



Superorganismality as defined by Wheeler is crucial for understanding major evolutionary transitions to caste-differentiated colonies

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Four decades of sociobiology have left us with multiple superorganism concepts that are mutually inconsistent and uninformative on how superorganismality originates. Wheeler's original concept did not have these problems; it gave early 20th century naturalists and geneticists a clear understanding of unconditional reproductive altruism and the irreversible acquisition of an unmated worker caste. Wheeler superorganismality was also consistent with Darwin's concept of family selection, which was later confused with group selection adding to the lack of conceptual transparency that has plagued our field. The sociobiology definition of eusociality has been a root cause of this problem, because it lumped a diverse spectrum of social systems into a single category so that fundamental differences in commitment to social life are glossed over. This was not because the original definitions of eusociality by Huxley (1930) and Batra (1966) were unclear – they were just never intended to include superorganismal lineages where all colony members belong to a single caste phenotype for life, but rather addressed advanced cooperative breeding where entire cohorts become helpers without becoming a life-time unmated caste. As it appears, controversies over the status of inclusive fitness theory emanate from the arbitrarily defined sociobiological concepts of superorganismality and eusociality, not from the theory itself. Hamilton's rule is the only generally accepted explanation for the evolution and maintenance of condition-dependent reproductive altruism, but can also be used to identify the necessary and sufficient conditions for the unconditional differentiation of permanently unmated castes. This offers a clear connection between inclusive fitness theory and the major evolutionary transitions paradigm, and shows that transitions to colonial superorganismality are analogous to origins of permanent multicellularity, as foreseen by both Wheeler and Huxley.