

Redefining eusociality: concepts, goals and levels of analysis

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Received 1 June 2005, revised version received 22 July 2005, accepted 1 July 2005

Lacey, E. A. & Sherman, P. W. 2005: Redefining eusociality: concepts, goals and levels of analysis. — *Ann. Zool. Fennici* 42: 573–577.

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.

Acknowledgements

We thank P. T. B. Starks for inviting us to participate in this forum and for his patience during the extended preparation of our contribution. For useful discussion and commentary, we thank H. K. Reeve, P. Nonacs, J. S. Sherman, and several anonymous reviewers. Finally, we acknowledge the many stimulating exchanges that have occurred over the past decade with the other participants in the "eusociality debate," notably J. Costa, B. Crespi, T. Fitzgerald, and D. Yanega.

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