A Novel Approach to Study Task Organization in Animal Groups

by

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A Dissertation Presented in Partial Fulfillment
of the Requirements for the Degree
Doctor of Philosophy

Approved October 2016 by the
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ARIZONA STATE UNIVERSITY
December 2016
ABSTRACT

A key factor in the success of social animals is their organization of work. Mathematical models have been instrumental in unraveling how simple, individual-based rules can generate collective patterns via self-organization. However, existing models offer limited insights into how these patterns are shaped by behavioral differences within groups, in part because they focus on analyzing specific rules rather than general mechanisms that can explain behavior at the individual-level. My work argues for a more principled approach that focuses on the question of how individuals make decisions in costly environments.

In Chapters 2 and 3, I demonstrate how this approach provides novel insights into factors that shape the flexibility and robustness of task organization in harvester ant colonies (*Pogonomyrmex barbatus*). My results show that the degree to which colonies can respond to work in fluctuating environments depends on how individuals weigh the costs of activity and update their behavior in response to social information. In Chapter 4, I introduce a mathematical framework to study the emergence of collective organization in heterogenous groups. My approach, which is based on the theory of multi-agent systems, focuses on myopic agents whose behavior emerges out of an independent valuation of alternative choices in a given work environment. The product of this dynamic is an equilibrium organization in which agents perform different tasks (or abstain from work) with an analytically defined set of threshold probabilities. The framework is minimally developed, but can be extended to include other factors known to affect task decisions including individual experience and social facilitation. This research contributes a novel approach to developing (and analyzing) models of task organization that can be applied in a broader range of contexts where animals cooperate.
I dedicate this work to my parents, Dayo and Eunice, for being exemplars of diligence, perseverance, and kindness.
ACKNOWLEDGMENTS

This work bears the marks of so many teachers and mentors who have shaped my intellectual journey. I am deeply grateful to my advisors, Dr. Yun Kang and Prof. Jennifer Fewell for their stalwart commitment through this process and for showing me that the joy of research comes in the balance of structure and creativity. I am also grateful to my committee members Prof. Marco Janssen and Prof. Carlos Castillo-Chavez. Their invaluable insight, inspiration, and encouragement have been instrumental in my development as a researcher. I would also like to acknowledge the contributions of key allies in my mentor network including Kenneth Jones (ECSU), Noa Pinter-Wollman (UCLA), Nina Fefferman (UT-Knoxville), Janet Best, Ian Hamilton, Yuan Lou (Ohio State), as well as my high school counselor, Ms. Donna Yearwood, who set me on this path so many years ago.

I am grateful for the friendships I made here at ASU, especially at the Simon A. Levin Modeling Sciences Center and the Social Insect Research Group. Special thanks goes to Derdei Bichara, Ivy Worsham, Jordan Bates, Miles Manning, John McKay, Komi Messan, Fereshteh Nazari, Oscar Patterson Lomba, Dustin Padilla, Kehinde Salau, and many others with whom I share amazing memories from these past 4 years. I am truly indebted to the Manning family, for their loving generosity, and to Sherry Woodley and Margaret Murphy-Tillis who tirelessly went to bat for me. Finally, I give my most profound gratitude to my family–my parents Dayo and Eunice; and brothers Anise and Yani – for believing in me. I love you all. Oyi ugwa kona; Mi kyo ri imhe bha.

My journey was made possible through generous funding from the Alfred P. Sloan Foundation (MPHD program); the U.S. Department of Education (GAANN grant program); and ASU Graduate College’s Doctoral Enrichment Fellowship.
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4.7 Bifurcations of System (4.12) As a Function of $\delta_1/\delta_2$. Here, Agents Have Similar Preferences Across Tasks ($\theta_{11} = \theta_{12} = \theta_{21} = \theta_{22}$), but Have Different Relative Efficiencies ($\alpha_{11}/\alpha_{21}$ vs. $\alpha_{12}/\alpha_{22}$). Interior Equilibria $E^{(x_{11},x_{12})}_{(x_{21},x_{22})}$ Are Denoted as Stable Attractors (Blue) or Unstable (Orange) Whenever They Exist. Other Parameters: (a) $\theta_{11} = \theta_{21} = 0.95$, $\theta_{12} = \theta_{22} = 1$, $\Phi_1 = \Phi_2 = 1$, $\rho = 0.15$, (b) $\theta_{11} = \theta_{21} = 0.8$, $\theta_{12} = \theta_{22} = 1.7$, $\Phi_1 = 3\Phi_2 = 3$, $\rho = 0.05$.

4.8 Bi-stability of (4.12) in the Parameter Space Shown in Figure 4.7 b. We assume Agent 1 Has Greater Activity Costs than Agent 2 ($\Phi_1 > \Phi_2$), and that $\alpha_{11} = 1$, $\alpha_{22} = 3$, $\alpha_{12} = \alpha_{21} = 0.25$. (left) Plots Showing the Trajectory of Agents’ Behavior Probability Space Starting from Different Initial Conditions $x_{ij}(0)$ (open circles). (right) Resulting Effects on the Dynamics of Task Stimuli. The System Converges to the Interior Equilibrium With Greater Workload if Both Agents Have Higher Initial Probabilities on Their Least Efficient Task, and Agent 1 is Initially More Likely Be Inactive.
Chapter 1

INTRODUCTION

Social (group-living) animals are among the most ecologically successful species in nature (Oster and Wilson, 1978; Hölldobler and Wilson, 1990). A key reason for their success is they collaborate on activities needed to survive, grow and rear offspring. Social groups must also balance flexibility and robustness in their collective response to environmental changes (Charbonneau and Dornhaus, 2015). Achieving this balance depends on how individuals assess and respond social information in relation to the external environment. For instance, the ability of groups to exploit their environment when conditions are favorable depends on having behaviorally flexible members who can switch between roles that contribute to group success (Charbonneau and Dornhaus, 2015). However, groups must also regulate their collective activity across tasks in order to minimize costs/risks when conditions become unfavorable (Pinter-Wollman et al., 2013). This dissertation is primarily concerned with understanding how mechanisms underlying behavioral activity at the individual-level can shape collective behavior of groups and how they respond to work in fluctuating environments. As we will see, the answer to this question may depend on social context considered (i.e., the size and/or mix of individuals in the group) (Sih and Watters, 2005).

Social dynamics and task organization in animal societies

The proximate challenge of sociobiology is to understand how group-level patterns of organization refer from individual-level mechanisms (Beshers and Fewell, 2001). Mathematical models have been instrumental in this regard; specifically in showing how collective patterns often emerge as a product of interactions among group mem-
bers and their environment (Camazine, 2003; Hemelrijk, 2002). These models provide a powerful lens to see how conspicuous organizational strategies like division of labor, can self-organize from behavioral differences within groups. The paradigmatic mechanism for this is based on the concept of response thresholds (Bonabeau et al., 1998; Theraulaz et al., 1998; Jeanson et al., 2007). Response threshold models posit that division of labor can spontaneously develop in groups where: (i) individuals vary in their task preferences, (ii) the task behavior of one individual changes the social environment (and behavior of others), and (iii) these changes generate closed feedback loops in which behavior becomes amplified. This is because when one individual in a group performs a task (e.g., nest construction or foraging), they necessarily reduce the task need and so lower the likelihood that others will perform it in the future. Over time, this dynamic can generate a positive feedback that drives individuals with the lowest threshold for a task to become specialized (Fewell and Page Jr, 1999).

One perspective that almost never considered in emergence models of task organization is how individuals make decisions in costly environments. This question is particularly relevant to understand how group-level needs are functionally integrated with worker behavior in eusocial societies (Charbonneau and Dornhaus, 2015). Moreover, it is also relevant in broader contexts of sociality where individuals must balance the costs and benefits of cooperation (Fewell and Page Jr, 1999; Cahan and Fewell, 2004; Jeanson et al., 2008; Holbrook et al., 2013). My work argues for an analysis of proximate factors that determine how individuals decide what tasks to perform, and how much to perform it in relation to social information (Gordon, 1999). This perspective provides a general lens for understanding organizational patterns that develop when individuals interact in groups (Clark and Fewell, 2013), and how these interactions shape their collective ability to regulate work in changing environments (Charbonneau and Dornhaus, 2015).
Summary of Contribution

My work uses a combination of experimental analysis and mathematical modeling to examine how social dynamics shapes the individual-level components of behavior (i.e., activity and task choice) and its consequences for the task organization in animals groups. I explore this question in the harvester ant (Pogonomyrmex spp.) species living in both eusocial and communal contexts.

The first part of my dissertation examines how mature P. barbatus colonies regulate their foraging activity in response to changes in their environment. Harvester ant colonies subsist on water and nutrients metabolized from the seeds collected by specialized foragers. Because they live in arid habitats, the likelihood that any forager returns with food decreases with the amount of time she spends searching. Consequently, colonies must constantly balance desiccation costs (and predation risks) with the expected benefits of finding food when conditions are favorable. How do they achieve this balance? A recent study by Pinter-Wollman et al. (2013) identified two distinct processes that likely mediate colony-level activity. Undecided foragers inside the colony were more likely to leave in search of food after having a threshold number of encounters with successful foragers, but they were also more likely to retire into nest (i.e, other tasks) if they experienced long latency periods between encounters (Pinter-Wollman et al., 2013). Given that colonies operate in complex environments where resource abundance and predation risks fluctuate unexpectedly, it is still unclear how a forager decisions at individual-level can provide flexible yet robust system of regulating colony-level activity. Moreover, as noted in previous experimental studies like (Gordon, 2002; Gordon et al., 2011), colonies show characteristic differences in how they well respond to (and recover from) perturbations.

In Chapter 2, I discuss the results of a mathematical model we recently published
to understand this system (Udiani et al., 2015). A key goal of the study was to understand what parameters a colony might adjust to balance foraging flexibility and robustness in variable environments. Our analysis showed that foraging could undergo both forward and backward bifurcations depending on the overall rate at which individual foragers are (or become) available for recruitment. This result not only suggests the existence of parameter regions where colonies can be described as “risk-prone” and “risk-averse” in relation to their foraging behavior, but also provides some insights into empirically noted differences in foraging regulation of neighboring colonies Gordon (2013).

The second part of my dissertation relates to the role of social dynamics in shaping patterns of work within Pogonomyrmex foundress associations. Foundress associations are incipient colonies containing few numbers of recently mated (unrelated) queens who cooperate to raise the first generation of workers. As in mature colonies, the work demands of incipient nests are inherently variable. Thus, foundresses must mutually coordinate and divide their efforts to meet these demands and ensure brood survival. Although working benefits the group, its physiological toll can vary significantly from task to task (e.g., nest construction vs. brood care). Yet, observations of experimental associations show that foundresses consistently differentiate into specialist task roles despite its obvious costs (Fewell and Page Jr, 1999; Cahan and Fewell, 2004; Jeanson and Fewell, 2008). Although a simple response-threshold model can explain why task differentiation emerges in eusocial systems (where costs are evaluated at the group level), it provides an incomplete description of the factors likely to affect behavioral response in communal groups where individual and group benefit do not completely align. Moreover, while division of labor may generate organizational efficiencies as hypothesized for derived systems (Oster and Wilson, 1978; Chittka and Muller, 2009), it is not exactly clear whether similar benefits can originate via
emergent dynamics.

In Chapter 3, I discuss a behavioral experiment we developed to study the emergence and scaling of division of labor in artificially forced associations of *P. barbatus* ant foundresses. The choice of *P. barbatus* is particularly attractive because queens are normally solitary in the field, but tolerant of conspecifics in lab associations (Fewell and Page Jr, 1999). Moreover, because *P. barbatus* associations are de novo, we can be confident that queens’ behavior should reflect an emergent response to social environment (i.e., rather than a previously evolved strategy). We asked the following questions with experimental data: (a) what (if any) are the typical behavioral patterns (i.e., activity level and task choice) of queens in solitary nests, and (b) how do these patterns change in social settings (i.e., with the addition of more similar or different individuals). We also examined the relationship between division of labor and per-capita productivity (i.e., offspring production) across nests of different group sizes. The study revealed several interesting observations. For instance, that queens consistently decreased their performance of excavation in associations (a metabolically expensive task) in favor of brood tending and self-maintenance. Moreover, variation in per-capita productivity (i.e., number of offspring reared) across nests was less connected with levels of division of labor, than on how consistent queens worked over time. These results support the idea that both intrinsic and social factors shape individual patterns of behavior (both in activity level and task choice) within groups. But they also raise an interesting theoretical question about why particular structures of division of labor may enhance productivity for some groups and not others. This question is particularly relevant to understand how emergent dynamics might shape the outcomes of cooperation in natural foundress associations Cahan and Fewell (2004); Jeanson *et al.* (2008)
A Systematic Modeling Approach to Study Task Organization

The key to understanding why different patterns organization emerge in social groups is to study how individuals make decisions in relation to their environments. The existing modeling approach, which focuses only on the phenomenological concept of response-threshold, can only offer limited insights into how causal mechanisms of group behavior aggregate from the independent actions and decisions of individuals (Beshers and Fewell, 2001). Indeed a more parsimonious modeling approach would:

(i) identify the underlying factors that shape behavioral response at the individual-level, and (ii) study their resulting influence on the social environment and patterns of collective behavior. The tools of nonlinear dynamical systems provide a way to develop such models.

In Chapter 4, I propose a general framework to study the emergence of task organization in heterogeneous social groups. The framework is based on multi-agent dynamical systems and builds on several components from previous studies (Pacala et al., 1996; Bonabeau et al., 1997, 1998). Importantly, our model assumes that individuals make task decisions with reference to underlying rewards of different choices adjust their behavior in favor of alternatives that provide the highest return in given environment. This process of “melioration” has a neuronal basis (Giurfa, 2007; Guerrieri and d’Ettorre, 2010) and its (emergent) dynamics can be described theoretically by a system of replicator equations (Loewenstein, 2010). For this Chapter, I focused on groups where agents have fixed costs and assess their environment independently (without the effects of experience or social influences). Our analysis reveals some key findings. First, under the assumption that individuals have well-defined and ordered preferences across different tasks, the dynamics of task choice always leads to a division of labor with an equilibrium mix of task specialists, generalists and
inactive (non-contributors). In particular, we obtain threshold conditions in which
agents perform different tasks (or abstain from work) with an analytically defined
set of probabilities. However, in groups where individuals have similar preferences
across all tasks, the equilibrium organization may be sensitive to initial conditions.
Our results suggest this might specifically relate to differences among individuals in
their initial propensity to perform different tasks (as well as their work rates across
different tasks). Although the framework is minimally developed, it can be extended
to include other factors known to affect task decisions including individual experience
and social facilitation (Webster and Fiorito, 2001; Ravary et al., 2007).

Broader Significance

In sum, this dissertation highlights how the integration of empirical and mathe-
matical modeling can inform studies of task organization in both simple and complex
animal societies. Our assumption that individuals make decisions with reference
to underlying rewards follows from common behavioral theories (e.g., reinforcement
learning (Herrnstein and Prelec, 1991; Loewenstein, 2010)) and is consistent with em-
pirical evidence (Weidenmüller, 2004; Ravary et al., 2007; Giurfa, 2007; Guerrieri and
d’Ettorre, 2010). We believe this approach will lead to the development of more pow-
erful, explanatory models that can be applied in a broader range of contexts where
animals cooperate.
IDENTIFYING FACTORS THAT SHAPE THE REGULATION OF FORAGING IN COLONIES OF HARVESTER ANTS

Abstract

The behavior of an ant colony emerges from the actions and decisions of workers following simple rules. However, little is known about how colony behavior adapts in response to environmental changes. Here, we develop a mathematical model to study how harvester ants regulate their foraging behavior in risky environments. We propose a set of differential equations describing the dynamics of: (1) available foragers inside the nest, (2) active foragers outside the nest, and (3) successful returning foragers, to understand how individual-level processes (e.g., interaction rates,) shape colony response to foraging interruptions. Our analysis indicates that the model can undergo a forward (transcritical) bifurcation or a backward bifurcation, which translates to a risk-sensitive (vs. risk-averse) colony-level strategy. In the former case, foraging can persist only when the average number of recruits per successful returning forager is larger than one. In the latter case, the backward bifurcation creates a region of bi-stability in which the size and fate of activity depends on the distribution of the foraging workforce outside and inside the nest. We validate the model with experimental data from the ant (*Pogonomyrmex barbatus*) and perform a sensitivity analysis to rank parameters affecting model outcomes. Our study suggests that the degree to which foragers make flexible decisions at the nest increases the ability of colonies to forage efficiently in risky environments.
Introduction

Almost all complex behaviors observed in ant societies emerge from the interactions of individual workers following simple rules (Detrain et al., 1999). Foraging is no exception. Ant colonies must maintain a flow of information about their environment in order to locate and transport food from multiple sources without central control (Detrain et al., 1999; Gordon et al., 2008; Dussutour and Nicolis, 2013). Yet like any solitary animal, they must collectively respond to changes in their environment (Kacelnik and Bateson, 1996). Importantly, colonies face a trade-off between using strategies that allow them to flexibly exploit their environment when conditions are favorable versus strategies that are resilient to potential catastrophes (i.e., if conditions suddenly become unfavorable). This is a particularly cumbersome problem for the desert harvester ant *Pogonomyrmex barbatus*. Because harvester ants obtain most of their water from metabolizing seed fats (Lighton and Feener Jr, 1989), foraging colonies must balance desiccation costs with the expected benefits of finding food when conditions are favorable (Gordon et al., 2013). Achieving this balance requires a process of information sharing between foragers inside and outside the nest (Pinter-Wollman et al., 2013). Yet, we still lack an understanding of the fundamental mechanisms underlying this process and how they affect colony response in different environments (Gordon, 2002). In the subsequent section, we will review empirical studies aimed at understanding these questions using behavioral experiments on field colonies.

Mechanisms of Foraging Regulation in Harvester Ants

*Pogonomyrmex barbatus* is a granivorous ant species native to the southwestern United States. Colonies favor arid, chaparral habitats and subsist on grass seeds they
collect and store year round (Gordon, 1991). Although neighboring colonies compete for food, foraging intensity is mostly affected by changes in temperature and humidity (Gordon, 1991; Gordon and Kulig, 1996; Gordon, 2002). Ants foraging in hot, dry conditions lose water, but obtain water from metabolizing fats in the seeds that they eat (Lighton and Feener Jr, 1989). Foragers are also routinely disturbed by predation from horned lizards, which tend to hunt near active trails (Munger, 1984).

Previous work suggest that *P. barbatus* colonies change their foraging behavior in response to daily and seasonal conditions (Gordon, 1991). Colonies are most likely to forage on humid days following a heavy rainfall. This pattern is likely beneficial because food distributed by wind and flooding uncover seeds in the top layer of the soil (Gordon *et al.*, 2013). Within a day, foraging rate are partly mediated by the return of successful foragers who interact with inactive (recruitable) foragers near the colony entrance (Fig. 2.1). These interactions consist of brief antennal contacts during which recruits can detect the task-specific cuticular hydrocarbon profile of the other and whether it is carrying food (Greene and Gordon, 2003, 2007) Empirical observations suggest that inactive foragers require a threshold number of interactions with successful ones at a particular rate before they leave the nest to look for food (Greene *et al.*, 2013).

A recent study by Pinter-wollman et al. (2013) suggests that *P. barbatus* colonies may regulate foraging at two separate timescales. In an experiment to discern how colonies react to changes in forager return rates, the authors showed the average rate of interaction experienced by ants inside the vestibule (Fig. 2.1) corresponded with the arrival rate of successful foragers on a timescale of seconds (Fig. 2.2(a)). Forager availability was also influenced by return rates on the timescale a minutes. On average, the number of available foragers in the vestibule increased one to two minutes after an increase in the number of returning foragers (Fig 2.2(b)). In a
Figure 2.1: Nest Entrance of a Typical *P. barbatus* Colony from Pinter-Wollman et al. (2013). Uncommitted Ants Interact with Returning Foragers Inside the *Vestibule* (Region Outlined in Blue). Ants Move to and from the Inner Nest Using the Tunnels (Yellow Arrows). The Dotted Circle Denoted ROI Is the Area Where Most Interactions Occur Before Foragers Exit the Nest.

subsequent experiment to discern how colonies responded to foraging disruptions, the authors showed that the degree to which colonies recovered from simulated predation depended on the duration of the interruption. For short interruptions, the average amount of time it took for colonies to recover to their previous foraging levels was similar to the length of the perturbation. For longer interruptions, colonies recovered much more slowly suggesting that most inactive foragers in the vestibule went back into the nest. In sum, these experiments reveal that although inactive foragers in the *vestibule* are likely to be activated by encountering successful foragers (Greene and Gordon, 2007), they are also likely to retire back into nest (and perhaps do other tasks) if they experienced long latency periods between encounters.

Forager interactions are clearly important aspect of how harvester ants regulate
foraging in different environments. However, previous work suggest that P. *barbatus* colonies differ in how likely they are to adjust the rate of outgoing foragers to the rate of forager return (Gordon *et al.*, 2011). While most colonies can adjust foraging rate closely when conditions are good, only some do so in poor conditions. From a theoretical perspective, colonies also face a fundamental dilemma in how to insure foraging returns against short-term versus long-term disturbances (e.g., predation by horned lizards Munger (1984)). This trade-off is perhaps best understood from the perspective of risk analysis. The more foragers a colony sends out, the more food it will gather. However, colonies which consistently have more foragers outside the nest, rather than inside, will be more vulnerable to catastrophic perturbations than colonies where fewer foragers leave the nest. One way colonies might mange these risks is by regulating the number of recruitable foragers inside the *vestibule* (Fig. 2.1). This can be achieved if ants modify the way they move when forager return rate is high, to increase interaction rate (Pinter-Wollman *et al.*, 2011). Foragers may also vary the amount of time they spend without recruitment before retiring back inside (Pinter-Wollman *et al.*, 2013). However, it is not immediately clear what the costs and benefits of such strategies would be in relation to how colonies would respond to different kinds environmental disturbances. Mathematical models are useful tool to study these kinds of questions (Sumpter and Pratt, 2003).

A Mathematical Model

In a recent article, we developed a model of collective foraging in P. *barbatus* Udiani *et al.* (2015). The model captures the positive and negative mechanisms of information sharing within the colony based on forager interactions at the nest entrance (Fig. 2.3). In the subsequent section, I provide a brief description of this model and discuss a set of analyses I performed to understand its dynamics. Mathematical
Figure 2.2: Experimental Observations of an Active P. Barbatus Colony. (a) Time Series of Foragers Inside and Outside the Nest Following the Addition of Seeds to Foraging Trails; Arrows Shows Time Points When Seeds Were Added and Depleted by the Colony. (b) Cross-correlation Coefficients of Series as a Function of Time Lag ($\tau$). The Correlation Between Returning Foragers and Available Individuals (Left) and Between Returning and Outgoing Foragers (Right) Is Maximzed at $\tau = 1$ and $\tau = 0$ Respectively, Suggesting That Changes in the Forager Return Rate Affects Outgoing Foragers Almost Immediately, but Influences the Number of Ants in the Vestibule a Short While Later.
proofs are omitted for clarity; but are shown in full detail in the appendix. Instead, I
will highlight theoretical results and the biological insights they provide about mecha-
nisms driving foraging outcomes (e.g., conditions under which the colony can reliably
forage at stable levels). I conclude with a discussion of the model’s predictions and
how they might explain variation observed in natural colonies (Gordon et al., 2008,

Model Derivation

Let \( N(t) = A(t) + F(t) + R(t) \) represent the foraging workforce of a colony at time
t where \( A(t) \) denotes the number of available (recruitable) foragers at the nest, \( F(t) \)
denotes the number of active (outgoing) foragers on the trail, and \( R(t) \) denotes the
number of successful foragers returning to the nest. The foraging state of the colony
can be described as a time vector \( \mathbf{D} = (A, F, R) \), which evolves deterministically
according to the following system:

\[
\frac{dA}{dt} = k_1 - \beta AR + \gamma R - \frac{k_2 A}{1 + \omega R} \\
\frac{dF}{dt} = \beta AR - (\alpha + d_f)F \\
\frac{dR}{dt} = \alpha F - (\gamma + d_r)R. \tag{2.1}
\]

The biological assumptions underlying this model are discussed subsequently.

1. **Available Foragers** \( A(t) \): The number of available (recruitable) foragers at
the nest is influenced by the following factors:

   (a) The **immigration rate** \( \Lambda(t) \), which describes the movement of naive
workers from the inner nest to the vestibule. For simplicity, I assume this
rate is constant over the model’s timescale: \( \Lambda(t) = k_1 \). In nature, \( \Lambda(t) \)
might fluctuate due to changes in task allocation; but this will depend on
(b) The **recruitment rate** \( \Psi(A, R) = \beta AR \), which describes the increase in the number of active foragers via activation. This mass action formulation assumes that interactions between successful foragers and recruitable foragers inside the nest are density-dependent (Fig. 2.1). More specifically, I assume that (i) foragers contact a fraction \( \rho \) of successful returning foragers at an average rate of \( c \) interactions per unit time, (ii) interactions are independent of one another and are equally likely to occur anywhere in the vestibule, and (iii) each interaction has a fixed probability \( (\mu) \) of activation. Hence, the effective contact rate \( \beta \) is the number of interactions per unit time made by a successful, returning forager that activates an available forager: \( \beta = c \rho \mu \).
(c) The turnover rate $\Upsilon(R) = \gamma R$, which describes the rate at which returning foragers become re-available for recruitment. This rate will be influenced by the distance between the resource site and the nest, searching and handling times, as well as the total amount of time spent inside the nest after a successful trip (Beverly et al., 2009). I aggregate these effects into a single constant $(1/\gamma)$, which describes the average time spent as a returning forager.

(d) The emigration rate $\chi(A, R) = k_2 \frac{A}{1+\omega R}$, which describes the movement of available workers from the vestibule into the nest, where they cannot be directly recruited. In accordance with the observations of Pinter-Wollman et al. (2013), I assume that workers emigrate at a rate proportional to $k_2 A$, which is maximum when there are no returning foragers ($R = 0$). I also introduce a parameter $\omega$, which models the responsiveness of available workers to changes in the number of returning foragers. Note that as $\omega$ increases, the emigration rate decreases; that is, more workers will remain available in the vestibule for the same number of returning foragers ($\frac{\partial \chi}{\partial \omega} < 0$).

This leads to the following equation:

$$A' = k_1 - \beta AR + \gamma R - \frac{k_2 A}{1+R}.$$  

2. Active Foragers $F(t)$: In addition to the recruitment rate $\beta AR$, the number of active foragers is influenced by: (i) the rate at which they find, process and handle seed items $\alpha(t)F$, and (ii) the rate at which they become lost during their excursion $d_f F$. The effective seed density around a typical harvester ant colony
Parameter | Description | Range | Default  
---|---|---|---  
$k_1$ | Immigration of naive foragers \( (\text{ants} \cdot \text{sec}^{-1}) \) | (0, 5) | 0.5  
$k_2$ | Retirement of available foragers \( (\text{ants} \cdot \text{sec}^{-1}) \) | (0, 5) | 0.2  
$\omega$ | Adaptive response factor | (0, 2) | 1  
$\beta$ | Effective contact rate \( (\text{sec}^{-1}) \) | (0, 2) | 0.1  
$\alpha$ | Seed discovery rate \( (\text{sec}^{-1}) \) | (0, 1) | 0.04  
$d_f$ | Loss rate: outgoing foragers \( (\text{sec}^{-1}) \) | (0, 1) | 0.025  
$d_r$ | Loss rate: returning foragers \( (\text{sec}^{-1}) \) | (0, 1) | 0.025  
$1/\gamma$ | Avg. time successful foragers spend recruiting \( (\text{sec}) \) | (0, 90) | 30  

Table 2.1: Description of Parameters Used in the Foraging Model (2.1).

is generally several orders of magnitude greater than its workforce (Schafer et al., 2006), and might change over several days following rainfall Gordon (1991, 1993). For simplicity, I’ll assume that seed densities are relatively constant (i.e., \( \alpha(t) = \alpha \)), and that foragers search randomly until they discover a seed item (Beverly et al., 2009). This leads to the following equation:

\[
F' = \beta AR - \alpha F - d_f F.
\]

3. **Returning foragers** \( R(t) \): The number of returning (incoming) foragers on the trail depends on the rate at which active foragers discover food items, \( \alpha F \); as well as the rate of predation or loss while en route to the nest, \( d_r R \). As noted in my earlier discussion of recruitment and turnover rates, only a fraction of foragers successfully return to the nest at time \( t \). I assume these foragers spend an average of \( 1/\gamma \) units of time recruiting workers at the nest entrance before entering to cache their seeds. This leads to the following equation:

\[
R' = \alpha F - \gamma R - d_r R.
\]
Mathematical Analysis

In this section, I provide a complete mathematical analysis of model (2.1). The analysis, which includes a characterization of equilibrium bifurcations, will provide theoretical conditions under which foraging can reliably persist at different levels of activity. It also outlines the relationship between colony-specific and environmental parameters influencing foraging outcomes. I will begin by establishing the basic properties of solutions to the dynamical system (2.1).

- Given positive initial conditions, solutions remain positive and bounded for all time.

- There are at least 2, and at most 3, equilibrium foraging states.

- The system only admits equilibrium behavior: no periodic or chaotic solutions exist.

I will also provide a sensitivity analysis of the model to understand how changes in colony-specific parameters, such as forager interaction rates, and environmental parameters, such as food availability, might influence foraging dynamics and long-term outcomes. Finally, I will validate the model by comparing its dynamics under simulated perturbations to the experimental observations of Pinter-Wollman et al. (2013). Detailed proofs and analysis associated with system (2.1) (i.e., on well-posedness, global dynamics, and bifurcations) can be found at the end of this chapter.
**Well-posedness and Boundedness**

**Theorem 2.0.0.1.** [Compact Attractor] System (2.1) is positively invariant in \(\mathbb{R}^3_+\) and every trajectory starting in \(\mathbb{R}^3_+\) is attracted to the following compact set \(C\):

\[
C = \left\{ (A, F, R) \in \mathbb{R}^3_+ : \frac{k_1}{\max\{k_2, d_f, d_r\}} \leq N \leq \frac{k_1 + k_2^2}{\min\{k_2, d_f, d_r\}} \right\}
\]

where \(N = A + F + R\).

**Notes:** It is reasonable to expect that the number of workers the colony commits to foraging \(N(t)\) over the course of daily activity is bounded due to constraints from other tasks (Gordon and Kulig, 1996). Thus, theorem 2.0.0.1 suggests that model (2.1) is at least biologically plausible.

**Equilibria and Stability**

**Theorem 2.0.0.2.** [Existence & Stability of Equilibria] Model (2.1) can have one (\(E_0\)), two (\(E_0\) and \(E_2\)), or three equilibria (\(E_0\) and \(E_i, i = 1, 2\)) depending on the values of \(R_0, R_A\), and \(R_\Delta\). Sufficient conditions for the existence and local stability of these equilibria are summarized in Table (2.2).

<table>
<thead>
<tr>
<th>Equilibrium</th>
<th>Component</th>
<th>Existence Condition</th>
<th>Stability Condition</th>
</tr>
</thead>
<tbody>
<tr>
<td>(E_0)</td>
<td>(A_0^*, 0, 0)</td>
<td>Always</td>
<td>Locally stable if (R_0 &lt; 1) Saddle if (R_0 &gt; 1)</td>
</tr>
<tr>
<td>(E_1)</td>
<td>(A_f, \frac{\gamma + d_r}{\alpha} R_1^<em>, R_1^</em>)</td>
<td>(\tilde{R}_\Delta &lt; R_0 &lt; 1)</td>
<td>Always a saddle</td>
</tr>
<tr>
<td>(E_2)</td>
<td>(A_f, \frac{\gamma + d_r}{\alpha} R_2^<em>, R_2^</em>)</td>
<td>(\tilde{R}_\Delta &lt; R_0 &lt; 1; or \ R_0 &gt; 1)</td>
<td>Always locally stable</td>
</tr>
</tbody>
</table>

Table 2.2: Existence and Stability of Equilibria in (2.1). \(A_0^* = \frac{k_1}{k_2}, R_0 = \frac{A_f^*}{A_f}, R_A = \frac{\beta A_0^*}{\omega k_1 + \gamma}, R_\Delta = \frac{k_1}{\phi_{max}},\) and \(\tilde{R}_\Delta = \max (R_A, R_\Delta)\). \(A_f^*\) and \(\phi_{max}\) are given in (2.2) & (2.5) respectively.

**Notes:** The model predicts up to three possible equilibrium states. There is a unique inactivity state where the colony does not forage: \(E_0 = (A_0^*, 0, 0) = (\frac{k_1}{k_2}, 0, 0)\). There
are two additional interior activity states \( E_i = (A^*_f, F^*_i, R^*_i) = (A^*_f, \frac{\gamma + d_f}{\alpha} R^*_i, R^*_i) \ i = 1, 2 \) where;

\[
A^*_f = \frac{(\alpha + d_f)(\gamma + d_r)}{\alpha \beta} > \frac{\gamma}{\beta} \Rightarrow \beta A^*_f - \gamma > 0
\]  \hspace{1cm} (2.2)

and \( R^*_i \) are the roots of the equation:

\[
\phi(R^*) = \left[ k_1 - (\beta A^*_f - \gamma) R^* \right] \left( 1 + \omega R^* \right) = k_2 A^*_f.
\]

Explicitly, these roots \( R^*_i \) are given by:

\[
R^*_{1,2} = \frac{k_1}{2(\beta A^*_f - \gamma)} - \frac{1}{2 \omega} \pm \sqrt{\left( \frac{k_1}{2(\beta A^*_f - \gamma)} - \frac{1}{2 \omega} \right)^2 + \frac{k_1 - k_2 A^*_f}{\omega (\beta A^*_f - \gamma)}}, \quad R^*_1 < R^*_2.
\]  \hspace{1cm} (2.3)

Theoretically, \( \phi(R) \) represents the net average rate of forager availability; it describes how the net number of recruitable foragers in the system changes with number of successful (returning) foragers. Recall that forager availability is both negatively and positively affected by returning foragers. Returning foragers deplete the recruit pool by activating previously uncommitted foragers. Yet, they increase the recruit pool both by reducing forager retirement rates and by becoming recruitable themselves. The stability of foraging activity critically depends on how these forces interact to provide a balanced pool of recruits to meet recruiters at the nest entrance.

To this end, we now define the following quantities.

**Thresholds for Collective Foraging**

1. \( \phi(R) \) has a unique maximum \( \phi_{\text{max}} \) at its critical point:

\[
R_c = \frac{\gamma - \beta A^*_f + \omega k_1}{2 \omega (\beta A^*_f - \gamma)}.
\]  \hspace{1cm} (2.4)
Figure 2.4: Equilibria of Model (2.1) Classified as Attractors (Blue), Saddles (Green) or Repellers (Black). An Equilibrium Occurs When the Rate of Forager Availability $\phi(R)$ Equals the Maximum Rate Forager Retirement (dashed horizontal lines: $\phi_i = k_2 A^* i$, $i = 1, 2$). (a) If $R_c < 0$, Then $\phi(R)$ Is Strictly Decreasing With the Number of Returning Foragers $R$ ($\phi_1$). (b) When $R_c > 0$, $\phi(R)$ Is Non-decreasing for a Range of Returning Foragers ($\phi_{1,2}$).

Thus, $R_c$ represents the critical number of returning foragers above which the expected reduction in forager retirement rates is insufficient to increase overall availability. Thus, it follows that:

$$
\phi_{\text{max}} = \phi(R_c) = \frac{(\beta A^*_f - \gamma + \omega k_1)^2}{4\omega(\beta A^*_f - \gamma)} \geq \phi(0) = k_1
$$

(2.5)

is the maximum rate of forager availability.

2. The forager generation number is a dimensionless quantity given by:

$$
R_0 = \frac{A_0^*}{A^*_f} = \frac{\beta k_1}{k_2} \cdot \frac{\phi}{(\alpha + d_f)(\gamma + d_r)}
$$

(2.6)

$R_0$ represents the average number of recruits generated by a single returning forager when the colony is near the inactivity state. It is the product of the expected production rate of new foragers (via recruitment) and successful foragers (via
resource discovery) over the typical duration of a foraging trip.

3. The forager availability number is a dimensionless quantity given by:

\[
R_A = \frac{\beta k_1 / k_2}{\omega k_1 + \gamma}. \tag{2.7}
\]

\(R_A\) describes the relationship between forager recruitment and availability. The numerator describes the mean recruitment rate of a single returning forager when the colony is near the inactivity state. The denominator describes the mean rate of increase of available foragers via: (i) new worker arrivals from the inner nest, (ii) recent foragers joining the recruit pool, and (iii) reductions in the number of retiring (uncommitted) foragers.

**Global Dynamics and Bifurcations**

Based on our analytical results shown in Theorem 2.0.1-2.0.0.2, we can classify global dynamics of model (2.1) in terms of \(R_0\), \(R_A\), and \(R_\Delta\).
Corollary 2.0.0.1 (Global Dynamics). Depending on the values of $R_0$, $R_A$, and $R_\Delta$, the global dynamics of (2.1) can be classified into one of three scenarios (also see Table 2.3):

1. **No activity:** If $R_0 < \min\{1, R_A\}$ or $R_0 < \bar{R}_\Delta < 1$, then model (2.1) has only the non-foraging equilibrium $E_0 = (\frac{k_1}{k_2}, 0, 0)$ which is globally stable. In either scenario, the colony will be unable to maintain its foraging activity.

2. **Persistent activity:** If $R_0 > 1$, then model (2.1) has two possible equilibria: $E_0$ which is a saddle and $E_2$ which is globally stable. In this scenario, the colony will consistently reach stable foraging levels.

3. **Bi-stability:** If $R_0$ is intermediate such that $\bar{R}_\Delta < R_0 < 1$, then model (2.1) has three possible equilibria: $E_i$, which is always a saddle, as well as $E_0$ and $E_2$, which are both asymptotically stable. In this scenario, the colony may be able to maintain its activity; but this depends on initial conditions.

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Condition</th>
<th>Dynamics</th>
</tr>
</thead>
<tbody>
<tr>
<td>Only $E_0$</td>
<td>$R_0 &lt; \min{1, R_A}$ or $R_0 &lt; \bar{R}_\Delta &lt; 1$</td>
<td>Globally stable.</td>
</tr>
<tr>
<td>$E_0$ and $E_2$</td>
<td>$R_0 &gt; 1$</td>
<td>$E_0$ is a saddle and $E_2$ is globally stable</td>
</tr>
<tr>
<td>$E_i, i = 0, 1, 2$</td>
<td>$\bar{R}_\Delta &lt; R_0 &lt; 1$</td>
<td>Both $E_0$ and $E_2$ are locally stable and $E_1$ is a saddle.</td>
</tr>
</tbody>
</table>

Table 2.3: Global Dynamics of Model (2.1). $A_0^* = \frac{k_1}{k_2}$, $R_0 = \frac{A_0^*}{A_f}$, $R_A = \frac{\beta A_0^*}{\omega k_1 + \gamma}$, $R_\Delta = \frac{k_1}{\phi_{\text{max}}}$, and $\bar{R}_\Delta = \max (R_A, R_\Delta)$. $A_f^*$ and $\phi_{\text{max}}$ are shown in (2.2) & (2.5).

**Mechanism underlying the backward bifurcation**

The backward bifurcation is the result of two opposite nonlinear feedbacks in the model. The net effect of successful foragers on the pool of available recruits can
be positive or negative depending on the forager return rate. Foraging will persist whenever $R_0 > 1$ (i.e., every returning forager activates at least one new forager). However, if this fails ($R_0 < 1$), the colony may be unable to maintain its activity (Fig. 2.6). This potential depends on $R_A$ the mean ratio of recruited foragers to available foragers. If $R_A > 1$, the colony always has more workers outside the nest than inside. Hence, if every returning forager is unable to recruit another (i.e., $R_0 < 1$) then foraging cannot be sustained. On the other hand, if $R_A < 1$, the colony always has more workers inside the nest than outside. Under this condition, foraging may still be sustained even when $R_0 < 1$, provided forager return rates are not too low. The effective minimum number of forager recruits sufficient for the colony to maintain its activity is given by:

$$
\tilde{R}_\Delta = \max (R_A, R_\Delta) = \frac{R_A + R_\Delta}{2} + \frac{|R_A - R_\Delta|}{2} \tag{2.8}
$$

where $R_\Delta = \frac{\phi(0)}{\phi_{\text{max}}} = \frac{k_1}{\phi_{\text{max}}} = \frac{4\omega k_1 (A_f^* - \gamma)}{(A_f^* - \gamma + \omega k_1)^2} \leq 1$ is the relative ratio of the minimum and the maximum rate of forager availability. $\tilde{R}_\Delta$ represents a sub-critical threshold.
where (2.1) undergoes a saddle-node bifurcation (i.e., goes from having zero to two interior equilibria) (Fig. 2.5(b)). Biologically, it reflects a lower bound for $R_0$ below which foraging is completely unsustainable.

**Sensitivity of Foraging Basin of Attraction**

Under the condition: \( \max\{\bar{R}_\Delta, R_A\} < R_0 < 1 \), a two-dimensional separatrix in \( \mathbb{R}^3_+ \) partitions the basin of attraction for the null (\( E_0 \)) and foraging (\( E_2 \)) activity states. Biologically, the separatrix defines a critical foraging allocation: \( \bar{D} = (\bar{A}, \bar{F}, \bar{R}) \) below which the colony ultimately ceases foraging. Simulations suggest that there is a positive scaling relationship between $R_0$, $\bar{R}_\Delta$ and the basin of attraction for $E_2$ (cf. Fig. 2.7). To better understand and quantify how small changes in one (or more) model parameters will affect the size of this region, I employed the normalized sensitivity index:

\[
\Gamma^u_p := \lim_{\delta p \to 0} \left( \frac{\delta u}{\delta p} \frac{u}{p} \right) = \frac{p}{u} \frac{\partial u}{\partial p} \quad u \neq 0
\]

where $u$ is a differentiable output variable of interest and $p$ is a nominal input parameter (Arriola and Hyman, 2009). The normalized sensitivity index ($\Gamma^u_p$) effectively estimates the expected percent change of a focal quantity (e.g., $R_0$) given a unit percentage change (i.e., ±1%) of one of its component parameters (e.g., $\gamma$). Because parameters can be classified into those that are likely colony-specific (i.e., $k_1$, $k_2$, $\beta$ & $\omega$), and those that reflect environmental conditions (e.g., $\alpha$, $\gamma$, etc.), the sensitivity index provides a way to quantify the potential costs (or benefits) to colonies of regulating different components. Moreover, these indices can provide some intuition about what parameters most influences colony’s ability to recover foraging after an
Sensitivity Index ($\Gamma^*_p$)

<table>
<thead>
<tr>
<th>Parameter</th>
<th>$\xi$</th>
<th>$R_A$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$k_1$</td>
<td>+1.78</td>
<td>+0.05</td>
</tr>
<tr>
<td>$\beta$</td>
<td>+0.99</td>
<td>1.0</td>
</tr>
<tr>
<td>$\omega$</td>
<td>0.78</td>
<td>-0.94</td>
</tr>
<tr>
<td>$\gamma$</td>
<td>-0.8</td>
<td>-0.05</td>
</tr>
<tr>
<td>$k_2$</td>
<td>-1.0</td>
<td>-1.0</td>
</tr>
</tbody>
</table>

Table 2.4: Normalized Sensitivity Indices for $\xi = R_0 - \bar{R}_\Delta$ and $R_A$. Sensitivity Indices Describe the Expected Impact of a 1% Change in Focal Parameters. Although $k_1$ and $k_2$ Independently Have the Largest Effects on Decreasing $R_A$ and Increasing $\xi$ Respectively, $\omega$ Has the Largest Joint Effect.

Table 2.4 lists the predicted change in $\xi = R_0 - \bar{R}_\Delta$ and $R_A$, based on the parameter values in table 2.1. Results here suggest that increasing the rate at which foragers arrive at the nest entrance ($k_1$) should have the largest positive impact on $\xi$ (and potentially the foraging basin of attraction; Fig. 2.7). On the other hand, changes in retirement rates ($k_2$) should have the largest negative impacts on $R_A$ (equation 2.7), and thus increase forager availability (cf. 2.5). Finally, results suggest that changes in the colony response factor ($\omega$) may produce the largest favorable effects on foraging dynamics (i.e., by maximizing the difference between $\xi$ and $R_A$).

Experimental Validation

To examine whether our model simulates realistic responses to perturbations, we replicated in silico the experimental perturbation described in Pinter-Wollman et al. (2013). In multiple observations over a 3-day period, returning foragers of mature P. barbatus were artificially prevented from entering the nest for either 3 minutes or 10 minutes during periods of high foraging activity. Throughout the trial, the number of available foragers in the vestibule along with the number of outgoing and returning foragers were recorded. In most instances, the number of outgoing foragers declined interruption (Pinter-Wollman et al., 2013).
Figure 2.7: Region of Attraction for $E_2$ (blue) vs. $E_0$ (red) Assuming $R_A < 1$. The Separatrix Partitions the Set of Initial Conditions $(\tilde{F}, \tilde{R})$ For Which Foraging Persist for Any Fixed Number of Available Foragers. Plots Show That Decreasing $\xi = R_0 - \bar{R}$ by Less than 50% from 0.256 to 0.143 Doubles the Region for $E_0$. Thus, the Critical Number of Returning Foragers $\tilde{R}$ Necessary to Sustain Activity Scales Nonlinearly with the Number of Active Foragers $\tilde{F}$. Other parameters: $k_1 = .5$, $k_2 = .2$, $\gamma = .03$, $\alpha = .04$, $d_f = 2d_r = .005$.

Figure 2.8: Exploring the Influence of $k_1$ and $\omega$ on Foraging Outcomes. ‘Risk Prone’ Regions Indicate Equilibria where the Colony has a Larger Portion of Its Workforce Outside the Nest (i.e., $1 < R_0 < R_A$). ‘Risk Averse’ Regions Indicate Equilibria Where the Colony has a Larger Portion of Its Workforce Inside the Nest (i.e., $\max\{\bar{R}, R_A\} < R_0 < 1$). Numerical Scale reflects the size of the Attraction Region for $E_2$ (vs. $E_0$).

in response to the removal of returning and recovered to varying levels of activity once returning foragers were allowed to enter to the nest again. We estimated model
parameters using the averaged time-series for each colony (see Table 2.5). Along with fixed experimental parameters (e.g., times of removal) we generated best-fit response curves corresponding to observations for both 3 and 10 minute removals. Because the quality of fits did not vary extensively among colonies, I show results for a single colony (Fig. 2.9).

The estimates of $R_0$ and $\tilde{R}_\Delta$ after the perturbation indicate that colony activity was in the bistable foraging region during the 3 minute removals ($R_0 = .03$, $\tilde{R}_\Delta = .0011$) and 10 minute removal ($R_0 = .52$, $\tilde{R}_\Delta = .18$). These results are consistent with empirical observations noting that harvester ant colonies will suppress and sometimes suspend foraging altogether if there are persistent declines in the forager return rate (Gordon, 2002; Gordon et al., 2011). However, the low estimates of $\tilde{R}_\Delta$, particularly in the 3 minute removals, do not suggest that foraging can be recovered without recruitment. In the context of our model, the low values reflect the increased potential of colonies to recover from short-term versus long-term interruptions. Although inactive foragers can leave the nest independent of social recruitment (Gordon et al., 2011), we stress that the ability of colonies to maintain their activity, in the bistable foraging region (i.e., $\tilde{R}_\Delta < R_0 < 1$), depends critically on the distribution of the forager workforce between the available, active, and returning states (Fig. 2.7).

In terms of biological significance, these estimates likely reflect the fact that harvester ant colonies are not very sensitive to foraging interruptions once they have reached stable levels of activity (Gordon, 2002; Gordon et al., 2011).

Finally, I acknowledge some model limitations may have affected the goodness of fit. Most obviously, our model does not capture any biological stochasticity. Thus, I cannot comment extensively on the ability of our estimates of $R_0$ and $\tilde{R}_\Delta$ to predict the recovery dynamics after the perturbation when the number of foragers becomes very small. Furthermore, we did not account for spatial constraints of vestibule
Figure 2.9: Predicted Best Fit Model to Experimental Data from Pinter-Wollman et al. (2013). Plots Show the Mean ± SD Numbers of Available (Top), Outgoing (Middle), and Returning (Bottom) Foragers in Colony N7 during Removal Trials Lasting 3 Minutes (left panel) or 10 Minutes (right panel). Parameter estimates are shown in Table 2.5.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>3-min removal</th>
<th>SD</th>
<th>10-min removal</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\alpha$</td>
<td>.6354</td>
<td>.3930</td>
<td>8.251</td>
<td>15.325</td>
</tr>
<tr>
<td>$\beta$</td>
<td>.0386</td>
<td>.0236</td>
<td>.5003</td>
<td>.8878</td>
</tr>
<tr>
<td>$\gamma$</td>
<td>.4568</td>
<td>.2973</td>
<td>6.028</td>
<td>11.493</td>
</tr>
<tr>
<td>$k_1$</td>
<td>11.067</td>
<td>12.783</td>
<td>10.763</td>
<td>6.532</td>
</tr>
<tr>
<td>$k_2$</td>
<td>34.642</td>
<td>57.712</td>
<td>1.729</td>
<td>6.056</td>
</tr>
</tbody>
</table>

Table 2.5: Mean (scaled in minutes) and 1-SD of Parameters Estimated for Colony N7 Using the Nonlinear grey-box modeling toolbox in MATLAB®. Death Rates Were Fixed Before and After the Perturbation ($d_f = d_r = 0$, $t < 4$ & $t > 14$) and Estimated for Returning foragers in 3-minute removals: (a) $d_r = 1.01101 ± 0.39937$, $t \in [4, 7]$; and 10-minute removals (b) $d_r = 1.01085 ± 0.278261$, $t \in [4, 14]$. Baseline Parameter Values and Sampling Range are Shown in Table 2.1.

size and structure which will influence the baseline numbers of available foragers, interaction patterns inside the vestibule, and any delays affecting the re-availability of returning foragers once inside the nest. Indeed, a summary analysis of (Pinter-Wollman et al., 2013) data revealed a lagged correlation between the numbers of
ants in the vestibule and number of returning foragers (Pearson’s product-moment correlation, t = 1.9592, df = 13, p= 0.07189; Fig. 2.2(b)). Such delays should be accounted for in future models.

Discussion

Harvester ants face a fundamental trade-off between maximizing foraging returns while remaining both flexible and robust to environmental disturbances (Gordon, 2002; Gordon et al., 2011; Pinter-Wollman et al., 2013). The modeling study discussed in this chapter provides theoretical insights into how *P. barbatus* colonies might bridge these regimes. First, the model predicts the existence of several key thresholds (i.e., $R_0$, $R_A$, $\tilde{R}_\Delta$) that together determine long-term foraging outcomes. These predictions can be summarized as follows:

1. Foraging persists if the expected number of recruits per successful returning forager, over the typical duration of a foraging trip, is larger than one (i.e., $R_0 > 1$).

2. If $R_0$ is less than one, foraging may still be sustained if the colony has more foragers inside the nest than outside (i.e., $R_A < 1$).

Previous studies of foraging in *P. barbatus* have focused on interaction rates as the primary factor affecting colony response to changes in environmental profitability (Prabhakar et al., 2012; Gordon et al., 2013). Here, we provide a more complete discussion of factors that might affect colony response by defining the relationships between $R_0$ and $R_A$. In addition to variables set by the environment outside the nest (e.g., $1/\alpha$, the nominal length of a typical a foraging trip), $R_0$ is defined by parameters that likely reflect colony-specific attributes (see Eq. 2.6). For instance, empirical studies suggest that colonies can vary significantly in their foraging intensity.
in similar environments (Gordon, 2002; Gordon et al., 2011). This pattern might be due to differences in baseline rates of recruitment (i.e., $\beta A_0^*$), which the model predicts should depend on average number of foragers inside the nest (i.e., $k_1/k_2$). On the other hand, the inherent cost of having high baseline recruitment rates relative to rates of forager availability suggests that colonies ought to regulate $R_A$ in response to external conditions (see Table 2.4). Unlike $R_0$, $R_A$ depends only on colony-specific parameters (see Eq. 2.7) and could be used to evaluate tendency towards risk-prone versus risk-sensitive foraging strategies (Fig 2.8). For instance, colonies who tend to have foragers outside the nest, rather than inside ($R_A > 1$), might be more vulnerable to a large foraging disturbance, even if this only lasts for a short period of time.

What parameters might be under selection to optimize foraging in different environments?

Harvester ant colonies can vary in their collective response to changing foraging conditions on an hourly, daily, and seasonal timescale (Gordon, 1991; Gordon et al., 2011). Colonies also exhibit characteristic foraging behavior from year to year, which as noted in a recent survey (Gordon, 2013) can influence their lifetime reproductive success (measured in the production of offspring colonies). Although the model presented focuses on proximate mechanisms, it is important to understand how these mechanisms might be shaped by selection. We can examine this question using the sensitivity indices (see table 2.4). As noted previously, $R_0$ and $R_A$ may be consequential for evaluating a colony’s ability to rapidly increase foraging in favorable environments and minimize risks in unfavorable ones. The potential costs (or benefits) to colonies of regulating these quantities is reflected in the sensitivity indices (see Table 2.4). There is a clear trade-off between parameters that tend to increase $R_0$ ($k_1$, $\beta$) versus those that tend to decrease $R_A$ ($k_2$, $\gamma$). However, changes in colony
response factor $\omega$, tend to have a more balanced effect (Table 2.4). Thus, regulating $\omega$ may provide the greatest return to colonies in terms of balancing flexibility and robustness in fluctuating environments. Pinter-Wollman (2012) provides an excellent discussion of how colonies might achieve this through consistent variation among foragers' behavioral propensities.

Limitations

One limitation of the model is that it does not explain experimental observation that colonies can be perturbed into different (stable) levels of activity (Gordon, 2002; Gordon et al., 2011; Pinter-Wollman et al., 2013). This might be related to specific components not captured in the current model. For instance, inactive foragers often leave the colony at a baseline rate independent of forager return (Gordon et al., 2011). Moreover, we did not consider potential feedbacks between forager return rates and worker arrival rates or explore how spatial constraints might influence interaction patterns inside the vestibule (Fig. 2.1). All these factors have been empirically noted as important in the context of foraging regulation (Gordon et al., 2013; Pinter-Wollman, 2015). A simple modification of the model can link worker arrival rates to the number of available foragers, and employ a saturating forager recruitment term to capture the effect of fixed vestibule size. Another extension that can be explored is how forager learning shapes colony’s ability to exploit resources in complex settings. For instance, in high-competition environments where food sources are constantly being depleted, colonies might need to have a critical number of foragers outside the colony to find new food sources (and minimize risk of losing profitable foraging areas to neighbors) (Adler and Gordon, 2003; Sanders and Gordon, 2004). It would also be useful (and more realistic) to study the effects of stochasticity on the foraging basin of attraction in an alternate formulation.
Concluding remarks

In conclusion, our results support the evidence that a simple interaction-based recruitment strategy can provide a resilient system for regulating foraging in ant colonies (Pinter-Wollman et al., 2013; Greene et al., 2013). Furthermore, our model provides useful insights into how internal and external variables can impact foraging dynamics, including identifying potential sources of inter-colony variation (Gordon, 2013). Finally, since the model is based on information sharing via local interactions, it can extended to study analogous systems that rely on similar mechanisms (e.g., nest construction in social wasps Jeanne (1986), quorum-sensing in rock ants Pratt (2005) and others).

Proofs

Proof of Theorem 2.0.0.1

Proof. According to the formulation of the foraging model (2.1), the following holds for \((A, F, R) \in \mathbb{R}^3_+\):

\[
A'_{|A=0} = k_1 + \gamma R \geq k_1 \\
F'_{|F=0} = \beta AR \geq 0 \\
R'_{|R=0} = \alpha F \geq 0.
\]

Thus, applying the results of Theorem A.4, p.423 in Thieme (2003), we can conclude that the foraging model (2.1) is positively invariant in \(\mathbb{R}^3_+\).

Let \(N = A + F + R\), then we have

\[
N' = A' + F' + R' = k_1 - \frac{k_A}{1+R} - d_F F - d_R R.
\]
Thus, we have the following inequalities based on the positive invariance property:

\[
k_1 - \max\{k_2, d_f, d_r\} N \leq N' \leq \frac{k_1(1 + R) - k_2 A - d_f F - d_r R(1 + R)}{1 + R}.
\]

This indicates the following two cases:

1. **Bounded below:**

\[
N' \geq k_1 - \max\{k_2, d_f, d_r\} N \implies \liminf_{t \to \infty} N(t) \geq \frac{k_1}{\max\{k_2, d_f, d_r\}}.
\]

2. **Bounded above:**

\[
N' \leq \frac{k_1(1 + R) - k_2 A - d_f F - d_r R(1 + R)}{1 + R} = \frac{k_1(1 + R) - d_r R^2 - k_2 A - d_f F - d_r R}{1 + R} \\
\leq k_1(1 + R) - d_r R^2 - \min\{k_2, d_f, d_r\} N \\
\leq \frac{k^2}{4d_r} + k_1 - \min\{k_2, d_f, d_r\} N.
\]

This indicates that

\[
\limsup_{t \to \infty} N(t) \leq \frac{k_1 + \frac{k^2}{4d_r}}{\min\{k_2, d_f, d_r\}}.
\]

Therefore, we can conclude that every trajectory starting in \( \mathbb{R}_+^3 \) is attracted to the following compact set

\[
C = \left\{ (A, F, R) \in \mathbb{R}_+^3 : \frac{k_1}{\max\{k_2, d_f, d_r\}} \leq A + F + R \leq \frac{k_1 + \frac{k^2}{4d_r}}{\min\{k_2, d_f, d_r\}} \right\}
\]

which also implies that the foraging dynamics of model (2.1) can be restricted to the compact set \( C \). Now, let \( M = \frac{k_1 + \frac{k^2}{4d_r}}{\min\{k_2, d_f, d_r\}} \). Because model (2.1) is bounded by \( M \), the number of returning ants \( R \) is also bounded by \( M \). This implies that for any
\(\epsilon > 0\), there exists time \(T\) large enough, such that we have

\[ A' = k_1 - \beta AR + \gamma R - k_2 \frac{A}{1 + R} \geq k_1 - \beta(M + \epsilon)A - k_2 A \geq k_1 - (\beta(M + \epsilon) + k_2)A \]

for all \(t > T\). This indicates that \( \lim \inf_{t \to \infty} A(t) \geq \frac{k_1}{\beta M + k_2} \). Therefore, we can conclude that \(A\) is persistent in \(R_3^3\).

**Proof of Theorem 2.0.2**

**Proof.** Because the non-foraging equilibrium \(E_0 = (A_0^*, 0, 0) = (\frac{k_1}{k_2}, 0, 0)\) always exists, we focus on sufficient conditions that lead to the existence of the foraging equilibrium \(E_i = (A_i^*, F_i^*, R_i^*)\), \(i = 1, 2\) where \(A_i^* = (\frac{\alpha + d_f}{\alpha \beta}) (\gamma + d_r)\) and \(R_i^*\) are roots of the equation \(\phi(R) = k_2 A_i^*\) with

\[ \phi(R) = [k_1 - (\beta A_i^* - \gamma)R] (1 + R). \]

Therefore, the existence of \(E_i\) is determined by the positive intercept(s) of the quadratic function \(\phi(R)\) and the horizontal line \(k_2 A_f^*\), which can be classified into the following two cases depending on the sign of the critical point \(R_c = \frac{\gamma - \beta A_f^* + k_1}{2(\beta A_f^* - \gamma)}\) of \(\phi(R)\) (see Fig. 2.4(b)):

1. If \(R_c < 0\) (see Fig. 2.4(a)), then we have

\[ R_c = \frac{\gamma - \beta A_f^* + k_1}{2(\beta A_f^* - \gamma)} < 0 \Leftrightarrow A_f^* > \frac{k_1 + \gamma}{\beta} \Leftrightarrow R_0 = \frac{k_1}{k_2 A_f^*} < \frac{k_1}{k_2 (k_1 + \gamma)}. \]

In this case, the foraging dynamics can have \(E_0\) or \(E_i, i = 0, 2\) depending on the ratio of \(\frac{\phi(0)}{k_2 A_f^*} = \frac{k_1}{k_2 A_f^*} > 1\):

(a) If \(\frac{\phi(0)}{k_2 A_f^*} = \frac{k_1}{k_2 A_f^*} < 1\) (i.e., \(R_0 < 1\), see the purple horizontal line in Fig. 35.
2.4(a)), then either there is no intercept of the null clines or the intercepts of \( \phi(R) \) and the horizontal line \( k_2A_f^* \) are located in the black region (i.e., negative values). In this scenario, the foraging model (2.1) only has the non-foraging equilibrium \( E_0 \).

(b) If \( \frac{\phi(0)}{k_2A_f^*} = \frac{k_1}{k_2A_f^*} > 1 \) (i.e., \( R_0 > 1 \), see the cyan horizontal line in Fig. 2.4(a)), then there is a unique foraging equilibrium \( E_2 \). Thus, in this scenario, the foraging model (2.1) has the non-foraging equilibrium \( E_0 \) and the foraging equilibrium \( E_2 \).

2. If \( R_c > 0 \) (see Fig. 2.4(b)), then we have

\[
R_c = \frac{\gamma - \beta A_f^* + k_1}{2(\beta A_f^* - \gamma)} < 0 \Leftrightarrow A_f^* < \frac{k_1 + \gamma}{\beta} \Leftrightarrow R_0 = \frac{k_1}{k_2A_f^*} > \frac{k_1\beta}{k_2(k_1 + \gamma)}.
\]

In this case, the foraging dynamics can have \( E_0 \) or \( E_i, i = 0, 2 \) or \( E_i, i = 0, 1, 2 \) depending on the ratio of \( \frac{\phi(0)}{k_2A_f^*} = \frac{k_1}{k_2A_f^*} \) and \( \frac{\phi_{\text{max}}}{k_2A_f^*} \):

(a) If \( k_2A_f^* > \phi_{\text{max}} \geq \phi(0) = k_1 \), we have

\[
k_2A_f^* > \phi_{\text{max}} \geq \phi(0) = k_1 \Leftrightarrow 0 < R_0 = \frac{k_1}{k_2A_f^*} < R_\Delta = \frac{k_1}{\phi_{\text{max}}}.
\]

In this case, the horizontal line \( k_2A_f^* \) (see the purple horizontal line in Fig. 2.4(b)) is above the quadratic equation \( \phi(R) \), i.e., there is no foraging equilibrium. Thus, in this scenario, the foraging model (2.1) has only the non-foraging equilibrium \( E_0 \).

(b) If \( k_1 < k_2A_f^* < \phi_{\text{max}} \) (see the dark green horizontal line in Fig. 2.4(b)),
then we have the following equalities:

\[ k_1 < k_2 A_f^* < \phi_{\text{max}} \iff 0 < R_\Delta = \frac{k_1}{\phi_{\text{max}}} < \frac{k_1}{k_2 A_f^*} = R_0 < 1 < \frac{k_2 A_f^*}{\phi_{\text{max}}}. \]

In this scenario, the foraging model (2.1) has the **non-foraging equilibrium** \( E_0 \) and two **foraging equilibria** \( E_i, i = 1, 2 \).

(c) If \( \frac{\phi(0)}{k_2 A_f^*} > 1 \) (i.e., \( R_0 > 1 \), see the cyan horizontal line in Fig. 2.4(b)), then there is a unique foraging equilibrium \( E_2 \). Thus, in this scenario, the foraging model (2.1) has the **non-foraging equilibrium** \( E_0 \) and the **foraging equilibrium** \( E_2 \).

Now we focus on the local stability of the **non-foraging equilibrium** \( E_0 \) and two **foraging equilibria** \( E_i, i = 1, 2 \) when they exist. The local stability of \( E_0 \) is determined by the eigenvalues \( \lambda_i, i = 1, 2, 3 \) of the Jacobian matrix associated with the foraging model (2.1)

\[
J|_{E_0} := \begin{bmatrix}
-k_2 & 0 & -\frac{\beta k_1}{k_2} + k_1 + \gamma \\
0 & -(\alpha + d_f) & \frac{\beta k_1}{k_2} \\
0 & \alpha & - (\gamma + d_r)
\end{bmatrix}
\]

where

\[
\lambda_1 = -k_2, \quad \lambda_2 + \lambda_3 = -(\alpha + d_f + d_r + \gamma) < 0
\]

and

\[
\lambda_2 \lambda_3 = \frac{-\alpha \beta k_1}{k_2} + (\gamma + d_r)(\alpha + d_f) = (\gamma + d_r)(\alpha + d_f)[1 - R_0].
\]

This indicates that if \( R_0 < 1 \), then \( \lambda_i < 0, i = 1, 2, 3 \); while if \( R_0 > 1 \), then \( \lambda_i > 0, 2, 3 \). Therefore, \( E_0 \) is locally asymptotically stable if \( R_0 < 1 \) and it is a saddle if \( R_0 > 1 \).
The Jacobian matrix evaluated at $E_i, i = 1, 2$ can be represented as follows:

$$J|_{E_i} := \begin{bmatrix}
-\beta R_i^* - \frac{k_2}{1 + R_i^*} & 0 & -\beta A_{f}^* + \gamma + \frac{k_2 A_{f}^*}{(1+R_i^*)^2} \\
\beta R_i^* & -(\alpha + df) & \beta A_{f}^* \\
0 & \alpha & -(\gamma + dr)
\end{bmatrix}$$

whose eigenvalues satisfy the characteristic polynomial:

$$\rho(\lambda) = \lambda^3 + c_2 \lambda^2 + c_1 \lambda + c_0 = 0 \tag{2.10}$$

with

$$c_2 = \beta R_i^* + (\alpha + df + dr + \gamma) + \frac{k_2}{1 + R_i^*} > 0$$

$$c_1 = (\alpha + df + dr + \gamma) \left[ \beta R_i^* + \frac{k_2}{1 + R_i^*} \right] > 0 \tag{2.11}$$

$$c_0 = \beta R_i^* [(\gamma + dr)df + \alpha dr] - \frac{k_2 R_i^* (\gamma + dr)(\alpha + df)}{(1 + R_i^*)^2}$$

According to the Routh-Hurwitz criteria (Brauer et al., 2001), we conclude that the foraging equilibrium $E_i$ is locally asymptotically stable if and only if $c_1c_2 > c_0 > 0$. According to (2.11), we have

1. $c_1c_2 > \beta R_i^*(\alpha + df + dr + \gamma)^2$ indicates that

$$c_1c_2 - c_0 > \beta R_i^* (\alpha + df + dr + \gamma)^2 - \beta R_i^* [(\gamma + dr)df + \alpha dr] > 0.$$ 

Because $c_1c_2 > c_0 \Leftrightarrow c_1c_2 - c_0 > 0$, thus, we can conclude $c_1c_2 > c_0$ always holds for both $R_i^*, i = 1, 2$. 

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2. The following equivalent relationships hold:

\[ c_0 > 0 \Leftrightarrow \beta(1 + R_i^*)^2 [\gamma + d_r]d_f + \alpha d_r] - k_2(\gamma + d_r)(\alpha + d_f) > 0 \]
\[ \Leftrightarrow (1 + R_i^*)^2 > \frac{k_2(\gamma + d_r)(\alpha + d_f)}{\beta [\gamma + d_r]d_f + \alpha d_r} = \frac{k_2A_f^*}{\beta A_f^* - \gamma} \]  

(2.12)

Notice that \( 0 < R_1^* < R_2^* \) are roots of \( \phi(R) = k_2A_f^* \), thus we have

\[ \phi(R_i^*) = [k_1 - (\beta A_f^* - \gamma)R_i^*] (1 + R_i^*) \]
\[ = k_2A_f^* \Leftrightarrow \left[ \frac{k_1}{\beta A_f^* - \gamma} - R_i^* \right] (1 + R_i^*) = \frac{k_2A_f^*}{\beta A_f^* - \gamma}. \]

This indicates that

\[ c_0 > 0 \Leftrightarrow (1 + R_i^*)^2 > \left[ \frac{k_1}{\beta A_f^* - \gamma} - R_i^* \right] (1 + R_i^*) \]
\[ \Leftrightarrow 1 + R_i^* > \frac{k_1}{\beta A_f^* - \gamma} - R_i^* \]
\[ \Leftrightarrow R_i^* > \frac{k_1}{2(\beta A_f^* - \gamma)} - \frac{1}{2} \]

Recall that

\[ R_1^* = \frac{k_1}{2(\beta A_f^* - \gamma)} - \frac{1}{2} - \sqrt{\left( \frac{k_1}{2(\beta A_f^* - \gamma)} - \frac{1}{2} \right)^2 + \frac{k_1 - k_2A_f^*}{\beta A_f^* - \gamma}} \]  

(2.13)

\[ R_2^* = \frac{k_1}{2(\beta A_f^* - \gamma)} - \frac{1}{2} + \sqrt{\left( \frac{k_1}{2(\beta A_f^* - \gamma)} - \frac{1}{2} \right)^2 + \frac{k_1 - k_2A_f^*}{\beta A_f^* - \gamma}} \]

Then we have

\[ R_1^* < \frac{k_1}{2(\beta A_f^* - \gamma)} - \frac{1}{2} \Rightarrow c_0 < 0 \]

\[ R_2^* > \frac{k_1}{2(\beta A_f^* - \gamma)} - \frac{1}{2} \Rightarrow c_0 > 0 \]
The discussion above implies that if the foraging equilibrium $E_i$ exists, then $E_1$ is always a saddle and $E_2$ is always locally asymptotically stable.

\[ \square \]

**Proof of Corollary 2.0.0.1**

*Proof.* According to Theorem 2.0.0.1, every trajectory of (2.1) is attracted to a compact set $C$. Thus the dynamics of model (2.1) is restricted to this set. Based on the results of Theorem 2.0.0.2, we have the following three cases:

1. If $R_0 < \min\{1, \frac{k_1\beta}{k_2(k_1+\gamma)}\}$ or $\frac{k_1\beta}{k_2(k_1+\gamma)} < R_0 < R_\Delta$, then the foraging model (2.1) has only the non-foraging equilibrium $E_0 = (\frac{k_1}{k_2}, 0, 0)$ which is locally asymptotically stable. This implies that the foraging model (2.1) has bistability, i.e., depending on the initial condition, the trajectory may converge to the non-foraging equilibrium $E_0$ or the foraging equilibrium $E_2$.

2. If $R_0 > 1$, then the foraging model (2.1) has the non-foraging equilibrium $E_0$ and the foraging equilibrium $E_2$ where $E_0$ is a saddle and $E_2$ is locally asymptotically stable. Again, applying the results of Poincare-Bendixson trichotomy in 3D (Thieme, 1992), we can conclude that every trajectory starting with strict positive initial condition converges to $E_2$, i.e., and $E_2$ is globally stable.

3. If $\max\{\frac{k_1\beta}{k_2(k_1+\gamma)}, \frac{k_1\beta}{k_2(k_1+\gamma)}\} < R_0 < 1$, then the foraging model (2.1) has the non-foraging equilibrium $E_0$ and two foraging equilibria $E_i, i = 1, 2$ where both $E_0$ and $E_2$ are locally asymptotically stable. This implies that the foraging model (2.1) has bistability, i.e., depending on the initial condition, the trajectory may converge to the non-foraging equilibrium $E_0$ or the foraging equilibrium $E_2$.

\[ \square \]
Chapter 3

IDENTIFYING FACTORS THAT INFLUENCE DIVISION OF LABOR AND PRODUCTIVITY IN FORCED ASSOCIATIONS OF HARVESTER ANTS

Abstract

Division of labor (DOL) is a prominent feature of task organization in animal societies. Previous work suggests that it can develop via self-organizing feedbacks that amplify behavioral differences within groups. However, not much is known about how these feedbacks affect productivity especially in a context where individuals must weigh the costs of performing different activities. To explore these questions, we created foundress associations (groups of colony-founding queens) in a normally solitary ant species (Pogonomyrmex barbatus). We compared the behavior of queens nesting alone to those in groups containing between two to six individuals over a 6-week founding period. Our results demonstrate that individual task choice, and its consequences on productivity, was influenced by social context. Solitary queens spent relatively more time engaged in work activities (excavation and brood tending) than on self-maintenance (grooming and resting). In groups, queens tended to specialize more on excavation or brood care. Although division of labor was intensified in larger associations, it did not translate to increased productivity. Brood production (per-capita) declined with increasing group size in part because queens laid fewer eggs. However, nesting pairs reared more adult offspring than any other group. To explore possible causal mechanisms for this pattern, we developed an agent-based model of the system. We hypothesized that short-term declines in task availability (e.g., due to queen inactivity) might exacerbate costs of specialization in larger groups where
demands of offspring care likely fluctuate. Simulations of a model in which queens had a decreased likelihood of activity following consecutive periods when they were unable to find work showed a curvilinear relationship between group size and expected productivity (measured as the variability of work needed across tasks). This result was further amplified if queens had a tendency to engage in recently performed tasks. In sum, our analyses provide a nuanced understanding about the internal factors that might shape the efficiency of task organization across the range of group sizes typically found in most cooperative species.

Introduction

Division of labor (DOL), or the degree to which different individuals tend to perform different tasks, is an integral feature of task organization in animal societies. Its foundational component, individual specialization on task roles, is found ubiquitously in eusocial societies (Michener, 1974; Oster and Wilson, 1978; Hölldobler and Wilson, 1990; Fewell et al., 2009), but also in cooperative (non-eusocial) societies, which occur broadly across social taxa (Bednarz, 1988; Stander, 1992; Underwood and Shapiro, 1999; Gazda et al., 2005; Jeanson et al., 2005; Holbrook et al., 2013). Previous work suggests that DOL is an emergent property of sociality that self-organizes from behavioral variation within groups (Fewell and Page Jr, 1999; Cahan and Fewell, 2004; Jeanson et al., 2005; Jeanson and Fewell, 2008; Holbrook et al., 2013). These results motivate a set of mechanistic questions about how social dynamics shape division of labor and what effects they might have on productivity in different contexts.

Group size is an important driver of social organization, influencing the emergence of task organization across social taxa (Oster and Wilson, 1978; Anderson and McShea, 2001). For instance, empirical estimates of division of labor, using worker specialization and/or polymorphism as a metric, increase with colony size in several
species of wasps and ants (Jeanne, 1986; Gordon, 1989; Karsai and Wenzel, 1998; Thomas and Elgar, 2003); but see (Dornhaus et al., 2009). With respect to ultimate function, division of labor might generate organizational efficiencies that are selected for in larger groups (Bonner, 2004) and/or costs that are selected against in smaller ones (Oster and Wilson, 1978; Herbers, 1981; Karsai and Wenzel, 1998). However, the ways in which selection shapes DOL is likely different within cooperative taxa, where individual and group success are related but not completely aligned (Fewell et al., 2009). In wild dogs, for instance, the need for a certain number of helpers to carry out several tasks essential to the group (e.g., hunting, pup-guarding etc.) may diminish the benefits of dividing labor and increase individual costs below a critical group size (Courchamp et al., 2002). Similar effects are likely to exist in taxa where multiple individuals reproduce (Bernasconi and Strassmann, 1999). However, these systems remain relatively understudied despite the fact that they represent a potentially more generalizable model of social evolution (Clark and Fewell, 2013).

In this chapter, we use a combination of empirical and theoretical approaches to explore factors that influence task organization in foundress associations of the ant *Pogonomyrmex barbatus* (Fewell and Page Jr, 1999). Like most ant species, *P. barbatus* colonies are initiated by a solitary queen who performs all of the initial tasks necessary for nest construction and offspring care (Bartz and Hölldobler, 1982; Johnson, 2002). However, queens increasingly specialize on a single task when forced to initiate colonies laboratory pairs (Fewell and Page Jr, 1999; Cahan and Gardner-Morse, 2013). Here, we examine the proximate mechanisms underlying this pattern and its scaling effects by comparing the behavior of solitary founding queens to those in groups containing between two and six conspecifics. In doing so, we ask: (i) how division of labor scales with group size, (ii) whether individual specialization confers work benefits to groups in terms of per-capita output and offspring production,
and (iii) how the tension between individual costs and group benefit might shape productivity outcomes in small versus large groups.

How might division of labor (DOL) be proximately linked with group size? A leading self-organizational hypothesis, the response threshold model, predicts that DOL can emerge in a context where individuals vary in their sensitivity to task-related stimuli and modify their behavior using simple rules (Robinson and Page Jr, 1989; Bonabeau et al., 1996; Page and Mitchell, 1998; Theraulaz et al., 1998). Similar models also predict that DOL should increase with group size if work demands decline relative to the availability of individuals to perform tasks (Gautrais et al., 2002; Merkle and Middendorf, 2004; Jeanson et al., 2007). However, this result may change depending on what factors are assumed to drive behavior. For instance, some authors have proposed that individual experience can modulate task-related thresholds via positive feedback (Pasteels et al., 1987; Plowright and Plowright, 1988; Theraulaz et al., 1998). This might occur if individuals who are successful at a task are more likely to continue performing it, and vice versa (Hogeweg and Hesper, 1983; Ravary et al., 2007; Weidenmüller, 2004). Moreover, the addition of self-reinforcement as a mechanism of task choice can lead to increased specialization in larger groups (Merkle and Middendorf, 2004; Jeanson et al., 2007).

One question that is particularly relevant for studying division of labor in cooperative associations, but often ignored in self-organizational theories, is how individuals make decisions in costly environments. Existing models tend to focus on large eusocial societies, where individuals suffer negligible costs of activity and are theoretically motivated to maximize colony benefit (Gautrais et al., 2002; Merkle and Middendorf, 2004; Jeanson et al., 2007). However, this assumption is ill suited for studying systems where individuals must balance the costs and benefits of cooperation—a trade-off that is often shaped by group size (Elgar, 1989; Creel, 1997; Clutton-Brock et al., 2001;
Gusset and Macdonald, 2010; Kerhoas et al., 2014). In a context where there are underlying trade-offs from performing different tasks, individuals might regulate costs by abstaining from work during periods when demands are perceivably low or absent (Jeanson and Fewell, 2008). However, this strategy may have unexpected group-level consequences for task organization and potentially alter the benefits of sociality in different contexts. For instance, short-term declines in task availability (e.g., due to queen inactivity) might increase the variability of work output in larger, more differentiated groups particularly in environments where task demands tend to fluctuate (Charbonneau and Dornhaus, 2015).

Our study of *P. barbatus* will explore the proximate mechanisms underlying the emergence and scaling of division of labor in a *de novo* context of sociality. Because *P. barbatus* queens are normally solitary in the field, their behavioral repertoire in groups should reflect an emergent response to a novel social environment rather than an evolved strategy (Fewell and Page Jr, 1999). In keeping with the variance-based models of self-organization, we expect that division of labor should increase with group size as a consequence of decreased need for work relative to number of tasks to be performed (Jeanson et al., 2007). With regards to its resulting structure, we expect that queens should invest less in nest excavation when paired with a conspecific, and increasingly less in larger associations due to its high physiological costs (Johnson, 2000). Likewise, we expect that queens should perform more self-maintenance activities (e.g., grooming and resting) in groups than in a solitary context.

Our study also explores whether the emergence of division of labor in incipient groups like *P. barbatus* has related effects on task organization and productivity as a token of fitness. Division of labor (DOL) may provide functional benefits in the context of colony foundation, as seen in more evolved contexts (Oster and Wilson, 1978; Chittka and Muller, 2009). We hypothesize that dividing labor may reduce the
aggregate costs of task switching allowing groups to provide more consistent patterns of offspring care than solitary queens (e.g., feeding and monitoring larvae). Under this hypothesis, we expect that scaling of DOL with increasing group size should correspond to increased per-capita efficiency of offspring production in larger groups versus smaller ones.

Methods

Collection and Experimental Setup

Queens of the normally solitary ant *P. barbatus* were collected in Scottsdale, AZ, USA, shortly after a mating flight in August 2005; all had removed their wings and were in search of a nesting site. Each queen was placed into a ventilated 1.5 ml eppendorf tube with moistened pieces of paper towel for transport from the collection site to the laboratory at Arizona State University. In the laboratory, queens were weighed, individually marked with enamel paint, before being assigned to observation nests in groups of two (n=24), or six (n=23). Queen weights were normally distributed with a mean 45.6 mg and variance of 3.53 mg; so we divided queens into 3 equally apportioned weight classes: small (33 to 45.0 mg); medium (45.1 to 48.8 mg); large (48.9 to 58.6 mg). We paired queens with another of the same weight class in groups of two. Groups of six received two queens from each weight class. Each observation nest was constructed using 2 panes of glass (12.5 × 17.5 cm) separated by thin (0.32 cm) plastic strips, and were filled with moistened sifted soil from the collection site. Nests were maintained in the laboratory for 55 days (until the appearance of the first workers) under natural light conditions, and at a constant temperature of 28°C. Nests were also re-moistened approximately every 4 days, and provided with fresh seeds (Kentucky blue grass) ad libitum throughout the experiment.
Behavioral Observations (wk 1)

Behavioral scans began as soon as queens were placed in their nests. For the first 2 days, nests were continuously monitored for 40 minutes every hour for 8 daylight hours, during which all instances of nest excavation were noted. A bout of nest excavation occurred when a queen brought a piece of soil out of the nest and deposited it on the surface. Nest excavation is the first task activity performed by queens, before the appearance of brood and initiation of brood care. Starting on the third day, nests were briefly scanned once each hour, during which each queen’s behavior was noted. Behavioral actions fell under the general categories of: task, non-task, and self-maintenance. In addition to nest construction, other tasks included brood care (laying an egg, interacting or standing over the brood pile), and foraging (manipulating seeds in the mandibles). Non-task behaviors consisted of walking, social interactions (antennation), and agonistic contact (e.g., biting or dragging another queen). Bouts of self-grooming and inactivity (resting) were classified as self-maintenance behaviors.

Nest productivity (wk 1-6)

Queens began producing eggs by day 3. Starting on the fourth day, all eggs and larvae were counted every 2 days until day 18. Brood production was subsequently monitored every week until day 55.

Data Analysis

Several queens died within the first 4 days of nest initiation; and most of these deaths occurred in the large groups. About 58% of 2-queen nests (10 out of 24) and 78% of 6-queen nests (18 out of 23) experienced at least one instance of mortality by the end of day 4. Based on these observations, we reclassified the number of queens...
in each nest as the number surviving after day 4 for our analysis. We excluded nests that experienced more than two deaths, or where all queens died; we also pooled data for nests with four or more individuals for analyses, except where noted. Foraging occurred infrequently (<1%) relative to the volume of other tasks across nests (supplementary Fig. 3.1). This was expected since *P. barbatus* queens are fully claustral during nest founding (Johnson, 2002). Based on these observations, we subsumed foraging into brood care and classified other behaviors into the following categories (a) Self-maintenance (resting or grooming), (b) Non-tasks (walking or interacting with a nest mate), (c) Excavation, and (d) Brood care. We used the normalized $DoL_i$ statistic (Gorelick *et al.*, 2004; Dornhaus *et al.*, 2009; Holbrook *et al.*, 2011) to quantify the degree behavioral specialization in each nest, and examine how queen number influenced division of labor. To calculate $DoL_i$, we generated an activity matrix, in which
each cell contained the proportion of task observations in which a specific queen was seen performing excavation or brood care throughout the experiment. Observations of foraging behavior were not included, because the frequency of this behavior is much lower than the two other tasks. From this matrix, we calculated Shannon’s index of entropy, for the distributions of individuals across activities and mutual entropy for the entire matrix (see Gorelick et al. (2004) for detailed methodologies). Finally, dividing the mutual entropy by Shannon’s index yields a specialization intensity $DOL_i$ between zero (low) and one (high). We tested (post-hoc) the effect of group size on the mean DOL values over the 6-day observations using a single-factor ANOVA. We performed a one-way analysis of variance (ANOVA) to test for performance differences between queens in solitary and group contexts, and to examine the effects of group size on egg and worker production. Where necessary, we performed a post-hoc Tukey honesty significance difference (T-HSD) test to note where differences occurred at $p < .05$ significance alpha level. For each test, normality and homoscedasticity assumptions of sample data were validated using Shapiro-Wilk normality test and the Bartlett test of homogeneity of variances.

Results

Activity Budgets and Work Output

We compared the activity budgets among queens founding alone to those in pairs, and groups with at least four (or more) conspecifics in the first week of colony initiation. This period is important because queens must manage concurrent demands for nest excavation, and brood care. By the end of this period, queens were engaging primarily in brood care. Solitary queens spent more time performing the tasks of excavating, brood care and/or foraging, and less time on self-maintenance activities
(grooming and resting) than did individual queens in associations (supplementary Fig.
3.1). In contrast, paired queens spent more time on brood care than did any other

group (43% of observations). Non-task behaviors (i.e., walking and social contact)
were more common in large groups than small ones. Social interactions accounted
for 9% of observations among paired queens compared to 14% in groups with 4+
queens. Queens in larger groups had lower per capita performance of nest construc-
tion (ANOVA: $F_{2,39} = 6.61, p < 0.01$) (Fig 3.2). Solitary queens excavated about
twice more often per-capita than queens in pairs (Mean ± SE: 11.6 ± 1.7 vs. 6.25
± 0.7) or in groups with 4+ individuals (Mean ± SE: 4.7 ± 0.86) (Post-hoc analysis
for pair sets, T-HSD: $p < 0.01$). Group size had a significant, but more mixed effect
on performance of brood care (ANOVA: $F_{2,39} = 6.55, p < 0.01$). Post hoc analyses
indicated that solitary queens did not differ significantly in brood tending from either
queens in pairs or queens in larger groups, but queens in pairs did tend brood signif-
icantly more than queens in larger groups (Mean ± SE: solitary 17.2 ± 1.89; pairs,
20.8 ± 1.47; 4+ queens, 12.4 ± 1.76) (T-HSD: $p < 0.01$).

**Task Organization**

**Division of labor**

Group size also affected the level of division of labor in nests with multiple queens.
Calculated $DoL_i$ was significantly higher in groups with four or more queens (Mean
± SE: 0.4 ± 0.04) than in pairs (0.23 ± 0.03) (ANOVA: $F_{1,31} = 9.64, p < 0.01$),
indicating that the degree to which different queens specialized on different tasks in-
creased with group size. To examine individual task repertoires in more detail, we
independently ranked queens by their excavation performance in associations. For
every pair, the queen that excavated more frequently was classified as the higher fre-
Figure 3.2: Bars Show Mean ± SEM Performance of Work (Vs. Non Work) Activities Per-capita. Group Size Had a Super-linear Effect on Performance of Self-care (Grooming and Resting) and Non-tasks (Walking and Social Contacts). In Contrast, It Had a Sub-linear Effect on Excavation, and Curvilinear Effect on Brood Care.

quency excavator (HFE) and the queen that excavated less frequently was classified as the lower frequency excavator (LFE) (following Fewell and Page Jr (1999)). Likewise, in groups of four or more individuals, queens with the highest and lowest excavation frequency were designated as the HFE and LFE respectively. We then compared the brood care performance of HFE vs LFE queens, to determine: whether queens who performed more excavation were less likely to perform brood care, indicating that queens were specializing on different tasks; or alternatively whether individuals who performed more excavation were also likely to perform more brood care, suggesting queens varied in activity level rather than specialization. We also used these comparisons to explore differences between the level of specialization in small versus large groups (Fig 3.3).
Figure 3.3: Bars Show the Mean ± SEM Performance of Queens Ranked as the High and Low Frequency Excavators (HFE vs. LFE) in Associations. Bars Show the Average of Top 2 and Bottom 2 Excavators in Nests with 4+ Queens.

**Tasks:** The level of excavation performed by solitary queens was similar to that of the HFE queens in associations ($F_{2,39} = 1.132, p = 0.33$). This was not true for LFE queens (ANOVA: $F_{2,39} = 53.84, p < 0.01$). On average, solitary queens excavated more per-capita than did LFE queens whether they were in a nesting pair (Mean ± SE: $11.67 ± 1.69$ vs. $2.71 ± 0.69$) or in a group with four or more individuals ($0.4 ± 0.1$; T-HSD: $p < 0.01$), a result consistent with the response threshold expectation that performance of a task by one individual should reduce its performance by others in the group Fewell and Page Jr (1999). There was also a negative relationship between excavation and brood care. In pairs, LFE queens performed more brood care bouts than did HFE queens (Mean ± SE: $24.8 ± 1.84$ vs. $16.78 ± 2.1$, $F_{1,26} = 8.52, p < 0.01$). Interestingly, they also had higher rates of brood care performance than did solitary queens ($17.2 ± 1.89$, $F_{1,21} = 7.64, p < 0.01$).
Likewise, LFE queens performed more brood care than did HFE queens in groups with 4+ individuals (Mean ± SE: 13.15 ± 1.09; $F_{1,39} = 4.9$, $p < 0.05$). But their performance was not statistically different from solitary queens.

**Self-maintenance:** LFE queens performed more self-maintenance activities (grooming and resting) than HFE queens regardless of context (Pairs: 16.78 ± 1.24 vs. 11.84 ± 1.16; $F_{1,26} = 8.34$, $p < 0.01$; 4+ groups: 20.94 ± 1.3 vs. 13.48 ± 1.26; $F_{1,36} = 13.8$, $p < 0.01$). In pairs, LFE queens performed self-maintenance twice more often than solitary queens (Mean ± SE: 20.94 ± 1.43 vs. 10.5 ± 2.38, $F_{1,45} = 16.4$, $p < 0.01$), but no more often than the average LFE queen in groups with 4+ individuals (Fig 2). In pairs, HFE queens performed similar levels of self-maintenance as solitary queens ($p = 0.05$), but significantly lower than the average HFE queen in groups with 4+ individuals ($F_{1,45} = 6.2$, $p < 0.01$).

**Non-tasks:** HFE queens performed more non-task activities (i.e., walking and social contact) than did LFE queens regardless of context (Pairs: 9.57 ± 1.09 vs. 3.64 ± 0.71; $F_{1,26} = 20.5$, $p < 0.01$; 4+ groups: 14.2 ± 1.25 vs. 7.7 ± 1.35; $F_{1,36} = 12.5$, $p < 0.01$). In groups with 4+ individuals, the top 2 excavators performed non-tasks 1.2 times more often than HFE queens in pairs (11.6 ± 0.87 vs. 9.57 ± 1.09), and 1.6 times more often than solitary queens (7.2 ± 1.01). The latter result was significant ($F_{1,45} = 5.4$, $p < 0.01$). In contrast, solitary queens performed more non-tasks than LFE queens in pairs ($F_{1,21} = 8.8$, $p < 0.01$), but no more often than the average LFE queen in groups with 4+ individuals (Fig 3.3).

**Temporal patterns of behavior in solitary versus group founding context**

We assessed how behavioral activity differed on the timescale of hours among queens in solitary versus group-founding context (Fig. 3.4-3.6). We also examined how the temporal progression of work in solitary versus group-founding nests varied during
nest establishment. We observed progressive changes in task organization between day 3 and day 8 as queens shifted from nest excavation to brood tending. Prior to day 5, the solitary queens spent a majority of their time excavating (35%); followed by self-maintenance (30%) and non-task activities (25%). From day 5, however, they were spending increasingly more time tending brood (Fig. 3.4). Similar changes in task organization emerged in groups with notable differences in the timing of the shift towards brood care. For instance, among nesting pairs, queens were spending on average more than 50% of their time tending brood by day 6 (Fig. 3.5). This was not the case in groups with 4+ individuals, where queens spent most of their time prior to day 4 engaged in non-task behaviors, particularly social interactions (Fig. 3.6 ).

Figure 3.4: Temporal Activity of Solitary Queens. Average Fraction of Time Spent Daily by Solitary Queens on Task and Non-task Activities During the Experiment (left), and Frequency of Hourly Transitions Between Behaviors over 6 Days (right).
Figure 3.5: Temporal Activity of Paired Queens. Average Fraction of Time Spent by Nests on Task and Non-task Activities During the Experiment (left), and Frequency of Hourly Transitions Between Behaviors for HFE and LFE Individuals over 6 Days (right).

Figure 3.6: Temporal Activity of Groups with 4+ Queens. Average Fraction of Time Spent by Nests on Task and Non-task Activities During the Experiment (left), and Frequency of Hourly Transitions Between Behaviors for Highest and Lowest Frequency Excavators (HFE and LFE) over 6 Days (right).

Productivity

Brood and worker production

We monitored nests over 55 days to assess the effect of group size on per-capita productivity. Queens began laying eggs on day 3, and production continued to increase...
until day 10, which coincided with the appearance of the first larvae cohort (Fig.
3.8). There was a large decline in egg numbers after day 10, in part due to hatch-
ing, but also because the newly hatched larvae cannibalized large numbers of eggs
. Therefore, we assessed cumulative egg production at day 10 before the first larva
hatched. Group size had an effect on cumulative egg production at day 10 (ANOVA:
$F_{2,24} = 3.77, p < 0.05$). The per capita number of eggs was higher in pairs than in
groups of 4+ queens, but did not differ between solitary queens and queens in pairs.
(T-HSD: $p < 0.03$).

We also examined the maximum number of larvae, pupae, and adult workers
reared in nests that survived up to day 55 (4 of 9 solitary, 11 of 14 pairs, and 11 of 19
with 4+ queens; Fig. 3.9). Although larvae production per-capita was similar among
Figure 3.8: Effects of Group Size on per-capita Investment by Day 10. Plot Shows the Mean ± SEM per-capita Egg Production of Surviving Nests at Day 10. Egg Counts Peaked on Day 10, and Remained at Low Levels for the Remainder of the Experiment. Groups with 4+ Queens Produced Fewer Eggs on Average than Singles or Pairs.

solitary and group-founding treatments (ANOVA: $F_{2,23} = 0.21, p = 0.81$), worker production was not (ANOVA: $F_{2,23} = 5.17, p=0.014$). Queens reared twice as many larvae into workers in pairs than in groups with 4+ individuals (T-HSD: $p < 0.05$).

Across nests, the number of offspring on day 55 was significantly associated with the total fraction of time queens spent on brood care ($T_{25} =3.0, p < 0.01$) and non-tasks ($T_{25} =-2.9, p < 0.01$), but not with division of labor in groups ($T_{21} = −0.6, p=0.5$) (Fig 3.10). Moreover, nests exhibiting higher variance in work output between days 3-8 were less productive in subsequent weeks than those with smaller variance compared during the same period (Fig 3.11).

Theoretical Effects of Group Size on Variance in Productivity

Existing models of group size and DOL tend to focus on contexts where individuals are always available or motivated to perform tasks, mapping to the expectations for eusocial colonies with sterile workers (Gautrais et al., 2002; Jeanson et al., 2007).
Figure 3.9: Effects of Group Size on Per-capita Productivity by Day 55. Plot Shows the Mean ± SEM of Maximum Amount Brood Produced among Queens in Nests Surviving up to Day 55. Egg Production Declined with Increasing Group Size. As a Proportion, the Number of Larvae That Survived into Adult Pupae/workers Was Highest in Co-founding Pairs, Intermediate for Solitary Queens, and Lowest in Nests with 4+ Queens.

However, these assumptions may not hold in cooperative (non-eusocial) systems generally, in which individuals must balance the fitness costs of expressing different behaviors (as suggested here by our study of *P. barbatus* queens during nest foundation). Our empirical results show that queens varied their activity levels in the presence of conspecifics, and that this variation was associated with differential patterns of work output and productivity in small versus large groups (Fig. 3.3; Fig. 3.10). Here, we develop a model to explore possible individual-level causes for this pattern. In relation to our empirical results, the model tests the hypotheses that short-term declines in task availability (e.g., due to queen inactivity) might exacerbate the costs of specialization in groups where the demands of brood care are high relative to other tasks. Under the hypothesis that queens have a lowered probability of remaining ac-
Figure 3.10: Effects of Task Organization on Productivity Across Nests. (a) Fraction of Time Spent on Brood Care, (b) Fraction of Time Spent on Non-tasks, (c) Relative Degree of Task Specialization among Group-founding Queens.

Figure 3.11: Effects of Variability in Work Output on Productivity Across Nests. (a) We Compared the Relative Variance (i.e., Coefficient of Variation) in Task Performance During the 1st Week with the Relative Variance in Periodic Counts of Eggs and Larvae over the Subsequent 3-week Period. (b) We Compared the Relative Variance in Periodic Brood Counts Between Weeks 2-4 with Maximum Number of Adult Offspring by Day 55.

tive following periods in which they are unsuccessful in performing a task, we expect that work demand might fluctuate increasingly in larger groups where there are more queens available than tasks needed.
An Agent-based Model

Our model considers a social group with $N$ queens (agents) and $M=2$ tasks (i.e., excavation and brood care). Each task $j$ is characterized by a variable $S_j(t)$, which reflects its level of need in period $t$. Similar to previous studies (Gautrais et al., 2002; Jeanson et al., 2007), we define a task demand parameter $0 < \delta_j < 1$, which represents the fraction of simulation time $N$ queens must collectively spend working on task $j$ in order to keep its stimulus from growing between periods. Likewise, each queen $i$ is characterized by a parameter $(\theta_{ij})$ that describes her threshold for performing task $j$ as well as a variable $\tau_i(t)$ that models her homeostatic cost of activity. We assumed that thresholds remain fixed over time; but that a queen might become more or less active in the group depending on her success in finding and completing tasks previously. More specifically, we assume that $\tau_i(t)$ increases by $c$ units during periods when queen $i$ is active without a task, and decreases when she was engaged in a task. This dynamic captures the feedback between queen’s availability to work and her perceived need for work in the group. The model also includes a component of task fidelity; i.e. specifically that a queen’s likelihood of encountering a specific task might depend on her recent history (see table 3.1 and ODD protocol for details).

Simulations run in discrete time for a total of $T$ periods ($0 \leq t \leq T$). During each period, queens can be in one of three behavioral states: (1) inactive, (2) active without task, or (3) active in a task. We assume that inactive queens are unavailable to perform tasks, but that active queens might encounter a task (or switch between tasks) once every period. Similar to previous studies (Gautrais et al., 2002; Jeanson et al., 2007), we assume that work arises in each task at a fixed rate $\sigma_j$ that scales proportionally with group size (i.e., $\sigma_j \sim N_j^{\beta_j}$, $0 \leq \beta_j < 1$). We also model the delay between the start of nest construction and brood care using a piece-wise linear
function during the simulation (see appendix for details). Finally, we assume that all queens work at a fixed rate $\alpha$.

The model is implemented as follows. At the start of period $t$, each task regenerates its stimulus by $\sigma_j = \delta_j \alpha N_j^\beta$. Next, queens are randomly selected to make decisions based on their current state. First, inactive queens may become active with probability $P_A(t) = 1/\tau_i$. Next, active queens may encounter stimulus for either task 1 or 2 (i.e., excavation or brood care) and become engaged with if $S_j(t) > \theta_{ij}$. Finally, queens who do not become engaged in a task might enter an active, non-task state with probability $P_{NT}(t)$, or retire (i.e., become inactive) with probability $1 - P_{NT}(t)$. We assume that $P_{NT}(t)$ is nonzero at its baseline in period $t$, and increases with the fraction of the group currently active without tasks (see appendix for details). The model updates tasks only after all queens have made their decisions. During the update period, each task reduces its stimulus by a value of $\alpha$ multiplied by the number of queens engaged in it.

We explored how the task demand ratio ($\delta_1/\delta_2$) and queen’s fidelity to recent tasks ($\rho$) influenced work output and DOL with increasing group size. We use the coefficient of variation of task stimuli over the length of a simulation lasting $T$ periods as a proxy measure for expected productivity. Further details of our implementation including a table of parameter values used in simulations can be found in the ODD protocol section end of this chapter. Here, we highlight the following key results.

**Simulation Results**

We first considered a null model ($c = 0$) in which queens had an equal likelihood of encountering both tasks ($\rho = 0.5$) and were always available to work throughout model simulations (i.e., $\tau_i(t) = 1, \forall 0 \leq t \leq T$). Simulations recapitulated our experimental findings of a curvilinear scaling of work performance with increasing group
Figure 3.12: Predictions of Null Model in Which Agents Perform Tasks above a Fixed Threshold and Work Demands Scale Proportionally with Increasing Group Size (see ODD protocol for details). Plots Show the Predicted Activity Budget for a Typical Agent under the Hypotheses That She Always Available to Work (c=0) and Encounters Both Tasks with Equal Probability (\(\rho = 0.5\)) During Simulations. The Fraction of Time Spent on Excavation and Brood Care Declines with Group Size \(N\) When Tasks Have Equal Needs (left), but Increases for a Range of Sizes When There Unequal Need (right).

size. But this result developed only under assumption that queens faced unequal demands for excavation versus brood care tasks (i.e., \(\delta_1 << \delta_2\), Fig. 3.12). This result was amplified in a context where queens had increased likelihood of encountering recently performed tasks (Fig. 3.13). As expected, division of labor also increased with group size and larger groups had lower variance in work output than smaller ones.

Next, we considered the modified model \((c > 0)\) in which queens had a lower probability of activity following periods in the simulation when they were idle (i.e., active without performing a task). Here, we observed a nonlinear relationship between group size and expected productivity, depending on the level of fidelity to recent tasks \((\rho)\). In the absence of activity costs \((c = 0)\), larger groups had less variance in work output than smaller groups for any value of \(\rho\) (Fig. 3.14). However, groups tended to achieve their lowest variance for intermediate values of \(\rho\). In the presence of activity costs \((c = 1)\), smaller groups tended to have lower variance in work output than
larger ones (Fig. 3.14). Nonetheless, increasing task fidelity among queens tended to lower expected variance in larger groups, but only when it was sufficiently high ($\rho > 0.9$). These results are likely explained by the fact that queens in larger groups are less likely to find work (and thus become increasingly inactive) during the early parts of the simulation when excavation is the only task available. On the other hand, active queens are less likely to encounter tasks below their thresholds in larger groups, especially if they are also highly specialized.

Discussion

Existing theory suggests that division of labor (DOL) can develop via of self-organizing feedbacks that amplify (and stabilize) behavioral differences within groups (Robinson and Page Jr, 1989; Bonabeau et al., 1996; Page and Mitchell, 1998; Therault et al., 1998). However, not much is known about how these feedbacks scale with group size, or their consequences for productivity in a context where individuals must weigh the costs of performing different activities (Jeanson and Fewell, 2008; Holbrook et al., 2013). We examined these questions in an experimental social system: forced associations of the normally solitary ant *P. barbatus*. Our results support the assertion that DOL can spontaneously emerge in a *de novo* system (Fewell and Page Jr, 1999; Cahan and Fewell, 2004; Jeanson et al., 2005, 2008), but that its expression and consequences are proximately shaped by group size (Jeanson and Fewell, 2008; Holbrook et al., 2013).

On mechanisms driving the emergence and scaling of division of labor

Our empirical context, in which we forced solitary nesting queens into communal associations, allows us to assess how social environment influences individual task choice, and by extension task organization (Fewell and Page Jr, 1999). *P. barbatus*
queens perform two major tasks during the early stages of colony foundation: constructing a nest and caring for brood. As is typical for females of any solitary species,
queens initiating a nest alone spent most of their time alternating between tasks (Fig. 3.2, 3.4). However, when paired with a conspecific, a division of labor emerged in which one queen primarily performed excavation while the other provided brood care (Fig. 3.5). This differentiation increased with group size, indicating that tasks are increasingly monopolized by a subset of individuals in larger associations (Fig. 3.5).

One issue that is often ignored in models of division of labor is how individuals behave when there are intrinsic costs associated with performing different tasks. In the case of nest founding, evidence suggests that excavation may be a particularly expensive task in terms of mortality risk (Johnson, 2000; Cahan, 2001). Indeed, we observed that queens excavated most frequently when nesting alone and consistently less in larger associations (Fig. 3.2). However, a different pattern was seen for brood care. Although the number of eggs produced (per-queen) declined with increasing group size (Fig. 3.8), paired queens performed significantly more bouts of brood care...

Figure 3.14: Comparing Predictions of Null Model to Modified Model with Individual-level Costs ($c > 0$). Plots Explore the Combined Effects of Group Size ($N$) and Task Fidelity ($\rho$) on the Expected Variance in Work Output Assuming That Queens Are More Likely to Become Inactive Following Periods When They Are Idle Without Work ($c > 0$). (See Protocol for Details). In the Absence of Activity Costs ($c = 0$), Larger Groups Have Less Variance in Output than Smaller Groups; But Groups Tended to Achieve Their Lowest Variance for Intermediate Levels of $\rho$. In the Presence of Activity Costs ($c = 1$), Smaller Groups Tend to Have Lower Variance in Work Output than Larger Ones.
than individuals in any other context (Fig. 3.3).

The positive scaling of division of labor might have emerged due to a reduction in demand (i.e., the overall need for work relative to the amount of labor needed to complete tasks) (Jeanson et al., 2007). But if lower demand led to fewer queens working in larger groups, what were they doing instead? We observed that queens in associations spent significantly more time on self-maintenance behaviors (i.e., grooming and resting). This was particularly evident during the first couple of days when excavation was the primary task available (Fig. 3.5 - 3.6). We also found some ancillary behavioral differences among queens classified as excavation specialists (HFE) versus non-specialists (LFE). For instance, HFE queens were generally more active and tended to engage in non-task behaviors (i.e., walking and social contacts) with greater frequency than their LFE nest mates (Fig. 3.3). These differences varied across groups, suggesting that performance of either self-maintenance (or non-tasks) may intrinsically connect with a queen’s perception of work needed within the nest (i.e., given her specialist role).

Our results also suggest that the value of work (or performing a particular task) to individual queens was influenced by intrinsic and extrinsic factors. In general, queens showed a fair degree of behavioral fidelity during each day such periods of work tended to follow periods of work (and likewise for resting) (Fig. 3.4 - 3.6). We also observed a shift in task performance over several days, which varied between solitary and group founding nests (Fig. 3.4 - 3.6). We speculate that queens may reduce their digging rate once they have reached a critical nest volume and that the size of the brood pile may represent a cue triggering the transition to brood care. However, it is also possible they might have responded directly to the activity of other nest mates. In support of this idea, we found correlations between the activity of excavation specialists (HFE) and non-specialists (LFE) were influenced by group
size (Fig. 3.7). For instance, HFE queens were more likely to be observed displaying the same behavior as their LFE nest mate in pairs than in groups with four (or more) conspecifics (Fig. 3.7). These results highlight the roles of individual experience in shaping patterns of task choice within groups; and also that group size can influence these patterns.

*Functional costs of increased group size on task organization and productivity*

Division of labor might provide functional benefits in incipient social groups, as hypothesized for more complex and derived societies (Oster and Wilson, 1978; Chittka and Muller, 2009). However, the extent of these benefits may depend on the type of social group considered and the environment they inhabit (Dornhaus et al., 2009; Charbonneau and Dornhaus, 2015). For instance, while specialization can improve individual efficiency (Chittka and Muller, 2009), it might be especially costly in environments where work needs can fluctuate unexpectedly (Charbonneau and Dornhaus, 2015).

In the case of nest founding in *P. barbatus*, we hypothesized that dividing labor might allow queens to better regulate the costs of task switching in work critical for brood care (e.g., grooming, feeding, etc). Under this regime, one might have reasonably expected larger groups to benefit more from dividing labor than smaller ones. However, we observed an opposite pattern. Among surviving colonies, the number of adult offspring (per-capita) peaked among paired queens and declined in groups with four (or more) conspecifics. This difference developed despite the fact that larvae production was similar across nests (Fig. 3.9).

Some of the earliest studies of foundress associations showed an optimum curve of colony productivity with group size (reviewed by Bernasconi and Strassmann (1999)). These findings were typically ascribed to conflict interactions and competition among
queens that resulted in decreased per-capita productivity (Taki, 1976; Rissing and Pollock, 1987; Tschinkel, 1993). For instance, in associations of *S. invicta*, queens often consume the eggs of their nest mates (Tschinkel, 1993). Moreover, differential loss of mass from reproductive investments can affect survival (Bernasconi and Keller, 1996). Our study of *P. barbatus*, however, focused on a *de novo* context where queens are not likely to have evolved such strategies. Although we can not completely rule out the possibility of egg cannibalism, our data suggest queens had lower egg-laying rates in groups with four (or more) conspecifics (Fig. 3.8). This result is inline with previous work showing that queens contribute disproportionately to brood production when forced into associations (Cahan and Gardner-Morse, 2013)

An alternative viewpoint is that the declining productivity of larger group sizes may have emerged as a consequence of within-group dynamics that modified the brood rearing environment. We observed that queens tended to maintain a common brood pile in a narrow, isolated tunnel inside the nest. Thus, it was not surprising to find that co-founding queens were more likely to perform brood care together than specialists in larger associations (Fig. 3.3). However, nests where queens had less consistent work output during the nest initiation period were generally less productive in subsequent weeks compared to those with more consistent output during nest initiation (Fig 3.11). This finding suggests a possible link between the variability of brood care and offspring quality during experiment. The proximate costs of non-constant task availability is probably lower for brood care during egg-laying phase than in latter stages when larvae start to eclose. Ant larvae require near constant feeding and monitoring to minimize oophagy (Urbani, 1991; Liu *et al.*, 2001; Masuko, 2003). With increased specialization, there were likely fewer individuals nursing brood in larger groups. This pattern might have increased variability of care and resulted in higher rates of brood attrition.
What mechanisms might underlie the variability within groups? We hypothesized *P. barbatus* queens may conserve energetic resources by minimizing superfluous activity in their natural solitary founding context. This might be achieved via a strategy whereby queens decrease their likelihood of activity during periods when work demands are low or absent—a pattern suggested by our data (see 3.4 - 3.6). Simulations of a model in which agents employ a similar cost-mitigating strategy showed a curvilinear relationship between group size and expected productivity (measured as the variability of work needed across tasks). In general, the model suggests that specialization might be more beneficial in smaller groups, where there is sufficient demand for work in order for keep queens active, than in larger groups where queens are less likely to find work and become increasingly less active (Fig 3.13 - 3.14). Moreover, the model also predicts that group performance should be maximized at a “threshold” size, where there was sufficient need for work in order for queens to remain partially active across tasks. These predictions can be tested in empirically by analyzing productivity *P. barbatus* colonies reared in different experimental nests where queens have varying levels of access to the brood pile.

The comparison of naturally evolved associations to artificially created ones like *P. barbatus* can provide some insights into the fitness consequences of self-organized division of labor under different ecological and social contexts (Fewell and Page Jr, 1999; Cahan and Fewell, 2004; Jeanson et al., 2008; Holbrook et al., 2013). Division of labor (DOL) may present a barrier to sociality because it can generate disparities among individuals specializing on different tasks. Our results here suggest that these costs might be exacerbated by increased group size with measurable effects on productivity. Thus, we expect that selection, as a rule, should favor behavioral adaptations leading towards task sharing rather than specialization in order to maintain cooperation in these systems. Cahan and Gardner-Morse (2013) identified several
ways this could occur; for instance, decreasing response thresholds to social cues, changes in the connections between stimulus inputs and behavioral outputs to minimize performance of high-cost tasks, or adaptive modification of behavioral responses in response to group size or composition.

Concluding remarks

Our results support the assertion that division of labor can emerge from self-organizational processes drive specialization in de novo groups (Fewell and Page Jr, 1999; Jeanson et al., 2005, 2008; Jeanson and Fewell, 2008; Holbrook et al., 2013), but that these mechanisms likely have potentially negative consequences for productivity at larger sizes. In all, we argue based on these results and others (Jeanson and Fewell, 2008) that behavioral adaptations to minimize differentiation may have been necessary for the evolution of social groups in which individual and collective fitness are enhanced by cooperation.

Protocol for Agent-based Model

This section provides a model description of the main components of the model based on the ODD protocol of Grimm et al. (2010).

Purpose

The purpose of this study is to shed light on mechanisms that might explain the empirical relationship between division of labor (DOL), group size and per-capita productivity in de novo associations of colony-founding ant queens (Fig 3.11). Our data shows that queens divided labor in pairs and worked increasingly less in larger groups. However, this dynamic might have increased the cost of DOL in larger groups because there were fewer queens available to respond to changing demands of offspring.
care. We developed a model to examine the consequences of an individual-level mechanism which might explain patterns in our data. In it, agents increase/decrease their activity levels in response to consistent success/failure in finding/completing tasks. We explore how this dynamic influences the variability of work output in context agents also tend to specialize on tasks and how group size can exacerbate this cost.

**Entities, state variables and scales**

The model considers a social group with $N$ agents (queens) and $m$ tasks. Each task $j$ is characterized by its stimulus level $S_j(t)$, which reflects its work need in period $t$. Task stimuli are perceivable by all agents. However, this may depend on the agent’s task history (see submodel section for details). Agents can either be inactive, engaged in a task, or active without a task during each period. Each agent $i$ is characterized by an internal demand $\tau_i(t)$, which changes with her activity level and influences her probability of being available to work in future periods. The model runs in discrete time; each time steps represent a decision epoch during which agents can change their behavioral state.

**Process overview and scheduling**

At the start of each period, each task increases its stimulus by a fixed value $\sigma_j$. Next, depending on their current state, agents are randomly selected to make decisions. First, inactive agents may become active with activation probability $P_{A_i}(t)$. Next, active agents may encounter stimulus for some task $j$ (i.e., excavation or brood care) and become engaged with probability $P_{T_i}(S_j)$. The likelihood that an agent encounters either task may depend on previous performance. Finally, those who do not become engaged in a task remain in an active, idle state with probability $P_{NT_i}(t)$ or retire.
Table 3.1: Definition of Parameters Used in the Numerical (Agent-based) Model.

(i.e., become inactive) with probability $1 - P_{NT}(t)$. Tasks are updated immediately after each agent makes a decision. During the update period, each task reduces its stimulus by a fixed value $\alpha$.

**Design concepts**

**Basic principles**: Our study draws on previously published model of division of labor and group size (Gautrais *et al.*, 2002; Merkle and Middendorf, 2004; Jeanson *et al.*, 2007). A common assumption in these models is that agents are always available/motivated to perform tasks, and behave without reference to underlying costs. Here, we assume that agents suffer homeostatic costs from performing tasks, and act (myopically) to minimize these costs by reducing their activity during periods when work demands are low or absent.

**Emergence**: We will examine how division of labor (i.e., the degree to which different individuals tend to perform different tasks) scales with increasing group size. We will also explore how the combination of increased specialization and declining need for work in larger groups might theoretically influence work out-
put by assessing fluctuations in task stimuli throughout the simulations.

**Adaptation**: We assume all agents are initially available to work on any task that exceeds their intrinsic threshold. However, individuals who have an experience of not finding tasks to perform become less available to work in subsequent periods. We also assume that agents’ probability of encountering a task may depend on recent experience performing it (see *task fidelity* in submodels).

**Objectives**: Agents do not have any explicit objectives. Their actions are strictly based on their current internal state and/or their external environment.

**Learning**: Agents become less active over time if they continue to have an experience of not finding tasks to perform.

**Sensing**: Agents are aware of their internal state and task stimulus levels. They are also aware of the behavioral state of others in each period.

**Interaction**: Agents directly affect tasks by performing them. They can influence each other’s probability of remaining active (as opposed to becoming inactive) during idle periods (see *Probability of remaining active* in submodels section).

**Stochasticity**: The order in which agents are asked to make each decision is random. Each agent’s task response thresholds are drawn from a distribution with known mean and variance.

**Observation**: During the simulation, we store the number of times each agent transitions into a new state and stimulus levels across tasks. From these data, we can compute (at simulations end) the variability of task stimuli, how much time the individuals/group spends on different activities, and division of labor.
(DOL_i) statistic (Gorelick et al. 2004). Since this a stochastic model, we calculated the mean and variance of these quantities over 50 simulation runs.

**Modeling details**

**State variables**

**Tasks:** We assume that there are \( m = 2 \) tasks; each task \( j \) is associated with stimulus value \( S_j \in R^+ \), which denotes with its current need. The stimulus for task \( j \) increases at a rate \( \sigma_j(t) \), and decreases by the number of agents working on it \( Q_j(t) \) (multiplied by their work rate \( \alpha \)). Thus, the change in task stimuli between time periods is given by:

\[
\Delta S_j = \sigma_j(t) - \alpha Q_j(t).
\]

where \( \sigma_j(t) \) is the increase in stimulus intensity in period \( t \). Naturally, \( \sigma_j \) should reflect the demand for each task (i.e., total work required to complete it relative to total work force available)(Jeanson et al., 2007). Our data suggests that the demand for excavation and brood care scale differently with group size. For instance, paired queens produced twice as many eggs as single queens, but groups with 4+ queens produced less than four times as many. Task demand may also change over time. For instance, we observed there was usually a delay in commencing egg tending until excavation reached a certain depth. Moreover, the demands of brood care change as eggs develop into larvae. For our simulations, we assumed that demand is function of group size: \( \sigma_j(t) = \delta_j \cdot \alpha \cdot N^{(\beta_j)} \) where \( \delta_j \in [0,1] \) is the baseline need for task \( j \) and \( \beta_j \in [0,1] \) is a scaling factor. Notes: \( \delta_j \) can be interpreted as the proportion of the group that must perform in task \( j \) in period \( t \) in other to keep its stimulus from growing.
(i.e., $\Delta S_j < 0$). Moreover, $\beta_j$ provides a way of modeling how the needs of task $j$ increases with number of agents in the group.

**Individuals:** We model the effects of work on agent $i$’s internal state by introducing an activity variable $\tau_i(t) \in R^+$ Its value is updated between periods as follows:

\[
\tau_i(t+1) - \tau_i(t) = \begin{cases} 
+ c & \text{if agent } i \text{ is idle in period } t \\
- b \cdot \delta_j & \text{if agent } i \text{ performs task } j \\
0 & \text{Otherwise}
\end{cases}
\]

$\tau_i$ models agent $i$’s perceived costs of activity. It captures a sense of how agents valuate the profitability of the work environment. Agents become more motivated/available to perform tasks when perceived costs are low (e.g., $\tau_i = 0$) than vice versa. The update rule requires $\tau_i$ to increase $c$ units during periods when agent $i$ is active but unable to find work. In contrast, $\tau_i$ decreases $b \cdot \delta_j$ units during periods when agent $i$ is working on task $j$. Either changes will affect her probability of being active in subsequent periods (see activation probability in the next section).

**Submodels**

**Initialization:** Each simulation runs for 1440 time periods. At the beginning of each simulation, all agents are inactive. The stimulus for excavation is initially set at value of $S_1(0) = 50$, while the stimulus for brood care is set at zero $S_2(0) = 0$. Furthermore, the demand for brood care is set at zero ($\sigma_2 = 0$) until $t = 250$, when it is assumed queens start producing eggs. Similar to Gautrais et al. (2002), and Jeanson et al. (2007) each agent $i$ has a genetically deter-
mined threshold $\theta_{ij} \in R^+$ for performing task $j$. $\theta_{ij}$ is sampled from a normal distribution $N(50,5)$. Furthermore, each agent’s intrinsic demand is initialized to zero (i.e., $\tau_i(0) = 0$).

**Activation probability** $P_{Ai}(t)$: We assume each agent becomes active with probability $P_{Ai}(t) = 1/\tau_i(t)$ at the beginning of period $t$, depending on their internal demand variable $\tau_i(t)$. Otherwise, they remain inactive for the remainder of the period.

**Probability that agent $i$ performs task $j$** $P_{Ti}(S_j)$: Next, all active agents can encounter a stimulus for either task 1 or 2. The probability of agent $i$ performing in task $j$ conditional on encounter is:

$$P_{Ti}(S_j) = \begin{cases} 1 & \text{if } S_j(t) \geq \theta_{ij} \\ 0 & \text{Otherwise} \end{cases}$$

We assume that both tasks are initially encountered with equal probability.

**Probability of encountering recent task (i.e., task fidelity):** $\rho$: We allow for the possibility that agents may be more likely to encounter stimulus for recently performed task. This might reflects the spatial heterogeneity in the distribution of tasks and their associated stimuli (e.g., in $P. \text{barbatus}$ colonies, queens kept brood in the innermost chambers of the nest; away from parts being excavated). Specifically, let $k(i)$ denote the index of agent $i$’s most recent task. Also, let $\rho \in [0.5,1)$ represent the probability that agent $i$ encounters stimuli associated with task $k(i)$. If $\rho = 0.5$, then agents have equal likelihood of encountering both tasks. As $\rho \to 1$, agents are more likely to encounter their most recently performed task.
**Probability of remaining active (non-task) \( P_{NT}(t) \):** Agents who do not become engaged in a task may retire (i.e., become inactive) with probability \( 1 - P_{NT}(t) \) or remain active probability \( P_{NT}(t) \). We assume that \( P_{NT}(t) \) has a baseline value \( \epsilon \in [0, 1] \), but increases with the number of individuals who are currently idle in period \( t \) : \( P_{NT}(t) = \epsilon \cdot (1 + A(t)/N) \).

**Implementation**

The model was developed in Netlogo (http://ccl.northwestern.edu/netlogo/). A code is available on request.
A NOVEL MODELING FRAMEWORK TO STUDY TASK ORGANIZATION IN ANIMAL GROUPS

Abstract

We introduce a mathematical modeling framework to study factors that shape the dynamics and outcomes of task organization in social groups. Our approach, which is based on the theory of multi-agent systems, focuses on groups of adaptive (reinforcement learning) agents whose behavior is based on a valuation of alternative choices in a given environment. As an application, we analyze two representational models in which agents must manage demands for one or two tasks, while constrained by a fixed cost of activity. We obtain a number of theoretical results including threshold conditions under which agents are likely to become specialized on a task, contribute proportionally to both tasks, or abstain from work altogether. Simulations of a model where agents have similar preferences across tasks, but vary in their work rate, reveal parameter regions with multiple coexisting attractors that correspond to distinct group efficiency outcomes. This result highlights the importance of studying initial conditions as part of a broader analysis of factors that might shape variation in groups where individuals balance costs of performing different activities. In sum, our framework expands the scope of existing models to study the theoretical causes and consequences of task organization in animal groups.
Introduction

Much of the behavior and success of social (group-living) animals is dependent on their capacity to organize and regulate work (i.e., tasks needed to survive, grow and produce offspring) on a systematic basis (Charbonneau and Dornhaus, 2015). The degree to which they achieve this is often defined by flexibility of their members to switch between roles in response to environmental changes. Mathematical models have been instrumental in highlighting conditions under which groups can achieve emergent regulation of work via self-organization (Bonabeau et al., 1996, 1998; Page and Mitchell, 1998; Theraulaz et al., 1998). However, there is still a gap in our understanding of how the processes and outcomes of task organization at the group-level are shaped by behavioral mechanisms at the individual level. Here, we propose a novel modeling approach that aims to bridge this gap.

There is a great deal of interest in relating causes and patterns of task organization to understand the variation seen across social taxa (Fewell et al., 2009). Classical studies focused on patterns of division of labor and how its regulation might contribute to colony efficiency (Oster and Wilson, 1978). However, there has been a more recent shift towards a proximate theory (Beshers and Fewell, 2001), with a focus on principles that allow group-level regulation to emerge as a consequence of individual-level behavior (Hemelrijk, 2002). The key challenge of this analysis is to understand how individuals make task decisions in different environments. Existing models finesse this question by focusing on phenomenological rules that describe how they behave without reference to underlying mechanisms that produce them (Beshers and Fewell, 2001). The paradigmatic example of this is based on the concept of response thresholds (Robinson and Page Jr, 1989; Bonabeau et al., 1996, 1998; Page and Mitchell, 1998; Theraulaz et al., 1998). Response-threshold models hypothesize
that division of labor can self-organize within groups where individuals vary in their sensitivity to extrinsic task stimuli. This pattern develops in part due to a stigmergic feedback in which one’s performance of a task changes in the environment in ways that decreases the likelihood of others performing the same task (Theraulaz et al., 1998). For instance, in the case where individuals have fixed sensitivities, those with the lowest threshold for a task will consistently initiate it sooner than others reducing its need (and thus the likelihood that others will perform it in the immediate future) (Bonabeau et al., 1998). The response threshold model also offers an explanation for how groups can adaptively respond to changing conditions without central control. This is because increasing the demand for a specific task will cause its stimulus level to exceed the thresholds of a broader subset of individuals in the group, causing them to initiate work on the task (Detrain and Pasteels, 1991; Fewell and Page Jr, 1993; O’Donnell and Foster, 2001; Weidenmüller, 2004).

Although, threshold models have been instrumental for exploring conditions under which groups can self-organize around work, this approach has some limitations (Beshers and Fewell, 2001). First, by studying response thresholds as a phenomenological concept, we lose sight of a broader set of factors that shape decision-making at the individual-level. For instance, an individual’s decision to perform a task might relate with her current physiological state (e.g., energy reserves), or depend on prior experience of others in the group (Charbonneau and Dornhaus, 2015). From an adaptive perspective, it makes sense for animals to modulate their activity in response to their environment particularly, when there are costs of performing different behaviors. Second, the lack of underlying theory of task choice limits the power of threshold models to explain how group-level patterns of organization are shaped by individual-level characteristics (Schelling, 1971). For instance, even in groups where individuals have similar response thresholds, variation in work demand resulting from
differences in task ability might influence the resulting structure of division of labor. A phenomenological approach forecloses on the possibility to evaluate whether particular equilibrium patterns of task choice are utility maximizing for an individual, or systematically efficient for the group (Granovetter, 1978). Finally, for explanatory power, models of task organization should be as broad and integrative as possible with narrowly focused hypotheses that can be empirically tested (Beshers and Fewell, 2001). Existing approaches so far have been exploratory; in that they are designed to reveal the consequences of specific behavioral rules. Moreover, because they have been developed within a computational framework, there is little hope of gaining any analytical insights into their predictions.

In this article, we develop a mathematical framework to study task organization that integrates mechanisms of decision-making at the individual level (Fig. 4.1). Our approach, which is inspired by the theory of multi-agent systems (Sato and Crutchfield, 2003; Lerman et al., 2006) focuses on myopic, reinforcement learning agents, who valuate utilities of performing different actions and adjust their behavior in favor of alternatives that provide the highest expected return (Herrnstein and Prelec, 1991; Loewenstein, 2010). The framework combines some key features from existing RT models (Bonabeau et al., 1998; Theraulaz et al., 1998) because we assume that individuals are able to assess task needs through specific environmental stimuli and reduce their activity level if the task environment becomes less profitable. However, by modeling the tradeoffs associated with different task choices (rather than thresholds explicitly), our approach allows us to evaluate factors that shape behavioral response at the individual-level and explore their group-level consequences for work.

The rest of the chapter is structured as follows. First, we will present a general description of our framework along with a discussion of its assumptions. Next, we will analyze two representational models developed for a pair of agents managing
Figure 4.1: A Behavioral Modeling Framework (modified from Beshers and Fewell (2001)). Boxed Quantities Represent Factors Known (or Hypothesized) to Influence an Individual’s Task Choice. We Theorize That Behavior Should Be Adaptive, Reflecting a Balance Between Costs and Rewards of Activity in a Dynamic Task Environment.

a single task, and a pair of agents and tasks. In each scenario, we ask how the presence of competing work demands and intrinsic costs of activity influence each agent’s behavioral likelihood over time (e.g. to what degree they tend to perform tasks versus abstain from work altogether). The chapter concludes with a discussion of our main theoretical results in connection with previous studies and empirical data.

Model Derivation

State variables

We consider the behavior of $N$ agents denoted by $i$ in a group over discrete time periods $t, t + 1, \ldots$ etc. In each period, agents can be engaged in one of $M$ tasks, denoted by $j$ or inactive in a non-task state (e.g., resting). Now, let $x_{i0}(t)$ represent
the probability that agent $i$ is inactive at time $t$. Similarly, let $x_{ij}(t)$ represent the probability that agent $i$ performs task $j$ at time $t$. Then, the allocation strategy of agent $i$ is given by $\mathbf{x}_i(t) = \{x_{i0}(t), x_{i1}(t), ..., x_{iM}(t)\}$, where $\sum x_{ij}(t) = 1$. Moreover, the allocation profile for task $j$ is given by $\mathbf{x}_j(t) = \{x_{1j}(t), ..., x_{Nj}(t)\}$.

**Dynamics of task stimulus**

Let $S_j$ represent the intensity of stimulus associated with task $j$. Biologically, $S_j$ might refer to any quantitative cue that signals the demand for task $j$ (e.g., number of physical encounters, a chemical concentration, etc.). Naturally, $S_j$ should decrease proportionally with the total amount of work done by agents performing task $j$. However, $S_j$ may increase at a maximum (constant) rate $\delta_j$ due to exogenous factors (e.g., nest degradation, brood development, etc.) that drive up the need for work in task $j$ and require agents to continually invest some effort in performing each task. Following the work of (Bonabeau *et al.*, 1998), we will assume $S_j$ follows a linear rate dynamic:

$$
\dot{S}_j = \delta_j - \sum_{i=1}^{N} \alpha_{ij} \cdot x_{ij} \cdot S_j
$$

(4.1)

where $\alpha_{ij}$ is the maximum effective work rate of agent $i$ in task $j$.

**Reward values: $V_{ij}(t)$**

Similar to Bonabeau *et al.* (1998), agents ascribes a time-varying non-negative value $V_{ij}$ to each task $j > 0$ proportional to its stimulus intensity (i.e., $V_{ij} \propto S_j$). However, $V_{ij}$ may also depend on other factors such as self-reinforced behavior (preferences) where successful performance of an action increases the likelihood of future
performance (Theraulaz et al., 1998). Another possible factor is social facilitation where agents directly increase (or decrease) their propensity to express a behavior when it is expressed by others (Webster and Fiorito, 2001). For any agent $i$, let $x_{-ij} = \{x_{1j}, x_{2j}, \ldots, x_{(n-1)j}\}$ represent the allocation vector of other agents towards task $j$ at time $t$. In other words, $x_{-ij}$ holds the proportion of effort all agents ($i$ excluded) allocates to task $j$. We allow for the possibility of self vs. socially-facilitated reinforcement using a multi-variate weight function $F(x_{ij}, x_{-i}) \in [0, 1]$: \[
V_{ij}(S_j, x_{ij}, x_{-ij}) = \frac{S_j}{\theta_{ij}} \cdot F(x_{ij}, x_{-ij}), \quad j = 1, 2, \ldots, m
\] (4.2)

where $\frac{1}{\theta_{ij}}$ is agent $i$’s preference for task $j$ (in which case $\theta_{ij}$ is an “aversion” parameter). Generically, $F(x_{ij}, x_{-ij})$ should be some linear combination of $x_{ij}$ and $x_{-i}$. As an illustration, consider the following possibility:

\[
F(x_{ij}, x_{-ij}) = 1 + \underbrace{\epsilon_i \cdot x_{ij}}_{\text{self-reinforcement}} + \underbrace{\sigma_i \cdot \frac{1}{N-1} \sum_{k=1}^{N-1} x_{kj}}_{\text{social reinforcement}}, \quad k \neq i.
\]

where $\epsilon_i \in [0, 1]$ and $\sigma_i \in [-1, 1]$. If $\sigma_i = 0 \iff F = 1 + \epsilon_i x_{ij}$, then $V_{ij}$ does not depend on behavior of others. However, if $0 < \sigma_i \leq 1$, then $V_{ij}$ increases with $F$ (i.e., the value of task $j$ to agent $i$ increases when other agents are likely to perform it). Conversely, if $-1 \leq \sigma_i < 0$, then $V_{ij}$ decreases with $F$ (i.e., the value of task $j$ to agent $i$ decreases when other queens are likely to perform it).

**Intrinsic demand: $V_{i0}(t)$**

We also assume that agents are subject to intrinsic demands $V_{i0}(t)$ that might limit their availability to perform tasks in period $t$. In biological terms, this might reflect a need to perform self-maintenance activities (e.g., grooming, resting etc) to
maintain homeostasis. For simplicity, we subsume these demands into a single constant: \( V_{i0}(t) = \Phi_i \), which can be interpreted as agent \( i \)'s intrinsic cost of activity at time \( t \).

**Dynamics of behavior switching**

Now, suppose that in a small time-interval \( dt \), an agent in behavioral state \( j \) encounters a stimulus for an alternate state \( k \neq j \) with probability \( 1/M \). We make a sensible assumption that agents follow a simple rule: switch to new state \( k \) if its perceived reward value is larger than that of current state \( j \). This rule is commonly referred to as a reinforcement learning and has been used in previous multi-agent modeling contexts (Sato and Crutchfield, 2003; Lerman et al., 2006). We can order the value of each behavioral state to agent \( i \) such that: \( V_{i0} \leq V_{i1} \leq \ldots \leq V_{iM} \). Based on this switching dynamic, we can write down an expression for the expected rate of change of \( x_{ij} \) in period \( t + dt \):

\[
x_{ij}(t + dt) - x_{ij}(t) = \sum_{k=0}^{j} x_{ik} \cdot x_{ij} \cdot [V_{ij} - V_{ik}] \cdot dt - x_{ij} \sum_{k=j+1}^{M} x_{ik} \cdot [V_{ik} - V_{ij}] \cdot dt
\]

\[
= x_{ij} \sum_{k=1}^{M} x_{ik} \cdot [V_{ij} - V_{ik}] \cdot dt
\]

\[
= x_{ij} [V_{ij} - \bar{V}_i] \cdot dt
\]

(4.3)

where

\[
\bar{V}_i = \sum_{k=0}^{M} x_{ik} V_{ik} = \left( 1 - \sum_{k=1}^{M} x_{ik} \right) \Phi_i + \sum_{k=1}^{M} x_{ik} \frac{S_j}{\theta_{ij}}
\]

(4.4)
is the *weighted* average rate of return to agent $i$ over all possible activities. In the continuous-time limit, $dt \to 0$ the dynamics of (4.3) can be approximated by an $M + 1$ dimensional system:

$$
\dot{x}_{ij} = x_{ij}[V_{ij} - \bar{V}_{i}], \quad j = 0, 1, ..., M
$$

(4.5)

where $V_{ij}$ and $\bar{V}_{i}$ are defined accordingly by equations (4.2) and (4.4) respectively.

**General framework**

Combining the model equations (4.1) and (4.5), we get an $M \times (N + 1)$ dimensional dynamical system:

$$
\begin{align*}
\dot{x}_{i0} &= x_{i0}[V_{i0} - \bar{V}_{i}] \\
\dot{x}_{ij} &= x_{ij}[V_{ij} - \bar{V}_{i}] \quad i = 1, 2, ..., N \\
\dot{S}_{j} &= \delta_{j} - \sum_{i}^{N} \alpha_{ij}x_{ij}S_{j} \quad j = 1, 2, ..., M
\end{align*}
$$

(4.6)

where $x_{i0} = 1 - \sum_{k=1}^{M} x_{ik}$, and all parameters are positive. Moreover, $V_{ij}$ and $\bar{V}_{i}$ are given by (4.2) and (4.4). The generalized framework (4.6) can be used to study how the dynamics of task organization within a social group relates with the composition and behavior of its members. For instance, we can explore how varying parameters relating to individual preference/aversion for certain tasks ($\theta_{ij}$), intrinsic costs ($\Phi_{i}$), as well as environmental parameters (e.g., $\delta_{j}$) affects their long-term patterns of task performance.
<table>
<thead>
<tr>
<th>Parameter</th>
<th>Meaning</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\delta_j$</td>
<td>Task regeneration rate</td>
</tr>
<tr>
<td>$\alpha_{ij}$</td>
<td>Mean work rate of agent $i$ in task $j$</td>
</tr>
<tr>
<td>$\Phi_i$</td>
<td>Intrinsic constraint of agent $i$</td>
</tr>
<tr>
<td>$\theta_{ij}$</td>
<td>Aversion of agent $i$ for task $j$</td>
</tr>
<tr>
<td>$\epsilon_i$</td>
<td>Self reinforcement of agent $i$</td>
</tr>
<tr>
<td>$\sigma_i$</td>
<td>Social reinforcement of agent $i$</td>
</tr>
</tbody>
</table>

Table 4.1: Description of Parameters Used in the General Modeling Framework (4.7).

A baseline model

To begin, let’s suppose that agents are neither influenced by experience nor by social reinforcement (i.e., $\epsilon_i = \sigma_i = 0$). This reflects typical assumptions made in the fixed response-threshold model (Bonabeau et al., 1998). Suppose also that agents have fixed constraints. Under these conditions, the value of resting for each agent is constant: $V_{i0} = \Phi_i$, and the value of each task depends only on perceived demand: $V_{ij} = S_j/\theta_{ij}$ and (4.6) becomes:

$$
\begin{align*}
\dot{x}_{i0} &= x_{i0} \left[ \Phi_i - \bar{V}_i \right] \\
\dot{x}_{ij} &= x_{ij} \left[ \frac{S_j}{\theta_{ij}} - \bar{V}_i \right] \quad i = 1, 2, \ldots, N \\
\dot{S}_j &= \delta_j - \sum_i \alpha_{ij} x_{ij} S_j \quad j = 1, 2, \ldots, M
\end{align*}
$$

(4.7)

where $\bar{V}_i = \left( 1 - \sum_{k=1}^{M} x_{ik} \right) \Phi_i + \sum_{k=1}^{M} x_{ik} \frac{S_k}{\theta_{ij}}$.

Mathematical Analysis

In this section, I will study the dynamics of Model (4.7) using a combination of analysis and simulations. First, I discuss some general properties of (4.7) and comment on their biological implications in the context of how individual activity and specialization affects division of labor. Next, I focus on specific cases to provide some clear intuition about these results. The first study focuses on a pair of agents,
who must manage a single task while facing a constant physiological cost. The second study focuses on a pair of agents and tasks. These analyses help us understand how individuals behave when faced with multiple (dynamic) demands. Proofs for analytical results are located in section 4.

**Definition 4.0.0.1.** An equilibrium point of (2.1) satisfies $S_j^* = \frac{\delta_j}{\sum_{i} \alpha_{ij} x_{ij}^*}$ and $\sum_{i} x_{ij}^* > 0$ for every task $j$. Moreover, let $X = [x_{ij}]_{N \times (M+1)}$ denote the equilibrium matrix of (2.1) in which: (i) the $i^{th}$ row represents the work allocation strategy for agent $i$, (ii) the $j^{th} + 1$ column represents the allocation profile for task $j$:

$$X = \begin{bmatrix}
  x_{10}^* & x_{11}^* & \cdots & x_{1m}^* \\
  x_{20}^* & x_{21}^* & \cdots & x_{2m}^* \\
  \vdots & \vdots & \ddots & \vdots \\
  x_{n0}^* & x_{n1}^* & \cdots & x_{nm}^*
\end{bmatrix}_{N \times (M+1)}$$

**Remark.** $X$ is a row-stochastic matrix ($\sum_{j=0}^{M} x_{ij}^* = 1$) and has non-zero columns ($j > 0$)

**Definition 4.0.0.2.** Agent $i$ is a complete specialist for task $j > 0$ if she has zero probability in every other task: $x_{ij}^* + x_{i0}^* = 1$. Conversely, agent $i$ is a generalist if they have non-zero probability in every task: $0 < x_{ij}^* < 1$, $\forall j > 0$.

**Definition 4.0.0.3.** We define $D_{ij} = \frac{\delta_j}{\alpha_{ij}}$ as the expected (equilibrium) demand for task $j$ with agent $i$ as its sole specialist.

**Definition 4.0.0.4.** Let $\theta_{ij} \Phi_i$ represent the "inertia" of agent $i$ to perform task $j$. Moreover, the ratio: $R_{i/h} = \frac{\theta_{i/h} \Phi_h}{\theta_{i} \Phi_i}$ define the relative availability of agent $i$ (versus $h$) for task $j$. 

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General Properties

Lemma 4.0.0.1. The hyperplanes $x_{ij} = 0$ are invariant under the flow of (4.5). Moreover, every initial condition that satisfies: $x_{ij}(0) > 0$, $\sum_{j=0}^{M} x_{ij}(0) = 1$, $\forall i, j$ remains in the unit simplex:

$$S^M_i = \left\{ x_{ij} = \{x_{i0}, x_{i1}, \ldots, x_{iM}\}, \, x_{ij} \geq 0, \, \sum_{j=0}^{M} x_{ij} = 1 \right\} \tag{4.8}$$

for all time.

Some general results

Theorem 4.0.0.3. [Number zeros in the equilibrium matrix] Suppose that $N, M > 1$. If for any pair of agents \{g, h\} we have that: (i) $\theta_{gj} \Phi_g \neq \theta_{hj} \Phi_h$ and (ii) $\frac{\theta_{gj}}{\theta_{hk}} \neq \frac{\theta_{kj}}{\theta_{ik}}$, $k \neq j$, then every equilibrium matrix $X = [x^*_{ij}]$ of (4.7) has \textit{at least} $(N-1)(M-1) + 1$ and \textit{at most} $NM$ zeros in its entries.

Remark. This result proves that (4.7) cannot have a “work sharing” equilibrium where two (or more) agents work on all tasks (i.e., complete generalists). This result holds provided that agents differ in the ratio of preference for any arbitrary pair of tasks (i.e., $\frac{\theta_{ji}}{\theta_{ik}} \neq \frac{\theta_{ij}}{\theta_{jk}}$).

The following results follow as a consequence of theorem 4.0.0.3.

Corollary 4.0.0.2 (Specialist only equilibria). Suppose that $N \geq M$. Then model (4.7) has an equilibrium where every agent is active and specializes on a unique task $u$: $x^*_{iu} + x^*_{i0} = 1$, $x^*_{iu} \leq 1$. No such equilibrium exists if $N < M$.

Remark. In the former case ($x^*_{iu} = 1$), every task is performed at a high level. Thus, the group is characterized as having high work activity and equal division of labor (DOL) because all tasks are performed at the same level of effort. In the latter case,
if $\alpha_{iu} \frac{D_{iu}}{\theta_{iu} x_{iu}} < 1$, tasks may be performed at different levels depending on each agent’s constraint.

**Corollary 4.0.0.3** (Generalist + Specialist equilibria). Suppose that $N, M > 1$. Then, model (4.7) has an equilibrium where exactly one agent $h$ is a complete generalist: $0 < x_{hj}^* < 1$, $\forall j$, and others $i \neq h$ are specialists for some task $u$. At this state, one of the following conditions must hold: (a) $x_{h0}^* = 0$ with $0 < x_{iu}^* < 1$, or (b) $x_{hj}^* = \frac{D_{hj}}{\theta_{hj} x_{hj}} - \sum_{i \neq h}^{N} \frac{\alpha_{iu} x_{iu}^*}{\alpha_{hj}} \forall j > 0$.

**Remark.** In the case ($x_{h0}^* = 0$) agent $h$ is always active. Moreover, other agents $i \neq h$ may specialize on the same task or on different tasks. These cases are visualized below:

$$
\begin{bmatrix}
0 & x_{11}^* & x_{12}^* & \ldots & x_{1m}^* \\
0 & x_{21}^* & 0 & \ldots & 0 \\
\vdots & \vdots & \vdots & \ddots & \vdots \\
0 & x_{n1}^* & 0 & 0 & 0
\end{bmatrix}
\text{ vs. }
\begin{bmatrix}
0 & x_{11}^* & x_{12}^* & \ldots & x_{1m}^* \\
x_{20}^* & 0 & x_{22}^* & \ldots & 0 \\
\vdots & \vdots & \vdots & \ddots & \vdots \\
x_{n0}^* & 0 & 0 & 0 & x_{nm}^*
\end{bmatrix}
$$

**Corollary 4.0.0.4** (Non-contribution equilibria). Suppose that $N, M > 1$. Then, model (4.7) has an equilibrium where one agent $h$ is a complete generalist: $0 < x_{hj}^* < 1$, $\forall j$, and at least one agent $i \neq h$ is inactive (non-contributor): $x_{i0}^* = 1$.

$$
\begin{bmatrix}
x_{10}^* & x_{11}^* & x_{12}^* & \ldots & x_{1m}^* \\
1 & 0 & 0 & \ldots & 0 \\
\vdots & \vdots & \vdots & \ddots & \vdots \\
1 & 0 & \ldots & 0 & 0
\end{bmatrix}
$$

**Remark.** The number of equilibria with non-contributors should increase with the ratio of agents to tasks ($N/M$). If $N < M$, then the existence of one non-contributor
necessitates the existence of a task generalist. This need not hold if $N > M$ provided there at least as many (contributing) agents as there are tasks.

**Theorem 4.0.0.4** (Stability of specialization equilibria). Suppose that $N \geq M$. The set equilibria where every agent specializes on unique activity $u = l(i)$ such that: $x_{iu}^* = 1$, $x_{ij}^* = 0$, $\forall j \neq u$ is asymptotically stable under the following conditions.

(a). $\frac{S_u}{\theta_{iu}} > \max \left\{ \max_{j \neq u} \frac{S_j}{\theta_{ij}}, \Phi_i \right\}$ for all $i$ with $u > 0$ and

(b). $\Phi_i > \max \frac{S_j}{\theta_{ij}}$ for all $i$ with $u = 0$.

**Remark.** The first condition requires that every active (contributing) agent values their specialized task $u$ more than any other task (and also resting). The second condition requires that every inactive (non-contributing) agent values resting over performing any task.

**Biological implications**

The preceding results for the null system (4.7) have some direct implications for groups where agents have fixed constraints, and are driven solely by the demand for work.

- **Task organization:** The system does not admit equilibria where all tasks are performed by every agent (i.e., complete “work sharing”). In this sense, the dynamics of task choice always leads to an equilibrium allocation containing a mix of specialists, generalists and inactive (non-contributors). In the case where agents specialize, the resulting division of labor in the group may be equal (or unequal) depending on how each agent’s constraint compares to the demand of the task they specialize in (i.e., $\frac{D_{ij}}{\theta_{ij} \Phi_i}$). For instance, if $\frac{D_{ij}}{\theta_{ij} \Phi_i} > 1$ holds for all $i, j$, then each agent contributes equally (and maximally) to work and the group can be characterized as having high levels of activity.
**Predictable specialists:** Our analysis (and simulations) suggest that the system has only equilibrium dynamics and provide no evidence of coexisting stable states provided agents have ordered, well-defined preferences across tasks. This means that an agent’s initial task weight ($\theta_{ij}$) and intrinsic demand ($\Phi_i$) are sufficient to infer their equilibrium probability of activity and task. The former result is akin to prediction of fixed-response threshold models (e.g., Bonabeau et al. (1998)) that individuals with lowest task thresholds become its specialists.

**Inactivity in low demand environments:** The number of equilibria with non-contributors increases as the ratio of agents to tasks increases. This result is consistent with experimental observations of colony-founding *P. barbatus* ants (discussed in chapter 3), which showed queens became less active on work in larger groups (see Fig. 3.2).

To make the general results in the last section more concrete, I will now discuss some specific examples for pair of agents facing one or two tasks.

*Dynamics with a Single Task*

**One Agent, One Task**

If $M = N = 1$, model (4.7) can be expressed as:

\[
\begin{align*}
\dot{x}_{11} &= x_{11}(1 - x_{11}) \left( \frac{S_1}{\theta_{11}} - \Phi_1 \right) \\
\dot{S}_1 &= \delta_1 - \alpha_{11} x_{11} S_1.
\end{align*}
\]

A straightforward calculation reveals two possible equilibrium outcomes (see Table 4.2). The dynamics of (4.9) depends on the ratio: $\frac{D_{11}}{\theta_{11} \Phi_1}$, which relates the minimum (expected) demand for work (i.e, when the agent is fully active on the task) with the
intrinsic demands of the agent. When $\frac{D_{11}}{\theta_{11}\Phi_1} > 1$, the demand for work is perceivably higher than resting (and vice-versa). In the former case, the agent commits fully to work ($x_{10}^* = 0$) and the system converges to $E_{(1)}$. In the latter case, the agent works in exact proportion to the ratio ($x_{11}^* = \frac{D_{11}}{\theta_{11}\Phi_1}$) and the system converges to $E_{(*)}$.

<table>
<thead>
<tr>
<th>Equilibrium</th>
<th>Component</th>
<th>Existence</th>
<th>Stability</th>
</tr>
</thead>
<tbody>
<tr>
<td>$E_{(1)}$</td>
<td>$(1, \frac{D_{11}}{\alpha_{11}})$</td>
<td>Always</td>
<td>$D_{11} &gt; \theta_{11}\Phi_1$</td>
</tr>
<tr>
<td>$E_{(*)}$</td>
<td>$(\frac{D_{11}}{\alpha_{21}\Phi_1}, \theta_{11}\Phi_1)$</td>
<td>$D_{11} &lt; \theta_{11}\Phi_1$</td>
<td>Always</td>
</tr>
</tbody>
</table>

Table 4.2: Equilibria and Stability of Model (4.9). $E_{(*)}$ and $E_{(1)}$ are linked via a transcritical bifurcation, which occurs as $\frac{D_{11}}{\theta_{11}\Phi_1} = \frac{\delta_1}{\alpha_{11}\theta_{11}\Phi_1}$ passes through one.

Two Agents, One Task

When $M = 1, N = 2$, model (4.7) can be expressed as:

\[
\begin{align*}
    x_{11} &= x_{11}(1 - x_{11}) \left( \frac{S_1}{\theta_{11}} - \Phi_1 \right) \\
    x_{21} &= x_{21}(1 - x_{21}) \left( \frac{S_1}{\theta_{21}} - \Phi_2 \right) \\
    \dot{S}_1 &= \delta_1 - [\alpha_{11} x_{11} + \alpha_{21} x_{21}] S_1.
\end{align*}
\]

A lengthy but straightforward calculation provides the following results.

**Theorem 4.0.0.5.** (Global dynamics) Model (4.10) may have up to seven ($4 + 3$) equilibria $E_{(x_{11}, x_{21}^*)}$ depending on the values of $D_{11} = \frac{\delta_1}{\alpha_{11}}$ and $D_{21} = \frac{\delta_1}{\alpha_{21}}$. Sufficient conditions for the existence and local stability are summarized in Table 4.3. Moreover, the dynamics of (4.10) can be classified into two categories.

**Remarks**

Our analysis of model (4.10) reveals up to seven equilibrium possibilities (see Table 2.2). Here, we limit our discussion to $E_{(0,1)}, E_{(0,*)}, E_{(\nabla,1)}$ and $E_{(1,1)}$. Although
Table 4.3: Existence and Stability of Equilibria $E(x_{1i}^*,x_{2i}^*)$ in Model (4.10). Note: $E(1,0)$, $E(\ast,0)$, and $E(1,\ast)$ Can Also Exist Under Similar but Reflective Set of Conditions. Other Quantities: $D_{11} = \frac{\delta_1}{\alpha_{11}}$, $D_{21} = \frac{\delta_1}{\alpha_{21}}$

several of these equilibria can coexist, no pair can be simultaneously asymptotically stable. Simulations of (4.10) under the conditions given in Table ?? suggest these states are globally attracting if both agents initially have a non-zero probability of task performance ($x_{i1}(0) > 0$, $i = 1, 2$).

According to Theorem 4.0.0.5, the stability of these states depends on two important quantities. The first quantity $D_{21} = \delta_1/\alpha_{21}$ measures the (minimum) equilibrium demand for the task if agent 2 is fully active and works at maximum rate $\alpha_{21}$ (see Definition 4.0.0.3). The second quantity describes the relative availability of agent 2 for work compared to agent 1 ($R_{2/1} = \frac{\theta_{11}\Phi_1}{\theta_{21}\Phi_2}$) (see Definition 4.0.0.4). It is given by the ratio of each agents’ cost of activity ($\Phi_i$) weighted by their perceived costs of performing the task ($\theta_{i1}$).

1. **One agent is inactive**: Suppose that $R_{2/1} = \frac{\theta_{11}\Phi_1}{\theta_{21}\Phi_2}$, then the system converges to $E(0,1)$ where agent 2 performs the task with unit probability (i.e., $x_{21}^* = 1$) works at her maximum rate $\alpha_{21}$. Conversely, if $D_{21} > \theta_{21}\Phi_2$, then the system converges to $E(0,\ast)$ where she performs the task at a rate proportional to its demand (i.e., $x_{21}^* = \frac{D_{21}}{\theta_{21}\Phi_2}$). These results have a
clear biological interpretation: individuals should condition their behavior on the level work needed in the group and adjust their activity level to match its perceived costs.

2. **One agent is partially active:** Again, suppose that $R_{2/1} > 1$. $E_{(\nabla,1)}$ necessarily exists if agents vary in their work rate (i.e., $\frac{\alpha_{21}}{\alpha_{11}} \neq 1$). However, its stability only depend on agent 2 being more available than agent 1 (i.e., $R_{2/1} > 1$). This result is interesting because there is no requirement for the most efficient agent to work maximally on the task at equilibrium. For instance, suppose that agent 2 has significantly lower work rate than agent 1 ($\frac{\alpha_{21}}{\alpha_{11}} < < 1$). Then $E_{(\nabla,1)}$ is a likely attractor whenever the demand for work (even with agent 2 working at her maximum rate) is sufficiently large to spur agent 1 out of inactivity ($D_{21} > \theta_{11} \Phi_1$). Under this condition, agent 1 works at a rate proportional to the difference between $\frac{D_{11}}{\theta_{11} \Phi_1}$ and agent 2’s work rate on the task. Biologically, this outcome might reflects a cooperative scenario where one individual specializes on a task, while the other tailors its activity level to perform any leftover work the specialist is unable to handle.

3. **Both agents fully active:** $E_{(1,1)}$ always exist, but becomes a likely attractor whenever task demand is sufficiently larger than both agents intrinsic costs of activity (i.e., $\frac{\delta_1}{\alpha_{11} + \alpha_{21}} > \max\{\theta_{11} \Phi_1, \theta_{21} \Phi_2\}$).
Figure 4.2: Bifurcations of System (4.10) under the Assumption That Agent 1 Has Greater Inertia than Agent 2 ($\theta_{11} \phi_1 > \theta_{21} \phi_2$). Increasing the Ratio of Task Needs and Work Rate $\delta_1 / \alpha_{21}$ Can Cause an Exchange of Stability between Equilibria. For Instance, $E(\nabla, 1)$ and $E(1, 1)$ at $\delta_1 = (\alpha_{11} + \alpha_{21}) \theta_{11} \phi_1$.

**Dynamics with Multiple Tasks**

**One Agent, Two Tasks**

If $M = 2$, $N = 1$ model (4.7) can be expressed as:

\[
\begin{align*}
x_{11} &= x_{11} \left[ (1 - x_{11}) \left( \frac{S_1}{\theta_{11}} - \Phi_1 \right) - x_{12} \left( \frac{S_2}{\theta_{12}} - \Phi_1 \right) \right] \\
x_{12} &= x_{12} \left[ (1 - x_{12}) \left( \frac{S_2}{\theta_{12}} - \Phi_1 \right) - x_{11} \left( \frac{S_1}{\theta_{11}} - \Phi_1 \right) \right] \\
\dot{S}_1 &= \delta - \alpha_{11} x_{11} S_1 \\
\dot{S}_2 &= \delta - \alpha_{12} x_{12} S_2.
\end{align*}
\]

(4.11)

A straightforward calculation here also reveals two possible equilibrium outcomes (see Table 4.4).

The equilibrium dynamics of model (4.11) depends on the demand ratio for both
Table 4.4: Existence and Stability of Equilibria in (4.11). The Equilibrium Pair $E(x_{11}^*)$ Are Linked Through a Transcritical Bifurcation at $\eta = \frac{D_{11}}{\theta_{11} \Phi_1} + \frac{D_{12}}{\theta_{12} \Phi_1} = 1$, where $D_{11} = \frac{\delta_1}{\alpha_{11}}, D_{12} = \frac{\delta_2}{\alpha_{12}}$. Other Quantities: $x_{11}^* = \frac{\delta_1 \alpha_{12} \theta_{12}}{\delta_2 \alpha_{12} \theta_{12} + \delta_2 \alpha_{11} \theta_{11}}$ and $x_{12}^* = 1 - x_{11}^* = \frac{\delta_2 \alpha_{12} \theta_{12}}{\delta_1 \alpha_{12} \theta_{12} + \delta_2 \alpha_{11} \theta_{11}}$.

When $\eta > 1$, the need for work (i.e., in either task) is perceivably greater than the agent’s intrinsic demand. Under this condition, the agent will commit fully to work ($x_{10}^* = 0$) and balance her performance of each task in proportion its maximum (weighted) demand. Specifically, each task is weighted by the her preference for (and work rate in) the alternate task ($x_{11}^* \propto \delta_1 \alpha_{12} \theta_{12}$ and $x_{12}^* \propto \delta_2 \alpha_{11} \theta_{11}$) (see Fig. 4.3). On the other hand, when $\eta < 1$, she performs each task with probabilities $x_{11}^* = \frac{D_{11}}{\theta_{11} \Phi_1}$ and $x_{12}^* = \frac{D_{12}}{\theta_{12} \Phi_1}$ and rests for the remaining time.

Finally, simulations suggest that changes in the agent’s intrinsic demands (or activity costs), can have important effects on the transient dynamics of model (4.11). In particular, increasing $\Phi_1$ can amplify the variability of workload in the system if the she has unequal work rate across tasks (Fig. 4.4).
Figure 4.3: Bifurcations of System (4.11) as a Function of $\delta_1/\delta_2$ Assuming That the Agent Has Unequal Work Rates Across Tasks ($\alpha_{11} = .25$, $\alpha_{12} = 1$). Dashed Vertical Line Denotes the Threshold Level of Demand $\eta = \frac{\delta_1}{\alpha_{11}\theta_{11}\phi_1} + \frac{\delta_2}{\alpha_{12}\theta_{12}\phi_1} = 1$ Where Change in Dynamics Occur. As Demand Increases, the Probability That Performing of Her Least Efficient Task 1 Increases. In Contrast, Performance of Her More Efficient Task 2 Remains Constant below the Threshold $\eta$. Other Parameters: $\phi_1 = 3$, $\delta_2 = \theta_{11} = \theta_{12} = 1$

Two agents, Two Tasks

When $M = N = 2$, model (4.7) is a 6D system

$$
\dot{x}_{ij} = x_{ij} \left[ \frac{S_j}{\theta_{ij}} - \Phi_i \right] - \sum_{k=1}^{2} x_{ik} \left( \frac{S_k}{\theta_{ik}} - \Phi_i \right) \quad i = 1, 2
$$

$$
\dot{S}_j = \delta_j - \sum_{i} \alpha_{ij} x_{ij} S_j \quad j = 1, 2.
$$
Figure 4.4: Effects of $\Phi_1$ on the Dynamics of System (4.11) Assuming That the Agent Is More Efficient in Task 2 than Task 1 ($\alpha_{11} = .25, \alpha_{12} = 1$). Increasing $\Phi_1$, Which Models the Agent’s Intrinsic Cost of Activity Amplifies the Variability of Task Stimuli. Other Parameters: $\delta_1 = 0.25, \delta_2 = \theta_{11} = \theta_{12} = 1$.

This system has up to 24 ($4+8+12$) steady states classified into the following categories: (i) One agent is inactive, (ii) Both agents specialize, and (iii) specialist and generalist. Due to the inherent symmetry of (4.12), each equilibrium state can be paired with at least one other that is reflectively similar in structure (e.g. $E_{(0, 1)}^{(1, 0)}$ vs. $E_{(1, 0)}^{(0, 1)}$). Thus, it is possible to obtain a general classification of equilibria in system (4.12) by focusing on a subset of states. Here, we focus our discussion on equilibria where agent 1 abstains from work or specializes on a task. A lengthy but straightforward calculation provides the following results.

**Theorem 4.0.0.6.** (*Existence & stability of specialization equilibria*) Model (4.12) can have up to 12 equilibrium states $E_{(x_{11}, x_{12})}^{(x_{21}, x_{22})}$ where either one agent is inactive (4), or both agents specialize (8). Here, we focus on six states where agent 1 is either inactive or specializes on task 1. Table 4.5 summarizes conditions under which these
Equilibria are asymptotically stable.

<table>
<thead>
<tr>
<th>Equilibrium</th>
<th>Component</th>
<th>Existence</th>
<th>Stability</th>
</tr>
</thead>
<tbody>
<tr>
<td>$E_{(0,0)}^{(0,0)}$</td>
<td>$(0, 0, x_2, 1 - x_2, \theta_{21}, \theta_{22})$</td>
<td>Always</td>
<td>$1 &lt; \frac{D_2}{\theta_{21} \phi_2} + \frac{D_2}{\theta_{22} \phi_2} &lt; \min \left{ \frac{\theta_{11} \phi_1}{\theta_{11} \phi_2}, \frac{\theta_{12} \phi_1}{\theta_{12} \phi_2} \right}$</td>
</tr>
<tr>
<td>$E_{(s, s)}^{(0,0)}$</td>
<td>$(0, 0, D_{21}, D_{22}, \theta_{21}, \theta_{22})$</td>
<td>$\frac{D_2}{\theta_{21} \phi_2} + \frac{D_2}{\theta_{22} \phi_2} &lt; 1$</td>
<td>$\min \left{ \frac{\theta_{11} \phi_1}{\theta_{11} \phi_2}, \frac{\theta_{12} \phi_1}{\theta_{12} \phi_2} \right} &gt; 1$</td>
</tr>
<tr>
<td>$E_{(s, 0)}^{(0,0)}$</td>
<td>$(\frac{D_1}{\theta_{11} \phi_1}, 0, 0, D_{21}, \theta_{11}, \theta_{12})$</td>
<td>$\frac{D_1}{\theta_{11} \phi_1} &lt; 1, \frac{D_2}{\theta_{21} \phi_2} &lt; 1$</td>
<td>$\frac{\theta_{11} \phi_1}{\theta_{11} \phi_2} &lt; 1, \frac{\theta_{12} \phi_1}{\theta_{12} \phi_2} &gt; 1$</td>
</tr>
<tr>
<td>$E_{(0, 0)}^{(1,0)}$</td>
<td>$(1, 0, 0, D_{11}, \theta_{22})$</td>
<td>$\frac{D_1}{\theta_{11} \phi_1} &lt; 1$</td>
<td>$\max \left{ \frac{\theta_{11} \phi_1}{\theta_{11} \phi_2}, \frac{\theta_{12} \phi_1}{\theta_{12} \phi_2} \right} &lt; \frac{\theta_{21} \phi_1}{\theta_{21} \phi_2}$</td>
</tr>
<tr>
<td>$E_{(0, 1)}^{(1,0)}$</td>
<td>$(1, 0, 0, 1, D_{11}, D_{22})$</td>
<td>Always</td>
<td>$\frac{D_1}{\theta_{11} \phi_1} &gt; \max \left{ \frac{D_1}{\theta_{11} \phi_1}, 1 \right}, \frac{D_1}{\theta_{11} \phi_1} &gt; \max \left{ \frac{D_1}{\theta_{11} \phi_1}, 1 \right}$</td>
</tr>
</tbody>
</table>

Table 4.5: Existence and Local Asymptotic Stability (L.A.S) of Model (4.12). Equilibria $E_{(x_1, x_2)}^{(0,0)}$, $E_{(x_1, x_2)}^{(s, s)}$, Denote Where (i) One Agent Is Inactive, or (ii) Both Agents Are Complete Specialists. Other Parameters: $D_{11} = \frac{\delta_1}{\alpha_{11}}, D_{12} = \frac{\delta_2}{\alpha_{12}}, D_{21} = \frac{\delta_1}{\alpha_{21}}, D_{22} = \frac{\delta_2}{\alpha_{22}}$.

Remarks

1. **One agent is inactive:** Our analysis of model (4.12) reveals at least two equilibria where agent 1 is inactive: $E_{(\Delta, \Delta)}^{(0,0)}$ and $E_{(s, s)}^{(0,0)}$. A necessary condition on these states is that agent 2 is more available than agent 1 to work on either task: $\mathcal{R}_{2/1} = \frac{D_1}{\theta_{22}} \min \{ \frac{\theta_{11}}{\theta_{21}}, \frac{\theta_{12}}{\theta_{22}} \} > 1$. $E_{(\Delta, \Delta)}^{(0,0)}$ is the likely attractor whenever the demand for work in both tasks exceeds agent 2’s intrinsic costs: $\eta = \frac{D_2}{\theta_{21} \phi_2} + \frac{D_2}{\theta_{22} \phi_2} > 1$. Otherwise, $E_{(s, s)}^{(0,0)}$ is the likely attractor. The exchange of stability at the threshold level $\eta = 1$ recapitulates the dynamics of model (4.11) with one agent and two tasks (see Table 4.4).

2. **Both agents are specialists:** Model (4.12) also has at least four equilibria where both agents specialize on a unique task (Table 4.5). Their stability necessarily requires that each agent $i$ ascribes greater value to the task they are specialized on than available alternatives. This valuation obviously depends on how both agents’ intrinsic demand relate with external needs of their preferred
task. For instance, suppose that agent 1 has lower inertia (or greater preference) for the first task compared to agent 2 ($\frac{\theta_{11}P_1}{\theta_{21}P_2} < 1$) and vice-versa for the second task (i.e., $\frac{\theta_{22}P_2}{\theta_{12}P_1} < 1$). Under these hypotheses, $E^{(0,1)}_{(1,0)}$ becomes an attractor whenever the demand both tasks exceeds each agent’s intrinsic costs: (i.e., $\frac{D_{11}}{\theta_{11}P_1} > 1$, $\frac{D_{22}}{\theta_{22}P_2} > 1$). Otherwise, $E^{(0,s)}_{(s,0)}$ is the likely attractor (see Table 4.5).

**Theorem 4.0.0.7** (Existence of specialist - generalist equilibria). Model (4.12) can also have up to 12 equilibrium states $E^{(x_{11},x_{12})}_{(x_{21},x_{22})}$ where one agent is a complete specialist while the other is a generalist. Here, we focus on three states where agent 1 specializes on task 1. Table 4.6-4.7 summarizes minimum set of conditions under which these equilibria might exist and be asymptotically stable.

<table>
<thead>
<tr>
<th>Equilibrium</th>
<th>Component</th>
<th>Existence</th>
</tr>
</thead>
<tbody>
<tr>
<td>$E^{(\nabla,0)}_{(\Delta,\Delta)}$</td>
<td>$\left(\frac{D_{11}}{\theta_{11}P_1} - \frac{\alpha_{11}x_{11}^<em>}{\alpha_{11}}, 0, x_{21}^</em> - 1 - x_{21}^*, \theta_{11}P_1, \frac{\theta_{11}P_1}{\theta_{21}P_2}\right)$</td>
<td>$\frac{\theta_{11}P_1}{\theta_{21}P_2} &lt; \frac{D_{21}}{\theta_{11}P_1} + \frac{D_{22}}{\theta_{22}P_2} &lt; \frac{\alpha_{11} + \alpha_{21}}{\alpha_{11}}, \frac{\theta_{11}P_1}{\theta_{21}P_2}$</td>
</tr>
<tr>
<td>$E^{(1,0)}_{(\nabla,s)}$</td>
<td>$\left(1, 0, \frac{D_{11}}{\theta_{11}P_1} - \frac{\alpha_{11}}{\alpha_{21}}, \frac{D_{22}}{\theta_{22}P_2}, \theta_{21}P_2, \theta_{22}P_2\right)$</td>
<td>$\frac{\alpha_{11}}{\alpha_{21}} &lt; \frac{D_{21}}{\theta_{22}P_2} &lt; \frac{\alpha_{11} + \alpha_{21}}{\alpha_{21}}, \frac{D_{22}}{\theta_{22}P_2} &lt; 1$</td>
</tr>
<tr>
<td>$E^{(1,0)}_{(\nabla,\Delta)}$</td>
<td>$\left(1, 0, 1 - x_{22}^* - x_{22}^*, \frac{D_{22}}{\theta_{22}P_2}, \theta_{21}P_2, \theta_{22}P_2\right)$</td>
<td>$\frac{D_{21}}{\theta_{22}P_2} &gt; \frac{\theta_{21}}{\theta_{22}}$</td>
</tr>
</tbody>
</table>

Table 4.6: Existence and Local Asymptotic Stability (L.A.S) of Model (4.12). Equilibria $E^{(x_{11},x_{12})}_{(x_{21},x_{22})}$ denote where Agent 1 Completely Specializes on Task 1 and Agent 2 Is a Generalist. Stability Conditions Are Necessary, but May Not Be Sufficient Otherwise. Other Parameters: $D_{11} = \frac{\delta_1}{\alpha_{11}}$, $D_{12} = \frac{\delta_2}{\alpha_{12}}$, $D_{21} = \frac{\delta_1}{\alpha_{21}}$, $D_{22} = \frac{\delta_2}{\alpha_{22}}$.

<table>
<thead>
<tr>
<th>Equilibrium</th>
<th>Stability (necessary)</th>
</tr>
</thead>
<tbody>
<tr>
<td>$E^{(\nabla,0)}_{(\Delta,\Delta)}$</td>
<td>$\frac{\theta_{11}P_1}{\theta_{21}P_2} &gt; 1$, $\frac{\theta_{11}}{\theta_{12}} &lt; \frac{\theta_{21}}{\theta_{22}}$</td>
</tr>
<tr>
<td>$E^{(1,0)}_{(\nabla,s)}$</td>
<td>$\frac{\theta_{11}P_1}{\theta_{21}P_2} &lt; 1$, $\frac{\theta_{11}}{\theta_{12}} &lt; \frac{\theta_{21}}{\theta_{22}}$, $\frac{D_{21}}{\theta_{22}P_2} &lt; \frac{\theta_{21}}{\theta_{22}}$</td>
</tr>
<tr>
<td>$E^{(1,0)}_{(\nabla,\Delta)}$</td>
<td>$\frac{D_{21}}{\theta_{22}P_2} + \frac{D_{22}}{\theta_{22}P_2} &gt; \left(\frac{\alpha_{11} + \alpha_{21}}{\alpha_{21}}\right) \cdot \max\left{1, \frac{\theta_{11}P_1}{\theta_{21}P_2}\right}$</td>
</tr>
</tbody>
</table>

Table 4.7: Stability of Equilibria $E^{(x_{11},x_{12})}_{(x_{21},x_{22})}$ in Model (4.12) where Agent 1 Completely Specializes on Task 1 and Agent 2 Is a Generalist. The Conditions given Are Necessary, but May Not Be Sufficient. Other Parameters: $D_{11} = \frac{\delta_1}{\alpha_{11}}$, $D_{12} = \frac{\delta_2}{\alpha_{12}}$, $D_{21} = \frac{\delta_1}{\alpha_{21}}$, $D_{22} = \frac{\delta_2}{\alpha_{22}}$.
Figure 4.5: Bifurcations of System (4.12) As a Function of $\delta_1/\delta_2$. Here, Agents Have Dissimilar Task Preferences ($\theta_{11} = \theta_{22} = .5$, $\theta_{12} = \theta_{21} = 1$, but Are More Efficient in Their Preferred Task ($\alpha_{11} = 1.5$, $\alpha_{22} = 3$, $\alpha_{12} = \alpha_{21} = 1$). Equilibrium points $E_{(x^1_1,x^1_{12})}$ Are Denoted as Stable Attractors (Blue) or Unstable Saddles (Green). The Dynamics of (4.12) Ultimately Converges to Specialist + Generalist Equilibria $E_{(\Delta,\Delta)}^{(1,0)}$ When Demand Is Sufficiently High.

Remarks

Our analysis of model (4.12) reveals 12 equilibria where one agent specializes on a unique task while the other works on both tasks. Theorem 4.0.0.7 focuses on three states in which agent 1 specializes on the first task: $E_{(\Delta,\Delta)}^{(1,0)}$, $E_{(\Delta,\Delta)}^{(\nabla,0)}$, and $E_{(\Delta,\Delta)}^{(1,0)}$. Intuitively, these equilibria might necessarily occur if agent 1 has a greater preference for the first task when available compared to agent 2 and vice-versa ($\frac{\theta_{11}}{\theta_{12}} < \frac{\theta_{21}}{\theta_{22}}$). However, there are several other factors in play including agents’ relative availability to work ($\Phi_1/\Phi_2$) as well as their relative efficiency on each task ($\alpha_{11}/\alpha_{21}$). Here, we discuss the intuition behind analytical conditions described in Theorem 4.0.0.7 and explore their veracity via simulations.
Figure 4.6: Effects of Relative Efficiency on the Outcomes of System (4.12). Here, Agents Have Distinct Task Preferences ($\theta_{11} = \theta_{22} = 0.5$, $\theta_{12} = \theta_{21} = 1$) and Equal Availability ($\phi_1 = \phi_2 = 1$). As Agent 1 Becomes Less Efficient (i.e., $\alpha_{11}/\alpha_{21} \to 0$), the Overall Workload Increases Forcing Agent 2 to Perform Both Tasks. However, Specialization is More Likely When Both Agents Are More Efficient on Their Preferred Task ($\alpha_{11}/\alpha_{21} > \alpha_{12}/\alpha_{22}$). Other Parameters: $\alpha_{21} = \alpha_{12} = 1$, $\alpha_{22} = 1.5$.

1. **Agent 1 is fully active**: At $E_{(\Delta, \Delta)}^{(1,0)}$, both agents have a maximum probability of being active on a task. However, agent 1 works exclusively on the first. $E_{(\Delta, \Delta)}^{(1,0)}$
necessarily exists if the weighted value to agent 2 of performing the first task (with agent 1 fully specialized on it) is greater than that of the second task: \( \frac{D_{11}}{\theta_{21}} > \frac{D_{22}}{\theta_{22}} \). This might occur if agent 1 tends to be less available than agent 2 (\( \Phi_1 > \Phi_2 \)) but has greater preference for the first task when available compared to agent 2 (i.e., \( \frac{\theta_{11} \Phi_1}{\theta_{21} \Phi_2} < 1 \)).

Suppose that \( \frac{\theta_{11}}{\theta_{12}} < \frac{\theta_{21}}{\theta_{22}} \). Under this hypothesis, agent 2 has a greater preference for the second task compared to agent 1 (regardless of availability). In this scenario, \( E^{(1,0)}_{(\nabla, \Delta)} \) likely becomes stable whenever the workload in both tasks is sufficiently large that it exceeds agent 2’s intrinsic costs of performing them (i.e., \( \eta = \frac{D_{21}}{\theta_{21} \Phi_2} + \frac{D_{22}}{\theta_{22} \Phi_2} > 1 \)). This result is supported by numerical analysis (Fig. 4.5).

2. Agent 1 is partially active: At \( E^{(\nabla,0)}_{(\nabla, \Delta)} \) agent 2 has maximum probability of being active on either task. In contrast, agent 1 works partially, but exclusively on the first task. \( E^{(\nabla,0)}_{(\Delta, \Delta)} \), necessarily exists if the expected workload of the second task with agent 2 specializing on it is less than that of task 1 with agent 1 working partially on it (i.e., \( \frac{D_{22}}{\theta_{22} \Phi_2} < \frac{\theta_{11} \Phi_1}{\theta_{21} \Phi_2} \)). This might occur if agent 1 tends to be less available compared to agent 2 (i.e., \( \Phi_1 > \Phi_2 \)).

Suppose that \( \frac{\theta_{11}}{\theta_{12}} < \frac{\theta_{21}}{\theta_{22}} \). Under this hypothesis, agent 1 has a greater preference for the first task than the second compared to agent 2. In this scenario, \( E^{(\nabla,0)}_{(\nabla, \Delta)} \) likely becomes stable whenever the workload in both tasks is sufficiently large that it exceeds agent 2’s intrinsic costs of performing them (i.e., \( \eta = \frac{D_{21}}{\theta_{21} \Phi_2} + \frac{D_{22}}{\theta_{22} \Phi_2} > 1 \)). This result is supported by a numerical analysis (Fig. 4.5).

3. Agent 2 is partially active: At \( E^{(1,0)}_{(\nabla, \nabla)} \), agent 1 has maximum probability
being active on the first task. In contrast, agent 2 works partially on both
tasks. $E_{(\nabla,s)}^{(1,0)}$ necessarily exists if agents vary in their work rate on the first task
(i.e., $\frac{\alpha_{11}}{\alpha_{11}} \neq 1$) and whenever its demand exceeds its perceived cost of perfor-

mance to agent 2: $\frac{D_{11}}{\theta_{21}x_{11}} > \frac{\alpha_{11}}{\alpha_{21}} \Leftrightarrow D_{11} > \theta_{21}x_{21}$. This might occur if agent 2 has
a significantly lower work rate on the task than agent 1 ($\alpha_{21} < \alpha_{11}$) or whenever $\delta_1$ is sufficiently large relative to $\frac{\alpha_{11}}{\alpha_{21}}$.

$\Rightarrow$ Suppose that $\frac{\theta_{11}}{\theta_{12}} < \frac{\theta_{21}}{\theta_{22}}$. Also, suppose that agent 1 is relatively for efficient
on the first task compared to agent 2 (i.e., $\alpha_{11} > \alpha_{21}$) but has lesser preference for it when available (i.e., $\frac{\theta_{11}x_{11}}{\theta_{21}x_{21}} < 1$). In this scenario, $E_{(\nabla,s)}^{(1,0)}$ might become stable when there roughly equal need for both tasks ($\delta_1/\delta_2 \approx 1$).
However, further increases in $\delta_1$ might move the system towards $E_{(\nabla,s)}^{(1,0)}$.
(see Fig 4.6).

Degenerate Cases

So far, I have focused my discussion of model (4.12) under the assumption that
agents have well-defined and ordered preferences across tasks (i.e., $\frac{\theta_{11}}{\theta_{12}} \neq \frac{\theta_{21}}{\theta_{22}}$). What
happens if the converse is true? As indicated in the following theorem, (4.12) may a
number of condition-dependent interior equilibria.

**Theorem 4.0.0.8** (Existence of interior equilibria). Suppose that $\frac{\theta_{11}}{\theta_{12}} = \frac{\theta_{21}}{\theta_{22}}$ and
that $x_{ij} = \rho \in (0,1)$ is fixed some agent $i$ and task $j$. Under these conditions, model
(4.12) may have up to 3 equilibrium states $E_{(x_{11},x_{12})}^{(1,0)}$ where both agents perform each
task with non-zero probability. Table 4.8 summarizes conditions under which interior
equilibria exist for a generic case where agent 1 is initially fixed on task 2 ($x_{12}(0) = \rho$).

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Table 4.8: Existence of Interior Equilibria in (4.12) Assuming That Agents Have Similar Preferences Across Tasks (i.e., $\frac{\theta_{11}}{\theta_{12}} = \frac{\theta_{21}}{\theta_{22}}$). Existence Conditions Are Defined Relative to Focal Agent’s Initial Probability on Either Task (i.e., $x_{ij}(0) = \rho$, for some $i,j$). Here, We Suppose $x_{12}(0) = \rho$. Other Parameters: $D_{11} = \frac{\delta_1}{\alpha_{11}}, D_{12} = \frac{\delta_2}{\alpha_{12}}, D_{21} = \frac{\delta_1}{\alpha_{21}}, D_{22} = \frac{\delta_2}{\alpha_{22}}$.

**Remarks**

Model (4.12) can have up to three interior equilibria if agents 1 and 2 have similar preferences across both tasks (i.e., $\frac{\theta_{11}}{\theta_{12}} = \frac{\theta_{21}}{\theta_{22}}$). A necessary condition for their existence is that one agent has a fixed probability of performing either task (i.e., $x_{ij} = \rho$, for some $i,j$). Here, we explore the stability these states relative to agent 1’s initial probability of performing task 2 (i.e., $x_{12}(0) = \rho$). As discussed below, the dynamics of (4.12) may be subject to initial conditions when these equilibria exist (cf. figure 4.7-4.8.).

- At $E_{(\triangle,\triangle)}^{(\triangledown,\cdot)}$, agent 2 has a maximum probability of being active on either task.

In contrast, agent 1 has a possibility of being inactive. An opposite pattern develops at $E_{(\triangledown,\triangledown)}^{(\cdot,\cdot)}$; specifically agent 1 has a higher probability of activity than agent 2. Finally at $E_{(\triangle,\triangle)}^{(\cdot,\cdot)}$ both agents have maximum probability of being active.

- $E_{(\triangle,\triangle)}^{(\triangledown,\cdot)}$ and $E_{(\triangledown,\triangledown)}^{(\cdot,\cdot)}$ can co-exist in a context where agent 1 is less efficient at work compared to agent 2 ($\alpha_{11}/\alpha_{21} < 1, \alpha_{12}/\alpha_{22} < 1$) if demand for both tasks exceeds agent 2’s perceived costs (i.e, $D_{21} > \theta_{11} \Phi_1, D_{22} > \theta_{12} \Phi_1$). However, simulations suggest that they cannot be simultaneously stable.
E_{(\Delta,\Delta)}^{(\bullet,\bullet)} is likely to exists when the workload for both tasks exceeds both agents intrinsic costs of activity (e.g. if $\delta_1/\delta_2$ is sufficiently high). Moreover, simulations it can be simultaneously stable with one (or more) boundary equilibria (see Fig ??). One reason for this is the dynamics of (4.12) has the effect of creating “emergent” preferences at equilibrium if agents vary in their work rates across tasks. For instance, consider a scenario where agent 1 has greater efficiency on the second task than agent 2 (and vice-versa for the first task), but agent 1 also has initially high probability on least efficient task 1 ($x_{11}(0) >> x_{12}(0)$). Under this condition, $E_{(\Delta,\Delta)}^{(\bullet,\bullet)}$ can be stable along with a relatively less efficient equilibrium $E_{(0,1)}^{(1,0)}$ in a region where $\delta_1 > \delta_2$ (Fig 4.7). On the other hand, consider a scenario where agent 1 has is relatively inefficient on the second task compared to agent 2 ($\alpha_{12}/\alpha_{22} < 1$), and is also has greater activity costs ($\Phi_1 > \Phi_2$). Under this condition, the dynamics of (4.12) may converge to one of two attractors (Fig 4.7). If agent 1 has an initially low probability of activity ($x_{11}(0)+x_{12}(0) << 1$), and agent 2 has an equal likelihood of working on both tasks initially, the system converges to a boundary state where agent 1 tends to specializes on her more efficient task 1 (black and blue lines, Fig 4.8). Conversely, if agent 2 initially has a high probability of performing task 1 (on which she is least efficient in), the system converges to an interior state where agent 1 takes on performance of task 2 (on which she is least efficient in). This latter dynamic results in an inefficient group-level outcome where the overall workload in the system is greater with each agents are maximally active than with agent 1 partially active. (c.f. red lines, Fig 4.8).
Figure 4.7: Bifurcations of System (4.12) As a Function of $\delta_1/\delta_2$. Here, Agents Have Similar Preferences Across Tasks ($\theta_{11} = \theta_{12} = \theta_{21} = \theta_{22}$), but Have Different Relative Efficiencies ($\alpha_{11}/\alpha_{21}$ vs. $\alpha_{12}/\alpha_{22}$). Interior Equilibria $E^{(x_{11}, x_{12})}$ Are Denoted as Stable Attractors (Blue) or Unstable (Orange) Whenever They Exist. Other Parameters: (a) $\theta_{11} = \theta_{21} = 0.95$, $\theta_{12} = \theta_{22} = 1$, $\Phi_1 = \Phi_2 = 1$, $\rho = 0.15$, (b) $\theta_{11} = \theta_{21} = 0.8$, $\theta_{12} = \theta_{22} = 1.7$, $\Phi_1 = 3\Phi_2 = 3$, $\rho = 0.05$. 
We assume Agent 1 Has Greater Activity Costs than Agent 2 ($\Phi_1 > \Phi_2$), and that $\alpha_{11} = 1$, $\alpha_{22} = 3$, $\alpha_{12} = \alpha_{21} = 0.25$. (left) Plots Showing the Trajectory of Agents’ Behavior Probability Space Starting from Different Initial Conditions $x_{ij}(0)$ (open circles). (right) Resulting Effects on the Dynamics of Task Stimuli. The System Converges to the Interior Equilibrium With Greater Workload if Both Agents Have Higher Initial Probabilities on Their Least Efficient Task, and Agent 1 is Initially More Likely Be Inactive

**Discussion**

Social dynamics (i.e., emergent nonlinear effects of interactions on individuals) can play a critical role in the task organization of animal groups (Fewell *et al.*, 2009). Existing models generally assume that costs have a nominal influence on how individual task choice, and thus have limited applicability to study groups where individuals must weigh the utility of their actions. Here, we propose a general mathematical model that is applicable in a border set of contexts. Our models can be used to study how changes in task organization might emerge as a consequence of how individuals...
dynamically weigh the costs (and benefits) of working in a group setting. We obtain a number general theoretical results including threshold conditions under which individuals are likely to become specialize on task role, contribute proportionally to both tasks, or abstain from work altogether in the group.

1. In groups where individuals have well-defined and ordered preferences across different tasks, our models predict an equilibrium organization with at least one individual who tends to perform all tasks and individuals who tend to specialize on a task (c.f. Theorem 4.0.0.3 and Corollary 4.0.0.2-4.0.0.4).

2. However, in groups where individuals have similar preferences across all tasks, the equilibrium organization of work may be sensitive to initial conditions (cf. Theorem 4.0.0.8, Fig 4.7). This might specifically relate to differences among individuals in their initial propensity to perform different tasks (as well as their work rates across different tasks; Fig 4.8).

Our analytical results are inline with probabilistic self-organizational models of task organization (Bonabeau et al., 1996, 1998; Page and Mitchell, 1998; Theraulaz et al., 1998). In their basic form, these models posit that individuals have an intrinsic “response-threshold” above which they have an increased likelihood of performing different tasks in a social group. Assuming there is sufficient within-group variation in the initial distribution of thresholds, RT models predicts that individuals with lower thresholds for a specific task are more likely to become its specialists (Fewell et al., 2009). Our results here provides a richer description of components that might constitute individual’s “response-threshold” . Moreover, by separating intrinsic and extrinsic factors that might drive variation in task propensities within a social group, our modeling approach provide a much more parsimonious and generalizable framework for studying emergent mechanisms of task organization across biological contexts.
Self-organization might underpin the emergence of division of labor in most animal groups. However, not much is known about their consequences for productivity. Although division of labor might generate efficiencies that should theoretically increase task output at individual and/or group level (Chittka and Muller, 2009), these benefits may not automatically follow in an emergence context (Dornhaus et al., 2009). The costs and benefits of different mechanisms of work organization may depend on the types of tasks groups face and the environments they inhabit (Charbonneau and Dornhaus, 2015). Our results contribute a further insights into this question. Specifically, we show that specialization can be costly to group performance in the absence of a mechanism to coordinate individual’s initial performance of a task with its potential efficiency on it (Fig 4.7).

Concluding remarks

We emphasize the our multi-agent systems approach, provides a more general dynamical theory for understanding the emergence and consequences of task organization in animal groups. Our analysis provide useful set of thresholds that describes how individuals’ behavior on different tasks relate with their perceived costs and efficiency of performance (i.e., \( \Phi_i, \theta_{ij}, \alpha_{ij} \)). Biologically, these relationships allow us to connect individuals (and their behavioral dynamics) with group-level patterns of organization more concretely compared to previous models (Pacala et al., 1996; Bonabeau et al., 1998; Theraulaz et al., 1998). Ultimately, our results contributes theoretical understanding of social dynamics and task organization in animal groups by showing how an individual’s behavior not only depends intrinsic factors, but also emerges out of a collective experience of a shared environment.
Proofs

Proof of Lemma 4.0.0.1

Proof. From (4.5), \( \dot{x}_{ij} = 0 \) implies either (i) \( x_{ij} = 0 \), or (ii) \( V_{ij} = \bar{V}_i \) for all \( i \) and \( j \). Therefore, \( x_{ij} = 0 \) is invariant. Now, suppose that we restrict initial conditions:

\[
\sum_{j=0}^{M} x_{ij}(0) = 1
\]

Since \( x_{ij}(0) = 1 - \sum_{k \neq j}^{M} x_{ik}(0) \), and \( x_{ij} = 0 \) is invariant, then \( x_{ij} = 1 \implies x_{ik} = 0, \forall k \neq j \). Moreover, this indicates that \( V_{ij} = \bar{V}_i \implies \dot{x}_{ij} = 0, \forall i,j \). Therefore, \( x_{ij} = 1 \) is also invariant. Finally, it easy to check from (4.5) \( \sum_{j=0}^{M} \dot{x}_{ij} = 0, \forall i \). This indicates that \( S_i^M \) is invariant: any trajectory starting in \( S_i^M \) will remain confined for all time. \( \square \)

Proof of Theorem 4.0.0.3

Proof. First, we note the following about model (2.1): (a) \( \dot{S}_j = 0 \implies S_j^* = \sum_i^\delta_j x_{ij} < \infty \iff \sum_i x_{ij}^* > 0, \forall j \), (b) \( \dot{x}_{ij} = 0 \) implies either: \( x_{ij}^* = 0, x_{ij}^* = 1 \), or \( V_{ij} = \bar{V}_i \implies S_i^* - \Phi_i = \sum_{k=1}^{M} x_{ik} \left( S_k^* - \Phi_i \right) \), and (c) \( x_{ij}^* = 1 \iff x_{ik}^* = 0, \forall k \neq j \). Now, let \( Z(i) \) denote the number of zeros in the \( i \)th row of \( X \). The objective is to show that:

(a) \( \min_{0 \leq x_{ij}^* \leq 1} \sum_i^N Z(i) = 1 + (N-1)(M-1) \), and (b) \( \max_{0 \leq x_{ij}^* \leq 1} \sum_i^N Z(i) = NM \) under the constraint: \( \sum_i^N x_{ij}^* > 0, \forall j > 0 \). Note that if \( x_{ij} = 1 \), then \( Z(i) = M \). Conversely, if \( 0 \leq x_{ij}^* < 1 \), then \( 1 \leq Z(i) \leq M \).

1. Maximum zeros: The maximum possible number of zeros in each row of \( X \) occurs when \( x_{ij}^* = 1 \) for some \( j \). If every agent \( i \) performs a unique task \( u \) such that: \( x_{iu}^* = 1, x_{ij}^* = 0, \forall j \neq u \), then, we have \( \sum_i^N x_{ij}^* > 0, \forall j > 0 \). Clearly, this equilibrium only exists if \( N \geq M \). Nonetheless, we can infer under this condition that \( Z(1) = Z(2) = \ldots = Z(N) = M \) and, \( \max_{0 \leq x_{ij}^* \leq 1} \sum_i^N Z(i) = NM \).

2. Minimum zeros: Since \( Z(i)|_{x_{ij} \neq 1} \leq Z(i)|_{x_{ij}=1} \), the minimum possible number
of zeros in each row of $X$ should occur for equilibria that satisfy $x_{ij}^* \neq 1$, and $x_{ij}^* > 0$, $\forall j$. Note that the equilibrium constraint: $\sum_i x_{ij}^* > 0$, $\forall j > 0$ always holds under this condition. Suppose there exists an agent $h$ who satisfies: $x_{hj}^* > 0$, $\forall j$. Then, $V_{hj} = \bar{V}_h \implies S_{\theta_{hj}}^* = \Phi_h$, $\forall j > 0$. However, since $\theta_{hj} \Phi_h \neq \theta_{ij} \Phi_i$ for all other agents $i \neq h$, then $x_{ij}^* = 0$, $\forall i \neq h$. Under the preceding condition, $Z(h) = 0$, $Z(i) = M$, and $\sum_i Z(i) = (N-1)M$. Now, suppose $x_{ih}^* = 0$ and $x_{hj}^* > 0$, $\forall j > 0$. Then, $V_{hj} = \bar{V}_h \implies S_{\theta_{hj}}^* = S_{\theta_{hk}}^*$, $\forall k \neq j$. Likewise, suppose there exist an agent $i \neq h$ satisfies: $V_{ij} = \bar{V}_i \implies S_{\theta_{ij}}^* = S_{\theta_{ik}}^*$, $\forall k \neq j$. However, since $\theta_{ij} / \theta_{ik} \neq \theta_{hj} / \theta_{hk}$, then either $x_{ij}^* = 0$, or $x_{ik}^* = 0$. From this, we can deduce that if one agent $h$ satisfies: $0 < x_{hj}^* < 1$, then every other agent $i$ must satisfy either $x_{ij}^* = 0$ or $S_{\theta_{ij}}^* = \Phi_i$. Moreover, if there exists a $i \neq h$ such that: $S_{\theta_{ij}}^* = \Phi_i$, then it follows that $x_{ij}^* = 0$ $\forall i \neq g$. This indicates that (a) any task column $j > 0$ of $X$ has at most two non-zero entries, and (b) any row of $X$ has at most $M$ non-zero entries. Nonetheless, we can infer under the preceding condition that $Z(h) = 1$, $Z(i) = M - 1$, $\forall i \neq h$, and $\sum_i Z(i) = 1 + (N-1)(M-1)$. To establish that this is the minimum, it suffices to note that $1 + (N-1)(M-1) \leq (N-1)M$ for $N > 1$.

Proof of Corollary 4.0.0.2

Proof. From (2.1), $\dot{S}_j = 0 \iff S_j^* = \sum_{i} \alpha_{ij} x_{ij}^*$. Suppose that $N < M$. Clearly, if every agent performs a unique task $u$: $x_{iu}^* \leq 1$, $x_{ij}^* = 0$, $\forall j \neq u$, then there is at least one $j$ for which $\sum_i x_{ij}^* = 0 \iff S_j^* = \infty$. Hence, such a point cannot be an equilibrium. Now suppose that $N = M$. According to lemma 4.0.0.1 $x_{ij} = 1$ is invariant. Hence, if every task is performed (i.e., $u$’s are distinct) then $x_{iu}^* + x_{i0}^* = 1$ is always an equilibrium of (2.1). Alternatively, if $x_{iu}^* \neq 1$, then from (2.1) $V_{iu} = \bar{V}_i \iff S_u^* = 113
\[ \frac{\delta_u}{\alpha_{iu}x_{iu}} = \theta_{iu} \Phi_i \iff x_{iu}^* = \frac{D_{ui}}{\theta_{iu}} \Phi_i. \]

Hence, \( x_{iu}^* = \frac{D_{ui}}{\theta_{iu}} \Phi_i < 1, \quad x_{ij}^* = 0, \quad \forall \ j \neq u \) is also an equilibrium if \( u \)'s are distinct. Finally, if \( N > M, \) \( u \)'s cannot be distinct. Thus, we require \( \sum_i x_{ij}^* > 0, \quad \forall \ j > 0. \)

\[
\text{Proof of Corollary 4.0.0.4}
\]

**Proof.** Since \( 0 < x_{hj}^* < 1, \quad \forall \ j, \) we can infer that \( \sum_i x_{ij}^* > 0 \iff S_j^* < \infty, \quad \forall \ j > 0. \)

Moreover, from (2.1), \( x_{hj} = 0 \implies V_{hj} = \bar{V}_h \iff S_{hj}^* = \Phi_h = \sum_{k=1}^M x_{hk} \left( \frac{S_h^*}{\theta_{hk}} - \Phi_h \right). \)

1. First, suppose that \( x_{hj}^* > 0, \quad \forall \ j > 0. \) Then, \( V_{hj} = \bar{V}_h \implies S_{hj}^* = S_{hk}^* \iff \)

\[
\frac{\delta_j}{\alpha_{hj}x_{hj}^* + \sum_{i \neq h} \alpha_{ij}x_{ij}^*} = \frac{\delta_k}{\theta_{hk} \left( \alpha_{hk}x_{hk}^* + \sum_{i \neq h} \alpha_{ik}x_{ik}^* \right)}, \quad \forall \ k \neq j. \quad (4.13)
\]

At equilibrium, this equation must also hold for other agents \( i \neq h. \) However, since \( \frac{\delta_{ij}}{\theta_{ik}} \neq \frac{\theta_{hj}}{\theta_{hk}}, \quad k \neq j, \) there are no solutions to (4.13) for which \( 0 < x_{hj}^* < 1 \) and \( 0 < x_{ij}^* < 1 \) hold for all \( i, j. \) Thus, we make the following assumption.

**(A1)** Each agent \( i \neq h, \) specializes on an activity \( u \) such that \( 0 < x_{iu}^* < 1, \) and \( x_{ij}^* = 0, \quad \forall \ j \neq u. \) Under this condition, there is at least one \( j \) for which \( x_{hj}^* > 0, \) and \( x_{ij}^* = 0 \) for all \( i \neq h. \) Thus, (4.13) can be expressed alternatively in terms of \( j: \)

\[
\frac{\delta_j}{\alpha_{hj} \theta_{hj} x_{hj}^*} = \frac{\delta_k}{\theta_{hk} \left( \alpha_{hk} x_{hk}^* + \sum_{i \neq h} \alpha_{ik} x_{ik}^* \right)}, \quad \forall \ k \neq j \quad (4.14)
\]

where \( u = k. \) A necessary condition for solution is that the number of equations must be equal to number of variables. Thus, we make an additional assumption.

**(A2)** \( x_{h0}^* = 0 \iff x_{hj}^* = 1 - \sum_{k \neq j}^M x_{hk}. \) Notice that if \( x_{ik}^* = 0, \) or \( x_{ik}^* = 1 \forall i, \) then (4.14) is an \( M - 1 \) dimensional system for agent \( h \) that can be solved for a unique solution: \( \sum_{j=1}^M x_{hj}^* = 1. \) Conversely, if \( 0 < x_{ik}^* < 1 \forall i \neq h, \) then \( V_{ik} = \bar{V}_i \implies \)
\[ S_j^* = \Phi_i. \] Solving these equations along with (4.14) simultaneously yields a unique solution that satisfies: \[ \sum_{j=1}^{M} x_{hj}^* = 1, \text{ and } x_{ik}^* = \frac{\alpha_{hj} \delta_i \theta_{hj} \left(1 - \sum_{k \neq j}^{M} x_{hk}^*\right)}{\alpha_{ik} \delta_i \theta_{hk}} - \frac{\alpha_{hk} x_{hk}^*}{\alpha_{ik}}. \]

2. Now, suppose that \( x_{h0}^* > 0 \), and \( x_{hj}^* > 0 \) \( \forall \ j > 0 \). Then, \( V_{hj} = \bar{V}_h \implies S_j^* = \frac{\delta_j}{\alpha_{hj} x_{hj}^* + \sum_{i \neq h}^{N} \alpha_{ij} x_{ij}^*} = \theta_{hj} \Phi_h. \) Since \( \theta_{hj} \Phi_h \neq \theta_{ij} \Phi_i \) for all \( i \neq h \), we must seek solutions on the boundary. Assume that (A1) holds. Then, \( x_{hj}^* = \frac{\delta_j}{\alpha_{hj} \theta_{hj} \Phi_h} - \sum_{i \neq h}^{N} \frac{\alpha_{iu} x_{iu}^*}{\alpha_{hj}} \forall j > 0. \) Since \( x_{iu}^* \) must be on the boundary, we have the following scenarios: 

(a) If \( x_{iu}^* = 0, \forall i \), then \( x_{hj}^* = \frac{\delta_j}{\alpha_{hj} \theta_{hj} \Phi_h}. \) 

(b) If \( x_{iu}^* = 1, \forall i \), then 

\[ x_{hj}^* = \frac{\delta_j}{\alpha_{hj} \Phi_h} - \sum_{i \neq h}^{N} \frac{\alpha_{ij}}{\alpha_{hj}}. \]

\[ \] Proof of Theorem 4.0.0.4

Proof. The dynamics of (2.1) can be studied by analyzing the subsystem with \( \dot{x}_{ij} \) and \( \dot{S}_j \)

\[ \dot{x}_{ij} = F(x_{ij}, S_j) = x_{ij} \left[ \frac{S_j}{\delta_j} - \bar{V}_i \right] \quad i = 1, 2, \ldots, N \]

\[ \dot{S}_j = G(x_{ij}, S_j) = \delta_j - \sum_{i}^{N} \alpha_{ij} x_{ij} S_j \quad j = 1, 2, \ldots, M. \] (4.15)
The jacobian of (4.15) at a steady state has the following structure:

\[
\begin{pmatrix}
\frac{\partial F(x_{11}, S_1)}{dx_{11}} & \cdots & \frac{\partial F(x_{11}, S_1)}{dx_{11}} & 0 & \cdots & 0 & \frac{\partial F(x_{11}, S_1)}{dx_{11}} & \cdots & \frac{\partial F(x_{11}, S_m)}{dx_{11}} \\
\vdots & \ddots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\
0 & \cdots & 0 & \frac{\partial F(x_{11}, S_1)}{dx_{11}} & \cdots & \frac{\partial F(x_{11}, S_1)}{dx_{11}} & 0 & \cdots & 0 \\
\vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\
0 & \cdots & 0 & x_{1m}\left(\Phi_1 - \frac{S_m}{\theta_m}\right) & \frac{\partial F(x_{1m}, S_m)}{dx_{1m}} & \cdots & \frac{\partial F(x_{1m}, S_m)}{dx_{1m}} & 0 & \cdots & 0 \\
\vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\
-\alpha_{11}S_1 & \cdots & 0 & -\alpha_{1m}S_m & 0 & \cdots & -\alpha_{1m}S_m & 0 & \cdots & -\sum_{i} \alpha_{im}x_{im} \\
0 & \cdots & -\alpha_{1m}S_m & 0 & \cdots & -\sum_{i} \alpha_{im}x_{im} & \cdots & \cdots & \cdots & \cdots \\
\end{pmatrix}
\]

where:

\[
\frac{\partial F(x_{ij}, S_j)}{dx_{ij}} = (1 - 2x_{ij}) \left(\frac{S_j}{\theta_{ij}} - \Phi_i\right) - \sum_{k \neq j}^{M} x_{ik} \left(\frac{S_k}{\theta_{ik}} - \Phi_i\right). 
\]

1. Suppose that at equilibrium, every agent is mapped to a unique task \(u\) such that: \(x_{iu}^* = 1,\) and \(x_{ij}^* = 0, \forall j \neq u.\) To make this definition clear, let \(l(i) = u\) represent the index of the task for agent \(i.\) Then \(x_{il(i)}^* = 1 \Leftrightarrow S_{l(i)}^* = \delta_{l(i)}^* \frac{\sum_{i} \alpha_{ii} \delta_{l(i)}}{\sum_{i} \alpha_{ii}}.\) Thus, it follows that:

\[
\frac{\partial F(x_{ij}, S_j)}{dx_{ij}} = \begin{cases} \\
\Phi_i - \frac{S_j}{\theta_{ij}} & \text{if } j = l(i) \\
\frac{S_j}{\theta_{ij}} - \frac{S_{l(i)}}{\theta_{l(i)}} & \text{otherwise}. 
\end{cases} 
\]

Under this condition, the eigenvalues of (4.16) can be deduced by noting the following properties.

(a) The \(m^{th}\) order principal submatrix of \(P,\) obtained by deleting its first \(m^2\) rows and (same) columns, is a diagonal matrix with non-zero entries: \(\Lambda_0 = -\{\alpha_{iu}\} < 0.\)
(b) The leading principal submatrix of $P$ is given by:

$$
\begin{pmatrix}
\frac{\partial F(x_{ij}, S_i)}{\partial x_{ij}} & x_{i1}(\Phi_1 - \frac{S_i}{\theta_i}) & \cdots & x_{il}(\Phi_l - \frac{S_i}{\theta_i}) & \cdots & 0 & 0 & \cdots & 0 \\
x_{i1}(\Phi_1 - \frac{S_i}{\theta_i}) & \frac{\partial F(x_{ij}, S_i)}{\partial x_{ij}} & \cdots & x_{il}(\Phi_l - \frac{S_i}{\theta_i}) & \cdots & 0 & 0 & \cdots & 0 \\
\vdots & \vdots & \ddots & \vdots & \ddots & \vdots & \vdots & \ddots & \vdots \\
x_{il}(\Phi_l - \frac{S_i}{\theta_i}) & x_{il}(\Phi_l - \frac{S_i}{\theta_i}) & \cdots & \frac{\partial F(x_{ij}, S_i)}{\partial x_{ij}} & \cdots & 0 & 0 & \cdots & 0 \\
0 & 0 & \cdots & 0 & \frac{\partial F(x_{ij}, S_i)}{\partial x_{ij}} & x_{il}(\Phi_l - \frac{S_i}{\theta_i}) & \cdots & x_{im}(\Phi_m - \frac{S_i}{\theta_i}) \\
0 & 0 & \cdots & 0 & 0 & \frac{\partial F(x_{ij}, S_i)}{\partial x_{ij}} & \cdots & x_{im}(\Phi_m - \frac{S_i}{\theta_i}) \\
\vdots & \vdots & \ddots & \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\
0 & 0 & \cdots & 0 & 0 & 0 & \cdots & \frac{\partial F(x_{ij}, S_i)}{\partial x_{ij}} & x_{im}(\Phi_m - \frac{S_i}{\theta_i}) \\
0 & 0 & \cdots & 0 & 0 & 0 & \cdots & 0 & \frac{\partial F(x_{ij}, S_i)}{\partial x_{ij}}
\end{pmatrix}
$$

(4.19)

Now, let $L(i) = l(i) + (i - 1)M$. Since $x^*_{il(i)} = 1 \implies x^*_{ij} = 0$ $\forall j \neq l(i)$, the $L(i)^{th}$ column of (4.19) is zero everywhere but in its $L(i)^{th}$ entry. The $N(M - 1)$ order submatrix of $\hat{P}$, obtained by deleting the $L(i)^{th}$ row and column for each agent $i$, is a diagonal matrix with entries: $\Lambda_1 = \{S^*_j - \frac{S^*_{il(i)}}{\theta_{il(i)}}\}$, $\forall i, j \neq l(i)$. Moreover, the $M^{th}$ order submatrix of $\hat{P}$, obtained by deleting all except the $L(i)^{th}$ row and column, is also a diagonal matrix with entries: $\Lambda_2 = \{\Phi_i - \frac{S^*_{il(i)}}{\theta_{il(i)}}\}$, $\forall i$

(c) The preceding discussion indicates that the characteristic polynomial (4.16)

$$\det(P - \lambda I) = 0$$

has $M$ roots given $\Lambda_0$, $N(M - 1)$ roots given $\Lambda_1$, and $N$ roots given $\Lambda_2$. Note that $\Lambda_1 < 0 \iff \frac{S^*_{il(i)}}{\theta_{il(i)}} > \max_{j \neq u} S^*_j$, and $\Lambda_2 < 0 \iff \frac{S^*_{il(i)}}{\theta_{il(i)}} > \Phi_i$ for all $i$. Therefore, $(x^*_{ij}, S^*_j)$ with $x^*_{iu} + x^*_{i0} = 0$ is L.A.S.

if $S^*_u > \max_{j \neq u} S^*_j, \Phi_i$, $\forall i$ where $u = l(i)$.

2. Suppose that $N > M$. Under this condition, there can be up to $N - M$ agents indexed by $h$ who do not perform any tasks (i.e. $l(h) = 0$, $x^*_{h0} = 1$). Thus,

$$\frac{\partial F(x_{ij}, S_j)}{\partial x_{ij}} = \frac{S^*_j}{\theta_{ij}} - \Phi_h$$

for all $j$. In this case, $\Lambda_2 = \{\Phi_i - \frac{S^*_{il(i)}}{\theta_{il(i)}}, \frac{S^*_j}{\theta_{ij}} - \Phi_h\}$, $\forall j$

where $i = 1, 2, \ldots N$, and $h = N + 1, N + 2, \ldots, N - M$. A sufficient condition for $\Lambda_2 < 0$ that $\frac{S^*_{il(i)}}{\theta_{il(i)}} > \Phi_i$ holds and $\Phi_h > \max_j \frac{S^*_j}{\theta_{ij}}$ for all $h$. 

□

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Proof of Theorem 4.0.0.5

Proof. Proof of existence are left to the reader as an exercise. The stability of \( E_{(0,1)} \) and \( E_{(1,0)} \) and \( E_{(1,1)} \) can be obtained from Theorem 4.0.0.4.

1. At \( E_{(0,1)} \), agent 1 is inactive (i.e., \( l(1) = 0 \)) while agent 2 specializes on the task (i.e., \( l(2) = 1 \)). Thus, \( E_{(0,1)} \) is L.A.S. if \( \frac{S^*_1}{\theta_{11}} < \Phi_1 \) and \( \frac{S^*_2}{\theta_{21}} > \Phi_2 \). Combining these conditions, we get \( \theta_{21} \Phi_2 < D_{21} < \theta_{11} \Phi_1 \).

2. Conversely, at \( E_{(1,0)} \), agent 1 specializes on the task while agent 1 is inactive. Thus, \( E_{(1,0)} \) is L.A.S. if \( \theta_{21} \Phi_2 < S^*_1 < \Phi_1 \theta_{11} \iff \theta_{11} \Phi_1 < D_{11} < \theta_{21} \Phi_2 \).

3. Finally, at \( E_{(1,1)} \) both agents are specialists (i.e., \( l(1) = l(2) = 1 \)). Thus, \( E_{(1,0)} \) is L.A.S. if \( S^*_1 = \frac{\delta_1}{\alpha_{11} + \alpha_{21}} > \max\{\theta_{11} \Phi_1, \theta_{21} \Phi_2\} \).

The stability of the remaining equilibria of (4.10) can be determined directly from its Jacobian matrix

\[
J := 
\begin{pmatrix}
-\frac{(S^*_1 - \theta_{11} \Phi_1)(2x^*_1 - 1)}{\theta_{11}} & 0 & \frac{x^*_1 (1-x^*_1)}{\theta_{11}} \\
0 & -\frac{(S^*_2 - \theta_{21} \Phi_2)(2x^*_2 - 1)}{\theta_{21}} & \frac{x^*_2 (1-x^*_2)}{\theta_{21}} \\
-\alpha_{11} S^*_1 & -\alpha_{21} S^*_1 & -\alpha_{11} x^*_1 - \alpha_{21} x^*_2 \\
\end{pmatrix}.
\tag{4.20}
\]

4. At \( E_{(0,\ast)} \), the first eigenvalue of (4.20) is given by: \( \lambda_1 = \frac{\theta_{21} \Phi_2 - \theta_{11} \Phi_1}{\theta_{21}} \). The remaining eigenvalues satisfy: \( \lambda_2 + \lambda_3 = -\frac{\delta_1}{\theta_{21} \Phi_2} \), and

\[
\lambda_2 \lambda_3 = -4 \alpha_{21} \delta_1 \Phi_2 (\delta_1 - \alpha_{21} \theta_{21} \Phi_2) > 0.
\]

which holds whenever \( E_{(0,\ast)} \), exists (i.e. \( \frac{D_{21}}{\theta_{21} \Phi_2} = \frac{\delta_1}{\alpha_{21} \theta_{21} \Phi_2} < 1 \)). Therefore, \( E_{(0,\ast)} \) is L.A.S. if \( \lambda_1 < 0 \iff \frac{\theta_{11} \Phi_1}{\theta_{21} \Phi_2} > 1 \).

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5. A similar calculation at $E_{(\ast,0)}$ shows that: 

$$\lambda_1 = \frac{\theta_{11} \Phi_1 - \theta_{21} \Phi_2}{\theta_{21}}, \quad \lambda_2 + \lambda_3 = -\frac{\delta_1}{\theta_{11} \Phi_1},$$

and

$$\lambda_2 \lambda_3 = -4 \alpha_{11} \delta_1 \Phi_1 (\delta_1 - \alpha_{11} \theta_{11} \Phi_1) > 0.$$ 

which holds whenever $E_{(\ast,0)}$, exists (i.e., $\frac{\partial \lambda_1}{\partial \theta_{11} \Phi_1} = \frac{\delta_1}{\alpha_{11} \theta_{11} \Phi_1} < 1$). Thus, $E_{(\ast,0)}$ is L.A.S. if $\lambda_1 < 0 \iff \theta_{21} \Phi_1 > 1$.

6. At $E_{(\nabla,1)}$, the first eigenvalue of (4.20) is given by: 

$$\lambda_1 = \frac{\theta_{21} \Phi_2 - \theta_{11} \Phi_1}{\theta_{21}}.$$ 

The remaining eigenvalues satisfy: 

$$\lambda_2 + \lambda_3 = -\frac{\delta_1}{\theta_{11} \Phi_1},$$

and

$$\lambda_2 \lambda_3 = -4 \alpha_{11} \Phi_1 (\alpha_{21} \theta_{11} \Phi_1 - \delta_1) [\alpha_{11} \theta_{11} \Phi_1 + \alpha_{21} \theta_{11} \Phi_1 - \delta_1] > 0$$ 

which holds whenever $E_{(\nabla,1)}$ exists (i.e., $\frac{\delta_1}{\alpha_{11} \theta_{11} \Phi_1} < 1 \iff \frac{\partial \lambda_1}{\lambda_2 \lambda_3} = \frac{\alpha_{21}}{\alpha_{11}} \frac{\delta_1}{\alpha_{11} \theta_{11} \Phi_1} < 1 \iff \frac{\theta_{11} \Phi_1}{\theta_{21} \Phi_2} > 1$). Therefore, $E_{(\nabla,1)}$ is L.A.S. if $\lambda_1 < 0 \iff \frac{\theta_{11} \Phi_1}{\theta_{21} \Phi_2} > 1$.

7. A similar calculation at $E_{(1,\nabla)}$ shows that: 

$$\lambda_1 = \frac{\theta_{11} \Phi_1 - \theta_{21} \Phi_2}{\theta_{11}}, \quad \lambda_2 + \lambda_3 = -\frac{\delta_1}{\theta_{21} \Phi_2},$$

and:

$$\lambda_2 \lambda_3 = -4 \alpha_{21} \Phi_2 (\alpha_{11} \theta_{21} \Phi_2 - \delta_1) [\alpha_{21} \Phi_2 \theta_{21} + \alpha_{11} \Phi_2 \theta_{21} - \delta_1] > 0$$ 

holds whenever $E_{(\nabla,1)}$ exists (i.e., $\frac{\delta_1}{\alpha_{11} \theta_{21} \Phi_2} > 1 \iff \frac{\partial \lambda_1}{\lambda_2 \lambda_3} = \frac{\alpha_{11}}{\alpha_{21}} \frac{\delta_1}{\alpha_{11} \theta_{21} \Phi_2} < 1 \iff \frac{\theta_{21} \Phi_2}{\theta_{11} \Phi_1} < \frac{\alpha_{11} + \alpha_{21}}{\alpha_{21}}$). Thus, $E_{(\nabla,1)}$ is L.A.S. if $\lambda_1 < 0 \iff \frac{\theta_{21} \Phi_2}{\theta_{11} \Phi_1} > 1$.

Proof of Theorem 4.0.0.6 - 4.0.0.7

Proof. Proof of existence are left to the reader as an exercise.

1. The stability of $E_{(1,0)}$ follows directly from Theorem 4.0.0.4. Here, agent 1
2. At $E^{(1,0)}$ is L.A.S. if $\frac{S^*_1}{\theta_{11}} > \max\{\frac{S^*_2}{\theta_{12}}, \Phi_1\}$ $\Leftrightarrow$ $\frac{D_{11}}{\theta_{11}} > \max\{\frac{D_{22}}{\theta_{12}}, \Phi_1\}$, and $\frac{S^*_2}{\theta_{22}} > \max\{\frac{S^*_1}{\theta_{21}}, \Phi_2\}$ $\Leftrightarrow$ $\frac{D_{22}}{\theta_{22}} > \max\{\frac{D_{11}}{\theta_{21}}, \Phi_2\}$.

The stability of the remaining equilibria of (4.10) can be determined from its Jacobian matrix $J$:

$$
\begin{pmatrix}
\frac{\partial F(x_{1i},S^*_i)}{\partial x_{1i}} & x_{1i} (\Phi_1 - \frac{S^*_i}{\theta_{1i}}) & 0 & 0 & -\frac{\partial F(x_{1i},S^*_i)}{\partial x_{1i}} & -\frac{\partial F(x_{1i},S^*_i)}{\partial x_{1i}} \\
\frac{\partial F(x_{2i},S^*_i)}{\partial x_{2i}} & x_{2i} (\Phi_2 - \frac{S^*_i}{\theta_{2i}}) & 0 & 0 & -\frac{\partial F(x_{2i},S^*_i)}{\partial x_{2i}} & -\frac{\partial F(x_{2i},S^*_i)}{\partial x_{2i}} \\
0 & 0 & x_{2i} (\Phi_2 - \frac{S^*_i}{\theta_{2i}}) & 0 & -\frac{\partial F(x_{2i},S^*_i)}{\partial x_{2i}} & -\frac{\partial F(x_{2i},S^*_i)}{\partial x_{2i}} \\
0 & 0 & 0 & -\frac{\partial F(x_{2i},S^*_i)}{\partial x_{2i}} & 0 & 0 \\
0 & 0 & -\alpha_{1i}S^*_i & 0 & 0 & 0 \\
0 & -\alpha_{12}S^*_i & 0 & 0 & 0 & 0
\end{pmatrix}
$$

where $\frac{\partial F(x_{1i},S^*_i)}{\partial x_{1i}}$ is given by (4.17) for $i = 1, 2$.

2. At $E^{(1,0)} = \left(1, 0, 0, \frac{\delta_2}{\alpha_{22} \theta_{22} \Phi_2}, \frac{\delta_1}{\alpha_{11}}, \theta_{22} \Phi_2\right)$, (4.21) has six trivial eigenvalues given by: $\lambda_1 = -\alpha_{11}$, $\lambda_2 = \Phi_1 - \frac{S^*_1}{\theta_{11}}$, $\lambda_3 = \frac{S^*_1}{\theta_{21}} - \Phi_2$, $\lambda_4 = \frac{S^*_2}{\theta_{12}} - \frac{S^*_1}{\theta_{11}}$, and

$$
\lambda_{5,6} = -\frac{\alpha_{22}x^*_2}{2} \pm \sqrt{\frac{\alpha_{22}^2(x^*_2)^2}{2} + 4\alpha_{22}\Phi_2(x^*_2 - 1)}
$$

where $x^*_2 = \frac{\delta_2}{\alpha_{22} \theta_{22} \Phi_2} = \frac{D_{22}}{\theta_{22} \Phi_2} < 1$.

(a) Clearly, $\lambda_1 < 0$. Moreover, we have the following: (a) $\lambda_2 < 0 \Leftrightarrow \frac{S^*_1}{\theta_{11}} > \Phi_1$, (b) $\lambda_3 < 0 \Leftrightarrow \frac{S^*_1}{\theta_{21}} < \Phi_2$, and (c) $\lambda_4 < 0 \Leftrightarrow \frac{S^*_2}{\theta_{12}} < \frac{S^*_1}{\theta_{11}}$. Finally, the remaining eigenvalues satisfy: $\lambda_5 + \lambda_6 < 0$, and $\lambda_5 \lambda_6 = -\alpha_{22} \Phi_2(x^*_2 - 1) > 0$ which holds whenever $x^*_2 < 1$.

(b) In conclusion, the preceding discussion implies that $E^{(1,0)}$ is L.A.S. if: (i) $\frac{S^*_1}{\theta_{11}} > \max\{\frac{S^*_2}{\theta_{12}}, \Phi_1\}$ $\Leftrightarrow$ $\frac{D_{11}}{\theta_{11}} > \max\{\frac{\theta_{22} \Phi_2}{\theta_{12}}, 1\}$, and (ii) $\frac{S^*_1}{\theta_{21}} < \Phi_2$ $\Leftrightarrow$ $\frac{D_{22}}{\theta_{22}} < \frac{\theta_{22} \Phi_2}{\theta_{12} \Phi_1}$.
3. At $E^{(1,0)}_{(0,1)} = \left( \frac{\delta_1}{\alpha_{11} \delta_1}, 0, 0, 1, \theta_{11} \Phi_1, \frac{\delta_1}{\alpha_{22}} \right)$, (4.21) has six trivial eigenvalues given by: $\lambda_1 = -\alpha_{22}$, $\lambda_2 = \Phi_2 - \frac{S_2}{\theta_{12}}$, $\lambda_3 = \frac{S_1}{\theta_{21}} - \Phi_1$, $\lambda_4 = \frac{S_1}{\theta_{21}} - \frac{S_2}{\theta_{12}}$, and

$$\lambda_{5,6} = -\frac{\alpha_{11} x_{11}^*}{2} \pm \sqrt{\frac{\alpha_{11}^2 (x_{11}^*)^2 + 4 \alpha_{11} \Phi_1 (x_{11}^* - 1)}{2}}$$

where $x_{11}^* = \frac{\delta_1}{\alpha_{11} \theta_{11} \Phi_1} = \frac{\theta_{11} \Phi_1}{\theta_{12}} < 1$.

(a) Clearly, $\lambda_1 < 0$. Moreover, we have the following: (a) $\lambda_2 < 0 \iff \frac{S_2}{\theta_{12}} > \Phi_2$, (b) $\lambda_3 < 0 \iff \frac{S_1}{\theta_{21}} < \Phi_1$, and (c) $\lambda_4 < 0 \iff \frac{S_1}{\theta_{21}} < \frac{S_2}{\theta_{12}}$. Finally, the remaining eigenvalues satisfy: $\lambda_5 + \lambda_6 < 0$, and $\lambda_5 \lambda_6 = -\alpha_{11} \Phi_1 (x_{11}^* - 1) > 0$ which holds whenever $x_{11}^* < 1$.

(b) In conclusion, the preceding discussion implies that $E^{(1,0)}_{(0,1)}$ is L.A.S. if: (i) $\frac{S_2}{\theta_{22}} > \max\{\frac{S_1}{\theta_{21}}, \Phi_2\} \iff \frac{\theta_{11} \Phi_1}{\theta_{12} \Phi_2} > \max\{\theta_{11} \Phi_1, 1\}$, and (ii) $\frac{S_2}{\theta_{12}} < \Phi_1 \iff \frac{\theta_{11} \Phi_1}{\theta_{12} \Phi_2} < \frac{\theta_{11} \Phi_1}{\theta_{12} \Phi_2}$.

4. At $E^{(0,0)}_{(0,1)} = \left( \frac{\delta_1}{\alpha_{11} \theta_{11} \Phi_1}, 0, 0, \frac{\delta_2}{\alpha_{22} \theta_{22} \Phi_2}, \theta_{11} \Phi_1, \theta_{22} \Phi_2 \right)$ (4.21) has two trivial eigenvalues given by:

$$\lambda_1 = \frac{S_1}{\theta_{21}} - \Phi_2 \quad \text{and} \quad \lambda_2 = \frac{S_2}{\theta_{12}} - \Phi_1.$$ 

Hence, $\lambda_1 < 0 \iff S_1^* < \theta_{21} \Phi_2$. Similarly, $\lambda_2 < 0 \iff S_2^* < \theta_{12} \Phi_1$. The remaining eigenvalues are roots of the characteristic polynomial:

$$\rho(\lambda) = \lambda^4 + c_1 \lambda^3 + c_2 \lambda^2 + c_3 \lambda + c_4.$$ 

(4.22)
The coefficients of (4.22) can be written as:

\[ c_1 = \alpha_{11}x_{11}^* + \alpha_{22}x_{22}^* > 0 \]
\[ c_2 = \alpha_{11}x_{11}^*(1 - x_{11}) \Phi_1 + \alpha_{22}x_{22}^*(1 - x_{22}) \Phi_2 + \alpha_{11}\alpha_{22}x_{22}^*x_{11}^* > 0 \]
\[ c_3 = \alpha_{11}\alpha_{22}x_{22}^*x_{11}^*(\Phi_1(1 - x_{11}) + (1 - x_{22}) \Phi_2) > 0 \]
\[ c_4 = \alpha_{11}\alpha_{22}x_{22}^*x_{11}^*(1 - x_{22}^*)(1 - x_{11}^*) \Phi_1 \Phi_2 > 0 \]

(4.23)

where \( x_{11}^* = \frac{\delta_1}{\alpha_{11} \theta_{11}} \) and \( x_{22}^* = \frac{\delta_2}{\alpha_{22} \theta_{22}} < 1 \).

Using the Routh-Hurwitz criteria (Brauer et al., 2001), we can conclude that \( E_{(0,*)}^{(s,0)} \) is locally asymptotically stable if and only if (i) \( c_1 > 0 \), (ii) \( c_3 > 0 \), (iii) \( c_4 > 0 \), and (iv) \( c_3(c_1c_2 - c_3) > c_1^2c_4 \).

(a) Conditions (i)-(iii) whenever \( x_{11}^* < 1 \) and \( x_{22}^* < 1 \). Thus, it remains to show under what condition (iv) is satisfied.

(b) According to (4.23), we have:

\[ c_1c_2 - c_3 = \alpha_{11}^2(x_{11}^*)^2(1 - x_{11}^*) \Phi_1 + \alpha_{22}^2(x_{22}^*)^2(1 - x_{22}^*) \Phi_2 \]
\[ + \alpha_{11}\alpha_{22}x_{22}^*x_{11}^*(\alpha_{11}x_{11}^* + \alpha_{22}x_{22}^*) > 0. \]

(c) Similarly, we also have:

\[ c_1^2c_4 = \alpha_{11}\alpha_{22}x_{22}^*x_{11}^*(1 - x_{22}^*)(1 - x_{11}^*)(\alpha_{11}x_{11}^* + \alpha_{22}x_{22}^*)^2 \Phi_1 \Phi_2 > 0. \]
Moreover,

\[ c_3(c_1c_2 - c_3) > c_3 \cdot [\alpha_{11}^2(x_{11}^*)^2(1 - x_{11}^*)\Phi_1 + \alpha_{22}^2(x_{22}^*)^2(1 - x_{22}^*)\Phi_2] \]

\[ = \alpha_{11}\alpha_{22}x_{22}^*x_{11}^* [(\heartsuit - \spadesuit)^2 + 2\alpha_{11}\alpha_{22}x_{22}^*x_{11}^*(1 - x_{22}^*)(1 - x_{11}^*)\Phi_1\Phi_2] \]

\[ + \alpha_{11}\alpha_{22}x_{22}^*x_{11}^* [(\alpha_{11}^2(x_{11}^*)^2 + \alpha_{22}(x_{22}^*)^2](1 - x_{22}^*)(1 - x_{11}^*)\Phi_1\Phi_2] \]

where

\[ \heartsuit = \alpha_{11}x_{11}^*(1 - x_{11}^*)\Phi_1 \quad \text{and} \quad \spadesuit = \alpha_{22}x_{22}^*(1 - x_{22}^*)\Phi_2. \]

Since \( c_1^2 = (\alpha_{11}x_{11}^* + \alpha_{22}x_{22}^*)(\alpha_{11}x_{11}^* - \alpha_{22}x_{22}^*) + 2\alpha_{11}\alpha_{22}x_{11}^*x_{22}^* \), it follows directly from the preceding inequality that:

\[ c_3(c_1c_2 - c_3) > \alpha_{11}\alpha_{22}x_{22}^*x_{11}^* (\heartsuit - \spadesuit)^2 + c_1^2c_4 > 0. \]  \( \text{(4.24)} \)

(d) In conclusion, the preceding discussion implies that \( E^{(\ast,0)}_{(0,\ast)} \) is L.A.S if and only if: (i) \( S_1^* < \theta_{21}\Phi_2 \iff \theta_{11}\Phi_1 < \theta_{21}\Phi_2 \), (ii) \( S_2^* < \theta_{12}\Phi_1 \iff \theta_{12}\Phi_1 > \theta_{22}\Phi_2 \), (iii) \( x_{11}^* \equiv \frac{\rho_{21}}{\theta_{11}\Phi_1} < 1 \) and (iv) \( x_{22}^* \equiv \frac{\rho_{12}}{\theta_{22}\Phi_2} < 1 \).

5. At \( E^{(1,0)}_{(\nabla,\ast)} = \left(1, 0, \frac{\delta_{21}}{\alpha_{21}\theta_{21}\Phi_2} - \frac{\alpha_{11}}{\alpha_{21}}, \frac{\delta_{21}}{\alpha_{22}\theta_{22}\Phi_2}, \theta_{21}\Phi_2, \theta_{22}\Phi_2 \right) \) \( \text{(4.21)} \) has two trivial eigenvalues given by:

\[ \lambda_1 = \Phi_1 - \frac{S_1^*}{\theta_{11}} \quad \text{and} \quad \lambda_2 = \frac{S_2^*}{\theta_{12}} - \frac{S_1^*}{\theta_{11}}. \]

Hence, \( \lambda_1 < 0 \iff S_1^* > \theta_{11}\Phi_1 \). Similarly, \( \lambda_2 < 0 \iff S_2^*\theta_{11} < S_1^*\theta_{12} \).

The remaining eigenvalues are roots of the characteristic polynomial:

\[ \rho(\lambda) = \lambda^4 + c_1\lambda^3 + c_2\lambda^2 + c_3\lambda + c_4. \]  \( \text{(4.25)} \)
Now, suppose that \( \alpha_{11} = \alpha_{12} = \alpha_1 \), and \( \alpha_{21} = \alpha_{22} = \alpha_2 \). Moreover, let \( \eta = \frac{\mathcal{D}_{21}}{\theta_{11}\Phi_2^2} + \frac{\mathcal{D}_{22}}{\theta_{22}\Phi_2^2} = \frac{\delta_1 \theta_{22} + \delta_2 \theta_{21}}{\alpha_2 \theta_{21} \theta_{22} \Phi_2^2} \). The coefficients of (4.25) can be written as:

\[
\begin{align*}
    c_1 &= \alpha_2 \eta > 0 \\
    c_2 &= \alpha_2 \left[ \left( \eta - \frac{\alpha_1}{\alpha_2} \right) \left( 1 - \eta + \frac{\alpha_1}{\alpha_2} \right) + 2x_{21}^* x_{22}^* \right] \Phi_2 + \alpha_2^2 x_{22}^* (\eta - x_{22}^*) \\
    c_3 &= \alpha_2^2 x_{21}^* x_{22}^* (2 - \eta + \frac{\alpha_1}{\alpha_2}) \Phi_2 + \alpha_1 \alpha_2 x_{22}^* (1 - x_{22}^*) \Phi_2 \\
    c_4 &= \alpha_2^2 x_{21}^* x_{22}^* (1 - \eta + \frac{\alpha_1}{\alpha_2}) \Phi_2^2.
\end{align*}
\]

(4.26)

Using the Routh-Hurwitz criteria (Brauer et al., 2001), we can conclude that \( E^{1,(0)}_{(*,*,*),*} \) is locally asymptotically stable if and only if (i) \( c_1 > 0 \), (ii) \( c_3 > 0 \), (iii) \( c_4 > 0 \), and (iv) \( c_3 (c_1 c_2 - c_3) > c_1^2 c_4 \). This is left to the reader as an exercise.

6. At \( E^{1,(0)}_{(\triangle,\triangle)} = \left( 1, 0, 1 - x_{22}^*, x_{22}^*, \frac{\mathcal{D}_{22}}{\theta_{22}}, \frac{\mathcal{D}_{22}}{\theta_{22}}, \frac{\mathcal{D}_{22}}{x_{22}^*} \right) \) where \( x_{22}^* = \frac{\delta_2 (\alpha_{11} + \alpha_{21}) \theta_{21}}{\alpha_{21} \delta_2 \theta_{21} + \alpha_{22} \delta_1 \theta_{22}} \) and \( \mathcal{D}_{22} = \frac{\delta_2}{\alpha_{22}} \), the Jacobian matrix (4.21) has two trivial eigenvalues given by:

\[
\lambda_1 = \Phi_1 - \frac{S_1^*}{\theta_{11}} \quad \text{and} \quad \lambda_2 = \frac{S_2^*}{\theta_{12}} - \frac{S_1^*}{\theta_{11}}.
\]

Hence, \( \lambda_1 < 0 \Leftrightarrow S_1^* > \theta_{11} \Phi_1 \). Similarly, \( \lambda_2 < 0 \Leftrightarrow S_2^* \theta_{11} < S_1^* \theta_{12} \).

The remaining eigenvalues are roots of the characteristic polynomial:

\[
\rho(\lambda) = \lambda^4 + c_1 \lambda^3 + c_2 \lambda^2 + c_3 \lambda + c_4.
\]

(4.27)

Now, suppose that \( \alpha_{11} = \alpha_{12} = \alpha_1 \), and \( \alpha_{21} = \alpha_{22} = \alpha_2 \). Moreover, let \( \eta = \frac{\mathcal{D}_{21}}{\theta_{21}\Phi_2^2} + \frac{\mathcal{D}_{22}}{\theta_{22}\Phi_2^2} = \frac{\delta_1 \theta_{22} + \delta_2 \theta_{21}}{\alpha_2 \theta_{21} \theta_{22} \Phi_2^2} \). Then, the coefficients of (4.27) can be written
\[ c_1 = \alpha_1 + \alpha_2 + (\eta - \xi) \frac{\Phi_2}{\xi} \]
\[ c_2 = \alpha_2 (\eta - \xi) \Phi_2 + \kappa \]
\[ c_3 = \alpha_2^2 \eta x_{21}^* (1 - x_{21}^*) \Phi_2 + \kappa(\eta - \xi) \frac{\Phi_2}{\xi} \]
\[ c_4 = \alpha_2^2 \eta x_{21}^* (1 - x_{21}^*) (\eta - \xi) \frac{\Phi_2}{\xi}. \]

where \( x_{21}^* = 1 - x_{22}^* \), \( \xi = \frac{\alpha_1 + \alpha_2}{\alpha_2} \) and:

\[ \kappa = \alpha_2 (1 - x_{21}^*) \left[ \frac{2\eta x_{21}^* \Phi_2}{\xi} + \alpha_1 + \alpha_2 x_{21}^* \right]. \] (4.29)

Using the Routh-Hurwitz criteria (Brauer et al., 2001), we can conclude that \( E^{(1,0)}_{(\triangle, \triangle)} \) is locally asymptotically stable if and only if (i) \( c_1 > 0 \), (ii) \( c_3 > 0 \), (iii) \( c_4 > 0 \), and (iv) \( c_3(c_1c_2 - c_3) > c_1^2 c_4 \).

(a) Conditions (i)-(iii) necessarily hold if \( \eta > \xi = \frac{\alpha_1 + \alpha_2}{\alpha_2} \). Thus, it remains to show under what condition (iv) is satisfied.

(b) Suppose that \( \eta > \xi \). From (4.28), we have

\[ c_1c_2 - c_3 = \kappa(\alpha_1 + \alpha_2) - \alpha_2^2 \eta x_{21}^* (1 - x_{21}^*) \Phi_2 + \alpha_2(\eta - \xi) \left[ \alpha_1 + \alpha_2 x_{21}^* + (\eta - \xi) \frac{\Phi_2}{\xi} \right] \Phi_2 > 0, \]

which holds because:

\[ \kappa(\alpha_1 + \alpha_2) - \alpha_2^2 \eta x_{21}^* (1 - x_{21}^*) \Phi_2 = \alpha_2^2 (1 - x_{21}^*) [\eta x_{21}^* \Phi_2 + \xi(\alpha_1 + \alpha_2 x_{21}^*)] > 0. \]
(c) Next, we have:

$$c_1^2 c_4 = \alpha_2^2 \eta x_{21}^*(1 - x_{21}^*)(\eta - \xi) \frac{\Phi_2^2}{\xi} \left[ (\alpha_1 + \alpha_2)^2 + 2\alpha_2(\eta - \xi)\Phi_2 + (\eta - \xi)^2 \frac{\Phi_2^2}{\xi^2} \right].$$

Similarly,

$$c_3(c_1 c_2 - c_3) = c_3 \cdot [\kappa(\alpha_1 + \alpha_2) - \alpha_2^2 \eta x_{21}^*(1 - x_{21}^*)\Phi_2]$$

$$+ c_3 \cdot \alpha_2(\eta - \xi)\Phi_2 \cdot c_1.$$

This indicates that:

$$c_3(c_1 c_2 - c_3) > c_3 \cdot \alpha_2(\eta - \xi) \left[ \alpha_1 + \alpha_2 + (\eta - \xi)\frac{\Phi_2}{\xi} \right] \Phi_2.$$

From (4.28), we have that $c_3 > \alpha_2 x_{21}^*(1 - x_{21}^*) \left[ 2\eta(\eta - \xi)\frac{\Phi_2^2}{\xi^2} + \alpha_2 \eta \Phi_2 \right]$. Therefore, $c_3(c_1 c_2 - c_3) > \bigheartsuit \cdot \clubsuit$ where:

$$\bigheartsuit = \alpha_2 \eta x_{21}^*(1 - x_{21}^*)(\eta - \xi) \frac{\Phi_2^2}{\xi} \left[ 2(\eta - \xi) \frac{\Phi_2}{\xi^2} + \alpha_2 \right]$$

$$\clubsuit = \left[ (\alpha_1 + \alpha_2)^2 + (\eta + \alpha_2)(\eta - \xi)\frac{\Phi_2}{\xi} \right].$$

This indicates that:

$$c_3(c_1 c_2 - c_3) - c_1^2 c_4 > \alpha_2^2 \eta x_{21}^*(1 - x_{21}^*)(\eta - \xi)^2 \left[ 2(\eta - \xi) \frac{\Phi_2}{\xi^2} + \alpha_2 \right] \frac{\Phi_2^3}{\xi^2} > 0.$$

(d) The preceding discussion implies that under the condition $\alpha_{11} = \alpha_{12} = \alpha_1$ and $\alpha_{21} = \alpha_{22} = \alpha_2$, equilibrium $E_{(1,0)}^{(1,0)}$ is L.A.S. if: (i) $\eta = \frac{\theta_{21}}{\theta_{22}} \Phi_2 + \frac{\theta_{22}}{\theta_{22}} \Phi_2 > \xi$

where $\xi = \frac{\alpha_1 + \alpha_2}{\alpha_2}$, (ii) $\frac{S_1}{\theta_{11}} > \Phi_1 \Leftrightarrow \frac{\delta_1 \theta_{22} + \delta_2 \theta_{21}}{(\alpha_1 + \alpha_2)\theta_{11} \theta_{22}} > \Phi_1 \Leftrightarrow \frac{\eta}{\xi} > \frac{\theta_{11} \Phi_1}{\theta_{21} \Phi_2}$, and (iii)

$$\frac{S_1^*}{\theta_{12}} < \frac{S_1^*}{\theta_{11}} \Leftrightarrow \theta_{11} \theta_{22} < \theta_{12} \theta_{21}.$$
7. At $E^{(\nabla, 0)}_{(\Delta, \Delta)} = (x_{11}^*, 0, x_{21}^*, 1 - x_{21}^*, \theta_1 \Phi_1, \frac{\theta_1 \theta_{21}}{\theta_{21}})$, (4.21) has one trivial eigenvalue given by:

$$\lambda_1 = \frac{S_2^*}{\theta_{12}} - \frac{S_1^*}{\theta_{11}} x_{11}^* - (1 - x_{11}^*) \Phi_1$$

where $x_{11}^* = \frac{\delta_1}{\alpha_{11} \theta_{11}} - \frac{\alpha_2}{\alpha_{11}}$, $x_{21}^* = 1 - \frac{\delta_2}{\alpha_{22} \theta_{22} \Phi_1}$, and $x_{22}^* = 1 - x_{21}^*$. Hence, $\lambda_1 < 0 \iff \frac{S_2^*}{\theta_{12}} < \Phi_1 \iff \frac{\theta_{11}}{\theta_{12}} < \frac{\theta_{21}}{\theta_{22}}$. The remaining eigenvalues are roots of the characteristic polynomial:

$$\rho(\lambda) = \lambda^5 + c_1\lambda^4 + c_2\lambda^3 + c_3\lambda^2 + c_4\lambda + c_5.$$  \hspace{1cm} (4.30)

Now, suppose that $\alpha_{11} = \alpha_{12} = \alpha_1$, and $\alpha_{22} = \alpha_2$.

Also let $\eta = \frac{C_{21}}{\theta_{21} \Phi_2} + \frac{C_{22}}{\theta_{22} \Phi_2} = \frac{\delta_1 \theta_{21} + \delta_2 \theta_{22}}{\alpha_{22} \theta_{21} \theta_{22} \Phi_2}$ and $\omega = \frac{S_1^*}{\theta_{21}} = \frac{\theta_1 \Phi_1}{\theta_{21}} = \frac{S_2^*}{\theta_{22}}$. Then, the coefficients of (4.30) can be written as:

$$c_1 = \frac{\alpha_2 \eta \Phi_2}{\omega} + \omega - \Phi_2$$
$$c_2 = \alpha_2 (1 - x_{21}^*)(\alpha_1 x_{11}^* + \alpha_2 x_{21}^* + 2 \omega x_{21}^*) + \alpha_1 x_{11}^*(1 - x_{11}^*) \Phi_1 + \frac{\alpha_2 \eta \Phi_2}{\omega} (\omega - \Phi_2)$$
$$c_3 = \alpha_2 (1 - x_{21}^*) [\alpha_1 x_{11}^*(1 - x_{11}^*) \Phi_1 + \alpha_2 \eta x_{21}^* \Phi_2]$$
$$+ \alpha_2 (1 - x_{21}^*) [(\omega - \Phi_2)(2 \omega x_{21}^* + \alpha_1 x_{11}^* + \alpha_2 x_{21}^*)] + (\omega - \Phi_2) \alpha_1 x_{11}^*(1 - x_{11}^*) \Phi_1$$
$$c_4 = \alpha_2 (1 - x_{21}^*) [\alpha_2 \eta x_{21}^* \Phi_2 (\omega - \Phi_2) + (\omega + \omega x_{21}^* - \Phi_2) \alpha_1 x_{11}^*(1 - x_{11}^*) \Phi_1]$$
$$c_5 = \alpha_1 \alpha_2 \omega x_{21}^* x_{11}^*(1 - x_{21}^*)(1 - x_{11}^*) (\omega - \Phi_2) \Phi_1$$

where $x_{21}^* = 1 - x_{22}^*$, and $x_{22}^* = \frac{\delta_2 \theta_{21}}{\alpha_{22} \theta_{11} \theta_{22} \Phi_1}$ = $\frac{\theta_{11} \Phi_1}{\theta_{22} \Phi_2}$. Thus, $x_{22}^* < 1 \iff \frac{\theta_{11} \Phi_1}{\theta_{22} \Phi_2} < \frac{\omega}{\Phi_2}$. Note also that $0 < x_{11}^* < 1 \iff \frac{\omega}{\Phi_2} < \eta < \frac{\omega (\alpha_1 + \alpha_2)}{\alpha_2 \Phi_2}$. Using the Routh-Hurwitz criteria (Brauer et al., 2001), we can conclude that $E^{(\nabla, 0)}_{(\Delta, \Delta)}$ is locally asymptotically stable if and only if (i) $c_1 > 0$, (ii) $c_3 > 0$, (iii) $c_4 > 0$, (iv) $c_5 > 0$.
(iv) \( c_5 > 0 \), (v) \( c_3(c_1c_2 - c_3) > c_1^2c_4 \), and (vi)

\[
(c_1c_4 - c_5)[c_3(c_1c_2 - c_3) - c_1^2c_4] > c_5(c_1c_2 - c_3)^2 + c_1c_5^2.
\]

This is left to the reader as an exercise.

8. At \( E^{(0,0)} = (0,0,\triangle,\triangle) = (0,0,\delta_1\alpha_2\theta_21 - \delta_1\alpha_2\theta_22, \delta_2\alpha_2\theta_21 + \delta_1\alpha_2\theta_22, \delta_2\alpha_2\theta_21 + \delta_1\alpha_2\theta_22) \)

(4.21) has two trivial eigenvalues given by:

\[
\lambda_1 = \frac{S_1^*}{\theta_{11}} - \Phi_1 \quad \text{and} \quad \lambda_2 = \frac{S_2^*}{\theta_{12}} - \Phi_1.
\]

Hence, \( \lambda_1 < 0 \iff S_1^* < \theta_{11}\Phi_1 \). Similarly, \( \lambda_2 < 0 \iff S_2^* < \theta_{12}\Phi_1 \). The remaining eigenvalues are roots of the characteristic polynomial:

\[
\rho(\lambda) = \lambda^4 + c_1\lambda^3 + c_2\lambda^2 + c_3\lambda + c_4. \tag{4.31}
\]

Now, suppose that \( \alpha_{21} = \alpha_{22} = \alpha_2 \), and let \( \eta = \frac{\delta_{21}}{\theta_{21}\Phi_2} + \frac{\delta_{22}}{\theta_{22}\Phi_2} = \frac{\delta_1\theta_{22}\theta_{21} + \delta_2\theta_{22}\theta_{21}}{\alpha_{21}\alpha_{22}\theta_{22}}. \)

The coefficients of (4.31) can be written as:

\[
\begin{align*}
    c_1 &= \Phi_2(\eta - 1) + \alpha_2 \\
    c_2 &= \alpha_2(\eta - 1)\Phi_2 + x_{21}^*(1 - x_{21}^*)(2\eta\Phi_2 + \alpha_2) \\
    c_3 &= x_{21}^*(1 - x_{21}^*)(2\eta(\alpha_2 + (\eta - 1)\Phi_2) - \alpha_2\alpha_2\Phi_2) \\
    c_4 &= x_{21}^*(1 - x_{21}^*)\alpha_2^2\eta(\eta - 1)\Phi_2^2.
\end{align*} \tag{4.32}
\]

Using the Routh-Hurwitz criteria (Brauer et al., 2001), we can conclude that \( E^{(\triangle,\triangle)} \) is locally asymptotically stable if and only if (i) \( c_1 > 0 \), (ii) \( c_3 > 0 \), (iii) \( c_4 > 0 \), and (iv) \( c_3(c_1c_2 - c_3) > c_1^2c_4 \).

(a) Conditions (i)-(iii) hold whenever \( \eta > 1 \). Thus, it remains to show under
what condition (iv) is satisfied.

(b) Suppose that $\eta > 1$. Then according to (4.32),

$$c_3 = x^*_{21}(1 - x^*_{21})[2\eta c_1 - \alpha_2]\alpha_2 \Phi_2 < x^*_{21}(1 - x^*_{21})2\eta c_1 \alpha_2 \Phi_2.$$ 

Likewise,

$$c_1 c_2 = \alpha_2 [\eta - 1] \Phi_2 + x^*_{21}(1 - x^*_{21})(2\eta \Phi_2 + \alpha_2)] > \alpha_2 x^*_{21}(1 - x^*_{21})(2\eta \Phi_2 + \alpha_2).$$

Thus, it follows that:

$$c_1 c_2 - c_3 = c_1 \alpha_2 [(\eta - 1) \Phi_2 + \alpha_2 x^*_{21}(1 - x^*_{21})] > 0 \quad (4.33)$$

since $\eta > 1$. Next, notice that:

$$c_3(c_1 c_2 - c_3) = c_3 \cdot [c_1 \alpha_2 [(\eta - 1) \Phi_2 + x^*_{21}(1 - x^*_{21})(2\eta \Phi_2 + \alpha_2)]]$$

$$- \alpha_2 x^*_{21}(1 - x^*_{21})[2\eta c_1 - \alpha_2]\alpha_2 \Phi_2$$

$$= c_3 \cdot [c_1 \alpha_2 [(\eta - 1) \Phi_2 + \alpha_2 x^*_{21}(1 - x^*_{21})] + x^*_{21}(1 - x^*_{21})\alpha_2^2 \Phi_2] > 0.$$ 

Likewise,

$$c_1^2 c_4 = c_1^2 \cdot x^*_{21}(1 - x^*_{21})\alpha_2^2 \eta (\eta - 1) \Phi_2^2.$$ 

However, since $c_3 > x^*_{21}(1 - x^*_{21})\eta c_1 \alpha_2 \Phi_2$, we can infer that

$$c_3(c_1 c_2 - c_3) \geq x^*_{21}(1 - x^*_{21})c_1^2 \alpha_2^2 \eta (\eta - 1) \Phi_2^2$$

$$+ c_3[c_1 \alpha_2^2 x^*_{21}(1 - x^*_{21}) + x^*_{21}(1 - x^*_{21})\alpha_2^2 \Phi_2].$$

This implies that $c_3(c_1 c_2 - c_3) > c_1^2 c_4 > 0$. 

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(c) The preceding discussion implies that under the condition \( \alpha_{21} = \alpha_{22} = \alpha_2 \), equilibrium \( E^{(\Delta, \Delta)}_{(0,0)} \) is L.A.S. if: (i) \( \eta = \frac{D_{21}}{\theta_{21}\Phi_2} + \frac{D_{22}}{\theta_{22}\Phi_2} = \frac{\delta_1 \theta_{22} + \delta_2 \theta_{21}}{\alpha_2 \theta_{21} \theta_{22} \Phi_2} > 1 \), (ii) \( S_1^* < \theta_{11} \Phi_1 \Leftrightarrow \eta < \frac{\theta_{11} \Phi_1}{\theta_{21} \Phi_2} \), and (ii) \( S_2^* < \theta_{12} \Phi_1 \Leftrightarrow \eta < \frac{\theta_{12} \Phi_1}{\theta_{22} \Phi_2} \).

9. At \( E^{(\ast, \ast)}_{(0,0)} = (0, 0, \frac{\delta_1}{\alpha_{21} \theta_{21} \Phi_2}, \frac{\delta_2}{\alpha_{22} \theta_{22} \Phi_2}, \theta_{21} \Phi_2, \theta_{22} \Phi_2) \), (4.21) has two trivial eigenvalues given by:
\[
\lambda_1 = \frac{S_1^*}{\theta_{11}} - \Phi_1 \quad \text{and} \quad \lambda_2 = \frac{S_2^*}{\theta_{12}} - \Phi_1.
\]
Hence, \( \lambda_1 < 0 \Leftrightarrow S_1^* < \theta_{11} \Phi_1 \). Similarly, \( \lambda_2 < 0 \Leftrightarrow S_2^* < \theta_{12} \Phi_1 \). The remaining eigenvalues are roots of the characteristic polynomial:
\[
\rho(\lambda) = \lambda^4 + c_1 \lambda^3 + c_2 \lambda^2 + c_3 \lambda + c_4.
\] (4.34)

The coefficients of (4.34) can be written as:
\[
c_1 = \alpha_{21} x_{21}^* + \alpha_{22} x_{22}^* > 0
\]
\[
c_2 = \alpha_{21} \alpha_{22} x_{21}^* x_{22}^* + \left[ \alpha_{11} x_{21}^* (1 - x_{21}^*) + \alpha_{22} x_{22}^* (1 - x_{22}^*) \right] \Phi_2 > 0
\]
\[
c_3 = \alpha_{21} \alpha_{22} x_{21}^* x_{22}^* (1 - x_{21}^* + 1 - x_{22}^*) \Phi_2 > 0
\]
\[
c_4 = \alpha_{21} \alpha_{22} x_{21}^* x_{22}^* (1 - x_{21}^* - x_{22}^*) \Phi_2^2 > 0
\] (4.35)

where \( x_{21}^* = \frac{\delta_1}{\alpha_{11} \theta_{11} \Phi_2} < 1 \) and \( x_{22}^* = \frac{\delta_2}{\alpha_{12} \theta_{12} \Phi_2} < 1 \). Using the Routh-Hurwitz criteria (Brauer et al., 2001), we can conclude that \( E^{(\ast, \ast)}_{(0,0)} \) is locally asymptotically stable if and only if (i) \( c_1 > 0 \), (ii) \( c_3 > 0 \), (iii) \( c_4 > 0 \), and (iv) \( c_3 (c_1 c_2 - c_3) > c_1^2 c_4 \).

(a) Now, let \( \eta = \frac{D_{21}}{\theta_{21} \Phi_2} + \frac{D_{22}}{\theta_{22} \Phi_2} \). Then, conditions (i)-(iii) necessarily hold since \( \eta \equiv x_{21}^* + x_{22}^* < 1 \). Thus, it remains to show under what condition (iv) is satisfied.
(b) Suppose that $\eta < 1$. Then according to (4.35):

$$c_1 c_2 - c_3 = \alpha_{21} \alpha_{22} x_{21}^* x_{22}^* (\alpha_{21} x_{21}^* + \alpha_{22} x_{22}^*)$$

$$+ [(\alpha_{11} x_{21}^*)^2 (1 - x_{21}^*) + (\alpha_{12} x_{22}^*)^2 (1 - x_{22}^*)] \Phi_2 > 0$$

(c) Likewise, we have that:

$$c_1^2 c_4 = (\alpha_{11} x_{21}^* + \alpha_{22} x_{22}^*)^2 \alpha_{21} \alpha_{22} x_{21}^* x_{22}^* (1 - \eta) \Phi_2^2$$

$$< (\alpha_{11} x_{21}^* + \alpha_{22} x_{22}^*)^2 \alpha_{21} \alpha_{22} (1 - x_{21}^*) (1 - x_{22}^*) \Phi_2^2.$$ 

However, notice that:

$$c_3 (c_1 c_2 - c_3) > c_3 \cdot [(\alpha_{11} x_{21}^*)^2 (1 - x_{21}^*) + (\alpha_{12} x_{22}^*)^2 (1 - x_{22}^*)] \Phi_2$$

$$= \alpha_{21} \alpha_{22} x_{21}^* x_{22}^* [(\heartsuit - ♠)^2 + 2 \alpha_{21} \alpha_{22} x_{21}^* x_{22}^* (1 - x_{21}^*) (1 - x_{22}^*)] \Phi_2^2$$

$$+ \alpha_{21} \alpha_{22} x_{21}^* x_{22}^* [(\alpha_{11} x_{21}^*)^2 + \alpha_{22} (x_{22}^*)^2 (1 - x_{21}^*) (1 - x_{22}^*)] \Phi_2^2$$

where

$$\heartsuit = \alpha_{21} x_{21}^* (1 - x_{21}^*) \quad \text{and} \quad ♠ = \alpha_{22} x_{22}^* (1 - x_{22}^*).$$

Since $c_1^2 = (\alpha_{11} x_{21}^* + \alpha_{22} x_{22}^*) (\alpha_{11} x_{21}^* - \alpha_{22} x_{22}^*) + 2 \alpha_{21} \alpha_{22} x_{21}^* x_{22}^*$, it follows directly from the preceding inequality that:

$$c_3 (c_1 c_2 - c_3) > \alpha_{21} \alpha_{22} x_{22}^* x_{21}^* (\heartsuit - ♠)^2 \Phi_2^2 + c_1^2 c_4 > 0. \quad (4.36)$$

(d) In conclusion, the preceding discussion implies that $E^{(s,s)}_{(0,0)}$ is L.A.S. if and only if: (i) $S_1^* < \theta_{11} \Phi_1 \Leftrightarrow \theta_{21} \Phi_2 < \theta_{11} \Phi_1$, (ii) $S_2^* < \theta_{12} \Phi_1 \Leftrightarrow \theta_{22} \Phi_2 < \theta_{12} \Phi_1$, and (iii) $x_{21}^* + x_{22}^* \equiv \frac{\theta_{21}}{\theta_{21} \Phi_2} + \frac{\theta_{22}}{\theta_{22} \Phi_2} < 1$. 

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Proof of Theorem 4.0.8

Proof. Suppose that $\frac{\theta_{11}}{\theta_{12}} = \frac{\theta_{21}}{\theta_{22}}$. We seek solutions to (4.12) of the form $0 < x^*_i < 1$, $i, j = 1, 2$. From (??), the nullclines of system satisfy:

\begin{align*}
\dot{x}_{11} &= 0 \implies Y_1 = (1 - x^*_{11})S_1\theta_{12} - \theta_{11}x^*_1S_2 - (1 - x^*_{11} - x^*_{12})\Phi_1\theta_{11}\theta_{12} = 0 \\
\dot{x}_{12} &= 0 \implies Y_2 = (1 - x^*_{12})S_2\theta_{11} - \theta_{12}x^*_1S_1 - (1 - x^*_{11} - x^*_{21})\Phi_1\theta_{11}\theta_{12} = 0
\end{align*}

and

\begin{align*}
\dot{x}_{21} &= 0 \implies Y_3 = (1 - x^*_{21})S_1\theta_{22} - \theta_{21}x^*_2S_2 - (1 - x^*_{21} - x^*_{22})\Phi_2\theta_{21}\theta_{22} = 0 \\
\dot{x}_{22} &= 0 \implies Y_4 = (1 - x^*_{22})S_2\theta_{21} - \theta_{22}x^*_2S_1 - (1 - x^*_{21} - x^*_{22})\Phi_2\theta_{21}\theta_{22} = 0.
\end{align*}

(4.38)

An interior equilibrium point $(x^*_{11}, x^*_{12}, x^*_{21}, x^*_{22}, S^*_1, S^*_2)$ of (4.12) with $x^*_{11} + x^*_{12} \leq 1$ and $x^*_{21} + x^*_{22} \leq 1$ must necessarily satisfy:

\begin{align*}
Y_1 - Y_2 &= S^*_2\theta_{11} - S^*_1\theta_{12} = 0 \iff \frac{S^*_1}{S^*_2} = \frac{\theta_{11}}{\theta_{12}} \\
Y_3 - Y_4 &= S^*_1\theta_{21} - S^*_2\theta_{22} = 0 \iff \frac{S^*_1}{S^*_2} = \frac{\theta_{21}}{\theta_{22}}
\end{align*}

(4.39)

where $S^*_1(x^*_{11}, x^*_{21}) = \frac{\delta_1}{(\alpha_{11}x^*_{11} + \alpha_{21}x^*_{21})}$ and $S^*_2(x^*_{12}, x^*_{22}) = \frac{\delta_2}{(\alpha_{12}x^*_{12} + \alpha_{22}x^*_{22})}$. Under the condition $\frac{\theta_{11}}{\theta_{12}} = \frac{\theta_{21}}{\theta_{22}}$, every interior candidate must necessarily satisfy $\frac{S^*_1}{S^*_2} = \frac{\theta_{11}}{\theta_{12}} \implies \frac{\delta_1}{(\alpha_{11}x^*_{11} + \alpha_{21}x^*_{21})} = \frac{\delta_2}{(\alpha_{12}x^*_{12} + \alpha_{22}x^*_{22})}$. This leads to the following equilibrium cases with $x^*_{12} = \rho \in (0, 1)$.

1. First, suppose that $x^*_{11} = 1 - x^*_{12} = 1 - \rho$. Under this condition, $Y_1 = Y_2 \equiv 0$.

Moreover, if we also assume that $x^*_{22} = 1 - x^*_{21} \implies Y_3 = Y_4 \equiv 0$, then solving $\frac{S^*_1}{S^*_2} = \frac{\theta_{11}}{\theta_{12}}$ yields a unique solution $x^*_{21} = \frac{\delta_1\theta_{12}(\alpha_{11}\rho + \alpha_{22}) - \alpha_{11}\delta_2\theta_{11}(1 - \rho)}{\alpha_{21}\delta_2\theta_{11} + \alpha_{22}\delta_1\theta_{12}}$. 

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2. Again, suppose that \( x_{11}^* = 1 - \rho \implies Y_1 = Y_2 \equiv 0 \). If we instead assume \( x_{22}^* \neq 1 - x_{21}^* \), then solving \( \frac{S_1^*}{S_2^*} = \frac{\theta_{11}}{\theta_{12}} \) along with equations (??) yields a unique solution: \( x_{21}^* = \frac{\delta_1}{\alpha_{21} \theta_{11} \Psi_2} - \frac{\alpha_{11}}{\alpha_{21}} (1 - \rho) \) and \( x_{22}^* = \frac{\delta_2}{\alpha_{22} \theta_{12} \Psi_2} \frac{\alpha_{12}}{\alpha_{22}} \rho \).

3. Finally, suppose that \( x_{11}^* \neq 1 - x_{12}^* \). If we assume that \( x_{22}^* = 1 - x_{21}^* \implies Y_3 = Y_4 \equiv 0 \), then solving \( \frac{S_1^*}{S_2^*} = \frac{\theta_{11}}{\theta_{12}} \) along with equations (4.37) yields a unique solution: \( x_{21}^* = 1 - \frac{\delta_2}{\alpha_{22} \theta_{12} \Psi_1} + \frac{\alpha_{11}}{\alpha_{22}} \rho \) and \( x_{11}^* = \frac{\delta_1}{\alpha_{11} \theta_{11} \Psi_1} - \frac{\alpha_{11}}{\alpha_{21}} x_{21}^* \).
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