

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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