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14. ABSTRACT Due to the rapid growth of animal movement data obtained by GPS, radio tracking collars and other means, there is a growing recognition that classical models of encounter rates among animal populations should be revisited. Recent theoretical investigations have demonstrated that biologically relevant modifications to classical assumptions about individual behavior can bring about non-trivial changes in the formulation of population-scale dynamical systems. In particular, the combination of tracking data with habitat information has revealed the <del>substantial impact that environmental factors have on animal movement and sociality.</del>
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## Report Title

Final Report: The Stochastics of Movement Ecology

### ABSTRACT

Due to the rapid growth of animal movement data obtained by GPS, radio tracking collars and other means, there is a growing recognition that classical models of encounter rates among animal populations should be revisited. Recent theoretical investigations have demonstrated that biologically relevant modifications to classical assumptions about individual behavior can bring about non-trivial changes in the formulation of population-scale dynamical systems. In particular, the combination of tracking data with habitat information has revealed the substantial impact that environmental factors have on animal movement and sociality.

This project directly confronts popular models for animal movement that are neither mathematically sound nor ecologically coherent. In our work, we deconstruct the existing conventional wisdom that supports the use of so-called "Levy flight" models that seek to describe animal movement in the absence of environmental cues, and, through a few examples, we make the case that animal movement patterns should not be separated from the spatial environmental features that shape them. In fact, animal sensing and decision-making are "leading-order" effects, and their study gives rise to new ecological observations and novel mathematical challenges.

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**Enter List of papers submitted or published that acknowledge ARO support from the start of the project to the date of this printing. List the papers, including journal references, in the following categories:**

**(a) Papers published in peer-reviewed journals (N/A for none)**

<u>Received</u>	<u>Paper</u>
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**TOTAL:**

**Number of Papers published in peer-reviewed journals:**

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**(b) Papers published in non-peer-reviewed journals (N/A for none)**

<u>Received</u>	<u>Paper</u>
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**TOTAL:**

**Number of Papers published in non peer-reviewed journals:**

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**(c) Presentations**

Statistics and Nonlinear Dynamics in Biology and Medicine, Banff, AB, Canada, July 27 - Aug 1, 2014: "Sensing and Decision Making in Random Search."

University of Tampa, Mathematics Department Lecture Series, Sept 30, 2014: "Sensing and Decision Making in Random Search."

Number of Presentations: 2.00

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**Non Peer-Reviewed Conference Proceeding publications (other than abstracts):**

Received      Paper

**TOTAL:**

Number of Non Peer-Reviewed Conference Proceeding publications (other than abstracts):

---

**Peer-Reviewed Conference Proceeding publications (other than abstracts):**

Received      Paper

**TOTAL:**

Number of Peer-Reviewed Conference Proceeding publications (other than abstracts):

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**(d) Manuscripts**

Received      Paper

**TOTAL:**

Number of Manuscripts:

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**Books**

Received      Book

**TOTAL:**

Received

Book Chapter

**TOTAL:**

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**Patents Submitted**

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**Patents Awarded**

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**Awards**

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**Graduate Students**

<u>NAME</u>	<u>PERCENT SUPPORTED</u>	<u>Discipline</u>
Jason Flynn	0.50	
<b>FTE Equivalent:</b>	<b>0.50</b>	
<b>Total Number:</b>	<b>1</b>	

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**Names of Post Doctorates**

<u>NAME</u>	<u>PERCENT SUPPORTED</u>
<b>FTE Equivalent:</b>	
<b>Total Number:</b>	

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**Names of Faculty Supported**

<u>NAME</u>	<u>PERCENT SUPPORTED</u>	<u>National Academy Member</u>
Scott McKinley	0.33	No
<b>FTE Equivalent:</b>	<b>0.33</b>	
<b>Total Number:</b>	<b>1</b>	

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**Names of Under Graduate students supported**

<u>NAME</u>	<u>PERCENT SUPPORTED</u>
<b>FTE Equivalent:</b>	
<b>Total Number:</b>	

**Student Metrics**

This section only applies to graduating undergraduates supported by this agreement in this reporting period

The number of undergraduates funded by this agreement who graduated during this period: ..... 0.00

The number of undergraduates funded by this agreement who graduated during this period with a degree in science, mathematics, engineering, or technology fields:..... 0.00

The number of undergraduates funded by your agreement who graduated during this period and will continue to pursue a graduate or Ph.D. degree in science, mathematics, engineering, or technology fields:..... 0.00

Number of graduating undergraduates who achieved a 3.5 GPA to 4.0 (4.0 max scale):..... 0.00

Number of graduating undergraduates funded by a DoD funded Center of Excellence grant for Education, Research and Engineering:..... 0.00

The number of undergraduates funded by your agreement who graduated during this period and intend to work for the Department of Defense ..... 0.00

The number of undergraduates funded by your agreement who graduated during this period and will receive scholarships or fellowships for further studies in science, mathematics, engineering or technology fields:..... 0.00

**Names of Personnel receiving masters degrees**

<u>NAME</u> Jason Flynn	
<b>Total Number:</b>	<b>1</b>

**Names of personnel receiving PHDs**

<u>NAME</u>	
<b>Total Number:</b>	

**Names of other research staff**

<u>NAME</u>	<u>PERCENT SUPPORTED</u>
<b>FTE Equivalent:</b>	
<b>Total Number:</b>	

**Sub Contractors (DD882)**

**Inventions (DD882)**

## Scientific Progress

This is a final report for effort made at the University of Florida. The PI, Scott McKinley, moved from University of Florida to Tulane University in August 2015. Though this is a "final report", effort is continuing.

The overarching theme of this proposal is: sensing and decision-making in animal search. In this report, I will describe three distinct research efforts. Mathematically, this the development of models rests on (at least) these three components:

- Developing a model for resource (or prey) distribution (Projects A and B below)
- Developing a model for consumer (or predator) movement, especially in the way it is modulated by sensory perception (Projects A and C)
- Utilizing multi-scale methods to relate individual-based behavior to population-scale dynamics. (Project A, B and C)

To summarize progress: the mathematical and statistical work is completed for Projects A and B. A manuscript has been submitted for B and one is forthcoming for A. Progress on Project C has been more difficult to come by. But we see a way forward for progress.

#### A) "The Spread of Disease in Fractured Landscapes"

The most substantial progress over this reporting period relates to the spirit of the project proposed in Section 5 of my ARO proposal. The work has been spearheaded by my graduate student, Rebecca Borchering, (she was not funded by ARO because of existing funding that was available to her through an NSF IGERT program at U-Florida) with important contributions by Jason Flynn (graduate student funded by the ARO), Juliet Pulliam (Asst. Prof. at UF in Biology and the Emerging Pathogens Institute) and Steve Bellan (Postdoc at UT-Austin, Center for Computational Biology and Bioinformatics).

In this work we consider the process of pathogen spillover between two neighboring populations -- one of which is naive to the disease, while in the other, the disease is endemic -- and we consider the question of how changes movement patterns within the susceptible population might make them vulnerable to pathogen invasion. The question stemmed from observations made by Bellan while studying a jackal population in Etosha National Park under the guidance of his advisor Wayne Getz (UC-Berkeley). Bellan noted that when an anthrax outbreak attacked a local zebra population, this led to very large nightly congregations of jackals that would gather at the carcass site. While jackals do not appear to be affected by anthrax, it occurred to him that the increased interactions among jackals effectively changes the within-species encounter rate that informs the basic disease reproduction number  $R_0$ . Specifically, for a disease like rabies, which is consistently introduced to the jackal population by way of a local domesticated dog population, the increased conspecific encounters could cause a previously subcritical population to become supercritical with respect to the disease and vulnerable to outbreak.

To summarize, he basically wondered: Can anthrax in one species "cause" rabies in another just by changing their intrinsic movement behavior?

In the manuscript, for which the mathematical and statistical work is completed, we accomplished the following:

- We developed a consumer-resource model wherein consumers travel to the nearest resource assuming a resource lies within a limited range of perception;
- We estimate the potential magnitude of resource-induced spikes in consumer conspecific encounter rates, identifying the resource density that leads to the greatest behavioral changes. Interestingly, we observe an important sense in which small resource pulses can be far more dangerous than large ones.
- To put the above results in context, we equip the model with biologically relevant parameters informed by the data collected by Bellan and colleagues, as well as by known parameter estimates for the spread of rabies in carnivore populations. We show that the expected encounter rates are substantially larger than would be necessary to transition the jackal population from being subcritical with respect to rabies to supercritical.

In our theoretical setting, anthrax can indeed "cause" rabies!

More seriously, we believe that this paper will serve as an excellent start in developing a framework for studying the spread of disease in fractured landscapes. The next phase is to take our other developing work on animal movement to directly model the spillover interactions between neighboring populations.

#### B: On the relationship between movement and population settlement patterns.

The paper submitted in connection to this grant was developed in response to an opportunity to work with an exceptional ecologist Craig Osenberg (Univ. Georgia, School of Ecology) and his graduate student Elizabeth Hamman. The submitted manuscript, entitled "Spatial patterns of symbionts arising from propagule redirection" focuses on how coral occupants interact with their habitat to influence spatial patterns on reefs.

The ecological motivation for this work was the observation by my colleagues that the settlement patterns of fish that live in symbiosis with corals often exhibit a very high degree of heterogeneity. Ecologists would like to determine whether these settlement patterns are necessarily the result of disparities in the quality of coral habitat (some coral patches just might be nicer places to live); whether there is evidence that the fish larvae are attracted to or repelled from corals where other fish are already living; and whether the spatial configuration of the corals plays a significant role in the distribution of the settlers.

This work has important implications for coral conservation. Fundamentally, marine ecologists in the field would like to know: If I build an artificial reef upon which a new coral population can grow, am I creating more habitat, thereby increasing the overall population size of corals and their symbionts; or am I simply stealing symbionts from existing corals, thereby exacerbating the crisis?

While the ecological motivation for this work is very different than my other work, the underlying mathematical framework was, in fact, a launching pad for the models used in Project A. Coral patch locations are modeled as a spatial Poisson process and fish larvae are distributed uniformly in the relevant section of the ocean. The coral habitat produces a signal of some kind (the nature of the signal is not yet clear to field ecologists) and the fish larvae choose a place to settle by a weighting function that takes into account the relative quality of the coral patches. Once the settlers are on their respective coral patches, population dynamics ensue, with important density-dependent effects.

We characterize a fully parameter space using a mix of numerical and analytical methods from dynamical systems and stochastic processes theory. Much like the results from Project A, we found that the spatial configuration of the resource population (in this case the corals) can have profound effects on the consumer population dynamics.

The results from Projects A and B both serve to demonstrate that classical mean-field approximations for consumer-resource models can miss qualitatively important aspects of population dynamics.

Project C: Developing a transient encounter rate theory.

This has been a focused effort with ARO-funded graduate student Jason Flynn and has been much more difficult than we originally anticipated. One of the aims of the proposal is to revisit Smoluchowski's encounter rate theory in the context of animal movement encounters, using the tools of general Levy processes. The Smoluchowski approach is to consider an absorbing sphere (or circle in 2d) at the origin, that absorbs random walker as they make contact. It is a steady state PDE calculation, which has two intrinsic flaws for our purposes. The first is that the method does not work in two dimensions. Because random walkers are recurrent -- eventually visiting all locations in the plane -- all walkers are absorbed in the long-run, and so no non-trivial stationary distribution exists.

During the 2013-14 reporting period Flynn developed a simulation platform to analyze the problem of encounter rates in the short term. During the recent period we have analytically studied the problem for Brownian motion (several closely related problems appear in Redner's book "A Guide to First-Passage Processes", but there do not exist any formulations that we know of that start the analysis with a rigorously defined stochastic process) and have researched and settled on what process we will use for the non-Brownian problem.

The problem set-up is as follows: there is an inner circle of radius epsilon that absorbs any walkers that enter it. There is a fixed intensity, rho, for the walkers; and their initial distribution is given by a Poisson process with intensity rho in a circle of size R. We then estimate the expected value of the number of walkers who enter the inner circle as a function of time. Call this  $N(t)$ . The function is monotonically increasing and because random walk is neighborhood recurrent in 2d, eventually all walkers are absorbed and  $N(t)$  therefore approaches  $2\pi R^2 \rho$  (the mean value for the number of walkers in the model) as  $t$  tends to infinity. If we repeat the experiment for increasing values of R, that saturation point increases and increases, but at shorter time scales all of the curves overlap. As we take R to infinity, the sequence of truncated encounter functions approach a limiting function. We have estimates for this limiting function and see that it has a nonlinear power law scaling that depends both on dimension and the density.

Unfortunately, most of the methods that provide exact results in 1d -- in particular the reflection principle for Brownian motion (or the method of images for the heat equation) -- do not apply in higher dimensions. We will have to be more creative in our approach to divining the encounter rate for higher-dimensions and we have several ideas on how to proceed.

### **Technology Transfer**