

The eusociality continuum

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Eusocial societies are traditionally characterized by a reproductive division of labor, an overlap of generations, and cooperative care of the breeders' young. Eusociality was once thought to occur only in termites, ants, and some bee and wasp species, but striking evolutionary convergences have recently become apparent between the societies of these insects and those of cooperatively breeding birds and mammals. These parallels have blurred distinctions between cooperative breeding and eusociality, leading to calls for either drastically restricting or expanding usage of these terms. We favor the latter approach. Cooperative breeding and eusociality are not discrete phenomena, but rather form a continuum of fundamentally similar social systems whose main differences lie in the distribution of lifetime reproductive success among group members. Therefore we propose to array vertebrate and invertebrate cooperative breeders along a common axis, representing a standardized measure of reproductive variance, and to drop such (loaded) terms as "primitive" and "advanced" eusociality. The terminology we propose unites all occurrences of alloparental helping of kin under a single theoretical umbrella (e.g., Hamilton's rule). Thus, cooperatively breed-

ing vertebrates can be regarded as eusocial, just as eusocial invertebrates are cooperative breeders. We believe this integrated approach will foster potentially revealing cross-taxon comparisons, which are essential to understanding social evolution in birds, mammals, and insects. Key words: avian eusociality, cooperative breeding, eusociality, mammalian eusociality, reproductive skew, social system convergence. [Behav Ecol 6:102-108 (1995)]

The evolution of eusociality has been an important puzzle ever since Darwin (1859: 268) identified worker ants as presenting "one special difficulty, which at first appeared to me insuperable, and actually fatal to the whole theory." In 1966, Batra coined the term eusocial (meaning truly social) to describe halictine bees in which "the nest founding parent survives to cooperate with a group of her mature daughters, with division of labor" (p. 375). Subsequently, Michener (1969: 305) referred to bees as eusocial if they lived in "matrifilial family groups consisting of . . . mothers and daughters . . . [showing] division of labor with more or less recognizable castes (egg layers and workers)."

In 1971, Wilson broadened these criteria to include other insects. Following his lead, Hölldobler and Wilson (1990: 638) defined eusocial species as those exhibiting "cooperation in caring for the young; reproductive division of labor, with more or less sterile individuals working on behalf of individuals engaged in reproduction; and overlap of at least two generations of life stages capable of contributing to colony labor." Once thought to occur only in the orders Hymenoptera (ants, bees, and wasps) and Isoptera (termites), eusociality has now been reported in Japanese aphids (Homoptera: Aoki, 1982; Itô, 1989), Australian weevils (Coleoptera: Kent and Simpson, 1992), Australian thrips (Thysanoptera: Crespi, 1992), and African mole-rats (Rodentia: Burda and Kawalika, 1993; Jarvis and Bennett, 1993; Jarvis et al., 1991, 1994).

As detailed information has accumulated on the reproductive and social behavior of vertebrates and invertebrates, distinctions between eusociality and other social systems have become blurred. Indeed, a number of authors have identified striking evolutionary parallels between the social systems of cooperatively breeding birds and mammals and those of social insects (e.g., Alexander et al., 1991; Andersson, 1984; Emlen et al., 1991; Lacey and Sherman, 1991; Reeve and Sherman, 1991; Veh-

rencamp, 1979). Further, as Seger (1991: 346) noted, detailed studies of insects have revealed a broad spectrum of social organizations among species traditionally characterized as eusocial (e.g., see Keller, 1993; Michener, 1985; Ross and Matthews, 1991).

Not surprisingly, therefore, several authors (e.g., Crespi and Yanega, 1994; Tsuji, 1992) have recently questioned the adequacy of traditional definitions of eusociality. Problems have arisen primarily because the key defining characteristic—"reproductive division of labor, with more or less sterile individuals working"—is vague and thus ambiguous in its application. One solution is to define eusociality more narrowly. This approach has been adopted by Tsuji (1992) and Crespi and Yanega (1994), who argue that the term should be applied to only a subset of the insects currently recognized as eusocial. Alternatively, definitional problems could be reduced by expanding the eusociality concept to include all vertebrate and invertebrate societies with helpers.

We favor the latter approach. It seems more productive to recognize that similar social systems occur in birds, mammals, and insects than to debate whether particular insects are eusocial (e.g., Furey, 1992 versus Tsuji, 1992). Behavioral convergences between eusocial insects and cooperatively breeding vertebrates should long ago have focused our attention on common selective factors favoring sociality and alloparental care in these taxa (see Strassmann and Queller, 1989). Research on these groups has proceeded largely independently, however, and as a result there is currently one set of evolutionary explanations for cooperative breeding in birds and mammals (e.g., Brown, 1987; Emlen, 1991; Jennions and Macdonald, 1994) and a parallel, but distinct, set of explanations for sociality in insects (e.g., Seger, 1991; Trivers, 1985). We suggest that the evolution of sociality in both groups will be best understood if these explanations are merged.

As a first step toward this unification it would be useful to have a quantitative way to compare social systems across diverse taxa. Current schemes for comparing insect societies are qualitative, however, and emphasize traits that result only secondarily from reproductive differences among colony members. For example, some authors (e.g., Cowan, 1991; Eickwort, 1981; Michener, 1974) distinguish "advanced" from "primitive" eusociality. Advanced eusocial species inhabit large, long-lived colonies containing workers that typically are unable to mate and that are well-differentiated morphologically from queens, whereas primitively eusocial species live in small, often annual colonies containing workers that are morphologically similar to queens and, usually, capable of mating.

The advanced-primitive dichotomy was erected primarily to categorize morphological and social complexity, not unevenness in reproduction. As a result it only crudely discriminates between societies with weakly versus sharply defined reproductive divisions of labor. For example, worker reproduction occurs in many "advanced" eusocial ants (Bourke, 1988; Choe, 1988) but not in queenright colonies of some "primitively" eusocial bees (Michener et al., 1979) and wasps (reviewed by Reeve, 1991). Moreover, this dichotomy is difficult to apply to specific cases because variation in each of

the distinguishing attributes (e.g., morphological differentiation of colony members) is continuous, rather than discrete, both within and among taxa. Finally, the terms "primitive" and "advanced" are both value-laden and ambiguous, as they may refer either to social complexity (*sensu* Michener, 1969) or similarity to presumed ancestral forms (*sensu* Carpenter, 1991).

To resolve these ambiguities, we propose using variation in lifetime reproductive success (LRS) among members of cooperatively breeding social groups to quantify "reproductive division of labor." Reproductive differences are central to all definitions of eusociality, and they underlie much of the diversity among vertebrate and invertebrate societies (see Bourke, 1991; Vehrencamp, 1979). Such differences result from social competition and suppression within groups as well as ecological factors that preclude reproduction by some group members. Differences in LRS provide an evolutionarily relevant basis for interspecific comparisons because it is through such differences that natural selection shapes the morphology, physiology, and behavior of eusocial species.

One could standardize LRS variation in numerous ways. One possibility is the index of reproductive skew (S) developed by Reeve and Ratnieks (1993) and Keller and Vargo (1993):

$$S = \frac{N_b v + N_n}{N_b + N_n}$$

where N_n is the number of nonbreeding alloparents (helpers) in a group, N_b is the number of breeders in the group (some of which may also behave as alloparents), and v is a measure of the variation in reproductive success among breeders. In groups containing a single breeder, v is defined as 1.0; in groups with multiple breeders, v is the variance among breeders in their proportion of the summed LRS of the group divided by the maximum possible value for this variance. Thus, $v = N_b s^2$, where s^2 is the sample variance in the proportion of total offspring produced by breeders:

$$s^2 = \frac{\sum_{i=1}^{N_b} \left(p_i - \frac{1}{N_b} \right)^2}{(N_b - 1)}$$

(in this expression, p_i is the proportion of offspring produced by the i th breeder).

Using S , one can begin to compare the degree of reproductive skew within and among social species on a common scale that ranges from 0 to 1. When LRS is equal among group members, $S = 0$; when reproduction is restricted to a single individual and other group members never breed, $S = 1$. If, as seems likely, skews vary considerably among conspecific groups or populations, then species may be represented as segments of the scale rather than as points. The index of reproductive skew can be calculated for males only, females only, or both sexes, depending on who participates in alloparental care—e.g., females in species of social Hymenoptera, males in many cooperatively breeding birds, and both sexes in termites and some carnivores.

We emphasize that the S index of Reeve and Ratnieks (1993) and Keller and Vargo (1993) is used for illustrative purposes, as one possible way

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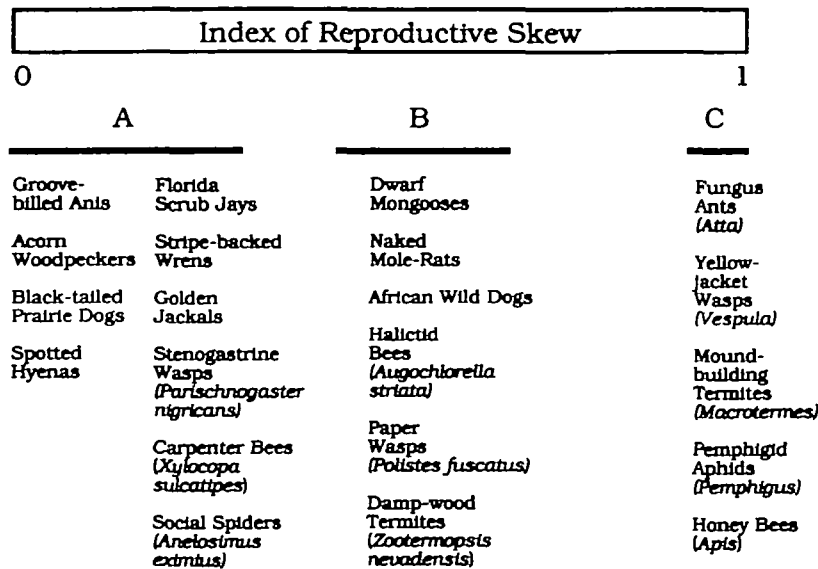


Figure 1
Intervals within which the societies of selected vertebrate and invertebrate cooperative breeders are expected to occur on a common scale of intragroup skew in lifetime reproductive success (see the text). There is no skew (i.e., 0) when LRS is equal among members of a social group; skew is maximal (i.e., 1) when reproduction is restricted to a single individual of each sex per group and helpers never breed. When skews vary considerably among conspecific groups or populations, species are best represented as line segments denoting intraspecific ranges. Indices of reproductive skew may be calculated for male group members only, females only, or both sexes, depending on who participates in alloparental care; for this figure, only female reproductive skews are considered. For clarity of presentation, societies that apparently exhibit similar reproductive skews are grouped together; intervals A, B, and C are not meant to denote separate categories in the eusociality continuum.

to construct a continuum for eusociality (see also Bourke, 1991). *S* provides only a rough summary of the distribution of LRS among group members, because different social groups with similar skew indices could have LRS distributions that differ in shape (e.g., in other continuous parameters such as skewness or kurtosis). Nonetheless, we suggest that *S* provides a useful preliminary method for identifying potentially similar social systems.

Although detailed data on LRS are not available for most social insects and cooperatively breeding vertebrates, existing behavioral and demographic information allows us to predict the relative positions of different societies along a scale of skew in LRS. At the low end of the scale (in subinterval A of Figure 1), lie helper-at-the nest/den societies with multiple reproductive individuals per group (e.g., "joint-nesting plural breeders," Brown, 1987). Examples of such societies include groove-billed anis (*Crotophaga sulcirostris*: Koford et al., 1990; Vehrencamp et al., 1988), acorn woodpeckers (*Melanerpes formicivorus*: Koenig and Mumme, 1987), black-tailed prairie dogs (*Cynomys ludovicianus*: Hoogland, in press), spotted hyenas (*Crocuta crocuta*: Frank, 1986; Frank et al., in press), lions (*Panthera leo*: Packer et al., 1988), and banded mongooses (*Mungos mungo*: Rood, 1986). Polyandrous cooperative breeders, in which male helpers mate with the breeding female (e.g., Arabian babblers, *Turdoides squamiceps*: Zahavi, 1990), will also lie at the lower end of the scale, but exactly where depends on how unevenly paternity is divided among the attending males.

Societies in which auxiliaries do not reproduce while helping (i.e., "singular breeders," Brown, 1987) but have a reasonable probability of successfully dispersing and producing offspring later in life are also expected to fall toward the low end of the scale. Reproductive skews for these societies will likely be higher than those for joint-nesting plural breeders because of helper mortality while behaving as alloparents. Examples of such societies

include Florida scrub jays (*Aphelcoma coerulescens*: Fitzpatrick and Woolfenden, 1988; Woolfenden and Fitzpatrick, 1984), splendid fairy-wrens (*Malurus splendens*: Rowley and Russell, 1990), stripe-backed wrens (*Campylorhynchus nuchalis*: Rabenold, 1990), green woodhoopoes (*Phoeniculus purpureus*: Ligon and Ligon, 1990), golden jackals (*Canis aureus*: Moehlman, 1986), pine voles (*Microtus pinetorum*: FitzGerald and Madison, 1983; Powell and Fried, 1992), and certain marmosets (*Saguinus* spp.: Snowdon and Soini, 1988), tamarins (*Callithrix* spp.: Stevenson and Rylands, 1988), stenogastrine wasps (Turillazzi, 1991), carpenter bees (Hogendoorn and Velthuis, 1993; Stark, 1992), and social spiders (e.g., *Anelosimus eximius*: Rypstra, 1993; Vollrath, 1986).

Toward the middle of the scale (subinterval B in Figure 1) will be singular breeding societies in which opportunities for direct reproduction by helpers are limited throughout life. In these cases, helping is not simply an ontogenetic stage through which most or all individuals pass prior to reproducing directly. Instead, because of limited opportunities for direct reproduction, only a fraction of helpers in these species will eventually produce offspring, usually via immigration to groups lacking a reproductive or superseded within groups. Examples include naked mole-rats (*Heterocephalus glaber*: Sherman et al., 1991, 1992), damaraland mole-rats (*Cryptomys damarensis*: Jarvis and Bennett, 1993; Jarvis et al., 1994), dwarf mongooses (*Helogale parvula*: Creel and Waser, 1991; Rood, 1986), African wild dogs (*Lycan pictus*: Frame et al., 1979; Malcolm and Marten, 1982), wolves (*Canis lupus*: Harrington et al., 1983), some halictid bees (e.g., *Augochlorella striata*: Mueller, 1991; *L. brevis*: Michener et al., 1979; *L. figueresi*: Wcislo et al., 1993), paper wasps (e.g., *Polistes fuscatus*: Klahn, 1981; Metcalf, 1980), small-colony termites (e.g., *Incisitermes schwarzi*: Luyckx, 1993; *Zootermopsis nevadensis*: Shellman-Reeve, in press) and many bumblebees (*Bombus* spp.: Free and Butler, 1959).

Finally, at the upper end of the scale (subinterval C in Figure 1) will be societies exhibiting consistent, pronounced intragroup differences in LRS due to the virtual absence of direct reproduction by most group members. Familiar examples are social insects with physiologically sterile or semi-sterile workers, such as Japanese aphids (*Pemphigus* spp.: Benton and Foster, 1992; Foster, 1990; Itô, 1989), fungus ants (*Atta* spp.: Hölldobler and Wilson, 1990), yellow-jacket wasps (*Vespa* and *Dolichovespula* spp.: Greene, 1991), large-colony termites (*Macrotermes* spp.: Wilson, 1971), and honeybees (*Apis mellifera*: Page and Metcalf, 1984).

Societies that lie at different positions along the scale of reproductive skew differ in several ways. Most importantly, those at the upper end live in larger groups, indeed usually orders of magnitude larger, than societies in the middle and at the lower end of the scale. Group size has two important evolutionary implications for the elaboration of alloparental care. First, as group size increases, the probability decreases that a particular individual will be able to fill any within-group breeding vacancy (see Reeve and Ratnieks, 1993). Thus, in species that live in large groups, individuals may transmit their genes more effectively by specializing physiologically, morphologically, and/or behaviorally to help relatives than they would by retaining

the capacity to personally reproduce and either waiting for a breeder's demise or attempting to reproduce in the breeder's presence. This is especially true if retaining the capacity to reproduce diminishes a helper's effectiveness, or if alloparental care greatly enhances group reproductive output. Second, a positive relationship between group size and specialization of helper phenotypes can also arise due to severe ecological conditions that strongly favor both the formation of large groups and alloparental care of young. Under these circumstances, natal philopatry and helping relatives may so consistently yield the highest inclusive fitness payoffs that irreversible specializations for helping evolve.

For these reasons the inability to reproduce may be obligate among large-colony societies, but facultative among small-colony societies. Direct conflict over reproduction is more characteristic of cooperative breeders that live in small groups (e.g., wolves: Zimen, 1976; dwarf mongooses: Creel et al., 1992; naked mole-rats: Faulkes et al., 1990; paper wasps: Reeve and Nonacs, 1992; Reeve and Ratnieks, 1993) than those that live in very large groups. The evolution of specialized helper phenotypes (e.g., castes) and intragroup breeding conflict thus are apparently related to group size, which is itself a function of the ecological advantages of group-living.

Societies that lie at different positions along the scale of reproductive skew should also differ in the distribution of LRS within social groups. Histograms of LRS for societies at the lower end will be roughly unimodal and symmetric or slightly skewed. For societies more toward the middle, LRS will be unimodal and strongly skewed, because some individuals produce many offspring but the majority produce only a few. At the upper end of the scale, histograms of LRS will be bimodal and lacking in intermediate classes: a few individuals produce all the young, whereas the rest do not reproduce (e.g., for data on honeybees, see Page and Metcalf, 1984). Bimodality is more evident at the high end of the scale because societies with extreme reproductive skews are mostly large-colony social insects in which maximum lifetime fecundity of queens versus workers is far greater than that of female breeders versus helpers in cooperatively breeding vertebrate societies.

These considerations suggest that eusociality is best viewed as a continuum rather than a discrete phenomenon. If eusociality is regarded as discrete, whatever "break point" on the scale of LRS skew is chosen as the defining cut-off would be arbitrary. Using the same logic, Shields (1993) recently argued against arbitrarily dichotomizing inbreeding versus outbreeding: because genetic relatedness among mates is a continuous variable, inbreeding also is a continuum. Although skews in LRS for social insects will often be greater than those for vertebrates, we expect these values to overlap, with no quantitative discontinuities between taxa. Given that most cooperatively breeding birds and mammals already meet two of the three traditional criteria for eusociality (overlap of generations and cooperative care of young), this implies that cooperative breeders can be regarded as "eusocial"—just as eusocial insects can be termed "cooperative breeders."

Some readers may balk at our attempt to broaden the concept of eusociality. Indeed, Crespi and Yanega (1995) propose to resolve ambiguities in the traditional definition by restricting eusociality to societies with irreversibly behaviorally distinct groups (castes), one or more of which is not "totipotent" (i.e., does not exhibit the full behavioral repertoire of the species). They further separate "facultatively eusocial" societies, in which only the "more-reproductive" caste is totipotent, from "obligately eusocial" societies, in which neither caste is totipotent. When there is reproductive division of labor and altruistic alloparental care, but no irreversible reduction in the behavioral repertoire of the alloparents, Crespi and Yanega term the society "cooperatively breeding." Such societies are further subdivided into "quasisocial" and "semisocial," depending on whether the distribution of LRS is unimodal or bimodal. This classification system roughly maps out as ordered segments along the continuum in our Figure 1 (e.g., proceeding from the left, quasisocial cooperative breeding, semisocial cooperative breeding, facultative eusociality, and obligate eusociality).

We have several reservations regarding Crespi and Yanega's definitional scheme. First, it categorizes societies as eusocial using a phenotypic feature ("irreversible behavioral distinctness") that is just one possible evolutionary outcome of reproductive differences among colony members. Crespi and Yanega state that "loss of totipotency is probably the most evolutionarily relevant event in social evolution, because it results in distinct, divergent, lifetime behavioral trajectories." This justification is insufficient, as it fails to indicate why lifetime differences in behavior are significant—simply stating that reductions in behavioral repertoires lead to increased behavioral specializations is not compelling. Although Crespi and Yanega go on to suggest that loss of totipotency is important because selection on the behavior of newly arisen castes "has become circumscribed," this argument confuses ontogenetic reversibility with potential for selective modification—concepts at two different logical levels of analysis.

Second, the Crespi-Yanega scheme effectively restricts eusociality to invertebrates. The separation of invertebrate from vertebrate societies tends to decouple evolutionary explanations for eusociality and cooperative breeding. This is unfortunate because vertebrate and invertebrate social systems are not fundamentally different, but instead vary quantitatively with respect to the same underlying evolutionary principles (e.g., Hamilton's rule; see Grafen, 1991). Under Crespi and Yanega's dichotomous scheme, however, similar social systems, such as those of naked mole-rats and sweat bees, are conceptually segregated, whereas rather dissimilar social systems, such as those of dwarf mongooses and social spiders, are lumped together.

Third, Crespi and Yanega place many societies that have traditionally been recognized as eusocial (e.g., some paper wasps, hover wasps, halictid bees, ponerine ants, and mole-rats; see Eickwort, 1986; Jarvis, 1981; Peeters, 1993; Turillazzi, 1991) into the quasisocial or semisocial categories, because they assume that workers are totipotent. Discovery of even one behavioral or physiological discontinuity, however, would cause such species to sud-

denly shift into the eusocial category. To accurately classify societies according to Crespi and Yanega's definitions requires knowing: (1) the behavioral repertoire of all groups of colony members in all social/environmental contexts, and (2) whether there is "obligate complementarity and mutual dependency of the castes." This leaves most species in limbo, because it is rarely known whether some or all colony members are totipotent in all environments. Further, because Crespi and Yanega include physiological attributes in their definition of caste, detailed knowledge of interindividual differences in physiology is also necessary to separate eusocial and cooperatively breeding species. Such data are difficult to obtain and relationships between physiological differences and behavioral totipotency are usually unknown.

The difficulties of using Crespi and Yanega's complicated definitional scheme are illustrated by attempts to classify the paper wasp *Polistes fuscatus*. They list it as (facultatively) eusocial, arguing that workers represent a distinct caste because, unlike foundress queens, workers cannot diapause or found new nests. However, *Polistes* workers do sometimes found nests (reviewed by Reeve, 1991). Further, there is no evidence that a replacement queen has a smaller behavioral repertoire than a foundress, because neither is likely to diapause after she has been a queen. Thus it is unclear whether *Polistes* species should be labeled as eusocial or cooperatively breeding.

A second example of these difficulties concerns the sweat bee *Halictus rubicundus*. According to Yanega (1989), reproductive competence in this species is determined by each female's mating success during the first few days after eclosion. Whether or not a female mates reportedly depends on the sex ratio at eclosion. Whereas females that mate become queens, females that do not mate become workers. Crespi and Yanega classify *H. rubicundus* as (facultatively) eusocial. From an evolutionary perspective, however, this bee is not very different from the superb fairy-wren (*Malurus cyaneus*), a cooperatively breeding bird in which limited access to mates because of a male-biased sex ratio forces males to stay in their natal group (Pruett-Jones and Lewis, 1990), where they may remain life-long helpers. Although the specific mechanisms enforcing reproductive asymmetries in the birds and bees differ, they nonetheless result in similar social systems, uneven partitioning of reproduction within social groups, and distinct (if not irreversible) lifetime trajectories of behavior and reproduction.

These problems could be largely avoided by using a measure of reproductive skew to classify cooperatively breeding societies. Skew is a fundamental attribute of all such societies—one that connects social evolution to its ecological and genetic foundations (Reeve, 1991; Vehrencamp, 1979, 1983a,b) and that can direct the evolution of key societal features, including the intensity of dominance interactions, the existence of castes, and the extent of caste specializations (i.e., "totipotency"; Keller and Reeve, 1994; Reeve and Ratnieks, 1993). Although the index of reproductive skew presented here is crude, it appears to describe much of the variation among social systems. Interestingly, Crespi and Yanega also embrace a continuous measure as part of their own classification scheme, using

Vehrencamp's (1979) index of mutualism/altruism (which is closely associated with our skew index) to describe the relative importance of personal reproduction versus indirect fitness effects in societies of cooperative breeders. We have simply extended this conceptual approach to its logical conclusion.

In sum, we agree with Crespi and Yanega (1995) that it is time to clarify the definition of eusociality. We believe, however, that it is more appropriate to expand than to contract the concept. Our approach emphasizes convergence and the roles of common selective principles underlying social evolution. The simple, continuous classification system that we propose unites societies exhibiting reproductive division of labor and alloparental helping of kin under a single theoretical and terminological umbrella, thus fostering potentially revealing cross-taxa comparisons. We believe this integrated approach is essential to understanding social evolution in both vertebrates and invertebrates.

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