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## The definition of eusociality

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*We describe more precise definitions for the term "eusociality" and other social systems. Our criterion for eusociality is the presence of castes, which are groups of individuals that become irreversibly behaviorally distinct at some point prior to reproductive maturity. Eusocial societies are characterized by two traits: (1) helping by individuals of the less-reproductive caste, and (2) either behavioral totipotency of only the more reproductive caste (facultative eusociality) or totipotency of neither caste (obligate eusociality). We define "cooperative breeding" as alloparental care without castes. Cooperatively breeding societies may comprise two types, semisocial (distribution of lifetime reproductive success bimodal), and quasisocial (distribution of lifetime reproductive success unimodal), but this hypothesis requires empirical analysis. Our definitions conceptually unify studies of arthropod and vertebrate sociality. Key words: cooperative breeding, eusociality. [Behav Ecol 6:109-115 (1995)]*

We propose that the term "eusociality" should be defined more explicitly and precisely. In this article, we describe the problem, propose a solution, and discuss the usefulness of the solution in theory and practice.

The term "eusocial" (truly social) was first used by Batra (1966) to describe nesting behavior in bees "in which the nest-founding parent survives to cooperate with a group of her mature daughters, with division of labor." Michener (1969) formalized the classification of bee social systems such that eusociality comprised three qualities: (1) castes and division of labor ("with both egg layers and workerlike individuals among adult females"), (2) generation overlap between mothers and their adult offspring, and (3) cooperative work on cells. Wilson (1971, 1975: 398) extended Michener's terminology to other social insects, and composed the definition of eusociality commonly used today: "(1) individuals of the same species cooperate in caring for the young; (2) there is a reproductive division of labor, with more or less sterile individuals working on behalf of fecund nestmates; (3) and there is an overlap of at least two generations in life stages capable of contributing to colony labor, such that offspring assist parents during some period of their life" (Table 1).

The primary reason that the definition of eusociality takes its present form is that it was developed for halictine bees in particular and borrowed for social arthropods in general. When the definition was first used, its flexibility may have been useful because the various forms of arthropod social systems were only then being discovered, and precise classification of poorly known taxa would have been

premature. Twenty years later, we have a much clearer understanding of the forms and causes of sociality in both arthropods (e.g., Aoki, 1987; Hölldobler and Wilson, 1990; Itô, 1989; Kent and Simpson, 1992; Michener, 1974, 1990a; Ross and Matthews, 1991) and vertebrates (e.g., Emlen, 1991; Stacey and Koenig, 1990). The discovery of the first vertebrates that are eusocial by Wilson's definition, two species of mole-rat (Jarvis, 1981; Jarvis and Bennet, 1993; Sherman et al., 1991), and the many recently noted similarities between social arthropods and cooperatively breeding vertebrates in the ecological causes, correlates, and forms of social behavior (Alexander et al., 1991) compel a clear definition of eusociality applicable to all animals.

The most serious problem with Wilson's (1975) definition is that the phrase "reproductive division of labor" has no single clear meaning. The phrase may be interpreted to refer to: (1) the presence of any individuals with zero reproduction because they help (West-Eberhard, personal communication); (2) "some females (reproductives) laying most or all of the eggs" (Cowan, 1991: 34), which implies a mean difference in reproduction between types of colony-mate; or (3) "deviation from a Poisson distribution of eggs per individuals" [Itow et al. (1984), referring to the thelytokous, queenless ant *Pristomyrmex pungens*]. Moreover, reproduction may be measured at any given time, over breeding episodes, or over entire lifetimes (Tsuji, 1992), and it may or may not involve inclusive fitness effects. All of these meanings are reasonable given Wilson's definition, but they have quite different implications for the classification of social forms.

The problems with Wilson's definition are neither academic nor purely semantic. For example, Furey (1992) considered age-related variation in reproduction as a suitable criterion for Wilson's definition (but see Tsuji, 1992). In a recent review, Seger (1991: 346-347) stated that "such [cooperatively breeding] species are at least temporarily eusocial, but the term is usually reserved for species in which colonies come to exhibit a more or less fixed division of reproductive labour, involving functionally sterile individuals that work on behalf of their parents." How should the terms "more or less" and "functionally sterile" be interpreted here?

The vagueness of Wilson's definition has permitted substantially different interpretations of the meaning of "reproductive division of labor" by different workers. The resulting conceptual ambiguity has, over the years, resulted in different taxa being classified as eusocial by divergent, often unspecified, criteria. For example, lists of purportedly eusocial taxa sometimes include all ants and some or all stenogastrine wasps (e.g., Seger, 1991: 348). However, many ponerine ant species have no queens, and dominance hierarchies among colony-members (Peeters, 1993; Peeters and Crozier, 1988), so that their social systems resemble those of many vertebrates. Similarly, many stenogastrine wasps with helping exhibit it only as a temporary ontogenetic stage (reviewed in Turillazzi, 1991), and thus resemble birds and mammals with helpers at the nest. We believe that the ambiguity in communication caused by the current vagueness of the term eusociality interferes with progress in recognizing convergences in social systems between diverse taxa, because the social systems being con-

**Table 1**  
**The traditional categorization of social insects, from**  
**Michener and Wilson**

	Coop- erative brood care	Castes	Gener- ation overlap
Communal	No	No	No
Quasisocial	Yes	No	No*
Semisocial	Yes	Yes	No
Eusocial	Yes	Yes	Yes

Castes are defined by Michener (1974: 371) as "functionally different groups among the females of a colony. The differences may be only behavioral or physiological, or may also involve structure. The differences are permanent, not merely due to age." Wilson (1975: 580) defines caste "broadly" as "any set of individuals of a particular morphological type, or age group, or both, that performs specialized labor in the colony" and "narrowly" as "any set of individuals in a given colony that are both morphologically distinct from other individuals and specialized in behavior." "Communal" societies exhibit nest-sharing. Wilson also categorizes societies as "Intermediate subsocial I or II," but these terms have rarely been used in the literature.

\* In Michener's scheme, quasisocial forms may or may not have generation overlap.

verged upon are unspecified, and vagueness allows categorization to be as easy as it is imprecise.

Our main criteria for a useful definition of eusociality are that the definition be *nonarbitrary* (categorizing societies by meaningful parameters), *universal* (applicable to all species), and *evolutionarily informative* in that it indicates differences between societies that differ in how natural selection affects behavioral interactions.

The purpose of our definition is twofold. First, the term eusociality should symbolize a pattern of behavioral interactions that exists in nature. The definition allows for recognition and identification of this pattern in any taxon, and it must include a description of the pattern that makes recognition unambiguous. Second, the term provides a necessary tool for conveyance of information about behavioral patterns between students of social behavior. This information serves as an essential framework and guide for ecological and evolutionary explanations of eusociality, because the search for convergence among diverse taxa requires consensus among workers about just what patterns have evolved. The more detailed and unambiguous the definitions of eusociality and other social systems can be made, within the context of describing actual patterns, the more information is conveyed and the more straightforward the search for convergence becomes. The existence of discrete patterns of behavior, rather than continuous variation, is an empirical question that can be solved by determining whether nonarbitrary behavioral criteria exist that separate taxa into discrete groups upon which natural selection has acted differently. As described below, we consider the evidence for the existence of a discrete eusocial pattern to be unequivocal.

We believe that the term eusociality should indicate the presence of distinct lifetime trajectories with respect to behavior and reproduction, such

that helpers have lower lifetime reproduction because they help others to reproduce. These distinct lifetime trajectories are recognized in practice via certain patterns of variation in behavior, including, but not restricted to, reproduction. Summed over their lifetimes, individuals of eusocial societies may be categorized along some set of behavioral axes into two or more distinct groups, and individuals of one of the groups help individuals of the other group to reproduce. The most important criterion of eusociality, which sets it apart from all other social systems, is that individuals become fixed into one of the behavioral groups at some point prior to reproductive maturity, such that transitions from one behavioral group to the other cannot and do not occur. These behavioral groups represent castes. Individuals of at least one caste irreversibly lose the capacity, at some point in development, to perform at least one behavior that is characteristic of individuals of the other group or groups (i.e., totipotency has been lost). In addition, one caste engages in alloparental behavior that increases the reproductive success of the other caste. The discrete behavioral gap between castes may involve any of the following: colony-founding, diapause, mating, colony defense, physiology, discrete morphological differences, or, in a few extreme cases, sterility.

In some eusocial societies, individuals of one caste are totipotent and specialize in reproduction (gynes), and individuals of the other caste or castes (workers and soldiers) are not totipotent and specialize in helping individuals of the more reproductive caste to reproduce. In other eusocial societies, the behaviors of the castes are complementary and mutually dependent, and neither caste is totipotent, as in *Apis* species where gynes cannot produce wax. We define totipotency as the potential, throughout life, to express the full behavioral repertoire of the population (even if never actually expressed), and the ability to produce offspring like oneself, exhibiting the full behavioral repertoire of the population, without help. For example, foundress gynes in many temperate polistine wasps and halictine bees can produce future gynes without help. However, helpers in such societies, even though capable of producing offspring, cannot diapause and found new colonies, and thus are not totipotent (e.g., Yanega, 1989). Similarly, foundresses of the thrips *Oncotrips tepperi* can produce the next generation of foundresses without help from their soldier offspring (if the gall is not invaded), and are therefore totipotent, but soldiers do not form galls or produce offspring like themselves, and are therefore not totipotent (Crespi, 1992, personal observation).

Our criterion of totipotency of one caste versus obligate complementarity of the castes logically subdivides eusociality into subsets that largely corresponds to Michener's (1974: 38) traditional categorization into "primitively eusocial" and "highly [or 'advanced'] eusocial," but are less value-laden (see also Kukuk, 1994). In facultatively eusocial societies, individuals of one caste are totipotent and individuals of the other caste are not totipotent. By contrast, in obligately eusocial societies, the presence of the other caste or castes is necessary for the production of offspring. Societies with these two types of behavioral variation differ fundamentally in how natural selection has shaped the inter-

actions within groups and in their expected ability to respond to future social selective pressures.

We specify that individuals become fixed into castes at some point prior to reproductive maturity rather than adulthood because there is evidence in halictine bees (Yanega, 1989, 1992) and polistine wasps (Mead and Gabouriaut, 1993) that caste is determined in the first few days of adulthood, but prior to the onset of reproduction. If individuals are capable of switching from one behavioral group to another, then the groups in question should at most be considered subcastes, that is, distinct behavioral groups within castes. For example, in many polistine wasps and halictine bees, foundresses and auxiliaries are subcastes of the gyne caste, whereas replacement queens and workers are subcastes of the non-gyne caste (Yanega, 1988, 1989). Although supersedure, the functional replacement of gynes by former workers, is common in societies such as these, categorized by Wilson as "primitively eusocial" (e.g., Eickwort, 1986; Reeve, 1991), productivity is not in itself sufficient to define a caste. Thus, an *Apis* worker that lays eggs in the absence of a queen would not be considered to have switched caste, nor should replacement reproductives in any other species, unless there is some other feature to distinguish them as a caste (such as the specialized, flightless "secondary reproductives" found in some termites). In many eusocial taxa, such as halictine bees and polistine wasps, the term queen has often been used to refer to the dominant egg-laying individual, and has been equated with caste. However, queens in such taxa may be members of either true, permanent caste (gynes and non-gynes), because both true castes are capable of dominance and reproduction (see also Peeters and Crozier, 1988).

Based on the considerations described above, we propose changes in the sociobiological lexicon to the following definitions, by which all societies can be categorized.

### Eusocial societies

Eusocial societies contain castes, which are groups of individuals that become irreversibly behaviorally distinct at some point prior to reproductive maturity. Individuals of one caste have higher mean lifetime reproduction (numbers of offspring), and at least one other caste exists that helps individuals of the other caste to reproduce. Individuals of the more reproductive caste are totipotent, or obligately complementary in behavior with individuals of the other caste or castes. Our definition of castes is similar to that of Michener (1974: 371), in that castes are permanent. However, in contrast to prior terminologies (Table 1), our definition makes no mention of presence or absence of overlap of generations, as it is not required to delineate functionally similar social patterns.

We divide eusocial societies into two categories. Facultatively eusocial societies are those with totipotency of the more reproductive caste only. Obligately eusocial societies are those with totipotency of neither caste; i.e., obligate complementarity and mutual dependency of the castes. Examples of taxa exhibiting facultative eusociality include some encyrtid wasps (Cruz, 1981, 1986; see also Grbic et al., 1992), thrips with soldiers (Crespi, 1992; Mound

and Crespi, in press), most aphids with soldiers (Aoki, 1987; Moran, 1993), many Halictinae, such as *Halictus rubicundus* (Yanega, 1989, 1993) and *Lasioglossum zephyrum* (Michener, 1974: 274–286), some Polistinae, such as *Polistes fuscatus* (Reeve, 1991), and, apparently, one spider (Rypstra, 1993). Examples of taxa exhibiting obligate eusociality include all Apinae, all Meliponinae, all nonparasitic Bombinae, some Halictinae (Brooks and Roubik, 1983), all nonparasitic Vespinae, all ants except some Ponerinae (cited below) and *Pristomyrmex pungens* (Tsuji, 1988, 1990), all Isoptera, and *Austroplatypus* beetles (Kent and Simpson, 1992). We consider the uncertain status of some Polistinae and Halictinae, with respect to whether eusociality is facultative or obligate, as an important challenge to students of sociality rather than a drawback of our categorization scheme.

### Cooperatively breeding societies

Cooperatively breeding societies contain, at any one time, behaviorally distinct groups, with individuals of one group specializing in reproduction and individuals of the other group or groups specializing in helping individuals of the more reproductive group to reproduce. All individuals, of all groups, are totipotent. Therefore, such societies do not contain castes, and individuals can and do switch between behavioral groups after reproductive maturity.

Cooperatively breeding societies can be divided into two categories, according to whether the frequency distributions of lifetime reproductive success (LRS) within populations are unimodal (quasisocial) or bimodal (semisocial) (Table 2). This distinction may be somewhat arbitrary, because unimodal distributions may grade insensibly into bimodal ones; indeed, if statistical tests were needed to distinguish the two types of distribution (e.g., Wyszomirski, 1992), then the distinction would be of limited usefulness. However, the current ease of classifying most well-studied cooperatively breeding societies by this criterion suggests that it corresponds to an actual pattern of variation in nature.

Examples of quasisociality may be seen in most vertebrates already considered to be cooperative breeders (Emlen, 1991; Fitzpatrick and Woolfenden, 1988: 308), some stenogastrine wasps (Carpenter, 1991; Turillazzi, 1991), possibly the bee *Eulaema nigrita* (Michener, 1974: 43), *Pristomyrmex pungens* (Tsuji, 1988, 1990), and some spiders (e.g., *Aebutina binotata*, Avilés, 1993). Semisocial societies may include those of naked mole-rats (Jarvis, 1981; Sherman et al., 1991), apparently, at least one polistine wasp (Sinha et al., 1993), some Ponerinae with gamergates (Ito, 1993; Ito and Higashi, 1991; Peeters, 1993), some Halictinae (e.g., *Halictus ligatus*, Packer and Knerer, 1986; *Augochloropsis sparsilis*, Michener, 1974: 261–264; Michener and Lange, 1959), and some Xylocopinae (e.g., *Xylocopa pubescens*, Hogendoorn and Leys, 1993; see also Michener, 1990b).

We have changed the defining features of the terms quasisocial and semisocial from those of Michener and Wilson (Tables 1 and 2). We have retained these terms, but altered their definitions, for two reasons. First, no or very few species are known to exhibit unequivocal quasisociality or

**Table 2**  
**A revised classification scheme for social animals**

	Alloparental care	Castes
Communal	No	No
Cooperatively breeding	Yes	No
Eusocial	Yes	Yes

We define alloparental care as feeding or defense of offspring that are not direct descendents, excluding cases of mistaken paternity or maternity and cases where the care is an incidental effect of other behaviors. We define castes as groups of individuals that become irreversibly behaviorally distinct at some point prior to reproductive maturity. Communal societies exhibit nest-sharing, but not alloparental care. Cooperatively breeding societies can be subdivided into semisocial (with a bimodal distribution of LRS) and quasisocial (with a unimodal distribution of LRS), but determining whether this distinction is nonarbitrary requires further empirical studies and analysis. LRS distributions should be compiled only for individuals who have survived to the onset of reproductive or nepotistic effort. Eusocial societies may be either facultatively eusocial (with totipotency of one caste, but not the other), or obligately eusocial (with totipotency of neither caste). When semisocial or quasisocial colonies occur within species having castes, only one caste is present (i.e., all gynes during pleometrosis, or all non-gynes after gyne death).

semisociality by Michener's or Wilson's definitions, although semisocial and quasisocial colonies are frequent occurrences during colony cycles in some bees and wasps. Semisociality is apparently restricted to temporary phases early in colony ontogeny (i.e., pleometrosis) or where the usual colony structure breaks down (i.e., foundress death or supercedure); quasisocial colonies are quite similar to semisocial ones, but lack a division of labor (Michener, 1974: 43–44). No species are definitively known to exhibit semisociality by Michener's and Wilson's definitions because none are known to have true (permanent) castes (Michener, 1974: 44–45; but see Schwarz, 1986, 1987 for a possible case). Second, all species or colonies that have been called semisocial or quasisocial, by Michener's and Wilson's classification, remain in these same categories with our changed definitions. Retention of these terms thus maximizes continuity in describing the social systems of noneusocial insects.

Cooperatively breeding vertebrates have usually been divided into two categories, those with "helpers-at-the-nest" (or den), which have a single reproductive pair or individual, and those with "communal breeders" (also called "plural" breeders, e.g., Smith, 1990), which have more than one reproductive of one or both sexes (Emlen, 1991). However, some researchers in this field have used the terms cooperatively breeding and communal synonymously (see Brown, 1978). To enforce consistency between researchers studying arthropods and vertebrates, we suggest that: (1) the term communal be reserved for societies with nest-sharing but not alloparental care, and (2) the term plural breeding be used for describing societies with multiple reproductives. This same classification system was advocated by Emlen (1991) in a recent definitive review. Smith (1990: 599) points out that, because

some taxa exhibit both helper-at-the-nest groups and plural breeding groups, the difference between them "is therefore only one of degree." Justification for retaining both terms is based on useful description, rather than clear, fundamental evolutionary differences. The arthropod equivalent of plural breeding is simply having multiple reproductives in a cooperatively breeding society.

It is important to recognize that many species may express more than one form of sociality. We therefore use the term societies rather than species, and our categories can be applied to populations or colonies when there is variation within a species. Within any of our categories, societies may differ in the expression of socially important traits, such as presence or absence of generation overlap, the degree to which individuals of helper castes reproduce, the degree of differentiation between castes, and, in cooperatively breeding societies, the frequency of independent colony-founding or the proportion of individuals who reproduce (e.g., from most or virtually all, in *Pristomyrmex pungens*, to relatively few, in pied kingfishers or white-fronted bee-eaters). We believe that it would be burdensome and unwise to attempt to create separate terms and categories for each of the possible combinations of these traits. For example, it is conceivable that each of our categories contains examples with and without generation overlap, and the basic similarities and differences between social structures may be obscured if each was granted its own category.

Variation in sociality among cooperatively breeding societies can also be usefully described along the quantitative axis developed by Vehrencamp [(1979), discussed in Emlen (1991: 332–333)], which permits estimation of the relative importance of inclusive fitness effects and personal fitness effects, and the degree to which the helping behavior is mutualistic or altruistic. If quantitative variables, such as the distributions of LRS or Vehrencamp's measure, eventually indicate that cooperatively breeding societies do form discrete categories, then division into subsets, such as semisocial and quasisocial, reflects nonarbitrary differences between societies in social patterns. By contrast, if empirical studies fail to reveal clear distinctions between different cooperatively breeding societies, then variation within this social system can best be described along continua such as Vehrencamp's.

#### Problems with the term eusociality

Sherman et al. (1995) have proposed that the term eusociality should refer to all social systems that involve alloparental care (see also Gadagker, in press), and that variation among such systems should be described by a single variable, the "index of reproductive skew" (Keller and Vargo, 1993; Reeve and Ratnieks, 1993). We believe that their approach is inappropriate for three reasons: (1) they are incorrect in their denial of the existence of discretely-different social systems; (2) their index of reproductive skew is a poor measure of variation in social level because variation in reproduction is due to many nonsocial causes as well as social ones; and (3) profoundly different frequency distributions of lifetime reproduction can yield the same index of reproductive skew.

The first problem with the ideas of Sherman et al. (1995) involves two questions: whether different types of alloparental social systems exist in nature, and, if so, how and by what criteria they differ. By different *types* of social system, we mean social systems that differ discretely in the patterns of behavioral interaction among members. Empirical identification of the existence of discretely different types of social systems requires measuring behavioral variables relating to sociality, and determining whether societies form clusters or vary continuously along some axis or axes. But what behaviors should be measured, and what axes of comparison are most directly indicative of variation among species in selection on social behavior?

Castes, as we have defined them, exist in some species but not in others. Societies in these two categories differ profoundly because in societies with castes, individuals follow one of multiple, discretely different, irreversible life history trajectories. The irreversibility of castes—the loss of switching between behavioral groups—represents an evolutionary threshold: once an individual has entered a caste, natural selection of its behavior has become circumscribed in its effects to modification within a specific, limited range of behaviors. We believe that such specialization of behavior evolves only under selective conditions substantially different from those that have produced noneusocial systems, and has profound evolutionary effects, and that elucidation of such conditions and effects is one of the main tasks of studies of social behavior.

The second problem with Sherman et al. (1995) is that their index of reproductive skew is a poor measure of information concerning social level, and therefore a poor, if not a seriously misleading, indicator of social convergence or divergence between disparate taxa. The index fails in its intended task because many of the major causes of variation in lifetime reproductive success, such as surviving parasites and predators, have little or nothing to do with social interactions. Thus, two populations may have exactly the same social system, but very different indices of reproductive skew because many individuals of one population succumb to disease and are included as nonbreeders in the skew computation. At best, the index will be correlated, to some unknown degree, with the amount of variation in reproduction due to social behavior.

A third problem with Sherman et al. (1995) is that a given value of skew could correspond to profoundly different distributions of reproduction. For example, consider two groups of ten breeding individuals, one with the distribution of lifetime offspring production 3,4,4,4,4,4,4,4,10, and the other with the distribution 1,2,3,4,5,5,6,6,6,7. The distribution is clearly bimodal in the former case, and continuous and unimodal in the latter, but the two groups have virtually identical values for the index of reproductive skew! Thus, the index conveys little information about the distribution of reproduction within societies. Using their measure, Sherman et al. (1995) would group species or populations together by the degree of skew obtained, without reference to how such skew arises. Such a process is analogous to addressing sex ratio evolution by grouping species according to the degree of skew in sex ratio, while ignoring the mode of sexual expression (e.g., hermaphrodites, sequential

hermaphrodites, or true males and females). We believe that the latter type of criterion is a much more appropriate basis for making evolutionary comparisons, and we use this type of criterion to address behavioral variation among animal societies: uniformity of behavior (communal), facultative behavioral alternatives (cooperative breeding), or permanent behavioral alternatives (eusociality).

The presence of important nonsocial causes of variation in lifetime reproduction, and the observation that very different distributions of reproduction yield the same values for skew, vitiate the claim by Sherman et al. (1995) that the index of skew can be used to recognize convergences between different taxa. Moreover, their statement that reproductive skew “directs the evolution of key societal features” is incorrect. The index of reproductive skew is simply a number closely related to the opportunity for selection (Arnold and Wade, 1984; Crow, 1958) that indicates only how rapidly a trait can evolve if there is selection upon it. As such, the index contains no information about how societies have been shaped or directed by the diverse interactions between environments and phenotypes that the sole cause of social evolution.

Sherman et al. (1995) argue that our definition of eusociality is inadequate for three reasons. First, they state that our definition is “so restrictive that many insects traditionally regarded as eusocial . . . would have to be reclassified.” We agree, because we believe that reclassification of many species is the first necessary step toward identification of convergences between diverse taxa. Moreover, we prefer a classification scheme that is precise, restrictive, and correct over one that is either inaccurate, all-encompassing, and uninformative (Sherman et al.'s) or ambiguous (Michener's and Wilson's).

Second, Sherman et al. (1995) claim that our definition is “difficult to apply.” We believe that this objection is both irrelevant and incorrect. The objection is irrelevant because whether a pattern or entity, be it eusociality or the Higgs boson, exists in nature has nothing to do with how difficult or easy it is for us to identify. The objection is incorrect because the detection of any switching between behavioral groups (putative castes), after reproductive maturity, is sufficient to indicate that a society is not eusocial.

Third, Sherman et al. (1995) state that totipotency is an arbitrary criterion for distinguishing social systems. As we have explained throughout this article, loss of totipotency is probably the most evolutionarily relevant event in social evolution, because it results in distinct, divergent, lifetime behavioral trajectories.

Clear and precise definitions of social terminology should clarify the genetic and ecological causes of social evolution, by delineating the boundaries and highlighting the similarities between all social animals. For example, our approach has led us to the insight that the only two cooperatively breeding birds in which helping is altruistic rather than mutualistic by Vehrencamp's measure, white-fronted bee-eaters and pied kingfishers, are the only alloparenting bird species which have both social dispersion patterns (colonial, nonterritorial; Smith, 1990: 598) and nest types (burrows in soil) similar to those of many Hymenoptera. Moreover, given that Stenogastrinae, some Polistinae, and even *Pris-*

*tomymex pungens* ants appear similar behaviorally and ecologically to some alloparental vertebrates (Strassmann and Queller, 1989), we should cast aside hesitations in calling a hymenopteran a cooperative breeder. Such taxonomic unification should lead to a host of new questions, such as whether cooperatively breeding ponerine ants are convergent with carnivores having helpers-at-the-den.

Progress in analyzing the causes of the different forms of sociality has become seriously hampered by vagueness of terminology. We believe that our revised lexicon expresses more accurately what most students of sociality mean when they say eusociality, and reflects more clearly the patterns existing in the natural world.

We are grateful to A. Bourke, B. Danforth, G. Eickwort, J. Herbers, L. Keller, P. Kukuk, C. D. Michener, U. Mueller, T. Seeley, P. Sherman, M. Schwarz, L. Vawter, M. J. West-Eberhard, W. Wcislo, M. Winston and two anonymous reviewers for helpful discussions and comments, many of them on earlier incarnations of this paper. This article began as a joint venture of B. Crespi with P. Sherman and E. Lacey. This research was supported by a grant from the Natural Sciences and Engineering Research Council of Canada.

Received 1 August 1993

Revised 31 January 1994

Accepted 7 February 1994

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