

Commentary

Social terminology revisited: Where are we ten years later?

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Introduction

The 1990s saw proposals for several amendments to terms used to describe or define degrees of sociality in animals, and particularly insect societies. The framework widely in use up to that time developed between 1928, with the work of William Morton Wheeler, and 1966, when Suzanne Batra coined the term “eusocial.” In its best known exposition (Wilson 1971), the framework included seven terms arrayed in a hierarchical manner: *subsoci*al, *communal*, *semisocial*, *quasisocial*, and *parasocial* (collectively termed *presocial*), plus *eusocial*, a category reserved for groups exhibiting overlapping adult generations, cooperative brood care, and reproductive altruism.

The proposals for change that were advanced in the mid-1990s were largely aimed at reconceptualizing eusociality in particular, not the entire framework. These papers, including Crespi and Yanega (1995), Sherman *et al.* (1995), and Keller and Perrin (1995), were prompted chiefly by (1) the growing diversity of the social bestiary, with the recognition that some complex forms of sociality did not precisely fit the three-trait criteria accepted as the defining characteristics of eusociality defined in 1966; and (2) a

desire to develop a more flexible concept that focused on the presumed hallmark of sociality: the tradeoff between personal reproduction and cooperation.

These proposals advocated redefining the term eusocial in various ways. Crespi and Yanega (1995) proposed defining eusociality in terms of the presence of morphological or behavioral castes. This was intended to extend the eusociality label to new groups discovered to possess soldier or defender morphs, including certain aphids (e.g., Itô 1989), gall thrips (Crespi 1992a, 1992b), and alpheid snapping shrimp (Duffy 1996, Duffy *et al.* 2000). Sherman *et al.* (1995) saw a “eusociality continuum” ordinated by intracolony reproductive skew, and in this same spirit Keller and Perrin (1995) proposed quantifying eusociality with a numerical “index” based on degree of skew. A very different proposal came from Wcislo (1997a), who argued that strictly defining any of the terms, including eusociality, is constraining, and advocated instead a “define as you go” approach: defining terms explicitly for each organism and study.

We contributed to the discussion (Costa & Fitzgerald 1996) within the context of the historical development of the terms and concluded that the framework under discussion was itself

flawed. Specifically, we argued that the framework developed over time in a “top-down” fashion with the demographic structure of particular taxa (bees, ants, wasps, and termites) fixed in advance at its apex. This meant that terms such as subsocial, presocial, etc. were defined in terms of traits lacking in comparison with the eusocial groups. We thought that such negative definitions — defining in terms of what is missing — was less satisfying than positive definitions. The hierarchical social terms are further flawed, we argued, in that they have teleological overtones and literally signify that groups with such monikers are not social or at best less than fully social. We further suggested that as the framework was developed with family-structured societies in mind, and its terms therefore explicitly defined stages of sociality in terms of degree of parent–offspring interaction, any group lacking parent–offspring interaction could never be considered very social no matter how intricate the interactions of group members. This is the plight of many group-living caterpillars, sawflies, and beetles, many with astonishing social repertoires.

The proposed amendments to the term eusocial did little to address its root problems, in our view. We argued that the hierarchy promotes a pre-occupation with the eusociality concept, leading to a subtle conflation of eusociality with sociality itself and reinforcing the impression that the non-eusocial species cannot teach us much about social evolution. A second, related, point was that the hierarchy leads to an under-

appreciation of social complexity in non-eusocial forms, and the focus on demography and reproductive skew directs attention away from cooperation. In view of these problems, we advocated dropping the sociality hierarchy terms in our 1996 paper, with the exception of the term eusocial which had become firmly entrenched in the literature.

The time is now ripe for revisiting this issue. Where are we ten years later? Despite some brief discussion precipitated by these proposals and critiques (Costa & Fitzgerald 1996b, Reeve *et al.* 1996, Wcislo 1997b) the issue seems to have been dropped. What has transpired since the 1995–1997 papers appeared?

New developments in social terminology

We researched the literature covered in the on-line Biological Abstracts/ISI Web of Science in the periods 1989–1996 and 1997–2004 — eight years prior to and following the 1995–1997 papers and critiques. Our findings suggest that insect sociobiologists are now defining terms in widely differing ways, each camp apparently following its own dictum from the respective 1995–1997 papers. For example, our Biological Abstracts search for *eusocial*, *subsocial*, *parasocial*, *quasisocial*, and *semisocial* in titles, keywords, and abstracts reveals a roughly comparable rate of usage before and following the 1995–1997 literature discussion for most terms (Table 1). Comparisons using literature databases are complicated by several factors, chief among them the use of target terms in contexts other than insect sociobiology (especially true of the term “communal” which was, accordingly, dropped from the analysis) and the increase in the number of primary journals over time, which has led to an overall increase in publication rate. Nor are book chapters covered in the database. The data in Table 1 thus cannot be interpreted too broadly, but serve as an indication that most of the social terms of the hierarchy have largely persisted if not increased in usage.

We interpret this to mean that most researchers have simply agreed to disagree, talking past one another and defining terms in their own ways.

Table 1. Results of Biological Abstracts/ISI Web of Science on-line literature searches (> 4000 journals) for six sociality terms of the traditional framework (Wilson 1971). Search conducted on 21 February 2005; parameters included article title, keywords, and abstract.

Term*	1989–1996	1997–2004
Presocial	0	3
Subsocial	46	75
Semisocial	17	8
Parasocial	2	6
Quasisocial	11	1
Eusocial	179	265

*The term “communal” was excluded due to broad usage outside of sociobiology.

For example, Weislo has followed his “define as you go approach” in his papers (e.g., box 1 in Weislo & Danforth 1997), while most researchers working on groups with soldier castes (certain gall aphids and thrips, and snapping shrimp) routinely employ the term “eusocial” following Crespi and Yanega’s (1995) redefinition of that term to focus on behavioral and morphological castes. We searched Biological Abstracts citations for papers combining the word eusocial with “aphid,” “thrips,” or “shrimp.” In the period 1989 to 1996, these numbered 3, 1, and 1 papers, respectively. In the period 1997–2004, in contrast, the papers numbered 12, 13, and 5, respectively. This non-traditional usage of the term eusocial has clearly increased after the 1995 papers and the 1996/1997 critiques.

We, too, have engaged in this practice. Following our own suggestion of referring to the various non-eusocial groups as social (Costa & Fitzgerald 1996), we subsequently so-labeled the caterpillar, sawfly, and beetle societies in papers we have published. Others have followed suit; we recorded nine “social + caterpillar” combinations from 1989–1996, but 23 from 1997–2004.

Finally, one exception to this general trend is the near-extinction of the term “eusociality index,” with but a single paper using the phrase (at least in title, keywords or abstract) since 1996. This does not mean that reproductive skew theory did not catch on; on the contrary, papers mentioning reproductive skew in our post-1996 literature survey number 128. Reproductive skew often refers to cooperative breeding, so of course there is much research on that front without reference to the eusociality index idea.

To further explore treatments of social terminology following the 1995–1997 discussion we also reviewed terminology usage in five recent entomology texts. As the primary books used to educate the next generation of entomologists, we were especially curious to see to what extent the literature debate was discussed. We were disappointed for the most part. Usage and definitions of sociality terms varied considerably, perhaps mirroring the diversity of usages in the primary literature. Two of the texts (Chapman 1998, Romoser & Stoffolano 1998) give the traditional sociality framework, with eusociality discussed strictly in terms of the Isoptera and Hymenop-

tera. While the other three texts largely limit discussion to the traditional eusocial groups, they also present expanded views of sociality, albeit in different ways. Elzinga (2000), for example, counts as “true societies” (= eusocial) the Isoptera, Hymenoptera, gall aphids, and gall thrips, and identifies parent–offspring overlap as “a prerequisite necessary for true socialization.” Gullan and Cranston (2000) broadly categorize insects as solitary, gregarious, subsocial, or eusocial. They are skeptical that any groups but the traditional ones in the Isoptera and Hymenoptera qualify as eusocial, and discuss in some detail why they treat gall aphids, thrips, and snapping shrimp as subsocial. (These authors even discuss sociality in other, non-soldier bearing thrips groups.) The authors of the final text in our survey, Triplehorn and Johnson (2005), also give a detailed and reasoned discussion of the sociality concept. They provide definitions for the terms in the sociality hierarchy, and list “Isoptera, Hymenoptera, and perhaps Coleoptera” as groups meeting the traditional eusociality criteria. They also mention that snapping shrimp and mole rats may fit the bill too. Unlike the other treatments, Triplehorn and Johnson point out that the sociality categories are not so neat and give several examples of exceptions or problems with fitting some social groups into the framework — thrips that have soldier castes but that remain reproductively competent, or lepidopterans that cooperate in many ways as larvae but are solitary as adults, etc.

Toward conceptual unity?

Where do we go from here in view of what seems to be a prevailing terminological free-for-all? Let’s first consider the pros and cons of expanding the eusociality definition to include defender morphs, focusing on behavioral or morphological castes as the main criterion for this category. After all, much usage in the literature seems to be moving in this direction. Is this a positive change? One benefit of such a change is accommodating taxonomically diverse groups, including invertebrates and vertebrates. It also retains the idea of reproductive altruism, which from the beginning was at the heart of the eusociality concept. There are drawbacks, however.

While recasting eusociality to accommodate castes in the broad sense may be an improvement we are concerned with some of the implications of this redefinition. First, this usage does not reflect evolutionary unity of eusocial species. Morphological castes arise in response to one set of pressures in thrips, aphids, and shrimp, groups Strassmann and Queller (1998) called “fortress defenders,” and in response to another set in the Hymenoptera and Isoptera, which exhibit a far more complex suite of foraging, defense, and other group tasks. Very few of these tasks are relevant in thrips, aphids, and snapping shrimp. This broad definition of eusociality means that extremely different social forms will be lumped together — uniting them as “eusocial” simply on the basis of one convergent trait (however interesting that particular trait may be) seems misleading. Another potential pitfall concerns breadth of applicability. Defining eusociality in terms of behavioral as well as morphological castes may mean that any species exhibiting reduced reproductive opportunity relative to others in its colony qualifies as eusocial. Cooperatively breeding birds and mammals, for example, with helpers at the nest that forgo reproduction, would be eusocial. Is there a danger of generalizing the term to the point of uselessness in this way?

We believe it may be least problematical to limit the the term eusocial to the societies of the Hymenoptera and Isoptera as originally intended by the 1966 and 1971 formulations. Indeed, problems arising from recent disagreements over which organisms ought to be included under the eusociality umbrella might be resolved by sharpening the traditional definition of eusociality. Adding to the definition the requirement of collective foraging and food sharing, for example, would unambiguously separate the traditional eusocial taxa from most of the “neo-eusocial” groups proposed since the early 1990s. Collective foraging refers to food retrieval, whether through recruitment, in joint or coordinated fashion, or by solitary foragers. This would accord with our intuitive sense that the later groups are far less complex than the traditional groups.

We stand by our earlier recommendation to drop the remaining teleological and often inconsistently applied terms in the hierarchy and refer to those organisms that the terms formerly

defined, including those traditionally classified as *communal*, *presocial* and *subsocial* arthropods, as simply “social.” Thus any group-living species exhibiting Wilson’s (1971) essential criterion of “reciprocal communication of a cooperative nature” would be considered social. This has the added benefit of facilitating conceptual unity with vertebrate societies, which typically are referred to as social without qualification (one exception being “eusocial” naked mole rats). To be consistent with the current insect-based hierarchy, different vertebrate societies would have to be termed *presocial*, *subsocial*, *quasisocial*, etc. — unlikely to be acceptable to vertebrate biologists. This would also be more consistent with the usage employed by arachnologists. Although terms like subsocial and quasisocial are sometimes applied to spider societies, our literature search revealed that these groups are more often just labeled “social”.

Finally, we encourage greater attention be given to breadth of social repertoire as an index of social complexity. A fuller understanding of social evolution is likely to come from comparative study of diverse social forms for which details of life history and behavioral ecology are well documented. Studies at the level of mechanism — of communication and other factors mediating nestbuilding, foraging, defense, cohesion, broodrearing, etc. — combined with intrinsic and extrinsic parameters are necessary for understanding convergence patterns in social solutions to ecological problems. Identifying the communicative and cooperative modes exhibited by different taxa can yield surprising or counter-intuitive insights that may have been missed by relying on the hierarchical sociality labels. Consider sociality in the gall thrips *Oncothrips tepperi* from Australia (Crespi 1992a,b) and the lichen-feeding *Anactinothrips gustaviae* from Central America (Kiestler & Strates 1984). The former is an example of a gall thrips with soldier morphs, making them eusocial by the caste definition. However, there appear to be no other cooperative interactions in its colonies. *A. gustaviae*, in contrast, has no castes, yet its social repertoire is richer: these thrips establish nest or bivouac sites from which they central-place forage for their fungal food. They reportedly move in single file to and from their food site,

and multiple adults jointly care for the juveniles of the group, possibly by chemical defense. It is telling that *A. gustaviae*, which seems to exhibit cooperative oviposition, defense and trail following with the use of trail pheromones, is little known. One might argue that the soldier bearing gall thrips have radiated greatly while *A. gustaviae* is but one species, justifying the difference in attention paid the two groups. This may be true, but perhaps more might be known of the other 15 described species of new world *Anactinotrips* if this form of sociality was better recognized and appreciated as complex. We believe that labels can make a significant difference in visibility and interest.

Explicitly acknowledging the range of social interaction as reflecting social complexity has the further advantage of including groups that vary widely in demographic and family structure. Under the classic terminological hierarchy, for example, all larval societies have been considered to be *communal* (or *presocial*), and, lacking adult–offspring interaction, they are especially low on the sociality scale. Yet consider that the best studied social larvae, the tent caterpillars, exhibit a range of group behaviors that exceeds that of many family-societies: group defense, nestbuilding, thermoregulation, and recruitment-based cooperative foraging. Breadth of cooperative interaction, and group synchrony, may be better hallmarks of social sophistication than mere demographic makeup, degree of parent–offspring interaction, or reproductive skew.

Once the full range of social interaction is recognized convergence patterns become more apparent, setting the stage for further empirical and theoretical investigation. Recruitment in eastern tent caterpillars, for example, meets Seeley's (1985) description of collective flexibility in honeybee foraging: the ability to evaluate patch quality, recruit to patches of high profitability, and abandon patches of low profitability. What factors have led to convergence in the basic foraging strategy of these taxa?

In summary, we have found that in the nearly 10 years following the mid-1990s discussion over how best to amend the sociality framework, little progress has been made. Continued disagreement over what constitutes eusociality is part of the problem, as is disagreement over

the utility of the remaining hierarchical terms. We suggest limiting the term eusocial primarily to the taxa traditionally placed in this category (of the later candidate groups, only naked mole rats are clearly convergent with the eusocial Hymenoptera and Isoptera), perhaps strengthening the traditional definition in some way to unambiguously delineate the highly complex societies. We reiterate our earlier argument for abandoning the other terms in the hierarchy, replacing them with the simpler and more neutral term “social”. Finally, we suggest that more attention be given to range of social repertoire as a gauge of social complexity.

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