Jay Love: Ecology and Evolution of Sociality

Overview – All living things behave, and all behaving things are social. That is, at least to some extent. From the narrowest biological scales to the broadest, we can see that the units of life interact with each other dynamically and often indirectly by sending and receiving information-containing signals; they exhibit a *social ecology*. Consistent patterns of social behavior form groups of organisms, and the structure and interactions within and between these social groups facilitate many of the processes wherein selection acts and which drive global ecology – from resource competition to mate choice to infectious disease dynamics to predator-prey dynamics to nutrient cycling. The fundamental dynamics of groups – how they form, are maintained, and change over time – must therefore dictate a profound influence over broad-scale ecosystem dynamics and the evolution of living things. If we are to understand foundational rules of life, we must pay close attention to the evolution of social groups. **Through my research, I seek to understand (1) how sociality evolves and (2) what role sociality plays in ecology.** Framed by these simple but engaging questions, this highly integrative research program lies at the intersection of ecology, evolution, and organismal biology. It will generate high-impact research products, funding opportunities from extramural sources, and training for undergraduate researchers.

(1) The evolution of social group cohesion

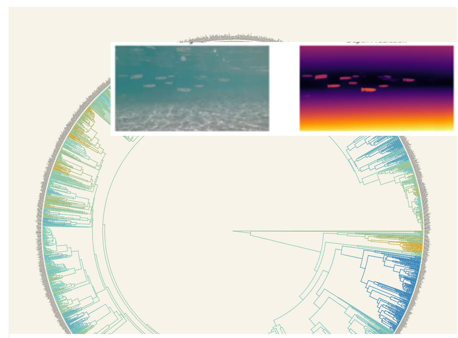

Fig. 1: Phylogenetic tree of 2973 Teleost species, with ancestral state reconstruction of group cohesion. Inset: monocular depth estimation of fish school, allowing for quantitative measurements of group cohesion from 2D images.

'Collective Behavior' refers to an emergent phenomenon that is observable in the behavior of a group of organisms and which arises as a result of the interactions of behavioral rules of individuals within the group. While collective behavior can confer strong fitness advantages, the evolutionary processes that cause collective behavior to evolve in one lineage while remaining absent in another are unknown. Using cutting-edge machine learning methods on publicly available text and image databases, I have documented the extant variation in collective movement (schooling) in fishes and placed that variation in a phylogenetic context (Love et al., forthcoming; Fig. 1). This variation illustrates a remarkable pattern: many clades show strong phylogenetic signal (closely related species share trait values), while many clades show very weak phylogenetic signal (closely related species do not share trait values). This constitutes an important evolutionary trend characterized by an attractor at the transition between behavioral states, which past theoretical work has predicted should occur under environmental instability. We also describe the dependence of diversification rates on sociality and go on to explore how the degree of sociality expressed by a species plays an important role in fitness-relevant ecological interactions, as in part 2, below.

Proposed research: My research program will use a mix of field, lab, and modeling methods to dig deeper into the richness of sociality. Building on my standard-setting work in Teleost fishes, we will first expand into other major vertebrate clades to determine if similar evolutionary patterns are found elsewhere. My past work with birds, which are also known to show extremes in social group cohesion, has introduced me to an amenable network of resources and potential collaborators. To begin, we will repeat our frontier language modeling methods to generate a coarse view of the diversity of group cohesion in the avian clade. Then, we will launch a field campaign to capture video of freely-behaving flocks of many species, targeting a sample defined through our first-pass methods. Using our monocular depth estimation pipeline, we will extract movement vectors from these flocking videos and fit movement models to the data. By quantifying variation in model parameters across species, we will contribute to a broader understanding of the relevant dimensions of collective movement. We will then expand to other systems, and in the future, conduct mechanistic evolutionary modeling of social cohesion under selection that is consistent with our observations. This work will be competitive for extramural funding from NSF (BIO, IOS panels) and private (e.g., Simons) sources. Undergraduate researchers will have opportunities to join the effort at every level – from roving data collection in the field to developing computational methods to quantifying collective behavior from those data. In this way, our work will be energetic, collaborative, and highly interdisciplinary. Students will be encouraged to focus deeply on one subject, but also dabble outside of their immediate interests, generating skillsets that will be useful throughout life.

(2) The ecology of sociality

Sociality plays an important role in determining the flows of energy and resources through ecological systems. For example, infectious disease moves more easily through denser populations, and individual transmission heterogeneity (determined in part by the social contact network degree distribution) can lead to outbreaks that erupt very quickly, but can be easily extinguished if the appropriate links in the transmission chain are targeted for interventions (Love et al. 2021 *Scientific Reports*; Love et al. *biorxiv*). In another vignette, very elaborate social interactions associated with mating can determine vital rates of populations, especially when under perturbation (Love and Goller 2021 *Ecology and Evolution*).

In new work, I focus on the ecological implications of sociality itself: the qualitative, rather than quantitative value. Collective movement is thought to allow group participants better predator avoidance and more efficient acquisition of patchy resources, but little empirical evidence has been garnered in support or in opposition of these mechanisms of selection. To investigate the role of predation pressure in driving the evolution of collective movement, we investigated the correlation of trophic level with schooling in fishes. Interestingly, species from clades that are uniformly strongly schooling or solitary show a strong negative correlation between trophic level and group cohesion, whereas species from clades with low phylogenetic signal in group cohesion do not. In a parallel investigation, we find a strong correlation between schooling and a patchily-distributed diet: schooling fish eat schooling fish, almost exclusively. These patterns are very clear when one makes the effort to collect the appropriate data, and I'm proud that we have been able to test long-held hypotheses. We find that patchy resource distribution favors initial social cohesion, while the refining of collective behavior occurs through additional selection via predation pressure.

Proposed research: My present work provides an excellent jumping-off point for more focused study of socio-ecological systems. Our future work will seek to quantify the role of sociality in determining the broad structure of ecosystems. For example, we will seek to understand the impacts of fisheries practices which target large schools on the stability of marine ecosystems: how does selecting against high social cohesion in this way impact the spatial distribution of species in adjacent positions in the food chain? This same framework underpins the ecology and evolution of predator-prey systems where either party is social, and undergraduate students will be encouraged to explore those systems (e.g., wolf-elk, with added influence of human hunting). A closely related branch of my research program will address the lingering question: given the adaptive benefits, why not be social? To that end, we will continue work on pathogen systems, modeling the ecological feedback between infectious pathogens and levels of sociality in populations. Students with interest in applied math will be recruited to explore ecosystem and infectious disease models that include social parameters, with the goal of fitting these models to data collected by students in part 1 of my research program, above.