.

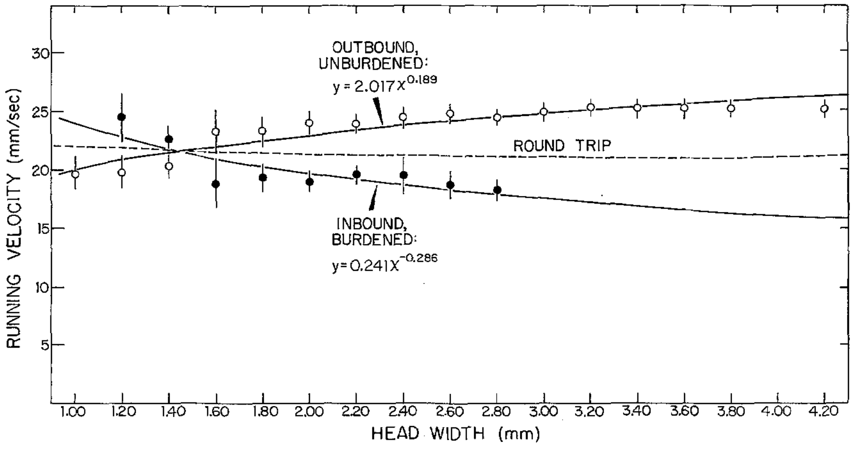

Fig. 8. Running velocity of workers traveling to the foraging arena unburdened and returning to the nest carrying fragments of leaves, as a function of head width. The measurements were taken in an ambient air temperature of 25 ± 1° C

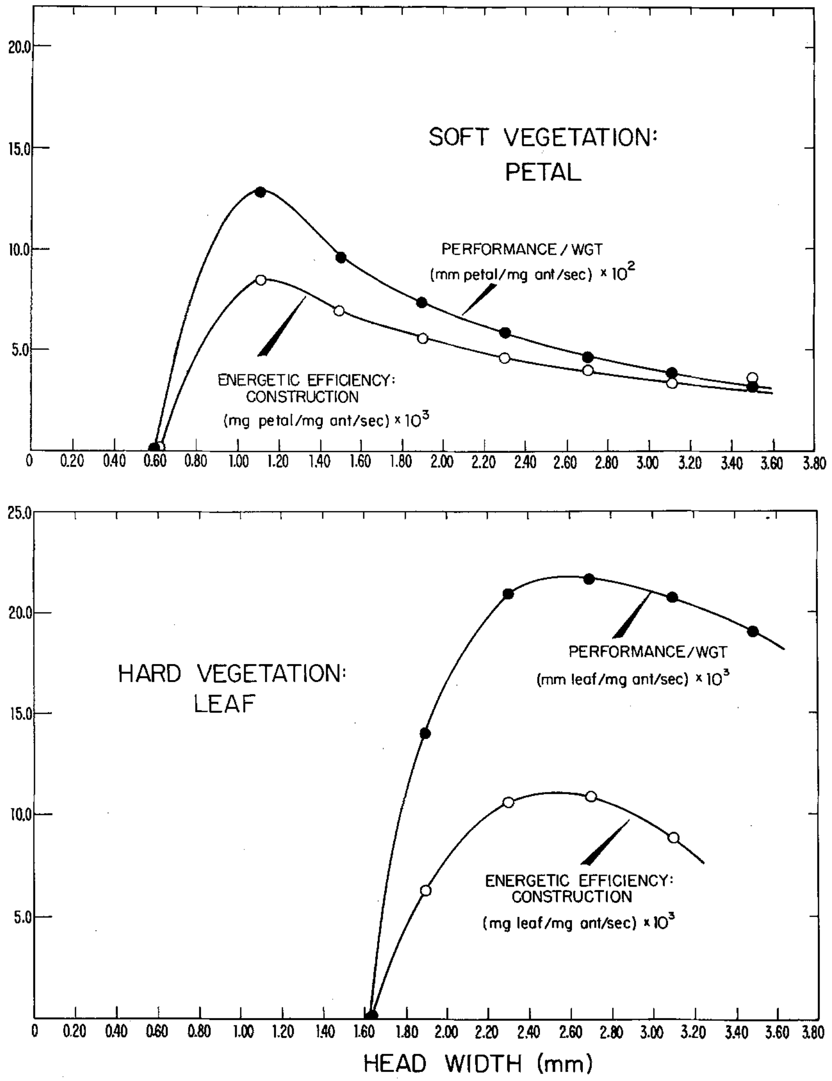

Fig. 9. The theoretical maximum performances and energetic efficiencies (construction criterion) of various worker size classes. These are the values obtained if every one of the workers in all size classes of the foraging force were attracted to the vegetation and all initiated cutting, but continued to display the size-dependent skill characteristic of the species. The numbers are consequently the skill in mg dry weight of vegetation cut per ant divided by the body dry weight of one ant, given for each size class in turn. (Compare with Fig. 10)

What *A. sexdens* has done is to commit the size classes that are energetically the most efficient, by both the criterion of the cost of construction of new workers (Figs. 2 and 3) and the criterion of the cost of maintenance of workers (Fig. 4). The two energetic criteria, cost and maintenance, turn out to be virtually indistinguishable; by optimizing with respect to one, the species at least approximately optimizes with respect to the other.

Moreover, *A. sexdens* has adapted more closely to hard vegetation, represented in the experiments by rhododendron leaves, than to soft vegetation, represented by rose petals. There has been a remarkably close match with the requirements posed by this kind of material, which can be seen by comparing the size-frequency distributions of foragers in the laboratory (Fig. 1) with the energetic efficiencies estimated by the pseudomutant technique (Figs. 2 and 3). The maximum energetic efficiency of rhododendron-leaf cutting is obtained by workers within HW 2.2–2.6 mm, which is also the mode of the size-frequency distribution of workers cutting rhododendron and most other forms of vegetation. Since the full size range of the worker caste is HW 0.6–5.4 mm, it is reasonable to say that the species is accurate to within (2.6–2.2)/(5.4–0.6) = 0.083, or about 10%, of the energetic optimum. This can be taken as the upper limit; the ants may have done better than 10%.

Why has the species fitted its innate polyethism curve more closely to hard vegetation than to soft vegetation? The answer, I believe, can be deduced from the skill curves presented in Fig. 7. The smallest workers capable of cutting rhododendron leaves are about HW 1.6 mm. Since most of the vegetation collected by free-living colonies of *A. sexdens* consists of at least moderately tough leaves (John Wenzel, personal communication), the colony will field a partly idle work force unless it utilizes workers over HW 1.6 mm.

In summary, the evidence clearly shows that *A.*

sexdens are operating at or close to the optimum defined by the criterion of energy harvesting. But are they *optimized*? This is a question seldom addressed in the literature of behavioral ecology. Translated into operational terms, it can be restated as follows: is there any direction in which *A. sexdens* can evolve further – short of a major anatomical or behavioral reorganization – so as to commit another size group that is even more energetically efficient than HW 2.2–2.6 mm? If not, then the species can be said to be truly optimized in an evolutionary sense. It sits atop an adaptive peak (see further discussion in Wilson 1975 p 24).

In order to answer the question of true evolutionary optimization at least in part, I treated the *A. sexdens* foraging system as a problem in design, considering which features might be changed readily in evolution and which cannot. On a priori grounds, the features most readily altered are behavioral, especially attraction to vegetation and initiative in cutting. These belong to broad categories of behavior that have changed most readily in genetic experiments on laboratory populations of other insect species (see, for example, Dobzhansky et al. 1972; Ehrman and Parsons 1976). The feature less readily altered is skill, which is a linear function of size, based on a head and mandibular form conventional for ants generally, and hence likely to be an evolutionarily stable trait. The relation between size and skill probably could not be significantly altered without large changes in the allometry of head shape, and even then all that might be affected is the slope of the allometric curve – with little final alteration redounding in the final relation between size and skill.

Consequently, I conducted a thought experiment in which attraction and initiative were allowed to evolve to uniform maximum levels for all size classes. The skill curves (Fig. 7) were not altered. Then new, theoretical maximum curves for performance and energetic efficiency, drawn across all size classes, were calculated on the basis of the empirical data for skill, dry body weight, and oxygen consumption. The results, given in Figs. 9 and 10, show that energetic efficiency in cutting petals is relatively insensitive to variation in worker size. But efficiency with reference to hard leaves remains very sensitive. It also does not shift very much: only from HW 2.2–2.4 mm to HW 2.6–2.8 mm, or about 8% of the total worker size range. Thus *A. sexdens* can be said to be within approximately 10% of the theoretical maximum level of energetic efficiency attainable by short-range evolution. It lies on or very close to the local adaptive peak. While it might be possible to design an imaginary leaf-cutting ant with higher levels of efficiency than *A. sexdens*, and in that sense identify a distant, higher adaptive peak, there appears to be no higher peak in the close vicinity of the *A. sexdens* genotype, and it is therefore likely that the species has stabilized with reference to its leaf-cutting behavior and performance.

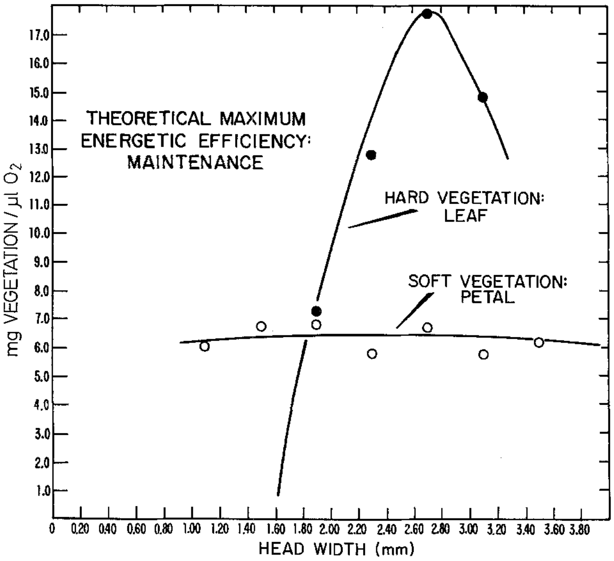

Fig. 10. The theoretical maximum energetic efficiencies (maintenance criterion), derived according to the same criteria employed to obtain the theoretical maxima with respect to the construction criterion (see Fig. 9). The values given are the skill in mg dry weight vegetation cut per worker divided by the oxygen consumption of one worker for each size class in turn

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