Summer Internship Project
Report

Collective Behaviour

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CERTIFICATE

This is to certify that that **C L Srinivas** has completed his summer internship, spanning a duration of two months **(from** 1st **June 2024 to** 31st **July 2024)** under **Prof. Vishwesha Guttal**, Indian Institute of Science, Bangalore.

Signature of project guide

Acknowledgement

I would like to express my heartfelt gratitude to all those who have supported and guided me throughout the journey of completing this project report.

First and foremost, I want to thank my project guide, Prof. Vishwesha Guttal, for his valuable insights and guidance. His expertise and encouragement have been instrumental in the completion of this project.

I would also like to extend my appreciation to my friends, seniors and fellow lab mates who have been a constant source of inspiration and assistance. Their willingness to share their knowledge and experiences has been invaluable in navigating through the complexities of this project.

Last but not least, I would like to acknowledge the collective support of my family, whose encouragement and understanding have been pivotal in ensuring the successful completion of this project.

Thank You
C L Srinivas

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Collective Behavior & Game Theory

C L Srinivas

Abstract

This report summarizes the outdoor observations, discussions, tutorials, papers, book chapters and other material that I have read during the course of the internship. Each individual summary of a paper/book chapter aims to highlight, primarily, the gist of the paper/chapter, important ideas and aspects that escaped my comprehension. The consistent theme of all the papers read was collective animal motion; general overview of collective systems in the biosphere, models, simulations for collective motion and their analysis. The two book chapters (from *"Game Theory and Animal Behavior"* by Lee Alan Dugatkin and Hudson Kern Reeves) deal with the PS Game and the game theoretic analysis of the evolution of cooperation.

1 INTRODUCTION

Biological systems provide a plethora of opportunities for theoreticians to model, simulate and analyse complex interactions, or better still, systems with simple local interactions leading to emergent complexity! The theme of emergent complexity is deeply embedded in living systems, as far as I can see. A collection of neurons forming intellectually capable networks (brains), gene regulatory networks making "decisions" (life of the λ phage), quorum sensing in bacteria (*Vibrio cholerae*) and collective animal motion are a few examples. Of these, collective animal motion is the most easily observable phenomenon that is a day to day experience for most of us. I think it is fairly justified to ask the question, how do these animals (birds, fish, ungulates etc.) move in cohesion without colliding with conspecifics or external obstacles? Especially when most of us have a first hand experience of what it feels like to avoid a collision in rush hour traffic. Akin to mechanisms in modern automobiles like obstacle detection and cruise control, animals rely on simple rules of thumb that allow them to exist in extremely compact, cohesive and mobile spatial structures. Variation in these local rules of interaction can give rise to variation in group level properties like polarization (p_{group}) and angular momentum (m_{group}). Another question worth asking is, what drives the formation of collectives in animal systems? Everything from group selection to selfish interests can be, and have been used to explain the formation of large herds. We look at the arguments for and against such rationale and also a minimalist model for group formation as a means of cover seeking that does not invoke the concept of group selection.

The papers summarized here cover some of the details of such processes, associated models, some mathematical details and some other interesting properties like collective memory (hysteresis).

Collective foraging entails complex social scenarios that are navigated by utilizing strategies that maximise individual payoffs. This domain of study is termed social foraging theory and one of the relevant games in this regard is the Producer-Scrounger Game or PS Game. Chapter II in the book *"Game Theory and Animal Behavior"* discusses this game and it's two variants, the rate maximising PS game and the shortfall minimising PS game.

The long standing question in the realm of evolutionary game theory has been the evolution of cooperation amongst selfish agents. Chapter III of the book introduces this concept and provides a gist of the various paths for the evolution of cooperation in the animal world.

2 COLLECTIVE BEHAVIOUR

2.1 GENERAL OVERVIEW

Article: - *"The principles of collective animal behaviour" by Vishwesha Guttal* [1]. The article does a splendid job of drawing fundamental parallels between physical systems and biological collectives. It also serves to highlight the abundance of interesting and complex problems that biological systems offer to researchers with a love for theory. I especially like the parallels drawn between physics and ecology. I was interested in modelling animal behavior (and hence my desire to work with this lab), I feel as though the ideas presented in that article helped me to concretely understand how one goes on about this.

Review paper: - *"The principles of collective animal behaviour" by D. J. T. Sumpter* [2]. This was a nice overview of the diverse instances of collective animal behaviour. From humans clapping in an opera theatre to ants deciding on a new nesting site. The author explains how one can distil the complex patterns generated by collective behaviour into a few fundamental, individual level rules. This is akin to an algorithm at the individual level. By identifying these fundamental rules, we can essentially generalise between different collective systems that follow similar dynamics. Hence, a bunch of schooling fish and a crowd of people trying to escape from a burning building might behave in the same manner at the collective level (given the fundamental rules are the same for individuals in both systems) even though as individuals humans are very different from fish.

Paper: - *"Complexity, Pattern, and Evolutionary Trade-Offs in Animal Aggregation" by Parrish et al.* [3] All animal aggregations may not necessarily be self-organized or driven by internal factors. External conditions like the state of the environment resource availability etc. can drive these processes. The patterns emerging from these collectives may or may not entail evolutionary benefits or adaptive value. Many a times, these patterns can be a mere artifact of the local rules and properties of individual behavior. Joining a group comes with certain trade-offs for the individual. The benefits of reduced predation (dilution and confusion effect), active retaliation (mobbing), increased awareness (group surveillance), protection (weaker juveniles protected by stronger adults by appropriate structuring and spatial distribution of the group) etc. comes at the cost of un-equitable distribution of benefits amongst the group members (skewed age wise spatial distributions in groups discussed above is disadvantageous to adults, skewed feeding benefits in groups where the vanguard individuals have access to greater resources as compared to the individuals on edge), sub-optimal group size etc. Given these pros and cons, groups (of sub-optimal sizes also) exist because at the individual level, it's better to be part of a group than be alone. However, given the un-equitable distribution of benefits in a group, selfish motives pose a threat to group integrity.

What I did not understand: -

1. What is mean field density of a swarm?
2. What is the diffusion approximation of random motion?
3. Why repulsion should have a greater non-linear density dependence than attraction? They are two sides of the same coin, right? (More attraction = less repulsion and vice-versa)
4. What are Lagrangian equations?

2.2 Models and analysis

Paper: - *"Novel Type of Phase Transition in a System of Self-Driven Particles" by Vicsek et al.* [4] The authors introduce a simple non-equilibrium model with novel type of dynamics in order to analyze phase transitions in a system of self-driven particles. In the model, all the particles are driven with an absolute velocity ν. The direction of velocity is updated at regular intervals, such that the new direction is equal to the average direction (the notion of "average direction" is a bit ambiguous, but has been clearly defined in the paper) of all neighbors within a radius $\mathbf{r}$, plus some random noise. This noise is parameterized by η {the noise term is chosen with a uniform probability from the interval $\mathbf{(-\eta/2,\ \eta/2)}$}. All the simulations are conducted in a 2D square of side $\mathbf{L}$. The density of self-propelled particles is $\mathbf{N/L^2} = \rho$. A kinetic order parameter is defined as,

$$v_a = \frac{1}{Nv}\left|\sum_{i=1}^{N} v_i\right|$$

The authors expect, based on the finite size scaling analysis, that the system will give phase diagrams analogous to a system of disordered ferromagnets with $\eta_\mathbf{c}$ playing the role of temperature and ρ playing the role of density of spins. Analysis shows that,

1. As the noise η decreases, the system transitions from a disordered phase to a coherent phase with particles moving in a uniform direction for a fixed density ρ in varying box sizes.
2. For a constant noise η, with increasing density ρ the system transitions from a disordered state to an ordered state of coherent motion.

What I did not understand: -

1. The scaling analysis part.
2. Thermodynamic limit of the model.
3. Why is it called spontaneous symmetry breaking of the rotational symmetry? I have intuitive understanding, but no concrete knowledge of what is symmetry breaking (in case something like that exists).

Paper: - *"Geometry for the Selfish Herd" by W. D. Hamilton* [5] *unrelated thought: - It would have been an awesome pun if researchers discovered similar dynamics in groups of crustaceans and named the paper "Geometry for the Shell-fish Herd"* The paper can be viewed in three sections:

1. Arguments against gregarious behavior and formation of collectives being a consequence of group selection, a.k.a., for the good of the species.
2. Discussion of marginal pruning as a mechanism for preserving or generating gregarious instincts/centripetal tendencies in prey species.
3. Introduction and discussion of a simple geometric model for explaining the dynamics of a "selfish herd" of cattle.

1. Arguments against group selection: -
    (a) The author first discusses a one-dimensional prey-predator model. It introduces the concept of the domain of danger; the area corresponding to a prey item such that, at every point in that area, that prey item is the closest one.
    (b) Using this concept and a series of logical arguments, the author describes how aggregation in prey items can be induced by "cover-seeking behavior". This can be seen as the first evidence to show that one can explain gregarious behavior without having to invoke any notion of group selection or "working for the good of the species".
    (c) In fact, if anything, such behavior could be detrimental to the species as a whole since such aggregations attract predators and offer a buffet of possible targets.
2. Marginal pruning : -

   (a) There are many examples where marginal pruning (predation from outside the herd causing members at the periphery to be preferentially predated) causes gregarious behavior in otherwise non-gregarious animals.
   (b) It is relatively obvious that marginal pruning can preserve centripetal tendencies, however, it can be shown that gregarious behavior can develop even when the predator is present amidst a field of unsuspecting prey.

3. Geometry for the selfish herd: -
   I feel that the idea behind this model can be summarized by the following quote, "If a tiger is chasing a bunch of men, in order to escape, you don't have to be faster than the tiger. You just have to be faster than the slowest man."
4. The assumptions for the model are as follows:
   (a) Each prey item (cattle) has its corresponding domain of danger.
   (b) The predator (a lion) will attack/try to capture the nearest prey item.
   (c) The predator's location is unknown and hence can be assumed to be anywhere.

5. Given this model it's easy to see that each prey item would try to minimize its domain of danger. The steps one individual must take in order to minimize its domain of danger are incredibly complex and nonapparent. This is because the movements of one individual will/should affect the decisions of the others. However, we can make some general observations about the situation with the information we have:
   (a) Movement towards the nearest neighbor does not guarantee maximum decrease in domain of danger. It can, in some cases, lead to an increase in the domain of danger, especially if the nearest neighbor is an isolated individual.
   (b) This tends to happen in cases where the prey item has a small number of neighbors, i.e., when the domain of danger is a polygon with a small number of sides (refer figure **??**).
   (c) When the individual has a many-sided domain, movement towards its nearest neighbor is almost inevitably accompanied by a decrease in the domain of danger.
   (d) We can conclude, that in general, it is useful for cows to approach their nearest neighbor. In fact, such tendencies have been shown in many animal systems.

6. In real life, the herds observed are much larger than the herd sizes observed in simulations. The author postulates that once smaller, primary groups have formed, secondary condensations can lead to the unification of these smaller groups based on similar principles discussed above. An infinite series of these condensations can hence lead to large herds.

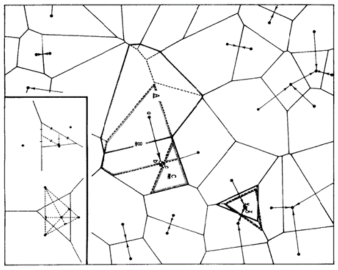

Figure 1: Domain of danger of prey items on a 2D plane

What I did not understand:

1. The figure in the paper (refer figure 1) is very difficult to read, hence some nuances of the model analysis were difficult to understand.

Paper: - *"Collective Memory and Spatial Sorting in Animal Groups" by Iain Couzin et al.* [6] The authors introduce a simple, yet biologically meaningful model for collective motion. They do so by incorporating abstractions of the attraction and repulsion tendencies of animals into their model. The paper also examines a novel type of "group memory" or hysteresis that had never before been explored. The model is as follows:
The group consists of N individuals $\{i = 1, 2, 3, \dots, N\}$. Each individual's position and orientation are denoted by the vectors $\mathbf{c}_i$ and $\mathbf{v}_i$ respectively. Time is simulated in discrete steps τ.
There are three spatial zones defined for each individual:

1. *zor*: Zone of repulsion. This is a spherical volume of radius r_r around the focal individual.
2. *zoo*: Zone of orientation. This is a spherical shell of width $\Delta r_o = r_o - r_r$ around the focal individual.
3. *zoa*: Zone of attraction. This is a spherical shell of width $\Delta r_a = r_a - r_o$ around the focal individual.

The direction of the i-th individual at time $t+\tau$ is denoted by $\mathbf{d}_i(t+\tau)$. $\mathbf{d}_i(t+\tau)$ follows the following rules:

1. If the number of neighbors in *zor*, $N_r \neq 0$, then
   $$\mathbf{d}_i(t+\tau) = \mathbf{d}_r(t+\tau),$$
   where $\mathbf{d}_r$ is given by,
   $$\mathbf{d}_r(t+\tau) = -\sum_{j \neq i}^{N_r} \frac{\mathbf{r}_{ij}(t)}{|\mathbf{r}_{ij}(t)|}.$$
2. If $N_r = 0$ or if $\mathbf{d}_r$ is a null vector, then $\mathbf{d}_o(t+\tau)$ is defined as,
   $$\mathbf{d}_o(t+\tau) = \sum_{j=1}^{N_o} \frac{\mathbf{v}_j(t)}{|\mathbf{v}_j(t)|}.$$

3. And $\mathbf{d}_a(t+\tau)$ is defined as,

$$\mathbf{d}_a(t+\tau) = \sum_{j\neq i}^{N_a} \frac{\mathbf{r}_{ij}(t)}{|\mathbf{r}_{ij}(t)|}.$$

4. If $N_a = 0$, then $\mathbf{d}_i(t+\tau) = \mathbf{d}_o(t+\tau)$.
5. If $N_o = 0$, then $\mathbf{d}_i(t+\tau) = \mathbf{d}_a(t+\tau)$.
6. If N_a and $N_o \neq 0$, then

$$\mathbf{d}_i(t+\tau) = \frac{1}{2}\left(\mathbf{d}_o(t+\tau) + \mathbf{d}_a(t+\tau)\right).$$

7. In case $\mathbf{d}_i(t+\tau)$ is a null vector, or there are no neighbors, then $\mathbf{d}_i(t+\tau) = \mathbf{v}_i$.

Some random noise is added to $\mathbf{d}_i(t+\tau)$ to simulate the stochastic effects that decision-making in animals is subjected to. This noise is added by rotating $\mathbf{d}_i$ through an angle obtained from a spherically wrapped Gaussian distribution with standard deviation σ.
Following the above rules, each individual updates its direction by turning at the rate θ. If the angle between $\mathbf{v}_i(t)$ and $\mathbf{d}_i(t+\tau)$ is less than or equal to the maximum turning angle $\theta\tau$, then $\mathbf{v}_i(t+\tau) = \mathbf{d}_i(t+\tau)$. Else, the individual turns $\theta\tau$ degrees/rads in the direction of $\mathbf{d}_i(t+\tau)$.

Analysis of the model: -

Two global properties are defined for the system for analysis:

$$p_{\text{group}}(t) = \frac{1}{N}\left|\sum_{i=1}^{N} \mathbf{v}_i(t)\right|$$

$$m_{\text{group}}(t) = \frac{1}{N}\sum_{i=1}^{N} \mathbf{r}_{ic}(t) \times \mathbf{v}_i(t),$$

where

$$\mathbf{r}_{ic} = \mathbf{c}_i - \mathbf{c}_{\text{group}}$$

$$\mathbf{c}_{\text{group}}(t) = \frac{1}{N}\sum_{i=1}^{N} \mathbf{c}_i(t).$$

The individual in front is defined as the individual with the greatest minimum distance from the plane perpendicular to $\mathbf{d}_{\text{group}}$ and passing through $\mathbf{c}_{\text{group}}$:

$$\mathbf{d}_{\text{group}}(t) = \frac{1}{N}\sum_{i=1}^{N} \mathbf{v}_i(t).$$

Results of Analysis: -
A change in the width of the behavioral zones Δr_o and Δr_a elicits sharp transitions between behavioral states of the system mentioned below (refer figure 2):

1. *Swarm*: An aggregate with cohesion but very low polarization. Occurs at high values of Δr_a and low values of Δr_o (virtually zero).
2. *Torus*: Individuals perpetually rotate around an empty core. p_{group} is small but m_{group} is large. Occurs at high values of Δr_a and low values of Δr_o.
3. *Dynamic parallel group*: Occurs at intermediate values of Δr_o and intermediate or high values of Δr_a.
4. *Highly parallel group*: Here p_{group} is very high, almost equal to 1. Occurs at high values of Δr_o.

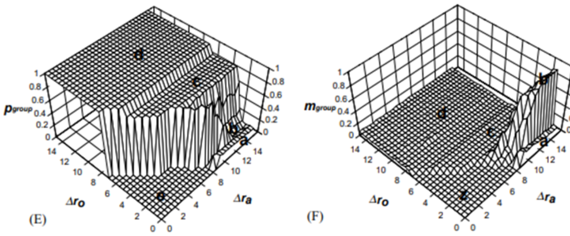

Figure 2: This figure shows how p_{group} and m_{group} vary with different values of r_o and r_a.

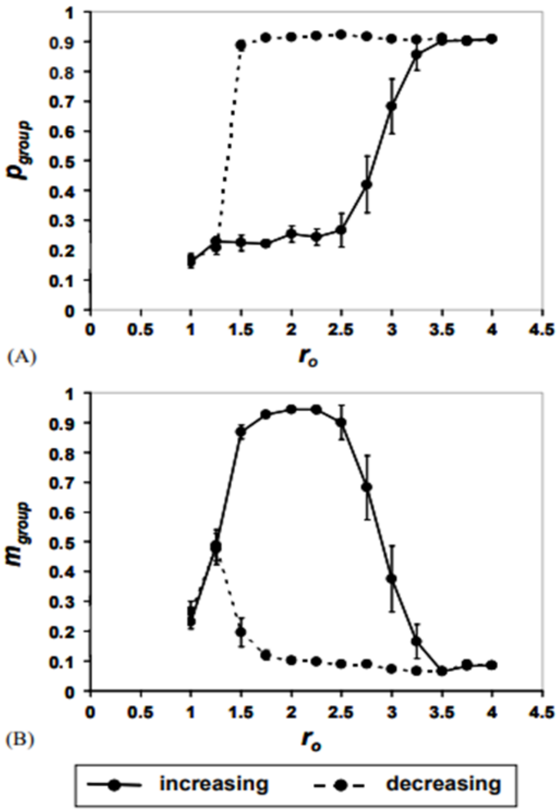

Figure 3: The system showing hysteresis behavior when p_{group} and m_{group} were measured as a function of r_o.

In the "e" region characterized by low Δr_o and low Δr_a, the groups have a greater than 50
As group size decreases, torus and dynamic parallel groups tend to become more restricted in the parameter space.

The field of perception α also plays a significant role in determining group dynamics. As α diminishes, torus becomes more common. Parallel groups become elongated along their principal axis as α diminishes. When it reaches 230° group fragmentation becomes common across the entire parameter space.

Turning rate essentially re-scales the parameter space.

r_o was increased and decreased back for a system. At each r_o step value, 2000-time steps were simulated. These r_o values were plotted against p_{group} and m_{group} on the y-axis. The increasing and decreasing plot lines show significant differences (refer figure 3), indicating that the previous history of the group influences transition between behavioral states (hysteresis).

Individual movement patterns can influence the position of individuals within the group. Individuals can essentially change their local position with respect to the group center ($\mathbf{c}_{\text{group}}$) even when they have no knowledge of their current position within the group or of the global group structure. For example, speed is strongly correlated with being in front of the group.

Individuals with smaller r_r tend to be near the center of the group. For all parameters, the strength of correlation tends to increase with an increase in variation among the individuals.

What I did not understand

1. This was a very easy-to-read (exciting) paper. Currently, I feel like I could understand all the aspects of the model and analysis presented here except for what is a spherically wrapped Gaussian.

Paper: - *"Flocks, Herds and Schools: A Distributed Behavioral Model" by C. W. Reynolds* [7] The paper presents a model for collective motion in an algorithmic fashion, emphasizing the lack of requirement of a global control system for a flock of moving objects (from here onwards, "boids"). The model presented here is very similar to the one discussed in the previous paper *"Collective Memory and Spatial Sorting in Animal Groups"*. The author's primary intention in developing said algorithm for simulating collective movement of boids, is to make the life of animators easier. Classical animation relies on the animator having to define the position of all objects in each frame, the trick being, that the animator would progressively and gradually alter the position/shape/lighting of a subset of those objects, giving the illusion of movement.

This algorithm aims to simulate flock movement by treating each boid as an independent computational unit that makes its own local decisions. As a result of each boid's local decisions, an emergent flock-like behavior appears. Hence, animators no longer need to tediously animate the flight paths of each and every boid in a flock, rather, the computer takes care of it. All one has to do now is set a global path or target for the flock (this target itself can be animated i.e. moved between frames), and the flock will follow this target in a natural fashion.

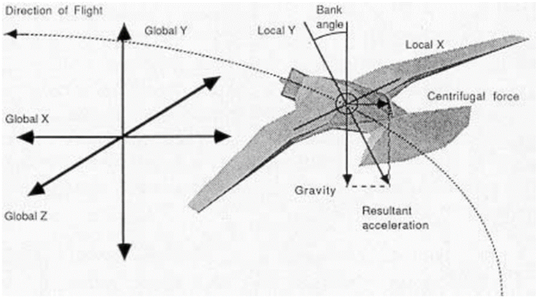

Figure 4: Geometric flight

Key Features of the Simulator: -

1. Unlike many particle systems where the particles involved can be approximated as tiny spheres or point masses, the boids involved here have a definite geometry, local spatial coordinates (implying local coordinate axes x, y, and z) and a local direction or orientation (defined as the direction of the local z axis).

2. **Geometric Flight:** Unlike in traditional animation, the path (3D curve) of the object is not defined beforehand but rather is incrementally updated using the local rules/algorithm followed by each boid. Each boid moves by incremental translations in its local positive z axis. These increments are intermixed with steering rotations (pitch and yaw) that align its local z axis appropriately with respect to the global coordinates (refer figure 4).

3. **Banking:** During steering, there is a lateral component of acceleration. While turning, centrifugal force and gravity form a diagonal resultant force. Correct banking aligns the local Y axis with this resultant force. In the limiting case of infinite velocity, the centrifugal force dominates over gravity and the local Y axis points at the center of the arc of curvature.

4. **Arbitration of Independent Behaviors:** There are three behavioral urges. They are listed below in the order of decreasing priority:

    (a) **Collision avoidance:** Avoid collision with nearby flock mates.

    (b) **Velocity matching:** Attempt to match the velocity with nearby flock mates.

    (c) **Flock centering:** Attempt to stay close to nearby flock mates.

    At each time interval, each behavioral urge produces an acceleration request. This is a 3D vector that is truncated to unit magnitude or less by the system. The task of merging, prioritizing, and arbitrating between the various acceleration requests is performed by the navigation module. The navigation module performs what is called **prioritized acceleration allocation**, whereby all the acceleration requests are

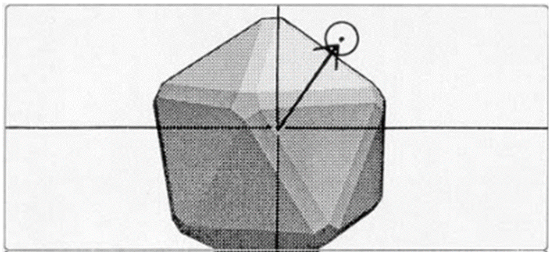

Figure 5: Steer to avoid method

considered in priority order (priorities of acceleration requests follow the priority order of the behavioral urges that generate them) and added to an accumulator. The magnitudes of the acceleration requests are added to another accumulator. This process continues till the sum of the magnitudes of all acceleration requests in the accumulator exceeds the maximum acceleration value (this is an intrinsic parameter of the boid). The magnitude of the last acceleration request is trimmed back to compensate for the excess accumulated acceleration magnitude. There is a finite amount of acceleration under the control of the navigation module; this acceleration is then parceled out to satisfy the acceleration requests. In emergency situations, if all available acceleration is used up by high-priority acceleration requests, some behavioral urges may remain temporarily unsatisfied.

5. **Simulated Perception:** The perception model tries to make available to the behavioral model the same information that would be available to a real animal in a flock. The behaviors that are responsible for the flock model are stated in terms of "nearby flock mates". Here the concept of neighborhood is defined as a spherical volume of sensitivity centered at the boid's local origin. The sensitivity is expressed as an inverse exponential of the distance. Hence, the neighborhood is defined by two parameters, a radius and an exponent.

6. **Scripted Flocking:** The migratory urge built into the boid model allows the animator to control the flock in time and space. The migratory urge can be a global direction vector (migratory direction) or a global position coordinate (target). This target can itself be animated. The target or global direction parameter can be passed on to the flock, which can then be passed on to each individual boid. Each boid then maintains its own "migratory goal register".

7. **Obstacle Avoidance:** The boid uses a **steer to avoid** method of obstacle avoidance (refer figure 5). The steps involved in this are as follows:
   (a) The boid considers only objects directly in front of it. This is accomplished by finding intersection points of its local positive Z axis with any obstacle.
   (b) Then, working in its local perspective space, it finds the object's silhouette edge closest to the point of eventual impact.
   (c) A radial vector is computed that will aim the boid at a point one body length beyond that silhouette edge.

What I did not understand

1. How do the boids incorporate the migratory urge? Does that entail an additional acceleration request at each time step on top of all the other basic requests? If this is indeed the case, then is it not sufficient to pass on the global target/direction to a subset of the boids, as the others will follow suit anyways? If yes, is there a threshold number? What is that number? What all does this threshold depend on?
2. In case of emergencies, do pending acceleration requests affect the subsequent time steps?
3. If acceleration is parceled out to meet several acceleration requests (weighted by their magnitudes), then is it not functionally similar to the weighted average?
4. What is a phase portrait of a force field?

3 Tutorial

The following topics were covered in the tutorials

(click the icon to view embedded PDF) 📎: -

1. Dynamic Processes
   (a) Discrete
   (b) Continuous
2. Random Variables
   (a) Discrete
   (b) Continuous
3. Probability Mass Function
4. Joint Density Function
5. Conditional Density
6. Marginal Density
7. Expectation
8. Variance
9. Correlation and Coefficient of Correlation
10. Markov Property
11. Ideal Independent Distribution (IID)
12. Random Walk
13. Brownian Motion
14. Stochastic Calculus
15. Reimann-Steiltjes and Stratonovich integrals
16. Stationary Process
17. Autocorrelation
18. Cross-correlation and Leader-Follower Dynamics
19. White Noise
20. Consensus in foraging ants
21. Marching locusts

4 OBSERVATIONS

1. **Ants:** We have observed colonies of weaver ants around campus. We were lucky enough to observe and capture images of nest building behavior. Utilizing the GoPro and a gorilla tripod, we have recorded continuous video footage (40 minutes) of weaver ant traffic from and to their nests. Additionally, we recorded short video footage of weaver ants transporting food items such as dead millipedes, insects, and even other ant species!

2. **Bats:** We observed and recorded huge groups of bats flying Westward coherently at dusk (6:15-7:00pm). It remains to be ascertained whether this behavior is driven by collective instincts or other factors, as the groups are very widely spread out (low density) and the individuals do not seem to show any signs of collective motion. Although the group is very polarized (towards South-West direction).

3. **Red Bugs (Cotton Tree Silk Bug?):** We found massive groups of these vibrant red bugs inside the plant nursery inside campus.

4. **Parakeets:** We observed and recorded flocks of parakeets moving to the safety of trees to take shelter for the night. Large flocks come and perch on trees to the point where there are more birds on the tree than leaves.

5. **Fish:** We observed schooling behavior in what we think are juvenile fish on our visit to Sanky Tank Lake. The tiny fish formed a dense school around what we think were the parent couple. Thanks to JVH having a pool with a lot of fish in it, we could observe the dynamic nature of schooling behavior in the fishes, whereby they form tight, polarized schools when threatened and disperse once they no longer perceive the threat.

6. **Swans:** Thanks to their fearless and docile nature, we could get good videos of groups of swans swimming in tight formations. We could also notice how the formations changed from a strict line, to a V shape and back, etc.

7. **Pigeons:** We have instances of large groups of pigeons (20-30) feeding. There seems to be brief interactions of competition, aggression, and territorialism between the individuals whilst feeding. The collective aspect of such groups (if any) remains to be investigated.

8. **Flies (Nematoceran Flies or Gnats):** We have observed drosophila-like flies (maybe even smaller) flying in tight ball-like formations, hovering in a fixed space for a considerable duration. This seems like a very intriguing case of collective motion.

9. **Millipedes:** We have observed millipedes around the campus for about 2 weeks now. They tend to occur in groups (about 3-4 individuals/m^2), although lone individuals are also spotted frequently. From observation, it would seem that the aggregation of these millipedes is driven by a pursuit for resources, mating opportunities, and favorable conditions more than anything else. Unobservable factors like soil condition, pH, etc. might also affect the millipede distribution. They are relatively immobile for the major part of their day (aka lazy). They spend most of their day munching on fallen and rotten fruits, moss, algae, and probably other vegetation. They seem to avoid or ignore their conspecifics when encountered. This is done by either changing their direction of motion when confronted with a conspecific or alternatively, climbing over the conspecific so as to get away from them. There is great polymorphism in the size, shape, and coloration of the millipedes. We cannot ascertain whether there are multiple species or whether it is intraspecific variation.

5 GAME THEORY

5.1 GAME THEORY AND SOCIAL FORAGING [8]

The field of "Social Foraging Theory" deals with the economic modelling of optimal foraging strategies using game theory in situations where there is frequency dependant payoffs. There can be simple dependence, as in the Ideal Free Distribution (IFD) *n-person, alternative option* game, or compound dependence, as is the case in the Producer-Scrounger Game (PS Game). Compound dependence refers to the situation where the payoff associated with a particular strategy depends on the frequency of players using that particular strategy and also on the frequency of players using alternate strategy.

5.1.1 THE CLASSIC PRODUCER-SCROUNGER GAME

Let q be the proportion of producers in a population, so that the number of scroungers is $1 - q$. The fitness of each strategy falls as an inverse function of its frequency (refer figure 6.

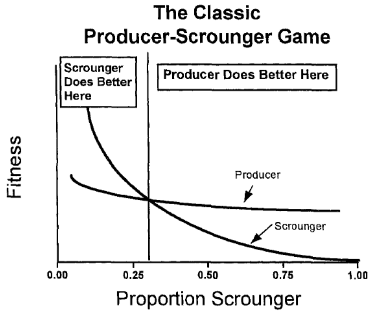

Figure 6: Characteristic fitness functions of a PS game

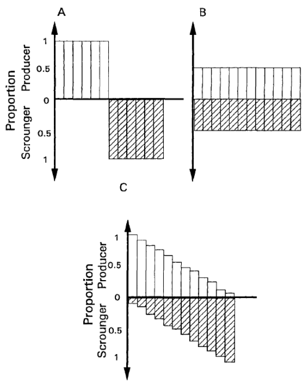

Figure 7: Three theoretically possible frequencies of producer and scrounger alternatives within a group of twelve foragers

In such a scenario, we expect the population to exist in equilibrium condition (refer figure 7) such that,

$$W(q^*|P) = W(q^*|S)$$

and,

$$dW(q|P)/dq|_{q=q^*} < dW(q|S)/dq|_{q=q^*}$$

5.1.2 Rate Maximizing PS Game

In this game, the hypothesized currency of fitness is the mean gross energy intake *(I)* over some time horizon T. The equilibrium frequency of producers can be found to be,

$$a/F + 1/G = q^*$$

Thus, the equilibrium proportion of producers in a population depends on two factors, the group size ($1/G$) and the "finders share" (a/F) (refer figure 8).

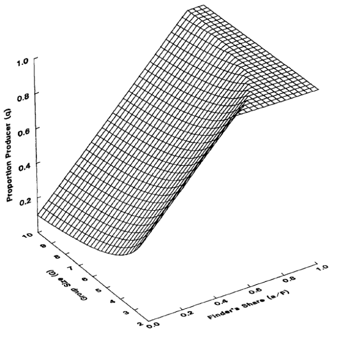

Figure 8: Equilibrium proportion of producers q^* as a function of $1/G$ and finders share a/F

5.1.3 Shortfall Minimizing PS Game

In this model, the assumption that fitness increases linearly with energy obtained is challenged. Here, the optimality criterion becomes the "probability of an energetic shortfall". This probability is a function of the physiological minimum energy requirement, energy expenditure entailed by the foraging strategy, expected energetic payoff and the variance of this payoff. The total number of food items procured by a producer follows a "Poisson-binomial" probability function with mean and variance,

$$E[X_i(T)] = \theta c\lambda T$$

$$V[X_i(T)] = \theta c\lambda T(1 - \theta + \theta c)$$

The total number of food items procured by a scrounger also follows a "Poisson-binomial" function with mean and variance,

$$E[X_j(T)] = (1 - \theta)cG_p\lambda T/G_s$$

$$V[X_j(T)] = ((1-\theta)cG_p\lambda T/G_s)(1-(1-\theta/G_s)+((1-\theta)c/G_s))$$

where, θ = the probability of a food item within a food patch being consumed by the producer, $(1 - \theta)/G_s$ = the probability of a food item being consumed by a scrounger, λ = the rate of patch encounter by a producer, c = the number of food items in each patch. It is interesting to note that in cases where the minimum energy requirement $R < \langle E \rangle$, the strategy with least variation in energy payoff is preferred, whereas, when $R > \langle E \rangle$, the strategy with greater variance in energetic payoff is preferred. The probability for energetic shortfall for a producer is denoted by z_p and that for a scrounger is z_s such that,

$$z_p = (R - \theta c\lambda T)/\{\theta c\lambda T(1 - \theta + \theta c)\}^{1/2}$$

$$z_s = (R + \rho - \{(1 - \theta)cG_p\lambda T)/G_s\}/\{V[X_j(T)]\}^{1/2}$$

where ρ = the energetic cost of playing the scrounger strategy.

The effect of rate of patch encounter, future food requirement, cost of scrounging ρ, physiological requirement R and group size on the equilibrium proportion of producers can be theoretically derived and experimentally tested.

5.2 Game Theory and Cooperation [9]

The chapter deals with the applications of game theory in behavioral evolution as a tool to explain the emergence of cooperation amongst a collection of selfish agents (individuals). There are three major ways in which cooperation might evolve as described in the book:

5.2.1 Reciprocal altruism

The primary game used to explore the emergence of cooperation through reciprocity is the infamous Prisoners Dilemma or PD game. Axelrod and Hamilton proved the evolutionary stability of TFT by proving that for sufficiently high w, also called shadow of the future, neither ALLD nor ALTDC can invade a population of TFT. The authors enlist a plethora of papers on PD variants and their novelties, inspired by Axelrod and Hamilton's initial paper.

Examples of cooperation selected by reciprocal altruism:

1. Egg swapping in hermaphroditic fish: Hermaphroditic fish engage in pairwise egg and sperm release. One turn consists of eggs released by one individual met by sperms from the other and vice-versa. This behavior can be modelled as a PD game where b is the benefit gained by fertilizing eggs (assume sperms are free i.e. do not cost anything to produce), c is the cost of producing eggs, p is the probability that a defector will release eggs on its turn without "defecting". For $p < 1$, this qualifies as a PD game and TFT can become a stable solution for $w > c/b$. However, in nature, individuals seem to be employing a forgiving variant of TFT like Generous TFT, because pairs only reciprocate 80% of the time and yet they stay together for long periods of time.

2. Reciprocal grooming in Impala: There is strong evidence for reciprocal allogrooming in impala. The benefits of grooming include reduction in tick load and other ectoparasites. Costs include energy expenditure, loss of vigilance, and loss of electrolytes via saliva. The degree of reciprocity is astounding in that there is almost a one-to-one correlation between the number of grooming bouts delivered and those received.

5.2.2 Group selection

The group selection theory of evolution of cooperation is fairly simple. The notion of a group here refers to a "trait group" i.e. a collection of individuals such that every individual feels the effect of every other individual. Group selection can operate in cases where the cost to the individual performing the act (intra-group costs) is overcompensated by the competitive advantage gained by the group over other groups (inter-group benefit). The necessary condition here is that groups with higher frequency of cooperators should be able to outcompete those with lesser number of cooperators. Note that the success of TFT can be alternatively viewed as a case of group selection rather than reciprocal altruism.
Examples of group-selected cooperation:

1. Raiding and warfare in chimpanzees: Chimpanzees form "all-male" raiding groups and patrol the territorial boundaries. These raiding parties avoid the use of vocalizations and move stealthily. Raids involve the killing of a small number of members of the raided group and entail the capture of females. There is strong within-group selection against individuals being part of these raiding groups (intra-group cost) and strong selection for groups that perform such raids (inter-group benefit)

2. Pleometrosis in Acromymex versicolor: Pleometrosis refers to a condition where colonies have multiple foundresses (queens). In Acromymex versicolor colonies, the queens forage after colony foundation. The forager queen shares the food with the other foundresses. Here the individual cost of foraging is borne by the cooperative queen (intra-group cost), which leads to a greater number of workers produced by the colony, which in turn leads to an increase in the probability of survival of the nest during the brood raiding period (inter-group benefit).

5.2.3 By-product mutualism/pseudo-reciprocity

By-product mutualism refers to the situation where by the act of performing bare minimum self-services, other individuals are benefited as a by-product. These are activities that a solitary individual must do regardless of the presence of others, such as hunting. The hierarchy of payoffs is $CC > CD > DC > DD$. The concept of pseudo-reciprocity refers to the act of investing in by-product mutualism. By-product mutualism and pseudo-reciprocity reduce the temptation to cheat that the individuals normally face in a PD game.
Examples of cooperation selected by by-product mutualism:

1. Cooperative territorial defense in pied wagtails: We can aptly title the following game as "the owner's dilemma". Wagtails defend riverside winter territories since they provide renewable resources that wash up. They forage their territories periodically allowing certain patches to renew their resources. Intruders who land on such territories are sometimes tolerated in exchange for shared territorial defense. However, it is interesting that the choice of whether to tolerate or evict an intruder depends on the status of the territory. During high food abundance, intruders are tolerated, whereas during periods of low food abundance, intruders are chased off. Hence the owner's dilemma. This illustrates that the costs and benefits of engaging in by-product mutualism can be condition-dependent and dynamic.

2. Controlled experiments on blue jays: The experiment is as follows, a pair of blue jays are given the option to peck on two buttons; a cooperate button and a defect button. The payoffs are controlled so that first, the pair engages in a PD game. Subsequently, the payoffs are altered so that the matrix corresponds to a by-product mutualism or M matrix. Finally, the payoffs are once again altered to bring the matrix back to a PD matrix or P matrix. Regardless of whether the birds could see each other or not, a consistent pattern was observed, that the birds cooperate in the M matrix but defect in the P matrix. Hence, their cooperation can be best explained as a case of by-product mutualism.

5.2.4 Challenging assumptions of established game theoretic models:

Assumptions:

1. Partner choice is random

2. Behavioral repertoire is discrete, with two alternative options; cooperate or defect. There is no continuum.

Challenge:

1. Predator inspection in guppy: Guppy form small predator inspections groups that break off from the main school to approach and inspect the oncoming danger. This has several benefits. Because of the costs and benefits of predator inspection, Milinsky (1987) suggested that inspectors were trapped in a prisoner's dilemma, where inspection equals cooperation and not doing so equals defection. Controlled experiments reveal that guppies, irrespective of their own strategy (cooperator or defector), prefer cooperative partners.

2. The extent of cooperation is signified by the distance of approach to the perceived danger on the first attempt. Thus, the extent of cooperation is a continuous variable and whether an individual is a cooperator or a defector is relative and specific to a pair. All cooperators are not equal.

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