

A NEW INTERPRETATION OF THE FREQUENCY CURVES ASSOCIATED WITH ANT POLYMORPHISM

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It is the purpose of the present paper to demonstrate that the distinctive size-frequency curves associated with the successive phylogenetic stages of ant polymorphism can be interpreted as the outcome of various degrees of divergence of two larval groups past a critical point in larval development. Also, it is proposed that the curves associated with the more elementary stages of polymorphism may be a simple function of larval competition. This concept has been derived principally from circumstantial evidence, and from the outset the writer freely admits that it represents but one of several explanations possible. The reason for discussing it now in its unproven form is that it brings to emphasis a little-known aspect of caste determination which must be carefully considered in the early years of experimental study ahead.

Worker polymorphism in ants arises phylogenetically by an extension of intranidal size variability sufficient to allow the expression of adult allometry (WILSON, 1953 *a*). The lower limits of polymorphism must therefore be expressed in terms of allometry alone and not polymodality of the size-frequency curve, as previously believed by many myrmecologists. At the same time changes in the frequency curve typically accompany changes in the allometric regression line, and in advanced stages of polymorphism the two conditions are closely correlated. The most widespread elementary stage of polymorphism is characterized by the allometric regression line having a single slope (termed "monophasic allometry" in the above publication) and the size-frequency curve being bimodal, with the two constituent curves broadly overlapping to form a distinctive asymmetrical figure (fig. 1A-center). Evolution in the frequency curve proceeds from this stage to complete dimorphism by a progressive separation of the two constituent curves and a final elimination of the intermediates.

The bimodal frequency curve would seem to be most simply and adequately interpreted as expressing two diverging groups of individuals. If a mathematical model were to be drawn consisting of two broadly overlapping frequency distributions, one larger than the other, the asymmetrical curve of figure 1A-center would be obtained. The gaps between the two curves would be filled, of course, by the summation of the overlapping

frequencies. If the two curves were now to be pulled gradually apart, the intermediate summation would rapidly decrease, and we would obtain after successive intervals the equivalence of the several phylogenetic stages connecting simple polymorphism and complete dimorphism. In terms of frequency distribution alone, we might conceive of caste determination as follows: there is a critical point, or zone, in larval development at which individual larvae embark on one or the other of two developmental

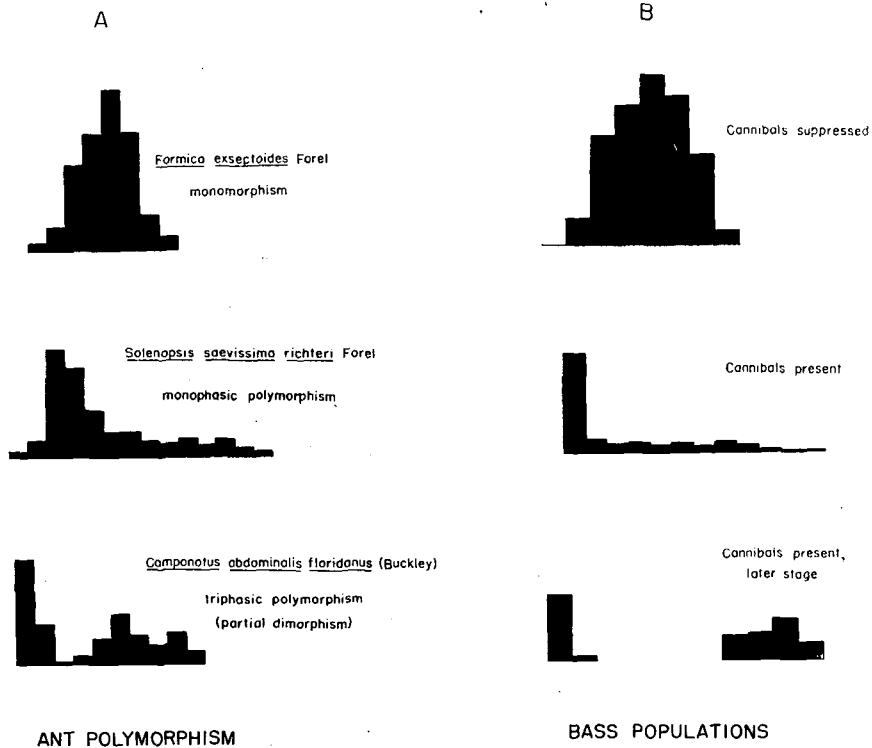


Fig. 1. — A, frequency curves associated with polymorphism in single colonies of three species of ants. B, frequency curves of populations of small-mouth bass, with and without cannibals (data from LANGLOIS, 1936).

pathways, which pathways may be distinguished by a feature as simple as a certain speed of development. It is obvious that the degree of divergence following the critical point, i. e., the degree to which the two resultant groups of larvae separate, will depend on the length of the growing period between the critical point and pupation and on how rapidly the two pathways diverge. It is theoretically feasible that the changes in frequency distribution which occur in the phylogenetic development of polymorphism can be explained entirely by one or both of two processes connected with the critical point of development: either the degree of divergence of the developmental pathways increases progressively after the critical point has been fixed in the larval life history, or the critical point

retrogresses away from the onset of pupal development back through larval life, or both. I have represented the first alternative in figure 2. Here the two developmental pathways increasingly diverge from a fixed critical point, resulting finally in a separation of the two size groups (complete dimorphism). I believe this particular scheme is favored by the very sparse data on larval development which is at our present disposal. FALCONER SMITH (1944) on *Camponotus* sens. str. and T. C. SCHNEIRLA (unpublished; personal communication) on *Eciton* have found evidences of an early divergence in these primitively polymorphic groups; the larger larvae in young broods tend to end their larval development larger, and in *Eciton* this may be associated with varying specific-growth-rates of the

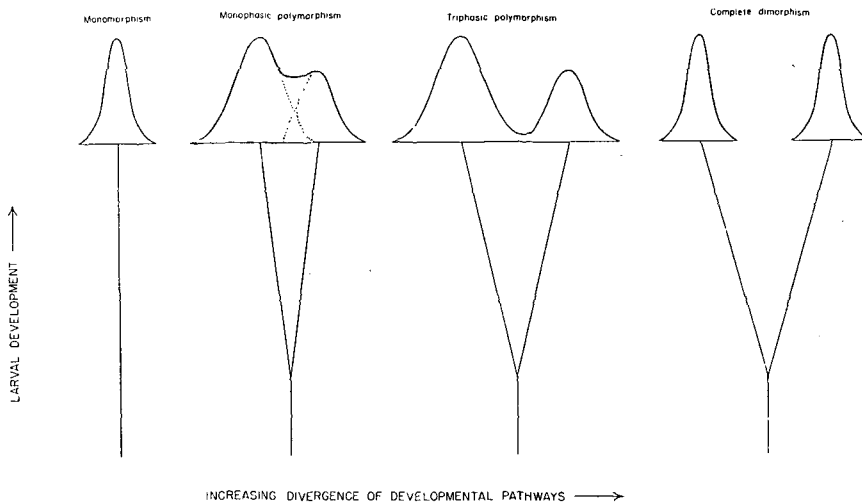


Fig. 2. — Hypothetical course of evolution of the polymorphism frequency curves. In larval development, the critical point appears in monophasic polymorphism, and evolution proceeds by a progressive increase in the divergence of the developmental pathways beyond the critical point. The resultant ideal frequency curves are shown above at the end of larval development.

limb imaginal discs. LEDOUX (1950) reports divergence of major and minor larvæ as early as the second instar in the partially dimorphic *Oecophylla longinoda*, and BRIAN (1952) has established the critical point of queen-worker divergence in *Myrmica rubra* as far back as the early part of the terminal instar, seeming to leave open the possibility of even earlier divergence with the statement, "Larger hibernating larvae tend to achieve this (queen path) more often than smaller ones in spite of the fact that they begin at a later stage of development." FLANDERS (1953) has proposed that the critical point exists at some period of embryonic development, but as I have shown elsewhere (WILSON, 1953 b), FLANDERS is most probably thinking only in terms of complete dimorphism and has no reasonable evidence, circumstantial or otherwise, with which to support his views as far as ants are concerned. Actually, existing experimental data oppose his hypothesis.

Whether the critical point is actually established primitively in early larval life or whether it is progressively pushed back remains to be seen. The important point made here is that the demonstrations of a simple mechanism involving one or both of these processes could explain fully the shape of the frequency curves associated with all of the known phylogenetic stages of polymorphism.

We are now in a position to consider the proposition that the frequency curves of elementary stages of polymorphism may be the outcome of direct larval competition. Specifically, the critical point may be nothing more than that stage of development at which a small group of larger larvae take the lead over their sisters and begin to pull away by virtue of their greater attraction to the adult nurses. An excellent analogy is provided by the case of the small-mouth bass *Micropterus dolomieu* (LACEPEDE) under rearing pond conditions as reported by LANGLOIS (1936). Fry placed in individual rearing ponds numbered up to 20,000 and were initially all about the same size and age. At first the entire population of a single pond swam in a closely knit school, but this tended to break up with growth and increased activity. As the entomostracan food supply diminished relative to the bulk of fish, certain larger individuals departed from the open water aggregation, stationed themselves in concealed niches around the pond margin, and began to feed on the remaining school fish. From this period on the cannibals rapidly diverged in their growth from the smaller open-water individuals. The frequency curves based on entire pond populations through the remainder of the growing period show a progressively marked bimodality strikingly similar to that seen in the phylogenetic development of ant polymorphism (fig. 1B). Populations in which cannibalism was prevented remained unimodal throughout the growing period.

The increasing bimodality of the bass curves resulted not from intrinsic growth difference between the two groups, but rather from the ability of certain larger individuals to accelerate their own growth at the expense of their fellows. In short, they acquired a food supply not available to the smaller fish. The act of cannibalism is itself of little concern in this relationship except that it provided the new food source; it obviously had no deleterious effect on the smaller individuals which escaped being eaten. The same type of opportunism may occur in ant broods. Certain larger larvae may attract the attention of their nurses enough to accelerate their own growth; the larger they become, the more attention they attract, and vice versa, resulting in an "autocatalytic" impetus to growth. The fact that worker ants often tend to segregate larvae of different sizes would no doubt contribute heavily to this process.

Larval competition has the greatest chance of being important in the more elementary stages of polymorphism, including monophasic and diphasic allometry (cf. WILSON, 1953 *a*). In triphasic allometry and complete dimorphism there is such a marked disparity between the castes, and such close correlation of the frequency curves with the allometry

curves, that it is almost necessary to assume that some sort of intrinsic physiological regulation is acquired at the critical point and operates past it. In addition, it seems doubtful that under conditions of competition alone the two constituent frequency curves would ever separate completely; in the bass the intermediates were presumably eliminated by the action of the cannibals.

There is one outstanding potential discrepancy in the foregoing comparison of bass and ants, but it is a discrepancy which stands a good chance of being resolved so completely as to actually contribute to the theory. This is the fact that the bass populations developed from individuals of the same age and initially of the same approximate size, whereas ant larvae are presumably hatched from eggs laid over a long period of time by the queen. It is reasonable to assume that if the ant larvae are of completely heterogeneous ages and if the frequency pattern is dependent on larval competition, a well-ordered bimodality will rarely or never emerge. Seemingly it could emerge only if there were some periodicity in oviposition—at least enough to separate the successive broods of larvae by a time gap amounting to a good part of the period of larval development. Such an ovipository cycle has been recorded in *Eciton* by SCHNEIRLA (1944), in *Myrmica* by BRIAN (1953), and in a small colony of *Lasius sittaensis* Pérg. by the present writer (unpublished), but virtually nothing is known about the majority of groups which show polymorphism at the level of monophasic and diphasic allometry.

Despite this lack of direct evidence, one generalization can be made about the reproduction of groups showing *elementary* polymorphism which may have utmost significance with respect to the question of ovipository periodicity: *these groups as a rule are characterized by monogyny*. The presence of a single nest queen does not necessarily result in periodicity, but it may greatly facilitate it. Examples of monogynous polymorphic groups include sections of *Myrmecia*, all of the *Dorylinæ*, *Pogonomyrmex*, *Atta*, *Solenopsis* s. str., *Melophorus*, *Myrmecocystus* and most *Camponotus*. Conversely, the groups which show marked polygyny, often associated with colony fusion, are nearly always, monomorphic or (infrequently) completely dimorphic.

Examples include *Ponera*, *Leptothorax*, *Meranoplus*, *Crematogaster*, *Iridomyrmex*, and many others. It is also noteworthy that within the genus *Monomorium* the well-known polygynous species are monomorphic (e. g., *floricola*, *minimum*, *pharaonis*, *viridum*), while in the genus *Camponotus* the one species known to us to be greatly polygynous, *Camponotus (Colobopsis) vitreus* F. SMITH, is completely dimorphic (*teste* W. L. BROWN). This relationship of simple polymorphism and monogyny seems too close to be due to chance alone, and the inference made here is that monogyny may be part of an ovipository regulating mechanism underlying the incipient bimodal frequency dispersion of castes.

Summary.

The frequency curves characterizing all stages in the phylogenetic development of ant polymorphism can be interpreted most simply on the basis of divergence of two size groups of larvae beyond a critical point in larval development. The degree of divergence, and with it the decrease of the medias, depends on the amount of development, or the rate of divergence, following the critical point. The frequency curves characterizing the more elementary stages of polymorphism can be explained on the basis of simple competition among larvae, providing that a fair degree of ovipository periodicity obtains. This interpretation is at present supported principally by inconclusive circumstantial evidence, and it is admitted that other explanations may be found to hold equally well.

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Le Gérant : GEORGES MASSON

Published in France

Dépôt légal 1954. - 1^{er} Trimestre - N° d'ordre : 1885 - Masson et C^{ie} Éditeurs, Paris.

Imprimé par l'Imprimerie CRÉTÉ, Corbeil-Essonnes (Seine-et-Oise), France.

Dépôt légal 1954 - 1^{er} Trimestre - N° d'ordre : 4391.