

Insect sociometry, a field in search of data

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Summary

The study of social insects has proceeded without adequate descriptive data on social insect attributes. The term “sociometry” is proposed for the collection and analysis of the physical and numerical attributes of social insect colonies and their inhabitants. Sociometry can be seen as having 3 levels – the compilation of data, the distribution patterns of the attributes among species (comparative studies), and the detection of relationships of the attributes to each other. Many sociometric attributes may be linked, hence evolve under constraint from other attributes. The study of social insects would benefit greatly through the organized collection of sociometric data.

Introduction

I have become convinced that we social insect researchers have “skipped a grade” in our studies of social insects. While many fields develop first through a descriptive stage before proceeding to more theoretical levels, the study of social insects seems not to have tarried long enough in this descriptive stage. We seem to have become so fascinated with what controls the machine, that we have failed to draw adequate blue-prints. As a result, not only are a lot of data on basic attributes of social insects simply not available, but we are probably missing critical relationships among these attributes and are devising unrealistic schemes of social insect evolution.

For purposes of focusing and identifying the discussion, I am applying the term “sociometry” to describe the field to which I wish to draw attention. The word has been used by sociologists in relation to human society, but has no present currency in biology. “Insect Sociometry” can be defined as the collection and analysis of the physical and numerical attributes of social insect colonies and their inhabitants. I see the field as having three levels – the compilation of data, the distribution patterns of attributes among species (comparative studies), and the detection of relationships of the attributes to each other.

Compilation of descriptive data: the first level of sociometry:

We are accustomed to the descriptions of individual insects. They consist of a list of physical and numerical characters – almost anything we can count, measure or

describe. The sum of those characters and their variation among conspecific individuals amounts to a species description.

Among social insects, not only can individuals be described in the classic way, but the colonies in which they live must also be characterized by a variety of physical and numerical attributes. These colony attributes are as much characters of each social species as are the individual attributes. Thus, an insect colony has a "somatic size" measurable as total biomass, together with the number of workers, queens, brood and sexuals; it has a lifespan, a rate of turnover of the components of its "soma"; it grows to a characteristic size in a characteristic period of time, and begins to reproduce by emitting sexuals of certain sizes in certain numbers at a certain time in its life cycle. The individual components of the colony, the queen, workers, alates and brood, can also be described by physical and numerical attributes. Table 1 lists examples of sociometric data. The list is not exhaustive, though collecting the data could be exhausting.

Comparative studies: the second level of sociometry:

Once compiled, such sociometric data can be used in comparative studies to determine the evolution and distribution of each particular sociometric attribute across social insect species. Unfortunately, such comparative studies have often languished or been arrested at theorizing because of a lack of data. For example, knowledge of queen number during the stages of the colony life cycle is so fragmentary as to hamper understanding of the factors affecting queen number (Hölldobler and Wilson, 1977). Little is known about the number of times sexual social insects mate, though this is a subject of obvious interest to genetics (Cole, 1983). Data on colony growth rates, sizes at first reproduction and maximum sizes are scarce, yet studies of population dynamics must be founded on them. Adaptive demography has received theoretical attention as a subject of importance (Oster and Wilson, 1978), yet we have very few data on the life spans of colony members, let alone colonies as a whole. We theorize about territory (Hölldobler and Lumsden, 1980), but we have only a handful of estimates of territory size, and even these are usually not related to a colony census. We talk about investment in sexuals, yet there are almost no data on the fraction of colony production invested in sexuals, let alone the relation of this investment to colony size. And so on it goes.

So far, I am just arguing that we don't have adequate descriptions of the colony-level attributes even of much studied social insects, and that such data are necessary for a full species description as well as comparative studies among species. The next level of analysis of these data, however, is likely to raise more pulse rates.

Linkages among attributes: the third level of sociometry:

For an individual insect, morphometric analysis explores the relationships among measures and attributes. Through such an analysis, insect morphometry has established a number of linkages among parts that amount to rules of how insects grow

Table 1. Examples of primary sociometric data

<i>Colony</i>	<i>Nest and Territory</i>
Size at maturity (no. workers, biomass)	Territory size and type
Time and size to 1st reproduction	Foraging distance (mean, S.D., max.)
Time and size to maximum size	Usable nest area or volume
Longevity or population turnover	nest type and location
Mode of founding (claustral, fission, budding, etc.)	<i>Brood</i>
Numbers of minims produced during founding	Number and caste (regressed vs. colony size)
	Size by caste and instar
	Rate and development (specify)
<i>Workers</i>	<i>Alates</i>
Size and size-variation relative to colony size	Size
Size of minims (if present)	Number (regressed vs. colony size)
Allometry (size/shape relationships)	Body composition (% fat, protein, carbohydrate)
Life span (regressed vs. body size, if applicable)	Sperm per male
Turnover rate (%/day)	Number mating flights per year (mean, S.D.)
Production rate (regressed vs. colony size)	No. sexuals released/flight (mean, S.D.)
Number of ovarioles	Total production by sex (regressed vs. colony size)
Egg-laying rate (conditions)	
<i>Queen (King)</i>	
Size	
Life span	
Number at founding	
% weight lost during founding	
Number at colony maturity	
Egg-laying rate (maximum, or regressed vs. colony size)	
Number and length of ovarioles	
Number males mating with queen	
Initial number of sperm in spermatheca	
Egg size	

and change shape, both within a single life cycle and during evolution of taxa (Huxley, 1932). Equally important, it has established a set of constraints on what development and evolution can produce, and has linked a large number of characters to one another. Growth gradients and allometric growth tell us that body parts often cannot evolve changes of size or shape completely independently of others (for an example from ants, see Franks and Norris, 1987). They are linked by the rules of growth.

Returning to social insects, we can perform similar analyses of the relationship of each attribute to other such attributes (hence the analogous term "sociometry"). Generally, colony attributes are discussed as though evolution acted to change them one at a time, independently of other attributes. But what if, in a fashion analogous to the morphometric linkages seen in individual insects, some of the attributes of social insects and their colonies are *linked* by the rules of "sociometry". What if a change evolving in one character necessarily resulted in changes in other social

attributes? In other words, what if there are *constraints* on the combinations of attributes evolution can produce in insect societies?

In fact, there is evidence that this is so, as a few examples will show. Worker size has been considered an important ecological characteristic of ant colonies (Davidson, 1977), and it has been suggested that niche separation in sympatric desert ant species is based partly on worker size. But if evolution acted to change worker size, a number of other important ecological attributes would necessarily change as well. Most important of these is colony size. Larger body size is correlated to greater longevity in a wide array of animals (Peters, 1983). Large workers of the polymorphic fire ant, *Solenopsis invicta*, live longer than do smaller ones. It seems reasonable to expect this to be true across other species of ants as well. In fact, though the data are skimpy and hard to compare because temperature is rarely specified, there is a tendency for larger ant species to have greater life spans than smaller ones. Our newly evolved larger workers would thus live longer, resulting in a lower worker turnover rate. Even though the queen's fecundity remained constant, the decreased turnover of workers would cause the colony's size to increase, with whatever ecological consequences this might have. One obvious one is an increase in territory size, and a decrease in colony density. Basic to all these is the size-relatedness of the individual's metabolic rate, though I hesitate to include it under the heading sociometry.

As another example, let us assume that a colony evolves to a larger size. We have already seen that producing larger workers is one way to achieve this. Can workers evolve greater longevity without increasing body size? Probably, but the increase may be limited. Data are not available. The most obvious manner in which to increase colony size is an increase in queen fecundity (egg-laying rate). But not even this is a single character; to a limited extent fecundity can be increased by speeding the movement of eggs down the ovarioles, probably resulting in smaller eggs (Tschinkel, 1988a). Does egg size affect worker size? There is certainly a clear negative correlation between egg size and worker size within the life cycle of *S. invicta* (Tschinkel, 1988a). If so, increasing colony size by decreasing egg size could have repercussions on worker size.

Alternatively, the queen may evolve more and/or longer ovarioles (Wilson, 1971; Tschinkel, 1988b), probably the most common mode of fecundity increase. More ovarioles require changes in queen proportions, number of sperm stored in the spermatheca and produced by males (Tschinkel, 1988b) and possibly in the relative size of queen and workers.

These examples should suffice to show that many interesting relationships, rules and constraints await discovery through the analysis of sociometric data. In Figure 1, I suggest some non-trivial possible linkages among the attributes listed in Table 1. Discovery of these rules will allow us to reason more realistically about how social insects evolve their particular attributes.

Discussion

The purpose of this paper is to increase awareness of the factual treasures that lie buried in sociometry, waiting to be exhumed. Accumulation of sociometric data

must be a communal effort. Each of us ought to spend part of our time collecting at least some of the sociometric data on our subject species. Or, if some of us have been doing so all along, but not publishing it, this information should be published. Certain basic facts about the social insects we work on must be generally available (Tab. 1).

As researchers with a common interest, we should communicate on whether or not we wish to develop some sort of data bank, and if so, what form it should take, and what data should be included. Such information would be of inestimable value to researchers who wish to pursue comparative studies, tease out the relationships among attributes or attack more general questions on the evolution of the social insects.

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