

Running Commentaries: Defining Eusociality

Annales Zoologici Fennici has instituted several changes in recent years. While all are designed to provide the reader a better view of the field of zoology and its research innovations, several changes stand out amongst the others. We have expanded the number of issues each volume from four to six, have edited thematic special issues (e.g., *Extinction Thresholds* vol. 40(2) and *Recognition Systems* vol. 41(6)), and have published featured articles covering issues of importance to the field (e.g., Pigliucci 2002, Roff 2003, Frankham & Brook 2004). This issue contains another first for us — a running commentary.

Running commentaries are designed to share discussions on points of disagreement. In many ways these can serve as excellent springboards to a larger discussion on topics of interest. Certainly they share the philosophy behind disagreements in a way that is often unclear when stated within the confines of a single article. This issue contains a running commentary on the definition of eusociality (Costa & Fitzgerald 2005, Wisclo 2005, Crespi 2005, Lacey & Sherman 2005).

This is a particularly apt discussion for our first running commentary as it addresses two issues of great significance: the general value of a uniform language and, specifically, a disagreement over how to define a social system that Darwin himself felt provided challenges to his theory of natural selection (Darwin 1859). With respect to the former, this journal has recently stressed the importance of a unified language (e.g., see Starks 2004). Simply stated, uniformity of terms facilitates comparisons across systems. These comparisons may be used scientifically, for example, to uncover examples of convergent evolution, or used practically, for example, to introduce research techniques from one system to another. With respect to eusociality, any discussion on a topic considered of special importance for biology's primary unified theory is of great relevance within the field of zoology.

Future commentaries will be considered, and the editors will welcome proposals. We at *Annales Zoologici Fennici* hope you enjoy the following running commentary and find it informative.

Philip T. Starks, Editor & Juha Merilä, Editor-in-Chief

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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: *subsocal*, *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 (Kiester & 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 *Anactinothrips* 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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Social labels: we should emphasize biology over terminology and not *vice versa*

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Costa and Fitzgerald revisit a decade-old exchange over how best to categorize (non-human) animal societies (this issue pp. 559–564, hereafter CF; all page numbers refer to this publication unless indicated otherwise). They use citation data to assess whether or not this debate has led to substantive advances in studies of social evolution. Subsequently, they make recommendations for standardized definitions of social groupings in an effort to achieve nomenclatural stability among biologists working on different taxonomic groups, and thereby hopefully facilitate conceptual unity.

CF conclude that there is a “prevailing terminological free-for-all” (p. 561). They discuss reasons why, but they omit one possibility. Their assessment is consistent with arguments in my paper (Wcislo 1997a; hereafter WTW). CF describe my contribution to the debate as advocating a “define as you go” (p. 559) approach. This summary is not incorrect, but it omits the essential details: WTW emphasized the importance of categorizing comparative data in a manner appropriate for the question(s) of interest, and precisely defining the units of comparison. My emphases have different connotations than “free-for-all” or “define as you go”. Their summary of my views is very abbreviated, so it is useful to briefly recapitulate them to try to discern areas of consensus or bases for dis-

agreement. My current views are substantially unchanged from WTW, which provides additional examples and discussion.

As discussed by Michener (2000: p. 71) and others, classifications generally are meant to be useful. To make useful classifications, we need to know their purpose. To illustrate my contention that social classifications are artificial — unlike the natural classifications possible in taxonomy (Panchen 1992) — WTW took imaginary examples from human social behavior. If you are interested in economic social exchanges, you might first categorize societies as industrial, agrarian, etc. But if you are interested in the origins of ethical systems, a more useful classification might be as monotheist, animist, etc. WTW gave parallel examples from insect societies, showing how you might use the *same* comparative data to categorize the *same* societies in *different* ways, depending on your question. Thus, I agree with CF that comparing recruitment and group foraging in forest tent caterpillars and honey bees is interesting, although I disagree that the comparisons have not been made simply because one is classified as “presocial” and one as “eusocial.”

CF argue that the traditional framework used for describing kinds of societies is seriously flawed because (1) it is hierarchical with eusociality at the top; (2) it was developed “with the

demographic structure of particular taxa...fixed in advance at its apex" (p. 560); and (3) societies are defined by "traits lacking in comparison with the eusocial groups" (p. 560). A fundamental problem for the first century (after Darwin) of social insect studies concerned intra-specific phenotypic divergence among already-sterile individuals, and therefore a focus on the evolution of eusociality was appropriate. I agree with CF that we now should broaden our horizons. I disagree with their second and third points for the following reasons. CF take as their starting point Wilson's (1971) summary of a social classification. Yet Wilson (1971: p. 4) followed the "most recent and sound classification" developed by Michener (1969). It is instructive to read Michener's paper. Michener (1969) developed his classification to review behavior that ranged from solitary to eusocial, with diverse kinds of social organizations in between. He also hypothesized that eusocial behavior may evolve and then be secondarily lost in some lineages, indicating that he did not view eusociality as the acme of evolution; this hypothesis has empirical support (see e.g., Wcislo & Danforth 1997, Danforth *et al.* 2003). Second, the assertion that groups were defined in terms of traits they lack is incorrect. For example, communal groups are those in which (i) females of the same generation live together, and (ii) females are structurally similar. Semisocial groups, by comparison, share traits (i) and (ii) in common with communal groups, but also possess (iii) division of labor, and (iv) females work cooperatively on brood cells. To say that communal societies are those that *lack* division of labor and cooperative work is short-hand to avoid repeating the defining characteristics that distinguish communal individuals from solitary ones. Although these criteria appear to be insect-biased, they can be modified readily to accommodate comparisons with vertebrates. For example, criterion (iv) is easily generalized as "females cooperatively rear young." In general, invertebrate-vertebrate comparisons are facilitated by precisely specifying the question of interest, and thus comparisons can be made using specific behaviors or life-history traits (see WTW for details; also Nonacs 2001).

CF also suggest that a concern with hierarchy reinforces "the impression that the non-eusocial species cannot teach us much about social evolution" (p. 560). Again it is informative reading Michener (1969). He clearly emphasized that some taxa, such as solitary and weakly social halictine bees, were appropriate for questions about the *origins* of social behavior, while already-eusocial taxa were appropriate for understanding the *maintenance* of social behavior. Furthermore, he discussed attributes that are important for understanding social evolution, which included, for example, development of aggregations and colonies; communication and integration; defense; and control of physical conditions. This list includes topics that CF believe are neglected because of the traditional hierarchical social classification, which undercuts their argument that the traditional classification impedes more catholic comparative studies.

In an effort to achieve conceptual unity, CF propose to limit the term "eusocial" to "highly complex societies..." (p. 563). Presumably by "highly complex" they mean societies like those of termites and stingless bees that have hundreds or thousands of individuals, even though Batra developed the term for sweat bees (Halictinae) (see Batra 1995), which can have eusocial colonies with as few as two or three females, among which adults usually do not share food (e.g., Batra 1966a, 1966b, Wcislo 1997b). CF then propose to add criteria of collective foraging and food-sharing, to "unambiguously separate the traditional eusocial taxa from most of the 'neo-eusocial' groups..." (p. 562). These additional criteria would *exclude* some of the "traditional" societies for which Batra originally coined the term! I contend this will lead to confusion rather than conceptual unity.

CF further propose to retain the term "eusocial" but drop the "remaining teleological and often inconsistently applied terms" (p. 562) and describe group-living but non-eusocial arthropods as "social." I believe that "social" is a very useful umbrella term to cover *any* group-living organisms, without specifying more details of the association, as in common usage. Moreover, for some questions, it matters whether societies are comprised of individuals with equal oppor-

tunities or not, or whether they are comprised of family (kin) groups, and so on, and valuable information can be lost by lumping together disparate kinds of group organization. Indeed, CF make the same point when discussing ideas to modify the definition of eusociality, because they are concerned that lumping very different social forms together would not “reflect evolutionary unity of eusocial species” (p. 562). If their main point is that evolutionary history matters, then I agree. Indeed, WTW reviewed an effort by Michener (1974) to derive a statistical system for classifying societies. Using a diverse array of behavioral and morphological traits, for a diverse array of species, Michener expected to obtain principal components clusters based on social level (i.e., solitary, communal, eusocial, etc.), whereas he obtained clusters based on taxonomic grouping (evolutionary history). Although Michener used species in this analysis, he was careful to mention that social classifications are *not* generally applicable at the species level, because of extensive intra-specific variation, except for some permanently eusocial taxa (e.g., stingless bees, ants). WTW emphasized that important *intraspecific* variation is masked by species-level classification (*see* also Michener 1969, 1974), which is neglected by CF and others (for an exception, *see* Nonacs 2001). Thus, species-level social classifications may promote typological thinking, despite arguments by Mayr (1942, 2004) and others that typology is an intellectual impediment for biologists.

WTW noted that labels sometimes are a kind of word-magic, if one equates naming things with understanding them. CF also are concerned with social labels, because they may make “a significant difference in visibility and interest” (p. 563). I agree. But labels are intended to be descriptive, and facilitate communication by quickly summarizing distinctions known to be important. In that spirit, colleagues and I even referred to a social pompilid wasp (*Auplopus*) as a “communal cleptoparasite” (Wcislo *et al.* 1988), because we wanted to emphasize the intense social competition among group-living females. This juxtaposition raises the curious point that nearly all the attempts at uniform social classifications are incomplete because they exclude social parasit-

ism, even though it represents a major, if dark, side of social evolution (*see* Wcislo 2000).

CF suggest that breadth of social repertoire might be used as an index of social complexity, and urge more attention be given to the full repertoire. Although I fully agree that we should pay more attention to other interesting social behaviors, size of repertoire as an index of social complexity is problematic (*see* discussion in Carneiro 2003, de Waal & Tyack 2003, Bonner 1988). Unidimensional metrics, whether they intend to measure social complexity or reproductive skew, inevitably capture fewer of the rich biological details that make up social life and so will be unsatisfactory for many questions. Moreover, breadth of social repertoire is too poorly known in general to serve as a basis for comparative studies.

In sum, CF do an admirable service by drawing attention to the fact that many taxa have fascinating social behavior yet are under-represented in studies of social evolution. They also raise interesting questions about why these taxa have been excluded from the dominant clique of social invertebrates (termites, ants, paper wasps, corbiculate bees). CF are correct that we need a sustained effort to document the rich natural history of these under-represented taxa, especially in the tropics where we are rapidly losing so many species. They are also correct that redressing this imbalance will likely enrich our understanding of social evolution. CF have not convinced me, however, that we need a new standardized system of social labels to achieve conceptual unification. To the contrary, conceptual syntheses are new ways of looking at the world, which invariably rupture the *status quo* (Sulloway 1996). A rigid classification scheme may act as a roadblock, or make for a bumpy ride, on the road to unification.

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Social sophistry: logos and mythos in the forms of cooperation

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In Plato's cave, humans chained to a wall see the world only as flickering shadows of statues, removed by several degrees from the 'real' world of ideas and forms. As the cave-dwellers communicate thoughts about the statues, their words add yet another layer of removal and distance, here between each others' perception and thought-pictures. Over ten years ago, I asked a number of the philosopher queens and kings of social insect biology how they conceived and applied the term 'reproductive division of labor', the core of the traditional definition of eusociality. From each person I received a different answer. I reckoned then that social terminology systems required an attempt at meeting of minds, to avoid implicit confusion and to foster progress in recognizing social convergences. Down the hall I went to Paul Sherman and his erudite mind. We compared our flickering shadows, decided to write a paper together, and started — but then realized that we viewed the wall quite differently, and two contrasting papers were the ultimate result.

The conceptual impact of the papers by Sherman *et al.* (1995), Crespi and Yanega (1995), and later Costa and Fitzgerald (1996), Wcislo (1997), and Crespi and Choe (1997) may be assessed in several ways. First, the papers have been cited 80, 45 and 22 times respectively (for the first three papers, Web of Science), which sug-

gests that workers are aware of the importance of cave-shadows in defining societies. Indeed, recent authors are usually careful to explain their use of social terms (e.g., Burda *et al.* 2000), probably more careful and explicit now than pre-1995. I see this as progress — at least we know that we are in a cave like Plato's.

Second, tabulation of how often various social terms were used before *vs.* after 1995 (Costa & Fitzgerald 2005) can demonstrate any trends, though the connections between word use and application of concepts is difficult to judge.

Third, we can seek to assess conceptual impact by determining if any of the specific suggestions of the authors have been implemented. For example, Crespi and Yanega (1995) proposed that some 'traditionally eusocial' ants, bees, and termites should be considered as cooperative breeders. Search for the combined terms 'insects' and 'cooperative breeding' on BIOSIS for 1985 through 1994 yielded 12 citations, with only one on social insects (ants). By contrast, 1996 to 2005 produced 27 hits, including two papers on ants, two on termites, five on wasps, and three on bees. A search for 'eusociality continuum' over this period gave only one empirical paper, on Zambian mole rats. I take this as suggestive evidence that some workers have adopted at least one central idea of Crespi and Yanega (1995), that insects can be cooperative

breeders, and that the eusociality continuum is proving difficult to apply in practice.

Of course, the science of social insect biology exists not just in the literature, our equivalent of the Greek *logos*, linear and logical communication meant to convey facts. Perhaps more importantly, it exists in our minds, hodge-podges of scientific lifetimes of mentors, colleagues, and students, thousands of papers and talks, and communing with our own favorite social creatures. To reach and change minds the Greeks used *mythos* — word-pictures, stories, analogies and metaphors that convey deep truths and values. Here, I have used Plato's cave as *mythos* for our thoughts concerning the forms of sociality.

So are there 'real' forms of sociality behind us, casting shadows? I like to think so — at least 'real' in the sense of unambiguous convergence on small suites of core social traits, as opposed to Wcisloian (1997) truths beyond history, or the heuristic phenomenology of Nonacs (2001). A large set of species is unique in having evolved reduced reproduction by some individuals, in association with a trade-off between helping and offspring production. In some, 'eusocial' forms, the tradeoff involves two permanently-distinct types of individual, and this permanence results in two independently-evolving phenotypic systems. In other, 'cooperatively-breeding' forms, the difference between 'breeders' and 'helpers' is not permanent — individuals are 'totipotent' and can switch roles. Transitions from cooperative breeding to eusociality probably occur very rapidly (Crespi 2004), such that transitional forms will seldom blur this distinction. Finally, in 'communal' forms, there is only one type of individual, who both breeds and engages in helping — and this social system appears never to evolve into cooperative breeding or eusociality, or vice versa (Crespi 1996).

All three social systems described above include vertebrates and invertebrates, and in all of them colonies, populations and species may vary in social sophistication, behavioral repertoire, complexity, skew, degree of reciprocal communication, or whatever. Convergences may be sought for any social traits, at any levels — wherever one finds interest. But in my view the tripartate scheme above is the most fundamental division, which is ignored only with peril,

because these three social systems are *different*.

Costa and Fitzgerald (2005) argue that the term eusociality should apply only to traditional 'advanced' eusocial forms among Hymenoptera, Isoptera, and naked mole rats, because only these species exhibit reproductive division of labor plus complex social repertoires, cooperative foraging, and food-sharing. All other species should simply be referred to as 'social'. Thus, instead of using one explicitly-applied core convergent trait (reproductive division of labor, be it permanent, temporary or absent) as the foundation of their terminology system, they use what I consider to be several arbitrarily-chosen traits (the latter three criteria), and they retain the very vagueness in the term 'reproductive division of labor' that led us into this flickering cave ten years ago. Their viewpoint will not, in my view, fuel the hunt for broad convergences. Indeed, I posit that it has been only via the conceptual application of the term eusocial to some shrimp, beetles, thrips, and aphids that we came to recognize the presence of two clear modes of eusocial forms, the factory-fortress inhabitants (including some termites and naked mole rats) and the central-place foragers (Crespi 1994, Strassmann & Queller 1998), that has each evolved convergently. Rather than seeing such a distinction as 'potentially misleading' (Costa and Fitzgerald 2005), I perceive it as providing important new insights into how ecological factors can generate reproductive division of labor. Would having called many of these taxa simply 'social', lumping them with marmosets, some caterpillars, and some spiders, have led to this inference?

Finally, most readers will have noticed that the contrasting visions of social terminology described in these papers reflect the taxa and theories of their authors: Sherman and Reeve (1995) working with 'eusocial' mole rats and skew theory for the continuum, Costa and Fitzgerald (1996, 2005) seeking recognition for the social sophistication of caterpillars, and Crespi (Crespi and Yanega 1995) elevating the lowly thrips to the altruistic alter of ants, bees and termites. Whether or not the memes of these authors are self-serving, the usefulness of their views in recognizing convergence, posing new questions, and structuring the minds of the next generation of students is the ultimate question. The controversy over social terminology has, I

think, served at least one fundamentally-important purpose: showing us that to reach the next truths in the study of social evolution, we should engage in continued shadow-dispelling discourse on the many meanings of being social.

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Redefining eusociality: concepts, goals and levels of analysis

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Introduction

A decade ago, we contributed to a series of publications that explored the terminology used to characterize the social systems of cooperatively breeding animals (Crespi & Yanega 1995, Keller & Perrin 1995, Sherman *et al.* 1995, Reeve *et al.* 1996, Wcislo 1997). Ostensibly, this was a semantic debate that focused on the definition of “eusociality,” a term coined by Batra (1966) to describe the social systems of bees that (1) live in multi-generational groups and (2) engage in alloparental care of young, and in which (3) reproduction is restricted to a few individuals per group. For the next 20 years, these criteria remained unchallenged and the term “eusocial” was applied only to insects in the orders Hymenoptera and Isoptera (e.g., Wilson 1971, Hölldobler & Wilson 1990). During the 1980s, however, the array of species characterized as eusocial began to increase, leading to confusion regarding the exact nature and phylogenetic distribution of this type of social system. The multiple reviews of eusociality published in the mid-1990s revealed markedly divergent viewpoints regarding not only terminology, but also the goals and processes of comparative studies of animal societies. Thus, what began as a semantic

argument became a discussion of fundamental conceptual issues in evolutionary research.

As is evident from the commentaries in this issue, the passage of time has not produced a consensus. Conceptual analyses of social behavior remain divided among schema that attempt to differentiate eusociality from other cooperative societies (e.g., Crespi & Yanega 1995), those that view eusociality as part of a spectrum of cooperative social systems (e.g., Sherman *et al.* 1995), and those that rely on phylogenetic relationships to delineate social structure (e.g., Wcislo 1997). As a result, the terms used to characterize animal societies remain diverse and largely unchanged (Costa & Fitzgerald 2005). Concomitantly, the proposed development of a lexicon that encompasses all cooperative societies (Costa & Fitzgerald 2005) promises to expand the range of social systems under consideration, thereby adding new complexities and points of disagreement to an already contentious issue.

We believe that terminological unification and simplification are needed. We were — and still are — proponents of the eusociality continuum, a conceptual framework that unites all occurrences of group living and alloparental care under a single terminological umbrella (Sherman *et al.* 1995). Here, we review the foundations

of the continuum perspective, with emphasis on criticisms of this viewpoint that have arisen during the past decade. We then consider two general sources of confusion that contribute to ongoing disagreements concerning the definition of eusociality. Finally, we suggest several directions for future research that may help to resolve current points of terminological contention.

The eusociality continuum

Sherman *et al.* (1995) proposed that animal societies characterized by multi-generational groups and alloparental care form a continuum based on the degree of reproductive skew (Vehrencamp 1983) within groups. The concept of the continuum arose from the authors' observations that the three attributes traditionally used to identify eusociality in hymenopteran and isopteran insects (Batra 1966, Wilson 1971) occur in a phylogenetically diverse array of animals, including several other orders of insects (thrips: Crespi 1992; beetles: Kent & Simpson 1992; aphids: Stern & Foster 1996) as well as mammals (e.g., African mole-rats: Sherman *et al.* 1991, Bennett & Faulkes 2000; dwarf mongooses: Creel & Waser 1994; meerkats: Clutton-Brock *et al.* 2004), birds (Florida scrub jays; acorn woodpeckers; Seychelles warblers: Stacey & Koenig 1990, Koenig & Dickinson 2004) and crustaceans (snapping shrimp: Duffy *et al.* 2000). All of these taxa are group living, alloparental, and exhibit some degree of reproductive skew (Reeve & Keller 1995, Sherman *et al.* 1995). However, because skew is a facultative response to ecological conditions (Komdeur 1992, Hirata *et al.* 2005) that is expected to vary continuously among species (Sherman *et al.* 1995, Hart & Ratnieks 2005), no objective distinction can be drawn between these societies. Thus, all cooperatively breeding (i.e., alloparental) vertebrate species are eusocial and, conversely, all eusocial insects are cooperative breeders.

Criticisms and challenges

Criticisms of the eusociality continuum have focused on either the mechanics of estimating reproductive skew or the choice of skew

as the sole axis for comparing social structure (e.g., Crespi & Yanega 1995, Costa & Fitzgerald 2005). Regarding the former, there has been a tendency to conflate the concept of the continuum with the quantification of reproductive skew (Crespi & Yanega 1995). Indeed, the failure of the specific index of skew suggested by Sherman *et al.* (1995) to gain favor in the literature has led some investigators to conclude that the eusociality continuum is "dead" (Costa & Fitzgerald 2005, P. Nonacs pers. comm.). We agree that better measures of skew are desirable, but we see this challenge as fundamentally distinct from the conceptual argument that skew varies continuously among alloparental taxa. We note that indices of skew are being developed that focus specifically on inequalities in reproduction resulting from social structure (e.g., dominance, kinship: Reeve *et al.* 1998, Nonacs 2003). Nevertheless, the eusociality continuum as a conceptual construct for understanding and comparing alloparental species is independent of any specific measure of the reproductive division of labor within social groups.

The eusociality continuum was developed in the context of redefining eusociality and, hence, using reproductive skew as the basis for comparing taxa is both logical and evolutionarily compelling. All species included in the continuum are group living and alloparental; traditionally, it is the third criterion for eusociality — a reproductive division of labor — that has been controversial and obscure. As originally defined, skew refers to variation in direct fitness that occurs due to an individual's social environment (Vehrencamp 1983). As the degree of skew within social groups increases, the routes by which breeding versus non-breeding animals achieve fitness diverge, with non-breeders increasingly restricted to "indirect" forms of fitness such as helping kin to reproduce (Reeve 1998). Concomitantly, specializations for either successful breeding or effective alloparental care are favored, potentially leading to behavioral, physiological, and morphological differences between breeders and non-breeders, as well as among non-breeding individuals. Thus, in addition to being an obvious basis for contrasting alloparental species, reproductive skew is a fundamental, causal axis for comparing cooperative societies.

Roadblocks to consensus

At least two more general issues appear to contribute to the ongoing debate regarding definitions of eusociality. One of these concerns the goals of comparative evolutionary research. In our opinion, a fundamental objective of such studies is to identify the general principles underlying patterns of social system diversity (Reeve & Sherman 1993, 2001, Dugatkin 2001, Reeve 2001, Autumn *et al.* 2002). When searching for general explanations, comparative data sets are most useful if they include all taxa known to exhibit the phenomena of interest. Accordingly, the eusociality continuum (Sherman *et al.* 1995) brings together a phylogenetically diverse collection of complex, cooperative animal societies under a single conceptual and terminological framework, thereby facilitating potentially revealing cross-taxonomic comparisons (e.g., Andersson 1984, Shellman-Reeve 1997, Korb & Schmidinger 2004). In contrast, the alternative schema proposed by Gadagkar (1994), Crespi and Yanega (1995), and Costa and Fitzgerald (2005) are intended to differentiate among cooperative societies, which limits their utility for exploring general adaptive explanations for evolutionarily convergent aspects of animal social structure (Keller & Reeve 1994, Reeve & Keller 1995, 2001). Similarly, phylogenetically based classifications (Wcislo 1997) tend to divide, rather than to unite, behaviorally convergent societies.

Although originally presented as alternatives, the eusociality continuum of Sherman *et al.* (1995), the dichotomous definition proposed by Crespi and Yanega (1995), and the phylogenetic approach outlined by Wcislo (1997) are, in fact, complementary because they represent different levels of analysis (Sherman 1988, Reeve *et al.* 1996). The eusociality continuum emphasizes differences in personal reproduction, which is an ultimate- or adaptive-level approach to variation in social structure. In contrast, definitions of eusociality based on the occurrence of behavioral or morphological castes are proximate- or mechanistic-level explanations for the reproductive differences exploited by the continuum perspective. Finally, phylogenetically based categories represent evolutionary- or historical-level distinctions between societies.

For biologists interested in understanding *how* reproductive differences among group members are maintained, behavioral or morphological castes may provide a useful means of distinguishing between species. The fitness consequences of failing to breed, however, are the same regardless of the mechanisms that maintain skew and, hence, for biologists interested in understanding *why* group living, alloparental care, and a reproductive division of labor (i.e., eusociality) occur, the presence of castes will, at best, provide only indirect information regarding the adaptive reasons for this form of sociality. Similarly, while phylogenetic analyses add valuable information regarding the evolutionary histories of eusocial species, they do not provide direct evidence of the adaptive significance of social structure.

Toward a unified lexicon of sociality

The divergent perspectives on eusociality outlined a decade ago remain evident in the present collection of commentaries. Eusociality continues to be used in two different contexts, namely to (1) unite taxonomically diverse societies that are characterized by alloparental care and reproductive skew, and (2) differentiate these societies based on the presence of castes or evidence of distinct phylogenetic histories. These objectives are necessarily disparate, making it difficult for one term to fulfill both functions. In practice, this could be resolved by adopting different terms for each purpose, but this solution would sidestep the more substantive issue of whether insect societies traditionally recognized as eusocial are truly distinct from other forms of cooperative breeding.

Costa and Fitzgerald (2005) provide a clear illustration of the increasingly schizophrenic demands on the social lexicon. On the one hand, they call for a more limited definition of eusociality — one that restricts use of this term to the hymenopteran and isopteran societies for which it was originally developed. On the other hand, they call for (1) greater consideration of other measures of social complexity and (2) terminology that includes groups that cooperate

in apparently non-reproductive contexts (e.g., tent caterpillars). We suspect that cooperation and self-sacrifice in all these societies have evolved due to their effects on the subsequent survival and fitness of group members, making reproductive skew a critical element of this expanded organizational scheme. But, if researchers are unable to agree upon a definition for eusociality, how likely is it that they will find a mutually acceptable conceptual and terminological framework that encompasses all complex, cooperative societies?

We suggest that elucidating the goals of comparative research, the criteria for comparing social systems, and the levels of analysis used to examine social structure are essential steps toward resolving the current terminological confusion. At a minimum, efforts to address these issues will lead to greater understanding of the differences among the various definitions and schema currently in circulation. If these conceptual challenges can be overcome, attention can then be redirected to identifying the best metrics for comparing social systems. This list of suggestions may seem pessimistic in that it appears to create, rather than to eliminate, roadblocks to a unified social lexicon. We hope, however, that it will serve as a heuristic challenge that, ultimately, will help to advance our understanding of complex, cooperative animal societies.

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