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海外特別研究員最終報告書

独立行政法人日本学術振興会 理事長 殿

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海外特別研究員としての派遣期間を終了しましたので、下記のとおり報告いたします。
なお、下記及び別紙記載の内容については相違ありません。

記

1. 用務地（派遣先国名）用務地： テンピ （国名： 米国 ）

2. 研究課題名（和文）※研究課題名は申請時のものと違わないように記載すること。
社会性昆虫の意思決定における集団的知性の進化プロセスの解明

3. 派遣期間：平成 30 年 4 月 1 日 ～ 令和 2 年 3 月 21 日

4. 受入機関名及び部局名
アリゾナ州立大学 生命科学科

5. 所期の目的の遂行状況及び成果…書式任意 **書式任意（A4 判相当 3 ページ以上、英語で記入も可）**
（研究・調査実施状況及びその成果の発表・関係学会への参加状況等）
（注）「6. 研究発表」以降については様式 10－別紙 1～4 に記入の上、併せて提出すること。

Research background

Collective behaviors by grouping animals form various spatial patterns, including coordinated movement and nest structures. In pattern formation, individuals follow a simple set of behavioral rules for local interactions, slightly varying within and among species, to produce a large diversity of shapes. As most of the studies have focused on the behavioral mechanism of each species, comparative analysis or comprehensive view across species are critically lacking, which limits the understanding of the origin and evolution of the behavioral mechanisms regulating collective behaviors. In termites, various collective behaviors, including tunneling through the soil, construction of complex structures, and nest emigration, have evolved several times independently, accompanying the evolution of nesting strategies. In this project, I will perform a comparative study of collective behaviors among species or across taxa, especially focusing on the collective building of termites. To examine and evaluate the behavioral rules of multiple species, I'll use both detailed behavioral observations and data-based modeling. With the results, I will infer the evolutionary process of sophisticated collective behaviors by grouping animals.

During two years, I worked on several projects relating to the evolution of behavioral rules. I summarize the outcome of each project below.

1. Complex relationship between individual behavior and tunnel structures in termites

Termites show a variety of nesting habitats across species. Among these, multiple-piece nesters, which nest across multiple-pieces of wood, build tunnels through the soil by collective excavation (Abe 1987). This behavior has evolved several times independently in lower termites. Despite this diversity, tunneling behavior has been studied only in the species of Rhinotermitidae. These studies have found that branching patterns of tunnels can vary among species, group size and soil environments (Su and Bardunias 2011), but little is known about the behavioral mechanisms underlying tunneling variations.

In this study, I focused on the mechanical relationship between individual behaviors and group-level patterns for tunnel building in termes. To observe tunneling behaviors of termites, including distinct phylogenetic groups, I used three subterranean termite species. *Paraneotermes simplicicornis* (Kalotermitidae) evolved tunneling independently from *Reticulitermes tibialis* and *Heterotermes aureus*

(Rhinotermitidae). We observed tunnel development at two different scales: the patterns of tunnel branching and the behavior of each termite.

First, by comparing *R. tibialis* and *H. aureus*, I found that two related species share a common rule set but build tunnel patterns that differ in their degree of branching. In both species, excavators transport sand particles individually from the tunnel face; when crowding prevents them from reaching the tunnel face, they choose between two behavioral options, waiting for the tunnel to clear or beginning excavation at the sidewall. The two species differ only in the probabilities of these actions, such that the one favoring waiting reduces the number of branches. The data-based simulation confirmed that the above different branching patterns between *R. tibialis* and *H. aureus* result from parameter tuning of the same behavioral rules. Second, I found that *P. simplicicornis* independently evolved low-branched patterns using different building rules. Rather than dig individually, excavators of this species work in a bucket-brigade; in a crowded tunnel, they receive and pass back sand grains rather than excavate the sidewalls. Simulations for this species underestimated the branching patterns, suggesting that this species may have a different mechanism for branching

These results elucidate the complex relationship between individual behavior and group-level patterns; in some cases, distinct behaviors can produce similar structures, but in others, the regulation of a common behavior can yield distinct patterns. The finding is parallel to the relationship between gene expression and morphology, emphasizing that evolution follows the same principle across different biological levels.

There are several reasons this work will attract attention from a broad readership beyond those interested in animal behavior. First, our result is parallel to findings in evolutionary developmental biology. Just as that discipline seeks the relationship between individual morphology and developmental processes, we have shown how a colony's external morphology (its nest construction) is related to collective behavioral processes. Second, our result clearly emphasizes the challenge of solving the inverse problem; that is, inferring underlying mechanisms from system-level properties. This is fundamental to complexity science, and has particular implications for the paleontological inference of behavior from trace fossils. Finally, our discovery that termites have two distinct behavioral solutions for the same tunneling problem can inspire distributed algorithms for swarm robotics and other artificial systems.

I performed the experiments and the simulations, with the advice from Stephen C. Pratt (Arizona State University) and Paul M. Bardunias (SUNY College of Environmental Science and Forestry). This study was presented in several international conferences (Behavior 2019, ASAB 2019, ESA 2019). Also, I've submitted the manuscript to *American Naturalist*, which is under revision.

Mizumoto N.*, Bardunias P. N. & Pratt C. S. Parameter tuning facilitates the evolution of diverse tunneling patterns in termites bioRxiv DOI:10.1101/836346
Mizumoto N.*, Bardunias P. N. & Pratt C. S. Complex relationship between tunneling patterns and individual behaviors in termites (under review)

2. Soil excavation behavior across different contexts in termites

I further examined how the above behavioral rule for tunneling can be shared within a species. Individual actions for collective building are often consistent across different socio-environmental conditions, which enables colonies to build a variety of structures with minimal change in behavior. In ants and termites, worker castes often specialize in nest building activities and perform most of these works (Emerson 1938; Oster and Wilson 1978). However, some other castes also inevitably involve in nest building processes, e.g., colony foundation pairs (Cronin et al. 2013). In this study, I asked how the individual-level actions for nest building can be consistent among different morphological castes within each species.

Subterranean termites engage in soil excavation in two different contexts in their life history: foraging for resources by workers and initial nest excavation by colony foundation pairs. Our comparison of tunneling behaviors by founders revealed distinct transporting mechanisms; *Heterotermes aureus* and *Gnathamitermes perplexus* carry sand particles only using their mandibles, while *Paraneotermes simplicicornis* use their legs to kick sand particles backward. The observed behaviors are consistent with those of workers in each species, despite a substantial dimorphism of body size, especially in *G. perplexus*. Furthermore, the behavioral difference is associated with tunnel development and task allocation patters. This study suggests that individual behavior of nest building in termites is less variable with contexts or functions within a species but can change among species, emphasizing the fruitfulness of comparative studies in future research.

I performed the experiments and analysis, with the advice from Stephen C. Pratt. Gillian H. Gile provided alates of *G. perplexus*. This work will be contributed as a part of special issue in the journal of

Mizumoto N.*, Gile H. G. & Pratt C. S. Behavioral rules for soil excavation by colony founders and workers in termites. (under review)

3. Phylogenetical analysis for shelter-tube construction in termites

Phylogenetic analysis of the collective building in termites lacks since Emerson (1938), although there are substantial revisions of the phylogeny after that time. In this study, we examined the evolutionary patterns of shelter-tube construction behavior of termites by literature survey with phylogenetical analysis. I collected information of shelter-tube construction potential in lower termites from the literature by executing a search on Google Scholar combining the terms for shelter-tube ("shelter-tube," "runway," "covered trail," "shelter-gallery," "mud-tube" and "covered-pathway") and each genus name. Also, I looked for the visual information of shelter-tube construction for each species, even including the results of Google search by images or videos. After searching, I mapped the natural use of shelter-tube construction and the potential to build shelter-tubes (observation of shelter-tubes only in laboratory condition) on the phylogeny. The natural use of shelter-tube corresponds to the multiple-piece (or separate) nesting habitats with the observation of shelter-tube constructions, while the potential to build shelter-tubes is mainly based on the observations in the laboratory condition with surrounding information of each species.

The use of shelter-tubes in the natural condition, corresponding to multiple-piece nesting (and separate nesting), has evolved four times independently in lower termites. However, when we also counted their behaviors observed in laboratory conditions, there is a behavioral potential to construct a shelter-tubes in many species even in the species classified as one-piece nesters. With this information, our phylogenic analysis suggests that the ability to build shelter-tubes was retained and probably present in the common ancestor of all termites. This result suggests that every species may share the behavioral rules and the potential to create various patterns, while species-specific parameters make the current observable patterns. Thus, the phylogenetic analysis provides the novel hypothesis about the evolution of collective behaviors in termites, which encourages future studies focusing on the comparative analysis of behavioral rules.

With this result, I wrote an article about the evolution of collective building in termites, which is almost published in the journal, *Ecology and Evolution*. This is a collaboration work with Thomas Bourguignon (Okinawa Institute of Science and Technology) who provided the phylogeny information. Stephen C. Pratt (Arizona State University) and Paul M. Bardunias (SUNY College of Environmental Science and Forestry) gave me a lot of idea through the discussion.

Mizumoto N.* & Bourguignon T. A potential role of parameter tuning in the evolution of termite construction (Accept with minor revision) *Ecology and Evolution*.

4. Comparison of tandem running behaviors between ants and termites

Ants and termites often show a similarity in their collective behaviors. A key question is if this convergent evolution of collective behaviors is achieved by the same underlying mechanism or differentiated behavioral rules. However direct comparative studies between species have rarely been conducted. One remarkable convergent patterns can be observed in tandem running (Mizumoto and Dobata 2019). Ants perform tandem running during nest relocation and group foraging, in which a single well-informed worker (leader) guides a naive nestmate (follower) to a target site. In termites, tandem running is used after a nuptial flight as a mechanism to maintain cohesion between a mated pair as they explore the environment in search for a new nest location, in which the male follows the female.

By introducing an information theoretic methodology, we found that ants engage in bidirectional communication during tandem runs, while termites only performed unidirectional signaling from a leader to a follower. We also found that ants show a regulation mechanism of information flow, as observed in the communication of human beings.

This work is the collaboration with Gabriele Valentini (Arizona State University) who collected the data of ants and performed the analysis, with the supervisions by Theodore P. Pavlic, Stephen C. Pratt, and Sara Imari Walker (Arizona State University). I provided the data of termites and joined the discussion. The manuscript is under review in the journal, *eLife*. The results were presented in the IUSSI2018 (the largest international conference on social insects) and Behavior 2019.

Valentini G., **Mizumoto N.**, Pratt S.C., Pavlic T.P.* & Walker S.I.* Revealing the structure of information flows discriminates similar animal social behaviors. (under review) bioRxiv DOI:10.1101/765198

5. Density dependent change of movements in termite mate search

Animals move to search for food, mates, and nests, which are essential for survival and reproduction. The optimal movements vary with the surrounding environments, which may explain the observation that animals often switch their movement patterns depending on conditions. Theories predict that animals change movements for search according to the density of targets to improve encounter rates; however, most studies have lacked empirical tests using actual animals because of the difficulty to measure the encounter dynamics.

I addressed this problem by observing the termite mate search process across different density conditions After a dispersal flight, termites drop their wings and walk to search for a mate; when a female and a male meet, they form a female-led tandem pair and search for a favorable nesting site. If a pair is separated, they have two search options: reunite with their stray partner, or seek a new partner. I hypothesized that the density of individuals affects separation-reunion dynamics and thus the optimal search strategy.

I observed the searching process across different densities and developed a data-based simulation. I found that termite pairs were often separated but obtained a new partner quickly at higher density. After separation, while females consistently slowed down, males increased their speed according to the density to increase mating encounters. Males at very low densities did best to move slowly and thereby reduce the risk of missing their stray partner, who is the only available mate. On the other hand, males that experienced higher densities did better to move fast because the risk of isolation is low, and they must compete with other males to find a partner.

This result is contrasted with previous observations of animals foraging for food resources who often slow down at a higher density of targets. Our study suggests that optimal search strategies change with type of target. This challenges many theoretical studies that acknowledge searching can be for arbitrary types of targets (food, mates or habitats), but have mostly assumed, explicitly or implicitly, that searching is for food.

There are several reasons this work will attract attention from a broad readership of those interested in animal ecology. First, we empirically evaluated the behavioral change of males by observing not only movement patterns but also encounter dynamics across densities, which is lacking in the field of animal search behavior (Bartumeus et al. 2016). Second, I formally tested the classical argument that males often increase moving speed at a higher density in mate search, by introducing random search. This can inspire further studies because movement pattern is rarely taken into account in many mate search studies, compared with foraging. Finally, by connecting movement and encounter dynamics, the discovery has implications for population-level ecological phenomena. For example, a density-dependent change of mate search strategy is a crucial mechanism that determines the strength of Allee effects.

I performed the experiments in University of Florida as a collaboration with Thomas Chouvenc. I submitted the paper for this research to the journal, Journal of Animal Ecology, which is under review.

Mizumoto N.*, Rizo A., Pratt S.C. & Chouvenc T. Termite males enhance mating encounters by changing speed according to density (under review)

6. Inferring collective behavior from a fossilized fish shoal

Collective motion by animal groups can emerge from simple rules that govern each individual's interactions with its neighbors. Studies of extant species have shown how such rules yield coordinated group behavior, but little is known of their evolutionary origins or whether extinct group-living organisms used similar rules. In this study, I analyzed the positions and heading directions of fossilized fish individuals to find the evidence consistent with coordinated collective motion in a fossilized group of the fish *Erismatopterus levatus*†, and infer possible behavioral rules that underlie it. To identify interaction rules of individuals in the group, I examined how distance to the nearest individual would change at the next moment after the snapshot preserved on the slab. I found repulsion at short distances, switching to attraction as distance increased, which is similar to rules for social interaction used by extant fish. Moreover, the fossilized fish showed group-level structures in the form of oblong shape and high polarization, both of which I successfully reproduced in simulations incorporating the inferred behavioral rules. Although it remains unclear how the fish shoal's structure was preserved in the fossil, these findings suggest that fish have been forming shoals by combining sets of simple behavioral rules since at least the Eocene. This study highlights the possibility to explore the social communication of extinct animals, which has been thought to leave no fossil records.

I performed this research by the collaboration with Shinya Miyata (Oishi Fossils Gallery of Mizuta Memorial Museum Josai University Educational Corporation) and Stephen Pratt (Arizona State

University). The finding was published in journal *Proceedings of the Royal Society B*.

Mizumoto N.*, Miyata S. & Pratt S. C. (2019) Inferring collective behavior from a fossilized fish shoal. *Proceedings of the Royal Society B* 286: 20190891 DOI: 10.1098/rspb.2019.0891

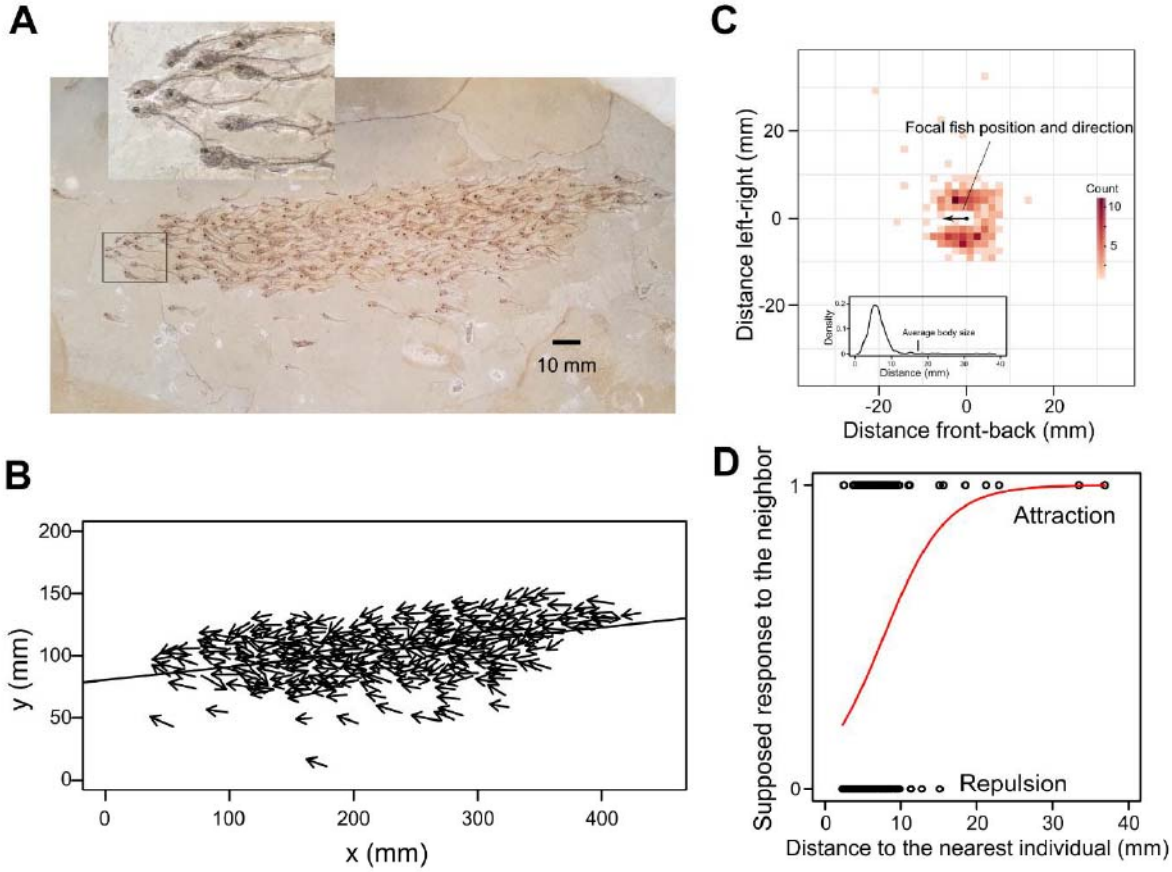

Fig. 1. Collective behavior in a fossil fish school. (A) Analyzed fossil of a group of *Erismatopterus levatus* in specimen FPDM-V8206 from the Eocene (Green River Formation). (B) Representation of the length and heading of each fish. The long line passes through the center of the group (average x and y) in the direction of the average heading. (C) Frequency distribution of each fish's nearest neighbor, showing that most are positioned laterally. Insert shows the density plot of the distance between individuals. (D) The projected short-term change of the distance to the nearest individual as a function of the observed starting distance. Initially, close neighbors tend to move away (repulsion) while initially distant neighbors move closer (attraction). Red line indicates fitted logistic regression.