68-15,954

TOPOFF, Howard R., 1941-
POPULATION CHARACTERISTICS, REVERSIBLE PHYSIOLOGICAL CONDITIONS AND BEHAVIOR IN SPECIES REPRESENTING THREE DORYLINE ANT GENERA.

The City University of New York, Ph.D., 1968
Zoology

University Microfilms, Inc., Ann Arbor, Michigan

POPULATION CHARACTERISTICS, REVERSIBLE PHYSIOLOGICAL CONDITIONS AND BEHAVIOR IN SPECIES REPRESENTING THREE DORYLINE ANT GENERA

by

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A dissertation submitted to the
Graduate Faculty in Biology in partial
fulfillment of the requirements for the
degree of Doctor of Philosophy,
The City University of New York.

1968

This manuscript has been read and accepted for the University Committee in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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ACKNOWLEDGMENTS

I wish to thank Dr. T. C. Schneirla, the principal sponsor of this research. I would like particularly to extend my appreciation to him, not only for his assistance and guidance throughout the study, but also for his theoretical contributions concerning problems of behavioral development on all phyletic levels. Through an understanding of his approach to behavioral studies, the significance of the present investigation has increased greatly.

I also wish to thank the many people who assisted in the investigation. I would like to acknowledge the valuable assistance of Miss Ann Young, who participated in all aspects of the field and laboratory work. The field work was conducted at the American Museum of Natural History's Southwestern Research Station, in Portal, Arizona, and I wish to thank Mr. Vincent D. Roth, the Station's director, for his cooperation. The following people, as student participants in the American Museum of Natural History's Undergraduate Research Program, also assisted in the field and laboratory program: Mr. Steven Vaeth; Mr. Steven Chernesky; and Miss Rona Lieberman. Dr. June Tice assisted in the final preparation of the manuscript.

This research was conducted during a three-year period, as a recipient of a National Defense Education Act Fellowship, awarded through the City University of New York.

A large part of the work conducted in the doryline laboratory at the American Museum of Natural History, was made possible by financial support from the National Science Foundation, to Dr. T. C. Schneirla, principal investigator of the doryline project. Field work at the Southwestern Research Station during the summer of 1964 was made possible by a grant from the Lincoln Ellsworth Foundation of the American Museum of Natural History. Support for the summer of 1965 was provided by a grant from the City University of New York.

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INTRODUCTION

Description of the Nomadic-Statary Functional Cycle in Two Neotropical Species of Eciton

In biology, the "success" of a taxon is often evaluated in terms of its evolutionary history (as far as it can be determined) and its present ecological status. These, in turn, are measured by species diversity, population size and geographical range, and the biological role that the group plays in the ecosystem of its habitat. By these criteria the ants of the subfamily Dorylinae may be considered an extremely successful group.

The doryline or army-ants have evolved in both the Old and the New World under the influence of the complex ecological factors that exist in tropical environments. This aspect of their phylogenetic history undoubtedly provided many of the conditions necessary for the evolution of the complex behavior patterns and population characteristics that typify army-ant life. These patterns and characteristics include the interrelationships between group raiding in populations of large size, an essentially carnivorous diet, and the periodical shifting of home nest sites. This paper is an attempt to evaluate a series of field and laboratory investigations designed to elucidate the biological bases of doryline colony behavior.

The relationships between the massive foraging and periodic changing of nest sites by tropical army-ants, which were well known to the early field naturalists and biologists, logically suggested food exhaustion as the explanation for the basis of nomadic activities (Heape, 1931; Fraenkel, 1932). This was quite consonant with Wheeler's (1928) contention that a predominantly carnivorous way of life could not be maintained in a social insect species having such large populations with permanent nesting sites. Thus changes in home nests were reported as being sporadic and irregular, reinforced entirely by the need for new sources of food by the population (Vosseler, 1905). An interesting case was Müller's (1886) earlier observations of colonies of the army-ant, Eciton burchelli, in Brazil, in which he noticed a marked reduction in the strength of foraging and raiding activities corresponding to the time when the colony's massive mature larval brood entered the enclosed pupal stage of development. Schneirla (1933, 1938, 1960) has discussed the implications of Müller's observations and has summarized other aspects of the history of doryline research.

These early reports of army-ant nomadism and behavior based on the food-exhaustion hypothesis, together with the suggestions derived from Müller's observations, provided the groundwork for a preliminary series of field investigations of army-ant behavior and biology in tropical America (Schneirla, 1933, 1934, 1938, 1944a).

The adequacy of the food-exhaustion hypothesis was first tested, in Panama, during the course of several short studies of colony behavior in the column raider *Eciton hamatum*, a neotropical doryline species ranging between 26°N. and 26°S. (Schneirla, 1933, 1934). This was followed by a long-term study during the rainy season of 1936 (Schneirla, 1938). Finally, a similar project was initiated in 1938 (Schneirla, 1945), for colonies of the swarm raider and closely related, sympatric species *Eciton burchelli*.

As a result of these studies it became increasingly clear that the emigrations reported by the earlier field biologists were not random displacements of army-ant populations based upon local food shortages. Instead, Schneirla's investigations provided the description of an organized and highly consistent pattern of colony behavior and related biological processes. Studies on both *E. hamatum* and *E. burchelli* yielded evidence for a marked regularity in fluctuations of colony activity, related to a reversible, cyclic pattern, divisible into two functional phases: the nomadic phase and the statary phase.

For both of these surface-adapted species the nomadic phase, which lasts for 16 - 18 days in *E hamatum* and 12 - 17 days in *E. burchelli*, is one of high and continuously increasing colony activity, in which successive massive daily raids typically end in an emigration to a new nest site or bivouac. This is followed by a statary interval lasting 19 - 20 days in *E. hamatum* and 19 - 22 days in *E. burchelli*, characterized by a marked reduction in population activities, especially in terms of the intensity of diurnal raiding and the absence of colony emigrations (Schneirla, 1938, 1944a, 1949, 1957a, 1965).

Major differences in levels of general colony activity during both behavioral phases, include patterns of raiding, the quantity and quality of pillaged food or booty, and locations of temporary nests. During the nomadic phase, foraging in the column raider *E. hamatum* is carried out on relatively stable chemical trails consisting of digestive products or fecal material (Schneirla, 1944b; Schneirla and Brown, 1950; Watkins, 1964, Blum and Portocarrero, 1964). In this species, these trails develop daily into a tri-dendritic pattern of main trails, each with many branched columns, that end in small separate terminal groups. During this phase booty consists not only of soft-bodied larval and pupal broods of other species of ants, but of substantial amounts of the hard-bodied adults as well. At the end of each diurnal raid during the nomadic phase a bivouac, consisting entirely of the clustered bodies of the army-ant workers, is established on or above the surface of the forest floor (Schneirla *et al.*, 1954; Schneirla, 1957a).

A very different set of processes obtains during the relatively quiet statary interval. Colony raiding is markedly reduced in terms of the numbers of participating individuals and usually takes place on a single basal column, which originates from the statary bivouac and remains connected with it. In addition the terminus of the column has a much less complex dendritic pattern (Schneirla, 1934, 1957a, 1965). Throughout the statary phase the amount of pillaged booty is far below the quantity brought back to the bivouac during the nomadic phase, and consists almost entirely of the soft-bodied broods of other ant species. Finally, the single statary nest which lasts all through this phase is constructed in a relatively well-sheltered place such as the inside of a hollow tree stump or log.

Although the abundance of food in local areas may have played an important part in the evolution of nomadism in animal populations of large size, for the dorylines an interpretation based more upon processes existing within the colonies has been advanced. The causal basis of the behavior cycle described for colonies of neotropical army-ants lies in relationships between the massive developing broods and the adult worker population; for both the nomadic and statary phases begin and end in close correspondence with the manifold biological changes associated with the condition of the brood throughout its larval, pupal, and newly eclosed (callow) stages of development (Schneirla, 1940, 1944a, 1957a, 1968).

At the beginning of a nomadic phase a mature brood completes its pupal development and emerges from the cocoons as lightly-pigmented callow workers. The callows are at the same time very attractive and highly excitatory to the adult workers. As a result the callows enter into an intensive trophallactic relationship with the workers. In this context "trophallaxis" refers to the mutual transfer of nutrient and other bio-chemical substances as detailed in Wheeler's (1928) original theory, as well as its extension by Schneirla (1941, 1946) to include inter-individual stimulation involving the olfactory, gustatory, and tactual modalities as well. The workers respond to the callows by stroking, licking, and dropping pieces of booty on them. This sudden and intensive social stimulation, originating through callow-adult interactions, is transmitted throughout the bivouac by communication between adults, and starts the colony off on a new nomadic phase. During the early days of this phase, the callows mature and become visibly (and presumably physiologically) indistinguishable from the adults, with the result that their chemical and chemotactual excitatory effects wear off. Nomadic activities in the colony are now maintained by comparable stimulation imparted to the adult workers by a brood of developing larvae, hatched from eggs laid approximately mid-way during the previous statary phase. Later, as this maturing larval brood, consisting of 80,000 individuals in *E. hamatum* and 200,000 in *E. burchelli* (Schneirla, 1965, 1968), enters into and develops throughout the pupal stage, the adult worker population receives only minimal stimulation, and the colony passes into the statary phase. Midway through this phase the colony queen lays a new batch of eggs which begin development as embryos, and hatch into microlarvae at approximately the time that the present pupal brood ecloses. This initiates a new nomadic phase and the cycle is repeated.

In the American tropics this sequence of alternating nomadic and statary phases normally continues uninterrupted throughout the entire year. The only major deviation from the basic pattern occurs at the beginning of the dry season, when processes associated with the development of an annual sexual brood typically lead to the division of a colony into two daughter colonies (Schneirla and Brown, 1950, 1952). For *E. hamatum* a sexual brood consists of approximately 1500 male individuals and six queens. The sexual larvae develop at a faster rate than those of an all-worker brood, resulting in a concomitant shortening of the nomadic phase. Still, the trophallactic relationships between the sexual brood and the adult workers as the basis for nomadism, are fundamentally equivalent to the reciprocal stimulative interactions described for all-worker broods

(Schneirla and Brown, 1952). For a fuller discussion of sexual brood production in relation to colony division, see Schneirla (1949, 1956a).

Extension of Brood-Stimulative Theory, as the Basis for Phase Alternation, to Species of the Doryline Genus, *Neivamyrmex*

The doryline genus *Neivamyrmex* differs from *Eciton* in several important aspects of its ecology. In comparison with *Eciton*, which has approximately 13 described species, *Neivamyrmex* is a much larger genus with over 113 species described (Borgmeier, 1955). Also, while species of *Eciton* are essentially tropical, *Neivamyrmex* ranges well into the north and south temperate zones, from approximately 45°N. to 45°S. The surface raids and bivouac locations of *E. hamatum* and *E. burchelli* enable these to be classified as epigaeic species (Schneirla, 1957a). Although several species of *Neivamyrmex* carry out raiding activities on the surface of the forest floor, much of the foraging is conducted in subterranean root systems. This, together with the fact that colonies of most species of *Neivamyrmex* nest in the soil, in hollowed-out root systems of dead trees, or in rotted tree stumps, characterizes this genus as relatively hypogaeic (Schneirla, 1958). Especially significant for those species of *Neivamyrmex* that extend into the temperate regions, is the problem of the adaptation of each aspect of colony life to ecological conditions associated with an annual winter (Schneirla, 1963).

Various aspects of the behavior and biology of species of *Neivamyrmex* have been discussed in the literature (Wheeler, 1900, Smith, 1927, 1942). Additional references to the earlier literature concerning *Neivamyrmex* have been cited by Schneirla (1958). Based upon preliminary observations of neotropical colonies of *Neivamyrmex pilosus*, *N. sumichrasti*, and *N. gibbatus*, in which large numbers of newly emerged callow workers were found in emigrating columns, Schneirla (1958) hypothesized a set of mutual stimulative relationships, centered around brood production as related to cyclic colony function, comparable to those described previously for *Eciton*. Later, he proposed a theory of army-ant behavior based upon colonies having a distinct nomad-statary cycle, for the nearctic species *Neivamyrmex nigrescens* in the Southwestern United States, similar to that for species of *Eciton* in the tropics (Schneirla, 1958, 1961). Although both the adult population and brood size in colonies of *N. nigrescens* is considerably smaller than in either of the two species of *Eciton* studied, the cycle in both genera nevertheless depends upon stimulative effects from the brood as necessary factors, and continues all through the functional season. In the area studied, cyclic functions end in September when brood production by the colony queen ceases. Then, during the spring months of the following season, the gradual rise of afternoon and especially of nocturnal temperatures activates the workers and initiates sub-surface and later surface foraging. As temperatures continue to increase, the resumption of raiding to a level at which large amounts of booty are again brought back into the nest facilitates increased queen feeding. With the subsequent laying and hatching of her first brood of the new season, nomadic colony functions resume (Schneirla, 1963).

Occurrence of the Characteristic Nomadic-Statary Behavior Pattern in the Old World Doryline Genus, Aenictus

The genera *Eciton* and *Neivamyrmex* belong to the New World tribe Ecitonini, which also includes the genera *Labidus* and *Nomamyrmex* (Borgmeier, 1955; Rettenmeyer, 1963). Two other tribes of doryline ants which have evolved in areas of humid tropical forests in the Eastern Hemisphere, are the Aenictini and Dorylini (the driver ants).

Aenictus, the predominant genus in the tribe Aenictini, has a wide geographical distribution, extending from Africa into Indo-Malaysia and Australia (Wilson, 1964; Schneirla and Reyes, 1966). On the basis of morphological considerations, Borgmeier (1955) and Wilson (1964) have found *Aenictus* closely related to the Old World Dorylini. However, a degree of *functional* affinity between species of *Aenictus* and the New World Ecitonini was indicated, because the recent observations of colonies of Aenictus by Chapman

(1964) and Wilson (1964) suggested that the characteristic nomad-statary behavior pattern described for the New World dorylines, also exist in certain surface-adapted species of *Aenictus* (Schneirla, 1965; Schneirla and Reyes, 1966). In three annual projects carried out in the Philippines on colonies of *A. laeviceps* and *A. gracilis*, Schneirla (1965) and Schneirla and Reyes (1966) demonstrated that cyclic colony behavior in these species is maintained through intra-colonial effects of fluctuating intensities of social stimulation derived from processes of brood development and feeding, and functionally is therefore quite comparable to the biological bases underlying the nomad-statary patterns described for *Eciton* and *Neivamyrmex*.

Significant differences occur, however, between *Aenictus* and the genera in the New World tribe Ecitonini, especially in the details of their raiding, emigrating, and nesting behavior. For example, during the nomadic phase colonies of *Aenictus* can initiate raiding at almost any time during the day or night. This contrasts with the situation found in surface-adapted species of *Eciton* in which nomadic raiding takes place diurnally, and the surface active species *Neivamyrmex nigrescens* which typically raids at night. Other properties of the *Aenictus* functional cycle which distinguishes this genus from other dorylines, have been discussed by Schneirla and Reyes (1966) and Schneirla (1968).

Species of *Eciton* and *Neivamyrmex* that have been studied in detail also exhibit differences in many important aspects of their colony behavior patterns which, as in *Aenictus*, arise from collateral variations in the structure and ecology of their populations. Still, colonies in these three genera are all characterized by regular and clearly alternating nomadic and statary phases. In all species of these genera that have been investigated the transition from one functional phase to the other has been found to depend upon coinciding fluctuations in the levels of trophallactic social stimulation between the adult worker population, the single colony queen, and a brood that changes synchronically from one developmental stage to another. On this basis Schneirla (1965, 1968) has combined the New World genera *Eciton* and *Neivamyrmex* with the Old World genus *Aenictus*, into a group-A complex, based on evidence suggesting a common evolutionary origin for the three genera in this group.

Irregular Colony Activities in the Old World Doryline Genus, Dorylus and in the New World Genera, Labidus and Nomamyrmex

In contrast to the cyclic colony behavior in the group-A complex, a qualitatively different kind of rhythmic sequence of colony activities has been found for the African driver ants, especially the subgenus, *Dorylus* (*Anomma*) (Raignier and Van Boven, 1955; Schneirla, 1957a,b). Instead of a regular alternation of nomadic and statary phases, colonies of this subgenus exhibit long intervals of sedentary nesting and raiding which are interrupted by single, prolonged colony movements (or emigrations) lasting up to several days. The statary-like intervals between emigrations are irregular and of variable duration. For *Dorylus* (*Anomma*) *wilverthi* the mode interval between emigrations is somewhere between 20 and 25 days, but intervals as short as six days and longer than 50 days have been recorded. In the related species *D.* (*Anomma*) *nigricans* intervals between bivouac changes may be as long as 100 days. Significantly, when the infrequent colony emigrations of driver ants have been observed, a major part of the brood present was completing the pupal stage of development, just prior to eclosion as callow workers (Raignier and Van Boven, 1955). Observations on colonies of the New World genera *Labidus* and *Nomamyrmex* (Schneirla, 1957a; Rettenmeyer, 1963) suggest an irregular cyclic pattern of single emigrations occurring at variable intervals, similar to the pattern described for *D.* (*Anomma*). On this basis, Schneirla (1965, 1968) has combined these three genera into a group-B complex, and has suggested that the emigrations characteristic of species in this group arise on the basis of a callow excitatory effect acting on the adult worker population in a way that is functionally equivalent to the chemical and chemotactual stimulation responsible for the *onset* of nomadism in colonies of the group-A complex. In *Dorylus* (*Anomma*), *Labidus*, and *Nomamyrmex* however the larval excitatory effect necessary to maintain increased levels of raiding and related colony activities associated with nomadism is absent, and the emigrating colonies soon settle into a new subterranean nest and renew their successive statary-like raids from this bivouac.

The factors underlying both the regular, alternating nomadic and statary phases described for the group-A complex, and the variable phases existing in species belonging to group B, are found in the interrelationship between the size of the colony's adult and brood population, and the periodicity and duration of egg laying by the functional colony queen. In the genera of group A, egg laying is restricted to a relatively short interval (e.g., seven days in *E. hamatum* and 10-12 days in *E. burchelli*, Schneirla, 1957a) occurring midway in the statary phase. This synchronization persists as the embryos hatch into larvae, as the larvae undergo pupation, and as the callow workers emerge from the pupal stage. Brood synchronization throughout all developmental stages insures that the fluctuations in trophallactic brood-adult interactions will also be synchronized, and that levels of raiding throughout the nomadic phase will be above the threshold necessary for an emigration to arise from it (Schneirla, 1957a).

In Dorylus (Anomma), Labidus, and Nomamyrmex, egg laying by the queen is more variable and extended in duration. In this group the queen may lay eggs more or less continuously, with peaks of ovulation occurring at intervals during the prolonged statary phase. This lack of brood synchrony normally prevents levels of stimulation from rising above the threshold values necessary for colony emigration, except at pupal maturity. An additional factor, arising from the immense size of both the adult and brood populations in group B, is a reduced efficiency in brood-adult and adult-adult communication. As a result, only when intracolonial developmental processes produce a sudden eclosion of a substantial part of the pupal brood within a relatively short temporal interval, does activity in the colony increase to the point of an emigration to a new nest site.

In all of the species of doryline ants studied so far, it has been found that cyclic behavior is dependent upon trophic and reproductive processes, expanded through interactions between members of the adult and brood generations, and is really independent of periodicities in the physical environment (Schneirla, 1957a). Nevertheless, for each species, significant differences have been described in every aspect of colony behavior. For example, the genera *Eciton*, *Neivamyrmex* and *Aenictus* probably evolved under somewhat similar climatic and habitat conditions; but each genus also has had an equally long history of strict ecological adaptations and specializations which has produced those patterns of raiding, emigrating, and bivouacking (and the relationships between them) that are characteristic of all its species.

The Concept of Polymorphism

Species differences in colony cyclic behavior are based upon many comparable variations in both individual and group organic properties. Anatomy, physiology, and behavior are complexly interrelated throughout the ontogeny of any individual in the colony, and organisms differing in these properties often have quite contrasting functions in colony life. Numerous examples have been described of functional and physiological differences in army-ant workers, associated with variations in morphological characteristics. These include correlations between the size of worker ants and the size of the load carried during emigrations and in the bivouac, the spatial position of the ants in the bivouac during its formation, rates of experimental desiccation, and levels of excitability in raiding and in defensive activities (Schneirla, 1953a,b,c, 1968).

For zoologists studying the biological bases of physiological and behavioral integration in populations of social insects, these intra- and intercolonial morphological variations are often described within the framework of the concept of polymorphism.

However, since current population-oriented evolutionary studies have led to an appreciation of the fact that all individuals in sexually reproducing populations exhibit structural and functional variations, much research has been canalized along lines aimed at providing information about the genetic, physiological, morphological, and ecological (including behavioral) bases of population polymorphism in general. As a result, "polymorphism" has few equals in the number of qualitatively different biological phenomena used to describe it.

As one example, population geneticists restrict the definition of "polymorphism" to: the existence in a population of two or more discontinuous genetic types, resulting from the simultaneous occurrence of several different genetic factors (Ford, 1961, 1964; Mayr, 1963).

Other workers have associated this term with studies of sex determination in the Hymenoptera. Here, sexual polymorphism (more commonly referred to as sexual dimorphism) is based upon the classical Dzierzon rule (cited in Woyke *et al.*, 1966), in which males arise from unfertilized eggs and females from fertilized eggs. Interestingly, this theory of haploid-diploid sex determination has recently been modified to include a population, multiple-allelic mechanism (Whiting, 1943; Rothenbuhler, 1957, 1967; Woyke et al., 1966).

For the present discussion, "polymorphism" will be defined as the existence within a colony of two or more intrasexual castes, without regard to their genetic or environmental origin (Wilson, 1953). In this context a caste may be considered as a group of morphologically differentiated organisms with a specialized function. In the social Hymenoptera, polymorphic studies are often restricted to variations in the female sex, including the anatomical and physiological discontinuities separating queens from workers, and the interindividual differences within a worker polymorphic series. To be sure, not all biologists are in strict agreement with this definition. Michener (1961), for one, prefers to restrict the term caste only to queen-worker divergence, and so refers to distinct forms within the worker caste as subcastes.

The strongest caste differences exist in several subfamilies of ants, in which strong queen-worker divergence is accompanied by distinct morphological diversity within the worker series. Examples of this kind of polymorphic system are the genera Eciton and Neivamyrmex in the ant subfamily Dorylinae. Weaker systems are exemplified by honeybees, bees of the tribe Meliponini (Michener, 1961), and several groups of ants, including the doryline genus, Aenictus. In Aenictus, queen-worker divergence is pronounced, but the workers are all morphologically and, at the same age, functionally much alike. The weakest caste structure exists in most social bees (other than the tribes Apini and Meliponini), social wasps (Richards and Richards, 1951) and some ant species in the subfamily Ponerinae. These groups are characterized by a minimum of morphological discontinuity between workers and the reproductive females, although physiological differences may be quite strong in some. Of course these examples do not exhaust the kinds of polymorphic systems, as many intermediate types of variation between these systems have been described (see for instance, the analyses of polymorphic differences in Halictine bees by Knerer and Atwood, 1966).

All of the above studies, in their relation to the factors that contribute to caste differentiation and to the role of castes in colony integration, have been reviewed for social insects by Light (1942, 1943), Brian (1957), Bier (1958), Michener (1961), and Weaver (1966). Included in these reviews are the termites, in which polymorphic differences exist in both the male and female sex. For a review of the factors influencing caste differentiation in termites, especially the role of social hormonal conditions, see Lüscher (1960, 1961). The origin and evolution of polymorphism in ants has recently been discussed by Wilson (1953).

Application of Allometry to Studies of Insect Polymorphism

Since the 1920's, many investigations have applied analyses of polymorphic differences to insect populations through studies centered on allometric growth of individuals during nymphal and larval stages of development, on adult allometry, and on intracolonial size-frequency distributions at all stages of the life cycle.

In its broadest sense, "allometry" refers to differences in proportions as related to changes in absolute magnitude of an entire organism or any of its parts. The variations under consideration may be morphological or physiological, and the size differences may arise during ontogeny, during phylogeny, or through any static adult comparison presumed to be a final result of intrapopulation ontogenetic processes (Gould, 1966).

Disproportionate variation, especially when related to static linear dimensions of anatomical parts of adult social insects, has frequently been described in terms of the power equation, $y = bx^k$ (Huxley, 1932). In this equation, y is a variable -usually the linear dimension of the anatomical part under consideration- whose change through the population range is studied in relation to another organismic variable x, which may represent a different dimension of the same organ, a dimension of another organ, or a measure of the size of the total body. This power function may be converted to a logarithmic form, resulting in the equation $\log y = k \log x + \log b$. This form of the equation specifies that a rectilinear graphic form will result if the logarithms of the original dependent and independent variables are plotted on rectangular coordinates. In the logarithmic equation, k is the slope of this rectilinear plot, while b is the value of y when $x = 1$. Recently, White and Gould (1965) and Gould (1966) have intensively reviewed the entire subject of allometric considerations, including its mathematical quantification and applications to a multitude of biological phenomena.

In the dorylines, polymorphic differences between individuals of a colony of *E. burchelli* have been analyzed in terms of correlative differences in the duration of development of larval series (Schneirla and Brown, 1952). Tafuri (1955) studied the developmental morphology of all-worker larval broods of *E. hamatum*, in relation to colony cyclic behavior, and he related differences in such anatomical characteristics as the developing imaginal leg discs with changes in over-all body length of the larvae during successive nomadic days. Instead of using the power function, as defined above, to analyze the non-linear relationship between leg disc dimensions and total-body length, Tafuri made use of the related exponential formula, $y = ab^x$, in which the independent variable appears as the exponent in the equation. In the larval samples studied, Tafuri found that the leg discs have different allometric growth rates in the minima, the intermediate, and the maxima larvae.

Comparable evidence of differences in developmental growth rates among polymorphic size groups of *E. burchelli* was presented by Lappano (1958). She also found histological evidence that the production of labial secretions in the early days of the nomadic phase, as well as changes in this same gland to produce precursors of the cocoon-spinning material at the end of the nomadic phase, occurs first in the maxima larvae, next in the intermediates, and last in the minima larvae.

Unpublished studies in our laboratory disclose a slower rate of development in the all-worker larval broods of colonies of the nearctic doryline, *Neivamyrmex nigrescens* sampled in the period of spring resurgence (Schneirla, 1963) than in those of normal colonies in the regular season. Schneirla (1961) has also demonstrated a relatively faster rate of development of larval series comprising a sexual brood.

A recent study by Schneirla, Gianutsos, and Pasternack (in ms.) was directed at studying differentiations in allometric growth within the larval broods of three genera of doryline ants. First, individuals of the same brood series from the same colonies were compared with respect to allometric growth; then the degree of differences in larval allometric growth rates was compared between broods from colonies of the genera *Eciton*, *Neivamyrmex*, and *Aenictus*. Using the exponential function to express the relationship between overall larval body length and leg disc area, the authors found that larval broods of *Eciton* and *Neivamyrmex* are polymorphic, while those of *Aenictus* are best characterized as quasi-monomorphic.

Finally, Schneirla (1968) has related polymorphic growth and developmental patterns in the group-A complex with those of group B. For this study Schneirla has shown how factors of developmental convergence (defined as the continuous reduction in temporal range of developmental events throughout embryonic, larval, and pupal stages) are related to the maintenance of the regular versus the irregular nomad-statary cyclic patterns that characterize the two respective group complexes. Thus in *E. hamatum*, for example, a difference of about one week separates the first-laid eggs from the last-laid eggs. Throughout the nomadic phase, however, caste specific differences in allometric growth rates enable the smallest larvae to "catch up" to the largest larvae, so that at the end of pupal development the time interval of eclosion between the workers maxima and the workers minima, has been reduced to only two or three days. The result is that at the start of the following nomadic phase, the brood can impart a much more intensive stimulative impact to the adult workers than would be possible if the developmental interval occurring at egg laying persisted throughout larval and pupal development.

The series of studies just described are all analytically comparable in that each investigation involved a developmental morphological comparison of successive brood samples that are longitudinal with respect to time. In contrast to this, aspects of doryline polymorphism have also been considered by means of cross-sectional approaches, involving the application of the power function -as defined above- to adult, static morphological comparisons.

Huxley (1927) first studied size-frequency variations in adult workers of the doryline subgenus *Anomma*, and attempted to interpret polymorphic differences both in terms of larval allometric growth and fixed adult allometric comparisons. Cohic (1948), also working with *D.* (*Anomma*) *nigricans*, described four distinct morphological types, largely on the basis of a quadrimodal size-frequency distribution of the sample. Later, Hollingsworth (1960) re-examined Cohic's methods of procedure and quantification, and reported, for the same species, a continuous (i.e., unimodal) morphological sequence from the smallest to the largest workers, when total body length was plotted on an arithmetic scale. In addition, Hollingsworth found that the proportion of the total-body length that any anatomical part comprised, was different for the minima, the intermediate, and the maxima adult workers. A similar distribution pattern was described for *D.* (*Anomma*) *wilverthi* (Raignier and van Boven, 1955), together with a positive allometric relationship between head width and body length. These allometric studies were continued by van Boven (1957) in which, on the basis of head-width and head-length measurements in relation to overall body length in all worker size groups, he was able to distinguish four distinct morphological castes. Working with the less polymorphic Old World species, *Aenictus gracilis*, Chapman (1964) nevertheless reported different ratios in head dimensions (expressed as head width divided by head length X 100) in the largest and smallest adult workers.

Comparison of the Doryline Functional Cycle with Behavioral Phases Occurring in Other Insects

I have noted that there are marked fluctuations in the intensity of doryline raiding activities associated both with diel periodicities in environmental stimuli such as the intensity of light incident on the forest floor, and with the contrasting stimulative condition of the brood during the nomadic and statary phases. Superficially, this might indicate that doryline behavioral phases are fundamentally similar to any of the great variety of environmentally controlled activity phases of cycles or rhythms that are known for insects generally (see reviews by Schneirla, 1953a,b,c; Harker, 1958; Bünning, 1967). However, Schneirla (1968) has contrasted such generalized *activity* cycles which are regulated principally by the interaction of physical environmental stimuli and intraorganic neurophysiological processes, with the much more complex functional cycles present in doryline colonies; for in this case aspects of the physical environment must also interact with interindividual stimulative processes (centered on trophic and reproductive conditions in queen and workers) that change continually through both phases of the cycle in relation to progressive changes in the brood or broods present.

For the dorylines, the concept of a functional behavioral phase implies that many aspects of an individual's physiological and behavioral condition are affected by levels of stimulative conditions within the colony. In addition to changes in levels of general activity, these may include metabolic differences and changes in the thresholds of response to a variety of physical and biotic environmental stimuli, affecting individual sensory modalities as well as many colony functions (e.g., nesting). On these grounds, Schneirla (1957a) has postulated for adult workers during the early part of the nomadic phase, a callow-induced "metabolic trace" factor, which is principally responsible for maintaining increased levels of raiding during the interval when callow excitation is diminishing.

Although the functional phases of doryline ants may be unique, especially with respect to the biological factors underlying the transition from one phase to the other, nevertheless, similar functional behavioral and physiological phases have been described for other insects.

The density-dependent type of phase variation that is found in some acridid locust species, has been reviewed by Key (1950), Kennedy (1956, 1961), and Uvarov (1961). The most impressive difference between locust phase variation and doryline phase alternation, is that in the locusts, any individual or group can develop into either the "solitaria" or the "gregaria" phase, depending upon the effects of certain physical environmental parameters, such as the degree of crowding during early development, on physiological and endocrinological aspects of nymphal and adult growth and development. Once the developmental pathway leading to either of the two phases has been established, individual locusts exhibit phase-specific differences in morphology and color (Kennedy, 1961; Uvarov, 1961; Nickerson, 1956), rates of growth and development (Albrecht, 1959), levels of resting metabolism (Gardiner, 1958; Norris, 1959, 1961), and response to the presence of other individuals in the group (Ellis, 1956).

A phase variation similar to that of the locusts, but not nearly as well known, exists in larvae of certain species of the family Noctuidae, known as armyworms. As in the locusts, the degree of crowding in the larval population affects numerous morpho-functional characteristics of the larvae and, later, of the adults (Iwao, 1963). With regard to behavioral differences, the deeply pigmented black larvae, which develop in crowded populations, were found to be more active than the pale larvae which predominate in less dense populations (Iwao, 1963, 1967a,b). In addition, other physiological and behavioral differences exist between the dark and light phases, including resistance to starvation, and reactions of the larvae to light stimulation.

SUBJECT AND LOCALITY

This project deals with an analysis of the population characteristics of three species of doryline ants, *Neivamyrmex nigrescens* Cresson, *Eciton hamatum* Fabricius, and *Aenictus laeviceps* F. Smith, and with changes in the physiological and behavioral condition in groups of ants, associated with the nomad-statary functional cycle, in one representative species, *N. nigrescens*.

The population study is related to two prime considerations concerning the biology of these three doryline species. First, how do differences in those aspects of the ecology and behavioral ontogeny that have been described for these dorylines, correlate with the observed and calculated population characteristics? Second, how are the variations in the population structure of each species related to corresponding variations in the physiological and behavioral integrative mechanisms underlying the adaptive cyclic patterns previously described for each of them?

Studies of population characteristics, computed by taking selected morphological measurements of pupal individuals, were done in the doryline laboratory, at the American Museum of Natural History, in New York City.

The physiological study consisted of measuring levels of oxygen consumption in groups of freely-moving ants, comparing their activity metabolism during successive nomadic and statary phases.

The behavioral tests consisted of recording differences in reactions of groups of ants in a "choice" situation involving a high and low intensity light stimulus, during the nomadic and statary phases.

Both behavioral and physiological tests described were carried out with equivalent samples of the same colonies taken at different times during consecutive nomadic and statary phases. Both series of tests were conducted during the summer months of 1964, 1965, and 1966, at the American Museum of Natural History's Southwestern Research Station, located on the eastern slope of the Chiricahua Mountains, Cochise County, five miles west of Portal, Arizona. The Station, at an altitude of 1600 meters, is in an oak-woodland association with light-to-medium ground cover. The area of research is composed of a section of the floor of Cave Creek Canyon, as well as the numerous hills at its rim. The rainfall and temperature patterns as related to doryline colony activity throughout the functional season have been described (Schneirla, 1958, 1961, 1963).

Field methods involved established procedures of longitudinal observations of colony location, and raiding and emigration routes. At the beginning of each summer, nightly searches were conducted until several colonies were found. Then, before the start of each night's work, a colony was selected for testing, based upon its functional phase and the number of days elapsed since its previous test. When weather and colony conditions permitted, the colonies were tested in a regular sequence.

At sundown each evening, all nomadic colonies were briefly checked. Then collections were made from the colony selected for testing, and brought to the laboratory. On nights when more than one colony was tested, the entire procedure was repeated. After completion of testing, all colonies were revisited to locate and establish the positions of new and existing bivouacs.

MATERIALS AND METHODS

Population Studies

The material used consisted of all-worker pupal broods collected by cross-sectional methods (previously described by Schneirla, 1958), mid-way through the pupal stage of development. This stage of development can be recognized by the constricted, adult-like shape of the petiole and the relative absence of cuticular pigmentation. (Due to differential development of the various castes at the stage in question, some areas of pigmentation are in evidence at the anterior region of the major workers, especially around the periphery of the mandibles.)

Pupae rather than adults were chosen for measuring population characteristics of all doryline species studied. It is easier to collect an entire brood of a colony of ants than the entire adult population, which can range from 100,000 individuals in species of *Aenictus*, to 150,000 individuals in *N. nigrescens*, up to one million individuals in the swarm raider, *E. burchelli* (Schneirla, 1965). Random sampling of adult army-ants in the field is just as difficult as collecting the entire population, due to a strong spatial localization of the different worker castes both on the raiding and emigration trails, and in the bivouac.

Specimens from all colonies studied were stored in the doryline laboratory of the Department of Animal Behavior, in the American Museum of Natural History. The pupal broods were collected in the field by Dr. T. C. Schneirla, fixed in Bouin's solution, and preserved in 70 percent ethyl alcohol.

In the laboratory the brood samples were randomly divided in an aluminum pan (33 cm. long by 25 cm. wide by 2 cm. deep) partitioned into two equal halves by an adjustable, upright sheet of glass. The entire pupal sample was placed in the pan and enough 70 percent ethyl alcohol added to the pan to just cover the specimens. The sample was thoroughly mixed with a strip of heavy paper and the glass partition then lowered into place along the midline of the pan. Each half of the entire sample was placed into jars and the entire procedure repeated until the desired number of divisions was obtained.

To estimate total-body length, the pupae were positioned on their sides, with their heads toward the left. Rapid positioning was accomplished in a petri dish that was filled half-way with hardened beeswax that was darkened with powdered lampblack. Two thin strips cut from a cover slip of a glass slide were inserted into the wax at right angles to each other. This formed a waxsurfaced enclosure for the pupae, with glass borders below and to the left. Rapid and homogeneous orientation was accomplished by sliding the pupae into the enclosure, measuring their over-all length and then sliding them out of the enclosure. This assembly-line technique was found to be an efficient way of rapidly size-classing thousands of ant pupae.

The head of an ant pupa is characteristically flexed in a ventral direction, and is tucked in underneath the anterior part of the thorax. With the head in this position, the most anterior point of the organism lies in the vertex area of the head. In an adult that has its head extended, the most anterior point would correspond to the labrum or mandible.

Worker pupae of _N. nigrescens_ and _A. laeviceps_ are "naked" in that the larvae do not spin cocoons at the time of pupation. To record the over-all length of these pupae the specimens were oriented in their sides in the petri dish, and a lateral measurement was taken from the margin of the vertex to the tip of the gaster. The pupae of _E. hamatum_ are enclosed in cocoons, and for this species, total-body length was estimated simply by measuring the length of the entire cocoon. This method was sufficiently accurate for computing size-frequency distributions of _E. hamatum_. However, those specimens that were selected for measurements associated with the allometry phase of the work, were individually removed from their cocoons and measured by the procedure used for N. nigrescens and A. laeviceps.

For studying pupal allometry in each of the three doryline species, the range of total-body lengths was divided into ten equal size classes. For each of the thirty specimens selected from each of the three species, the following pupal anatomical parts were measured: overall body length; length of the tibia; length of the first tarsal segment; length of the second tarsal segment; length of the third tarsal segment; width of the head across the eyes; and width of the head just dorsal to the point of articulation of the mandibles. To record leg measurements, the left metathoracic leg (determined by positioning the specimen with its head pointing towards the left) was severed across the femur, and the leg held in place on the waxed dish with an insect pin. Head-width measurements were facilitated by decapitation and antennectomy.

All measurements were done with a binocular dissecting microscope and a calibrated ocular micrometer.

Physiological Studies

All of the physiological and behavioral tests were conducted in a basement laboratory room divided into light-tight booths, using plaster wall boards and black plastic curtains.

Oxygen consumption tests were carried out in a differential respirometer constructed largely from plexiglass materials (fig. 1). The base of the respirometer consisted of a test chamber and a compensatory chamber, both permanently affixed and set apart upon a rectangular plastic sheet. The cover consisted of a plastic sheet large enough to cover both chambers. Four vents consisting of pieces of plastic tubing were cemented vertically into four holes in the cover. Two of the holes were positioned above the test chamber, and the other two positioned above the compensatory chamber. The "U"-shaped manometer was permanently affixed to the cover. It was obtained by severing the closed arm of a standard Warburg manometer below the level of attachment of the flask side-arm. One arm of the manometer was connected to the inner vent above the test chamber, and the other arm connected to the inner vent above the compensatory chamber. The manometer was filled with Brodie solution (specific gravity = 1.033).

In order to minimize the handling of test specimens, a portable cartridge was constructed. This same cartridge was used both in the field as an aspirator for collecting the test organisms, and as a container which was placed inside of the test chamber during an oxygen consumption test. This unit (fig. 2) consisted of a plastic cylinder (5 cm. in diameter by 2 cm. high) with a removable, tight-fitting lid on the top and on the bottom.

Fig. 1. Diagram of the differential respirometer used to measure oxygen uptake. The test cartridge and blank cartridge are shown in place in the test and compensatory chambers. Details of the respirometer's construction are given in the text.

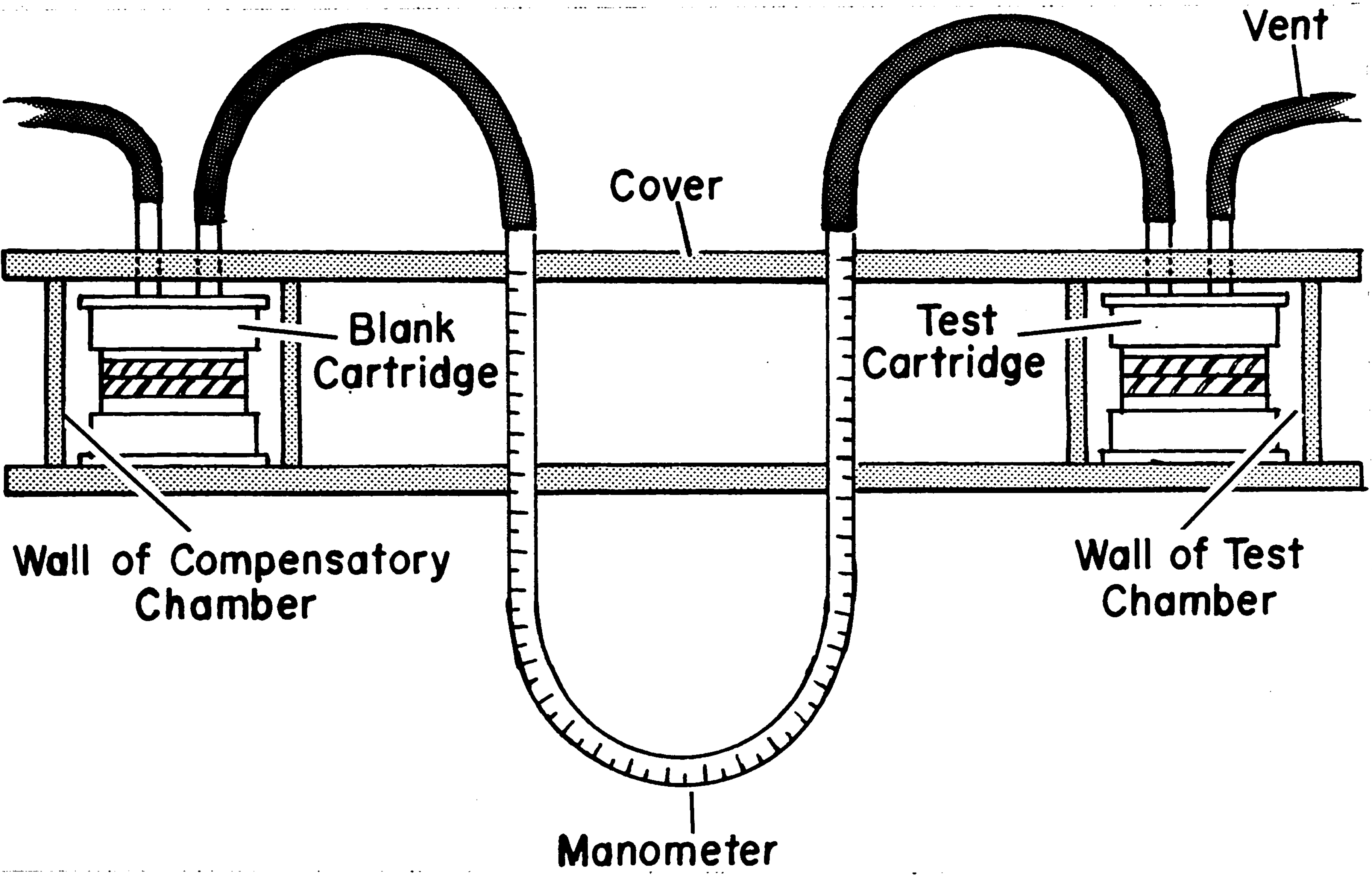

Vent
Cover
Blank Cartridge
Test Cartridge
Wall of Compensatory Chamber
Wall of Test Chamber
Manometer

Fig. 1

Fig. 2. Diagram of the test cartridge used in the physiological studies. When assembled for use in the field, the ants are aspirated into the space between the two steel-mesh discs. After collecting the specimens, the rubber tubing and "L"-shaped plastic tube are removed. The dimensions of the cartridge are given in the text.

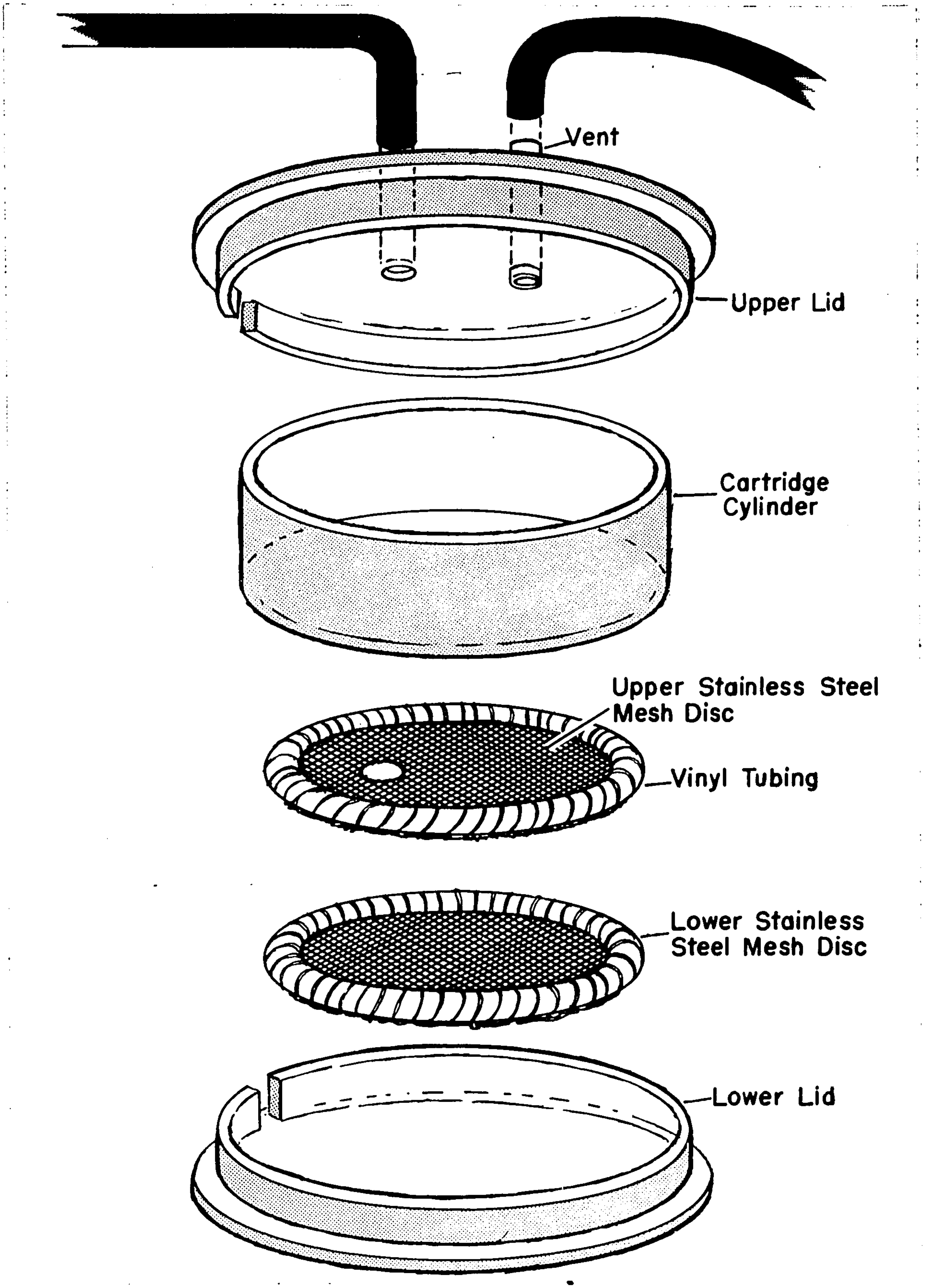

Vent
Upper Lid
Cartridge Cylinder
Upper Stainless Steel Mesh Disc
Vinyl Tubing
Lower Stainless Steel Mesh Disc
Lower Lid

Fig. 2

Two holes (7 mm. in diameter) were drilled through the top lid, one in the center and one near the perimeter. A tubular plastic vent (2 cm. high) was permanently set into the eccentric hole. The lower end of this vent was then covered with nylon mesh. Two discs of stainless steel mesh, having the same diameter as the inner wall of the cylinder, were sewn with nylon thread onto two rings of vinyl tubing. The screen discs were placed in the cylinder so that their vinyl borders fit snugly against its inner wall. By independently sliding either of the two mesh discs up or down in the cylinder, the air gap between them could be varied. For this experiment the discs were juxtaposed to provide a 7 mm. space for the test organisms. A hole was drilled into the center of the upper mesh disc so that, when assembled, it was directly below the hole in the center of the upper lid.

When the cylinder was used in the field as an aspirator, the mesh discs were inserted into it, and the upper and lower lids attached. A piece of rubber tubing was placed over the plastic vent in the upper lid, and the short arm of an "L"-shaped piece of plastic tubing was inserted down through the center hole in the upper lid until it was flush with the corresponding hole in the center of the upper mesh disc. By a suction applied through the rubber tubing, between 15 and 25 intermediate-sized worker ants were aspirated into the space between the two screen discs. The upper and lower lids were then removed, and a plug inserted into the hole in the center of the screening.

In the laboratory, two discs of filter paper were each moistened with 1 cc. of a 10 percent potassium hydroxide solution, and one placed in the bottom of each chamber. The cartridge containing the ants was lowered into the reaction chamber and a blank cartridge placed in the compensatory chamber. A thin film of petroleum jelly was spread around the rims of both chambers, and the covers pressed down upon them and clamped into place. The entire apparatus was allowed to equilibrate for three minutes. The outer vents above both the test and compensatory chambers were then clamped. Readings of changes in the level of manometric fluid were taken at five minute intervals, for twenty minutes. The flask constant was calculated according to the procedure outlined in Umbreit *et al*. (1964). Throughout all tests the booth was illuminated with a 7.5-watt red light source, and air circulation was provided by an oscillating wall fan. At the end of each test the ants were counted, weighed, and preserved.

Behavioral Studies

The behavioral tests were carried out in a circular plexiglass arena divided into four equal areas by a combination of opaque rectangular partitions and a central cylindrical cartridge (fig. 3). The arena was illuminated from above so that the light intensity in the quadrants of the arena was 16,000 lux. By placing several layers of onion skin paper on two opposite quadrants of the experimental arena's transparent cover, the intensity of light in the two corresponding chambers below was reduced to 160 lux. The cartridge and arena were constructed so that at the beginning of a test, four slit-like openings at the bottom of the cartridge gave the ants equal access to either the brightly-illuminated or the dimly-illuminated arena quadrants. A control test, in which all of the arena quadrants were uniformly dark, was run at the same time as the bright-dim test.

In the experimental booth a 22-watt, cool white fluorescent light ring (15 cm. in diameter) was attached to an adjustable wooden frame (omitted from fig. 3), with the height of the light source positioned to illuminate the four arena quadrants as described above. To insure that this intensity of light was equal over the entire surface of the arena when it was placed on the table below the light source, the fluorescent light was diffused through a sheet of neutral ground glass. In addition, the frame holding both the ring of light and the diffuser was wrapped in a cylinder of white glossy cardboard.

A mirror was positioned at a 45-degree angle, below the arena table, approximately mid-way between it and the floor. A tripod with a camera attached was positioned in front of the table so that the camera lens was at the same level as the mirror and was focused, through the mirror, on the transparent base of the arena. Either Kodak Plus-X or Tri-X film was used in the camera.

The control booth was constructed in the same way as the experimental booth. Instead of using fluorescent light, however, infrared light (at approximately 800 mμ) was diffused through a sheet of neutral ground glass. This was provided by four General Electric 150-watt photoflood lamps, each sealed behind a Kodak gelatin filter (No. 88A). In order to record the movements of the test ants, Kodak High-Speed Infrared film (HIR 421-1) was used in the camera.

The plastic arena (fig. 4) consisted of a shallow cylinder with opaque walls (29 cm. in diameter by 4 cm. high), cemented onto a flat basal disc. The four rectangular partitions were cut from pieces of black plastic and were cemented onto the base of the arena in a plane perpendicular to both the base and wall of the arena. These partitions extended from the arena wall towards the center of the arena to a point at which they were in contact with the vertical wall of the cartridge when it was in place in the arena.

To minimize handling of the specimens (as in the experiment on oxygen consumption) the cartridge was constructed for use in the field as an aspirator as well as a test chamber in the arena (fig. 5). It consisted of a small plastic cylinder (8 cm. diameter by 2.5 cm. high) with opaque walls, held in place 6 mm. above a basal disc by four plastic struts positioned at 90-degree intervals around the circumference of the cylinder. When the cartridge was in place in the arena, this provided four equi-distant and equal-sized channels (6 mm. high) between the center cartridge and the arena. The lid of the cartridge had one central and one eccentric hole drilled through it. A plastic vent was inserted through the central hole and cemented in place with one-fourth of its length projecting on the under side. A small patch of nylon mesh was placed over the lower end of this vent to prevent the test ants from being aspirated into the mouth.

When the cartridge was used in the field as an aspirator, a thin plastic ring was slipped over it on the outside to effectively seal the four open slits. A piece of rubber tubing (25 cm. long) was attached to the upper end of the vent in the cartridge lid and the short arm of an "L"-shaped tube was inserted into the eccentric hole.

An effort was made to collect ants from raiding columns that were 1-3 feet from the bivouac and from which the traffic was predominantly exiting from the bivouac. This procedure worked wll during the nomadic phase, but on many statary nights the number of individuals raiding was so small that it was necessary to collect the test ants further away from the bivouac. For each test an attempt was made to aspirate 40-60 ants into both the experimental and control cartridges, but often more than 60 ants were collected.

After they had been loaded with specimens, the cartridges were put into a cardboard box and carried to the laboratory. Standardization of the amount of time that the ants spent in the cartridge during transit to the laboratory was difficult, due to the highly variable and constantly changing distance between the colonies and the laboratory. This elapsed time ranged from a minimum of two minutes to a maximum of six minutes. For each test the exact transit time was recorded nightly, and when the upper limit of six minutes was reached, no further tests were performed on that colony.

In the laboratory, a 7.5-watt red light bulb was turned on in both the experimental and control booths. This provided a minimum of disturbance to the ants while the arena and cartridge were set in place upon the transparent table. In each booth the cartridge was placed in the arena between the four partitions (fig. 3). Initially the cartridge did not sit flush with the floor of the arena, but was supported by four small plastic cubes which projected centrally from the inner base of each arena partition, just far enough to meet the outer slip ring of the cartridge. The arena cover was then placed over the cartridge in both booths. To start the test the vent projecting up from the center of the cartridge lid, which was protruding through a hole in the center of the arena cover, was pushed down. This caused the cartridge to slide down through the supported slip ring, with the result that all four slit-like channels separating the cartridge from the arena opened simultaneously.

Both the experimental and control tests were started at the same time. In the experimental booth, the fluorescent light was turned on at the same time that the channels were opened to the test ants. The light remained on throughout the test and a photograph was taken every five seconds, recording the position of the ants in both the cartridge and in all four arena quadrants. This was facilitated by a buzzer that was electrically programmed to deliver a one-second pulse of sound every five seconds, which enabled the photographic records from both the experimental and control booths to be well synchronized.

The infrared photography set-up in the control booth required some technical modifications. Because the infrared light source was provided by flood lamps that were filtered to pass only in spectral light longer than 720 mμ, the problem of heat, melting the filters and being absorbed by the dark-bodied ants in the arena, was of prime consideration. To overcome this the infrared light source was electrically programmed and synchronized with the electric buzzer. The flood lamps were automatically lit for 1.5 seconds out of every five-second interval, and this 1.5-second interval was made to coincide with the one-second sound pulse produced by the buzzer every five seconds. This not only eliminated the heat factor but also solved the problem of taking photographs in a booth that was almost totally free from visible light. The photographer was assured that as long as he snapped the camera shutter while the buzzer was sounding, the infrared light source would be on.

Fig. 3. A schematic representation of the apparatus used in the behavioral tests, showing the relative positions of the light source, ground glass, arena cover, arena, mirror, and camera. The cartridge is shown in place in the arena. In this diagram the apparatus is not drawn to the same scale as in figs. 4 and 5. For the control tests, the fluorescent light was replaced by an infrared light source. A complete explanation of the apparatus and its dimensions is given in the text.

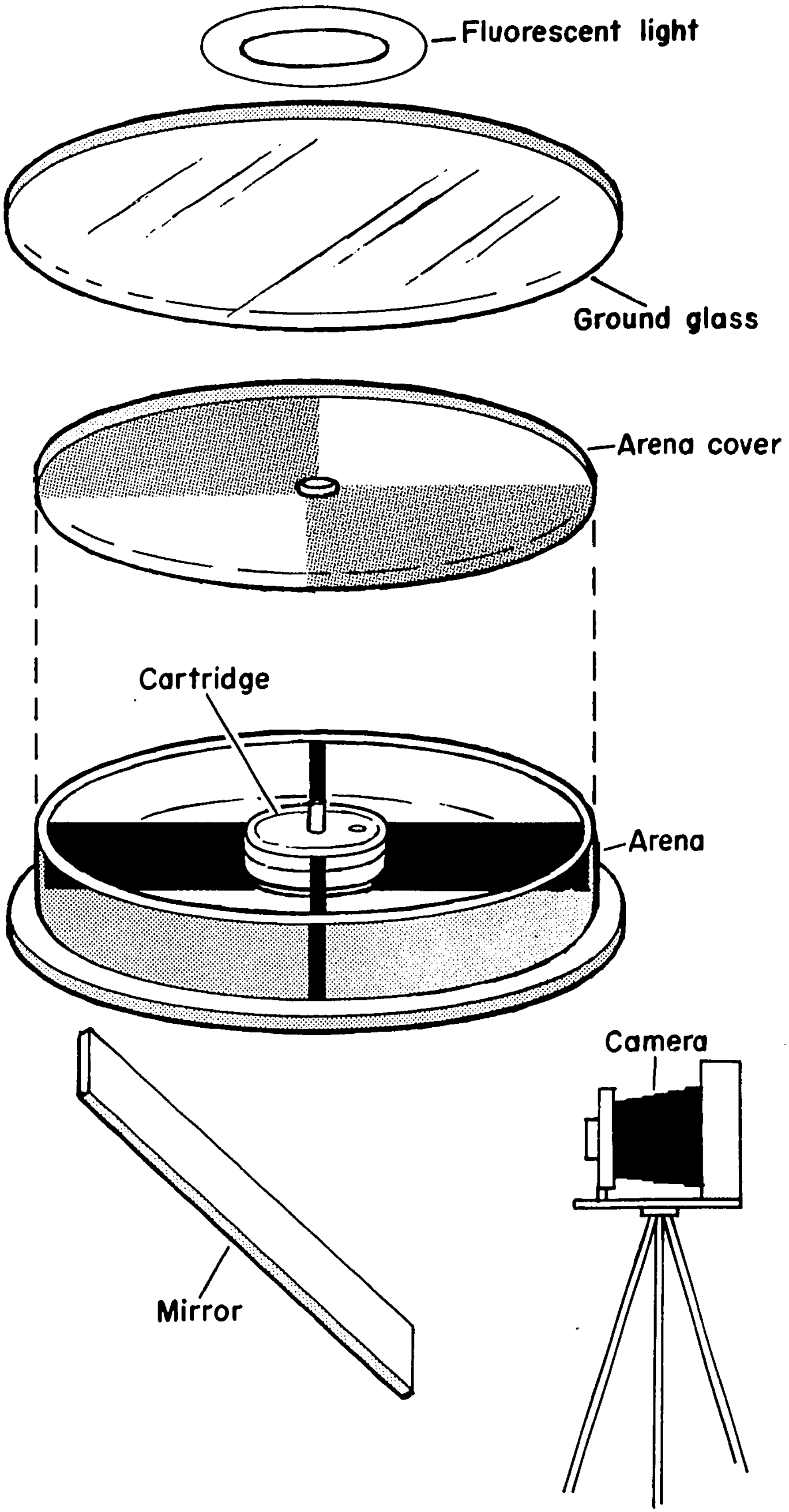

Fluorescent light
Ground glass
Arena cover
Cartridge
Arena
Camera
Mirror

Fig. 3

Fig. 4. Diagram of the test arena (above) and its cover (below). Details of the construction of the arena are given in the text.

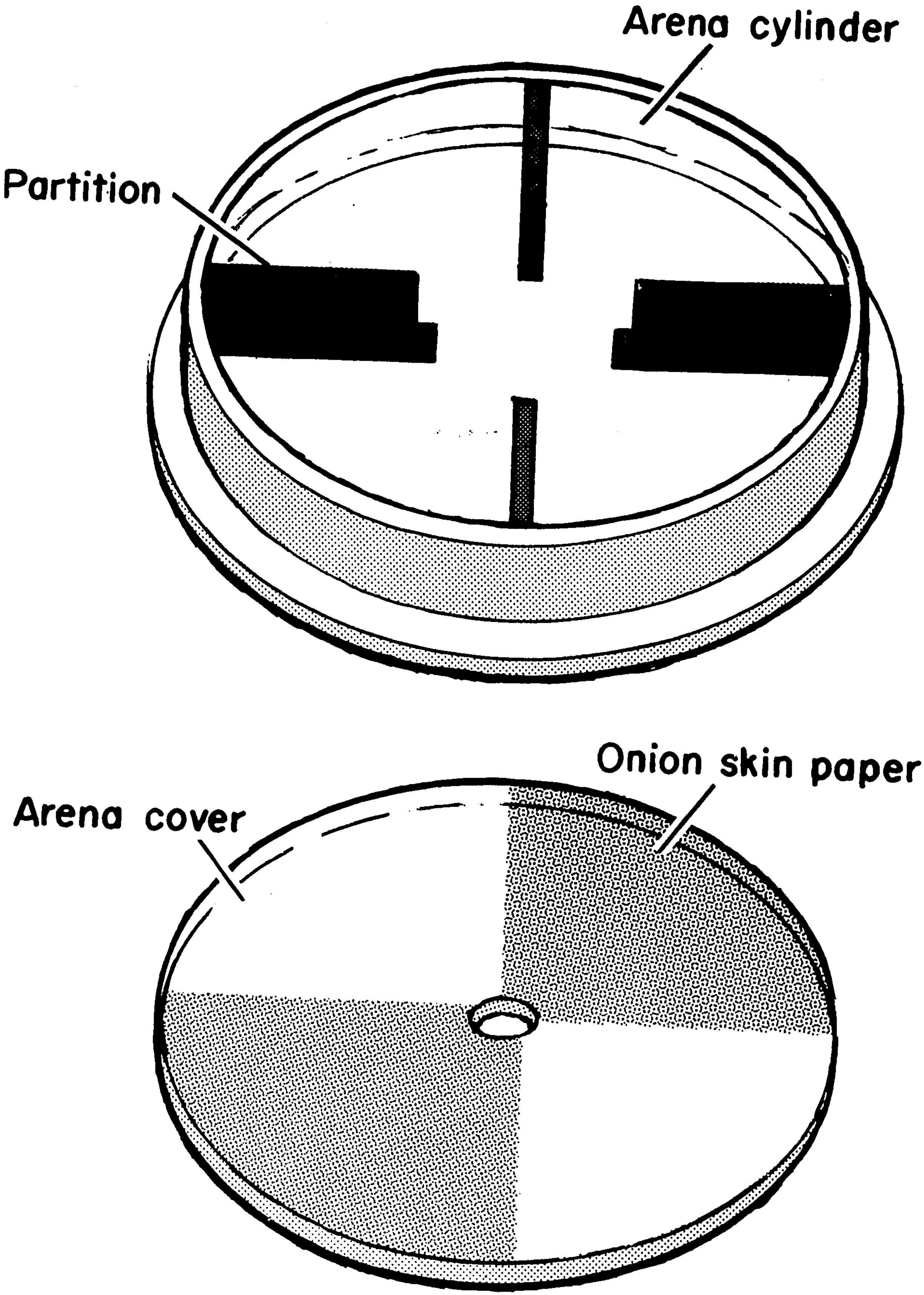


Fig. 4

Fig. 5. Diagram of the cartridge used in the behavioral tests. When used in the field as an aspirator, the plastic slip ring is placed over the outside of the cartridge to effectively seal the four exit slits. After collecting the specimens, the rubber tubing and "L"-shaped plastic tube are removed from the cover of the cartridge. The dimensions of the cartridge are given in the text.

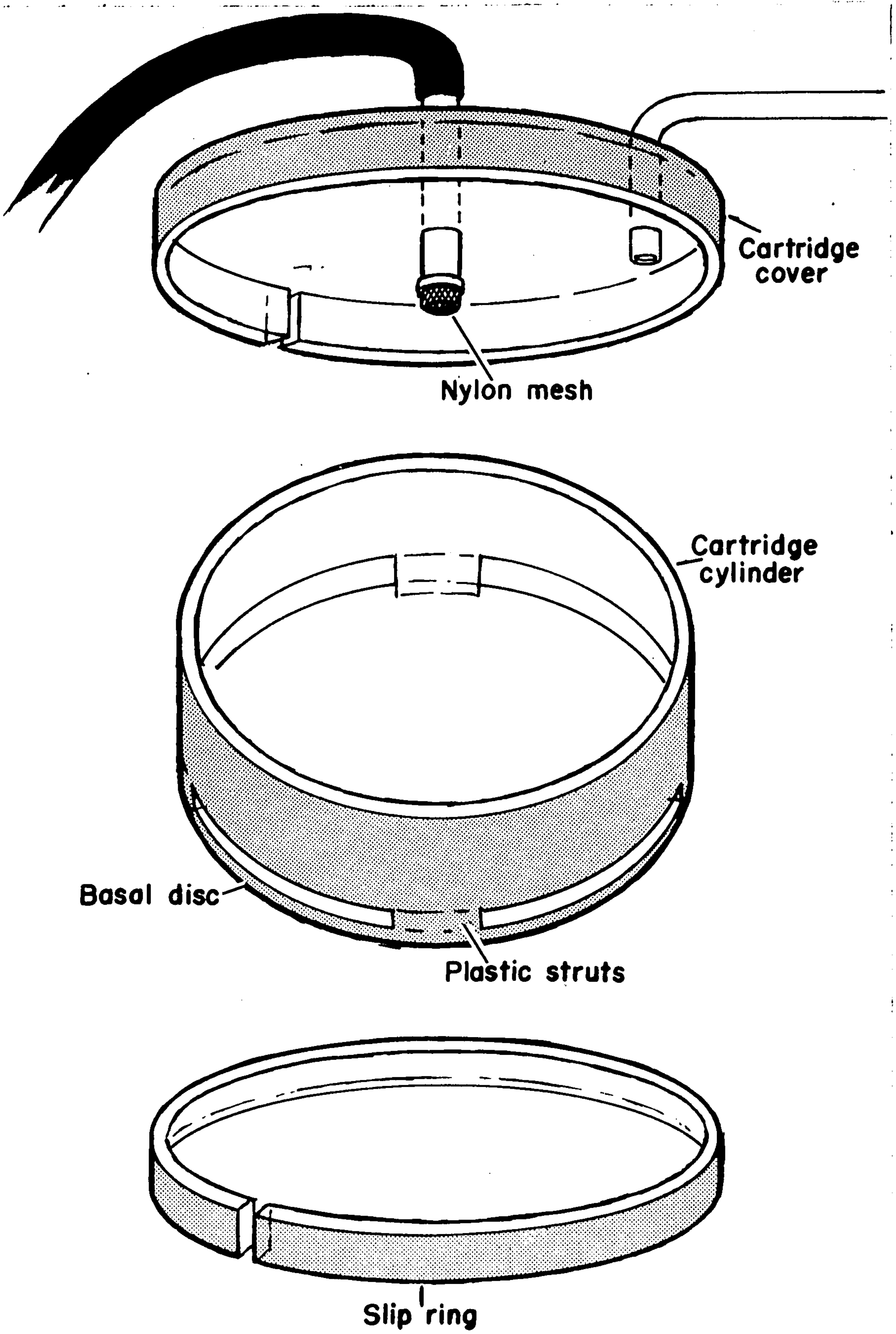

Cartridge cover
Nylon mesh
Cartridge cylinder
Basal disc
Plastic struts
Slip ring

Fig. 5

RESULTS

Population Studies

Obtaining Pupal Samples that are Representative of their Respective Populations:

The population characteristics of the three genera that will be described below are based primarily upon single pupal samples extracted from cross-sectionally collected pupal brood populations. Because the objective of a sampling procedure is to acquire a portion of the total population, with the hope that some knowledge can be gained about the entire population, the two essential considerations that must be taken into account in adequate sampling procedures are randomness and representativeness. Randomness insures that every unit in the population has an equal chance of being selected for study in the sample, thus facilitating a good estimate of the sampling variation. Representativeness in sampling however, is also necessary in order to get as accurate a picture of the parameters of the population as is possible by studying any selected sample. Since much of the comparative population data to be presented below is based upon single samples randomly chosen from their corresponding brood populations, it was necessary to establish that the sampling procedure previously described, does in fact produce samples that are representative of the population as a whole.

One way to estimate the representativeness of a sample is by its reproducibility. If the distributions and other statistics of successive samples are similar, we may conclude that the samples are representative of the population (Wadley, 1967).

The brood population of Neivamyrmex nigrescens (colony '59 N - XIII) was randomly divided into eight parts, according to procedures previously described. Two samples (IA2 and IIA1) were arbitrarily chosen and each was further divided three more times. This resulted in the production of 16 pupal samples, each comprising 1/64 of the entire brood population. The test of the ability of the sampling procedure to produce samples that are representative, consists of arbitrarily selecting four of the 1/64's from IA2 and four from IIA1, and comparing the eight cumulative size-frequency distribution ogives. The reproducibility of this procedure is demonstrated by the similarity of the eight ogives represented in figure 6.

Comparison of Pupal Population Characteristics of Neivamyrmex nigrescens, Aenictus laeviceps, and Eciton hamatum:

Results of a comparison with respect to pupal size-relative frequency distributions between colonies of N. nigrescens, A. laeviceps, and E. hamatum, are shown in

Fig. 6. Graph comparing the cumulative frequencies of eight random samples from a pupal population of *N. nigrescens*. The similarity of the distributions indicates that the sampling procedure described in the text produces pupal samples that are representative of the population.

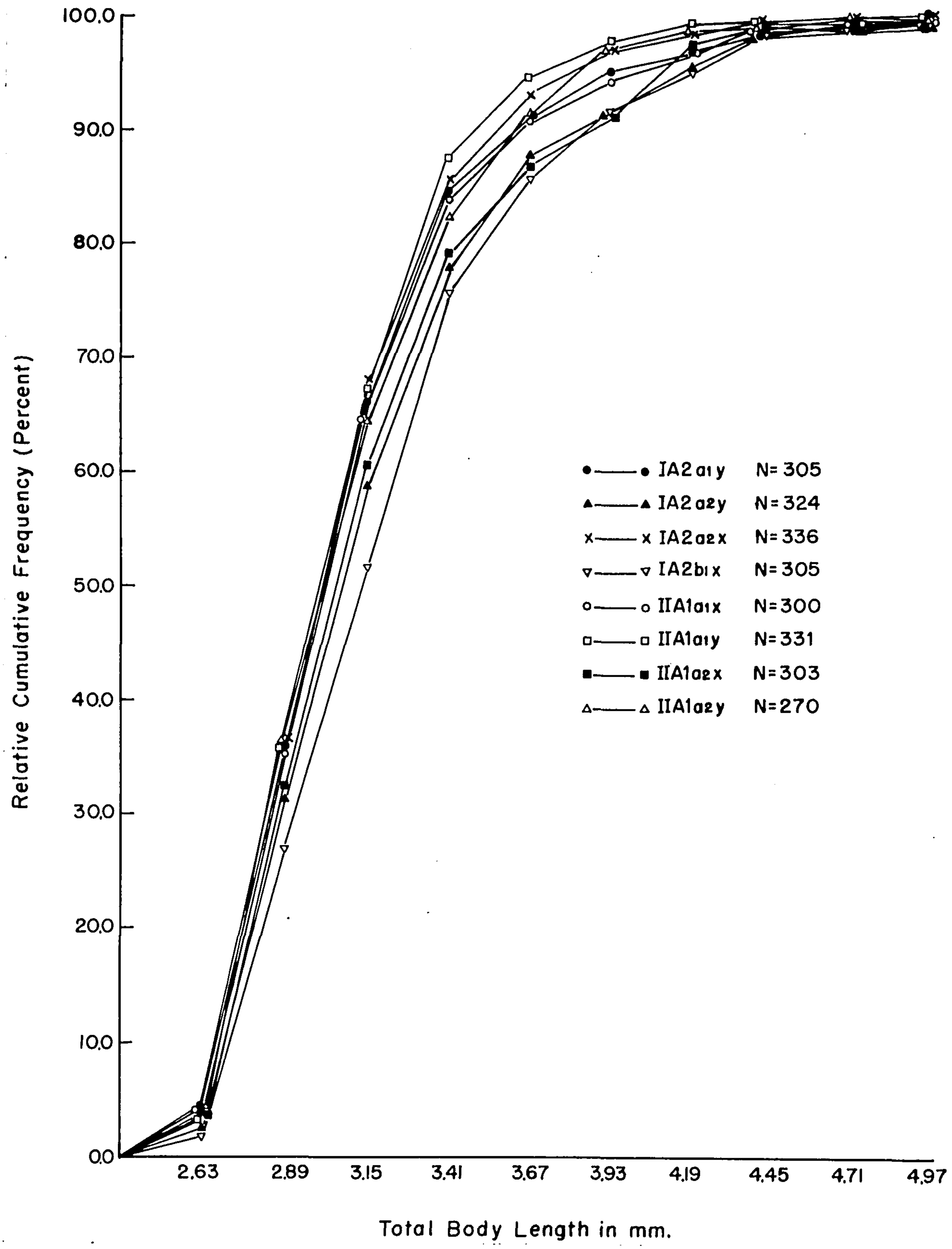

Relative Cumulative Frequency (Percent)
100.0
90.0
80.0
70.0
60.0
50.0
40.0
30.0
20.0
10.0
0.0
2.63
2.89
3.15
3.41
3.67
3.93
4.19
4.45
4.71
4.97
Total Body Length in mm.
●——● IA2a1y N=305
▲——▲ IA2a2y N=324
×——× IA2a2x N=336
▽——▽ IA2b1x N=305
○——○ IIA1a1x N=300
□——□ IIA1a1y N=331
■——■ IIA1a2x N=303
△——△ IIA1a2y N=270

Fig. 6

figure 7. Since there were eight measured samples for each of the three genera, one sample from each genus was randomly selected for the comparative study. In addition, the relative frequencies of each distribution were standardized in order that the areas under all three polygons would be the same.

The most obvious difference between the pupal samples is the contrasting ranges. The range of _N_. _nigrescens_ is 2.4 mm. (2.6 mm. - 5.0 mm.); for _A_. _laeviceps_ it is 0.6 mm. (3.2 mm. - 3.8 mm.); and for _E_. _hamatum_ it is 8.1 mm. (4.4 mm. - 12.5 mm.).

It is evident that the size-relative frequency polygons of _N_. _nigrescens_ and _E_. _hamatum_ are not symmetrical, in that there is a predominance of smaller-sized individuals. This assymetricity is termed positively skewed, towards the larger-sized workers. Several attempts were made to characterize quantitatively all three generic samples on the basis of the proportion of the total sample that each worker-caste comprises. Since in a symmetrically distributed sample the arithmetic mean and median are equal, a crude index of skewness for each sample could be determined by computing the difference between these two measures of central tendency. Another method involves testing each sample for symmetricity by comparing their respective indices of skewness (Snedecor, 1946), which is done by computing the sum of the cubed-deviations of over-all body length from the mean over-all body length. However, both of these methods proved unsatisfactory, because their interpretation is made less clear when the distribution under consideration differs significantly from a mesokurtotic pattern. Kurtosis is a measure of deviation from normality, which means that relative to the shoulders of a frequency distribution, the center and tails have too many or too few values for normality, even though the distribution may be perfectly symmetrical.

The most satisfactory means of comparing caste distributions of the three generic samples was found by redrawing the distributions as size-cumulative relative frequency curves, in which all the ranges were standardized and plotted on a proportional scale (fig. 8). This method of representing the asymetrical distributions provided much more flexibility of interpretation than either of the two previously considered tests. With the distributions thus represented, we could choose any of the ten arbitrary caste classes and compare them between any of the three genera.

In a normal distribution, if we select the point that is half-way along the total range (0.5 R), we find that 50 percent of the individuals from the sample are included below it, and 50 percent of them remain to be included. As an example, if we arbitrarily select this point for our comparison, it can be seen, for N. nigrescens, that

Fig. 7. Graph comparing the relative frequency distributions of pupal samples from colonies of *N. nigrescens*, *A. laeviceps*, and *E. hamatum*. The range of *N. nigrescens* is 2.4 mm.; for *A. laeviceps* it is 0.6 mm.; and for *E. hamatum* it is 8.1 mm.

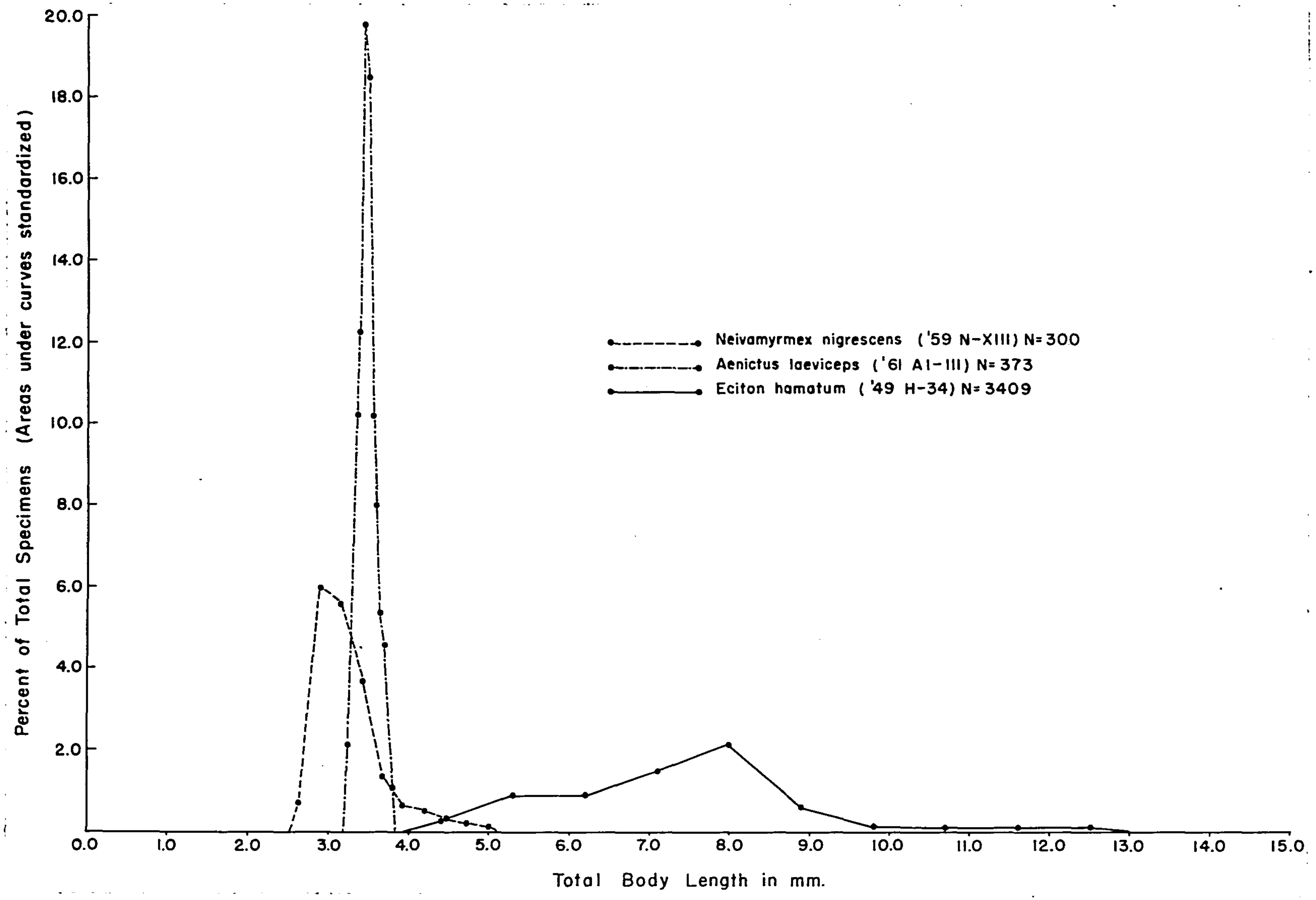

20.0
18.0
16.0
14.0
12.0
10.0
8.0
6.0
4.0
2.0
Percent of Total Specimens (Areas under curves standardized)
Neivamyrmex nigrescens ('59 N-XIII) N=300
Aenictus laeviceps ('61 A1-III) N=373
Eciton hamatum ('49 H-34) N=3409
0.0
1.0
2.0
3.0
4.0
5.0
6.0
7.0
8.0
9.0
10.0
11.0
12.0
13.0
14.0
15.0
Total Body Length in mm.

Fig. 7

Fig. 8. Graph comparing the cumulative frequencies of pupal samples from colonies of *N. nigrescens*, *A. laeviceps*, and *E. hamatum*. To facilitate a comparison of the degree of skewness of the distributions, the ranges of over-all body length are standardized.

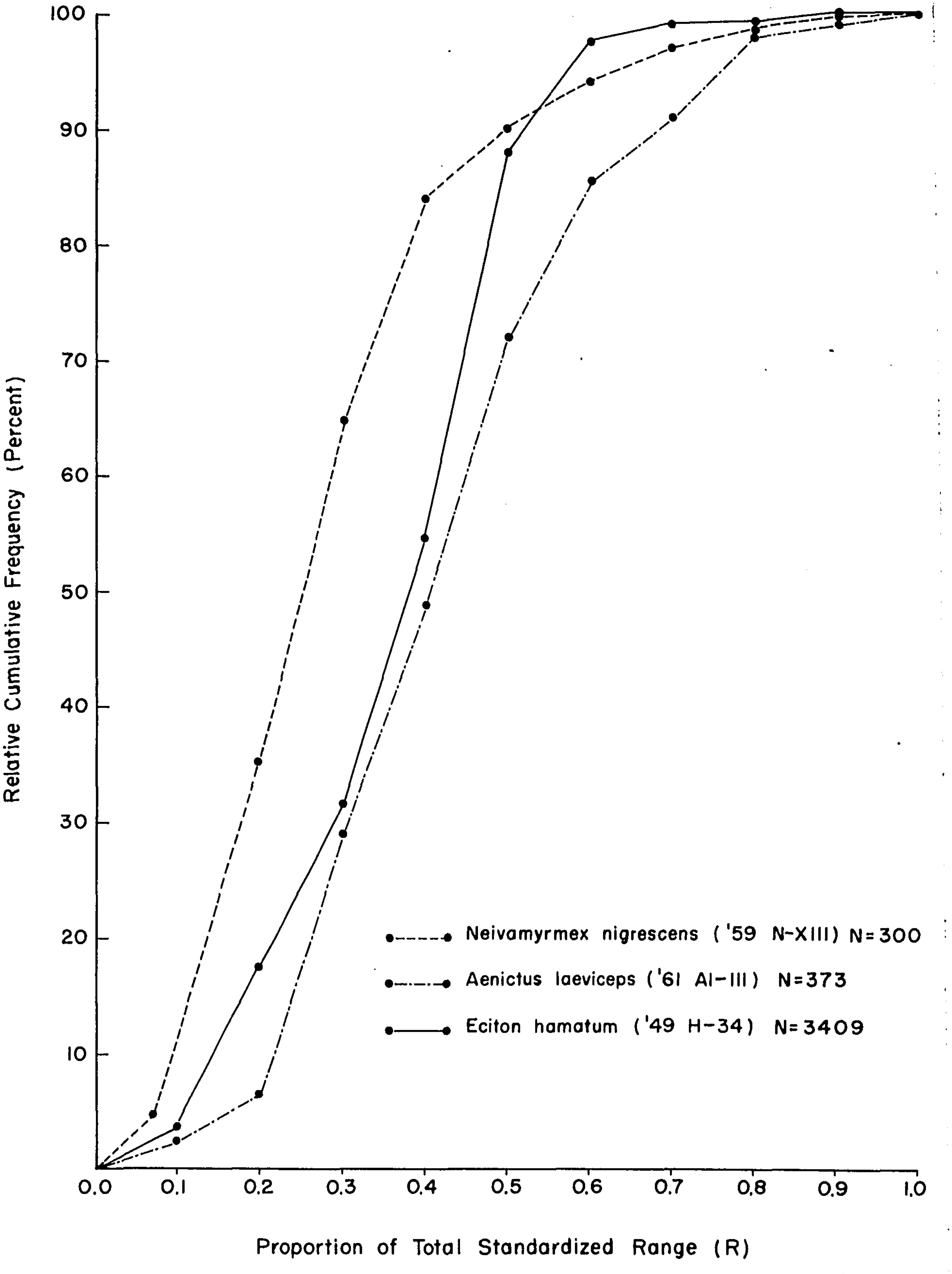

Relative Cumulative Frequency (Percent)
100
90
80
70
60
50
40
30
20
10
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
Proportion of Total Standardized Range (R)
Neivamyrmex nigrescens ('59 N-XIII) N=300
Aenictus laeviceps ('61 AI-III) N=373
Eciton hamatum ('49 H-34) N=3409

Fig. 8

by the time we have reached 0.5 R, 90 percent of the individuals have been included. At the same 0.5 R, 88 percent of the individuals from the *E. hamatum* sample have been included, while only 72 percent of the *A. laeviceps* sample have been included. Thus, at the level of 0.5 R, *N. nigrescens* has the greatest proportion of smaller-sized workers.

The advantage of this type of cumulative frequency distribution is that we can compare all of the samples at any point along the proportionate range scale. Thus, if we are interested in the relative abundance of workers minima, arbitrarily defined as all individuals included up to 0.3 R, inspection of the distribution shows that *N. nigrescens* has the greatest preponderance, with *E. hamatum* next. *A. laeviceps* has a worker distribution that is closest to being symmetrical. All three pupal distributions differ significantly from each other and all differ significantly from a symmetrical pattern ($\alpha = < .01$, as determined by a Kolmogorov-Smirnov two-sample test, with N = 10).

The three pupal broods represented in the generic comparative distribution in figure 8 were all collected from colonies that were not appreciably disturbed before the time of colony sampling, and were therefore judged to be normal. However, one of the colonies of *E. hamatum* ('52 H-P) in our laboratory, consisted of a cross-sectional pupal brood collected approximately 23 days after the smallest larvae, constituting an estimated 30 percent of an entire brood, were removed on the sixth day of the previous nomadic phase. This sample was then compared with the normal *E. hamatum* pupal brood ('49 H-34), by means of a similar cumulative frequency distribution (fig. 9). The interesting thing to note here is that although the over-all distributions are significantly different ($\alpha = < .01$, N = 10), this deviation in the cumulative proportion graphs is most manifest above 0.4 R, while below this portion of the range, the cumulative frequencies are very much alike.

Also represented in figure 9 is the cumulative distribution of a sample of adult workers from *E. hamatum* colony, '52 H-P. This distribution is significantly different from the corresponding pupal distribution of the same colony ($\alpha = < .01$; N = 10), and is also significantly more skewed than the pupal distribution of colony '49 H-34. The implications of these distributions will be discussed later.

Before presenting the comparative allometric data, I think that it is important to re-emphasize the nature of the material used for this study. Measurements were taken exclusively from individuals sampled from pupal brood populations, in which the adult form, including the allometric relationships of external organs, is present. Wilson (1953), Cock (1966), and Gould (1966) properly emphasize the difference between cross-sectional and longitudinal data,

Fig. 9. Graph comparing the cumulative frequencies of two pupal samples and one adult sample from two colonies of _E. hamatum_. The pupal distribution of colony '49 H-34 represents a sample of the population taken from a normal colony. The pupal distribution of colony '52 H-P represents a sample of a population taken from a colony in which approximately 30 percent of the smallest-sized larval individuals were removed during the previous nomadic phase. The adult distribution of colony '52 H-P represents a sample of a portion of the population collected along with the pupal brood.

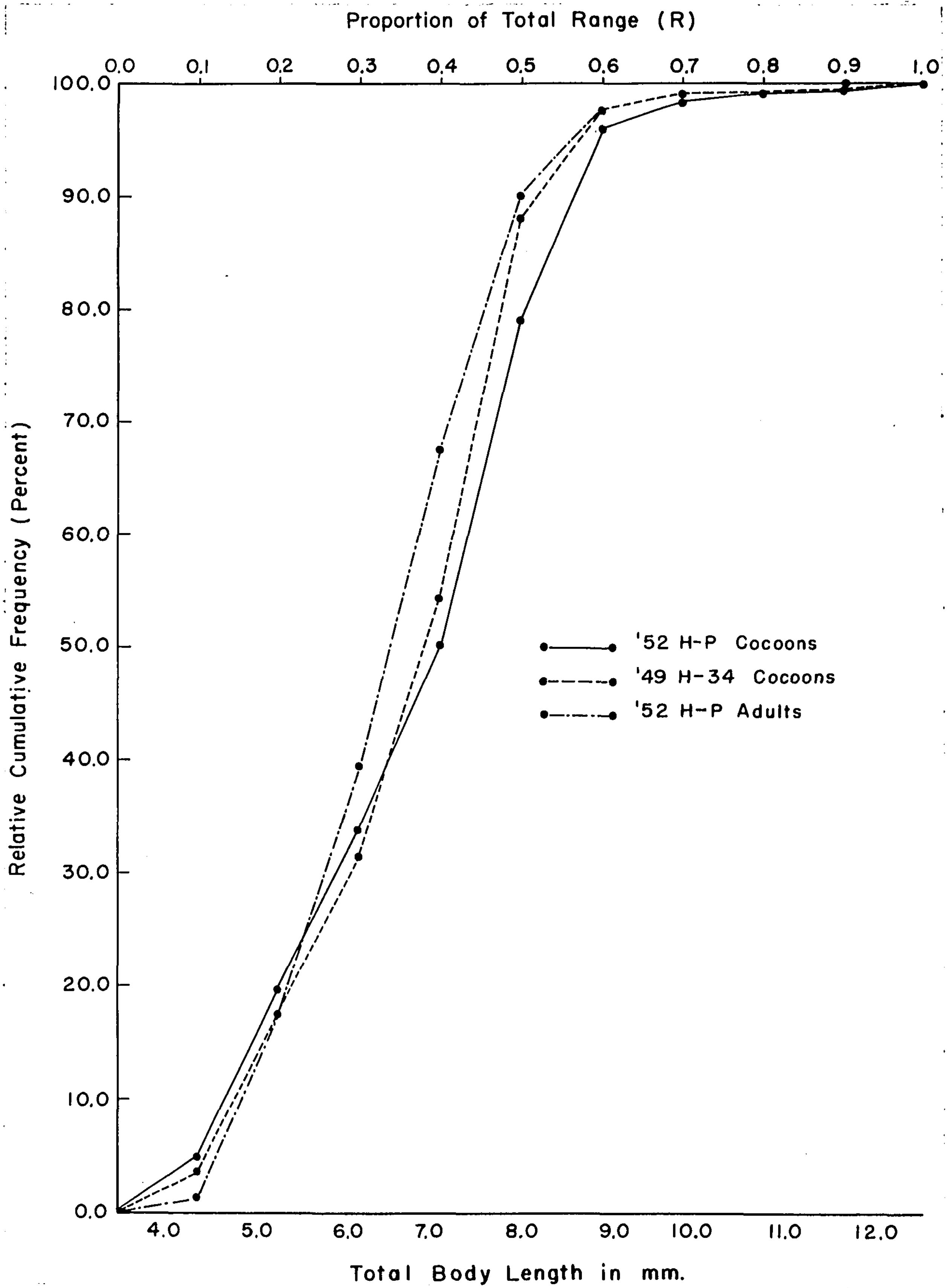

Proportion of Total Range (R)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
100.0
90.0
80.0
70.0
60.0
50.0
40.0
30.0
20.0
10.0
0.0
Relative Cumulative Frequency (Percent)
'52 H-P Cocoons
'49 H-34 Cocoons
'52 H-P Adults
4.0
5.0
6.0
7.0
8.0
9.0
10.0
11.0
12.0
Total Body Length in mm.

Fig. 9

and how each relates operationally to the proper applications of the allometric equation.

True ontogenetic allometric analyses can result only from series of measurements obtained from a single individual over a temporal interval. When practical considerations dictate that a specimen be permanently removed from its population and killed for purposes of measurement, then longitudinal samples containing individuals at various stages of development are often used instead (for applications of this type of ontogenetic allometric study, see Schneirla et al., in ms.).

Thus, the static comparative data gathered in this study, resulting from cross-sectional analyses of members of single populations at comparable growth stages, cannot be termed allometric growth, even though they obviously result from allometric growth processes (Gould, 1966).

As previously noted, Schneirla et al. (in ms.) chose the exponential over the power function as a means for describing allometric growth patterns in larval series of the same three genera of doryline ants that will be considered below. Nevertheless, on empirical grounds, based in part upon its simplicity and ease of interpretibility, the power function $y = bx^k$ has successfully been used to describe many diverse biological phenomena involving differences and changes in the size and shape of animals

(Huxley, 1927, 1932; Teissier, 1960). This power equation was expressed by Huxley and Teissier (1936) as $y = bx^{\alpha}$, while Schneirla _et al_. (in ms.) chose the form $y = ax^{b}$ as most suitable for their data. For this study, I have selected the notational form of the power function expressed as $y = bx^{k}$, which was used previously by Wilson (1953) in his discussion of adult formicid allometry.

The comparisons of the relationships between total-body length and linear dimensions of various anatomical appendages in pupae of the doryline species _E_. _hamatum_, _N_. _nigrescens_, and _A_. _laeviceps_ are shown in figures 10-16. In these figures, the logarithms of the original dependent and independent variables are shown plotted on rectangular coordinates. By this transformation of the power function $y = bx^{k}$ into its logarithmic form $\log y = k \log x + \log b$, we have specified that the resulting relationship appear in rectilinear graphic form. In these graphs _k_ represents the slopes of the double logarithmic plots and will be used as the key index in comparing changing anatomical relationships both within worker series of one species, and between populations of the species representing the three doryline genera.

The usefulness and validity of the power function (or of its transformation) depends in large part upon the assumptions underlying and the conclusions drawn from its application to biologically significant phenomena. Gould

(1966) details instances in which the power function has been misused, either because varying numbers of straight lines were fitted to wide curvilinear scatter, or because of the arbitrary and subjective selection of critical points representing discontinuous breaks in the allometric double logarithmic plot. He rightly points out that although the rates of change in allometric relationships are frequently more rapid (or slower) at corresponding important morphological and physiological transitions, still the fitting of straight lines to curvilinear data, even though it be done entirely for the convenience of demonstrating and interpreting intra-population differences in morphological characteristics, suggests that the changes are necessarily abrupt.[1]

In the data for the three genera represented in figures 10-16, selection of the points for plotting additional lines, where they exist, was determined empirically by examination of the specimens, by statistical procedures for determining lines of best fit, and also by extraction from arithmetic plots of the raw data in curvilinear form. These points, for each of the anatomical parts considered in each of the three species, is shown in table 1. Breaks in the regression lines of the double logarithmic plots represent increasing or decreasing rates of morphological relationships that suggest corresponding unique physiological and behavioral differences within certain segments of the worker populations in all three species and genera considered. However, although the extremes of polymorphic worker series are well separated morphologically and functionally, the transitions that are represented by the additional regression lines, are of varying degrees of abruptness, depending upon the anatomical parts being considered, and the species and genera under study. For my purposes, the power function has been selected because it is the most familiar mathematical expression with which to demonstrate intra- and inter-specific differences in morphological population parameters, and also because the specimens studied were, in effect, adults.[2]

The results of comparisons of the relationships between total-body length and linear dimensions of various anatomical appendages in pupae of *E. hamatum*, *N. nigrescens*, and *A. laeviceps*, are shown in figures 10-16. The equations of the straight regression lines resulting from the logarithmic transformations of the corresponding power functions are shown in table 1. In those cases in which only one regression line was fitted to the logarithmic plot, a test of significance of deviation from isometry was performed, by testing the significance of the deviation of the regression coefficient $\underline{k_1}$ from unity. When two regression lines were fitted to the data taken from a single population, a test of the significance of the difference between the two regression coefficients ($\underline{k_1}$ and $\underline{k_2}$) was made;

in addition a test of significance of deviation of both $\underline{k_1}$ and $\underline{k_2}$ from unity was made. The results of these tests are shown in table 2.

The regression lines for the width of the pupal head measured across the insertion of the mandibles are shown, for the three genera, in figure 11. For E. hamatum, as an example, $k_1 = 1.04$ and $k_2 = 2.26$. Thus over a range comprising 80 percent of the over-all body length, the width of the head bears an isometric relationship to the over-all body length. Over the remaining portion of the total-pupal length, the width of the head becomes disproportionately larger, demonstrating a strong positive allometry for each increment in over-all body length. If the original data for head-width versus over-all body length were plotted on rectangular coordinates, this abrupt and discontinuous change in the slopes of the two regression lines would appear as a moderately-sudden but nevertheless continuous alteration in the slope of the curvilinear relationship. To clarify further the relationship between the slope of the double logarithmic regression plot and isometric versus allometric anatomical relationships, the ordinate, representing the width of the head, was expressed as a percent of the total-body length (fig. 17). If any anatomical part bears an isometric relationship to over-all body length, then the percent of over-all body length that the part comprises remains constant over the entire range of total-body length. Thus in E. hamatum, for the width of the head measured across the mandible insertion (fig. 17), a value of k_1 = 1.04 corresponds to the first twenty points in figure 11, and shows that until 60 percent of the over-all body length of the size range comprising the pupal series has been reached, the width of the head comprises a constant 22 percent of the total-body length. The slope of k_2 (equal to 2.26) in figure 11, which indicates a strong positive allometric relationship, corresponds to the sharp increase in the ordinate in figure 17, thus demonstrating the disproportionate increase in head width in relation to further increments in over-all pupal size.

If we examine the regression lines for the total length of the leg in E hamatum (fig. 12), it can be seen that the first 21 points exhibit a strong positive allometry, while the last seven points show a nearly equally strong negative allometry. This change in the slope of the two regression lines corresponds to the rise and fall of the "percentage" ordinate in figure 18. Thus with respect to the length of the total leg, as pupal size increases throughout 60 percent of its total range, the length of the leg increases disproportionately. As pupal size increases still further however, the percentage of total-body length that the total leg comprises actually decreases.

Having graphically illustrated the isometric and allometric relationships between regression lines of the double logarithmic plots, rectangular coordinates, and the corresponding plots expressing linear dimensions of morphological appendages in terms of a proportion of the overall pupal body length, I would now like to consider in detail, the comparative population characteristics for the various anatomical parts illustrated in figures 10-16.

The values for width of the head in E. hamatum, whether measured across the mandible insertion or across the eyes, increase isometrically (or proportionately) as over-all pupal body length increases, up to approximately 75 percent of the total range (figs. 10, 11). Thus in individuals of E. hamatum in which the over-all length ranges from 4.4 mm. - 10.5 mm., head width varies isometrically. From figure 8 we can see that this range includes approximately 99 percent of the total E. hamatum population. In the remaining one percent of the population, in which overall length extends from 10.5 mm. - 12.5 mm., head width increases with a strong positive allometry (k_2 = 2.05 for head-width measured across the eyes, and k_2 = 2.26 for head-width measured across the mandible insertion).

For comparable head with measurements in N. nigrescens, a single regression line has been drawn throughout the range of total-body length (figs. 10, 11). In both cases head width in this species exhibits a slight positive allometry throughout the pupal range.

When the head-width in pupal individuals from populations of _A_. _laeviceps_ is considered, an interesting situation obtains. In individuals ranging from 3.2 mm. - 3.4 mm. (which includes approximately 50 percent of the total population), head width varies isometrically. For individuals ranging from 3.4 mm. - 3.8 mm. the width of the head hardly increases at all, resulting in a negative allometric relationship. However, in the case of _Aenictus_ it must be kept in mind that the regression lines have been exaggerated by the standardization of over-all body lengths in all three species under study. Because in _Aenictus_, we are dealing with a relationship between head width and a range of over-all pupal body length of only 0.6 mm., and because a relatively large scatter obtains (resulting in a correspondingly large standard error of the difference between $\underline{k_1}$ and $\underline{k_2}$, as shown in table 2) in this case a single regression line might have been drawn through all of the points.

When the allometric relationships of the leg and its various parts is considered for _E_. _hamatum_, a situation is found that is opposite to that for head width. Whether we consider the length of the tibia, the length of the first three tarsal segments, or the sum of these lengths, a moderately strong positive allometry exists over 80 percent of the range of over-all body length, followed by a correspondingly strong negative allometry over the remaining 20

Fig. 10. Graph comparing regressions of pupal head-width (measured across the eyes) on over-all pupal length, in *N. nigrescens*, *A. laeviceps*, and *E. hamatum*. The ordinate represents the logarithms of the head-width measurements, in mm. The abscissa represents the logarithms of the over-all body length measurements, in mm. For all three species, the ranges of over-all body length are standardized.

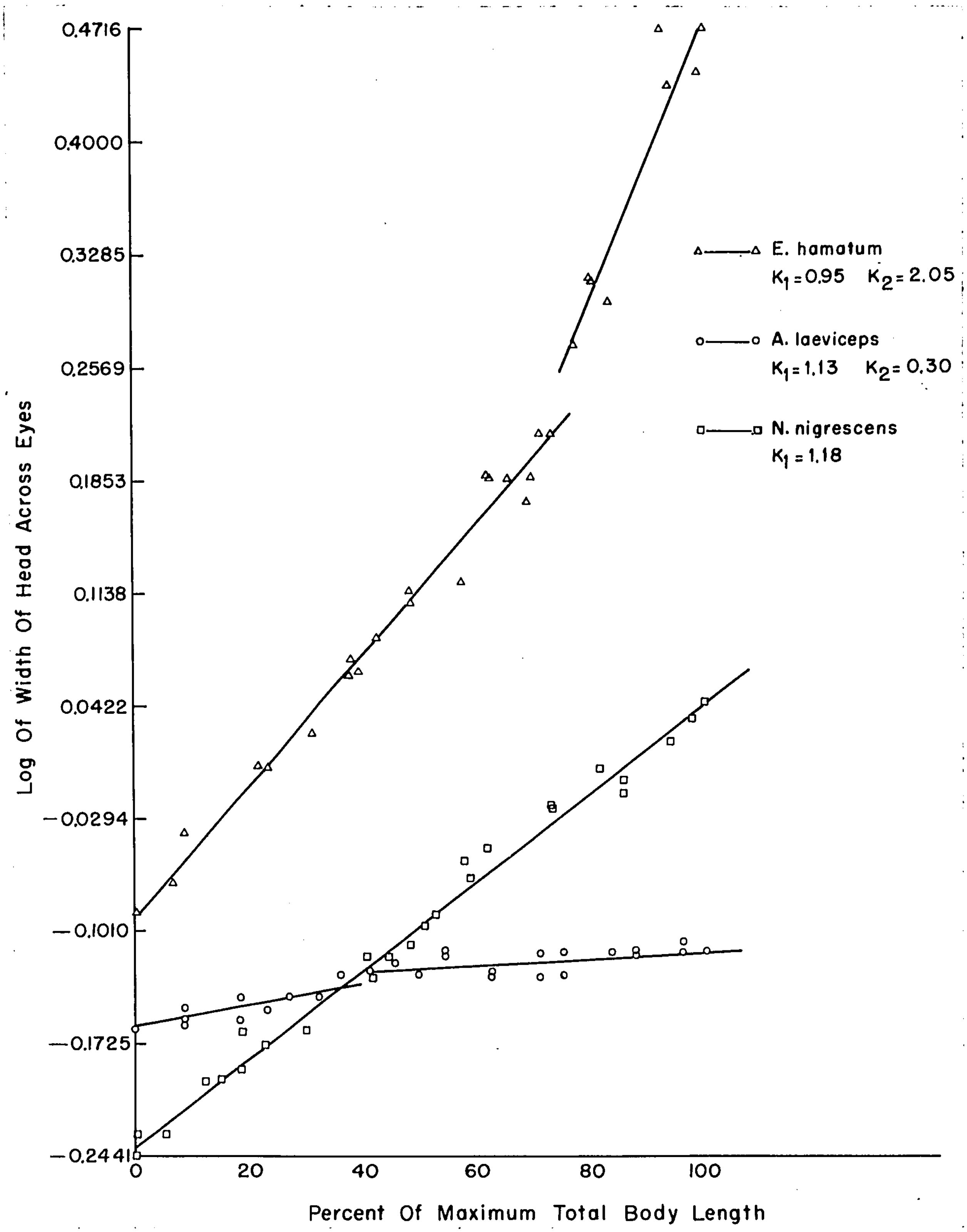

0.4716
0.4000
0.3285
0.2569
0.1853
0.1138
0.0422
−0.0294
−0.1010
−0.1725
−0.2441
Log Of Width Of Head Across Eyes
0
20
40
60
80
100
Percent Of Maximum Total Body Length
E. hamatum
K_1 = 0.95 K_2 = 2.05
A. laeviceps
K_1 = 1.13 K_2 = 0.30
N. nigrescens
K_1 = 1.18

Fig. 10

Fig. 11. Graph comparing regressions of pupal head-width (measured across the mandible insertion) on over-all pupal length, in *N. nigrescens*, *A. laeviceps*, and *E. hamatum*. The ordinate represents the logarithms of the head-width measurements, in mm. The abscissa represents the logarithms of the over-all body length measurements, in mm. For all three species, the ranges of over-all body length are standardized.

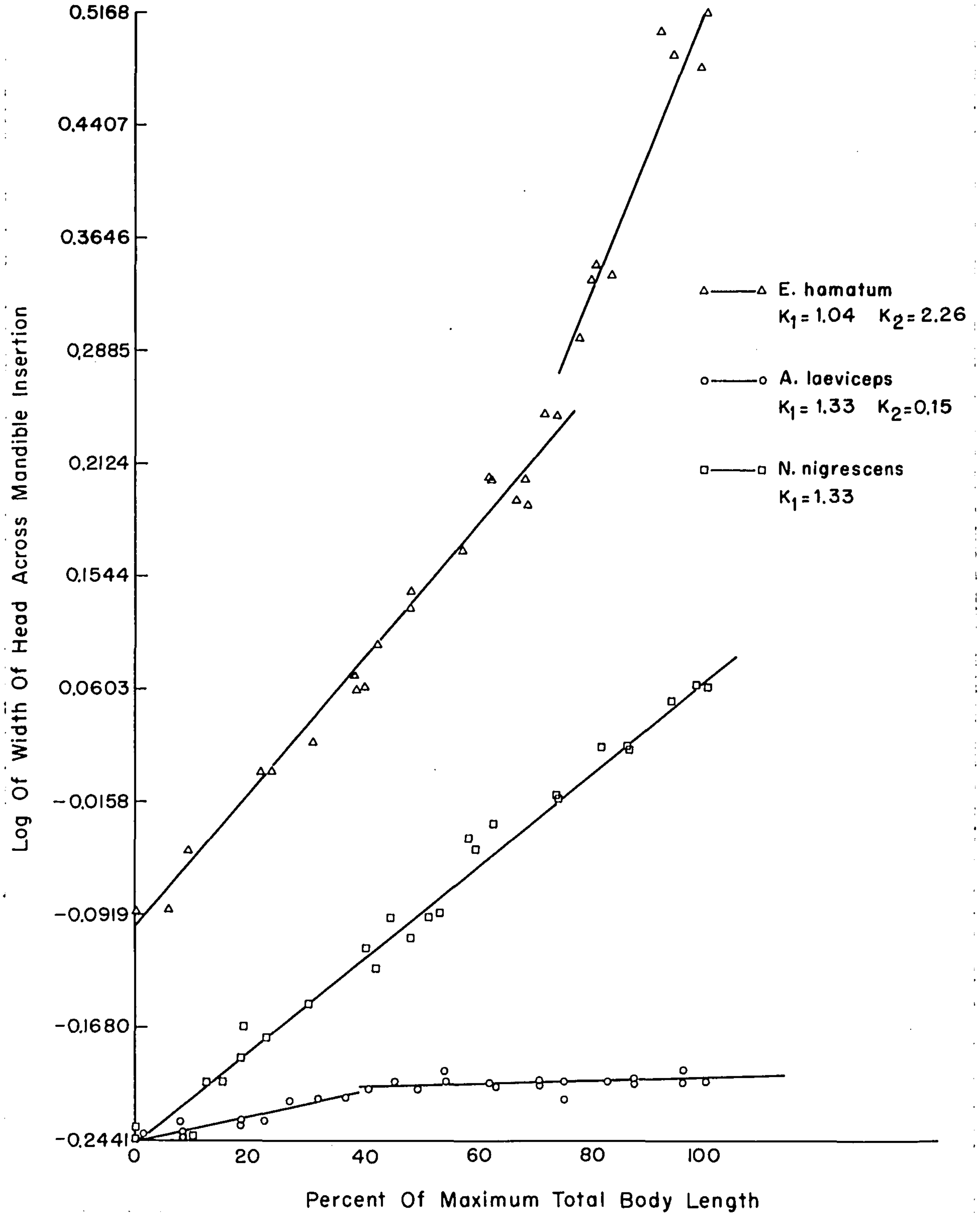

0.5168
0.4407
0.3646
0.2885
0.2124
0.1544
0.0603
-0.0158
-0.0919
-0.1680
-0.2441
0
20
40
60
80
100
Log Of Width Of Head Across Mandible Insertion
Percent Of Maximum Total Body Length
△——△ E. hamatum
K_1 = 1.04 K_2 = 2.26
○——○ A. laeviceps
K_1 = 1.33 K_2 = 0.15
□——□ N. nigrescens
K_1 = 1.33

Fig. 11

Fig. 12. Graph comparing regressions of the length of the total leg, on over-all pupal length, in _N_. _nigrescens_, _A_. _laeviceps_, and _E_. _hamatum_. The ordinate represents the logarithms of the leg-length measurements, in mm. The abscissa represents the logarithms of the over-all body length measurements, in mm. For all three species, the ranges of over-all body length are standardized.

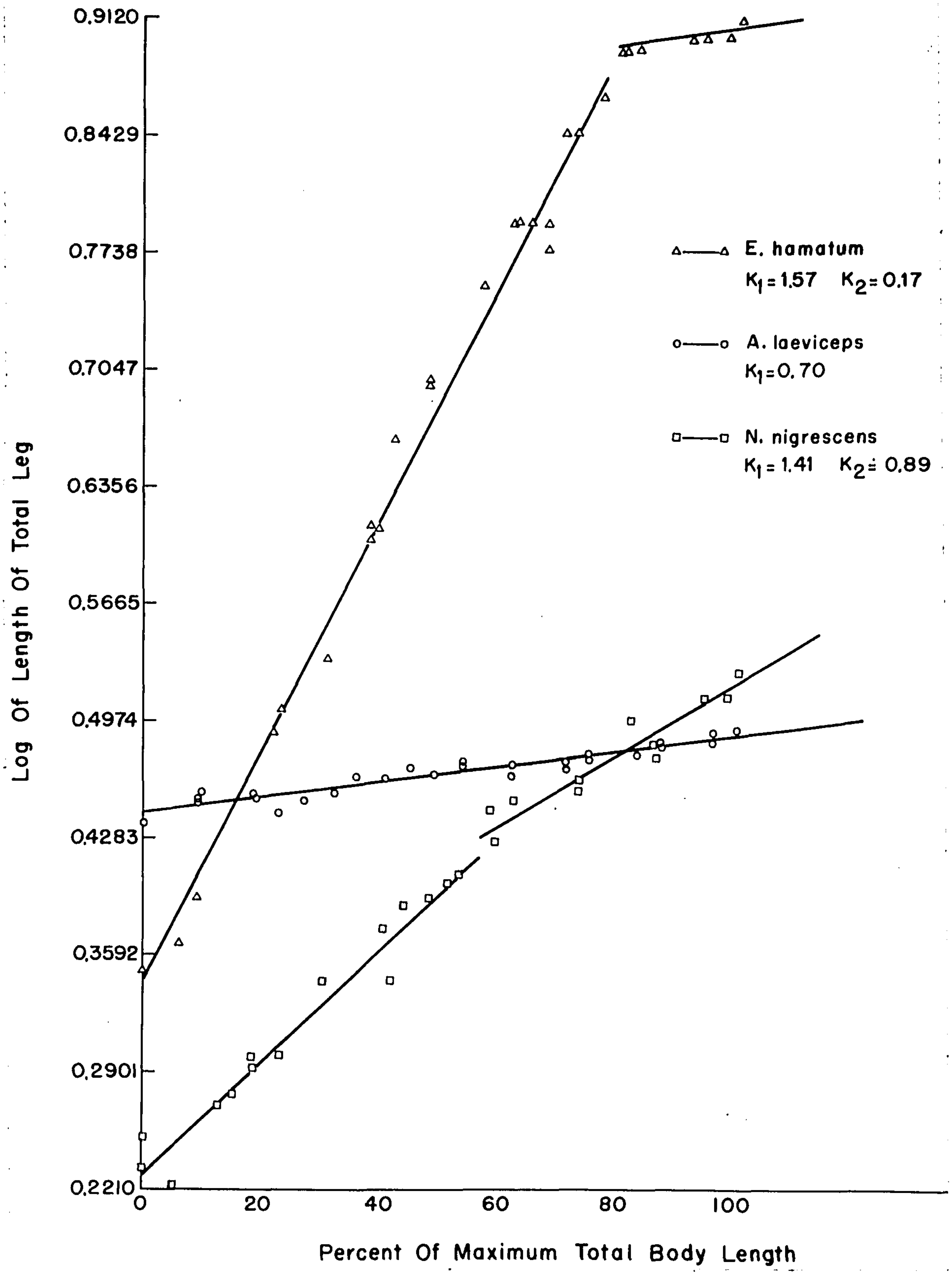

0.9120
0.8429
0.7738
0.7047
0.6356
0.5665
0.4974
0.4283
0.3592
0.2901
0.2210
Log Of Length Of Total Leg
0
20
40
60
80
100
Percent Of Maximum Total Body Length
△——△ E. hamatum
K1 = 1.57 K2 = 0.17
○——○ A. laeviceps
K1 = 0.70
□——□ N. nigrescens
K1 = 1.41 K2 ≐ 0.89

Fig. 12

Fig. 13. Graph comparing regressions of the length of the tibia, on over-all pupal length, in *N. nigrescens*, *A. laeviceps*, and *E. hamatum*. The ordinate represents the logarithms of the tibial-length measurements, in mm. The abscissa represents the logarithms of the over-all body length measurements, in mm. For all three species, the ranges of over-all body length are standardized.

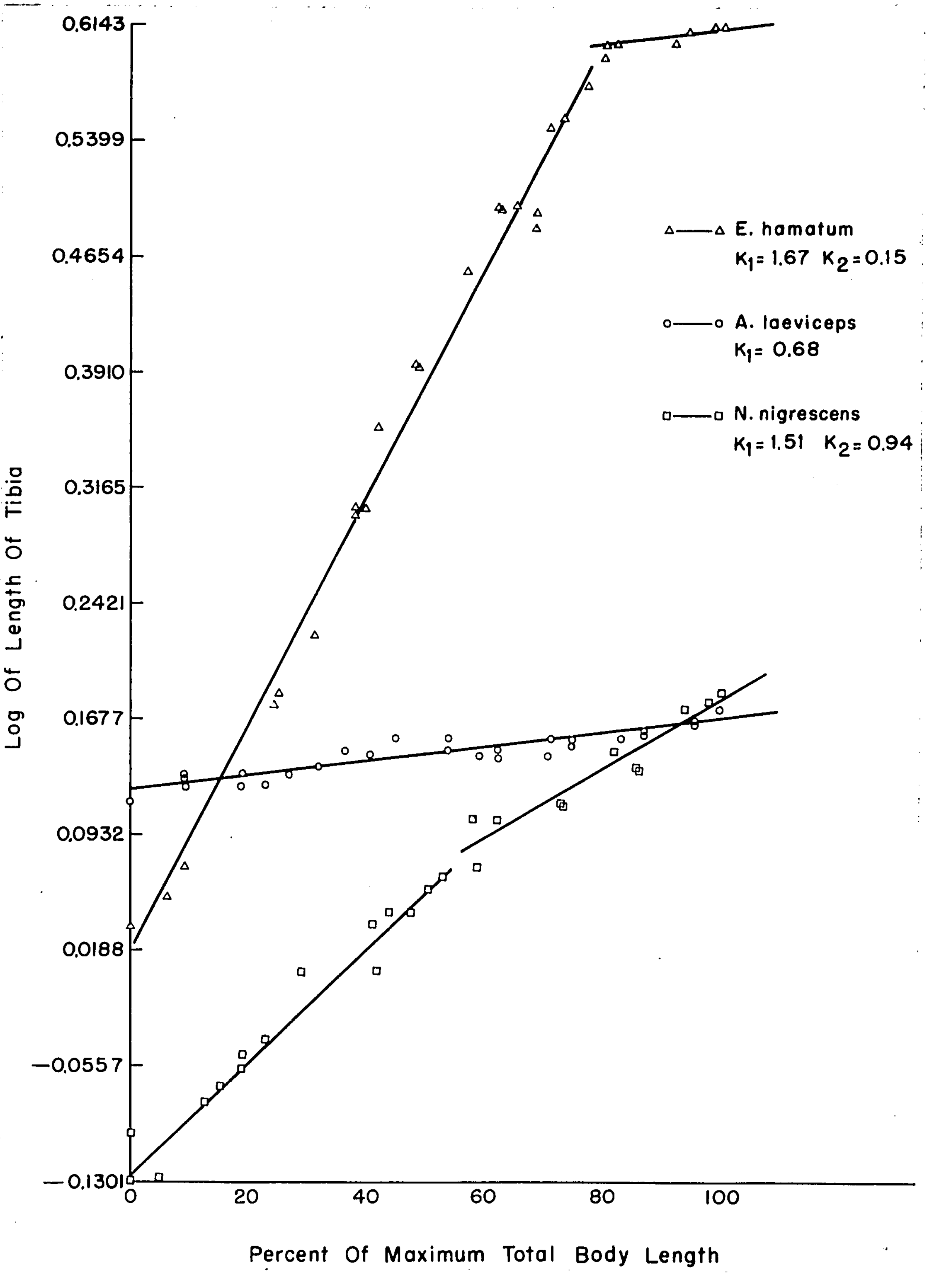
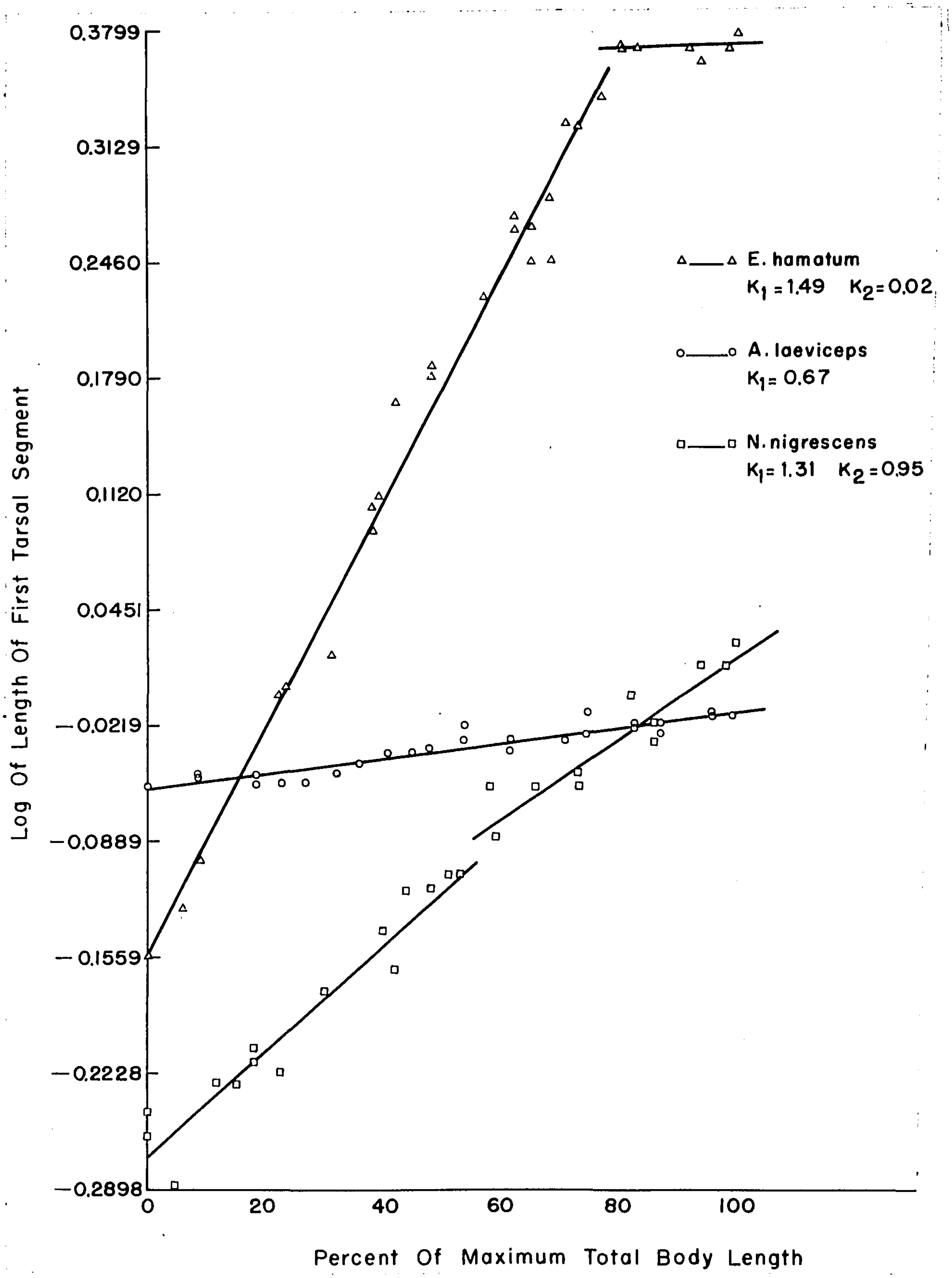

0.6143
0.5399
0.4654
0.3910
0.3165
0.2421
0.1677
0.0932
0.0188
−0.0557
−0.1301
0
20
40
60
80
100
Log Of Length Of Tibia
Percent Of Maximum Total Body Length
△——△ E. hamatum
K1= 1.67 K2=0.15
○——○ A. laeviceps
K1= 0.68
□——□ N. nigrescens
K1= 1.51 K2= 0.94

Fig. 13

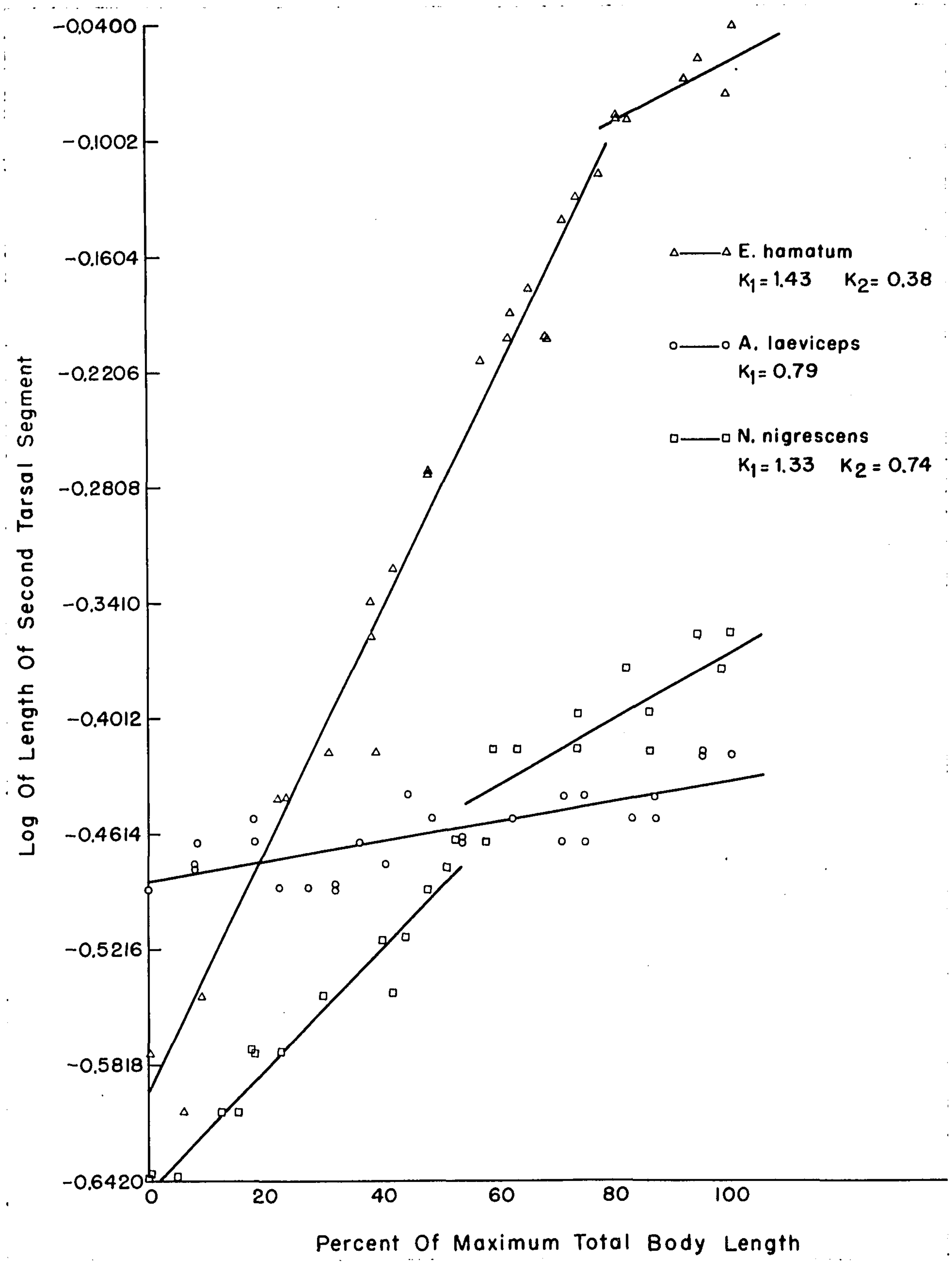
Fig. 14. Graph comparing regressions of the length of the first tarsal segment, on over-all pupal length, in *N. nigrescens*, *A. laeviceps*, and *E. hamatum*. The ordinate represents the logarithms of the tarsal-length measurements, in mm. The abscissa represents the logarithms of the over-all body length measurements, in mm. For all three species, the ranges of over-all body length are standardized.



0.3799
0.3129
0.2460
0.1790
0.1120
0.0451
−0.0219
−0.0889
−0.1559
−0.2228
−0.2898
0
20
40
60
80
100
Log Of Length Of First Tarsal Segment
Percent Of Maximum Total Body Length
△——△ E. hamatum
K1 = 1.49 K2 = 0.02
○——○ A. laeviceps
K1 = 0.67
□——□ N. nigrescens
K1 = 1.31 K2 = 0.95

Fig. 14

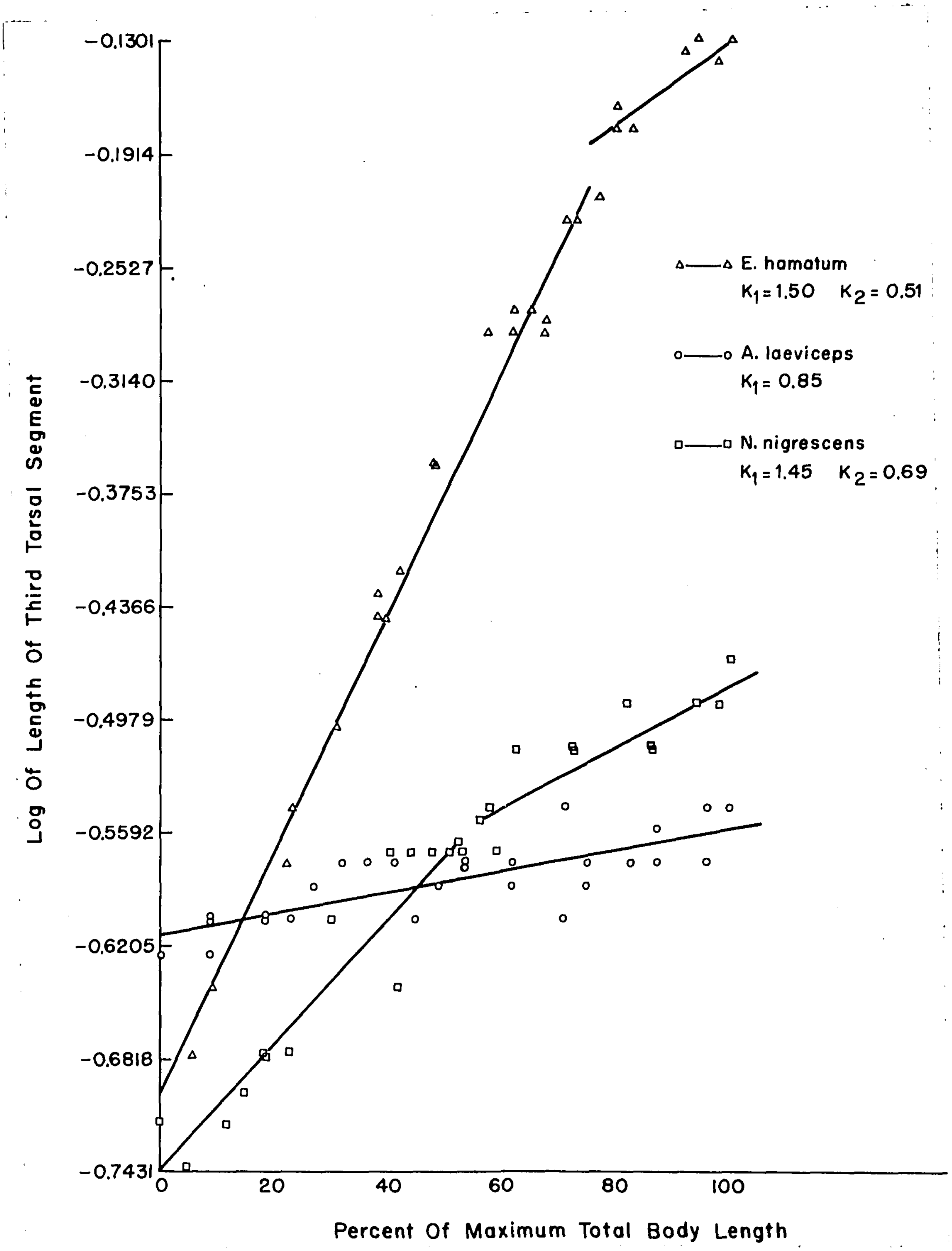
Fig. 15. Graph comparing regressions of the length of the second tarsal segment, on over-all pupal length, in *N. nigrescens*, *A. laeviceps*, and *E. hamatum*. The ordinate represents the logarithms of the tarsal-length measurements, in mm. The abscissa represents the logarithms of the over-all body length measurements, in mm. For all three species, the ranges of over-all length are standardized.



-0.0400
-0.1002
-0.1604
-0.2206
-0.2808
-0.3410
-0.4012
-0.4614
-0.5216
-0.5818
-0.6420
0
20
40
60
80
100
Log Of Length Of Second Tarsal Segment
Percent Of Maximum Total Body Length
△——△ E. hamatum
K_1 = 1.43 K_2 = 0.38
○——○ A. laeviceps
K_1 = 0.79
□——□ N. nigrescens
K_1 = 1.33 K_2 = 0.74

Fig. 15

Fig. 16. Graph comparing regressions of the length of the third tarsal segment, on over-all pupal length, in _N_. _nigrescens_, _A_. _laeviceps_, and _E_. _hamatum_. The ordinate represents the logarithms of the tarsal-length measurements in mm. The abscissa represents the logarithms of the over-all body length measurements, in mm. For all three species, the ranges of over-all body length are standardized.



Log Of Length Of Third Tarsal Segment
−0.1301
−0.1914
−0.2527
−0.3140
−0.3753
−0.4366
−0.4979
−0.5592
−0.6205
−0.6818
−0.7431
0
20
40
60
80
100
Percent Of Maximum Total Body Length
△—△ E. hamatum
$K_1 = 1.50$ $K_2 = 0.51$
○—○ A. laeviceps
$K_1 = 0.85$
□—□ N. nigrescens
$K_1 = 1.45$ $K_2 = 0.69$

Fig. 16

Fig. 17. Graph showing the relationship between pupal head-width and over-all pupal body length in _A_. _laeviceps_, _N_. _nigrescens_, and _E_. _hamatum_. For all three species, the ranges of over-all body length are standardized.

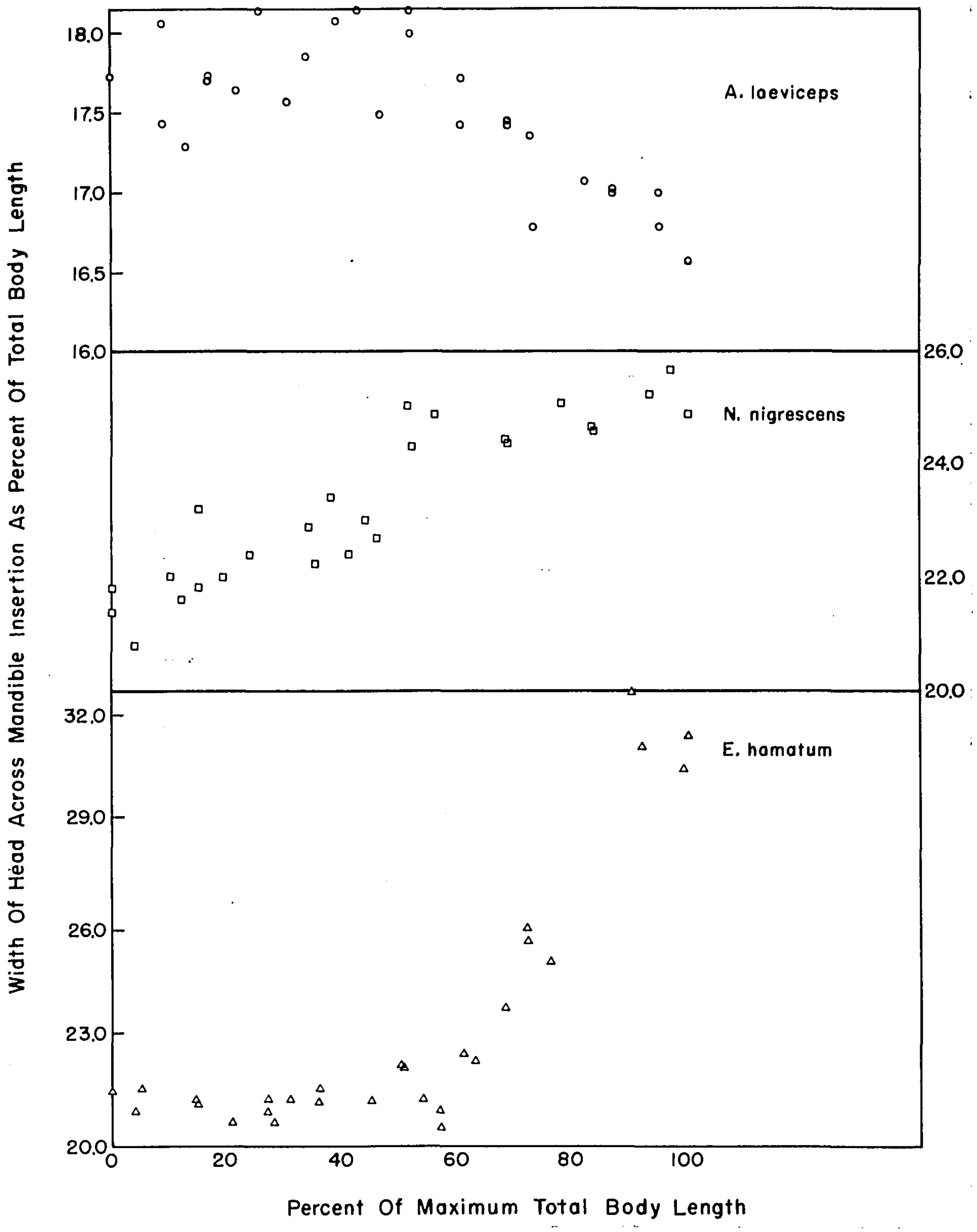

Width Of Head Across Mandible Insertion As Percent Of Total Body Length
18.0
17.5
17.0
16.5
16.0
32.0
29.0
26.0
23.0
20.0
26.0
24.0
22.0
20.0
A. laeviceps
N. nigrescens
E. hamatum
0
20
40
60
80
100
Percent Of Maximum Total Body Length

Fig. 17

Fig. 18. Graph showing the relationship between pupal leg-length and over-all pupal body length in *A. laeviceps*, *N. nigrescens*, and *E. hamatum*. For all three species, the ranges of over-all body length are standardized.

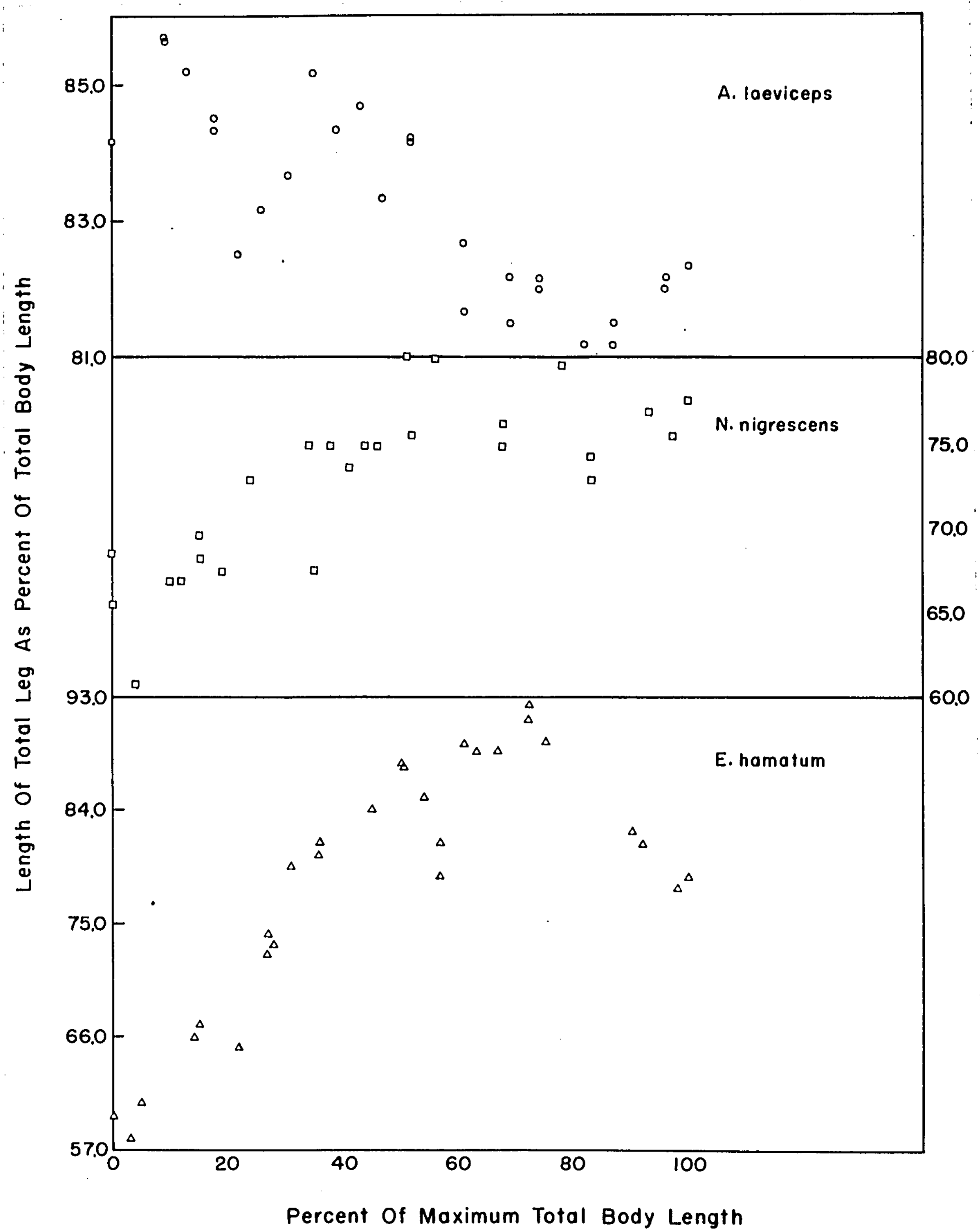

A. laeviceps
N. nigrescens
E. hamatum
85.0
83.0
81.0
93.0
84.0
75.0
66.0
57.0
80.0
75.0
70.0
65.0
60.0
0
20
40
60
80
100
Length Of Total Leg As Percent Of Total Body Length
Percent Of Maximum Total Body Length

Fig. 18

TABLE 1

EQUATIONS OF THE LINEAR REGRESSION LINES ILLUSTRATED IN FIGURES 10-16, AND THEIR TRANSFORMATION TO POWER FUNCTIONS

WIDTH OF HEAD ACROSS MANDIBLE

N. nigrescens	First twenty-six points	
	$Y = 1.3255X - 0.8088$	
	$Y = 0.1553X^{1.3255}$	
E. hamatum	First twenty points	Last eight points
	$Y = 1.0409X - 0.7012$	$Y = 2.2612X - 1.8664$
	$Y = 0.1990X^{1.0409}$	$Y = 0.0136X^{2.2612}$
A. laeviceps	First ten points	Last seventeen points
	$Y = 1.3223X - 0.9224$	$Y = 0.1456X - 0.2856$
	$Y = 0.1195X^{1.3223}$	$Y = 0.5180X^{0.1456}$

WIDTH OF HEAD ACROSS EYES

N. nigrescens	First twenty-six points	
	$Y = 1.1769X - 0.7362$	
	$Y = 0.1835X^{1.1769}$	
E. hamatum	First twenty points	Last eight points
	$Y = 0.9459X - 0.6357$	$Y = 2.0540X - 1.6049$
	$Y = 0.2314X^{0.9459}$	$Y = 0.0248X^{2.0540}$

A. laeviceps	First ten points	Last seventeen points
	$Y = 1.1340X - 0.7411$	$Y = 0.2996X - 0.2894$
	$Y = 0.1815X^{1.1340}$	$Y = 0.5136X^{0.2996}$

LENGTH OF TOTAL LEG

N. nigrescens	First fifteen points	Last eleven points
	$Y = 1.4144X - 0.3721$	$Y = 0.8943X - 0.0707$
	$Y = 0.4245X^{1.4144}$	$Y = 0.8500X^{0.8943}$
E. hamatum	First twenty-one points	Last seven points
	$Y = 1.5731X - 0.5643$	$Y = 0.1682X + 0.7357$
	$Y = 0.2727X^{1.5731}$	$Y = 5.4410X^{0.1682}$
A. laeviceps	First twenty-seven points	
	$Y = 0.7037X + 0.0817$	
	$Y = 1.2070X^{0.7037}$	

LENGTH OF TIBIA

N. nigrescens	First fifteen points	Last eleven points
	$Y = 1.5095X - 0.7645$	$Y = 0.9436X - 0.4456$
	$Y = 0.1720X^{1.5095}$	$Y = 0.3584^{0.9436}$
E. hamatum	First twenty-one points	Last seven points
	$Y = 1.6668X - 0.9405$	$Y = 0.1456X + 0.4634$
	$Y = 0.1147X^{1.6668}$	$Y = 2.9070X^{0.1456}$
A. laeviceps	First twenty-seven points	
	$Y = 0.6808X - 0.2270$	
	$Y = 0.5930X^{0.6808}$	

LENGTH OF FIRST TARSAL SEGMENT

N. nigrescens	First fifteen points	Last eleven points
	$Y = 1.3071X - 0.8278$	$Y = 0.9519X - 0.6123$
	$Y = 0.1486X^{1.3071}$	$Y = 0.2441^{0.9519}$
E. hamatum	First twenty-one points	Last seven points
	$Y = 1.4918X - 1.0126$	$Y = 0.0253X + 0.3465$
	$Y = 0.0971X^{1.4918}$	$Y = 2.2200X^{0.0253}$
A. laeviceps	First twenty-seven points	
	$Y = 0.6656X - 0.3997$	
	$Y = 0.3989X^{0.6656}$	

LENGTH OF SECOND TARSAL SEGMENT

N. nigrescens	First fifteen points	Last eleven points
	$Y = 1.3323X - 1.2128$	$Y = 0.7382X - 0.8541$
	$Y = 0.0613X^{1.3323}$	$Y = 0.1400X^{0.7382}$
E. hamatum	First twenty-one points	Last seven points
	$Y = 1.4303X - 1.4216$	$Y = 0.3841X - 0.4460$
	$Y = 0.0379X^{1.4303}$	$Y = 0.3581X^{0.3841}$
A. laeviceps	First twenty-seven points	
	$Y = 0.7935X - 0.8928$	
	$Y = 0.1280X^{0.7935}$	

LENGTH OF THIRD TARSAL SEGMENT

N. nigrescens	First fifteen points	Last eleven points
	$Y = 1.4527X - 1.4128$	$Y = 0.6929X - 0.9377$
	$Y = 0.0387X^{1.4527}$	$Y = 0.1154X^{0.6929}$
E. hamatum	First twenty-one points	Last seven points
	$Y = 1.4987X - 1.5675$	$Y = 0.5097X - 0.6510$
	$Y = 0.0271X^{1.4987}$	$Y = 0.2233X^{0.5097}$
A. laeviceps	First twenty-seven points	
	$Y = 0.8502X - 1.0496$	
	$Y = 0.0892X^{0.8502}$	

TABLE 2

TESTS OF SIGNIFICANCE OF THE DIFFERENCES BETWEEN THE REGRESSION COEFFICIENTS AND OF THEIR DEVIATION FROM ISOMETRY (K = 1)

(Head Width Measured Across Eyes)

	Test for Isometry $(K_1=1)$	Calculated Value of K_1		Calculated Value of K_2	Test for Isometry $(K_2=1)$
N. nigrescens		1.1769			
s.e.[a]		0.0264			
t[b]	6.7				
d.f.[c]	24				
p[d]	.01				
E. hamatum		0.9459		2.0540	
s.e.		0.0396		0.1639	
t	1.4		6.6		6.4
d.f.	18		24		6
p	.20-.10		.01		.01

	Test for Isometry (K_1=1)	Calculated Value of K_1		Calculated Value of K_2	Test for Isometry (K_2=1)
A. laeviceps		1.1340		0.2996	
s.e.		0.4407		0.2000	
t	0.3		1.7		3.5
d.f.	8		23		15
p	.80-.70		.20-.10		.01

[a] standard error of allometric coefficient

[b] calculated as detailed in Snedecor (1946)

[c] degrees of freedom

[d] probability

(Head Width Measured Across Mandible Insertion)

	K=1		K_1		K_2		K=1
N. nigrescens			1.3255				
s.e.			0.0299				
t		10.9					
d.f.		24					
p		.01					
E. hamatum			1.0409		2.2612		
s.e.			0.0458		0.1904		
t		0.9		6.2		6.6	
d.f.		18		23		6	
p		.40-.30		.01		.01	

	K=1		K_1		K_2		K=1
<u>A</u>. <u>laeviceps</u>			1.3233		0.1456		
s.e.			0.4464		0.2000		
t		0.7		2.4		4.3	
d.f.		8		23		15	
p		.60-.50		.05-.02		.01	

(Length of Total Leg)

	K=1		K_1		K_2		K=1
N. nigrescens			1.4144		0.8943		
s.e			0.0875		0.1280		
t		4.7		3.4		0.8	
d.f		13		22		9	
p		.01		.01		.50-.40	
E. hamatum			1.5731		0.1682		
s.e.			0.0377		0.1854		
t		15.2		7.4		4.5	
d.f.		19		24		5	
p		.01		.01		.01	

	K=1	K_1	K_2	K=1
A. laeviceps		0.7037		
s.e.		0.0431		
t	6.9			
d.f.	25			
p	.01			

(Length of Tibia)

	K=1		K_1		K_2		K=1
_N_. _nigrescens_			1.5095		0.9436		
s.e.			0.1066		0.1523		
t		4.8		3.0		0.4	
d.f.		13		22		9	
p		.01		.01		.70-.60	
_E_. _hamatum_			1.6668		0.1456		
s.e.			0.0376		0.1854		
t		17.7		8.0		4.6	
d.f.		19		24		5	
p		.01		.01		.01	

	K=1	K_1	K_2	K=1
A. laeviceps		0.6808		
s.e.		0.0545		
t	5.9			
d.f.	25			
p	.01			

(Length of First Tarsal Segment)

	K=1		K_1		K_2		K=1
N. *nigrescens*			1.3071		0.9519		
s.e.			0.1726		0.2491		
t		1.8		1.2		0.2	
d.f.		13		22		9	
p		.10-.05		.30-.20		.90-.80	
E. *hamatum*			1.4918		0.0253		
s.e.			0.0376		0.1854		
t		13.1		7.8		5.3	
d.f.		19		24		5	
p		.01		.01		.01	

	K=1	K_1	K_2	K=1
A. *laeviceps*		0.6656		
s.e.		0.0578		
t	5.8			
d.f.	25			
p	.01			

(Length of Second Tarsal Segment)

	K=1		K_1		K_2		K=1
N. nigrescens			1.3323		0.7382		
s.e.			0.0860		0.1241		
t		3.9		3.9		2.1	
d.f.		13		22		9	
p		.01		.01		.10-.05	
E. hamatum			1.4303		0.3841		
s.e.			0.0486		0.2401		
t		8.8		4.3		2.6	
d.f.		19		24		5	
p		.01		.01		.05-.02	

	K=1	K_1	K_2	K=1
A. laeviceps		0.7935		
s.e.		0.1285		
t	1.6			
d.f.	25			
p	.20-.10			

(Length of Third Tarsal Segment)

	K=1		K_1		K_2		K=1
<u>N</u>. <u>nigrescens</u>			1.4527		0.6929		
s.e.			0.1055		0.1522		
t		4.3		4.1		2.0	
d.f.		13		22		9	
p		.01		.01		.10-.05	
<u>E</u>. <u>hamatum</u>			1.4987		0.5097		
s.e.			0.0484		0.2390		
t		10.3		4.1		2.1	
d.f.		19		24		5	
p		.01		.01		.10-.05	

	K=1	K_1	K_2	K_1
A. laeviceps		0.8502		
s.e.		0.1413		
t	1.1			
d.f.	25			
p	.30-.20			

percent of the over-all pupal size range (figs. 12-16). Of additional interest is the similarity of the values of k_1 and k_2 for each of the parts contributing to the structure of the leg. For the tibia $k_1 = 1.67$; for the first tarsal segment $k_1 = 1.49$; for the second tarsal segment $k_1 = 1.43$; for the third tarsal segment $k_1 = 1.50$; and for the length of the sum of these parts $k_1 = 1.57$.

The allometric pattern of the leg in pupae of *N. nigrescens* is somewhat similar to that found in *E. hamatum*. Over 55 percent of the pupal size range, the parts of the leg exhibit a moderately positive allometry. This is followed, in the remaining size groups, either by an essentially isometric relationship (for the first tarsal segment, the tibia, and the total leg), or by a moderately negative allometric relationship (for the second and third tarsal segments).

In the case of *A. laeviceps*, one regression line has been fitted for all of the leg segments. They all exhibit a slightly negative allometry, and, as in the case of *Eciton*, all of the regression coefficients are similar.

Physiological Studies

Brief Description of Colonies of N. nigrescens:

The colonies of *N. nigrescens* used for the physiological and behavioral studies were visited nightly and followed throughout as many functional cycles as possible. With the exception of one colony ('64 N-VI) all were judged to be normal in size and activity. Before presenting the results of these tests, a very brief description of the colonies used is given. It should be mentioned also that five of the colonies were particularly interesting ecologically, either because of their own activities or as a result of their predatory interactions with other ant species.

The descriptions given below, of colony routine and behavior during the nomadic and statary phases are very brief. A detailed account of colony raiding and nesting activities in relation to the functional cycle in *N. nigrescens*, has been given by Schneirla (1958), and should be consulted for additional information concerning phase durations, bivouac sites, and levels of worker activity during the nomadic and statary phases.

Colony '64 N-II was found on July 3, with a weak raid in progress along the bank of the north fork of cave creek. It was completing a statary phase (judged at about statary day 15) and its bivouac was located beneath the surface of the loose soil above the creek bank. Weak raiding occurred for the remaining three statary days. On July 7, the colony entered the nomadic phase. It was followed for four more days until, on July 12, it emigrated into tall grass bordering the creek.

Colony '64 N-IV was discovered on July 17, on statary day 18. A very small raid was in progress in the area around the Station's water tank. On the first nomadic day (July 18), raiding was rather weak for the time; later that evening an emigration took place, but only a few hundred callows were observed in the column. Many mature pupae were being transported by the adult workers. Throughout the first week of the nomadic phase, raiding was only moderately strong, until nomadic day 11, when colony activities increased sharply. On August 3, probably the last nomadic day (N-17), this colony also emigrated into an area of very tall grass, with heavy ground cover.

Colony '64 N-V was discovered on July 30, on statary day 12. Raiding during the remaining statary days was very weak. On August 6 the first emigration was observed. On August 11, the colony was engaged in a long emigration to the east. At the same time, another colony ('64 N-VII) was in the process of emigrating to the north. In an area of dense grass, the two colonies crossed perpendicular to each other. At the point of contact both colonies completed their emigrations intact, with practically no interaction.

Colony '64 N-VI was found on August 2, engaged in a very weak raid to the south, from beneath a rock. On August 4, another very weak raid was in progress. The next night, worker activity was so reduced that it was unusual, even for a statary colony. Tests of oxygen uptake correlated well with this observation (fig. 19). Except for one evening, this pattern of very reduced activity and no emigrations, continued until August 12. I then decided to dig up the colony to set up a laboratory nest, but when the log under which the bivouac was turned, I found that the colony had a larval all-worker brood at a stage corresponding to that usual for nomadic day 15. All of the visible larval brood was heaped into one mass at the far end of the log, but it seemed as though the brood population was quite small. I collected all of the larvae and found only about 1000 individuals (in contrast to approximately 40,000 from a normal colony). I watched the complete emigration, which was caused by my disturbing the colony, and no larvae were observed being carried in the column. At the completion of the emigration, I dug up the area around the old nest site, but no brood was found. It is probable that the lethargic condition of this colony resulted from the presence of an abnormally small larval brood.

Colony '65 N-III was found on July 3, as it was completing a nomadic phase. At this time the colony was at a very high level of activity, with vigorous raids being followed by long emigrations. On July 6, the colony entered the statary phase. For the next seven days raiding was very reduced, and on two of these statary days, no surface activity was observed. After statary day 7 observations on this colony were discontinued.

Of particular ecological interest, were the events occurring on the evening of July 4 (nomadic day 17), when we checked the condition of the colony, bivouacked under a log. A colony of the myrmicine ant, Trachymyrmex sp. was nesting beneath the surface, two meters to the left of the log. At 7:10 p.m., when it was still light, a few doryline workers were observed, milling around the edge of the log. At 7:55 p.m., the army-ants surged out of their bivouac, in a strong raiding column, at a 90°-angle to the Trachymrmex nest. At precisely this moment, the entire Trachymyrmex population (including brood and winged males), "bubbled" out of their nest with such vigor, that it could best be described as looking like a small volvanic eruption.

This sort of interaction, between colonies of N. nigrescens and species representing potential sources of booty, merits further investigation. During the course of our field studies, we have often seen colonies of ants maintaining "vigils" directly outside of their nests. In Trachymyrmex the first stage of this reaction is marked by a general milling around the nest opening, by several adult workers. As the raiding columns approach the nest, the workers begin pouring out at increasing rates. Stage two of this reaction occurs when the entire Trachymyrmex colony is out of the nest, occupying a stationary circular area around the nest opening. The final stage is often marked by a single column moving in a direction away from the advancing dorylines.

This sequence of reactions is so predictable that we often used it to locate colonies of *N. nigrescens*. Whenever we found a colony of *Trachymyrmex* out of its nest at night, we immediately began searching the area for army-ants. This was done by starting at the *Trachymyrmex* nest and walking in a spiral pattern. In addition, the stage of the *Trachymyrmex* reaction was an index of how far from the nest to search.

It is doubtful that this reaction is **always** caused by the entrance of sub-surface raiding columns of the dorylines into the *Trachymyrmex* nest, for stage one of the reaction is often seen when the army-ants are quite far away. The most probable explanation for this reaction is that workers of *Trachymyrmex* are able to detect odors that are associated with the army-ants. An almost identical series of reactions is given by colonies of *Pheidole* sp. that are present in the area of doryline foraging.

Colony '65 N-IV, judged at about nomadic day 18, was discovered on July 9. Weak-to-moderate raiding was characteristic of this colony throughout the succeeding statary phase. During this interval the colony was bivouacked in an area composed of very loose rocks, in which several statary nest shifts (at distances of 1-5 meters) were observed. On July 29, a new nomadic phase began. The colony was followed and tested until August 16, or through nearly all of this phase.

Colony '65 N-V was discovered on July 13, when columns were seen emerging from several nest openings belonging to colonies of the dolichoderine ant, Dorymyrmex pyramicus. From the condition of the brood, collected that evening during an emigration, we estimated that the colony was in its third nomadic day. On the night of July 18, at 11:25 p.m., a raiding column formed along the foundation of our cabin. Later that evening the foraging column entered the foundation between our cabin and the adjoining one. Colonies of Pheidole, which were nesting between the foundations of the two cabins, were forced out of their nests and into our room, and within 20 minutes, thousands of the fleeing adults (many carrying brood) were climbing up the cabin walls, and covering our beds and clothing. Finally, a moderately-strong column of army-ants emerged from beneath the foundation, raided across the floor of the bathroom, and disappeared beneath the floor on the other side.

On the night of July 20 (nomadic day 10), the colony emigrated beneath the foundations of our cabin. Early that morning (about 3:00 a.m.) a sudden and violent rain storm wiped out the emigration column. Later that morning (at 6:00 a.m.) a circular mill, about three meters in diameter, was found outside our cabin. By 9:00 a.m. all of the ants in the circular column were dead.

The colony entered the statary phase on July 29, and exhibited very reduced levels of surface activity. During the 16 days of the statary phase that this colony was visited, no surface raiding occurred on seven of them.

Colony '65 N-VIII was found on July 26, on approximately its last nomadic day. Throughout the statary phase, raiding was highly variable in strength and duration. Small statary shifts were observed on two of the statary nights. On August 15, the colony began a new nomadic phase.

Colony '66 N-II was followed through the last week of a nomadic phase, through a statary phase of 18 days, through a second nomadic phase (lasting 17 days), a second statary phase of 18 days, and through the first week of a third nomadic phase. This period, lasting from June 29 to September 3 represents the longest interval that any colony was surveyed.

The first statary phase (July 5) was marked by greatly reduced surface activities, and on five of the 18 statary nights, no surface raiding occurred. On evenings when surface raiding was observed, they often did not begin until after midnight.

The onset of the second nomadic phase was associated with exceedingly high levels of worker activity, and heavy booty-laden columns. The third nomadic night (July 25) was particularly impressive in that a greater quantity of booty was brought back to the nest than was observed for any other colony. On nomadic night 10 (August 1), colony excitation during a 50-meter emigration was again at a very high level. The new bivouac was situated underground, with the only entrance being a single hole, approximately 2 cm. in diameter. The emigration column was so broad that the nest opening could accommodate only a small fraction of the advancing worker population. As a result of this "traffic jam" at the bivouac opening, most of the on-coming individuals ran past it, eventually forming a triangular-shaped mill. The emigrating ants entered the perimeter of this triangle at one apex, the opening to the new bivouac was located at the second apex, and a single raiding column left the triangle from the third apex.

A transition of much interest for the present investigation occurred between the second statary and third nomadic phase. The first nomadic day was August 29, and by this time in the season, evening temperatures were between 55°F. and 60°F. Except for the presence of callow workers in the emigration trails, the colony appeared to be at a low (statary) level in all of its raiding and emigration activities. Figure 21 shows that, for the first week of this last nomadic phase, the levels of oxygen uptake are not significantly different than for the previous statary phase. Significantly, no developing larval brood was found in the colony at this time, and it is probable that this was the colony's last nomadic phase of the season, before the onset of winter dormancy.

Colony '66 N-III was found on July 3, at the start of a statary phase. All of the statary evenings were characterized by relatively weak raiding and no shifting of nests occurred. This colony was followed throughout the statary phase, and into the first week of a new nomadic phase.

Colony '66 N-VI was located on July 10, on approximately statary day 17. A very weak raid was in progress, with the returning foragers disappearing below the ground in the middle of a loose cluster of rocks. The transition between the statary and nomadic phases was particularly abrupt for this colony. By July 22, on nomadic day 11, the colony had emigrated so far from the laboratory that we abandoned it.

Colony '66 N-VII was discovered on July 26 (approximately nomadic day 2). It was judged to be above average in total population size, and was exceedingly active throughout the nomadic phase. At 3:00 a.m., on nomadic day 2, a strong raid was in progress, with columns passing within five meters of a nest of the myrmicine ant, *Pheidole* sp. Although no surface "fighting" took place between the two colonies, the *Pheidole* population abandoned their nest and formed a moving column that extended 20 meters from their nest, and terminated half-way up a juniper tree. On subsequent nights during the nomadic phase, the colony was characterized by heavy raiding and very long emigrations (in one case the new bivouac was located over 90 meters from the previous nest).

The statary phase was distinguished by colony activities at a low ebb, with no surface raiding in evidence on nine of the 21 statary days.

Colony '66 N-XII was found on August 13, in its last nomadic day. The entire statary phase was characterized by extremely weak surface activities. On August 31, a new nomadic phase was initiated, but the columns were weak and slow moving. This situation is comparable to that observed for colony '66 N-II, at the end of the functional season. The levels of activity of this colony during the nomadic phase at this time of the season, are greatly below those of the previous nomadic phase.

Comparison of Oxygen Uptake by Groups of Adult Workers of N. nigrescens During the Nomadic and Statary Phases:

Oxygen consumption records for groups of adult workers from colonies of *N. nigrescens* during the nomadic and statary phases, are summarized in figures 19-21. The graphs have been combined into three groups, representing the three corresponding years during which the tests were carried out.

Colony tests were performed nightly, usually between 8:30 p.m. and midnight. Each night, a colony was selected for testing, depending upon the number of days

Fig. 19. Graph comparing oxygen uptake of groups of intermediate-sized workers of *N. nigrescens*, during the nomadic phase (indicated by solid lines) and during the statary phase (indicated by broken lines). Each point represents the mean value of four determinations, made at five-minute intervals. These tests were conducted during the summer of 1964.

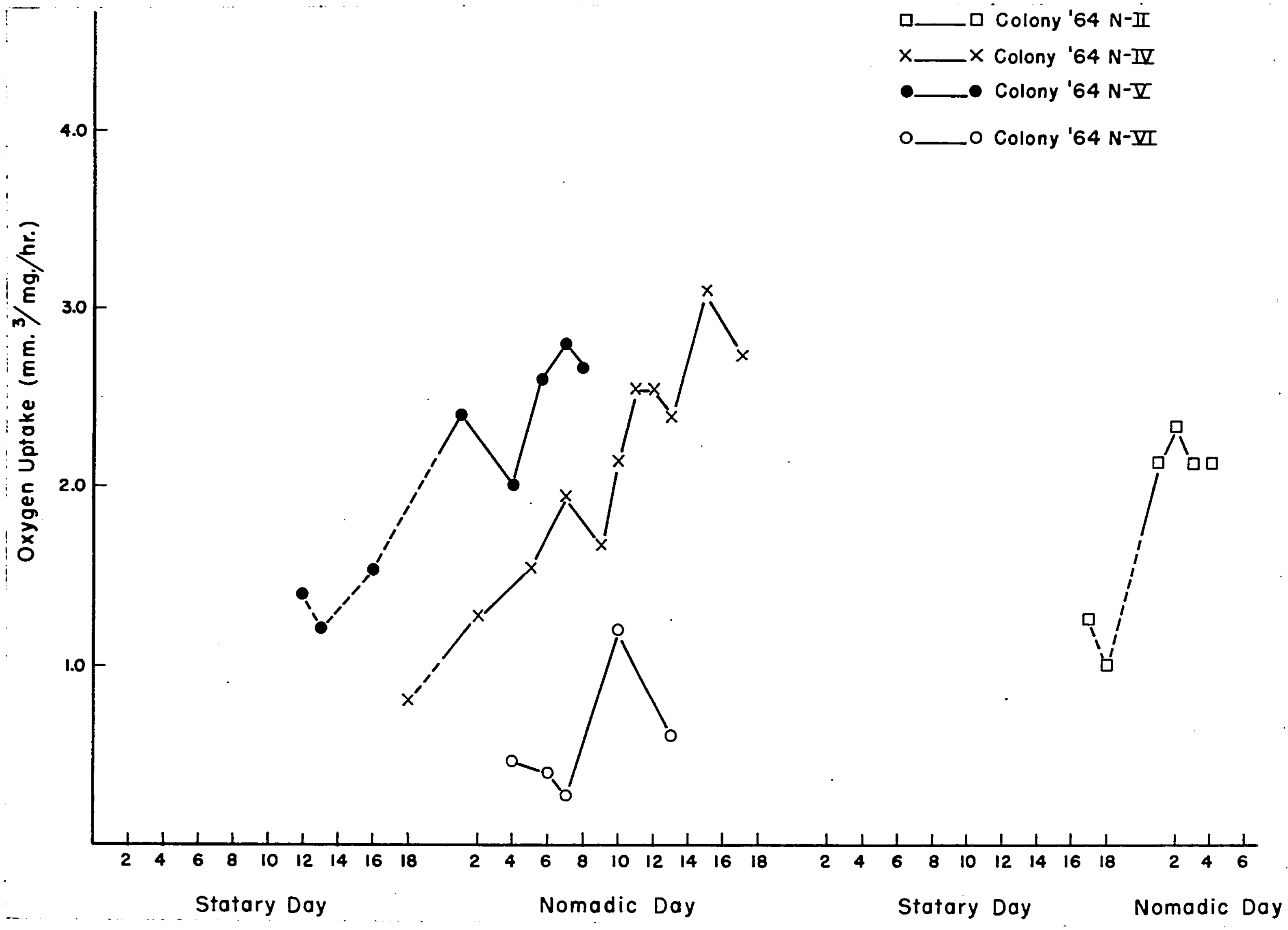

□——□ Colony '64 N-II
×——× Colony '64 N-IV
●——● Colony '64 N-V
○——○ Colony '64 N-VI
Oxygen Uptake (mm.³/ mg./hr.)
4.0
3.0
2.0
1.0
2 4 6 8 10 12 14 16 18
2 4 6 8 10 12 14 16 18
2 4 6 8 10 12 14 16 18
2 4 6
Statary Day
Nomadic Day
Statary Day
Nomadic Day

Fig. 19

Fig. 20. Graph comparing oxygen uptake of groups of intermediate-sized workers of N. nigrescens, during the nomadic phase (indicated by solid lines) and during the statary phase (indicated by broken lines). Each point represents the mean value of four determinations, made at five-minute intervals. These tests were conducted during the summer of 1965.

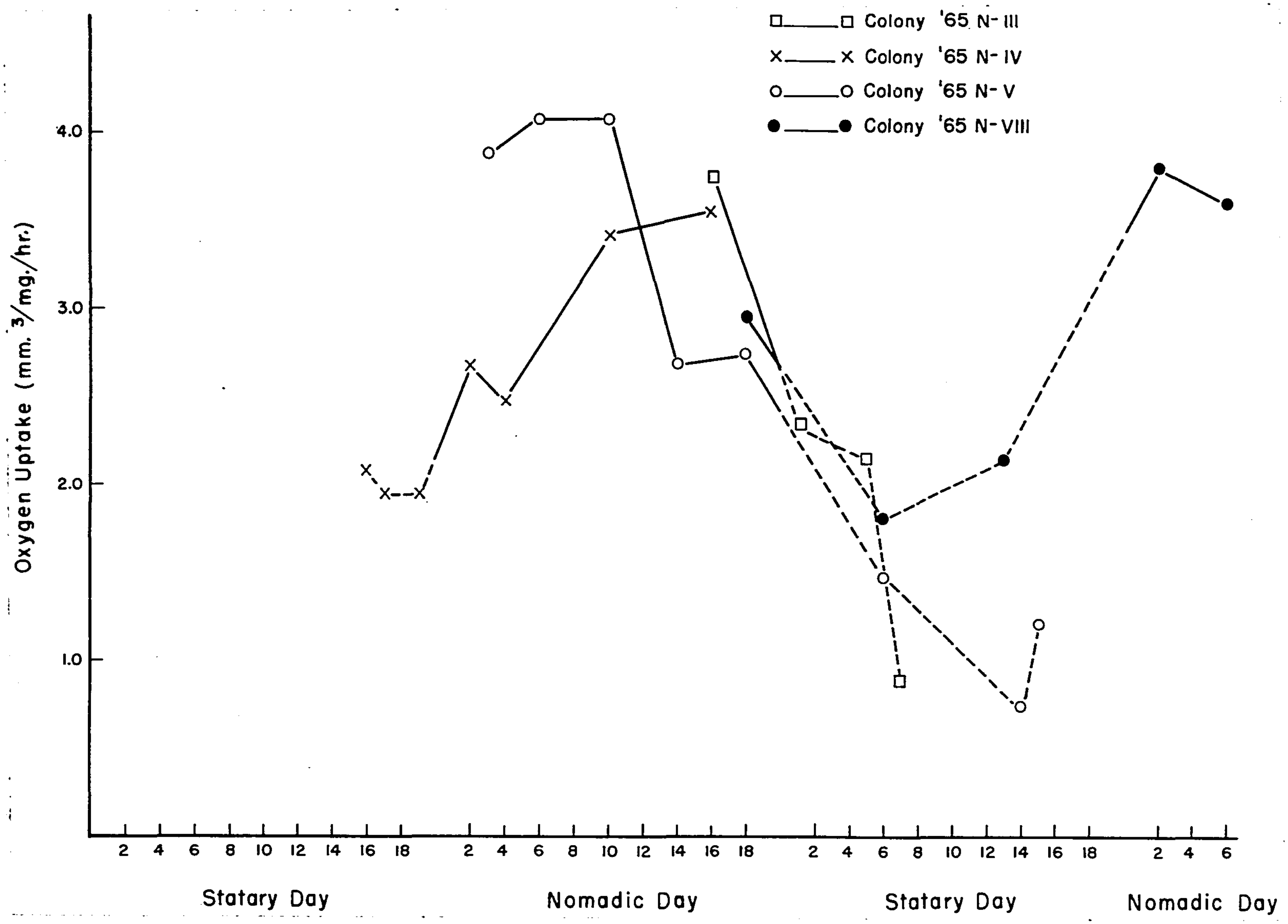

□——□ Colony '65 N-III
×——× Colony '65 N-IV
○——○ Colony '65 N-V
●——● Colony '65 N-VIII
Oxygen Uptake (mm.³/mg./hr.)
4.0
3.0
2.0
1.0
2 4 6 8 10 12 14 16 18
2 4 6 8 10 12 14 16 18
2 4 6 8 10 12 14 16 18
2 4 6
Statary Day
Nomadic Day
Statary Day
Nomadic Day

Fig. 20

Fig. 21. Graph comparing oxygen uptake of groups of intermediate-sized workers of *N. nigrescens*, during the nomadic phase (indicated by solid lines) and during the statary phase (indicated by broken lines). Each point represents the mean value of four determinations, made at five-minute intervals. These tests were conducted during the summer of 1966.

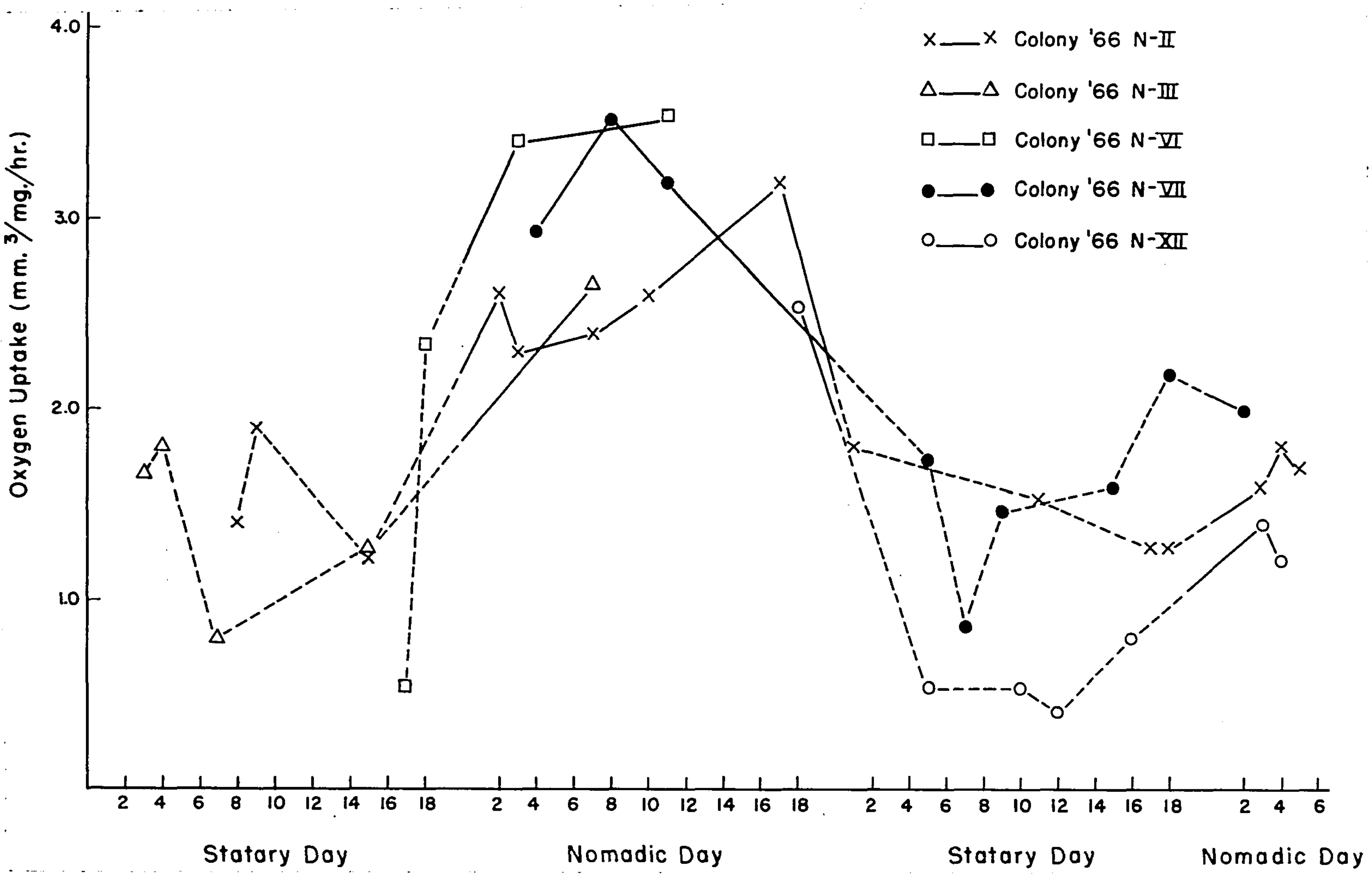

Colony '66 N-II
Colony '66 N-III
Colony '66 N-VI
Colony '66 N-VII
Colony '66 N-XII
Oxygen Uptake (mm.^{3}/mg./hr.)
4.0
3.0
2.0
1.0
2 4 6 8 10 12 14 16 18
Statary Day
2 4 6 8 10 12 14 16 18
Nomadic Day
2 4 6 8 10 12 14 16 18
Statary Day
2 4 6
Nomadic Day

Fig. 21

elapsed since its previous test, and the nightly colony situation. This last factor is especially important in disrupting our research schedule during the statary phase, for there were many nights on which we arrived at the bivouac site, only to find no surface activity.

The points representing levels of oxygen consumption on the graphs, are the mean values for four five-minute determinations of oxygen uptake for a single group of approximately 20 worker ants. The lines connecting them are either solid, to represent test performed during the nomadic phase, or broken, to represent tests conducted during the statary phase. All of the connecting lines are inserted only for convenience in tracing the trend of oxygen uptake for any one colony throughout both phases of the functional cycle. They are not intended to directly represent patterns of increasing or decreasing levels of oxygen consumption between any two evenings on which the tests were actually conducted (except on those few occasions when tests were performed on successive nights).

Not only is there considerable intra-colony variation in metabolic rates on successive nights during both phases, but each colony also seems to be relatively independent in its performance during either of the two phases. This is not surprising since each colony is also an independent ecological unit, determined by the location of its bivouacs (during the nomadic phase), the relative exposure of the immediate terrain, and the amount and quality of booty in the raiding area. All of these factors can influence intra-colony stimulative processes to varying degrees. As a result, each colony is somewhat unique in its nightly activity patterns.

In addition, the over-all levels of oxygen consumption seem to be rather low, especially since the workers are moving all through the tests. For studies on activity metabolism, higher values are expected. Several reasons can be suggested to account for these low absolute values. First, since the rates of oxygen consumption are expressed in relation to total-body weight, the inclusion of cuticular and other relatively inert tissues may be reponsible for the values obtained. However, the most probable explanation is that -to eliminate a potential source of external stimulation that would interfere with the test organisms' own condition- the test chambers were never shaken during the experiments. A similar procedure, in which the respirometer was not shaken, was performed by Allen (1959a) in his study of respiratory rates in worker honeybees of different ages. He stated that normal gaseous diffusion was sufficient to insure a constant supply of oxygen to the bees. In our case, it might be that gaseous diffusion was not sufficient for the KOH to absorb all of the CO_2 produced by the ants. If this were the case, we could not record the total respiratory rate of the workers.

Most important for this study is a consideration of the differences in levels of oxygen uptake between workers removed from colonies and tested during the nomadic phase, and workers comparably tested during the statary phase. Despite the large variation in oxygen uptake within any one colony during either of the two behavioral phases, or between different colonies, the over-all picture emerging is that, for any colony, respiratory rates are distinctly higher during the nomadic phase than during the statary phase. To determine the significance of these differences in metabolic levels exhibited by the workers, a Rank-Sum test was used. This non-parametric test is essentially the same as the Mann-Whitney test, except that it employs $\underline{R}$ (the sum of the ranks) as its statistic (Siegel, 1956).

Because tests on any one colony were conducted on only a few days during the nomadic and statary phases, this statistical test could only be used for three of the 13 colonies studied: '64 N-V; '65 N-V; and '66 N-II. For each of these colonies, differences in the magnitude of oxygen uptake between the two functional phases, are significant at the .05 level. But since in most of the colonies in which too few tests were performed for statistical analysis, the magnitude of the differences in metabolic levels is just as large as those found for colonies '64 N-V, '65 N-V, and '66 N-II, I can say with some confidence that if more tests were run on the other colonies, corresponding metabolic differences of equal significance would have been exhibited.

Behavioral Studies

Observations on Colonies of N. nigrescens in the Field as a Basis for Laboratory Experimentation:

This aspect of the present investigation results from the extension of brood-stimulative theory to *N. nigrescens* (Schneirla, 1958), in relation to field observations made on numerous colonies of this species.

After conducting systematic, longitudinal studies on colonies of *N. nigrescens* throughout successive nomadic and statary phases, it became clear that the time course of evening activities varied in the colonies, depending upon the phase of the functional cycle. It is a common observation that in the nomadic phase, colonies of *N. nigrescens* often begin foraging activities much earlier in the evening. In fact on several occasions during this phase, when a colony is highly excited, as in the presence of a newly eclosed worker brood, raiding may even be initiated in full sunlight. By contrast, this situation is never encountered for colonies during the statary phase. Also, as these evening raids develop and progress, there is a marked distinction in their organization and pattern, which also depends upon the phase in the cycle. With few exceptions it is relatively easy to determine whether a colony is in the nomadic or statary phase, by observing only the pattern of its nocturnal raiding.

During the nomadic phase, raiding in N. nigrescens, in addition to beginning earlier, involves greater numbers of individuals, and consists of the establishment of numerous branching columns (Schneirla, 1958, 1968). Also, the movement outward from the bivouac may remain at a peak for up to several hours, as the workers' excitement persists both at the raiding fronts (where the "battles" between the dorylines and their prey take place) and on the basal columns, extending to the bivouac. This increased level of excitation in the foraging columns facilitates the capture of a larger proportion of hard-bodied adult ants and other small insects.

During the statary phase, raiding is less vigorous, with fewer individuals participating in the foraging columns; on some nights during the statary phase raiding is absent altogether. These statary raids usually consist of a single basal column, which may have only a small terminal branching system at the raiding front. On successive nights this single column often emerges from the statary bivouac in a different direction, but because the outward surge usually peaks after only a few minutes, the extending basal column remains relatively thin. Throughout the night, worker activity and excitation is low, and booty consists almost entirely of the soft-bodied broods of other ant species.

These aspects of differences in raiding patterns in colonies during the nomadic and statary phases, are important to consider in relation to Schneirla's (1958) theory, in which the regular alternations of phases comprising a functional cycle are considered to be regulated by levels of stimulation resulting from fluctuating degrees of interaction between workers, brood, and queen. Accordingly, the two behavioral phases can be viewed as the outcome of a complex, interrelated set of "antagonistic" processes associated with conditions both in the colony's physical environment, and in the physiological state of all its individuals.

We can consider that the chemical and chemotactual excitatory effects imparted to the adult workers by the developing larval brood, function as a "driving force" in arousing the workers to a level above the threshold value necessary for the onset of evening raiding activities. At the same time, evidence exists that the workers are highly attracted to the developing brood, to the colony queen, and to each other (Schneirla, 1957a, 1958; Watkins and Cole, 1966), and this sets up an opposing force tending to keep the colony together in the bivouac. Finally, since under the thermal and other ecological conditions that exist in the habitat of _N. nigrescens_, the workers react negatively to photic stimulation, the light incident at the surface-hole or other entrance to the subterranean bivouac during the day must also act to keep the colony below ground. The workers are, so to speak, caught between the effects of these physical and biotic influences, which, under various conditions and in different combinations, may act either synergistically or in opposition to each other.

With this information as background material, we decided to bring the army-ants into the laboratory to further study variations in their responses to similar chemical and physical stimuli, as a function of their own changing physiological state. And since I have shown (in the previous section) that the workers' internal physiological state (presumably regulated by neural and endocrinological factors) changes significantly between the nomadic phase and the statary phase, I decided to compare reactions of adult workers in the test chambers to both photic and intra-colony chemical stimulation, to see if phase-specific differences could be found, that could be correlated with observations on these colonies in the field.

As previously described, two groups of 40-60 adult worker ants were each placed in the test situation. In one test, the organisms were permitted to leave a brightly-lit (16,000 lux) central cartridge, and to enter into either two equally-bright arena quadrants (also at 16,000 lux), or into two dimly-lit (160 lux) quadrants. In the second test, conducted concurrently, the effective illumination in the cartridge and in all the arena quadrants was close to zero.

Comparison of the Behavior of Groups of Ants in Laboratory Tests, During the Nomadic and Statary Phases:

That the inhibition of diurnal raiding in the field is partially dependent upon the adult workers' photonegative reaction to light stimulation, was immediately confirmed by these tests. With the exception of certain instances during the statary phase (which will be discussed later), as soon as the cartridge was lowered into the arena, thus opening the four exit slits, the workers almost invariably entered into either one or both of the dimly-lit arena quadrants. This was the usual reaction of the workers during either the nomadic or statary phase. Only occasionally, when groups of ants in the cartridge happened to be close to a brightly-lit quadrant at the start of a test, did a column enter into this bright quadrant. But unless the colony was in an extremely excited condition, as soon as connections were made with columns in either of the two dimly-lit quadrants, the ants in the bright quadrant would drain into the column in the dim quadrant and remain there. With the exception of certain times during the statary phase, of the more than 60 tests conducted, at the end of each test (lasting two minutes each) at least 75 percent of the individuals were located in the dim quadrants. The reason this figure does not always reach 100 percent is due to the construction of the apparatus. Once chemical trails are formed, the ants are restricted to running along them. If two groups of ants each settle in one of the dim quadrants, these trails must cross through the bright cartridge.

Under the conditions of this experiment, consistent differences in the ants' reaction to light stimulation during the nomadic and statary phases were not expressed (except in the most highly excited colonies), due to the presence of very significant and correlative differences in the responses of the same workers to their trail and other chemical secretions during both functional phases.

From the beginning, it was apparent that many aspects of army-ant behavior, concerned with activities regulated by the workers' response to chemical stimuli, correlated well with these same behavior patterns in the field. Specifically, the differences in characteristics of column formation and trail following in the cartridge and arena, were distinctly related to corresponding differences in these activities exhibited by colonies in the field. The outstanding difference was in the relative tendency of the army-ant workers during the statary phase, to remain together, either as a stationary group, or -when raiding- in a tightly packed unit. Figure 22 shows this tendency to remain together. It is a graphic summary of the difference in time that it takes for the ants to leave the cartridge (brightly-lit in one test and dark in the other) during the nomadic and statary phases. As an index of this I have recorded the percentage of the total number of ants remaining in the cartridge at the end of one minute (which is

Fig. 22. Graph comparing the relative tendency of groups of workers of *N. nigrescens* to remain together in the test cartridges, during the nomadic and statary phases. Many more nomadic days are represented because results from statary tests in which ants clustered, are omitted.

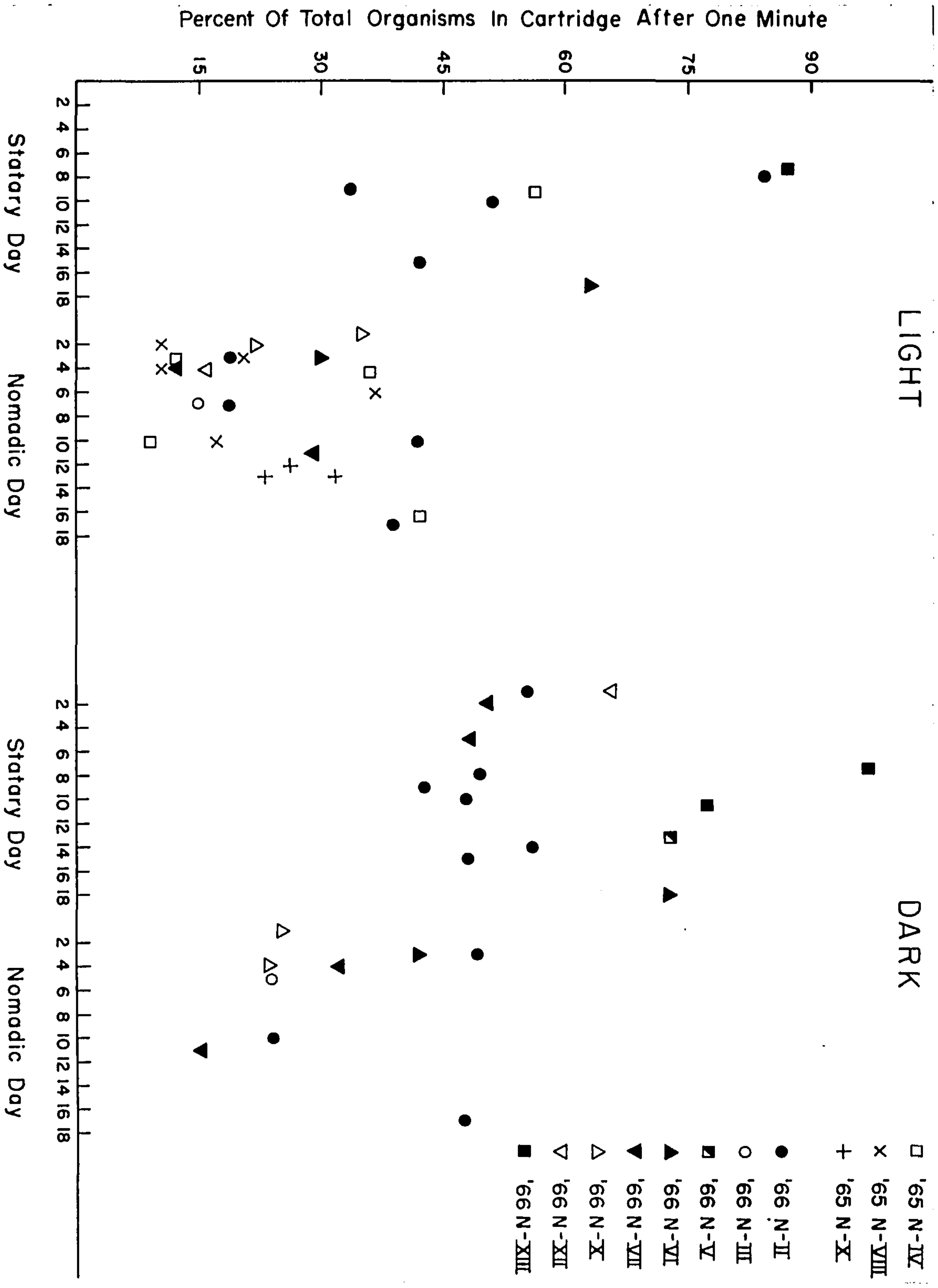

Percent Of Total Organisms In Cartridge After One Minute
15
30
45
60
75
90
LIGHT
DARK
2 4 6 8 10 12 14 16 18
Statary Day
2 4 6 8 10 12 14 16 18
Nomadic Day
2 4 6 8 10 12 14 16 18
Statary Day
2 4 6 8 10 12 14 16 18
Nomadic Day
□ '65 N-IV
× '65 N-VIII
+ '65 N-X
● '66 N-II
○ '66 N-III
▨ '66 N-V
▶ '66 N-VI
◀ '66 N-VII
▷ '66 N-X
◁ '66 N-XII
■ '66 N-XIII

Fig. 22

half-way through the test). It is clear that an over-all trend exists, in which the number of ants remaining in the cartridge is greater during the statary phase. During the summer of 1965 (when no equipment for control testing was available) we thought this reaction might be due, in part, to an effect of the light itself. But when ants from the same colonies were tested concurrently in almost total darkness (during the summer of 1966), the same trend appeared. In this experiment the light, which acts to force the ants out of the cartridge and into the dim arena quadrants, acts in opposition to the workers' tendency to remain together. In the field however, these two factors probably act synergistically, tending to keep the ants inside the nest.

Although for both tests, the time it takes for the ants to leave the cartridge is significantly different (at the .01 level) during the nomadic and statary phases, this difference is much more distinct than figure 22 illustrates. This is because numerous tests, conducted during the statary phase, were not included in the graph, hence there are many more nomadic days represented than statary days.

By way of explanation, it will be recalled that I previously mentioned (in connection with the workers' response to the light source) that there were instances during the statary phase, when the ants did not leave the cartridge at all. In these cases, the ants become associated very closely, in a condition I have termed clustering. When they occur, the clusters look like a mass of ants joined together in varying degrees of compactness. Although, in our first series of tests, this clustering reaction seemed to be a natural response to the effects of light (for by clustering the ants reduced their surface area of exposure), we subsequently found this same phenomenon in the control tests, under conditions of total darkness.

Occasionally the ant cluster, instead of remaining as a stationary mass throughout the test, moved as a single unit out of the cartridge and into one of the dim arena quadrants. Whenever this happened, the number of ants in the cartridge fell from 100 percent to almost zero in just a few seconds. It is for this reason that all tests in which a cluster formed (either moving or stationary) were omitted from the graph in figure 22.

Table 3 shows the frequency of this clustering phenomenon. Notice that it occurs only in ants taken from colonies during the statary phase, and that it appears in both the bright-dim tests and in the control tests. Clustering has never been observed in tests with any group of ants taken from a colony during the nomadic phase.

To illustrate the clustering phenomenon further, as well as differences in characteristics of trail following and other individual reactions during the nomadic and

TABLE 3

OCCURRENCE OF CLUSTERING DURING BEHAVIORAL TESTS CONDUCTED ON GROUPS OF WORKERS OF *NEIVAMYRMEX NIGRESCENS*

Colony No.	Bright-Dim Test	Control Test
'65 N-IV	Statary Day - 9	No Test
	Statary Day - 17	No Test
'65 N-V	Statary Day - 11	No Test
'66 N-II	Statary Day - 1	
	Statary Day - 16	Statary Day - 16
'66 N-V	Statary Day - 13	
	Statary Day - 16	Statary Day - 16
'66 N-VI	Statary Day - 18	
'66 N-VII	Statary Day - 2	
	Statary Day - 5	
	Statary Day - 7	Statary Day - 7
	Statary Day - 14	No Test
	Statary Day - 17	Statary Day - 17
'66 N-XII	Statary Day - 1	
	Statary Day - 10	No Test
	Statary Day - 14	No Test

'66 N-XIII	Statary Day - 1	Statary Day - 1
	Statary Day - 10	
	Statary Day - 13	Statary Day - 13

statary phases, and to relate them with observable conditions in the field, let us examine more closely several of the group patterns exhibited during the testing schedule.

A sequence of photographs illustrating the behavior of the army-ants in the test chambers, are shown in figures 23-28. The photographs have been selected as reliable representations of the standard responses by groups of workers during the nomadic and statary phases. For each colony, the photographs represent four time periods, selected from each two-minute test. As previously described, the photographs were taken through a mirror, situated below the experimental and control arenas. Because of this relation between the position of the camera and the test arenas, the ants in figures 23-28 are seen from their ventral surface. Also, regarding the technical aspects of the tests, the photographs of the ants in the bright-dim tests are slightly sharper in detail than those of the ants in the control tests. This is because a very high-speed infrared film was used for recording the photographic record in the dark chambers of the control tests.

To begin, a sequence of photographic frames taken during a test conducted on colony '66 N-III, judged at approximately nomadic day 7, is shown in figure 23. At the start of the test (fig. 23A) the ants are spread evenly around the perimeter of the cartridge. At this time, there are no clusters visible in the cartridge, and the ants are running along their chemical trails at a fast pace. Forty-five seconds later (fig. 23B) the ants have established columns in the lower dim quadrant (not seen in the photograph) and in the bright quadrant to the right of the cartridge. The fact that the ants are occupying both of the bright arena quadrants, attests to their very high levels of excitation. Normally, even on most days during the nomadic phase, ants in these columns rapidly enter the dim quadrants. Notice that the ants are spread out in the quadrants of the arena, and that there still is no indication of clustering, even around the edges of the partitions, where they are attached to the floor and wall of the arena. After one minute has elapsed (fig. 23C) the ants are still "raiding" in one of the bright arena quadrants, and are moving very quickly. Finally, at the end of the two-minute test (fig. 23D) most of the ants are still in the brightly-illuminated quadrant, with no indications of clustering.

A similar sequence of photographs illustrating a typical pattern of group "raiding" during the nomadic phase, is shown in figure 24. These pictures were taken during a control test (in almost total darkness) on colony '66 N-X, on nomadic day 6. At the start of this test (fig. 24A) the ants are grouped in the upper portion of central cartridge, near the exit slit leading to the upper arena quadrant. That this grouping of ants in the cartridge is not equivalent to ant clusters formed in the statary phase, can be seen by their pattern of column formation after the cartridge is lowered into the arena. Forty seconds after the start of the test (fig. 24B) "raiding" columns can be seen in the upper, left, and right arena quadrants. The columns appear to be radiating out from the central cartridge, with the workers well scattered and moving quickly. One column can be seen around the perimeter of the upper quadrant, but notice that no worker clusters have formed along the base of the arena wall. After 80 seconds (fig. 24C) the column in the upper quadrant is still prominent, with the ants "raiding" in a circular pattern around the perimeter of the quadrant. At the end of the test (fig. 24D) the column still exists in the upper quadrant, and there are still no clusters to be seen.

The patterns of "raiding" and group organization exhibited in the test chambers by army-ant workers during the statary phase, is very different from the patterns described above for groups of ants during the nomadic phase.

The behavior of the test organisms taken from colony '66 N-II during the first day of the statary phase, is shown in figure 25. At the start of the test (fig. 25A) the ants are found clustered near the center of the cartridge. Thirty seconds later (fig. 25B) most of the ants are still clustered in the cartridge, in approximately the same position. None of the ants have left the cartridge, and there are no columns within the cartridge. After one minute (fig. 25C) a second small group of ants has assembled above the large cluster, but it soon breaks up as the ants return to the primary cluster. At the end of the test (fig. 25D) the original cluster still exists, and consists of all but of the few of the ants, which can be seen running at the edge of the cartridge.

A very similar pattern of group clustering, occurring in total darkness, is shown in figure 26, which represents a photographic series of colony '66 N-XIII, tested on statary day 1. At the start of this test (fig. 26A) all of the individuals are in the cartridge, near its upper edge. After 45 seconds (fig. 26B) all but one of the ants are still in the cartridge. At this time, the ants in the cartridge are gathered loosely at its upper edge. After 100 seconds (fig. 26C) the group of ants in the cartridge is beginning to cluster more tightly. Finally, at the end of the test (fig. 26D) all of the ants are in the cartridge and the cluster has reformed.

During the statary phase, there is a large amount of variability in this tendency of army-ant workers to cluster together in the test chambers. A particularly tight cluster was discovered during a test conducted on colony '65 N-V, on statary day 13 (fig. 27). At the start of this test, as in the statary test on colony '66 N-II (described above), a tight cluster had formed in the upper part of the central cartridge (fig. 27A). During a normal test sequence, the cartridge is gently lowered into the arena. On this particular night the cartridge was accidently slammed down onto the floor of the arena, and the resulting mechanical shock immediately broke up the cluster and caused the ants to disperse throughout the cartridge and into one of the dim arena quadrants (fig. 27B). One minute later (fig. 27C) the cluster can be seen in the process of reforming, even though some of the dispersed ants are running in one of the bright arena quadrants. By the end of the test, however, all of the ants have reformed in the cartridge, into another tightly-packed cluster, whose position is very close to that of the original cluster at the start of the test (fig. 27D).

During the statary phase there are many nights when no stationary cluster at all forms in the test cartridge. On most of these nights, however, the patterns of column organization and trail following are still quite different from those described for ants tested during the nomadic phase.

A pattern of column formation characteristic of army-ants during the statary phse, can be seen in the photographic record taken of colony '66 N-II, tested on statary day 16 (fig. 28). At the start of the test (fig. 28A), the ants are seen clustered in the upper portion of the central cartridge. In the figure the ants in the cartridge are difficult to see. This is because of special processing to enable the ants to be seen in the dim arena quadrants. After 55 seconds have elapsed (fig. 28B) a very tight column has started to move into the upper dim arena quadrant. Contrast this pattern of column formation and trail following, with those described for ants during the nomadic phase (figs. 23, 24). After 65 seconds (fig. 28C) this dense, slowly-moving column is beginning to form a cluster in the upper dim quadrant. At the end of the two-minute test (fig. 28D) the cluster has become tighter with the ants in the cartridge draining into it.

Fig. 23. Photographic series illustrating characteristic patterns of group "raiding" during the nomadic phase. This series is from a two-minute test conducted on _N_. _nigrescens_ colony '66 N-III, judged at approximately nomadic day 7. A. At the start of the test. B. After 45 seconds. C. After 60 seconds. D. At the end of the test. In A, the experimenter's hand is seen, removing the "U"-shaped plastic support which prevents the cartridge from prematurely sliding down onto the floor of the arena. A complete explanation is given in the text.

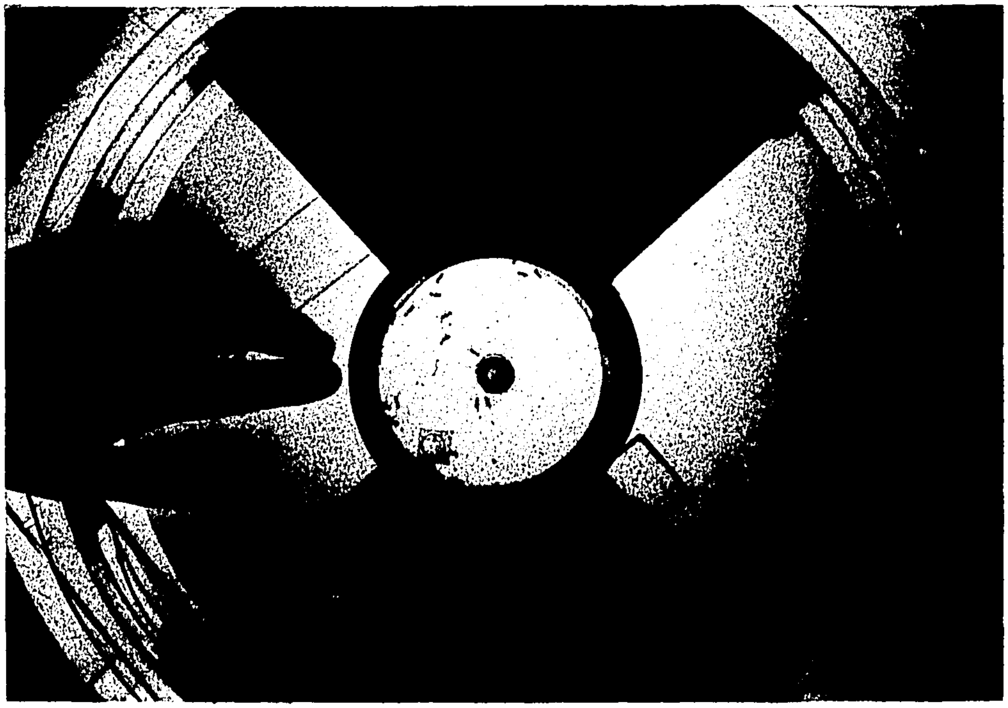


Fig. 23A

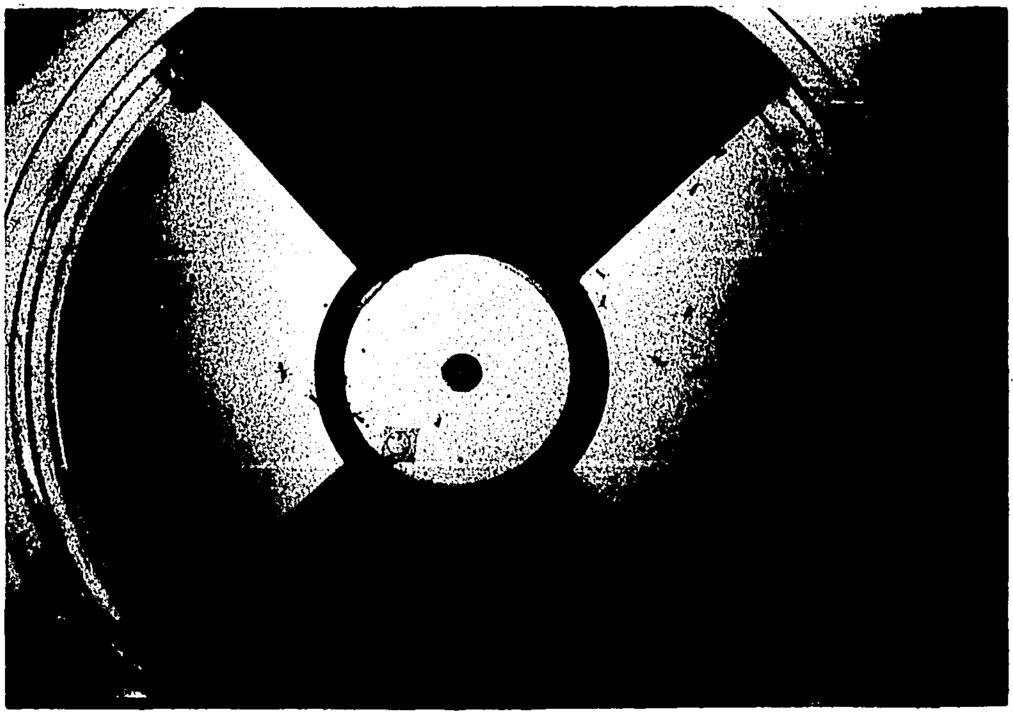


Fig. 23B

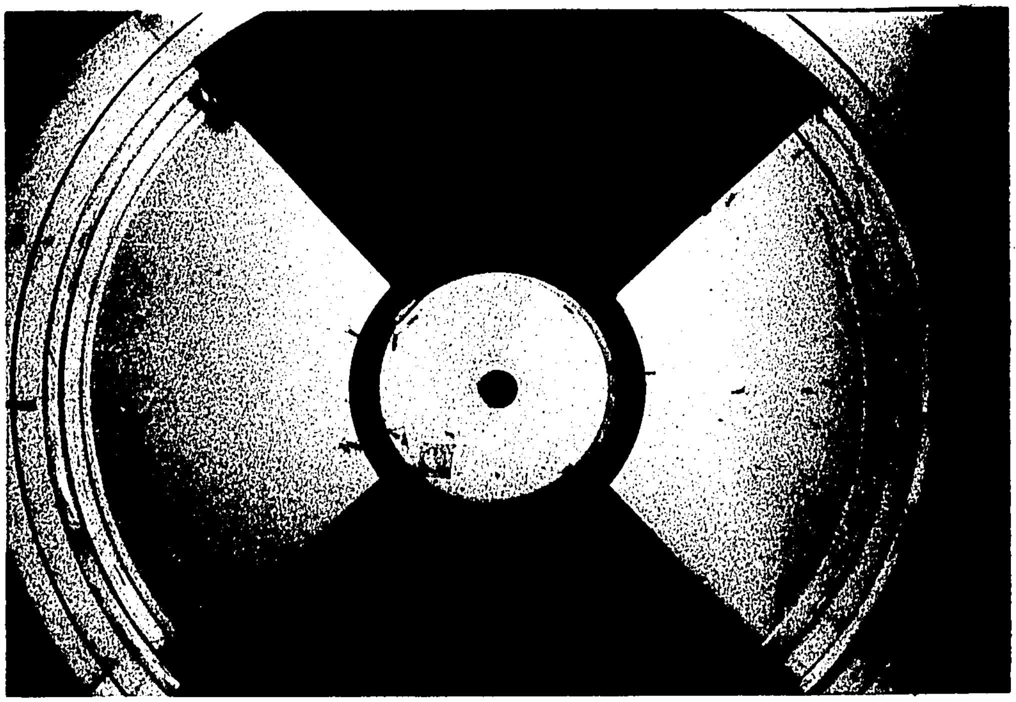


Fig. 23C

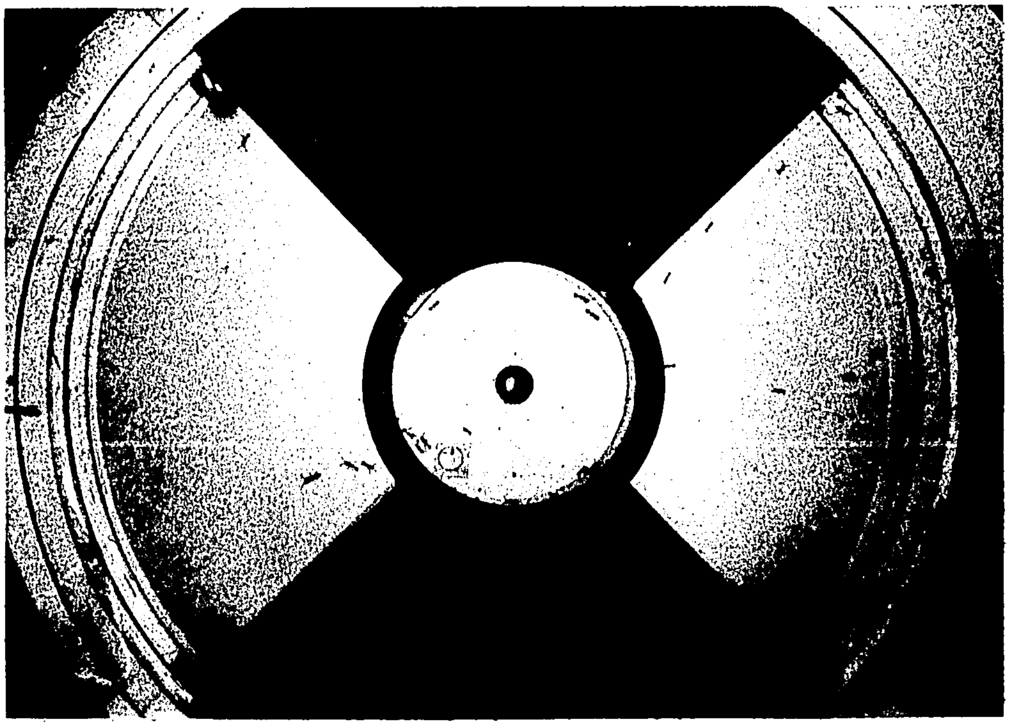


Fig. 23D

Fig. 24. Photographic series illustrating characteristic patterns of group "raiding" during the nomadic phase. This series is from a two-minute test conducted on *N. nigrescens* colony '66 N-X, judged at approximately nomadic day 6. A. At the start of the test. B. After 40 seconds. C. After 80 seconds. D. At the end of the test. A complete explanation is given in the text.

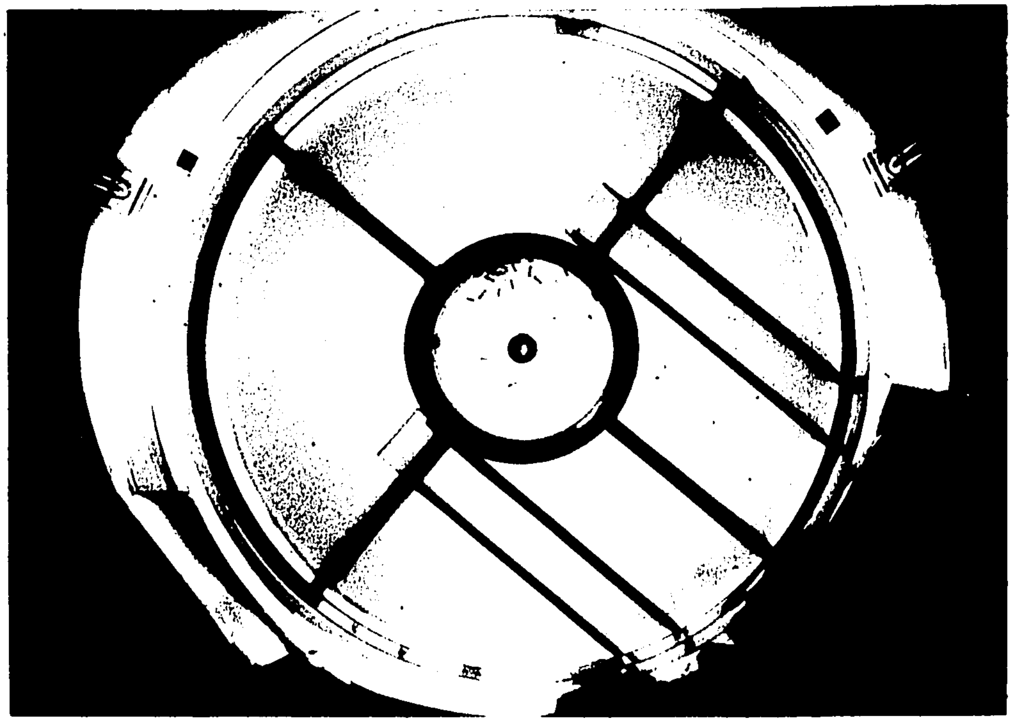


Fig. 24A

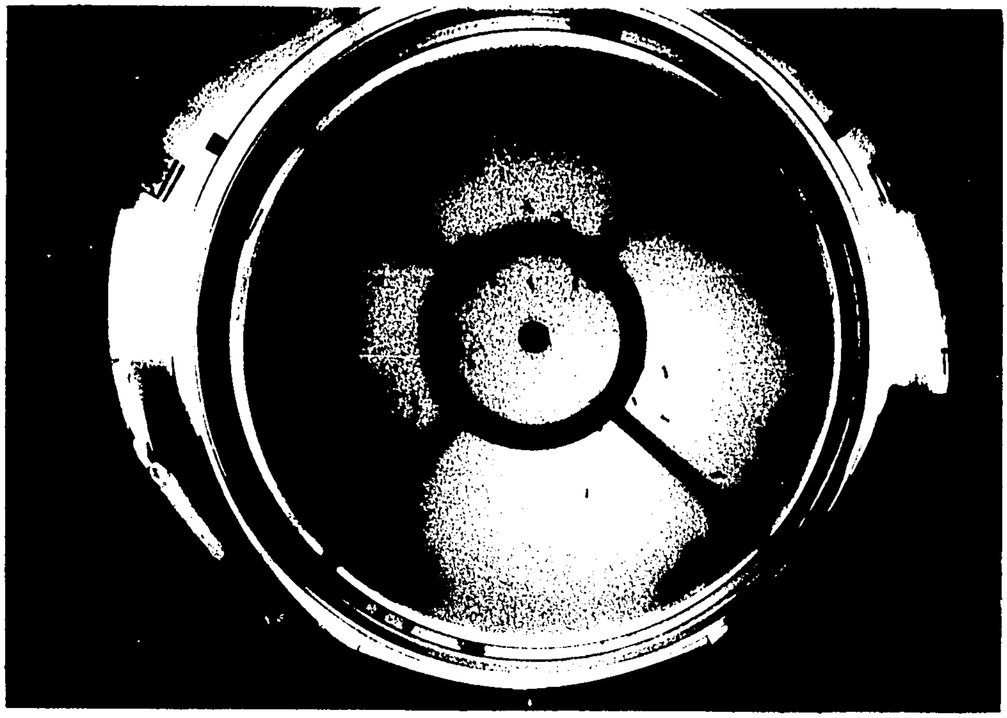


Fig. 24B

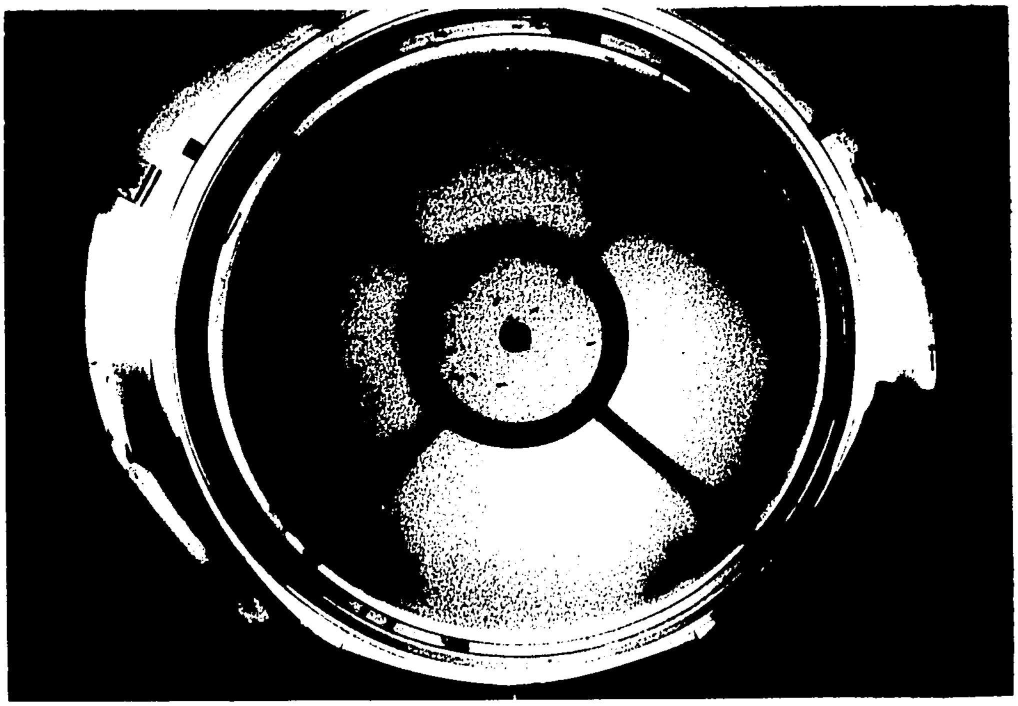


Fig. 24C

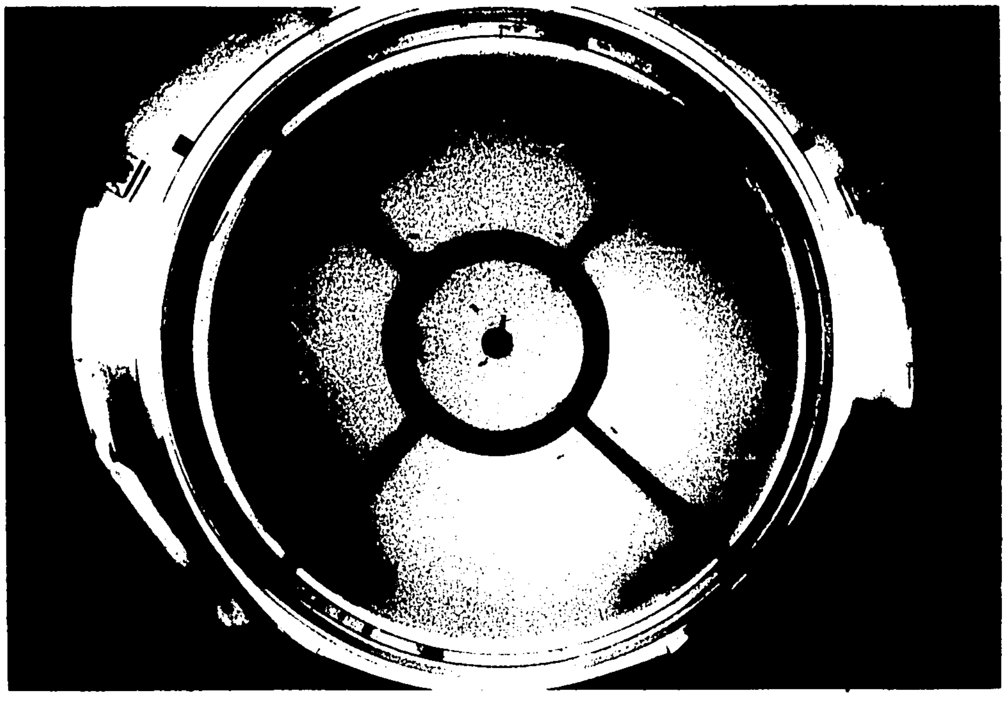


Fig. 24D

Fig. 25. Photographic series illustrating the phenomenon of clustering during the statary phase. This series is from a two-minute test conducted on *N. nigrescens* colony '66 N-II, judged at approximately statary day 1. A. At the start of the test. B. After 30 seconds. C. After 60 seconds. D. At the end of the test. A complete explanation is given in the text.

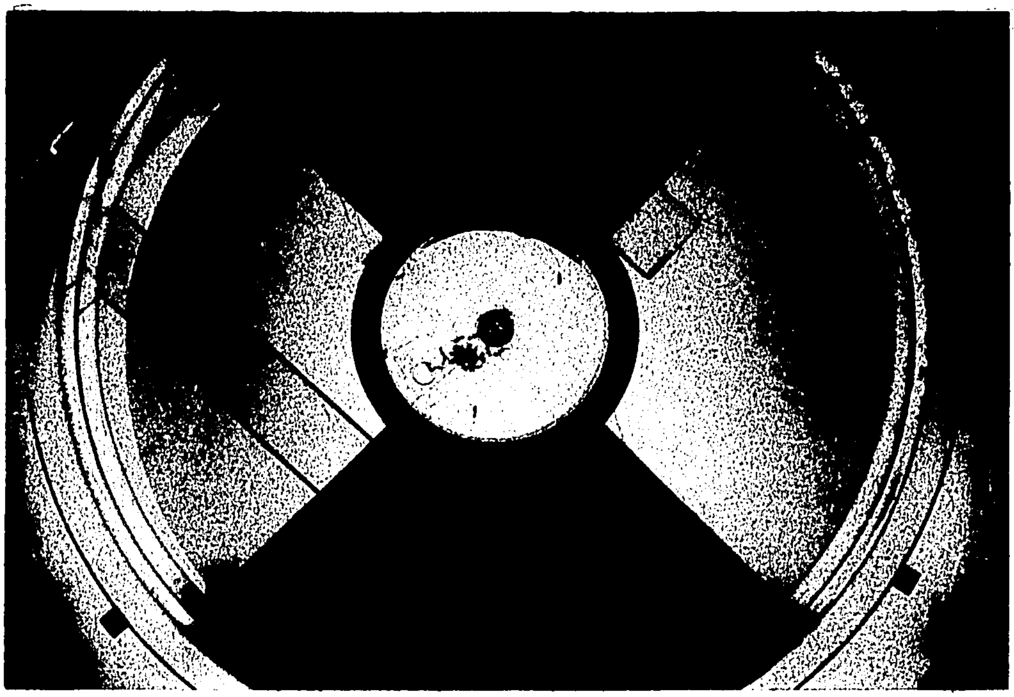


Fig. 25A

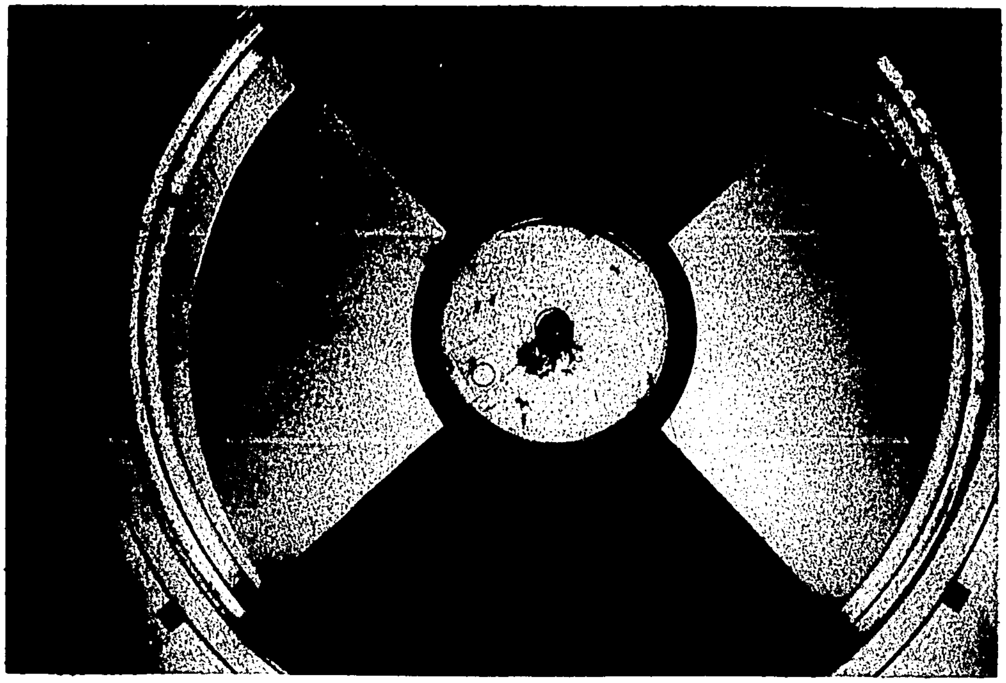


Fig. 25B

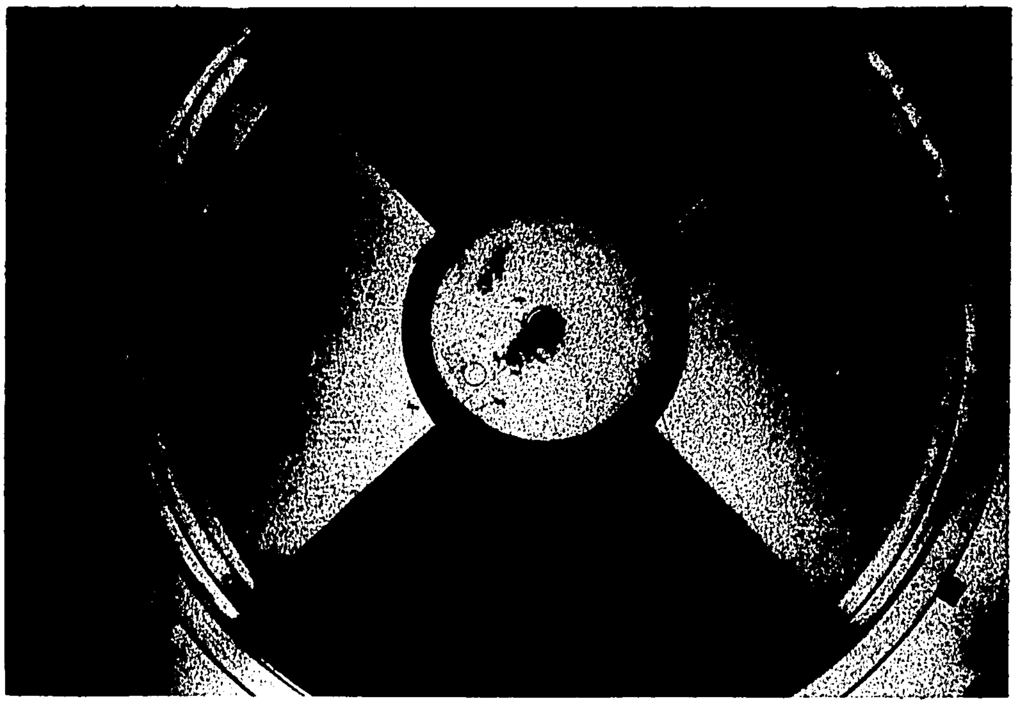


Fig. 25C

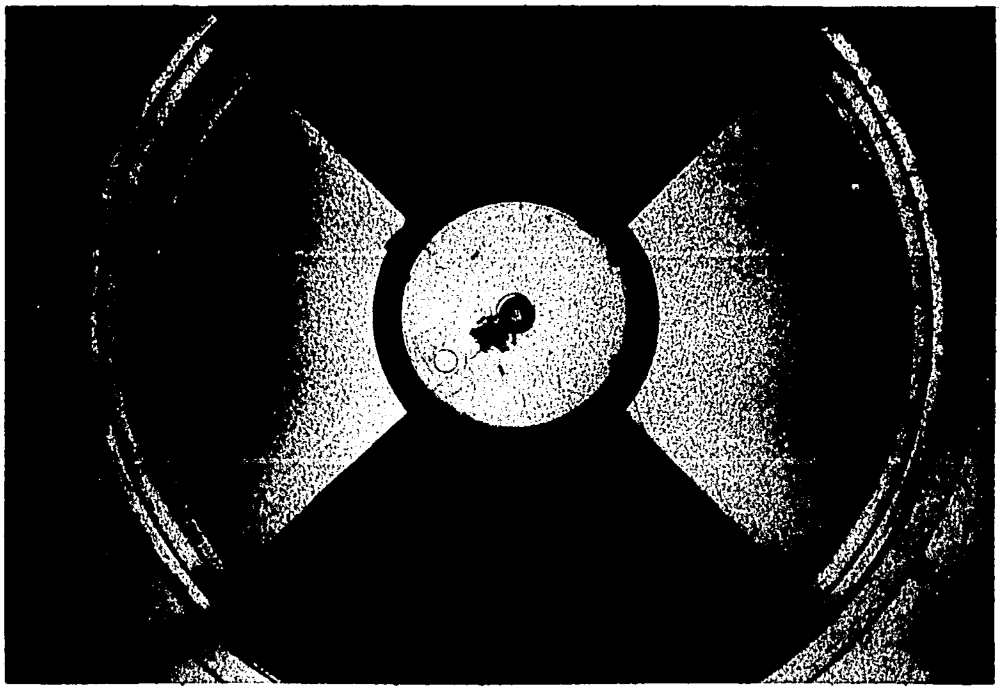


Fig. 25D

Fig. 26. Photographic series illustrating the phenomenon of clustering during the statary phase. This series is from a two-minute test conducted on *N. nigrescens* colony '66 N-XIII, judged at approximately statary day 1. A. At the start of the test. B. After 45 seconds. C. After 100 seconds. D. At the end of the test. A complete explanation is given in the text.

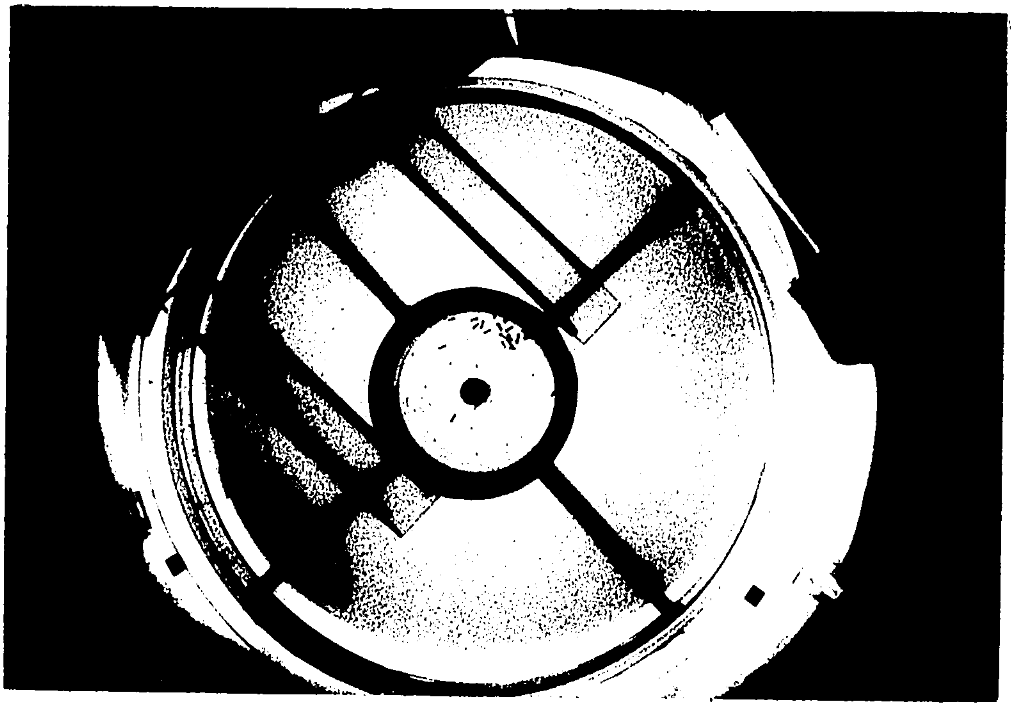


Fig. 26A

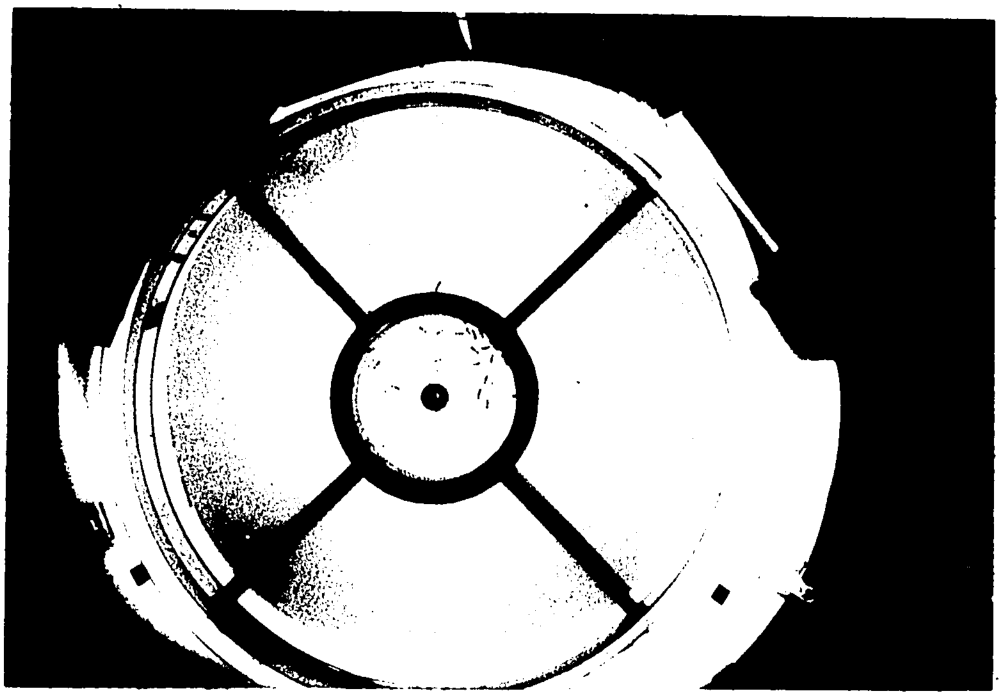


Fig. 26B

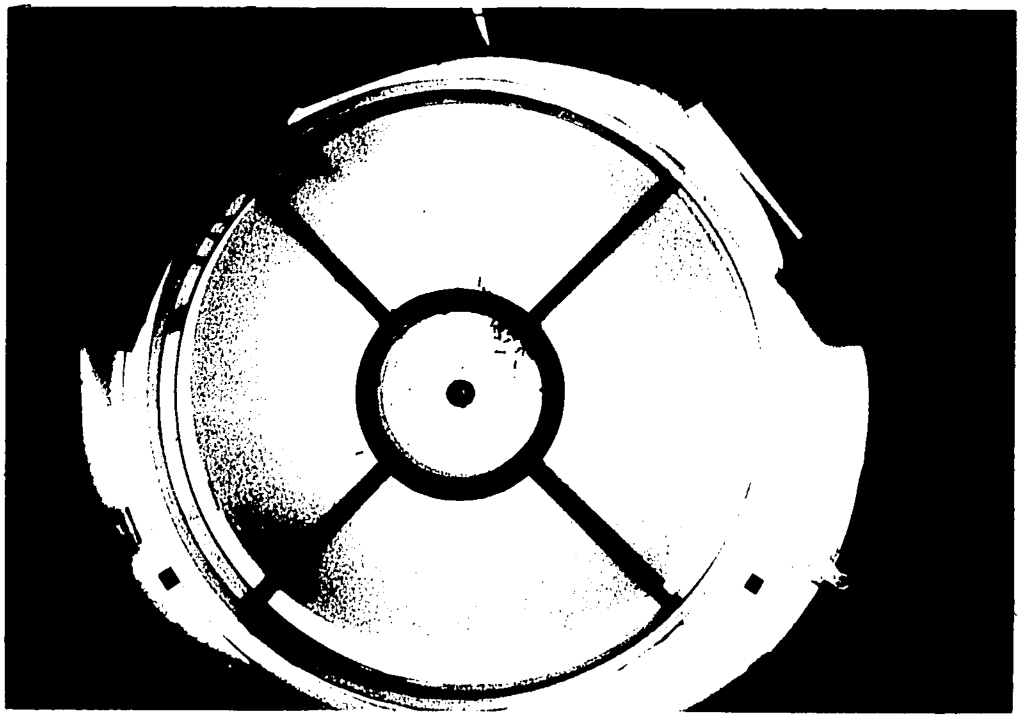


Fig. 26C

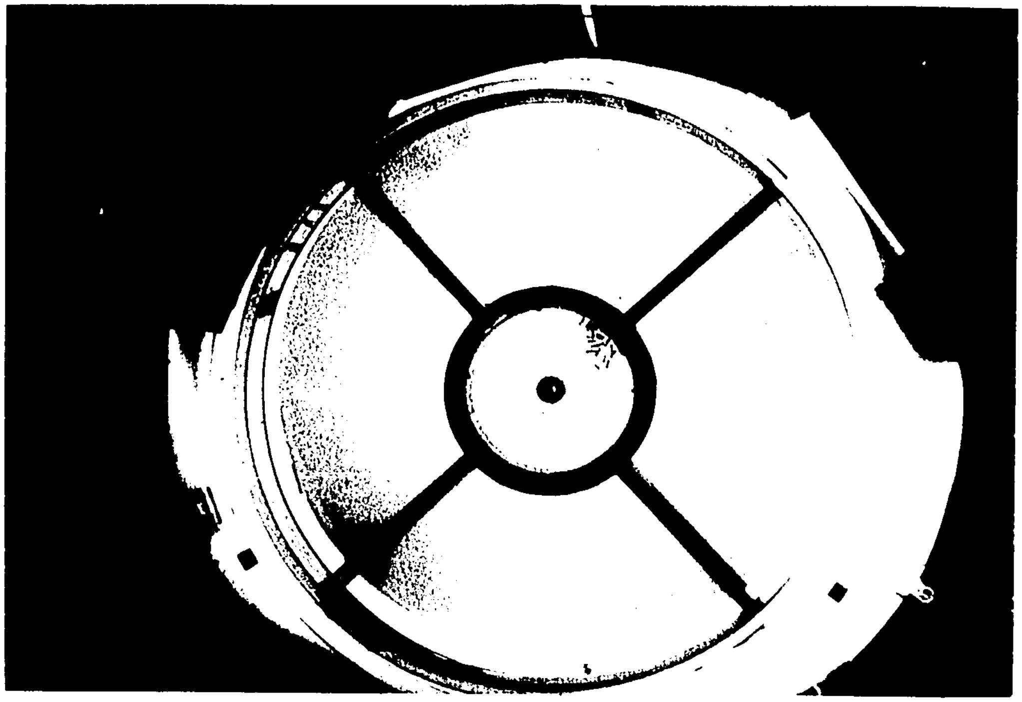


Fig. 26D

Fig. 27. Photographic series illustrating the phenomenon of clustering during the statary phase. This series is from a two-minute test conducted on _N. nigrescens_ colony '65 N-V, judged at approximately statary day 13. A. At the start of the test. B. After 15 seconds. C. After 60 seconds. D. At the end of the test. A complete explanation is given in the text.

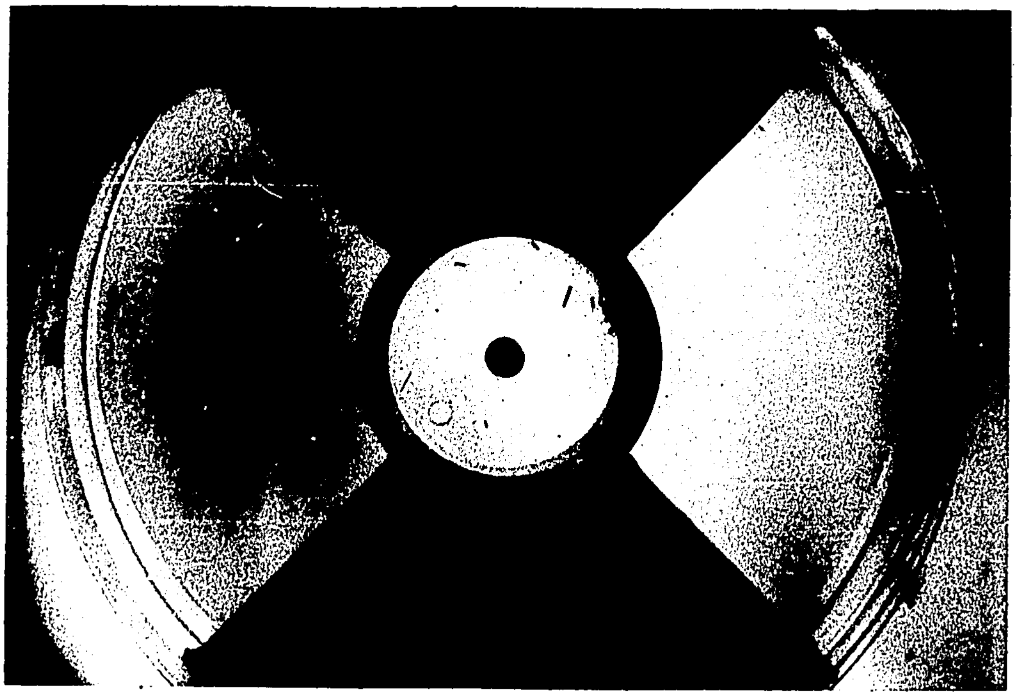


Fig. 27A

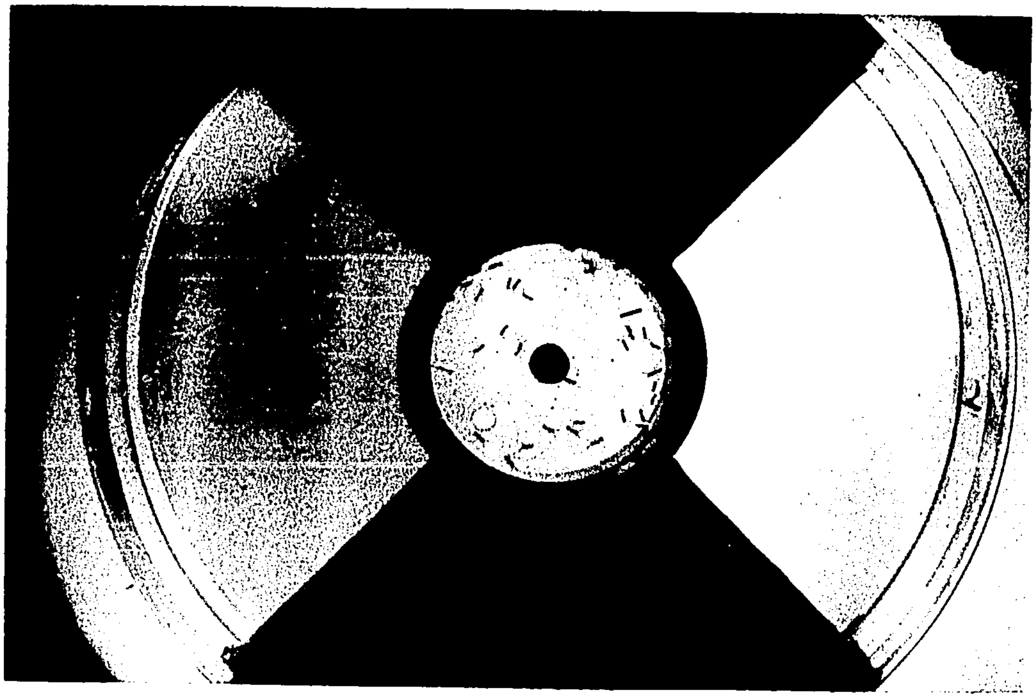


Fig. 27B

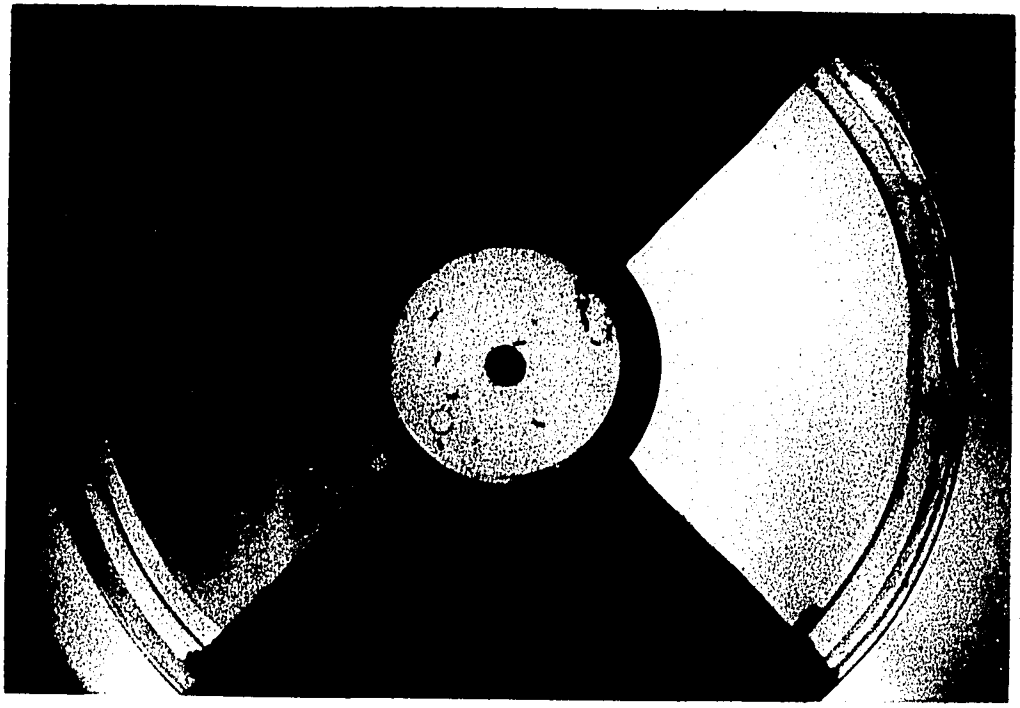


Fig. 27C

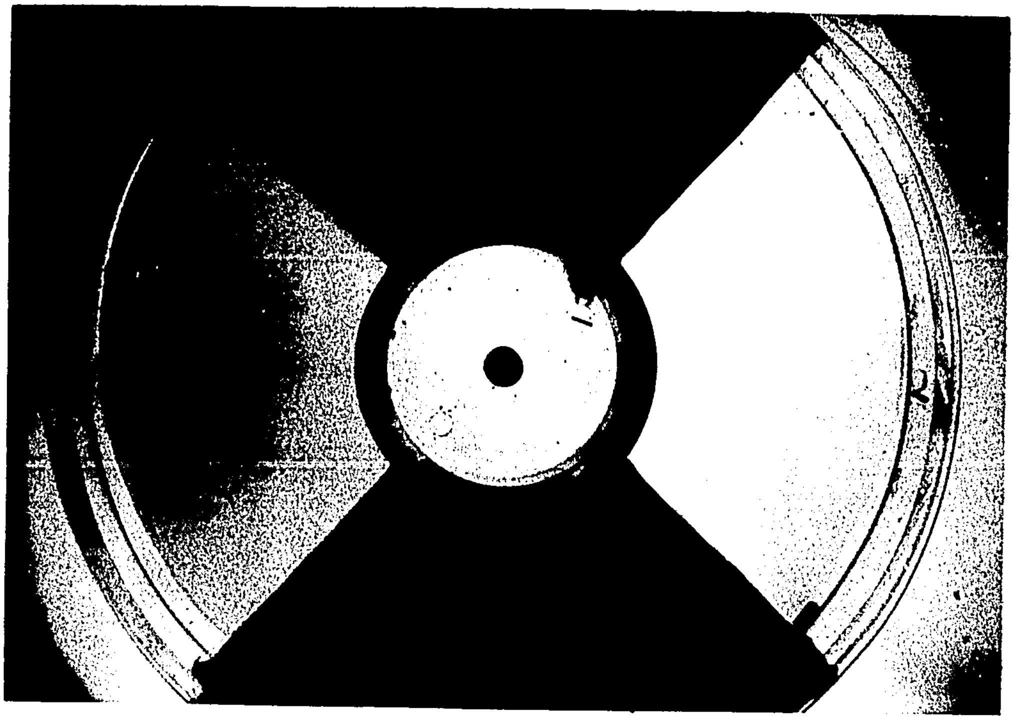


Fig. 27D

Fig. 28. Photographic series illustrating characteristic patterns of group "raiding" during the statary phase. This series is from a two-minute test conducted on N. nigrescens colony '66 N-II, judged at approximately statary day 16. A. At the start of the test. B. After 55 seconds. C. After 65 seconds. D. At the end of the test. A complete explanation is given in the text.

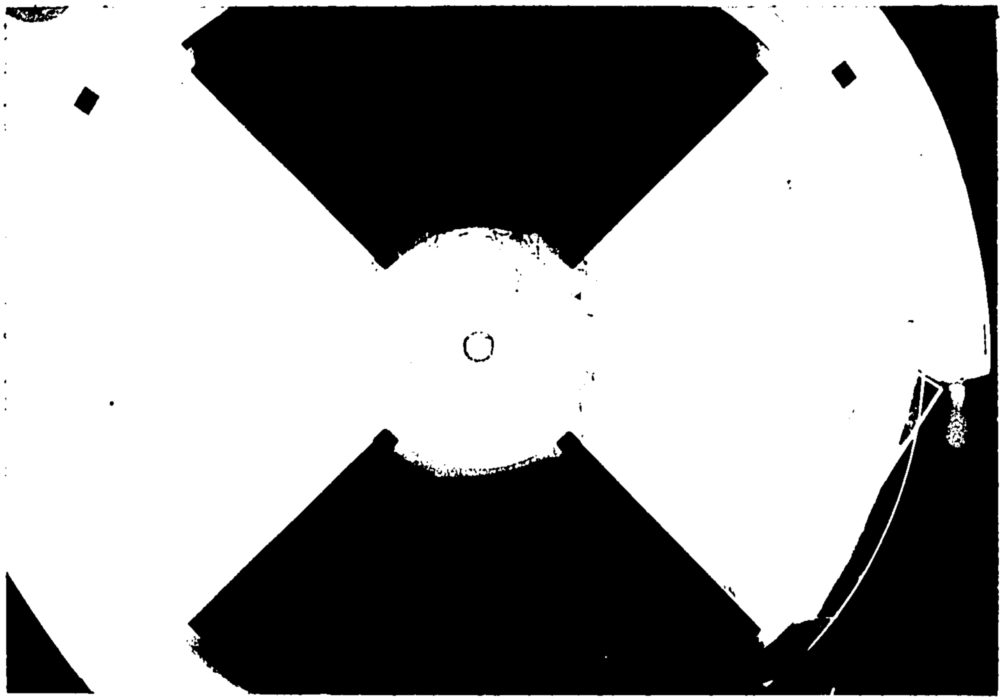


Fig. 28A

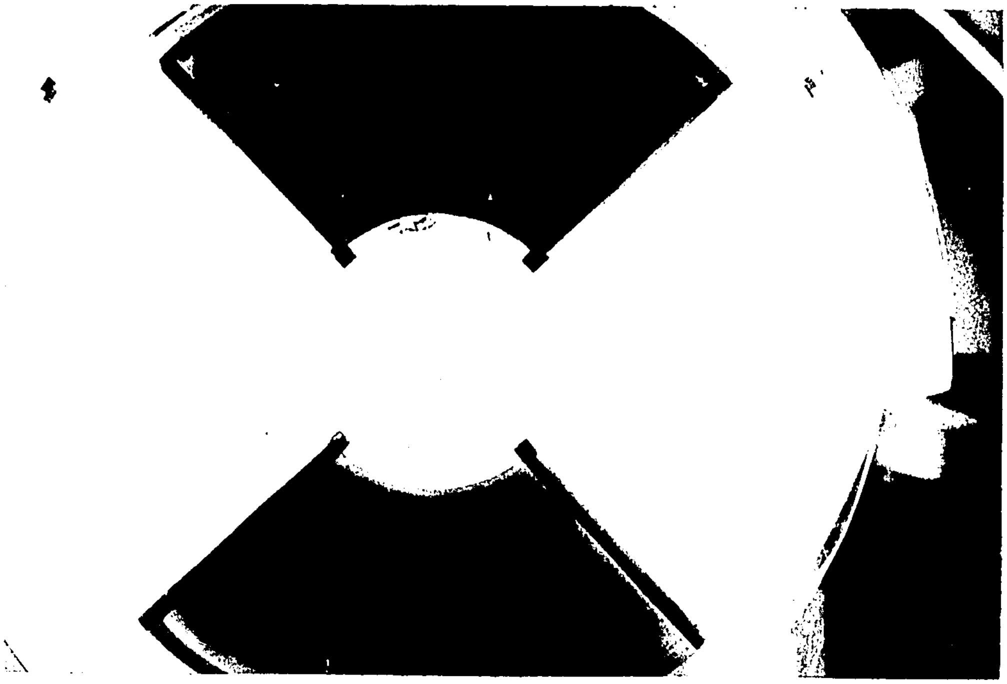


Fig. 28B

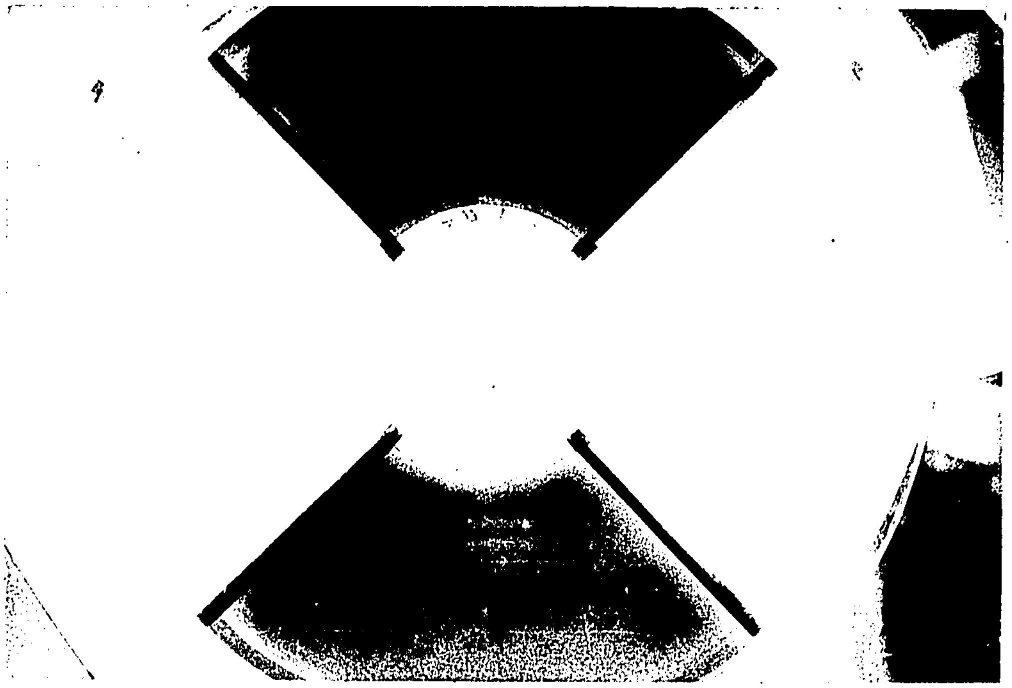


Fig. 28C

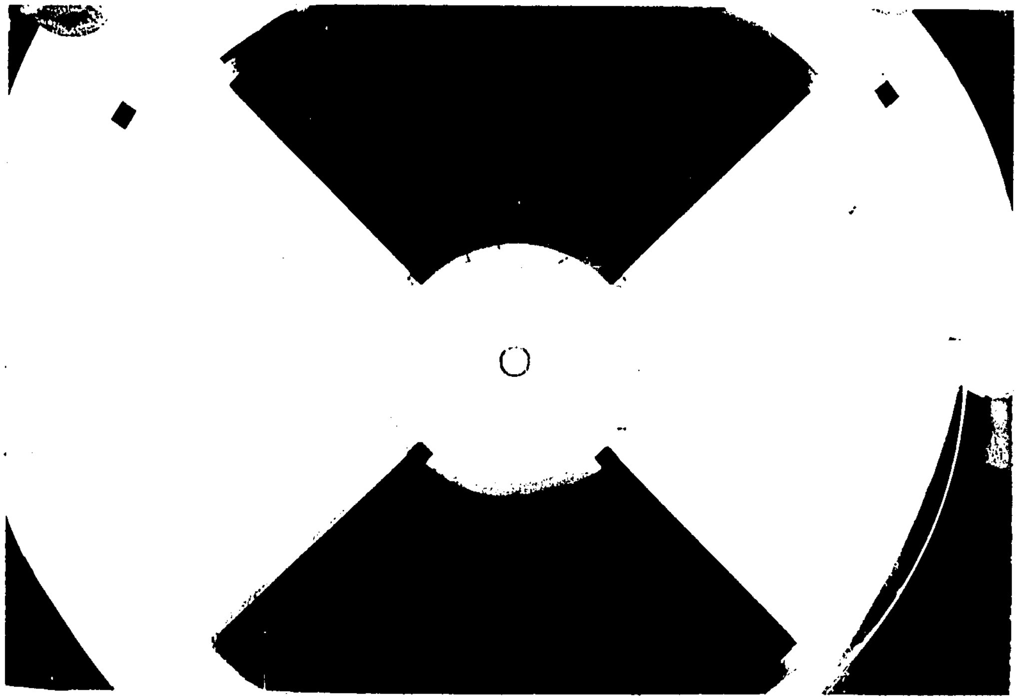


Fig. 28D

Footnotes

[1] Justification for plotting linear regression lines to fit raw curvilinear data would be further enhanced if equally abrupt changes in functional attributes, associated with morphological specializations, could be demonstrated. In this case preliminary additional support arises from our knowledge concerning structure-function relationships in colonies of these ants; and as a result experiments are presently being initiated in our laboratory, to determine the thresholds of behavioral responses in relation to morphological characteristics, in army-ant workers of all castes.

[2] That abrupt changes in anatomical relationships do exist, is demonstrated by a comparison of figures 12 and 18. For *E. hamatum*, the break in the log-log regression line representing total-leg allometry (fig. 12), corresponds to the point at which the curve expressing leg-length as a percent of total-body length, reverses direction (fig. 18).

DISCUSSION

Population Studies

Generic Comparison of Polymorphism and its Relation to Caste-Specific Behavior:

Both the size-frequency distributions (figs. 7, 8) and the allometric relationships considered (figs. 10-16) show that large differences in the degree of polymorphism exist between the species representing the doryline genera, Eciton, Neivamyrmex, and Aenictus. Nevertheless, it is still difficult to define these contrasting degrees of polymorphism in any strict quantitative manner. Wilson (1953) has devised a mathematical index of polymorphism which takes into account the size-range of the population as well as its allometry. This index is applicable to comparisons of different species showing the same type of allometry, and is especially useful for populations that exhibit comparable degrees of polymorphism. Because the allometric relationships existing in the three doryline genera used in the present study are not qualitatively alike, this polymorphic index could not be computed.

In N. nigrescens the width of the head (whether measured across the eyes or across the mandible insertion) bears a monophasic allometric relationship to over-all pupal body length. In the terminology used by Wilson (1953), this relationship is exemplified by an allometric regression line having a single, unbroken slope (figs. 10, 11), and a unimodal size-frequency curve for the population. But when the length of the leg is considered (fig. 12), the allometric line breaks into two. This condition may represent a transition between monophaic allometry and the diphasic allometric condition described by Wilson, in which the distribution of the population as well, is bimodal.

For E. hamatum, both the head-width and leg-length measurements are represented by broken log-log allometric regression lines (figs. 10-12), even though there is no indication of bimodality in the population size-frequency curve. Finally, even in A. laeviceps, in which the population consists of relatively uniform-sized individuals (with the largest and smallest workers separated by only 0.6 mm.), the regression line representing head-width allometry has a slight break in it (figs. 10, 11).

In their review of allometric considerations in ontogeny and phylogeny, White and Gould (1965) and Gould (1966) stress the importance of stating the size interval over which the allometric equation is considered valid. In our study, the interval consists of the ranges in total-body length between the largest and smallest-sized pupal individuals in all three species considered. Similarly, in view of the variations in allometry existing between different morphological structures in each species of the three genera studied, the anatomical part considered should always be stated when polymorphic systems are to be compared. Thus, when one population is said to be more or less polymorphic than another, a logical question is: more polymorphic with respect to what anatomical structure? It is reasonable to assume that the relationships between different anatomical parts (and their associated physiological characteristics) could vary independently of each other, with the result that they very often have different roles in the functioning of each species. This point is clearly brought out by the recent study by Schneirla *et al*. (in ms.). In their assessment of allometric growth in larval series representing species of *Eciton*, *Neivamyrmex*, and *Aenictus*, these authors found that the intra-colony ranges of the equilibrium constant (i.e., the slope of the growth curve) in the larval populations studied, are larger for *N. nigrescens* than for *E. hamatum*. They rightly point out, however, that this relationship holds only for rates of change in the brood stages actually studied; for in the adult workers, *E. hamatum* has a much greater allometric differential over a greater size range than *N. nigrescens*.

Although strict quantification of polymorphic differences cannot be made at this time, the results of this study on pupal allometric relationships generally support the conclusion reached by Schneirla *et al*. (in ms.), from their studies of allometric larval growth in *E. hamatum*, *N. nigrescens*, and *A. laeviceps*. Expressing the relationships of body length and leg-disc area by use of the exponential function, these authors concluded that larval broods of *Eciton* and *Neivamyrmex* are polymorphic, whereas those of *Aenictus* are classified as quasi-monomorphic.

For *Eciton*, as in many other polymorphic species of ants, the adult worker individuals exhibit various functional specializations that are associated with their morphological variation. For example, as Schneirla (1953a,b,c; 1968) has pointed out, the intermediate-sized workers perform most of the general colony functions, both in the bivouac, and on the raiding and emigration trails. By contrast, the workers minima predominate in handling the eggs and newly hatched larvae, as well as in feeding the smallest larvae throughout development. The submajors are especially useful for carrying large pieces of booty back to the bivouac, for transporting large larvae to new nest sites during the emigrations, and for dismembering prey insects. Finally, the major workers also serve as predominant "defensive" units of the colony.

The disproportionately large head width in the major workers of *E. hamatum* (as indicated by the increase in slope of the regression line in figure 10, from an isometric condition with $k_1 = 0.95$, to a strong positive allometric condition with $k_2 = 2.05$) is probably due to the enormous musculature that is necessary for the operation of their sickle-shaped mandibles.

The defensive role of the submajors in the colony is probably also served by the allometric relationship of their legs. Starting with the smallest individuals and continuing up to 0.8 R, the pupal leg exhibits strong positive allometry ($k_1 = 1.57$ in fig. 12). As a result, the submajor workers have the longest legs in relation to their over-all length (fig. 18). The relative size of their legs may make it easier for them to anchor themselves in the soil while they are spreading the legs of a foreign insect that must be dismembered before being carried back to the bivouac. In addition, this disproportionately long leg is especially useful to the submajors during the emigrations, as it enables them to easily transport the largest larvae without having to drag them over the surface of the ground.

The increase in leg length, in proportion to total-body length, does not continue into the range comprising the major workers. In fact, from 0.8 R, across the remaining portion of the range of over-all body length, the leg becomes disproportionately smaller ($k_2 = 0.17$ in fig. 12). The possibility exists that if the positive allometric trend exhibited by the leg from the smallest workers up to 0.8 R, continued through the major workers, their legs would be so long, in relation to their body length (and weight), as to make them inefficient even for adequate walking.

This differentiation in worker functions serves to increase the complexity of organization in all aspects of group behavior in the colony. In polymorphic populations we therefore expect to find individual differences in levels of excitability and thresholds of response to a variety of physical and biotic environmental stimuli. But the relation between structure and function in social insects has further implications. For when we consider the ontogeny of behavior patterns, it is evident that few of them are present in the newly-eclosed callow individuals. In many instances, a period of maturation lasting up to several days is essential before certain responses can be identified in their adult forms. As an example, preliminary experiments by Miss Ann Young and myself, have shown that callow workers are not capable of responding to the "arousal" pheromones extracted from the mandibular glands of adult individuals.

These observations, together with the fact that the patterns of many behavioral reactions in the adults are elicited by different intensities of stimulation, depending on the morphological (or caste) position of the individual in the colony, suggest that the developmental sequence of behavioral maturation also is caste-specific. Experiments in progress in our laboratory are designed to test the hypothesis that, depending upon the caste of the individual callow worker, different periods of maturation are required before they can respond to "arousal" pheromones, and to the chemical trails laid down by the adult workers.

All of these morphological, physiological, and behavioral variations existing in polymorphic doryline species, undoubtedly contribute to colony integration and organization, and are essential, therefore, for the maintenance of the regular functional cycles that characterize the three doryline species used in the present study. But the studies on larval growth by Schneirla *et al*. (in ms.), as well as the present pupal study, demonstrate that *Aenictus* is a small ant, of almost uniform population size, and with weak allometry. Therefore, in contrast to the strong functional differences existing in the more polymorphic genera, such as *Eciton* and *Neivamyrmex*, *Aenictus* has very limited potential for differences in physiological or behavioral variation between individual workers. Even though colonies of *Aenictus* still maintain the predatory, nomadic behavior patterns characteristic of species of *Eciton* and *Neivamyrmex*, the relative lack of variation between individuals has significant consequences for colony behavior as related to cyclic functions. These include simple and relatively direct communicative relationships between the workers, brood, and queen, with the result that the response of the population as a whole to any major intra-colony or extrinsic environmental event is more simple, direct and variable than in either *Eciton* or *Neivamyrmex*. Schneirla (1965, 1968) and Schneirla and Reyes (1966) have discussed the effects of these relatively primitive relationships on many aspects of colony behavior, including patterns of raiding, emigrating, and bivouac formation.

The cumulative frequency distribution of a sample of adult workers from E. hamatum colony, '52 H-P is also shown in figure 9. This distribution is significantly different from the corresponding pupal distribution of the same colony ($\alpha = < .01$; N = 10). This is expected since the area of significant disagreement between the adult and pupal samples lies over the range of intermediate-sized individuals (approximately 0.4 R - 0.6 R), and this is precisely the range in which compensatory frequency reduction has occurred, thus shifting the pupal distribution curve towards the right. Up to 0.3 R, the adult and pupal distributions are quite similar.

However, the adult distribution of colony '52 H-P is also significantly more skewed than the pupal distribution from colony '49 H-34, which had been taken from a colony characterized as normal.

Several explanations are possible to account for the contrasting distributions between these adult and pupal samples. But first we must ask: how similar should we expect the distributions to be when a pupal and adult sample of any doryline colony are compared? Throughout this study pupal samples have been used exclusively because of the relative ease of collecting entire pupal populations in the field, and then randomly dividing them into manageable samples in the laboratory. To do a comparable study using the approximately one-half million adult individuals from an E. hamatum colony would be an extremely tedious job. In addition, there are many factors that can affect the adult distribution pattern, such as differential mortality related to caste-specific "offensive" and "defensive" behavior of major workers, that have not been thoroughly investigated. Still, Schneirla (1968, Chap. 2) has compared the size-frequency distribution of 29,000 adult workers with 32,000 enclosed pupae from a colony of E. hamatum ('33 H-K), and demonstrated almost identical size-distribution patterns between them. In a comparable study of E. burchelli (colony '33 B-IV), the polygons for 10,000 adult workers and 22,000 pupae were also identical. Furthermore, evidence also exists with respect to certain allometric population parameters, that pupal and adult samples are again almost identical.[3]

Part of the answer may be found by considering the methods used in collecting the adults of colony '52 H-P. This colony of E. hamatum consisted of a cross-sectional pupal collection of approximately 80 percent of the entire brood present. Since this pupal "grab" was performed by entering the statary bivouac at noon when only a small raid was out, thousands of adults were also collected along with the statary brood.

In the dorylines, adult caste-specific polarization exists throughout all phases of colony behavior (after about nomadic day six), and activities associated with larval brood feeding and handling in the bivouac seem to be performed mainly by the smaller-sized intermediate adult workers (Schneirla, 1952, 1957a, 1968). In addition, there exists a distinct spatial orientation of the brood in the bivouac center, whose position changes with the developmental stage of the larvae (Schneirla *et al.*, 1954). During the period immediately following egg laying, the brood consists of a single bolus situated in the upper center of the bivouac, immediately below the queen. Early during the nomadic phase this single brood bolus is divided into several fringe-like boluses. As larval development proceeds, the brood comes to occupy an expanding circular area in the bivouac, with the largest larvae placed concentrically in the periphery around the smaller individuals. In the statary phase the cocoons of the pupae are situated throughout all but the lowest parts of the bivouac, piled in variable-sized heaps in spaces among the strands of workers, roughly size-assorted with the smallest in the center.

The most likely explanation for the increased numbers of adult intermediate workers in the distribution is that a strong bias was introduced at the time of collection, by taking only those adults that were spatially associated with the pupal brood. Thus, even though the strong localization of particular adult size groups with the developing brood during the nomadic phase does not exist in the statary bivouac, nevertheless it is likely that certain adult-pupal interactions, including handling and positional changes within the bivouac, are still performed predominantly by intermediate and sub-intermediate adult workers.

Relationship Between Larval Allometric Growth and Pupal Static Allometry:

At this stage of our work, we possess considerable information concerning the morphological and histological correlates of polymorphism in three genera of doryline ants representing the group-A complex. The longitudinal studies of Tafuri (1955), Lappano (1958), and Schneirla *et al.* (in ms.), together with the present comparative cross-sectional studies, have provided much information about larval allometric growth and pupal anatomical relationships in *E. hamatum*, *N. nigrescens*, and *A. laeviceps*. Of particular importance for this discussion is the study by Schneirla and co-workers (cited above), dealing with the comparative allometry of larval broods in these three doryline genera, because the species they selected to represent the three respective genera are the same ones used for the present study. It might seem, therefore, to be a relatively straightforward task to relate such ontogenetic studies of allometric growth in larval populations to the static allometric relationships eventually existing in cross-sectional pupal (or adult) series from the same populations. But the situation is, in fact, very complex. I will start by considering the nature of the material used for the comparison of the populations that have been studied.

In holometabolic insects, in order to study the relative growth of any morphological characteristic (in relation to either time, or to some other characteristic that varies with time during development), it is necessary to select structures that are accessible to measurement throughout all stages of larval development. For the longitudinal larval studies cited above, the area of the imaginal leg discs was chosen as the most accessible morphological characteristic, and for this reason the present study of pupal allometry pays particular attention to the anatomical relationships of the individuals' metathoracic legs.

The structure, growth, and differentiation of the imaginal leg discs in doryline ant larvae, have been described by G. Wheeler (1943) and Lappano (1958). As in all endopterygote insects, these imaginal discs first appear as paired thickenings of hypodermis situated on the ventral surface of the three thoracic segments. As larval development proceeds, the actively dividing discs proliferate, and they gradually become set off from the surrounding hypodermis by a peripodal cavity. As they continue to grow, they extend in an antero-posterior direction, and become increasingly submerged beneath the surface of the integument. As a result, near the end of larval development, there is a steady decrease in their visible area. As Lappano points out, furthermore, the leg-discs initially appear in the larvae at a different time in each of the different size-groups considered. In the first samples, taken from the colonies during the last statary and first nomadic days, the leg discs are found only in the largest larvae (the potential workers maxima), while in subsequent samples the discs are found in the intermediate and, finally, in the smallest-sized larval individuals.

Because the measurements used in all of the previous larval allometric studies consisted of computing the area of that portion of the leg discs visible from the surface, it is difficult to correlate the leg-disc parameters with the morphology of the adult-like legs existing after pupal metamorphosis. That is, it is then impossible to say whether the segments of the adult leg are represented by proportional lengths of leg-disc tissue that may have been hidden in the larva, or whether the pupal proportions first appear during the reorganization that takes place during metamorphosis. Let us now consider some of the relationships that may exist as consequences of ontogenetic allometric growth patterns, in view of the static morphological variations described for the pupal samples.

For this study, I will use just one species, Eciton hamatum, and will compare three graphs representing longitudinal and cross-sectional population studies of larval and pupal series of this species. Figure 29 is a composite of these three graphs. Figure 29A, modified after Schneirla et al. (in ms.), shows the differences in over-all relative larval growth between individuals representing the potential workers maxima and minima. It can be seen that at the start of larval development the largest and smallest larvae are separated by a gap of approximately 1 mm. But because the largest larvae increase their length at a faster rate than the smallest individuals (as indicated by the steeper slope of the growth curve of maxima larvae), this gap in total-body length increases to about 8 mm. at the end of the nomadic phase.

Figure 29C is a hypothetical, arithmetical reconstruction made by combining two graphs: a plot of the relation of leg-disc area to over-all body length, as a function of time (Lappano, 1958); and a semilogarithmic plot of leg-disc area, as a function of larval body length (Schneirla et al., in ms.). In the latter graph, the authors show that when relative growth of the leg discs are computed, the faster rate of growth (indicated by the steeper slope of the semilogarithmic plot) occurs in the minima larvae, not in the maxima larvae. Thus, while over-all body length increases at a faster rate in the largest-sized larval indi-

Fig. 29. Graph showing the relationship between larval over-all body growth, larval leg-disc growth, and the resulting static pupal-leg allometry, in *E. hamatum*. A complete explanation is given in the text.

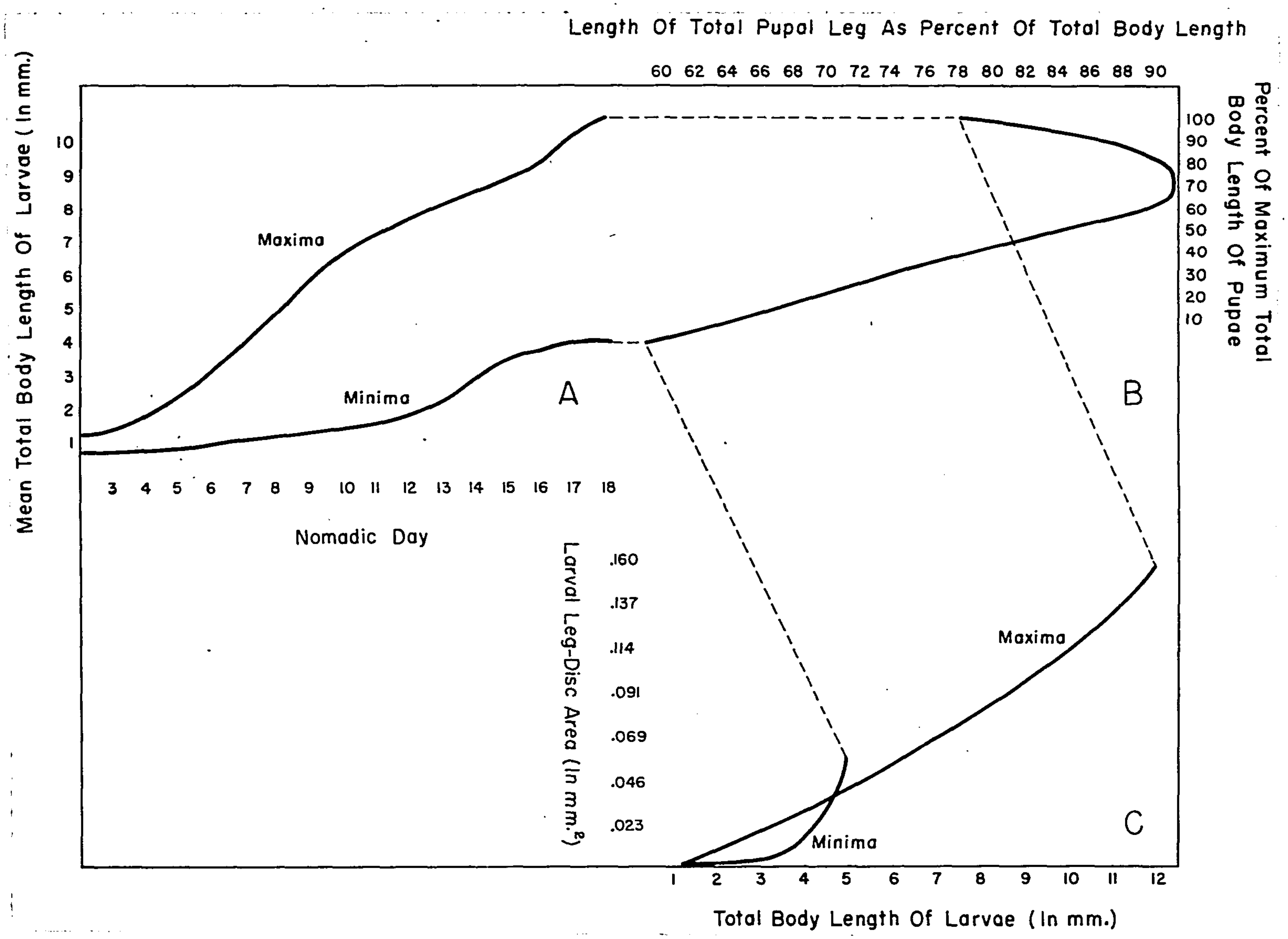

Length Of Total Pupal Leg As Percent Of Total Body Length
60 62 64 66 68 70 72 74 76 78 80 82 84 86 88 90
Percent Of Maximum Total Body Length Of Pupae
100 90 80 70 60 50 40 30 20 10
Mean Total Body Length Of Larvae (In mm.)
10 9 8 7 6 5 4 3 2 1
Maxima
Minima
A
B
3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
Nomadic Day
Larval Leg-Disc Area (In mm.²)
.160 .137 .114 .091 .069 .046 .023
Maxima
Minima
C
1 2 3 4 5 6 7 8 9 10 11 12
Total Body Length Of Larvae (In mm.)

Fig. 29

viduals, the fastest rate of growth in leg disc area takes place in the potential workers minima. The explanation for this apparent discrepancy, despite the fact that leg discs begin to proliferate at a later developmental time in the smaller larvae than in the larger ones, is that the faster growth of these imaginal discs enables the smaller larvae to "catch up" to the largest larvae. As a result, at the end of the nomadic phase, the individual larvae representing all morphological castes complete their larval development and begin to pupate within only two or three days of each other. This temporal "catching up" (due to caste-specific differential growth rates in the larvae), has been termed developmental convergence (Schneirla, 1968).

Figure 29B is the lower section of figure 18, redrawn with the coordinates rotated. It represents a plot of the length of the pupal leg, as a function of total pupal body length in _E_. _hamatum_. In connection with this graph, it has already been mentioned that as the total body length of any pupa increases, the leg becomes disproportionately larger ($k_1 = 1.57$). This trend continues only until over-all body length reaches approximately 10 mm. Then, the leg becomes disproportionately smaller ($k_2 = 0.17$).

Primarily, it is this continuously changing relationship between leg length and over-all body length in pupae representing different morphological castes that makes it difficult to directly relate larval allometric growth to static adult anatomical relationships resulting from it. The three graphs in figure 29 clearly show that no simple relationships exist between over-all body growth and leg-disc growth. It is apparent, on the contrary, that relationships between these two ontogenetic processes are continually changing, both as functions of time (throughout the nomadic phase), and as functions of over-all size and leg-disc size at any one developmental stage. Evidently, in the course of evolution, selective processes have modified embryological events, to combine these two aspects of growth in a manner so complex that no simple extrapolation from growth processes can predict the final adult anatomical relationships.

Evidence for Regulation of Larval Development in *E. hamatum*:

For many years, larval, pupal, and adult populations from colonies of *Eciton*, *Neivamyrmex* and *Aenictus* have been collected in the field and randomly divided in our laboratory. Because the population characteristics of any one species show surprisingly little variation when different colonies are compared, it would be interesting to know if the dorylines possess mechanisms to regulate patterns of larval development. Evidence from one pupal sample suggests that they do.

I have previously mentioned that one of the pupal broods in our laboratory (from *E. hamatum* colony, '52 H-P) was collected about 23 days after the smallest-sized larval individuals were removed from the colony. In figure 9, the distribution of a sample from this pupal population is compared with a pupal brood sample from a normal undisturbed colony of _E_. _hamatum_ ('49 H-34). The over-all distributions of the two samples are significantly different, but below 0.5 R, the cumulative frequencies are very similar. Thus in spite of the fact that one-third of the larval brood, comprising all individuals up to 0.3 R, was removed from the colony, developmental compensatory processes acting over a two-week period have produced a pupal brood in which the smaller-sized individuals exhibit a distribution approximating that of a normal colony. In addition, figure 9 shows a marked reduction in the number of intermediate-sized pupae from colony '52 H-P, in the range from 7.0 mm. to 9.0 mm. This reduction in frequency may be the result of a compensatory decrease in growth rates during the previous nomadic phase, of those potential intermediate-sized larvae that would have developed into pupae with an over-all length range of 7.0 mm. - 9.0 mm.

A hypothetical schema, illustrating how such processes of compensatory development may operate, is shown in figure 30. In this diagram the growth curves for the largest and smallest-sized larvae are modified from previous studies on larval broods of _E_. _hamatum_ (Schneirla, _et al_., in ms.). The curves representing growth rates in a

Fig. 30. Diagram to illustrate how processes of larval developmental compensation may operate to restore the normal frequency of the smallest larval individuals. A complete explanation is given in the text.

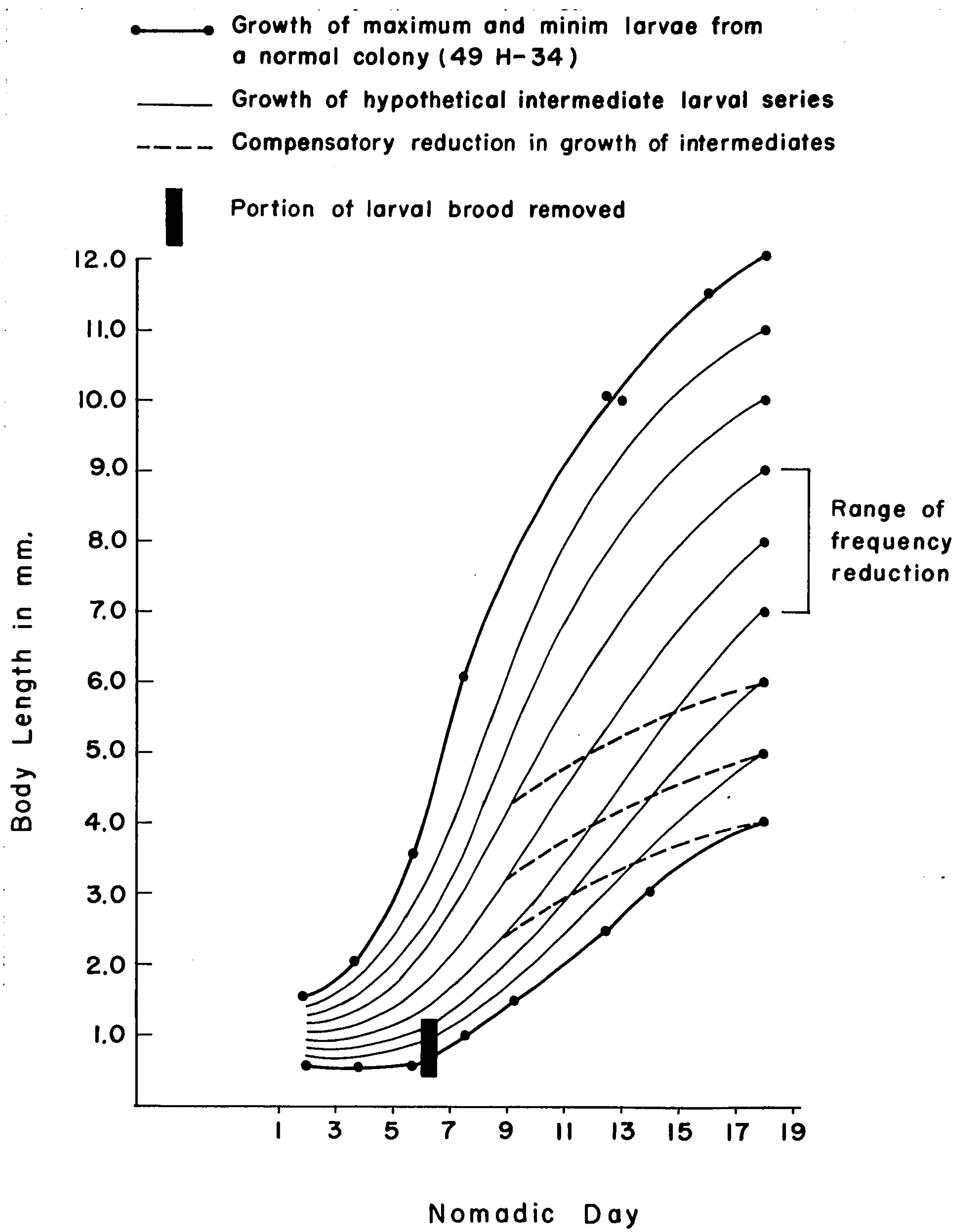

Growth of maximum and minim larvae from a normal colony (49 H-34)
Growth of hypothetical intermediate larval series
Compensatory reduction in growth of intermediates
Portion of larval brood removed
12.0
11.0
10.0
9.0
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.0
Body Length in mm.
1
3
5
7
9
11
13
15
17
19
Nomadic Day
Range of frequency reduction

Fig. 30

graded series of intermediate-sized larvae are hypothetical. The solid vertical bar represents that portion of the larval brood (approximately 30 percent) removed from the colony on the sixth day during the previous nomadic phase. In this case the normal frequency of pupae comprising the smallest individuals, results from a decrease in the rate of growth of larvae above them in the over-all size series.

How such developmental processes actually operate is not at all clear, although a shift in the magnitude of stimulative and trophic relationships between the adult workers and the smaller-sized brood may be involved. This scheme is offered here only as one of many possible explanations. It is certain that this entire procedure should be replicated and extended to determine more precisely the degree to which developmental processes may compensate for natural and artificial population disturbances. We hope to be able to remove various portions of developing larval populations at different times during the nomadic phase, and to compare the resulting pupal or adult distributions. Thus we plan to remove increasingly larger portions of larval broods from colonies at equivalent developmental stages during the nomadic phase; in addition, we also plan to remove a constant proportion of larval broods from colonies during successive days of this phase, to determine the critical developmental periods during which this potential compensation may be realized.

Ontogenetic Considerations of Polymorphism in Social Hymenoptera:

I have shown that three species of ants from different genera in the subfamily Dorylinae exhibit contrasting population characteristics, as measured by the range and relative abundance of size groups of workers in the population, and by relationships between the linear dimensions of various anatomical parts. These discontinuities exist despite the fact that (for each species considered) functionally equivalent ontogenetic processes associated with feeding and reproduction act to regulate and maintain cyclic colony behavior in all. This similarity in the patterns of behavior in colonies of Eciton, Neivamyrmex, and Aenictus attests to the adaptive value afforded to species of doryline ants that possess regular, alternating cyclic behavior regulated by stimulative processes originating within the colonies themselves. It is reasonable to assume that many steps were involved in the evolution of nomadism by the predoryline ancestors (Wilson, 1958, Schneirla, 1968), but once having established the relationship between large colony size, a carnivorous diet, and intracolonial processes that insured regular cyclic functional cycles, the dorylines emerged as a dominant insect group.

Even within this subfamily we must not confuse the causal implications of the adaptive value of these similar behavior patterns; for although the developmental events underlying colony functions in the three genera placed in group A may be homologous, still the morphological differences in the caste structures of these populations indicate that the relationships between embryological, ecological, and behavioral factors in the colonies of the species studied may be unique for each. In order to compare and relate the ecological conditions found in colonies of Eciton, Neivamyrmex, and Aenictus, I think it is necessary to consider the methodology and terminology commonly used in studies of polymorphism in social Hymenoptera.

Briefly, castes in social insects are said to be determined genetically, blastogenically, or trophogenically (Brian, 1957; Michener, 1961; Weaver, 1966).

Genetic determination results from inherited genomic discontinuities in the fertilized eggs, with the result that developmental processes occurring in the normal (i.e., species-typical) environment produce individuals that differ phenotypically as well as genotypically. This is the kind of morphological determination that the population geneticist has in mind when he uses the term "polymorphism." In the social insects, the outstanding and most frequently cited example of genetic determination occurs in the Meliponini genera Melipona and Trigona (Kerr, 1950a,b).

Blastogenic determination is due to differences in the fertilized eggs, other than the individual's own genotype. This includes differences in the size of the egg, the amount of ribonucleic acids in its cytoplasm (Bier, 1954), or the amount of yolk present in the eggs at the time of their oviposition (Flanders, 1945, 1952, 1962). Often, blastogenic determination includes the genetic differences as well, and will be used as so meaning in this discussion.

In trophogenesis, it is primarily the quantity and quality of food, as well as its temporal sequence of presentation to the developing brood, that determines the subsequent adult caste of any individual. The classical studies on female dimorphism in the honeybee offer a good example of trophogenic determination (Shuel and Dixon, 1960).

To the reader, it might seem superfluous for me to reiterate these three classical conceptual modes of caste differentiation, especially in view of the recent review articles cited above. Nevertheless, as long as investigators persist in dividing what are clearly interdependent developmental processes into distinct and mutually exclusive categories, the resulting terminological confusion must be eliminated.

As a behaviorist I have always been impressed by the analogy between the blastogenic-trophogenic dichotomy pertaining to caste development in social insects, and the dichotomy involving a distinction between innate and acquired characteristics to explain species-typical behavior in adult animals.

In behavioral studies, the concept of "innate" usually refers to adult behavior patterns that unfold and occur with an inborn coordination, and that are relatively independent of extrinsic (with respect to the organism) effects. I think that the similarity between this ethological concept of innate behavior and the population zoologists' concept of blastogenic determination is clear. But the question arises: how instrumental are either of these concepts in their ability to provide a framework for studying problems involving both morphological and behavioral development?

Schneirla (1956b, 1957c, 1966) has repeatedly questioned the concept of innate and acquired as the proper methodological tools with which to investigate species-typical behavior in animals of all phyletic levels, and concluded that they do not represent separable entities in behavioral determination. He goes on to point out that during the interval between the onset of cleavage in the fertilized egg and the behavior of the mature organism, lie the complex processes of development. This development is mediated by continuous interactions between intraorganic processes and the effects of agencies (both external and internal) in the developing medium. Most important is the understanding that these extrinsic influences occur at many levels, and may range from direct physiological effects at one extreme, all the way to advanced patterns of learning at the other extreme. Thus, not only are innate and acquired factors inseparable, but the extrinsic affects may mediate ontogenetic processes at many levels, depending in part upon the phyletic position of the organism.

I believe that it is only through the application of similar developmental concepts involving an appreciation of the numerous levels of factors that can combine with intraorganismic developmental events, that we can really elucidate processes of caste differentiation. I would like to submit that the terms "blastogenic" and "trophogenic" be replaced by a methodological framework consisting of a "levels of developmental interaction" approach, as detailed below.

Figure 31 is an outline of the factors involved in caste determination in social insects. I have divided these factors into three levels, broadly categorized as the ecological, the physiological, and the biochemical-genetic. These three groups are not intended to necessarily represent a strict functional trichotomy of ontogenetic processes, and I think this approach admits a great deal more information and more thought concerning interactions between different kinds of extrinsic and intrinsic factors in developmental processes in general, than the old blastogenic-trophogenic dichotomy.

In addition, the factors included within all three levels certainly do not represent either an exhaustive list, nor are all of the possible interrelationships shown between them. The most important aspects to be considered here are the relationships between the three levels, during the on-

Fig. 31. Diagram illustrating interactions between ecological, physiological, and biochemical-genetic factors in the development of polymorphism in social insects. A detailed explanation is given in the text.

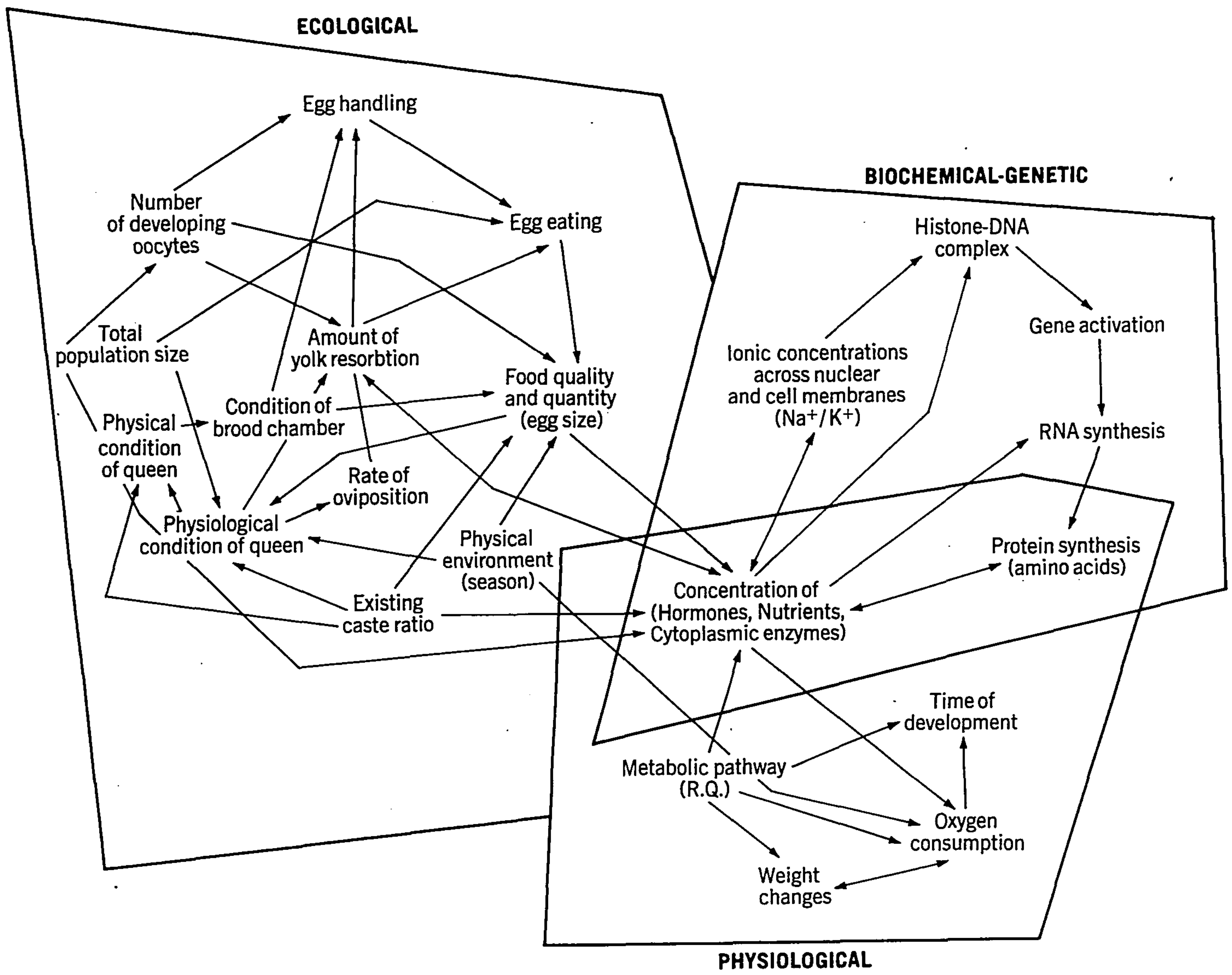

ECOLOGICAL
Egg handling
Number of developing oocytes
Egg eating
Total population size
Amount of yolk resorbtion
Food quality and quantity (egg size)
Physical condition of queen
Condition of brood chamber
Rate of oviposition
Physiological condition of queen
Physical environment (season)
Existing caste ratio
BIOCHEMICAL-GENETIC
Histone-DNA complex
Gene activation
Ionic concentrations across nuclear and cell membranes (Na+/K+)
RNA synthesis
Protein synthesis (amino acids)
Concentration of (Hormones, Nutrients, Cytoplasmic enzymes)
Time of development
Metabolic pathway (R.Q.)
Oxygen consumption
Weight changes
PHYSIOLOGICAL

Fig. 31

togeny of social insects.

Most of the studies of caste determination have been performed at the ecological level. It encompasses aspects of environmental influences in insect development that fall into the classical category of trophogenic determination, and also includes many studies which were formerly a part of the non-genetic, blastogenic terminology. There is no need to review the literature pertaining to those factors included in this level of research, since the majority of bibliographic citations appearing in the reviews on caste determination, cited above, deal with these factors.

The physiological level of approach towards problems of morphological differentiation is less known and even less developed. It is aimed at describing physiological differences in adult individuals representing all castes, or in immature forms at selected intervals during their ontogeny. Most of the research at this level has been cross-sectional, demonstrating different physiological conditions at one developmental stage. However, a few longitudinal studies, tracing patterns of physiological differences among individuals belonging to different castes, have been reported. In the honeybee, Melampy and Willis (1939) used standard Warburg techniques to measure the oxygen consumption of larvae that were being reared in queen cells and larvae being reared in worker cells. They found that in 3-day old larvae, those in the queen cells consumed 50 percent more oxygen than worker larvae of equivalent age. In addition, the respiratory quotient (R.Q.) was 1.16 for queen-determined larvae, and 1.42 for worker-determined larvae. In a related study (Melampy et al., 1940) they demonstrated significant differences in tissue composition between queen-determined and worker-determined larvae at 3 - 4 days of age. The tissues of the queen larvae contain a higher percentage of lipids and a lower percentage of nitrogen. The subsequent change in tissue composition throughout larval development was also found to be caste specific.

Lukoschus (1956) correlated the volume of the corpora allata with the data on oxygen consumption reported by Melampy and Willis, and showed that after the fourth day of larval development, endocrine organs were significantly larger in queen larvae than in worker larva. These endocrine differences must develop between the first and fourth days of larval life, since in one-day old worker and queen larvae the corpora allata were approximately equal in size (Pflugfelder, 1948; Lukoschus, 1955). Rembold and Hanser (1964) measured the oxygen consumption of individual three-day old honeybee larvae reared on royal jelly in the laboratory, and found that larvae which subsequently developed into queens had a much higher oxygen consumption than those that later developed into workers. Shuel and Dixon (1959) concluded that metabolic differences between queen larvae and worker larvae must be established very early in larval development. Using a sensitive Cartesian diver to measure gas exchange during the first 24 hours after hatching, they demonstrated a much higher rate of carbon dioxide evolution on a substrate consisting of royal jelly than on the diet characteristically supplied to worker larvae. Concomitant with these differences in metabolism, Canetti *et al.*, (1964) presented histological evidence for caste differences in endocrine activity during the critical period of determination in larvae of honeybees. Weaver (1957) provided evidence for a true physiological dichotomy in the development of the reproductive system of queen and worker larvae. Continuing their physiological studies on honeybee larvae, Liu and Dixon (1965) used starch-gel electrophoresis to illustrate striking differences in hemolymph protein patterns between the various castes. Finally, Lue and Dixon (1967) examined the concentrations of free amino acids in the hemolymph during eight stages of larval development, and implicated differences in the concentration of aspartic acid as a criterion of dimorphism.

In the family Formicidae, Brunnert (1967a,b) used starch-gel electrophoresis to analyze the hemolymph proteins and amino acids in metamorphosing queens and workers of *Formica polyctena*. He compared the protein patterns for the two female castes at nine different developmental stages, and showed that the distribution pattern of the protein fractions was caste specific. In an excellent related series of papers, Schmidt (1961, 1962, 1967) investigated the physiological differences of males, females, and workers of Formica polyctena, during seven stages of metamorphosis. The respiratory quotient (R.Q.) values during metamorphosis were 0.89-0.98 for workers, 0.79-0.95 for males, and 0.74-0.86 for queens. He also presents data of caste specific differences in oxygen consumption, nitrogen content, concentrations of phospholipids and amino acids, and weight changes during metamorphosis. Hultin (1947) measured the volume of the corpora allata in Tapinoma erraticum, and found it to be three times greater in females than in workers.

Other examples of caste specific differences in physiological conditions have been provided by Flanders (1945, 1953, 1962). By analogy with the effects of ovisorption on the eggs of some parasitic Hymenoptera, he suggested that determination of caste in ants may be influenced by similar processes. Thus, prior to ovulation by the queen, the period of exposure of the ovarian egg to absorbtive processes may determine the quantity of food available for the developing embryo. In addition, it is to be expected that extraorganic environmental conditions also contribute to variations in egg characteristics (e.g., weight-Roberts and Taber, 1965).

The last level of research to be considered represents one of the most exciting fields in biology today. It concerns the regulation of gene action in insect development (Kroeger and Lezzi, 1966), and involves longitudinal, ontogenetic studies of continually changing relationships between genomic and cytoplasmic factors.

On the level of biochemical-genetic studies, the analogy between caste differentiation in social insects and cell differentiation in tissues of one individual, has been made by Wigglesworth (1961, 1966). In the case of caste differentiation, a series of genetically similar eggs enter into different developmental pathways, due to extrachromosomal factors which regulate differential genic activation. In cell differentiation, beginning with the onset of cleavage, the progeny of a single fertilized egg also enters into selective developmental pathways, that differ according to specific sequences of gene activation or repression.

I know of no studies aimed at investigating the biochemical-genetics of embryology in social Hymenoptera that have distinct caste systems. I think that caste development would afford an excellent tool for such research, but it is understandable that the majority of this work has been done using the polytene chromosomes characteristically found in certain tissues of dipteran flies. The chromosomal picture in most Hymenoptera is not nearly as clear.

At certain times during the development of these insects, puffs appear in the polytene chromosomes, which consist of chromosomal segments in which the normal banding pattern is modified (Kroeger and Lezzi, 1966; Beerman, 1959; Kroeger, 1963a,b). The most significant biochemical change evident in a chromosomal segment undergoing puffing is an increase in its RNA content. This indicates that the puff can be considered as the site of genetic transcription, in which DNA serves as a template for RNA synthesis. During the course of development particular chromosome segments in dipteran salivary glands undergo puffing at different times, and these puffs are apparently linked to specific developmental events. Significantly, enzyme activities and concentrations of other chemicals undergo fluctuations in precise patterns which often correspond to the activity patterns of the chromosomal segments (Laufer, 1963).

The regulation of gene activity, as indicated in changes in patterns of puffing, is always dependent upon the biochemical milieu and its interaction with the genetic material. For example, the hormonal control of puffing has been investigated by injecting various amounts of the insect molting hormone ecdysone, into developing larvae (Clever and Romball, 1966). These investigators showed that the size of the puff produced is a function of the quantity of the hormone administered. There has also been extensive research on the role of differing concentrations of ions in regulating puffing patterns. In Chironomus thummi, Kroeger (1963b) demonstrated that entire series of puffing patterns can be initiated by proper adjustment of the specific sodium-to-potassium ionic ratios in the explant medium.

At the molecular level, current theories suggest that chromosomal DNA is chemically bound to regulatory progeins called histones (Stedman and Stedman, 1950). Accordingly, the ability of a segment of chromosomal DNA to act as a template for RNA synthesis, would depend upon a temporary elimination (or reduction) of the repressing action of the histone molecules. Butler and Johns (1964) have provided evidence that the DNA-histone linkage is affected by changes in the ionic concentration of the chromosomal milieu.

To take stock, I have described three levels of interaction of factors that influence embryological processes in all organisms. Why is this division more useful than that of the earlier blastogenic-trophogenic dichotomy, and how can it eliminate much of the confusion in the literature, concerning the development of caste-specific morphology, physiology, and behavior in social insects?

Many biologists realize of course that the separation of developmental phenomena into the relative contributions of genetic versus environmental factors, is only a methodological convenience, and are aware of the interdependence of such factors at all levels. If this is the case then perhaps it is time to consider a conceptual schema that is just as convenient and, in addition, approximates more closely those interactions of developmental processes that have been elucidated.

The point I wish to make can be stated briefly as follows: in so far as the development of any organism is the result of the differential activation and repression of chromosomal segments, in precise temporal patterns that differ for each caste, then *all* caste determination is a biochemical-genetic event. In so far as the differential pattern of genic activation depends upon metabolic differences and changing concentrations of hormonal, enzymatic, and nutrient factors interacting with the genome, *all* caste determination is a physiological event. And finally, in so far as these physiological discontinuities, which exist early in development, are a function of corresponding differences in any of the numerous ecological factors, then *all* caste determination is an ecological event.

The second most important point to establish is that although all three levels of developmental interaction are always involved in all caste determination, nevertheless, the relative contributions of each level depends upon the species of organism in question. Furthermore, there does not seem to be any a priori method of determining the relative importance of the effects of any of the three levels on the development of population structure, either in any of the more than 10,000 species of ants, or in any of the other social Hymenoptera. Thus, when caste determination in such a social insect as *Melipona* or *Trigona* is said to be genetic (Kerr, 1950a,b), this does not necessarily imply that the entire genetic program for "queenness" or "workerness" is somehow encoded in the sequence of bases on the DNA molecules in the fertilized eggs. It may mean, however, that the eggs have enough genomic and cytoplasmic differences (e.g., in hormonal levels, yolk content, or enzymes) to insure that developmental processes will be canalized along two different paths, and that the relative contribution of ecological factors is minimal (but usually not zero). Even in the case of *Melipona*, the ecological factors play a small but significant role; for Kerr and Nielsen (1966) have recently concluded that food quantity acts as an effectuator, in close dependence with the doubly-heterozygous condition necessary for queen production. Of course in the case of the honeybee, the ecological events are very crucial, especially the amount and quality of food administered to the developing brood during the first three days of larval life (Shuel and Dixon, 1960).

Levels of Developmental Interaction Applied to Comparisons of Polymorphism in Doryline Ants:

In the dorylines, as with many other formicid groups, our developmental analysis of caste structure must include a consideration of factors underlying the discontinuity separating queens from workers, as well as the continuous polymorphic series (in those species in which it exists) ranging from workers minima at one extreme to workers maxima at the other extreme.

For species of *Eciton* and *Neivamyrmex* the production of single, annual sexual broods, on processes affecting the queen and the colony, has been reviewed by Schneirla and Brown (1950). For two surface adapted species of *Eciton*, Schneirla and Brown (1952) have summarized the characteristics associated with sexual brood production as follows: seasonal timing; restriction to one sexual brood per colony per season; a dimorphic makeup consisting of a few females and many males; the size of the sexual brood population within a species-typical range constituting a fraction of the total for an all-worker brood; a precocious development and emergence of queens; a shorter period of larval development, with a different time rate of change than in worker broods; and graduated individual differences in size approximating a normal frequency distribution.

For *E. hamatum*, a sexual brood consists of approximately 1500 male individuals and about six queens. This presents a striking contrast with a typical all-worker brood consisting of more than 80,000 individuals. Although this discussion will not concern the development of the males, it is reasonable to assume that the portion of the sexual brood that develops into male individuals arises from eggs that are not fertilized by the queen. This is the situation found in social Hymenoptera generally, even though recent studies have demonstrated that it is not necessarily the haploid condition per se that gives rise to the production of males (Whiting, 1943; Mackenson, 1951; Rothenbuhler, 1967; Woyke et al., 1966). In keeping with this genic balance theory of the authors cited above, I should point out that although no evidence exists to support the conclusion that doryline males arise from diploid eggs that are homozygous at many genic loci, still we do know that the apterous condition of the doryline queen must admit some instances of inbreeding, evidently differing in frequency for the different group-A genera (Forbes, Schneirla, and Cazier, in prep.).

What is the relative contribution of factors from the physiological and ecological levels to queen determination in a doryline such as E. hamatum? Physiological differences between the egg series of a sexual brood and that of an all-worker brood would be expected if, for example, supplementary contributions to the total brood were made by egg-laying workers. For any sexual or worker brood, however, all individuals are approximately the same age, and are precisely synchronized with subsequent broods. This is strong evidence that they are produced by the single colony queen.

Other differences may arise from correlative genetic differences in the eggs of sexual larvae. Because the male is probably a haploid individual, his contribution to each of the queen's offspring is genetically identical (assuming only one male parent to each brood). As far as the queen is concerned, however, since normal segregation occurs in oogenesis her genetic contribution to each offspring is not identical (as is often assumed), but depends upon her own state of heterozygosity or homozygosity (Rothenbuhler, 1967). This raises several fundamental questions. Are genomic differences that may exist in the eggs at the particular season when sexual broods are typically produced, strong enough to account for the faster rate of development as well as the many other morphological and physiological correlates that are characteristic of queen larvae? Or, must we pay particular attention to the unique ecological conditions existing in the colonies at the onset of the dry season, to account for those aspects of queen development that have been studied? The evidence points to a strong implication of ecological factors which I will now consider.

In species of _Eciton_ and _Neivamyrmex_, the onset of nomadism is associated with a sudden increase in levels of social stimulation and trophic conditions, resulting from the eclosion of thousands of callow workers. During the first few nomadic days these callows resemble larvae in that they feed voraciously. This establishes a degree of competition in the bivouac between the callow workers and the newly hatched, first instar larvae, for the limited resources available (Schneirla and Brown, 1952). But since the total population of a sexual brood is only a fraction of that of an all-worker brood (approximately three percent), the competition between the sexual male and female larvae, and the callow workers is much less intense. Also, the total excitatory effect of an early larval sexual brood far exceeds that of a worker brood. This leads to larger and more intensive raids, and consequently, to more food being brought back to the bivouac. The probable result is that the highly aroused adults heap a disproportionately large amount of food upon the sexual microlarvae. This imparts to these female larvae enough of an early trophic impetus to activate those genetic systems essential for queen development. This genetic activation undoubtedly must be induced at an extremely early critical period during larval life, probably even before the termination of the first instar. In addition, an even earlier trophic advantage may be given to the sexual microlarvae immediately after hatching, if part of their first diet consists of undeveloped, residual eggs that the queen has laid. It is possible that at the end of the five or six days of the statary phase during which time the eggs are laid, those that have not yet hatched (presumably the last-laid eggs) are fed to the first instar larvae (having hatched from the first-laid eggs). In some myrmicine ants such as Myrmica rubra, the first instar larvae typically feed on adjacent eggs in the egg mass (Weir, 1959).

In Eciton and Neivamyrmex, since the number of individuals in a sexual brood constitutes only about three percent of a comparable all-worker brood, it is likely that the queen does lay more than the number of eggs that normally develop into sexual individuals (Schneirla and Brown, 1952).

Whether the initial trophic impetus gained by the sexual microlarvae results from their early feeding on increased quantities of food brought into the bivouac as booty, or from qualitative nutritional differences in the residual colony eggs, once this impetus is established, it is both self perpetuating and self accelerating. The superior attractiveness of the sexual brood for adult workers of E. hamatum have been described (Schneirla and Brown, 1950). The workers in the bivouac cluster very closely about the young queens in all larval stages, and they soon begin to be established as centers of aggregation, which eventually leads to a true polarization in the bivouac. This situation is not found when a worker brood is present in the bivouac. Furthermore, this increased attraction of the adults for the sexual larvae -both male and female- is maintained even in activities taking place outside the bivouac, and which are not concerned with larval feeding. I am referring specifically to the patterns of emigrations that occur during the nomadic phase. Schneirla (1961) has described the increased levels of activity of the adult workers when sexual larvae are being transported to a new bivouac. During the summer of 1964 I came upon a massive nocturnal emigration of a colony of N. nigrescens, with adult workers running in columns that measured up to 25 cm. across, and with the level of worker excitation far greater than I had ever seen with all-worker broods. This was the first colony containing a sexual brood that I had encountered in the field.

All of this increased attractiveness and levels of social stimulation in the colonies containing sexual broods, undoubtedly leads to ever increasing bouts of feeding by the developing larvae, and this tends to accelerate their growth even more. The result is that the queen larvae evidently begin to pupate after approximately 8-10 days from the onset of the nomadic phase. Contrast this with the resulting durations of nomadic phases of 16-18 days when an all-worker brood of E. hamatum is present. The trophic advantage afforded to the sexual larvae at all stages consequently results in their exhibiting population characteristics that differ markedly from an all-worker brood at comparable times throughout the nomadic phase. In the developmental curves for sexual broods, there is an earlier acceleration of growth than for a worker brood (Schneirla and Brown, 1952, p. 15). During the first third of a nomadic phase, larval worker broods exhibit a slow rate of development, in contrast to the early rapid acceleration of sexual broods. In addition, when the increase in rate of larval worker development appears, it is never so rapid as the earlier increase exhibited by the sexual larvae.

When we consider the contribution of the three levels of interaction to differences between polymorphic and monomorphic worker series in the dorylines, it is clear that very different factors are involved for the genera *Eciton* and *Neivamyrmex*, as compared to *Aenictus*.

Once again, we have to account for the genetic differences that exist in a worker egg series produced by a queen that is relatively heterozygous. Unlike the situation in a sexual brood, where only about six eggs finally develop into queens, here we are dealing with broods that range from 35,000 in *Aenictus laeviceps*, to 50,000 in *Neivamyrmex nigrescens*, to 80,000 in *Eciton hamatum*. This admits the possibility of relative, genetically controlled cytoplasmic, enzymatic, and other biochemical differences in potential worker egg series. And again the question arises as to whether genetic differences, if indeed they exist, are strong enough to account for the continuous polymorphic series existing in adult workers of *Eciton* and *Neivamyrmex*. In the absence of laboratory tests in which all developing larvae are given food of identical quantity and quality, this question cannot presently be answered. In addition, it would be interesting to know if mechanisms of yolk resorption postulated by Flanders (1945, 1952) are in operation here. With so many thousands of eggs being produced it is certainly reasonable to assume that they are retained in the ovarioles of the queen for varying intervals, during the five or six days when the eggs are laid.

As is the case for sexual broods, more information exists concerning contributions from the ecological level, with the evidence suggesting that these factors act as essential effectuators of the plastic genetic systems that probably are present in the worker egg series. Many interesting correlations can be made between the ecological situation in colonies of *Eciton*, for example, during the last third of the statary phase, and the population characteristics of their adult workers.

To account for the skewed distributions of worker series of *E. hamatum* and *N. nigrescens*, along with the related allometric variations within each polymorphic series, the effects of differential patterns of larval feeding again appear to be crucial. The evidence elucidated so far points to a competition by the larval brood for the limited amount of booty available (see also Wilson, 1954; Schneirla, 1968).

The microlarvae from the very large (hence potential) all-worker broods are at a substantial trophic disadvantage as compared to a sexual brood. First, it is doubtful that a substantial number (if any) of residual, undeveloped eggs are present in the bivouac for the first instar larvae to feed upon. If this is the case the result is that all of the eggs complete embryonic development and emerge as a massive brood of "hungry" first instar larvae. But since an all-worker larval brood of E. hamatum contains around fifty times the number of individuals in a sexual brood, the competition for the limited amount of booty (which in the absence of residual eggs comprises their only supply of food) is manifestly more intense. This competition exists not only as the adults distribute the booty among the developing larval individuals, but also as a substantial portion of the food is consumed by the newly eclosed callow workers. The result of this trophic "rationing" that occurs at the transition between the statary and nomadic phases, is that regardless of any differential or preferential feeding of larvae, the critical period for gene activation of developmental systems essential for queen determination, is already past.

But in Eciton and Neivamyrmex, a great deal of developmental plasticity still exists, as evidenced by the continuous, polymorphic adult worker series that arise in species of both genera. For both E. hamatum and N. nigrescens the pupal populations are significantly skewed towards the larger-sized individuals. Also, not only do colonies of these two species contain a preponderance of smaller-sized workers, but the patterns of the distributions are quite similar. As we move across the range of over-all body length, a rapid rise in the frequency of individuals is followed by a corresponding decrease, with a tail that is prolonged over the range comprising the workers maxima (figs. 7, 8). This similarity in pattern suggests the formulation of a simple hypothesis relating this population characteristic in E. hamatum and N. nigrescens, to trophic conditions existing in the statary bivouac. I have already attempted to explain the morphological and physiological discontinuities between queens and worker series, by contrasting the time-course of early larval feeding. Can we now account for the continuous differences in morphology existing within the worker population of each species, in terms of comparable trophic gradations in the bivouac shortly after egg laying?

For both E. hamatum and N. nigrescens, the single colony queen lays eggs over about a one-week period, midway during each successive statary phase. If we possessed enough information concerning the rate of egg laying during this interval, to construct a rate-frequency distribution polygon, it is tempting to predict that it would strongly resemble a mirror image of the size-frequency distribution polygons constructed for the pupal populations (fig. 7). Indeed, this would be the simplest explanation of the relationship between trophic conditions in the colony at the time when the larvae complete their embryonic development, and the morphologically graded worker series that has been described for the pupal populations. It is suggested that the relatively small number of first-laid eggs are also the first to hatch and therefore the first to begin feeding. This initial trophic advantage enables their own larval development to be accelerated, as they enter into early trophallactic relationships with the workers of the adult generation. The adults are attracted to these first hatched larvae and soon begin to feed them preferentially. This developmental advantage, held by the larvae that will differentiate into workers maxima, is maintained even after the bulk of the larvae have subsequently hatched. Thus the hypothesis is that a progression in the rate-frequency of egg laying by the queen is followed by a comparable gradation in the temporal onset and intensity of larval-adult stimulative and nutritive interrelationships. This in turn establishes a related temporal pattern in the onset and intensity of larval feeding by the adult workers. The result is that individual variations in developmental physiology activate genetically-regulated embryological systems to produce adult castes that exhibit continuous differences in size, form and function. The influence of trophic differences on larval development in colonies of _E. hamatum_ and _N. nigrescens_ is manifold. Regression analyses of calculated allometric-growth curves for these two species show that significant differences (at a probability level of .001) exist between the maxima and minima larvae, with the maxima larvae having the flattest allometric curves and the minima larvae the steepest (Schneirla _et al._, in ms.). Data on related larval physiological characteristics such as caste-specific differences in oxygen consumption and respiratory quotient during development, as well as patterns of hormonal, nutrient, and enzymatic concentrations, are not yet available.

Throughout the discussion of the influence of patterns of feeding on developmental physiology, I have combined the genera *Neivamyrmex* and *Eciton*. For the two species used to represent these genera, fundamentally similar ecological factors have been described to account for the continuous variations in size and morphology exhibited by the two populations. However, the almost uniform size range found in workers of *Aenictus* (3.2 mm. - 3.8 mm.), plus the fact that species in this genus are very similar to those of *Eciton* and *Neivamyrmex* in the queen's schedule of egg delivery during the statary phase, indicates that very different sets of processes related to brood-adult interactions, must be in operation.

Returning to the population-genetic structure of colonies of *Aenictus*, there is no reason to believe that the *Aenictus* queen is any less heterozygous than queens of *Eciton* and *Neivamyrmex*; and if comparable genetic variation does indeed exist in the egg series produced by queens of the three genera, then we cannot account for the difference between the strong morphological variations of populations of *Eciton* and *Neivamyrmex*, and the structural uniformity exhibited by workers of *Aenictus*, on the basis of genetically controlled, cyto-physiological variations in the eggs. But what about the role of non-genetic physiological and biochemical factors. For Eciton and Neivamyrmex the possibility was considered, of differential resorbtion of yolk from eggs as they passed along the ovarioles in the queen. Schneirla (1965, 1968) has suggested how comparable effects may be involved in early brood development in Aenictus. First, the oocytes may have undergone resorbtive processes to such a degree that they all begin development at a uniformly low physiological level. Secondly, in this condition, the eggs are far less attractive to the workers than in Eciton or Neivamyrmex. Lastly, by a combination of this relative unattractiveness of the eggs, and the unresponsiveness of the adult workers due to their own decreased physiological condition, the eggs of the brood generation begin development in nearly the same condition, and at very nearly the same time (approximately statary day 22).

Considerable information exists concerning factors that determine the rate of early embryonic development in insects. One obvious fact is that, within limits, developmental processes are accelerated by high temperatures and retarded by low temperatures. Development may also be delayed by low humidity (Schipper,1938), and in many insects the eggs must absorb a certain amount of water for development to continue (Johnson, 1937). In addition, many insects undergo a developmental arrest -or diapause- even under optimum external environmental conditions. This suppression of growth processes occurs at specific developmental stages, and is under biochemical control. Reviews of factors underlying the onset of diapause has been provided by Andrewartha (1952), Hinton (1954), Lees (1955, 1956), and Harvey (1962). That insects can enter into diapause at any stage, depending upon the species considered, is significant in view of the relatively slow rate of early development of *Aenictus* egg series. Of special importance here is that the physical and physiological environment of the female parent, can influence the onset of diapause in her progeny. Exposing female chalcid wasps to low temperatures during oogenesis, can induce diapause in her next brood (Schneiderman and Horwitz, 1958), and a similar maternal effect has been demonstrated in larvae of the blowfly, *Lucilia caesar* (Ring, 1967). Fukuda (1952) showed that a hormone produced by the subesophageal ganglion of the silkworm, *Bombyx mori*, controlled the production of conditions associated with diapause in the eggs of the subsequent generation. Finally, respiratory rates in relation to diapause have been measured in the beetle, *Galeruca tanaceti* (Siew, 1966) and in the moth, *Hyalophora cecropia* (Schneiderman and Williams, 1953), while the biochemical basis of diapause has been considered in insects by Agrell (1951), Schneiderman and Williams (1954a,b), and Ludwig and Barsa (1955). It would be extremely interesting to measure the oxygen consumption of *Aenictus* worker eggs, and to compare them with similar studies on the eggs of Eciton and Neivamyrmex. If relative to their size, eggs of Aenictus indeed exhibit decreased values of respiratory rates, then studies of Aenictus queens might be undertaken to look for corresponding differences in nutritive and hormonal interactions that may be partly responsible for the physiological differences existing in the eggs.[4]

Finally, evidence also exists of cases in which stimuli specific to hatching are essential to initiate larval development. In mosquitoes for example, this stimulus may be either the reduction of dissolved oxygen in the medium, below some critical level (Gjullin et al., 1941), or the physical and physiological effects of egg crowding (Thomas, 1943).

Any of these factors may play a part in delaying development of the egg series in Aenictus. But that the adult army-ant workers themselves may play an equally important role in enhancing either the onset or rate of embryonic development in Aenictus is a particularly intriguing thought, especially when we consider the condition of the workers at the time of egg laying. For unlike the situation found during the statary phase in colonies of Eciton and Neivamyrmex, in which over-all colony activities are reduced, in both A. laeviceps and in the closely related species A. gracilis, the statary phase approaches a real dormancy. Schneirla and Reyes (1966, p. 139) reported, for four colonies studied throughout their statary phases, that surface raids ceased entirely after the first five days, and for the next 17-22 statary days surface raiding was totally absent. In addition, when the infrequent statary raids do occur, they usually consist of a brief exodus which is often soon reversed, with no booty brought back to the bivouac. Overall, the workers appear generally dormant, and probably fall much lower in metabolic level than workers of *Eciton* and *Neivamyrmex* at comparable times during the statary phase. Whether the eggs (or embryos) require a certain amount of mechanical stimulation to promote development, or lack certain essential chemical secretions due to the relative decrease in egg handling by the workers, is not yet known.

Physiological Studies

Studies of insect respiration can be divided into three areas of investigation. The first concerns the transport of oxygen from the atmosphere to the tissues of the organism, and the corresponding route of carbon dioxide elimination. These studies include descriptions of the structural development and functional anatomy of the tracheal system, as well as the neural basis of diffusion regulation through the spiracles. The second class of studies concerns the chemical changes which the constituents of the living body undergo, especially the intermediary metabolism of carbohydrate, nitrogenous, and lipid compounds to produce the energy essential to maintain activity. Lastly, there is a great amount of research concerning the exogenous and endogenous effects of physical, physiological, and chemical factors on the rate of respiratory gaseous exchange, usually expressed in terms of the amount of oxygen consumed or carbon dioxide produced.

It has been pointed out that a rising rate of respiration with increasing temperatures, is one of the most over-confirmed facts in insect physiology (Keister and Buck, 1964). Nevertheless, temperature effects are still completely dependent upon the age, nutrition, and past thermal experience of the organism (Edwards, 1953). Also, temperature not only controls the rate of respiration, but respiratory processes can indeed influence external temperatures. Thus, honeybees can regulate temperatures in the hive by "fanning" and "shivering" (Woodworth, 1936). Doryline ants can also regulate bivouac temperatures by physical processes involving close clustering (Schneirla _et al._, 1954), but it is not known if increased physiological processes also contribute to this social homeostatic mechanism. The entire subject of the effects of temperature on respiration in insects, has been reviewed by Uvarov (1931), Edwards (1953), Keister and Buck (1964), and Wigglesworth (1965).

Much information also exists concerning changes in respiratory rates taking place during insect development.

Reference to some of these studies has already been made, in connection with the physiology of caste determination in social hymenoptera.

The relation between oxygen uptake of intact embryos, their homogenates, and intracellular constituents of the grasshopper, Melanoplus differentialis, has been studied by Bodine (1950) and Bodine and Lu (1950). Related studies on respiratory rates in diapausing eggs have been reported by Burkholder (1934) and Bodine and Boell (1936). The biochemical basis of respiration in eggs of the Japanese beetle, Papillia japonica was studied by Ludwig (1958), Rothstein (1952) and Ludwig and Wugmeister (1955).

In holometabolic insects, a generalized pattern of fluctuating respiratory rates has been described, starting with the onset of larval development, and continuing to the end of the pupal phase. For most insects the larval rate increases steadily until the last larval (or prepupal) instar, after which it drops and remains at a low level throughout pupal development. In the adult, the respiratory rate again rises. This "U"-shaped respiratory pattern during growth and metamorphosis, resulting from the interaction between processes of gaseous exchange, nutrition, histolysis, and histogenesis, has been described in Diptera (Dobzhansky and Poulsen, 1935), Coleoptera (Fink, 1925), and Hymenoptera (Melampy and Willis, 1939).

In connection with these studies of respiratory physiological processes during growth, a recent and fascinating area of research concerns the pheromonal control of development (reviewed in part by Butler, 1967). Indirect evidence for a relationship between pheromones and respiratory processes during development, has been provided by Norris (1954). In the locust, *Schistocerca gregaria*, he has shown that pheromones secreted by mature males accelerate maturation in immature individuals of both sexes. That these pheromones themselves are under hormonal control within the individual, was suggested by Loher (1961). Finally, similar group-effects in growth and maturation have been shown to exist in the cricket, *Acheta domesticus* (Chauvin, 1958; McFarlane, 1962, 1966a,b).

I have so far provided two examples of factors that influence respiratory rates: the effects of environmental temperatures; and the physiological conditions associated with individual and group developmental stages. Although neither of these is directly related to the present study, they have been chosen to illustrate the modification of respiratory rates by an exogenous and an endogenous factor. Other external factors, that have not been considered here, include humidity and atmospheric oxygen tension. But the studies on oxygen consumption of workers from colonies of *N. nigrescens* during the nomadic and statary phases, must also include strong considerations of internal physiological effects, even though they undoubtedly interact with variations in the external environment (especially temperature) throughout both functional phases. Therefore, I would now like to consider some studies concerning the effects of physiological and behavioral conditions on metabolic processes.

In many organisms, the influence of internal physiological conditions on the cyclic magnitude of recorded respiratory rates, can be related to comparable fluctuations in the individual's physical and chemical environment. For example, diel fluctuations in temperature, oxygen, and carbon dioxide, associated with such activities as nesting, may act directly on cellular metabolic processes, or indirectly through increased ventilation due to higher levels of activity. Diel rhythms in respiration in mealworm larvae and pupae have been described (Michal,1931), and similar rhythms exist in the beetle, _Dytiscus_ (Poljakov, 1938, as cited by Edwards, 1953).

But in addition, there are many fluctuations in rates of respiration that persist even under conditions of constant temperature, humidity, and chemistry of the medium (Harker, 1958; Bünning, 1967). In the cockroach, _Periplaneta americana_, as Harker (1956, 1960) has shown, locomotory rhythms are under the influence of the subesophageal ganglion (but compare this with recent contradictory reports by Roberts, 1966 and Nishiitsutsuji-Uwo _et al._, 1967, in which other neurosecretory organs are implicated as the controlling source). During larval development in insects, metabolic rhythms occurring in each instar have been described for Galleria mellonella (Sehnal and Sláma, 1966), for Bombyx mori (Hsueh and Tang, 1944), and for Pyrrochoris apterus (Sláma, 1960).

These studies on metabolic rhythms are important, especially in relation to the cyclic behavior patterns described for all species of Neivamyrmex so far studied. Results obtained in this project show that oxygen consumption increases through the nomadic phase, and subsequently decreases with the onset of statary conditions. In view of these striking and repetitive differences in the same individual's physiological condition, exactly what relationships can be accepted between the changing behavioral conditions existing in the colonies, and the variations in magnitude of physiological processes recorded in this experiment?

For the tests of oxygen consumption, groups of approximately 20 intermediate-sized worker ants were removed from a raiding column in the field, placed in a test chamber in the laboratory, and their activity metabolism recorded. A question to be raised at this point is: if worker army ants are indeed more active (both on raiding trails and in the bivouac) during the nomadic phase than during the statary phase, shouldn't we expect these fluctuating levels of activity in the field to be reflected in corresponding variations in respiratory metabolism in the laboratory? After all, increases in respiration associated with high levels of activity have been described for many insect groups, including species representing the Orthoptera (Krogh and Weis-Fogh, 1951), the Lepidoptera (Kalmus, 1929), the Diptera (Davis and Fraenkel, 1940; Chadwick, 1947), and the Hymenoptera (Jongbloed and Weirmsa, 1934).

But the army ants exhibit fundamental and significant differences from the studies cited above, concerning metabolic rates in relation to levels of activity. A striking fact that appears in the graphs of the longitudinal tests on oxygen consumption (figs. 19-21) is the regularity of the rise in oxygen consumption throughout the nomadic phase. To be sure, this effect may be explained in part as an artifact induced during the collection of the specimens, even though handling was absolutely minimized by using the same container both as an aspirator in the field and a test chamber in the laboratory. A second and clearly more important hypothesis, however, arises from continuous studies of colonies of N. nigrescens in the field, under the influences of the highly fluctuant ecological conditions characteristic of the habitat of investigation, namely that the physiological changes may have an extrinsic basis. Were this the case, however, one would expect respiratory levels to be more variable during the nomadic phase, then measurements indicate. The point is that, regardless of the predictable changes internal to the colonies through the two phases of the functional cycle, the doryline workers respond in all of their field activities, to diel periodicities in temperature, precipitation, and the quantity and quality of booty available. Thus, on relatively cool nights during the nomadic phase, I have often been surprised to find levels of oxygen consumption above the values predicted by observation of the activity of the workers as they left the bivouac at the start of an evening's raid. On many such evenings, worker ants (exhibiting decreased activity relative to levels of excitation on warmer nights), became much more active in the higher and more uniform temperatures that were characteristic of the insulated laboratory room. If these respiratory tests could be conducted in the field, much more variation in levels of activity metabolism would probably be recorded throughout both behavioral phases.

As a result of the relatively uniform rise in oxygen consumption during the nomadic phase, it appears as though the physiological condition of the workers is continually modulated outside the bivouac by aspects of the existing physical and biotic environment. But when the workers are placed in the laboratory situation where nocturnal temperatures are both stable and above those occurring in the field, their increasing stimulative organic condition is expressed more directly in the test chamber of the respirometer. That the army-ant workers <u>can</u> retain these internal physiological states (or metabolic traces) for varying periods after being removed from their colony, has previously been suggested by Schneirla (1957a), as one factor maintaining increased levels of raiding by workers of _E_. _hamatum_ early in the nomadic phase, when the callow excitatory effect is diminishing, and before the larval-excitatory effect enters as the main source of colony social stimulation.

These considerations, together with the related changes in thresholds of response of the workers to chemical stimuli existing in the colony, suggest that we are here dealing with physiological differences based upon intraorganic conditions in addition to processes associated only with levels of activity. It is still of interest, however, to determine the relationship between "basal" metabolic rates and the activity metabolic rates measured in this experiment during both the nomadic and statary phases.

Basal metabolic studies are designed to measure the amount of oxygen consumption necessary only for organismic maintenance, and it might be feasible to measure the oxygen consumption of homogenate preparations of army-ant workers as an index of basal conditions. Bodine and Lu (1950) measured the oxygen consumption of intact embryos, and their homogenates, of the grasshopper, _Melanoplus differentialis_. They found that the oxygen uptake of the homogenates is always less than that of the intact embryos. But, more important, they found the relative difference in oxygen consumption of homogenates from active versus diapausing embryos, to be practically identical with the corresponding relative difference between active and diapausing intact embryos. Comparable tests on workers of army-ants should be performed to determine if constant relations do exist between the oxygen uptake of the intact workers and their homegemates.

One difficulty that must be overcome before such studies can be made successfully with homogenates, is that the homogenate of an adult ant, unlike the condition found in the soft-bodied embryo, is a very complex and "messy" mixture. Because of this, many investigators have tried to compromise between the relatively "crude" activity metabolism and the respiratory studies based on homogenate techniques. It is possible, for example, to measure resting metabolism in insects that stay quiescent for long periods, or that can be physically secured to eliminate activity.

By a similar method, Allen (1959a,b) compared the resting metabolism of worker honeybees at different ages and at different temperatures, and also compared differences in respiratory rates of drone versus worker larvae. Of special significance for the present study of oxygen uptake of adult army-ant workers during the nomadic and statary phases, are the studies on the resting metabolism of the locust, Schistocerca gregaria (Gardiner, 1958; Norris, 1959, 1961). These authors showed that both the nymphs and adults from the "gregaria" phase have higher resting metabolic rates than individuals of the same developmental stages taken from the "solitaria" phase.

Although it may appear that the resting metabolism is the simplest reliable index of internal physiological states, this measurement cannot always be compared between organisms. Unless the test animal is normally motionless for periods long enough to record its oxygen uptake, some sort of restraining apparatus must be employed. For measuring metabolic rates of worker honeybees at different ages, Allen (1959a) placed the test organisms into a copper gauze cylinder that permitted only very slight movements. But for most social insects that usually are active at the time of testing, this procedure would make it very difficult to eliminate endocrine-related "stress" effects introduced by the subjects' struggling. I have repeatedly attempted to physically immobilize workers of _N. nigrescens_, but the usual patterns of activity they exhibit immediately after being released makes it clear that artificial and prolonged physiological changes are introduced by this method.

If, as the evidence so far suggests, the regular fluctuations in levels of activity metabolism exhibited by adult workers of _N. nigrescens_ during the nomadic and statary phases, are dependent upon corresponding variations in internal physiological processes, in which organic systems might these processes be clearly reflected? I suggest that a fruitful line of research would involve studies of changes in the neuroendocrine systems in the workers of this doryline species, during both phases of the functional cycle.

The corpora allata are spherical or oval shaped glandular structures, which arise by budding of epidermal cells between the mandibular and maxillary segments. The first morphological study, on a comparative basis, suggesting their endocrine function, was made by Nabert (1913). The corpora allata have since been found to secrete juvenile hormone which maintains larval characteristics in immature insects, controls the deposition of yolk in developing eggs of mature female insects, and influences many aspects of general insect metabolism.

In 1945, Pfeiffer concluded, from experiments on the effects of allatectomy on the adult female grasshopper, <u>Melanoplus</u> <u>differentialis</u>, that the corpora allata tend to increase basal metabolism. In the blowfly, <u>Calliphora erythrocephala</u> allatectomized females exhibit a decrease in oxygen consumption of approximately 24 percent (Thomsen, 1949). Thomsen and Hamburger (1955) later demonstrated the same effects, using castrated female grasshoppers, and concluded that the action of the corpora allata hormone is therefore direct, and not caused by an increase in oxygen consumption by the developing ovaries in the sexually mature female. A similar reduction in oxygen uptake was demonstrated in allatectomized adults of the Colorado beetle, *Leptinotarsa decemlineata* (deWilde and Stegwee, 1958, as cited by El-Ibrashy, 1965), and in *Locusta migratoria* (Roussel, 1963a,b). Levels of oxygen uptake in the female cockroach, *Leucophaea maderae* increase after implantation of corpora allata (Sägesser, 1960); here again the effect was the same for castrated females, thus indicating that the endocrine effect is a direct one. Additional evidence for this was supplied by Clarke and Baldwin (1960) in which they demonstrated an increase in oxygen uptake in isolated mitochondria preparations from *Locusta migratoria*, after the addition of corpora allata extract, and they suggested that the site of action of the hormone lies within the citric acid cycle. Stegwee (1960) suggested that this cellular effect of the corpora allata hormone on respiratory metabolism may be achieved between succinate and cytochrome *c*.[5]

These studies have shown that endocrine secretions are able to control metabolic processes in many solitary insects. Unfortunately, few comparable studies have been performed on social Hymenoptera. In view of the evidence presented so far, I suggest that the differences in physiological conditions exhibited by worker ants taken from colonies of *N. nigrescens* during the nomadic and statary phases, result from related disparities in the secretory activity of the corpora allata and associated neuroendocrine glands. To support this hypothesis, I would like to digress for a moment, to discuss some of the existing evidence concerning the hormonal control of egg production in sexually mature female insects.

In addition to its role in regulating metabolism, the corpora allata also control egg maturation in the ovaries of female insects. This effect was first reported by Wigglesworth (1936), from demonstrations that an active corpus allatum is essential for egg maturation to occur in the bug, *Rhodnius prolixus*. Following allatectomy, the growth of the eggs ceases due to the degeneration of the follicle cells. Since then, a similar gonadotrophic effect of the corpora allata has been shown to exist in the grasshopper, *Melanoplus differentialis* (Pfeiffer, 1940), in the cockroaches, *Leucophaea maderae* (Scharrer, 1946; Scharrer and von Harnack, 1958) and *Periplaneta americana* (Bodenstein, 1953), in the bugs, *Oncopeltus fasciatus* (Johansson, 1954) and *Pyrrhocoris apterus* (Sláma, 1964), in the beetle, *Leptinotarsa decemlineata* (deWilde and deBoer, 1961), and in the mosquitoe, *Culex pipiens* (Clements, 1956).

In the doryline species Schneirla (1965) placed in group A by virtue of their regular alternation in behavioral phases, egg laying by the single colony queen usually takes place mid-way through each statary phase. During the last few days of the nomadic phase, the larvae undergo physiological and biochemical changes that lead into their subsequent development as relatively quiescent pupae (which in some species -e.g., *E. hamatum*- are actually enclosed in cocoons).

At this time the high levels of excitation and activity exhibited by the adult workers, have not yet worn off, and they begin to attend to the queen with increasing vigor. At this time the queen is fed intensely and must receive, in addition, excessive amounts of concentrated chemical and chemotactual stimulation. Significantly, in the last few days of the nomadic phase, colony queens of Eciton (Schneirla, 1949; Schneirla and Brown, 1950) and of Neivamyrmex and Aenictus (Schneirla, 1957a) regularly show a distention of the gaster that soon accelerates towards physogastry. By extension of the work cited above, concerning the role of the corpora allata in controlling oocyte maturation, experiments in progress in our laboratory are designed to test the hypothesis that increases in nutritive and chemical products, and in social stimulation at the transition of the nomadic to the statary phases, activates the queen's corpora allata to secrete amounts of gonadotropic hormone that are above the threshold value necessary for the onset of egg maturation. Circumstantial evidence from experiments on other (non-social) insects supports this hypothesis.

First, there are many insects which produce successive gonotrophic cycles of oocytes, and in all cases studied so far, the corpora allata exhibit corresponding fluctuations in secretory activity, as indexed by variations in over-all volume and nuclear size (Highnam, 1964). Furthermore, totally isolated corpora allata do not exhibit such periodicities (Pflugfelder, 1937, Engelmann, 1959). In most insects the corpora allata receive neural connections from both the brain (through the nervi corporis allati) and the subesophageal ganglion. As a result it is expected that these glands are controlled, in turn, by numerous internal and external factors. The hypothesis of internal neural control is supported by the investigations of Engelmann and Lüscher (1956) on the reproductive physiology of the adult female cockroach, Leucophaea maderae. It has also been shown that environmental factors such as temperature, humidity and photoperiod can influence the degree of neurosecretory activity in the Colorado beetle, Leptinotarsa decemlineata (deWilde and Stegwee, 1958, cited in Highnam, 1964).

These studies demonstrate that numerous cases are known for insects in which cyclical fluctuations in neurosecretory activity exist. Unfortunately, more is known concerning the internal regulation of these endocrine glands than about the role of external physical and biotic factors. I have suggested for doryline colony queens belonging to species of the group-A complex, that sensory stimuli affecting many modalities, may play a role in neuroendocrine regulation. I would now like to propose an analogous hypothesis to account for the phase-specific variations in oxygen consumption exhibited by the adult workers of N. nigrescens.

Comparatively little is known about the structure or function of the corpora allata in worker ants. Indirect evidence that they are less active in worker ants than in the reproductive individuals, comes from the investigations of Weyer (1928). He showed that in workers of *Formica rufa* and *Camponotus ligniperda*, the eggs develop somewhat as in the queen, but only up to the stage of yolk deposition; they are then reabsorbed. A direct study of differences in size and activity in the corpora allata from nine species of queen and worker ants was performed by Hultin (1947). He concluded, on the basis of histological preparations, that the volume of the glands in the various castes of the ants studied exhibit considerable individual variation. In the species *Tapinoma erraticum*, the volume of the corpora allata (in proportion to the size of the body) is approximately three times greater in the queen than in the workers.

Since worker ants of most species do not normally lay eggs, it is reasonable to expect that their corpora allata are not as large (or as active) as those found in sexually mature queens. Nevertheless, the workers do possess functional corpora allata. It is therefore entirely possible that fluctuations in levels of neurosecretory activity by the corpora allata may occur in worker ants, even though the concentration of the hormone in the organisms' circulatory system is always below the threshold levels necessary for the completion of egg maturation.

Throughout the nomadic phase, the adult workers of *N. nigrescens* engage in mutual nutritive, chemical, and chemotactual interrelationships with the developing massive larval brood. This social stimulation falls to near zero with the onset of statary conditions as the mature larvae enter the pupal phase of development. This situation in which the workers receive fluctuating, phase-specific intensities of stimulation involving many modalities, is very much like the condition, described above, regulating egg production in the queens. And again the hypothesis is that brood-induced stimulative processes responsible for the maintenance of levels of activity associated with nomadism, have far-reaching effects on numerous physiological and biochemical processes that are regulated by the worker ants' neuroendocrine system. In our laboratory, we are now planning to investigate the relative activity of the corpora allata in workers of _N. nigrescens_, removed from their colonies during the nomadic and statary phases.

Behavioral Studies

Factors Influencing Behavioral Orientation in Insects:

The results of the behavioral tests (described above) indicate that distinct differences may exist in the organization and pattern of processes relating to group raiding, during the nomadic and statary phases. These difference result from variations in the reactions of workers of _N. nigrescens_ to their own pheromones and other chemical secretions. Although variations in patterns of group activities exist in the laboratory testing situation during both behavioral phases, still, the over-all trend of phase-specific differences in behavior, appears to be reliable, especially when we correlate these observations with our field studies of raiding, and bivouacking during the nomadic and statary phases.

Before attempting to account for the observed differences in army-ant behavior in the laboratory, in terms of what we know about variations in developmental, physiological, and behavioral processes associated with maintaining and regulating the regular alternations in phase exhibited by colonies of _N. nigrescens_, I would like to consider some of the existing evidence concerning relationships between internal physiological states and behavioral orientation in insects.

Most biologists no longer consider the behavior of insects as instinctive, in the sense that the organism emerges with an inborn, genetically pre-determined coordination which typically results in behavior that is adaptive for it. Instead, investigators are concentrating increasingly both on developmental processes contributing to the appearance and pattern of behavior during ontogeny, and to the effect of external physical factors and internal physiological states on the organization of behavioral responses in adult organisms. For in order to be complete, behavioral studies must include considerations of the organic setting of the behavior, and of the environmental setting in which it appears (Schneirla, 1953a,b,c).

The responses of all organisms to stimuli of constant physical intensity, are profoundly influenced by numerous external environmental and internal physiological effects. Included in the category of internal effects are the age, sex, nutritional state, and physiological condition of the organism. Moreover, these variations in behavioral responses occur not only in organisms possessing well-developed nervous systems, for some of the earliest experiments demonstrating the influence of temperature on orientation with respect to a source of light, were performed using acellular flagellates (Mast, 1911). In a more recent study on Hydra pirardi (Rushforth, 1964), it was shown that the presence of a food source (or of its chemical extract) in the medium can inhibit the contractions normally caused by mechanically stimulating the organism.

For insects, considerable evidence also exists that external temperatures can influence phototactic responses. Working with the waterscorpion, Ranatra, Holmes (1905) showed that high temperatures produce a positive phototactic response, while low temperatures make the animal photonegative. After numerous experiments in which he altered other environmental parameters as well, he concluded that any circumstances which reduce the excitability of an organism, tend to produce a negative response to light. In a similar manner, the positive light reaction of the mayfly nymph, Epeorus is also shifted by decreasing temperatures (Allee and Stein, 1918). Comparable studies, demonstrating that temperature critically influences behavioral responses to stimulation by light, have been performed using the drone fly, Eristalis tenax (Dolley and Golden, 1947; Dolley and White, 1951), the beetles Blastophagus piniperda (Perttunen, 1958, 1959, 1960) and Trypodendron lineatum (Graham, 1959; Francia and Graham, 1967), and the mosquitoes Aedes japonicus and Culex pipiens (Chiba, 1967a,b).

Temperature is not the only environmental factor that can modify an organism's response to photic stimulation. In the mealworm, Tenebrio molitor, the organism's characteristic photonegative response shifts to positive under conditions of severe desiccation (Perttunen and Lahermaa, 1958). The adult beetle, Trypodendron lineatum is photonegative at 100 percent relative humidity, but when the humidity decreases to 34 percent, it reacts indifferently towards light. Finally, as desiccation continues the beetle becomes photopositive (Pulliainen, 1965). Relative humidity has also been shown to interfere with phototactic orientation in the flour beetle, Tribolium castaneum (Amos and Waterhouse, 1967), and in the beetles, Meligethes aeneus (Pulliainen, 1964a) and Myrrha 18-guttata (Pulliainen, 1964b).

These investigations clearly show, for a variety of insects and related groups, that changes in behavioral orientation with respect to photic stimulation, can be produced by varying any one of numerous physical parameters in the external physical environment of organisms. As a result, these studies demonstrate the importance of considering the ecological situation in which a particular behavior pattern appears. But none of these studies have considered how such physical factors act to modify the organisms' internal physiological condition, and how processes of neural integration mediate between these intraorganic states and the observed shifts in phototactic orientation. At this stage all we can say is that, with very few exceptions, any environmental agent that either reduces over-all activity in organisms or lowers their metabolic rate, tends to increase their negative photoreactivity. As an example, mayfly nymphs are normally photonegative, but approximately 20 percent of the nymphs taken from any population tend to be more photopositive. Allee and Stein (1918) have shown that the photopositive nymphs exhibit higher levels of carbon dioxide production. Similarly, in the studies concerning effects of temperature on behavioral orientation towards light stimulation (described above), the possibility exists that shifts in sign of the phototactic responses, are caused by corresponding increases and decreases in over-all metabolism.

Changes in internal physiological condition are not caused by the effects of such environmental factors as temperature and humidity alone. During development, in all insects, processes associated with growth and maturation result in continuous variations in hormonal and other physiological states that could also influence behavioral orientation. The newly hatched larva of the hawk moth, *Smerinthus ocellata* is strongly photopositive (Beetsma *et al.*, 1962), but just prior to pupation, the mature larvae become increasingly photonegative. These investigators also showed that injections of the hormone ecdysone, extracted from the prothoracic glands of *Locusta migratoria*, could induce this photonegative reaction. Immature larval tabanid flies are relatively indifferent to stimulation by light, but when they are mature they also become intensely photonegative (Shamsuddin, 1966). Even within a single larval instar, alterations in photoreactivity have been described. Thus, the response of the milkweed bug, *Oncopeltus fasciatus* to light undergoes a shift in sign within the fifth instar (Barrett and Chiang, 1967), and a comparable effect has been reported for the hawk moth, *Smerinthus ocellata* (de Ruiter and van der Horn, 1957).

Still other shifts in photic orientation have been recorded, in relation to variations in intraorganic physiological conditions. Mosquitoes are normally activated at dusk by decreasing light intensities, and they respond by moving towards the evening light. But when they are rendered wingless, the resulting physiological changes act to maintain their negative photoreactivity until after dusk (Rao, 1947). Dolley and Golden (1947) have shown that physiological differences associated with sexual dimorphism in the drone fly, *Eristalis tenax* interact with the effects of temperature to modify behavioral orientation differently in the male and in the female. Finally, Wheeler (1933) has shown that physiological changes associated with mating and wing loss in queen ants result in an increased negative photoreactivity.

All of the studies described so far, deal with the interrelationships between environmental and physiological factors, as they regulate insects' behavioral orientation with respect to stimulation by light. This aspect was emphasized, because the behavioral studies of this investigation have shown that photic stimulation markedly affects certain aspects of group behavior in workers of *N. nigrescens*. But these studies also demonstrate that chemical stimuli may play an even more important role in the organization of these group processes. Therefore, I would now like to consider some of the evidence concerning environmental and physiological regulation of orientation towards chemical stimuli.

The study of insect chemoreception has been the subject of numerous thorough reviews (Dethier, 1953; Hodgson, 1964). Unfortunately, as with much of the research on visual orientation, these treatments usually emphasize peripheral discriminatory mechanisms. But as is the case for light, olfactory thresholds of response may also be profoundly influenced by environmental and internal physiological factors.

In relation to the present investigation, which indicates that workers of N. nigrescens may respond quite differently to their own chemical secretions or trails, depending upon their physiological state, the most significant correlative evidence in an insect has been provided by Goldsmid (1967) through his studies on the behavior of the blue tick, Boophilus decoloratus. Newly hatched tick larvae exhibit a strong negative reaction towards light. At this developmental stage, however, they also tend to aggregate together in clusters, and this clustering tendency overrides the individuals' negative response towards light. If the cluster is mechanically broken and the larvae scattered within their container, they frequently reaggregate in approximately the same position. After one week, changing physiological conditions associated with larval maturation, eliminate the tendency to aggregate, and at this time the larvae also become markedly photopositive.

Other groups of insects also aggregate together as their physiological condition changes. In the ant, Oecophylla smaragdina, the workers cluster together in response to decreasing temperatures (Gupta, 1966). In this case, the author suggested that the response in question might be due to the presence of a pheromone. Another instance of mass aggregation occurs in several acridid locust species, in which such environmental parameters as the degree of crowding during early development, can affect physiological and endocrinological aspects of growth, leading to either the "solitaria" or "gregaria" phase. For these locusts, Ellis (1956, 1962) has shown that phase-specific differences exist in their responses to the presence of conspecific individuals. A similar form of aggregation occurs in nymphs of the African grasshopper, *Phymateus purpurascens* (Rowell, 1967). As the nymphs mature, the aggregations break-up due to physiological processes which result in asynchronous molting cycles.

Behavioral Differences in N. nigrescens During the Nomadic and Statary Phases as Related to Corresponding Changes in Physiological Conditions:

Having presented evidence that thresholds of responses in insects, to light and chemical stimuli, are not innately fixed, but are highly variable, depending upon the organisms' physiological condition (as it, in turn, is regulated both by external ecological factors, and internal events related to its sex, nutritional state, and developmental stage), we are now in a position to return to the dorylines.

On most nights during any nomadic phase, workers of N. nigrescens are often out of the bivouac for long periods, taking part in the massive raids that typically occur during this phase. The workers are highly excited and extremely active, a condition which usually results in the formation of foraging columns consisting of numerous branching trails (Schneirla, 1958, 1961). In the behavioral tests conducted in the laboratory during this phase, workers of this species correspondingly are also very active, both in the "bright-dim" test and in the control test (under conditions of almost total darkness). On evenings when levels of worker excitation are particularly high, as when a callow brood emerges at the beginning of the nomadic phase, the ants may even spend much time in the brightly-illuminated arena quadrants. Also, during the nomadic phase, the columns in the cartridge and arena quadrants are relatively dispersed, with the ants continually running along their chemical trails (throughout the two-minute testing period).

As one outcome of this investigation, a reasonable hypothesis can be proposed to relate the behavior of the ants in the laboratory test situation with their behavior in the field during the nomadic phase. It is well known for N. nigrescens (Schneirla, 1958) that the nomadic phase is initiated by intense social, chemical, and chemotactual stimulation, resulting from interactions between the adult workers and a callow brood (consisting of over 40,000 individuals) that ecloses within a very short interval (occasionally one day only, as found in the present study). As the callows mature, nomadic activities are maintained by equivalent stimulation derived from a developing larval brood. The results of the present investigation suggest that increases in worker excitation and activity are accompanied by more fundamental physiological changes, which persist when the workers are removed from the colony and tested in the laboratory. Schneirla (1957a), on an empirical basis, termed this a metabolic trace effect. It appears likely that the increased metabolic condition of the workers during the nomadic phase, influences their reactions to light and to chemical stimuli. Under the conditions of this experiment the workers are only slightly less sensitive to light during the nomadic phase. But their response thresholds to chemicals secreted by other workers (and perhaps by the brood and queen as well) seem to be distinctly increased, as there is little tendency for groups of workers, confined in the laboratory test chambers, to remain together.

At the end of the nomadic phase, the larval brood completes its development and begins to pupate, resulting in a sharp decline in the quantity of stimulation imparted to the adult workers. In the field the most noticeable effect associated with the onset of statary conditions is that the intensity of surface raiding is greatly reduced (or absent together). The workers spend considerably more time in the statary bivouac, and raiding during this phase, when it occurs, begins later in the evening than during the nomadic phase. In the laboratory workers of _N. nigrescens_ have a tendency to remain closely associated in clustered groups, and this tendency often overrides their individual negative photoreactivity. Since the physiological tests (described above) have shown that levels of worker activity metabolism are significantly lower during the statary phase, it is likely that the decrease in thresholds of olfactory responses exhibited by the workers is related to their lower metabolic condition. To illustrate this compare the photographic series, representing a behavioral test conducted on colony '65 N-V during the statary phase (fig. 27), with the description, given above, of phototactic and chemotactic orientation in the blue tick as a function of phasic behavioral development (Goldsmid, 1967). In both the tick and the army-ants, specific physiological conditions are correlated with distinct differences in thresholds of olfactory responses to other individuals in the group. The early instars of the tick, characterized by decreased larval activity, an intense photonegativity, and a strong tendency to cluster (which overrides their individual photonegativity), may be considered analagous to the statary phase in _N. nigrescens_, in which worker activity is low, in which the ants are strongly photonegative, and in which there is a strong tendency to cluster (which also can override their individual photonegativity). Similarly, the later instars of the tick, characterized by increased levels of larval activity, a positive phototactic response, and no tendency to cluster, may be considered analagous to the doryline nomadic phase, which is similarly characterized by increased worker activity, a slightly less photonegative reaction, and no tendency to cluster.

In the army-ants, as in the blue tick, phasic processes are accompanied by corresponding sharp fluctuations in over-all metabolic conditions in the colony. In the tick, these phases have been represented by larval individuals selected from the beginning and end of this growth stage, and as such they represent extreme points of an intraorganic physiological continuum, associated with the normal sequence of development. In the army-ants, by contrast, even though phase alternations are also associated with significant differences in levels of metabolic processes, in this case phase-specific physiological conditions are activated by stimulation originating from sources external to the workers, namely the callow and larval broods.

Footnotes

[3] Working in connection with this project, as a participant in the Museum of Natural History's undergraduate research program, Miss Rona Lieberman computed allometric relationships between the width of the head across the eyes and tibial length, in samples from a colony of E. hamatum. Using a double logarithmic plot she found the pupal and adult regression coefficients almost identical. Thus, for the pupae $k_1 = 0.5$ and $k_2 = 3.5$; for the adults $k_1 = 0.5$ and $k_2 = 3.2$.

[4] The control of yolk formation and egg maturation by the corpora allata was first demonstrated by Wigglesworth (1936) in Rhodnius prolixus. It has subsequently been confirmed in many other insects (Novák, 1966). If it is found that egg series from Aenictus queens do have reduced quantities of yolk, this also could be explained as due to a different set of relationships between hormonal levels and reproductive processes in the queens.

[5] An unrelated but very important consideration of the direct effects of neurosecretion on metabolism at the cellular level, involves cycles of molting in the crayfish. These animals exhibit a distinct molt cycle which is correlated with many other cyclical phenomena, including oxygen consumption. McWhinnie and Kirchenberg (1962),

McWhinnie and Chua (1964), and McWhinnie and Corkill (1964) demonstrated reciprocal variations in levels of activity of the Embden-Meyerhoff and hexose-monophosphate shunt during the intermolt and premolt periods. Significantly, these investigators were able also to demonstrate by reciprocal injection experiments that extracts from the eye-stalks influence the cyclical variation in activity of the two oxidative pathways.

GENERAL DISCUSSIONS

Species of ants in the subfamily Dorylinae all possess an almost strictly carnivorous way of life, based upon group foraging activities. Throughout the subfamily, these group activities exist within adaptive patterns of cyclic colony functions that have been characteristically modified or specialized in the various doryline species. But in all species that have been studied so far, these cyclic functions (both the regular phase alternations of species in the group-A complex, and the irregular rhythmic colony activities characteristic of species in group B) appear to be based on colony arousal mechanisms resulting from intracolony reproductive and nutritional processes (Schneirla, 1957a,b; 1968).

The present investigation has attempted to determine how intracolony morphological, physiological, and behavioral factors interact with aspects of the external environoment, to sustain and regulate the behavioral phases characteristic of doryline functional cycles.

In N. nigrescens, for example, the regular alternations of nomadic and statary phases are accompanied by correlative events within the colony, and in the relationship between the colony and its physical environment. As the primary colony "energizer," the larval and callow broods enter into intensive trophallactic relationships with the adult worker population. The response of the worker population to the resulting chemical and chemotactual stimulation is abrupt and manifest. From the onset of the nomadic phase, the workers exhibit highly increased levels of activity and excitement, and in the laboratory, groups of worker ants exhibit significantly higher levels of oxygen uptake. A logical question that arises from this part of the study is: during the nomadic phase, is this increase in the level of oxygen consumption due to the ants' increased activity, or does their increased activity result from more fundamental changes in their physiological condition? The results of this study support the latter alternative, which we have now formulated into a testable hypothesis concerning the possible role of endocrinological and other physiological factors in maintaining increased levels of metabolism exhibited by the worker ants during the nomadic phase.

In addition to these differences in activity metabolism, this study has shown how thresholds of responses to light and especially to chemical stimuli, also change significantly during the two phases of the functional cycle.

It must be remembered, that as members of a social insect colony, the workers of *N. nigrescens* tend to remain together in response to their nest situation and to other individuals in the group. The group, in turn, possesses certain stimulative properties which affect individual behavior and provide a basis for all interrelated activities in the colony. Schneirla (1952) has pointed out that the collective population in its organic and environmental setting creates certain physico-chemical conditions to which all individuals in the population are aroused and controlled. But the magnitude of this arousal and control is certainly not invarient. In fact, both the physico-chemical environment existing in the bivouac, and the reactions of the adult workers to them, change continually throughout both behavioral phases. We have already seen how the workers respond to each other in the laboratory tests during the nomadic and statary phases, and I have attempted to interpret these phase-specific differences in group activities related to raiding and trail following, in terms of corresponding changes in physiological conditions resulting from brood stimulation.

Although the hypothesis, relating metabolic levels in the workers to corresponding shifts in their response thresholds to physical and biotic stimuli, is clear, still we do not know how these alterations in worker physiological conditions operate neurophysiologically, to produce changes in photic and olfactory sensitivity in them. The insect central nervous system can integrate afferent impulses from peripheral receptors on various parts of the body, with impulses arising from enteroceptors which continually monitor the individual's internal physiological condition. But in only a few instances is the neurophysiological basis of these processes understood.

The outstanding example of studies concerning the neurophysiological basis of sensory integration involving peripheral olfactory receptors and enteroceptors, comes from the work of Dethier and Bodenstein (1958) on the regulation of feeding in the blow fly. In this insect, the threshold of response to food is regulated by information originating in the foregut and passing by way of the recurrent nerve to the brain, where it inhibits the effect of sensory input from the oral receptors.

Information also exists concerning the neurophysiological basis of sensory integration involving peripheral modalities. Huber (1965) has shown that the male cricket, _Gryllus campestris_ exhibits a withdrawal response to mechanical stimulation of the cerci. But this response varies in threshold, and often disappears completely during sexual activity. On the basis of electrophysiological recordings, Huber concluded that impulses from the brain can inhibit impulses from the cerci, and that this inhibition takes place at the synapse between the abdominal giant fiber and the metathoracic ganglion.

At this stage of our investigations we do not know which integrative processes are operating in the dorylines. From the two cases cited above on other insects, it is clear that sensory integration, resulting in drastically altered thresholds of responses to stimuli, can occur at many levels, and it is possible that many such processes are in operation in the dorylines.

Throughout the present investigation, two aspects of doryline colony functions have been emphasized. I have considered physiological conditions of groups of worker ants, in relation to behavioral differences during the nomadic and statary phases. I have also considered the behavior of groups of ants in relation to phase-specific differences in their physiological condition.

In both the physiological and the behavioral tests, this investigation has emphasized observations and measurements of groups of worker ants. But the morphological structures of the populations we have observed in the field and tested in the laboratory, indicate that individual differences in behavior and physiology are probably very important in their contributions to over-all group processes. The morphological structure of a polymorphic population such as _N. nigrescens_, for example, suggests that we must also consider caste-specific differences in physiology and behavior throughout the size range of the worker series, within the nomadic or statary phase, as well as differences exhibited by the workers of all size groups between one phase and the other. Thus, if individual worker ants had been used in the behavioral tests, the results probably would have been quite different. The results of the behavioral tests indicate that sensitivity to light in individual workers, increases sharply during the statary phase; but in the group situation, the individual worker's response to the light itself often is not expressed, due to a correlative increase in her sensitivity to chemical stimuli produced by other ants in the test chambers.

The contributions of individual physiology and behavior to the regulation of cyclic behavior in a worker group, are also probably very different in such polymorphic species as E. hamatum and N. neivamyrmex, from such quasi-monomorphic species as A. laeviceps. I have also discussed relationships between structure and function in ant populations, and their contribution to colony organization in polymorphic and monomorphic species, and Schneirla and Reyes (1966) have shown specifically how uniform worker sizes result in less complex integrative processes in species of Aenictus. The profound differences in caste structure exhibited by N. nigrescens, E. hamatum, and A. laeviceps, are providing the groundwork for continued investigations in our laboratory, as we are now considering individual behavior and development as related to social integrative processes within the colony situation. Specifically, we are interested in knowing the extent to which worker sensitivity to intracolony chemical stimuli is correlated with morphological specialization. Also, we hope to determine whether caste-specific behavioral differences in the adult workers, are accompanied by corresponding differences in their appearance during the period of callow maturation.

The present investigation, together with the results of investigations carried on in our doryline laboratory for many years, have made it clear that developmental and cross-sectional studies concerning the relationships between structure, physiology, and behavior are essential for a more complete understanding of the functioning of populations of doryline ants.

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