Comparison of Metastability Frameworks in a Simplified Model of *C. Elegans* Locomotion

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Abstract

Organisms must navigate a trade-off between robustness and flexibility as they enact adaptive behaviors. Behaviors must be stable enough for repetition yet flexible enough for reuse in varying contexts. One way organisms manage this trade-off is by employing a repertoire of metastable behavioral states. Recently, the types of mechanisms that can give rise metastability have received significant attention. As an example, we consider metastability in two different neural models of forward-reversal behavioral transition in *C. elegans*. We first show how fundamentally different mechanisms can give rise to the same phenomenology under noisy conditions. We then analyze the deterministic aspects of these mechanisms to expand on their differences clarifying the theoretical relationship between them. Our work contributes toward a theoretical understanding of metastability in adaptive systems.

Keywords: metastability, c. elegans, dynamics, heteroclinic networks, ghost networks, theoretical neuroethology

1 Introduction

Organisms must perform adaptive behaviors to maintain conditions conducive to their survival in constantly changing environments (cite). These behaviors emerge from the interaction of heterogeneous systems operating across multiple spatial and temporal scales (cite), often exhibiting complex nonlinear dynamics characterized by long-lived transients (cite). Yet behavior remains remarkably structured, with organisms relying on repertoires of behaviors that are repeated across different contexts (cite). Such behaviors need to be temporary yet stable under various conditions - a phenomenon called metastability (cite).

Metastability has been studied across disciplines including neuroscience, biophysics, and robotics (cite). Recent work in neuroscience has highlighted how different mathematical frameworks capture unique aspects of metastable dynamics. From a topological perspective, metastable states emerge through two fundamental mechanisms: generalized heteroclinic channels or ghost states (cite). Heteroclinic networks achieve metastability through carefully aligned saddle structures, while ghost networks rely on dynamical features near bifurcation points where attractors have recently disappeared (cite). These mechanisms differ in their structural requirements and analytical tractability, yet both can produce similar behavioral phenomenology. Distinguishing between them is crucial for rigorously defining notions of behavioral state.

We examine these mechanisms in the foraging behavior of *Caenorhabditis. elegans* behavior, where transitions between forward and reversal locomotion provide a clear case study for metastability. *C. elegans* exhibits stereotyped movement patterns that correspond to both neural activity states and bodily poses, where transitions between states occur quickly relative to time spent within states. We use this system as a case study for clarifying two different topological interpretations of metastable states.

Using generalized Lotka-Volterra (GLV) equations and continuous-time recurrent neural networks (CTRNNs), we construct two distinct metastable models: one employing heteroclinic networks and the other ghost networks. We first demonstrate that both models reproduce key features of the worm's behavioral statistics despite their different underlying mechanisms. Through bifurcation analysis and phase space topology, we then clarify how these mechanisms differ in their deterministic structure and implications for adaptive behavior. Our work provides a concrete comparison of how heteroclinic and ghost networks can implement similar functional outcomes through different dynamical mechanisms.

2 Related Work

Metastability has been fundamental to work in biochemistry (cite), motivating the adoption of topological dynamics to study metastable systems. Similarly, ecology has heavily utilized metastability, producing several excellent reviews of the underlying mathematics (cite).

The concept of metastability has since been adopted in psychology and neuroscience (cite). Kelso and colleagues have been key proponents of the concept (cite),

particularly in distinguishing metastability from multistability (cite). Heteroclinic networks, in particular, have been widely used to model metastability. Rabinovich and colleagues proposed the Winnerless Competition Principle (cite), demonstrating how ecological competition models can help explain and, in some cases, predict metastability in neural systems (cite). Morrison and Young (cite) further advanced this approach by using chaotic heteroclinic networks to model behavioral transitions in *C. elegans*.

Other approaches to modeling metastability have also gained traction. A significant body of work has explored metastability through chaotic itineracy (cite), driven dynamics (cite), and hybrid discrete/continuous systems (cite). Recently, a growing number of studies have investigated ghost attractors as a framework for metastability (cite).

Directly inspiring this work, metastability has found significant applications in *C. elegans* research. Kato et al. (2015) used whole-brain imaging to analyze neural dynamics during constrained and freely moving behaviors. They found that the pirouette foraging strategy is organized by a neural manifold, with distinct regions of the collective neural phase space corresponding to specific behavioral motifs. Similarly, Stephens et al. (cite) identified the same motifs from the perspective of dissipative systems (cite).

We construct the models in this paper using techniques developed by Postlethwaite and Ashwin. Their methods generate systems of ODEs with metastable networks matching the topology of a given adjacency matrix. By applying their framework for designing excitable and heteroclinic networks, we demonstrate its potential for advancing the study of metastable dynamics in adaptive behavior. Parameterization for such networks has been explore in (cite). These parameterizations are crucial for applying these mathematical techniques to recorded neural data.

Finally, we build on the work of Roberts et al. (cite), who constructed a Markov model of transitions between forward and reversal movements in *C. elegans* foraging. Their model offers a mesoscale approach, abstracting beyond individual neurons while still explaining experimental data. Our models are based on the topology of this Markov model.

3 Methods

Our goal was to extend the model developed in \cite{...} by replacing the Markov states with a coupled system of ordinary differential equations. We used different neural mass equations as building blocks, starting with a Generalized Lotka-Volterra (GLV) model. GLV models are commonly used to model the collective behavior of neurons during tasks requiring sequential activation \cite{...} and exhibit Winnerless Competition, a proposed mechanism underlying brain dynamics \cite{...}. The second model we used was a CTRNN (equivalent to a Wilson-Cowan model), which are universal dynamics approximators \cite{...} and have been previously applied to *C. elegans* neural dynamics \cite{...}.

We focused on modeling the neural dynamics of *C. elegans* during forward-reversal behavioral transitions. Following \cite{...}, we assumed each behavioral state

corresponds to a single neural mass, with peak activation marking the behavior's occurrence. This simplifies the dynamics by treating each state as a one-dimensional system in time. While our methods can be extended to systems with Lyapunov-stable solutions (cite), some analytic techniques may not apply in those cases (cite). We based our work on Roberts et al. \cite{...}, who developed a stochastic discrete neural mass model of *C. elegans* foraging. Their model involves two neural clusters: one (AVBL, AVBR, PVCL, PVCR) correlated with forward movement and another (AVAL, AVAR, AVDL, AVDR, AVEL, AVER) linked to reversals. Their model includes three behavioral states (forward, pause, reversal) but four neural states, accounting for pauses occurring when both clusters are active or inactive.

We created a continuous extension of this model by replacing the discrete system with a system on $\mathbf{R}^4$, where each dimension corresponds to a behavioral state: forward (f), pause- both cluster inactive (p_l), reverse (r), and pause- both clusters active (p_h). We used this 4-dimensional model to match the experimental data in (cite) as described in the (ref secction). However, for pedagogical clarity and ease of visualization, for the second and third sections of the results we use a 3-dimensional version of the model which corresponds to modeling the behavioral states rather than neural activity since in the 3-dimensional case we consider only a singular pause state.

For the GLV model, we used equations of the form:

$$\frac{dx_i}{dt} = x_i(1 - \sum_{j=1}^{n} \rho_{i,j} x_j^2) + Y \tag{1}$$

where and

$$x_i \in \{f, p_h, r, p_l\} \tag{2}$$

$$\rho_{i,j} = \begin{cases} \mu_i, & i = j \\ \alpha_i, & i = j - 1 \\ \beta, & \text{otherwise} \end{cases} \tag{3}$$

with noise $Y \sim \mathcal{N}(\mu, \sigma^2)$ with $\sigma = 1e - 4$ unless otherwise noted. Parameters α and β were chosen using methods from \cite{...} . The CTRNN model:

$$\frac{dx_i}{dt} = x_i(1 - \sum_{j=1}^{n} w_{i,j} f(x_j)) + Y \tag{4}$$

Where Y is the same as in the GLV case and

$$f(x) = \frac{1}{1 - e^{-x}} \tag{5}$$

$$w_{i,j} = \begin{cases} w_s, & i = j \\ w_p, & i = j - 1 \\ w_n, & \text{otherwise} \end{cases} \tag{6}$$

4

The values of the various w parameters were chosen based on the bifurcation diagram (ref) and insights from (cite). We explore these choices in more detail on the section on bifurcations (ref).

4 Results

For this work, we were interested in the implications of replacing a Markov model of behavioral states with a continuous ODE system. Biological systems are a subset of physical systems, and as such, while they can be modeled using computational techniques such as discrete-time Markov chains, they also emerge from many-body interactions governed by dynamic physical laws. ODEs provide a more natural framework for describing these temporal characteristics. Beyond this, ODE models offer several advantages over Markov chains; we direct the reader to (cite) for additional considerations.

### 4.0.1 Matching Empirical Data with Two Different Dynamic Models

We began by constructing two metastable models of the forward-reverse transition, as described in (cite). These models were numerically integrated using the Julia DifferentialEquations package (cite) , with simulations performed using the TSIT algorithm (cite) and adaptive step sizing. This approach successfully reproduced key features of the original stochastic model, including state sequencing, average dwell times, and high-velocity transitions.

Using the methods outlined in the Methods section, we found that both the GLV and CTRNN-based models could replicate the observed patterns in the data. To assess their performance, we plotted the mean dwell times alongside empirically observed values (ref). These empirical dwell times, originally measured in (cite), served as the basis for the stochastic model we extend in this work. The results demonstrate that both metastable models can closely match these observables.

We also examined typical noisy trajectories for the GLV and CTRNN models (ref). While both exhibited similar stochastic dynamics, their waveforms and amplitude ranges differed slightly. To further investigate these dynamics, we simulated the systems with a significantly smaller noise term, XX (ref). The deterministic behavior revealed a key distinction: the GLV model produced oscillations with increasing period, whereas the CTRNN model exhibited more classical oscillations with a fixed period. In the following sections, we will explore the differences between these behaviors and demonstrate how bifurcation theory can provide a unified understanding of the two models.

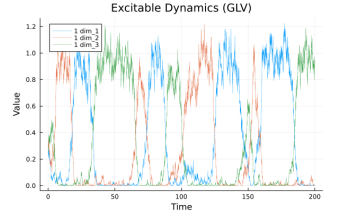## 4.1 Distinguishing the Mechanisms Underlying Metastability

In the case of *C. Elegans* locomotion, behavioral states are not directly observable. Instead, they must be inferred from the dynamics of the system. This has been achieved in real data by using a combination of video and neural recordings (cite). Several different techniques have been used to identify behavioral states within the recorded
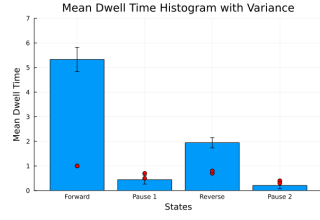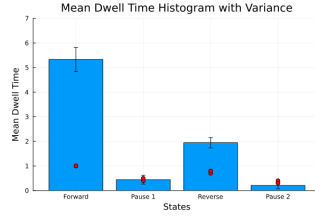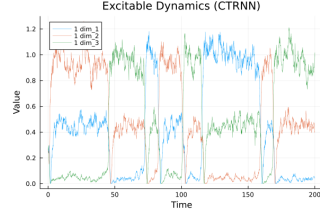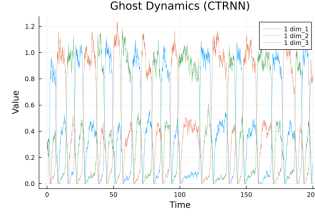
(a) GLV Excitable Time Series (b) GLV Excitable Time Series (c) GLV Excitable Time Series (d) C


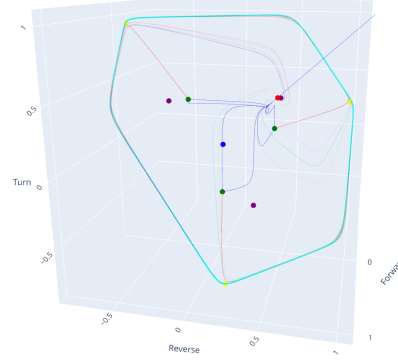(e) CTRNN Excitable Time Series (f) CTRNN Ghost Time Series

Fig. 1: (a) The dynamics of noisy GLV equations in the excitable regime. (b) The dynamics of noisy GLV equations in the heteroclinic regime. (c) The dynamics of noisy CTRNN equations in the excitable regime. (d) The dynamics of the noisy CTRNN equations in the ghost regime.

data. In fact, it has been shown that clustering (cite), slow region analysis (cite), and eigenmode decomposition (cite) can all be used to identify approximately the same behavioral states from data collected in experimental conditions. This suggests that such behavioral states are not artifacts of a specific analysis but rather a fundamental feature of the adaptive behavior of the worm. Theoretical investigation of different models may be able to elucidate what the physical bases of these observations are and explain why very different analyses can result in the identification of the same fundamental behavioral states.

Once behavioral states have been identified experimentally, they can be used to define a discrete state model which can then explain phenomena at longer timescales as in (cite). However, this approach cannot explain the emergence of these states themselves. To describe how behavioral states emerge in the real-time dynamics of the nematode, we must define them in terms of emergent features of the dynamics. Dynamic systems theory provides various mathematical constructs which can explain how a high-dimensional system can give rise to low-dimensional regions of state-space. An important limitation is that in all models we have chosen, the behavioral states correspond to single points of the phase space, which is a simplification that is not always valid. In real \textit{C. elegans}, the states are regions of the phase space with their own dynamical structure. The models can, in principle, be extended to include more complex "attractors" for the nodes of the network, which we suggest is a fruitful area for future research.

6
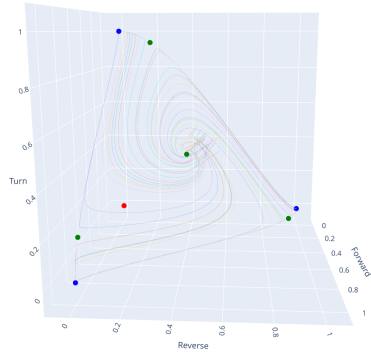
(a) GLV Phase Portrait   (b) CTRNN Phase Portrait

Fig. 2: (a)The Parameter chart of the GLV equations replicated from (cite).(b). The diagrammatic images represent the different classes of dynamics that exhibit switching dynamics (multistability: red, heteroclinic cycle: green, limit cycle: blue

Adaptive behavior is dynamically interesting not only because it exhibits metastable states but also because of the structured way in which adaptive systems quickly move between these states with incredible regularity. Explaining such behavioral transitions is not trivial, as it requires precise experimental measurements and is difficult to predict in models unless they contain explicit time-scale terms as in fast-slow systems (cite). For example, while most experimental work in \textit{C. elegans} behavior has emphasized dwell times and frequencies of various states (cite), few have examined how the transition process between these states is structured. Similarly, only a few models have actively explored state transitions (cite), as most assume discrete states to begin with (cite).

We examine the fundamental ways metastable systems can exhibit state transitions, quantifying this difference by explicitly associating transitions with different objects in the phase space. Although the models we present are simple, they span the space of possible topological requirements for the emergence of metastable behavior (cite). Here, we consider these phenomena in our simplified models of the forward-reversal transition, specifically examining how the structure of transitions differs between the classes of behavioral states we described previously.

4.1.1 Heteroclinic Channels in GLV

The assumption that behavioral states correspond to attractors is quite strong. In a generic system, most invariant solutions are more likely to be saddles rather than attractors (cite). Additionally, the attractor-based conception presupposes that the only reason state transitions occur is due to external perturbations. Several authors have argued that this is not a useful assumption for biological systems, since spontaneous transitions are common and noise is an intrinsic property of these systems rather than purely an external phenomenon (cite).

7

One alternative is to assume that behavioral states are partially stable—stable in some directions but unstable in others. This corresponds to saddle invariants in state space. We were interested in demonstrating this possibility in our models. As we will discuss in the section on model parameterization, while both models can exhibit behavioral states as saddle nodes, it is only in the GLV system that this phenomenon is observable.

We started by parameterizing the GLV system in the region of state space that exhibits saddle points (ref). Similar to our previous analysis, we solved the system numerically to find equilibria and linearized around them to determine stability. We found (cite) number of fixed-point solutions, with no attractors—despite the system exhibiting clear metastability in its time dynamics (ref). Instead, we identified saddle and unstable fixed points. However, not all saddles correspond to metastable states. To distinguish between them, we used the saddle value proposed by (cite), defined for saddle points as:

$$S_p = \frac{\mathrm{Re}(\lambda_s)}{\mathrm{Re}(\lambda_u)} \tag{7}$$

Metastable states are characterized by S_p, indicating dissipative saddles where trajectories approach over time. Coloring nodes by stability (and saddle value for saddles), we observed the state space structure in (fig). Four dissipative saddles emerged, with one acting as a strong entry point compressing trajectories onto the metastable subspace—a feature common in heteroclinic networks with multiple cycles (cite).

Heteroclinic networks enable state transitions without external perturbations, distinguishing them from excitable networks. Their defining feature is the alignment of stable and unstable manifolds between nodes: the unstable manifold of one node aligns with the stable manifold of another, creating cyclical dynamics. This "winnerless competition" (cite) arises from local excitation and long-range inhibition, where neural regions temporarily dominate one another.

To identify the heteroclinic network, we first computed the stable and unstable manifolds of equilibria via the Jacobian's eigenvalues. The stable manifold consists of points attracted to the equilibrium, while the unstable manifold consists of points repelled from it. Though exact manifolds are analytically intractable, we approximated them numerically. For the unstable manifold, we perturbed the state slightly from equilibrium and integrated forward in time—similar to separatrix identification. Integrating a trajectory offset along the eigenvector from a saddle yielded a heteroclinic channel between saddles, approximating our time-series dynamics. By examining network connectivity, we distinguished metastable saddles and plotted the heteroclinic network in figure (fig).

4.1.2 Haunted Invariants in CTRNNs

Unlike the heteroclinic and saddle cases, the metastable states in the CTRNN dynamics cannot be explained through standard invariant analysis. When behavioral states correspond to explicit invariants (e.g., fixed points or limit cycles), numerical solving

and continuation methods can directly identify and characterize them. However, for the CTRNN's metastable dynamics, this approach fails.

Performing standard fixed-point analysis reveals 8 equilibria, none of which align with the system's observed slow states (figure). This implies the metastable behavior arises from *ghost states*—structures absent from the real-plane vector field but inferred through dynamics. Recent advances now allow explicit design of ODEs with ghost states of desired topology (cite), but their analysis requires advanced techniques.

Without explicit singularities, ghost states must be identified indirectly via analytic continuation into the complex plane (cite). Here, we extended fixed-point identification by using complex initial conditions and analytically continuing the equations to operate in complex space. This approach works for point-like ghost states but becomes intractable for geometrically complex invariants (e.g., ghost limit cycles or tori). Stability analysis of such structures remains an open problem in criticality research (cite). Plotting both real fixed points and identified ghost states (figure), we see that while metastable states don't coincide with equilibria, the latter still shape the dynamics.

In heteroclinic and excitable networks, transitions rely on known invariants (e.g., saddle manifolds or separatrices). Ghost networks, however, lack exact states, requiring careful empirical study. To probe transitions, we first traced trajectories near approximate metastable states until they reached subsequent states. These trajectories clustered but didn't converge, suggesting an underlying cyclic mechanism.

Guided by CTRNN theory, we hypothesized a Hopf bifurcation-generated limit cycle drives transitions. Continuation analysis (via Julia BifurcationKit (cite)) confirmed this: the limit cycle mediates ghost-state transitions, and its disappearance via a SNIC bifurcation marks the shift from metastable to excitable dynamics (figure). This contrasts sharply with heteroclinic networks, where transitions arise from interlocking saddle manifolds. In ghost networks, linearization may fail to distinguish stable/unstable manifolds (cite), and metastability emerges from *haunted invariants*—structures (like limit cycles) perturbed by ghost states, rather than direct competition between states.

We plotted the limit cycle found through continuation along with the various equillibrium points found from the phase space analysis. We also plotted the real component of the two fixed point solutions that emerged in the complex. It should be clear that they lie along the limit cycle which is how long-lived states emerge on the cycle.

Quantifying haunted invariants remains challenging. Both ghost-state identification and the catalog of invariants they can haunt are open questions. Unlike winnerless competition, ghost-state transitions need not involve dominance by another state; a ghost may vanish independently, leaving no trace in the real-plane dynamics.

4.2 Different Models Exhibit Different Kinds of Metastability

Though heteroclinic and ghost cycles differ topologically—heteroclinic cycles rely on saddle connections, while ghost cycles emerge from destabilized limit cycles—bifurcation analysis reveals their shared origin in the collapse of multistability. Static phase portraits emphasize their distinct invariant sets, but parameter continuation exposes a deeper continuity: both regimes arise via codimension-one bifurcations

that destabilize attractors, redirecting trajectories along metastable pathways. In the CTRNN, saddle-node bifurcations collapse multistable attractors, forming a heteroclinic cycle through the collision of stable and unstable manifolds. In the GLV system, a Hopf bifurcation annihilates a stable limit cycle, leaving a ghost cycle as a transient manifold. Though their invariant structures differ, both transitions are governed by the same bifurcation sequence, with the heteroclinic and ghost phases occupying adjacent regions in parameter space.

This shared bifurcation structure clarifies why both systems exhibit a conserved ordering: the heteroclinic phase lies between multistable and ghost phases, regardless of the measure of the parameter regions they occupy. Numerical continuation shows that these phases are not isolated but linked by higher codimension bifurcations. For example, perturbing parameters near the heteroclinic cycle in the CTRNN destabilizes saddle connections, transitioning the system to a ghost-like regime with noise-sensitive transients . Similarly, in the GLV system, reversing the Hopf bifurcation restores the limit cycle, effectively "reanimating" the ghost cycle into a stable attractor, as was previously observed in (cite). These transitions demonstrate that heteroclinic and ghost cycles are dual outcomes of attractor destabilization, differentiated only by the stability of their underlying invariant sets.

By mapping bifurcation boundaries, we resolve a key paradox: despite differing topologies, both cycles mediate transitions between multistable and monostable regimes. Their structural divergence arises from how invariant manifolds reorganize during bifurcations—heteroclinic cycles preserve saddle connections, while ghost cycles inherit the geometry of a vanished limit cycle. However, bifurcation theory unifies them as complementary mechanisms for metastability, governed by the same parameter-dependent instabilities. This framework explains why both systems exhibit analogous transient dynamics despite distinct phase space architectures. Static analyses fail to capture this relationship, underscoring the necessity of bifurcation-driven parameter exploration to clarify the structural relationships underlying metastable systems.

4.2.1 Bifurcations of the GLV System

Bifurcations of the 3D GLV system have been analyzed previously in (cite). To replicate and extend these analyses, we performed numerical continuation studies using BifurcationKit.jl in Julia (cite), focusing on parameter ranges relevant to the network dynamics (0,3). Our results revealed three key bifurcation curves: (1) a diagonal Hopf bifurcation curve along the $\alpha = -\beta$ line, identified by tracking the central attractor; (2) two fold bifurcation curves at $\alpha = 1$ and $\beta = 1$, located by following attractors at their corresponding states; and (3) a degenerate Bogdanov-Takens bifurcation at the intersection of these curves.

These bifurcations partition the α, β parameter space into three distinct stability regimes (Fig. \ref{fig:bc}):

1. **Central Fixed Point Dominance**: For $\alpha < 1$ and $\beta < 1$, the system exhibits a single stable fixed point at the coexistence equilibrium. This regime corresponds to the region bounded below both fold curves, where mutual inhibition remains subcritical.

2. **Multistability**: Crossing either fold bifurcation curve ($\alpha > 1$ or $\beta > 1$) introduces bistability between dominance states. Here, the predecessor and successor populations act as mutual "switches," with hysteresis governed by the fold bifurcations.

3. **Heteroclinic Dynamics**: Near the Bogdanov-Takens point at $(\alpha, \beta) = (1, 1)$, the interplay of Hopf and fold bifurcations creates two regions supporting heteroclinic orbits. These manifest as slow switching dynamics between states when parameters approach the Hopf line from either side.

The degenerate Bogdanov-Takens bifurcation acts as an organizing center, mediating transitions between these regimes. Metastability emerges along the Hopf curve, where damped oscillations about the central fixed point coexist with slow transitions between saddle states. This structure aligns with earlier findings while clarifying how codimension-2 bifurcations shape the global stability landscape.

4.2.2 Bifurcations of the CTRNN System

The Neural Model we present here uses the commonly used neural mass node, the CTRNN (or equivalently the Wilson-Cowan model). This model reveals several important details for computational models of metastability. The first is the importance of numerical algorithms for the prediction of biological measurements. The second is that even outside of the measured parameter range, a parametric investigation of models can reveal new insights. And finally a way in which dynamical structure may be relate to network structure.

The behavioral states in the neural model are not invariant solutions as in the previous two models. Instead, we will show that the states are "ghost attractors." Although ghost attractors have been known as a possible mechanism for metastability, it has only recently been shown that they can form ghost networks which are analogous but different than heteroclinic networks.

Ghost networks can occur in purely deterministic systems similar to heteroclinic networks. However, unlike heteroclinic networks which are usually only robust under certain symmetries, ghost networks can be constructed in a wide range of systems. This makes them a useful tool for modeling metastability. They can be more easily observed than heteroclinic networks in a wider range of systems and are often more robust to perturbations. However, they are also more difficult to analyze because they are not as easily reduced to a simple set of solutions of the underlying equations.

While both the stable states of excitable networks and the saddle states of heteroclinic networks can be thought of as attractors, the structure of ghost networks is more complex. Ghost networks require non-stationary dynamics to maintain their structure. This means that they are harder to identify without a detailed analysis of the underlying dynamics. Additionally, ghost networks depend on the presence of ghost attractors, which are by definition not explicitly observable.

As we will discuss, this does not mean ghost networks cannot be analyzed. In fact, they can be analyzed using the same techniques as heteroclinic networks. However, the analysis is more nuanced and requires a detailed understanding of the underlying dynamics along with some additional assumptions about the structure of the system.
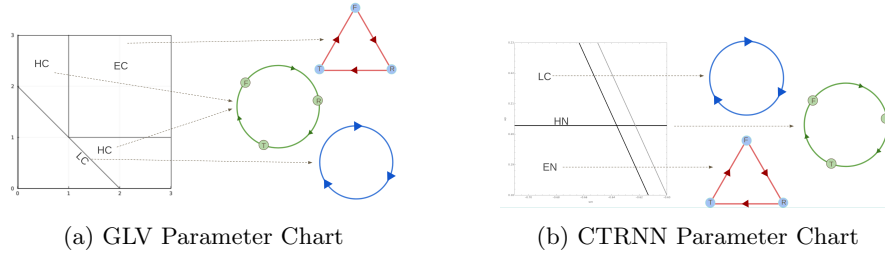
(a) GLV Parameter Chart   (b) CTRNN Parameter Chart

Fig. 3: (a)The Parameter chart of the GLV equations replicated from (cite).(b). The diagrammatic images represent the different classes of dynamics that exhibit switching dynamics (multistability: red, heteroclinic cycle: green, limit cycle: blue

The ghost network we consider was previously used to model the structure of *C. elegans* locomotion in [**?**]. It was constructed using the technique introduced in []. CTRNNs have been previously used to model the brain of *C. elegans* in previous work, however, our model abstracts away from specific neural topology for a phenomenological approach.

In the following section, we consider these models in three different contexts. Specifically, we first look at the ability of the models to match experimentally observed data as in the model by Roberts et al. (cite). Having demonstrated that these dynamical models are as expressive as the Markovian formalism, we take a theoretical approach and study these models in terms of state identification and transition structure. Our results show how metastability differs from multistability and how the two fundamental types of metastability differ from each other.

5 Discussion

5.1 Limitations

In this work, we limit our consideration to models of metastability where the metastable states are conceived of as points. This is an unrealistic assumption since behavioral states are not points in states space but rather complex dynamical structures. However, this choice allows us to significantly reduce the range of dynamical mechanisms that give rise to metastable dynamics.

However, not all forms of metastability are possible with this assumption. Some forms of metastability, those associated with chaotic itineracy, require significantly more complex attractor structures to emerge.

We justify this assumption in our preliminary work with two primary reasons. Firstly, in the models we have used so far the individual attractor states that represent the behaviors may be substituted with more complex attractors as in (cite). Secondly, work in topological dynamics shows that although state transitions may be caused by a range of structures the basic building blocks for such transitions are due to proximity to a bifurcation or the formation of hetero-clinic like structural symmetries (cite). This

means that although our analysis is far from exhaustive, the insights gleamed from it will have implications for most dynamical systems with a metastable structure.

5.2 Future Work

To address the afformentioned limitations future would could consider the role of more complex attractors. This would be particularly useful for embodied models where non-stationary states are the norm. Such work could look at the effects of introducing toroidal or chaotic attractors, the theory of which has already been studied in other contexts (cite).

Additionally, the methods and techniques used in this work could be applied to organisms other than *C. elegans* since it is known that behavioral state transitions are a common phenomena at organisms across many scales (cite). In particular, it could be useful to further disentangle the differences between these dynamical concepts in the context of organisms like E. Coli in which experimental control is sufficiently available for numerical considerations.

5.3 Conclusion

In this work, we analyzed questions about adaptive behavior in the context of 4 different dynamical models of varying complexity. We saw that some phenomena such as behavioral transtion and even decision-making can appear in these different models. We also observed how the different dynamical structures of the models give rise to different specific mechanism in how adaptive behavior can be analyzed or studied.

We also showed how the same phenomenological dynamics may become more complicated. In all cases, although the models produced metastability the means of analysis became more complex, requiring more assumptions and deeper numerical techniques. In particular, we saw how phenomena like criticality can smooth across multiple different mechanisms to give rise to more complex dynamics. However, this complexity could be unraveled with the tools and techniques we developed by studying simpler models.

We conclude that significantly more research needs to be done in the gap between low dimensional toy models (cite) and high dimensional experimentally motivated models. While toy models can give deep theoretical insights and experimental models can produce quantitative results, it is the gap between these models in which we can explicitly develop the tools and techniques to relates theoretical principles to quantitative outcomes. This work serves as a step towards this greater goal.