Using Dynamical Systems to make Micro- and Macroscopic Predictions in

Marine Biology

by

Joseph A. Landsittel

Submitted to the Graduate Faculty of

the University Honors College in partial fulfillment

of the requirements for the degree of

Bachelor's of Philosophy

University of Pittsburgh

UNIVERSITY OF PITTSBURGH DEPARTMENT OF MATHEMATICS

This thesis was presented

by

Joseph A. Landsittel

It was defended on

April 18th, 2022

and approved by

G. Bard Ermentrout, University of Pittsburgh Department of Mathematics

Klaus M. Stiefel, Silliman University Institute of Environmental and Marine Sciences

Jonathon E. Rubin, University of Pittsburgh Department of Mathematics

Andrew Mugler, University of Pittsburgh Department of Physics and Astronomy

Copyright © by Joseph A. Landsittel

Using Dynamical Systems to make Micro- and Macroscopic Predictions in Marine Biology

Joseph A. Landsittel, B.Phil

University of Pittsburgh,

Dynamical systems have successfully been shown to illustrate how components of a biological machine evolve together; this paper explores two examples of such. In one case, we investigate the stereotyped escape reflex of the marine goby. This governing neural circuit of this goby's escape has been observed to exhibit distinct behaviors depending on the threat level of predatory fish. We propose two ODE models to explore the feasibility of distinct biological possibilities regarding the circuit at play. In a second case, we investigate the mating strategies of wrasses and cephalopods. We simulate the life histories of the fishes with a piece-wise, discrete time dynamical system. Our results provide a framework for understanding the dependence between the evolutionary stability of various mating strategies with ecological factors and behavioral patterns being exhibited.

Table of Contents

Preface					
1.0	Th	e Shrimp-goby Escape Communication System	1		
	1.1	Introduction	1		
	1.2	Model 1: M-Cell Oscillations	2		
		1.2.1 Overview	2		
		1.2.2 Analysis	4		
		1.2.3 Results	8		
	1.3	Model 2: CPG Oscillations	9		
		1.3.1 Overview	9		
		1.3.2 Results	1		
	1.4	Conclusions	4		
2.0	Alt	cernative Mating Strategies in Cephalopods and Fishes 1	5		
	2.1	Introduction	5		
	2.2	Approach	6		
	2.3	Basal Wrasse Model	8		
		2.3.1 Overview	8		
		2.3.2 Results	0		
	2.4	Cephalopod Model	1		
		2.4.1 Overview	1		
		2.4.2 Results	3		
	2.5	Cichlids	4		
		2.5.1 Overview	4		
		2.5.2 Results	27		
	2.6	Stochastic Considerations	7		
		2.6.1 Overview	7		
		2.6.2 Results	9		

2.7 Conclusions	30
Appendix A. List of Equations for 1.3	32
Appendix B. Parameter Exposé for 2.0	37
Bibliography	40

List of Tables

- 1 Startle response of Zebrafish as sensory stimulus is increased. M-cells, fast motor neurons, central pattern genrating neurons, and slow motor neurons are considered. 12
- 2 Startle response of Gobies as sensory stimulus is increased. M-cells, fast motor neurons, central pattern genrating neurons, and slow motor neurons are considered. 13

List of Figures

1	The goby Amblyeleotris Rubrimarginatus stands by as the shrimp clears sand	
	from the burrow. Photography courtesy of Klaus M. Stiefel	2
2	Neural circuit reproduced by Model 1	3
3	Behavior of the simple model in three parameter regimes. Stimulus is applied at	
	$t = 25ms$, removed at $t = 225ms$. The parameter I_{max} is increased from 0.1 (a)	
	to 1.8 (b) to 3.5 (c)	6
4	Bifurcation diagram of Model 1 with respect to input strength (I_{max}) . Here	
	there is no asymmetry in the input received by the M-cells. That is, $q = 1$.	
	Red corresponds to a stable fixed point, black unstable. Green corresponds to a	
	stable limit cycle, blue unstable.	6
5	Bifurcation diagram of Model 1 with respect to input strength (I_{max}) . Here there	
	is asymmetry in the input received by the M-cells. That is, $q = 0.99.$	7
6	Two parameter bifurcation diagram following the location of the Hopf point	
	(dark blue) and the pitchfork bifurcation (light blue). Input strength (I_{max}) and	
	asymmetry (q) are varied. Notably this plot looks like a fish	7
7	Neural circuit reproduced by Model 2 [14]. Zebrafish and Goby variations are	
	included. The zebrafish model is put forth by Miller et. al. 2017 [18]. Both	
	M-cells may recieve stimulus, thought not necessarily equal doses	10
8	The Indo-pacific wrasse <i>Thalassoma lutescens</i> . Photography courtesy of Klaus	
	M. Stiefel	18
9	Wrasse transition diagrams for the mating season (blue) and growth season (red).	
	An arrow from one state to another indicates that such a transition has a nonzero	
	probability of occurring	19

10	Stability of the sneaker and dominant mating strategies among wrasses as we	
	iterate across values of food availability and predation. Isoclines corresponding	
	to observations are included; we can then make predictions of where cases lie	
	relative to each other in the parameter space [36, 37, 38, 3]	21
11	Cephalopod transition diagrams for the mating season (blue) and growth season	
	(red)	22
12	Two male cuttle fish (left) engaged in a conflict over a female (right). The nesting	
	male guarding the female is visibly larger than the intruder. Read the full story	
	here: [LINK]. Photography courtesy of Klaus M. Stiefel.	23
13	Stability of the sneaker and dominant mating strategies among cephalopods as we	
	iterate across values of food availability and predation. Isoclines corresponding	
	to observations are included; we can then make predictions of where cases lie	
	relative to each other in the parameter space [10, 20]	24
14	Predicted sneaker proportion at ESS as a function of Food Availability and Pre-	
	dation for wrasses (a) and cephalopods (b). $\ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots$	25
15	The specific effect each individual wrasse-cephalopod distinction has on ESS,	
	across variation in predator presence. The normalized food availability is set to	
	be 40	26
16	Cichlid transition diagrams for the mating season (blue) and growth season (red).	27
17	One dimensional parameter sweeps across food availability (α) and predator pres-	
	ence (β) . Cases with and without Hamilton's rule are considered	28
18	Simulations including a stochastic variable ξ . The extent of variation is judged	
	by its variance, σ^2 . Specifically in (a) $\sigma = 0.01$, (b) $\sigma = 0.04$, (c) $\sigma = 0.08$, and	
	(d) $\sigma = 0.15$	30
19	Presence of sneakers in the high food availability regime, dominants in the low	
	food availability regime, for increased stochasticity.	31

Preface

This paper is the sum of work pursued by G. Bard Ermentrout, Klaus M. Stiefel, and myself from 2019 through 2022. Though this project was a joint effort, their expertise in the fields of mathematical modeling and marine biology was the cornerstone. I'd like to recognize their phenomenal support and mentorship throughout my undergraduate career.

The work here includes two constituents parts that illustrate connections between dynamical and biological systems. Miles from the first and certainly not the last insights to come from this field, these projects share two cases of how modeling can better inform our understanding of neuroscience and ecology. The independent nature of the results for each lead one to view this more as a collection of short stories from the same book than a unified fable.

In 2021, the work of the first chapter was published by the Journal of Computational Neuroscience [14].

1.0 The Shrimp-goby Escape Communication System

1.1 Introduction

The 'startle response' of fishes after receiving an abrupt burst of stimulus is a well studied phenomenon [7, 30]. Notably, this process is realized as a one-sided 'tail whip' resulting from reciprocal inhibition between the left and right side of the CNS. Asymmetric activation of command neurons will result in an asymmetric firing of fast motor neurons. The product is a c-shaped, sudden movement that allows fish to escape approaching predation.

This underlying neurophysiology has been investigated in the context of hindbrain Mauthner (M-) cells present in zebrafish and goldfish [5, 30, 17]. Specifically, it has been experimentally demonstrated that the M-cell action potentials in these species of fish correlate with motor patterns in the escape reflex.

An alternate form of this escape reflex has been observed in the marine goby, which lives in tandem with the alpheid shrimp through mutualist symbiosis [13, 16, 14]. This relationship exists as follows: the shrimp, whose eyesight is poor, constructs a burrow to be used as shelter by both species [12]. The goby, maintaining good eyesight but lacking a burrowing ability, acts as an alarm providing the shrimp with tactile-based communication regarding nearby predation. In a sense the goby stands watch as the crustacean regularly clears the burrow of obstructions.

The exact behavior of the goby in the communication relationship is well documented [27, 13, 14]. Three distinct patterns emerge depending on the parameter regime in effect. In the absence of predatory fish, the goby remains still while its tail is in constant contact with the shrimp. For an intermediate presence of visual or auditory predation stimulus, the goby's tail briefly oscillates in what has been described as a 'tail flick.' This is to act as a warning for the shrimp. A sufficiently strong stimulus will trigger the c-shaped escape reflex, allowing the goby to retreat into the burrow without fear of being harmed by incoming threats.

We contrived two mathematical models in an attempt to explore how the neurophysiology of the goby's escape reflex deviates from that of zebrafish and goldfish. In both cases, we modeled the M-cells as point neurons as opposed detailing dendrites as a series of attached compartments [6]. In the first case, we model the 'tail flick' as an oscillation in firing between the two M-cells. In the second case, oscillations are produced downstream by a system of central pattern generating neurons (CPG).



Figure 1: The goby *Amblyeleotris Rubrimarginatus* stands by as the shrimp clears sand from the burrow. Photography courtesy of Klaus M. Stiefel.

1.2 Model 1: M-Cell Oscillations

1.2.1 Overview

We begin with a simple firing rate model that attempts to reproduce the tail flick behavior via oscillations between M-cells. It utilizes six differential equations to convey the behavior of four neurons. Two correspond to M-cells (M_{ℓ} and M_r), two to internal M-cell inhibition



Figure 2: Neural circuit reproduced by Model 1

 $(Z_{\ell} \text{ and } Z_r)$, and two to external inhibitors $(Y_{\ell} \text{ and } Y_r)$. The difference in stimulus received is governed by an asymmetry parameter $q \in (0, 1]$.

The equations are as follows:

Mauthner Cells:

$$M'_{\ell} = -M_{\ell} + f\left(\operatorname{Input}(I_{max}, t) - gY_r - rY_{\ell} - \beta Z_{\ell}\right)$$
(1)

$$M'_{r} = -M_{r} + f\left(\operatorname{Input}(I_{max}, t)q - gY_{\ell} - rY_{r} - \beta Z_{r}\right)$$
(2)

Inhibitory Neurons:

$$Y'_{\ell} = \left(-Y_{\ell} + \max\{M_{\ell} + \zeta \operatorname{Input}(I_{max}, t), 0\}\right) / \tau_y$$
(3)

$$Y'_r = \left(-Y_r + \max\{M_r + \zeta \operatorname{Input}(I_{max}, t)q, 0\}\right) / \tau_y \tag{4}$$

Mauthner Adaptation Proces:

$$Z'_{\ell} = \left(-Z_{\ell} + M_{\ell}\right) / \tau_z \tag{5}$$

$$Z'_r = \left(-Z_r + M_\ell\right) / \tau_z \tag{6}$$

Functions:

$$f(x) = \frac{1}{1 + e^{-x}} \tag{7}$$

$$Input(x,t) = xu(t-t_{on})u(t_{on} + dur - t)$$
(8)

where

$$u(x) = \begin{cases} 0 & \text{if } x < 0 \\ 1 & \text{if } x \ge 0 \end{cases}$$

The parameter values are g = 6, $\beta = 1.5$ r = 0.3, $\tau_y = 0.2$, $\tau_z = 5$, and $\zeta = 0.01$.

1.2.2 Analysis

We can show analytically that the symmetric system (q = 1) undergoes a Hopf bifurcation for increasing input strength (I). First notice that the external inhibitors Y_{ℓ} and Y_r respond to changes in M-cells with fast time, so they can be neglected for this purpose (then set $\tau_z = \tau$). Also assume M-cells are the sole receivers of input sensory data (i.e. $\zeta = 0$). The new system is stated here.

$$M'_{\ell} = -M_{\ell} + f(I - gM_r - rM_{\ell} - \beta Z_{\ell})$$
(9)

$$M'_{r} = -M_{r} + f(I - gM_{\ell} - rM_{r} - \beta Z_{r})$$
(10)

$$Z'_{\ell} = (M_{\ell} - Z_{\ell})/\tau \tag{11}$$

$$Z'_r = (M_r - Z_r)/\tau \tag{12}$$

Observe that this system has a fixed point which solves the following transcendental equation:

$$\xi(I) = M_{\ell} = M_r = Z_{\ell} = Z_r = f(I - \gamma \xi(I)).$$
(13)

Where $\gamma = g + r + \beta$. We can then state the jacobian matrix:

$$J = \begin{bmatrix} -(1+rf'(I-\gamma\xi)) & -\beta f'(I-\gamma\xi) & -gf'(I-\gamma\xi) & 0\\ \tau^{-1} & -\tau^{-1} & 0 & 0\\ -gf'(I-\gamma\xi) & 0 & -(1+rf'(I-\gamma\xi)) & -\beta f'(I-\gamma\xi)\\ 0 & 0 & \tau^{-1} & -\tau^{-1}\\ \vdots & & \end{bmatrix}$$
(14)

Which is in the form of:

$$J = \begin{bmatrix} A & B \\ B & A \end{bmatrix}.$$

Whose eigenvalues are the eigenvalues of A + B and A - B. The eigenvalues of A + B have strictly negative real parts. A - B's eigenvalues are:

$$\operatorname{Re}\lambda = (g-r)f'(I-\gamma\xi) - \tau^{-1} - 1$$
(15)

$$\mathrm{Im}\lambda = \pm \sqrt{-\left[(g-r)f'(I-\gamma\xi) - \tau^{-1} - 1\right]^2 + 4\tau^{-1}\left[f'(I-\gamma\xi(I))(\beta-g+r) + 1\right]}.$$
 (16)

Let $\nu = (f')^{-1}((\tau^{-1}+1)/(g-r))$. The fixed point will loose stability at:

$$I = \nu + \gamma \xi(I). \tag{17}$$

For the previously stated parameter values, $\nu = 1.00$ and $\gamma = -7.80$. We then see that a pair of complex conjugate eigenvalues will cross the imaginary axis for $I \approx 1.10$, $\xi \approx 0.27$. This is the initiation of the tail flick.



Figure 3: Behavior of the simple model in three parameter regimes. Stimulus is applied at t = 25ms, removed at t = 225ms. The parameter I_{max} is increased from 0.1 (a) to 1.8 (b) to 3.5 (c).



Figure 4: Bifurcation diagram of Model 1 with respect to input strength (I_{max}) . Here there is no asymmetry in the input received by the M-cells. That is, q = 1. Red corresponds to a stable fixed point, black unstable. Green corresponds to a stable limit cycle, blue unstable.



Figure 5: Bifurcation diagram of Model 1 with respect to input strength (I_{max}) . Here there is asymmetry in the input received by the M-cells. That is, q = 0.99.



Figure 6: Two parameter bifurcation diagram following the location of the Hopf point (dark blue) and the pitchfork bifurcation (light blue). Input strength (I_{max}) and asymmetry (q) are varied. Notably this plot looks like a fish.

1.2.3 Results

This model successfully reproduces the general behavior of the goby's startle response as sensory input is increased. In the high strength regime, there are two steady state firing rates and one significantly greater than the other, each occupied by a distinct M-cell (see figures 3, 4). If there is asymmetry in the input strength between the two M-cells, then the favored cell will be the one that fires (see figure 5). This will then be communicated downstream; unbalanced firing of fast motor neurons will produce a c-shaped response in the tail of the goby.

The sensitivity of this model to changes in asymmetry presents a weakness. As illustrated by figure 6, the Hopf bifurcation will only occur if the difference in input across the M-cells is less than 5% of the total. Though the extent of the limitation is subject to change with values of other parameters, the fact that oscillations between the M-cells remain highly sensitive to changes in asymmetry proves fishy. This result minimizes the possibility that oscillations strictly at the level of M-cells can reproduce the escape response of the goby in a complete sense, leading us to consider a more neuronal approach.

1.3 Model 2: CPG Oscillations

1.3.1 Overview

For this case we consider the circuitry of the goby escape reflex to be a modified case of that present in the zebrafish, as explored by Miller et. al. 2017 [18]. This is itself an an adaptation of the Morris-lecar framework [19, 6] with the purpose of investigating connections between the M-cell escape pathway and social dominance behavior.

The membrane potential of each cell abides by the following:

$$C\frac{dV}{dt} = -I_{Ca} - I_K - I_{KCa} - I_L - I_{syn} + I_{app}(t).$$
 (18)

Here calcium, potassium, calcium dependent potassium, and leak currents obey the following dynamics:

$$I_{Ca} = g_{Ca} m_{\infty}(V)(V - V_{Ca}) \tag{19}$$

$$I_K = g_K n(V - V_K) \tag{20}$$

$$I_{KCa} = g_{KCa} \left(\frac{[Ca]}{[Ca] + k} \right) (V - V_K)$$

$$\tag{21}$$

$$I_L = g_L (V - V_L). \tag{22}$$

The Calcium concentration evolves according to:

$$\frac{d[Ca]}{dt} = \epsilon \bigg(-\mu I_{Ca} - k_{Ca}[Ca] \bigg).$$
(23)

Regarding the gating variables m and n, m responds instantaneously to changes in voltages and n is dynamic.

Synaptic input governs inter-cellular connections, with this current following:

$$I_{syn} = g_{syn}(V - V_{syn}) \sum_{j} s_j.$$

$$(24)$$

In this case the synaptic variable s is controlled by the fraction of open channels.

$$\frac{ds}{dt} = s_{\infty}(V)(1-s) - \beta s \tag{25}$$

 $s_{\infty}(V)$ is another gating variable.

A complete list of equations and parameter values can be found in the appendix.

These equations are used to model the behavior of five categories of interest: M-cells, fast and slow motor neurons, CPG neurons, and inhibitory neurons. We expect silence in the negligible stimulus case, CPG fueled oscillation of slow motor neurons in the intermediate case, and Mauthner fueled activation of fast mostor neurons, inhibition of slow motor neurons in the strong case. A primary distinction from the basal zebrafish model lies in the existence of a rest state where the CPG neurons are inactive.



Figure 7: Neural circuit reproduced by Model 2 [14]. Zebrafish and Goby variations are included. The zebrafish model is put forth by Miller et. al. 2017 [18]. Both M-cells may recieve stimulus, thought not necessarily equal doses.

More accurately, there are a number of dissimilarities between the basal case and the goby case [14, 18]. For one, the zebrafish model includes a series of adaptation variables to

accommodate for social interaction that have been excluded. Additionally, instead of hosting a chain of stimuli (18 stimuli parameters are included in [18]), we consider only a single pulse of stimulus. That is we activate the system at a time *stimon* for a duration dur.

Of the distinctions present, two are critical to the 'tail flick' mechanism. (1) We propose a direct connection from sensory stimulus to the CPG neurons. At the time of stimulus being received, the CPG will receive a pulse to activate the system and then decay (with time constant τ_{cpgx}). Additionally, (2) in the absence of stimulus, the CPG system is silent. This is achieved by lowering a parameter corresponding to background applied stimulus (CPG_{iapp}) from 45 to 44.7. This way, the boost of stimulus from CPG_x is specifically required for the CPG to engage. The following equations summarize this.

$$\frac{d}{dt}CPG_{Goby} = \frac{d}{dt}CPG_{Zebrafish} + CPG_x - 0.3$$
(26)

Where

$$\frac{d}{dt}CPG_x = -CPG_x/\tau_{cpgx} + u(t - t_{on})u(dur - t - t_{on})(1 - CPG_x).$$
(27)

1.3.2 Results

We see that these modifications successfully reproduce the observed behavior of the goby's startle response [13, 16]. In the absence of stimulus, the model is tranquil, unlike in the zebrafish case where the CPG is constantly active. A weak stimulus will activate the CPG (and subsequently the slow motor neurons) for enough time for a tail flick to occur. A sufficiently capable sensory input will result in an M-cell firing, which will activate the corresponding fast motor neuron downstream. Notably in this case the inhibition of the slow motor neurons does not prevent the CPG from continuing to fire, as it does not interfere with the escape reflex. A summary of the results in the measure zebrafish case are summarized in table 1; the adapted results for the goby case are in table 2.



Table 1: Startle response of Zebrafish as sensory stimulus is increased. M-cells, fast motor neurons, central pattern genrating neurons, and slow motor neurons are considered.



Table 2: Startle response of Gobies as sensory stimulus is increased. M-cells, fast motor neurons, central pattern genrating neurons, and slow motor neurons are considered.

1.4 Conclusions

Our simulations promote the belief that a series of deviations from the M-cell mechanism present in zebrafish can accurately describe that of the marine goby. We require the CPG to exist in a tranquil state when the environment is void of visual or auditory sensory data. This corresponds to observations of the goby remaining still at the aperture of the shrimp's burrow [16, 13]. Additionally it appears highly likely that some explicit or implicit pathway exists connecting this sensory data to the CPG, hence bypassing the M-cells. We do not make claims about the anatomical nature of this pathway, only about its existence.

We are amenable to the possibility of another mechanism existing to explain this behavior, as it cannot be readily disproven. Simultaneously, we have confidence that these modifications are an immediately likely candidate given their simplicity and effectiveness.

Additionally, we do consider a second potential circuit (previously dubbed *Model 1*). However, this more elementary proposal has left itself open to criticism by requiring a narrow parameter regime in order to reproduce observed behavior. In other words, if the tail flick is the result of oscillations between the two M-cells, then the system will only activate if sensory input is received nearly equally on both sides of the CNS. If it had been observed that predatory fish approaching the goby from one side, hence leading to a lop-sided activation of the CNS, resulted in the fish failing to respond appropriately, then M-cell oscillation hypothesis presented by *Model 1* would be more enticing. We are not aware of such observations existing.

2.0 Alternative Mating Strategies in Cephalopods and Fishes

2.1 Introduction

Evolutionary game theory (EGT) models use theoretical results of intra and inter species competition to predict an Evolutionary Stable Strategy (ESS). The ESS, or distribution of strategies that maximizes total fitness, should be the end behavior of natural selection. An original framework for making ESS predictions, in the specific sense, revolves around articulating the potential strategies, payoffs of each strategy, and stability criterion [11]. A conventional setup for evaluating the fitness of short-term strategies was provided by the Hawk-Dove game [31]; this involves the analysis of a payoff matrix to evaluate a surrogate currency, which is assumed to be proportional to fitness. A range of methods have since developed in the context of EGT, including stochastic programming [4] and dynamic equations [15, 1].

A distinction has been presented in EGT between specific and general models (though in any practical sense the two lie on a continuum) [26]. A specific model will be designed around a precise interaction in biology, giving a result that is more quantitative with the general model's solution being considered qualitative. It is seen in the former case that parameters can often be readily measured, while this is not strictly true in the latter case. It will be revealed that our results coincide with that of a general model.

The focus of this work is to evaluate the evolutionary stability of various inter-species, alternative mating strategies as ecological parameters are varied. That is, we're interested in the phenotypic variation in mating behavior between male wrasses, cephalopods, and cichlids [23].

Seeking out a mate requires dedication to a series of strategic choices. In one case, the fish act as a sneaker by disregarding any underlying aspiration to settle down. They find themselves quickly seeking out a mate under the aphoristic radar of those who control the nests, waiting for them to be distracted. [4, 34, 24]. For the giant Australian cuttlefish, *Sepia Apama*, this means steering clear of dominants by adopting female color patterns

[21]. Nesting males by contrast gamble a trade off; they're willing to invest more time and energy in order to yield a higher rate of mating success. The winning strategy will almost be consequence of environmental factors; this is what we wish to articulate.

2.2 Approach

Our proposed model involves dividing the total population of interest into discrete states and then evolving the population distribution forward in time according to a piece-wise dynamical system. Thus we assume the life histories of the fish can be viewed as movement through a phase space, where at any fixed time a player can hold a certain energy level and have adopted a certain strategy. We use the term 'energy' to refer to whether or not a fish has grown sufficiently in order to seek out a mate.

If $\mathbf{x}[t]$ represents a state vector, a portrait of the of the population at time t, then $\mathbf{x}[t][i]$ is the proportion of the population at time t holding state i. Hence for an N state system,

$$\sum_{i=0}^{N} \mathbf{x}[t][i] = 1.$$
 (28)

We're interesting in proposing a mechanism to evolve the system:

$$\mathbf{x}[t] = \varphi_t(\mathbf{x}[0]). \tag{29}$$

During each fixed season, the population will iterate according to a discrete time Markov chain. The transition probabilities will alternate in time depending on the season. In other words, there are clear differences in the behavior of the fish depending on whether or not we are in a mating or growth season. During a mating season, those fish occupying a high energy state will have some probability of transitioning to a mating state. During a growth season, fish will have some probability of 'leveling up' from a low energy into a high energy state. Other distinctions will be revealed.

Though in any fixed season we utilize a Markov chain, the system as a whole will not be Markovian. More accurately it can be described as a time delay system [28, 2]. Why is this? It will be revealed that fish playing a given strategy will birth fish inclined to perform the same strategy. (Whether not they switch strategies will depend on the case study.) Thus the proportion of new births that occur that result in fish initially playing strategy x will depend on the proportion of matings that occurred in the previous season as a result of a male playing strategy x.

More specifically, we run simulations that alternate between a 60 day mating season and a 300 day growth season. The transition probabilities during the growth season will have dependence on the values taken on by taken on by the state vector during the previous mating season. Let μ be an array of ecological parameters. Given t days have passed, let $\omega(t)$ be the number of days the simulation ran for before the start of the previous mating season; that is we have the integer part of the number of years that have passed, times the number of days in a cycle. We can state the following:

$$\omega(t) = 360 \left\lfloor \frac{t}{360} \right\rfloor$$

$$\mathbf{x} \to P\mathbf{x}$$
 if $t - \omega(t) < 60$ where $P = P(\mu) \in \mathbb{R}^{NxN}$ (30)

$$\mathbf{x} \to Q\mathbf{x}$$
 if $t - \omega(t) \ge 60$ where $Q = Q(\mu, \mathbf{x}[\omega(t) + \tau] \tau \in \{0, \cdots, 59\}) \in \mathbb{R}^{NxN}$. (31)

Here, P corresponds to the transition matrix of the mating season, Q the growth season.

We view a strategy (or mixed strategy) as being evolutionary stable if a uniformly distributed initial state will migrate towards that strategy in time. In any practical sense this effective strategy will be revealed after a series of iterations corresponding to 50 mating cycles. This framework for determining ESS is in contrast to previously discussed specific models [32, 11]. In cases such as the Hawk-Dove game where the strategy is a choice of a single action, it is reasonable to view the outcome of evolution as being carved into a proverbial stone. Though in the evaluation of these alternative mating strategies, there is a dependence on environment.

2.3 Basal Wrasse Model

2.3.1 Overview

The two strategies will be referred to as "sneaker" and "dominant." The wrasse model we begin with involves transitions between seven states: a 'dead' state (X), low and high energy states for both the sneaker and dominant (LS, HS, LD, HD) and mating states for each strategy (MS and MD). During the mating season the dead state will be absorbing; during the growth season movement away from this state corresponds to new births. Additionally during the growth season wrasse can switch strategies for a trade off of loosing energy.



Figure 8: The Indo-pacific wrasse *Thalassoma lutescens*. Photography courtesy of Klaus M. Stiefel.



Figure 9: Wrasse transition diagrams for the mating season (blue) and growth season (red). An arrow from one state to another indicates that such a transition has a nonzero probability of occurring.

We move forward by initializing a state vector $\mathbf{x} \in \mathbb{R}^7$ corresponding to the population being uniformly distributed between the four low and high energy states. The vector will then be iterated according to previously described transition matrices. Here the location (i, j)corresponds to P_{ij} , the probability in that in a single day a member of state j transitions to state i. We will use the notation P_{ij} and Q_{ij} to refer to the (i, j) location in the mating and growth matrices, respectively.

The goal moving forward will be to identify parameter dependence for the transition matrix elements. Relations between transition probabilities and key parameters will be explained here; proportional constants and further explanation are included in Appendix B. We define two parameters: α and β to correspond to food availability and predation, respectively. We suggest the following relations:

$$P_{XZ}, Q_{XZ} \sim \beta/\alpha \tag{32}$$

$$P_{LZHZ}, Q_{LZHZ} \sim 1/\alpha$$
 (33)

$$Q_{HZLZ} \sim \alpha. \tag{34}$$

Here, Z is an arbitrary strategy or state. Transition probabilities in the form P_{ZZ} are chosen specifically such that the sum of the column elements is unity. Otherwise equation (28) would flounder.

One aspiration of ours is to redistribute new births in the growth season according to the relative success of each strategy in the previous mating season. Fix t days having passed such that $t \ge \omega(t) + 60$ (i.e. the time corresponds to some point in a growth season). Define the following:

$$\mu(t) = \sum_{k=\omega(t)}^{\omega(t)+59} MS[k] \qquad \nu(t) = \sum_{k=\omega(t)}^{\omega(t)+59} MD[k]$$

Here $\mu(t)$ is proportional to the number of sneaker matings that occurred in the previous mating season, $\nu(t)$ dominant matings. Let $\delta \leq 1$ correspond to a pseudo birth rate of the population. Then we define,

$$Q_{LSX}(t) = \frac{\mu(t)\delta}{\mu(t) + \nu(t)}, \qquad Q_{LDX}(t) = \frac{\nu(t)\delta}{\mu(t) + \nu(t)}.$$
(35)

2.3.2 Results

Our results come as predictions regarding where observed wrasse populations come in the parameter space of food availability and predation. Alonzo et al., 2000 observe the wrasse *Symphodus ocellatus* off the coast of Corisca, France, finding 67% playing the dominant strategy [3]. Warner and Swearer 1991 observe the wrasse *Thalassoma bifasciatum* off the coast of the US Virgin Islands, finding an equal presence of both strategies [38]. Warner and Hoffman 1980 and Warner 1982 observe the wrasses *Thalassoma bifasciatum* and *Thalassoma bifasciatum* off the coast of Panama, finding between 85% and 99% of the wrasses playing the sneaker strategy [37, 36].

Figure 10 summarizes our predictions regarding ecological parameter differences between these populations. We note that making any claims regarding absolute differences in calorie or predator density is beyond the scope of our model; we instead are focused on comparing these quantities in a relative sense.



Figure 10: Stability of the sneaker and dominant mating strategies among wrasses as we iterate across values of food availability and predation. Isoclines corresponding to observations are included; we can then make predictions of where cases lie relative to each other in the parameter space [36, 37, 38, 3].

2.4 Cephalopod Model

2.4.1 Overview

Though evolutionary convergence has spurred numerous behavioral similarities between cephalopods and fishes, the most recent common ancestor was pre-Cambrian, indicating that the alternative mating tactics likely evolved independently [25]. As such, a variety of distinctions have been well documented, and we are interested in four of these. Notably the cephalopods (1) do not switch strategies, (2) mate only once per lifetime, (3) engage in cannibalistic tendencies, and (4) grow at a much faster rate [21, 10, 20].



Figure 11: Cephalopod transition diagrams for the mating season (blue) and growth season (red).

The second of these behaviors is known as semelparity; it is characterized by each fish participating in a single large spawning aggregation before its death [10]. The giant Australian cuttlefish *Sepia Apama* typifies this behavior. We incorporate this into our model by producing an instantaneous reset of our state vector $\mathbf{x}[t]$ towards the dead state after each mating season and before the subsequent growth season. This does not correspond to the model holistically resetting though, as information regarding the previous mating season is still encoded in the values of Q_{LXD} and Q_{LSX} .

It has also been noted that dominant cephalopods exhibit cannibalistic tendencies towards their smaller counterparts [22]. As such, the probability of a sneaker migrating to the dead pool will be updated each day according to the following relation:

$$Q_{XLS}[t+1], \ Q_{XHS}[t+1] \sim (\beta/\alpha)(LD[t] + HD[t])$$
 (36)

Notably those playing the sneaker strategy are more likely to migrate toward the dead state; however, (36) demonstrates that these transition probabilities are updated according to the same mechanism.

The diagonal transition probabilities Q_{ZZ} are updated accordingly so that (19) holds.

Finally, the growth probabilities Q_{HSLS} and Q_{HDLD} were increased by a factor of two and the strategy change probability Q_{LDHS} was set to zero.



Figure 12: Two male cuttle fish (left) engaged in a conflict over a female (right). The nesting male guarding the female is visibly larger than the intruder. Read the full story here: [LINK]. Photography courtesy of Klaus M. Stiefel.

2.4.2 Results

Our results come as predictions regarding where observed cephalopod populations come in the parameter space of food availability and predation. Hanlon et al., 2002 observe the squid *Loligo vulgaris* off the coast of South Africa, finding 86% playing the dominant strategy [10]. Naud et al., 2004 observe the cuttlefish *Sepia Apama* off the coast of Southern Australia, finding only 17% playing the dominant strategy [20]. The relevant environmental predictions are summarized by figure 13.

Figure 15 summarizes the impact each of the four modifications has on the basal wrasse model. Specifically we note that the cannibalistic mechanic and the increased growth speed sway the favor toward the dominant strategy, while the lack of an option for a fish to transition strategies provides benefit to the sneakers.



Figure 13: Stability of the sneaker and dominant mating strategies among cephalopods as we iterate across values of food availability and predation. Isoclines corresponding to observations are included; we can then make predictions of where cases lie relative to each other in the parameter space [10, 20].

2.5 Cichlids

2.5.1 Overview

We move our interest towards one final species Lamprologus Callipterus which is endemic to the African lake Tanganyika [35, 29]. For the purpose of our model, certain males in this population (sneakers and dominants) behave equivalently to previously discussed wrasses. However, there exists a third genetically determined class which we will refer to as dwarf males (LW, HW, and MW for the low energy, high energy, and mating dwarf states,



Figure 14: Predicted sneaker proportion at ESS as a function of Food Availability and Predation for wrasses (a) and cephalopods (b).

respectively). These are one fortieth the size of the dominant counterparts and have no ability to switch strategies.

An additional behavioral complexity relevant to this cichlid lies in a visible presence of altruism. That is, an individual will receive an evolutionary bonus if it aids in the reproduction of sufficiently related members of the population. The condition for an act of altruism to make evolutionary sense has been articulated by Hamilton: [8, 9, 33]

$$b > cr. \tag{37}$$

Here b is the benefit of an altruistic act, c is the cost, and r is the relatedness of the two participants. In our case, the dominant males are presumed to receive an altruistic benefit when dwarf males utilize their nests.

We assume a mean relatedness between any given dwarf and dominant male to be fixed throughout the population. The explicit benefit from Hamilton's rule is provided to the dominant fish is then proportional to the total dwarf male population. Then we update the dominant growth probability according to the following at each timestep:

$$Q_{HDLD}[t+1] \sim \alpha + LW[t] + HW[t]. \tag{38}$$

In other words, we model the altruistic benefit as being materialized in the form of an increased growth speed.



Figure 15: The specific effect each individual wrasse-cephalopod distinction has on ESS, across variation in predator presence. The normalized food availability is set to be 40.



Figure 16: Cichlid transition diagrams for the mating season (blue) and growth season (red).

2.5.2 Results

We find that, as is the case for wrasses and cephalopods, the dominant strategy is most preferred in a regime where food is readily available. As is the case for the wrasse, but not the cephalopod, a very small predator presence can also incite fish to play the dominant strategy. An altruistic bonus for dominants provides favor to that strategy at the expense of both of the other two. Figure 17 summarizes these thoughts.

2.6 Stochastic Considerations

2.6.1 Overview

We additionally wish to see how the stability of various strategies depends on the variability of our ecological parameters. It is conceivable that for a sufficiently stochastic environment, a fish may be able to get away with a strategy that otherwise would not be an



Figure 17: One dimensional parameter sweeps across food availability (α) and predator presence (β). Cases with and without Hamilton's rule are considered.

appropriate way of maximizing fitness. That is, the result of a simulation for any given α , β ecological parameters can itself be viewed as a stochastic variable.

More accurately introduce a random variable, ξ , that we allow to fluctuate in time. Let $\xi > 1$ correspond to a relatively high food availability and a relatively low predator presence, $\xi < 1$ be the similar opposite. At the time of any seasonal transition, $\xi = 1$ is reset. Within a season, ξ is updated according to a random normal distribution:

$$\xi[t+1] = N(\xi[t], \sigma).$$
(39)

In a sense ξ takes a random walk during each season before being reset. During a mating

season we preform the following updates for each day:

$$P_{LSHS} = \frac{1}{\xi} P_{LSHS} \qquad P_{LDHD} = \frac{1}{\xi} P_{LDHD}. \tag{40}$$

And during the growth season:

$$Q_{LSHS} = \frac{1}{\xi} Q_{LSHS} \qquad Q_{LDHD} = \frac{1}{\xi} P_{LDHD}$$
(41)

$$Q_{HSLS} = \xi Q_{HSLS} \qquad Q_{HDLD} = \xi Q_{HDLD}. \tag{42}$$

2.6.2 Results

We simulate the parameter space with the set up of the original wrasse model.

The parameter σ can be interpreted as the characteristic percentage an ecological parameter may change during a given day. For instance, figure 18 (d) shows the results of a simulation where the environment takes a random walk changing typically 15% per day. This is an extreme case used to illustrate the result of there existing more variability than we would reasonably expect.

The extent to which stochasticity impacts an environment depends on that environment itself. When running the simulation in the limit of low food availability, the ESS holds relatively constant at 1 - 2 % as our variability increases. To contrast, the proportion of sneakers in a realm corresponding to much greater food availability rises steadily with σ .



Figure 18: Simulations including a stochastic variable ξ . The extent of variation is judged by its variance, σ^2 . Specifically in (a) $\sigma = 0.01$, (b) $\sigma = 0.04$, (c) $\sigma = 0.08$, and (d) $\sigma = 0.15$

2.7 Conclusions

Our results are summarized as predictions regarding how the ESS of an alternative mating strategy may change as we vary (1) food availability, (2) predation, (3) stochasticity, and (4) behavioral patterns. This allows us to produce claims relative claims regarding environments of different observed populations. For example, we believe the French wrasse observed by Alonzo et al. in 2000 has a much more plentiful supply of food when compared with the central American populations documented by Warner and Hoffman in the early 1980s [3, 37, 36].



Figure 19: Presence of sneakers in the high food availability regime, dominants in the low food availability regime, for increased stochasticity.

We suspect that the behavioral differences between the wrasses and the cephalopods result in distinctions regarding parameter dependence. For instance, we believe that the dominant strategy can reasonably be stable for the wrasse in a very low predation environment. We cannot say the same for the cuttlefish (assuming sufficiently low environmental variability). In the case of the cichlid *Lamprologus Callipterus*, we suspect that the dominant population may receive an altruistic benefit towards its genetic fitness since its nests are utilized by a dwarf population.

With the inclusion of a stochastic environment, we recognize that a mixed strategy output from our simulations for a given parameter set is itself a random variable, whose mean depends on the position in the parameter space that the setting is categorized as. In particular, there is asymmetry in this effect in that the sneaker strategy is more likely to prevail in a stochastic, high food availability environment than the dominant strategy in a comparably variable but scarce case.

Appendix A List of Equations for 1.3

Mauthner Cell Functions:

$$m_{inf}(v) = 0.5(1 + \tanh((v - v_{f1})/v_{f2}))$$
(43)

$$w_{inf}(v) = 0.5(1 + \tanh((v - v_{f3})/v_{f4}))$$
(44)

$$\tau_w(v) = \frac{1}{\cosh((v - v_{f3})/(2v_{f4}))}$$
(45)

$$mw_{inf}(v) = 0.5(1 + \tanh((v - v_{f3})/m_{vf4}))$$
(46)

$$m\tau_w(v) = \frac{1}{\cosh((v - v_{f3})/(2m_{vf4}))}$$
(47)

$$m_{sinf}(v) = \frac{1}{1 + \exp(-(v + \theta_s)/m_{ss})}$$
(48)

$$m_{syn1} = mg_{syn}ms_2(m_{v1} - mv_{syn})$$
(49)

$$m_{syn2} = mg_{syn}ms_1(m_{v2} - mv_{syn})$$
(50)

$$pul(t) = u(t)u(dur - t)$$
(51)

Mauthner Cell Differential Equations:

$$m_{v}[1,2]' = (mb_{iapp} + m_{stim}[j]pul(t - stimon[j]) - g_{ca}m_{inf}(m_{v}[j]) (m_{v}[j] - v_{ca}) - g_{k}m_{w}[j](m_{v}[j] - v_{k}) - g_{l}(m_{v}[j] - v_{l}) -m_{syn}[j] - gkca(m_{ca}[j]/(m_{ca}[j]/(m_{ca}[j] + ca_{0}))(m_{v}[j] - v_{k}))/cm$$
(52)

$$m_w[1,2]' = m_\phi(m_{winf}m_v[j] - m_w[j])/(m_{\tau_w}m_v[j])$$
(53)

$$m_s[1,2]' = m_\alpha (1 - m_s[j]) m_{sinf} m_v[j] - m_\beta m_s[j]$$
(54)

$$m_{ca}[1,2]' = m_{\epsilon}(-\mu g_{ca}m_{inf}m_{v}[j](m_{v}[j] - v_{ca}) - m_{ca}[j]kca)$$
(55)

Fast Motor Neuron Functions:

$$fmn_{syn1} = fmng_{syn}ms_1(fmnv_1 - fmnv_{syn})$$

$$\tag{56}$$

$$fmn_{syn2} = fmng_{syn}ms_2(fmnv_2 - fmnv_{syn})$$
⁽⁵⁷⁾

Fast Motor Neuron Differential Equations:

$$fmn_{v}[1,2]' = (fmn_{iapp} - g_{ca}m_{inf}fmn_{v}[j](fmn_{v}[j] - v_{ca}) - g_{k}fmn_{w}[j](fmn_{v}[j] - v_{k}) - g_{l}(fmn_{v}[j] - v_{l}) -$$
(58)

$$fmn_{syn}[j] - gkca(fmn_{ca}[j]/(fmn_{ca}[j] + ca_0))(fmn_v[j] - v_k)/cm$$

$$fmn_w[1,2]' = fm_\phi(w_{inf}fmn_v[j] - fmn_w[j])/(\tau_w fmn_v[j])$$
(59)

$$fmn_{ca}[1,2]' = fm_{\epsilon}(-\mu g_{ca}m_{inf}fmnv[j])$$

$$(fmn_{v}[j] - v_{ca}) - fmn_{ca}[j]kca)$$
(60)

Inhibitory Interneuron Functions:

$$mti_{syn} = mtig_{syn}(m_{s1} + m_{s2})(in_v - iv_{syn})$$
 (61)

$$mtis_{inf}(v) = \frac{1}{(1 + exp(-(v + \theta_s)/mtis))}$$
(62)

$$its_{syn1} = i2mng_{syn}in_s(smnv_{v1} - i2mnv_{syn}) \tag{63}$$

$$its_{syn2} = i2mng_{syn}in_s(smnv_{v2} - i2mnv_{syn}) \tag{64}$$

Inhibitory Interneuron Differential Equations:

$$in'_{v} = (iiapp + g_{ca}m_{inf}in_{v}(in_{v} - v_{ca}) - g_{k}in_{w}$$
$$(in_{v} - v_{k}) - gl(in_{v} - v_{l}) - mti_{syn} -$$
(65)

 $gkca(in_{ca}(in_{ca}+ca_0))(in_v-v_k))/cm$

$$in'_w = i_\phi(w_{inf}in_v - in_w)/(\tau_w in_v) \tag{66}$$

$$in'_{s} = i_{alpha}(1 - in_{s})(mtis_{inf}in_{v} - i_{\beta}in_{s})$$

$$(67)$$

$$in'_{ca} = i_{\epsilon}(-\mu g_{ca}m_{inf}in_v(in_v - v_{ca}) - in_{ca}kca) \tag{68}$$

CPG Functions:

$$cpg_{syn1} = cpgg_{syn}cpg_{s2}(cpg_{v1} - cpg_{vsyn})$$

$$\tag{69}$$

$$cpg_{syn2} = cpgg_{syn}cpg_{s1}(cpg_{v2} - cpg_{vsyn})$$

$$\tag{70}$$

$$i2cpg_{syn1} = i2cpgg_{syn}in_s(cpg_{v1} - i2cpg_{vsyn})$$

$$\tag{71}$$

$$i2cpg_{syn2} = i2cpgg_{syn}in_s(cpg_{v2} - i2cpg_{vsyn})$$

$$\tag{72}$$

CPG Differential Equations:

$$cpg'_{x} = -cpg_{x}/\tau_{cpgx} + (stimon)pul(t - stimon)(1 - cpg_{x})$$
(73)

$$cpg_{v}[1,2]' = (cpg_{iapp} + cpg_{x} - g_{ca}m_{inf}cpg_{v}[j]$$

$$(cpg_{v}[j] - v_{ca}) - g_{k}cpg_{w}[j](cpg_{v}[j] - v_{k}) -$$

$$g_{l}(cpg_{v}[j] - v_{l}) - cpg_{syn}[j] - i2cpg_{syn}[j] - gkca$$

$$(cpg_{ca}[j]/(cpg_{ca}[j] + ca_{0}))(cpg_{v}[j] - v_{k}))/cm$$
(74)

$$cpg_w[1,2]' = cpg_\phi(w_{inf}cpg_v[j] - cpg_w[j])/(\tau_w cpg_v[j])$$
(75)

$$cpg_w[1,2]' = cpg_\alpha(1 - cpg_s[j])s_{inf}(cpg_v[j]) - cpg_\beta cpg_s[j]$$

$$\tag{76}$$

$$cpg_{ca}[1,2]' = cpg_{\epsilon}(-\mu g_{ca}m_{inf}cpg_{v}[j](cpg_{v}[j] - v_{ca}) - cpg_{ca}[j]kca)$$

$$\tag{77}$$

Slow Motor Neuron Functions:

$$smn_{syn1} = smng_{syn}cpg_{s1}(smn_{v1} - smn_{vsyn})$$

$$\tag{78}$$

$$smn_{syn2} = smng_{syn}cpg_{s2}(smn_{v2} - smn_{vsyn})$$
⁽⁷⁹⁾

Slow Motor Neuron Differential Equations:

$$smn_{v}[1,2]' = (smn_{iapp} - g_{ca}m_{inf}smn_{v}[j](smn_{v}[j] - v_{ca}) - g_{k}smn_{w}[j](smn_{v}[j] - v_{k}) - smn_{syn}[j] - its_{syn}[j] - (80)$$
$$(gkca)smn_{ca}(smn_{ca}[j]/(smn_{ca}[j] + ca_{0}))(smn_{v}[j] - v_{k}))/cm$$

$$smn_w[1,2]' = sm_\phi(w_{inf}smn_v[j] - smn_w[j])/(\tau_w smn_v[j])$$

$$\tag{81}$$

$$smn_{ca}[1,2]' = sm_{\epsilon}(-\mu g_{ca}m_{inf}smn_{v}[j]$$

$$(smn_{v}[j] - v_{ca}) - smn_{ca}[j]kca)$$
(82)

Parameter Values: $v_{f1} = -1.2, v_{f2} = 18, v_{f3} = 12, v_{f4} = 17.4, g_{ca} = 4, v_{ca} = 120, g_l = 2, g_k = 8, v_l = -60, v_K = -84, iapp = 45, \phi = 0.23, ss = 0.2, \theta_s = 0, v_{syn} = 30, g_{syn} = 0.1, cm = 20, kca = 1, g_{kca} = 0.25, \mu = 0.2, ca_0 = 10, mv_{syn} = -50, mg_{syn} = 0.5, m_{\beta} = 0.08, m_{\alpha} = 10, miapp1 = 3, miapp2 = 0, mbiapp = 40.5, mss = 4, mv_{f4} = 17, m_{\epsilon} = 0.005, m_{\phi} = .23, fmngsyn = 0.4, fmnvsyn = 30, fmniapp = 38, fm_{\epsilon} = 0.005, fm_{\phi} = 0.225, 2agfmn = 0, fmnw = 0.5, mtigsyn = 0.2, ivsyn = 30, i_{\alpha} = 10, i_{\beta} = 0.00035, iiapp = 40.4, mtis = 1, i = 0.005, i = 0.225, 2agin = 0, i2mngsyn = 0.6, i2mnvsyn = -50, iinw = 1, cpgvsyn = -30, cpggsyn = 0.3, cpg_{\beta} = 0.2, cpg = 10, cpgiapp = 44.7, cpg_{\epsilon} = 0.005, cpg_{\phi} = 0.005,$

 $\begin{aligned} 0.23, & i2cpggsyn = 0, & i2cpgvsyn = -50, & smngsyn = 0.37, & smnvsyn = 25, & smniapp = 40.4, & sm_{\epsilon} = 0.005, & sm_{\rm l}phi = 0.23, & \tau_{cpgx} = 300, & dur = 50, & stimon = 2000, & cpgx = 300 \end{aligned}$

Appendix B Parameter Exposé for 2.0

For the mating and growth seasons, respectively, we define transition matrices:

$$P = \{P_{ij}\}, \quad Q = \{Q_{ij}\}.$$
(83)

Chapter 2 outlined a series of statutes for choosing reasonable values to act as entries of these matrices, some of which are worthy to be restated. No-change probabilities (P_{ii}) will be balanced by equation (28). Equations (32) - (34) demonstrate the influence of food availability and predation on transition elements, while equation (35) summarizes the occurrence of new births in the growth season (with $\delta = 0.2$ chosen). The probability of leaving the mating state on any given day is set to be one. Any transition probability gone unmentioned can be presumed to be zero; the astute reader will observe such omissions to be consistent with the transition diagrams (figures 9, 11, and 16).

The articulation of proportionality constants remains to be specified. These choices are made with the following guiding principles in mind:

- The sneaker male is more likely to increase its energy level in a given day than the dominant male.
- Though the dominant male is slower to evolve, it is less likely to subsequently loose energy.
- The sneaker male is more likely to die than the dominant.
- The sneaker male is less likely to transition from the high energy state to the mating state than the dominant male.

Baseline Parameters (Wrasse):

Initialize keystone parameters α , β . For the two dimensional parameter sweeps, α was swept from 1.20 to 2.00, β from 10⁻⁵ to 0.02. This choice magnifies the curve of change in ESS. These have been re-scaled to a 1 to 100 scale for the purpose of figures. Low Energy Sneaker Transitions:

$$P_{XLS} = Q_{XLS} = 4\beta/\alpha$$
$$Q_{HSLS} = 0.0625\alpha$$

High Energy Sneaker Transitions:

$$P_{XHS} = Q_{XHS} = 1.6\beta/\alpha$$
$$P_{LSHS} = Q_{LSHS} = 0.008/\alpha$$
$$P_{MSHS} = 0.1$$
$$Q_{HSLD} = 0.001$$

Low Energy Dominant Transitions:

 $P_{XLD} = Q_{XLD} = 2.6\beta/\alpha$ $Q_{HDLD} = 0.0125\alpha$

High Energy Dominant Transitions:

$$P_{XHD} = Q_{XHD} = 0.8\beta/\alpha$$
$$P_{LDHD} = Q_{LDHD} = 0.06\alpha$$
$$P_{MDHD} = 0.4$$

Modified Behavior:

Unless otherwise stated, the transition probabilities in the cephalopod and cichlid cases will be the same as those listed for the wrasses.

In the case of cephalopods, Q_{XLS} and Q_{XHS} need to be be updated each day of the growth season to account for cannibalism; equation (36) summarizes this mechanism. The

proportionality constants here are 4 and 1.6 for the low and high energy cases, respectively, as in the wrasse case. To incorporate an increased growth speed, the probabilities Q_{HSLS} and Q_{HDLD} were multiplied by two relative to the wrasse case. The probability Q_{LDHS} was set to zero.

In the case of cichlids, altruism is accounted for by updating Q_{HDLD} each day according to the following specification:

$$Q_{HDLD} = 0.0124\alpha + 0.03(LW[t] + HW[t]).$$

Here the 0.03 proportionality constant can be interpreted as a mean relatedness from Hamilton's rule [8, 9]. The food availability sweeps shown in figure 17 fixed $\beta = 0.001$, while the predation sweeps fixed $\alpha = 1$. The remaining transition probabilities for the dwarfs are listed below.

High Energy Dwarf Transitions:

 $P_{XHW} = Q_{XHW} = \beta/\alpha$ $P_{LWHW} = Q_{LWHW} = 0.008/\alpha$ $P_{MWHW} = 0.25$

Low Energy Dwarf Transitions:

$$P_{XLW} = Q_{XLW} = \beta/\alpha$$
$$Q_{HWLW} = 0.5\alpha$$

Given these values, one could fill in the transition matrices P and Q, and then apply equations (30) and (31) to simulate a population.

Bibliography

- [1] J. McNamara M. Mangel A. Houston, C. Clark. Dynamic models in behavioral and evolutionary ecology. nature. *Nature*, 332:29–34, 1988.
- L. J. Allen. An Introduction to Stochastic Processes with Applications to Biology, 2nd Edition. Chapman and Hall / CRC Press., 2010.
- [3] S. Alonzo, M. Tabosrky, and P. Wirtz. Male alternative reproductive behaviours in a mediterranean wrasse, symphodus ocellatus: Evidence from otoliths for multiple life-history pathways. *Evolutionary Ecology Research*, 2:997–1007, 2000.
- [4] S. H. Alonzo and R. R. Warner. Dynamic games and field experiments examining intra- and intersexual conflict: explaining counterintuitive mating behavior in a mediterranean wrasse, symphodus ocellatus. *Behavioral Ecology*, 11:56–70, 1999.
- [5] R. C. Eaton, W. A. Lavender, and C. M. Wieland. Identification of mauthner-initiated response patterns in goldfish: Evidence from simultaneous cinematography and electrophysiology. *Journal of Computational Physiology*, 144:467–485, 1981.
- [6] G. B. Ermentrout and D. H. Terman. *Mathematical foundations of neuroscience*, volume 35. Springer Science Business Media, 2010.
- [7] M.E. Hale, H.R. Katz, M.Y. Peek, and R.T. Fremont. Neural circuits that drive startle behavior, with a focus on the mauthner cells and spiral fiber neurons of fishes. *Journal of Neurogenetics*, 30(2):89–100, 2016.
- [8] W. D. Hamilton. The evolution of altruistic behavior. *The American Naturalist*, 97(896):354–356, 1963.
- [9] W. D. Hamilton. Altruism and related phenomena, mainly in social insects. Annual Review of Ecology and systematics, 3(1):193–232, 1972.
- [10] R. Hanlon and K. Hall. Principal features of the mating system of a large spawning aggregation of the giant australian cuttlefish sepia apama (mollusca: Cephalopoda). *Marine Biology*, 140(3):533–545, 2002.

- [11] A. I. Houston and J. M. McNamara. John maynard smith and the importance of consistency in evolutionary game theory. *Biology and Philosophy*, 20:933–950, 2005.
- [12] Z. Jaafar and Z. Yiwen. Visual acuity of the goby-associated shrimp, alpheus rapax fabricius, 1798 (decapoda, alpheidae). *Crustaceana*, 85(12-13):1487–1497, 2012.
- [13] I. Karplus and A. Thompson. The partnership between gobiid fishes and burrowing alpheid shrimps. *The Biology of Gobies*, pages 559–607, 2011.
- [14] J. A. Landsittel, G. B. Ermentrout, and K. M. Stiefel. A computational model of the shrimp-goby escape communication system. *Journal of Computational Neuroscience*, 49:395–405, 2021.
- [15] D. Liao and T. D. Tlsky. Evolutionary game theory for physical and biological scientists. ii. population dynamics equations can be associated with interpretations. *Interface Focus*, 4(4), 2014.
- [16] P.J. Lyons. The evolution of mutualism between alpheid shrimp and gobiid fishes: a balance between benefits and costs. PhD thesis, Stony Brook University, 2012.
- [17] V. Medan and T. Preuss. The mauthner-cell circuit of fish as a model system for startle plasticity. *ScienceDirect*, 108(2-3):129–140, 2014.
- [18] T. H. Miller, K. Clements, S. Ahn, C. Park, E. H. Ji, and F. A. Issa. Social status-dependent shift in neural circuit activation affects decision making. *Journal of Neuroscience*, 37:2137–2148, 2017.
- [19] C. Morris and H. Lecar. Voltage oscillations in the barnacle giant muscle fiber. Biophysical Journal, 35:193–213, 1981.
- [20] M. Naud, R. T. Hanlon, K. C. Hall, P. W. Shaw, and J. N. Havenhand. Behavioural and genetic assessment of reproductive success in a spawning aggregation of the australian giant cuttlefish, sepia apama. *Animal Behaviour*, 67(6):1043–1050, 2004.
- [21] M. D. Norman, J. Finn, and T. Tregenza. Female impersonation as an alternative reproductive strategy in giant cuttlefish. *The Royal Society: Proceedings B*, 266:1347– 1349, 1999.

- [22] R. K. O'Dor. Squid life-history strategies. FAO Fisheries Technical Paper, pages 233–254, 1998.
- [23] R. F. Oliveria, M. Taborsky, and H. J. Brockmann. *Alternative Reproductive Tactics: An Integrative Approach.* Cambridge University Press, 2008.
- [24] K. Ota and M. Kohda. Description of alternative male reproductive tactics in a shellbrooding cichlid, telmatochromis vittatus, in lake tanganyika. *Journal of Ethology*, 24:9–15, 2006.
- [25] A. Packard. Cephalopods and fish: The limits of convergence. *Biological Reviews*, 47(2):241–307, 1972.
- [26] G. A. Parker and J. M. Smith. Optimality theory in evolutionary biology. Nature, 348:27–33, 1990.
- [27] J. L. Preston. Communication systems and social interactions in a goby-shrimp symbiosis. Animal Behavior, 26:791–802, 1978.
- [28] J.P. Richard. Time-delay systems: an overview of some recent advances and open problems. *Automatica*, 39(10):1667–1694, 2003.
- [29] D. Schütz and M. Taborsky. Giant males or dwarf females: what determines the extreme sexual size dimorphism in lamprologus callipterus?. Journal of Fish Biology, 57(5):1254–1265, 2000.
- [30] T. Shimazaki, M. Tanimoto, Y. Oda, and S. Higashijama. Behavioral role of the reciprocal inhibition between a pair of mauthner cells during fast escapes in zebrafish. *Journal of Neuroscience*, 39(7):1182–1194, 2019.
- [31] J. M. Smith. The theory of games and the evolution of animal conflicts. *Journal of Theoretical Biology*, 47:209–221, 1974.
- [32] J. M. Smith. Evolutionary game theory. *Physica D: Nonlinear Phenomena*, 22:43–49, 1986.
- [33] K. M. Stiefel. Why are there no eusocial fishes? *Biological Theory*, 7:204–210, 2013.

- [34] M. Taborsky. Sneakers, satellites, and helpers: parasitic and cooperative behavior in fish reproduction. Advances in the Study of Animal Behavior, 23(1):e100, 1994.
- [35] M. Taborsky. The evolution of bourgeois, parasitic, and cooperative reproductive behaviors in fishes. *Journal of Heredity*, 92(2):100–110, 2001.
- [36] R. R. Warner. Mating systems, sex change and sexual demography in the rainbow wrasse, thalassoma lucasanum. *Copeia*, pages 653–661, 1982.
- [37] R. R. Warner and S. G. Hoffman. Population density and the economics of territorial defense in a coral reef fish. *Ecology*, 61(4):772–780, 1980.
- [38] R. R. Warner and S. E. Swearer. Social control of sex change in the bluehead wrasse, thalassoma bifasciatum (pisces: Labridae). *The Biological Bulletin*, 181(2):199–204, 1991.