**ULTRSOCIALITY, GOODS THEORY, AND PRIMITIVE AGRICULTURE IN
COSMOPOLITAN EARTH AND PUTATIVE EXTRATERRESTIAL
MICROBIAL SYMBIONTS**

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ABSTRACT

Farming microbes select vital tradeoffs favoring economics-reliant ultrasociality, a superior collective state derived from multilevel sociogenetic effects. This public-goods interpretation yields better insights into sociobiological transitions on Earth and model habitable worlds, including consumer drivers of life histories and biospheres.

BACKGROUND

Goods theory remains a popular tool for studying and describing competitive and cooperative microbial behaviors across differing ecological situations (Box 1). But, where lie the limitations of public goods theory for explaining microbial sociobiology? Rauch et al. (24), for example, importantly find both fixed and conditional investment strategies beat public goods game dilemmas for microbes confronting eco-evolutionary tradeoffs that threaten long-term viability of predominant cooperator subpopulations against their freeloader rivals. The authors generalize the outcomes of their yeast-sucrose model system as a predictable case from public goods game theory, where the ability to regulate economic investments through gene-supported smart or rational social strategies allow organisms to colonize more challenging environments over short to long timescales. While these conclusions certainly offer insights into the fundamental nature of social conflict instigation and resolution, Rauch et al. (24), among other scientists, fail to confront severe trending criticisms concerning the value of public goods theory for understanding broader contexts of complex social microbial behavior (e.g., 23,30,31), including possible farming-unique ultrasociality and the use of fallible rational and irrational economic-based decisions to maximize generational and transgenerational outcomes for survival and reproduction. If found to be powerful and internally and externally valid within and across microbiota systematics, such consumer-based effects may be expected to play major roles in shaping the life histories of microbes and the structures and processes of microbial communities, with particular dramatic influence over the origins and evolution of niches to biospheres for habitable worlds beyond Earth. Unfortunately, the sociobiology of early life, or life at any stage of evolution and development for that matter, is often given little to no scientific significance by astrobiologists. Future unmanned and manned exploration of our solar system and elsewhere in the universe will give unprecedented opportunities to appraise contemporary sociobiological thinking and to apply those foundational efforts to practical empirical and theoretical investigations into the origins and evolution of life and societies.

ECONOMICS STRUCTURE OF ULTRASOCIALITY

Ultrasociality, a sophisticated form of mass social organization dependent on division of labor and public-goods-based agricultural subsistence (cf. 17), is considered the evolutionary pinnacle of social-group expression, with robust complex contributions from genes, culture, and other motivating factors. Despite innovative social organization and competencies of simple animal and nonanimal life, sociobiologists rarely credit ultrasociality to clades of organisms older than the Ecdysozoa-Lophotrochozoa divergence (17,25), believing ultrasociality is exemplified by humans and few other members of Kingdom Animalia. Nevertheless, a major microbiota taxon – Dictyostelids – produce complex cosmopolitan societies exhibiting essential traits of ultrasociality, including biomass proliferation, habitat diversity and dominance, sophisticated

Box 1. Forecasting the Economic Origins of Microbial Ultrasociality

Application of economics theory in sociobiology continues to garner strong interest among scientists as a means to explain and predict the evolution and behavior of all social microbiota. The basis of economics theory involves the types and exchange of goods supplied and demanded. Goods may fall within categories for private, club, common-pool, and public resources and (commoditized) services. Private and club goods are associated with property owner rights or some level of excludability, whereas common-pool and public goods are non-excludable. Scarcity of goods motivates rivalry between consumers and may influence acquisition of excludable private goods and non-excludable common-pool goods. Club and public goods are non-rivalrous or minimally rivalrous properties. Scientists for decades have developed and presented arguments of varying soundness or cogentness for excludable/nonexcludable and rivalrous/nonrivalrous microbial societies. Trends in empirical observations for public and private goods behavior in microbes suggests that multilevel selection pressures forced individual-group tradeoffs responsible for convergent evolution of ultrasocial life and sustained elevated viability over both evolutionary and ecological time periods. Microbes displaying these characteristics offer good models to study further the eco-evolutionary complexity of societal formation, stability, and transition, perhaps giving opportunities to reveal similar (or dissimilar) eco-evolutionary processes occurring at other locations in the universe.

division of labor, kinship-(in)dependent conflict instigation/mediation, and tendencies of managed livestock-/crop-like farming (4,5,29,33). Appreciation of near ultrasocial microbial characteristics puts all animal-centric views of ultrasociality evolution into a necessary larger frame. Without such details, scientists arguably cannot fully explain multilevel sociogenetic selection pressures that force individual-group tradeoffs and convergent evolution of ultrasociality and other social forms within and across systematics (cf. 21.22).

An example may be developed from Thutupalli et al. (31), who conclude the nematode *Caenorhabditis elegans* farms soil bacteria in a qualitative different manner than behaviorally unsophisticated microbial systems, which, with possible exception of the cellular slime mold *Dictyostellium discoideum*, depend on metabolic costs of goods synthesis, such as that used by the fungus *Saccharomyces cerevisiae* (24), and not exploration-exploitation strategies and other phenomena. Using related claims, some scientists now judge instances of microbial sociality as illusory outcomes of life-history tradeoffs and nonsocial multiple fitness traits selected by deterministic or stochastic eco-evolutionary pressures (23,30). Such claims strongly contest the power and validity of applying public goods game theory to microbe-salient scenarios, including that espoused by Rauch et al. (24), where regulation of economic investments through gene-supported fixed or conditional social strategies permits microbes to colonize exigent time-varying environments. But, in reaching their conclusions, Thutupalli et al. (31) and additional scientists avoid a significant opportunity to elaborate and strengthen their too narrow animal-centric arguments on evolved public-goods-dependent social structure and function – an outcome that directly impacts scientific interpretations of ultrasociality evolution.

**ECONOMICS-DRIVEN EMERGENCE
OF PRIMITIVE MICROBIAL AGRICULTURE**

Similar to ultrasocial ants and termites (17), sociogenetic features of adaptive microbial symbioses promote economics-dependent ultrasociality in caste-like cosmopolitan (super)colonies. Experimental findings confirm different microbe types, via single or multiple gene mutations, phenotypic switching, and learned behavioral modification (4,5,25,29), can alter their social status within a colony. Social mobility, induced by supply-stressed environmental resources and cell-cell communications reporting community-transformation needs, compels management of individual-group tradeoffs to optimize survival and reproduction. Sometimes individual or group goals are achieved through ruthless, selfish Machiavellian-type rivalry and deception and other times more peaceable, honest altruistic actions are taken (e.g., 1,2,26,32). Whether through these sorts of reciprocating, policing, or alternative social constraint methods, microbes demonstrate remarkable aptitudes to harness intracolony resources to cope with their niche and to conquer additional ones, as observed for microbes transitioning from hunter-/gather-subsistence (e.g., predation, phototrophism, free-nutrient absorption) to (tended/untended) agrarian-type communities that help direct group versatility toward ultrasociality (4,5,28,33).

Making farming-based economics a criterion for ultrasociality, as done for animals (17), requires special attention to *D. discoideum* primitive agriculture (4,5,29,31,33), which evolved as a clone-specific trait that influences life history and fitness. While these microbes and possibly additional ones surely cannot match the farming technology and financial market sophistication of humans, their prowess to survive, reproduce, and establish kin-dependent niche dominance through complex behaviors and exploration-exploitation tradeoffs should not be underestimated. *D. discoideum* farmers proliferate in ecological conditions of low nutrient availability, when solitary hunting is abandoned and ordered motile social collectives, called slugs, are formed to begin fruiting body differentiation and sporulation. Slugs comprised of farmers, as compared to non-farmers, migrate shorter distances to relocate in more favorable, if imperfect, ecological settings as well as prudently harvest bacteria to reserve stores for later consumption during codispersal. The symbiosis between farmer and bacterial livestock is furthermore selective. Farmer amoebae carry proportionately higher populations of preferred-eating bacteria, with additional mixed populations of herd-dog bacteria to help secure and privatize livestock. Taken together, the qualities of *D. discoideum* primitive agriculture support dynamic consumer marketplaces, with structural and operational capabilities of kinship groups effecting sound trading partner choices, creation of strong local business connections, efficient diversification and specialization, high-return indispensable partnerships, ruthless competition elimination, and prudent saving for lean times (cf. 33). These scaled adaptations of Dictyostellids phylogenetically predate socioeconomics-driven change in animal ultrasocieties, strengthening Rauch et al.'s (20) public goods arguments for fungus sociality as well as revealing an exceptional alternate paradigm to Thutupalli et al.'s (31) *C. elegans* model and to other animal models useful for investigating ultrasociality and additional kinds of economics-supported social organization and operation.

RATIONALITY OF MICROBIAL CONSUMER DECISIONS ON ULTRASOCIAL TENDANCIES

That said, convincing application of public goods theory to explain and predict the origins and evolution of social microbial behaviors still needs better elucidation. Martinez-Garcia and Tarnita (21) importantly find and caution that use of dimensionally compacted fitness measures,

Box 2. Traditional Learning and Rational Winning Behavior in Social Microbes

Like animals, certain taxa of microbes, especially heterotrich ciliates, have been shown to encode and apply stored information about spatiotemporally sensitive relationships (i.e., associations) between unconditioned and conditioned stimuli, as in classical conditioning, or between responses and consequences (i.e., reinforcers), as in instrumental conditioning, to perfect social decision making, such as the economics-based maneuverings of mates and rivals during paired reproductive events. These associative phenomena, unlike epigenetic processes, represent traditional forms of learning that underpin intuitive social logics and flexible goal-directed social reciprocity. As informal inferential systems used by humans, animals and microbes, intuitive social logics typically fail to conform to the axioms of categorical, propositional and predicate logics and of probability calculus. The fallibility of intuitive logics was initially revealed by the groundbreaking research of Nobel-prize-winning scientists who studied simple strategies called representativeness and availability heuristics in humans. Representativeness heuristics reduce inferential tasks to quick exemplar or similarity comparisons. When traits or events used for judgments are unrepresentative or provide only indefinite dimensions for categorization, such as level of mating fitness and availability, the heuristic may become a nonnormative guide to decision making. Availability heuristics employ readily accessible information to judge the frequency, probability and causality of traits and events. Because decisions result from the accessibility of perceived and/or retrieved information, these simple rules of thumb may be corrupted by inaccurate trait or event base rates under the control of subjective factors. Under such conditions, like representativeness heuristics, availability heuristics become a nonnormative guide to decision making.

such as reproductive success, can lead to paradoxical experimental results and spurious conclusions about the sociality of microbes. They cite, as example, the observed occurrence of reproductive skew in wild and laboratory *D. discoideum* chimera. Reproductive skew in the densities of these cellular slime mold subpopulations is typically attributed to social dominance hierarchies caused by strain conflicts over group viability and limited resource availability. However, because chimera populations show fair coexistence and heterogeneity in natural settings, rather than predictable conflict-induced progressive loss of species-wide genetic diversity, some scientists now believe: 1) many, if not all, instances of microbial sociality are illusory and 2) reproductive skew is instead an outcome of life-history tradeoffs and nonsocial multiple fitness traits selected by deterministic and/or stochastic eco-evolutionary pressures. These kinds of experimental findings and interpretations cast doubt on the complexity and rationality or purposefulness of microbial social behavior (cf. 3,11,13-16,18-20,27). To help resolve some of these important issues, improved identification of nonassociatively and/or associatively learned social interactions, as opposed to the mostly genetic and epigenetic components now under widespread investigation, should be stressed.

Traditional forms of learning (Box 2) play significant roles in the adaptation and cultural transmission of traits linked with ultrasocial animals (4,5,29,32). Recent theories (17) are not unique on this matter and one may also expect similar levels of contribution from learning and complex heritable traits in microbial ultrasociality (cf. 6-14,18,20). Thus, inclusion of certain microbes, such as learning-capable Dictyostelids (cf. 28), within the boundary of public-goods-

dependent ultrasociality will only help shape and advance taxonomically valid sociobiological theory otherwise unachievable with strictly animal-centric interpretations of ultrasocial form and deed. The instance of Dictyostelids learning to switch their economic approach to farming, between largely unregulated public goods and herd-dog-secured private goods models, over lifespans and across generations underscores the need to move beyond animal-centric interpretations of sociobiology and to better evaluate the conserved relationship of traditional learned and inherited goal-direct behaviors with marketplace-influenced organismal adaptation, health, longevity, and life histories. Yet learning in social microbe contexts is best understood in protozoa (6-14) and bacteria (18,20), leaving the need to further refine different taxonomic models of ultrasociality with respect to learned reliability, accuracy, speed, and application of social information processing. Models, such as those involving Dictyostelids, nevertheless offer great potential for unprecedented fuller analysis and understanding

CONCLUSIONS

Recent theory on the origins of ultrasociality perpetuates the notion that only certain animal clades evolved ultrasocial form and deed, largely because of societal transitions to agriculture and farming-based economic systems (17). In contrast to this animal-centric perspective, extant microbial communities capable of economics-driven primitive farming also fulfill many characteristics of ultrasociality, such as global biomass proliferation, niche diversity and dominance, sophisticated division of labor, physically and communally organized groups, resource management, and social conflict instigation and mediation. Emergence, transfer, and modification of ultrasocial traits in microbial communities, very counter to Martinez-Garcia and Tarnita's (21) assertions about illusory social behavior in *D. discoideum*, seem to depend on adaptive processes analogous to the multilevel genetic and culture contributions of animal ultrasocieties and may provide exceptional models to investigate the convergent evolution and resilience/stability of economy-favoring ultrasociality within and across taxonomic boundaries and generations of life. That said, Martinez-Garcia and Tarnita's findings raise concerns that apparent ultrasocial tendencies of microbes may be erroneously interpreted as such, emphasizing the need to use similar rigorous scientific methods to more carefully scrutinize any further claims. Such work should also examine the contribution of learning and social logics in effecting winning and/or losing outcomes that benefit an individual microbe and groups of microbes and the impact that these kinds of outcomes have on short- to long-term social structures and processes. Even a putative crude version of ultrasociality and its economics affords microbes a complex, flexible capacity for driving significant environmental changes capable of widespread eco-evolutionary modification of worlds, extinct and extant livable worlds that Earthlings may now or soon explore through man and unmanned space missions. Future astrobiological research should endeavor to understand better the sociobiology of microbes in anticipation and support of potential extraterrestrial life detection.

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