

RELATIVE MOTION AS AN ECOLOGICAL MECHANISM

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Relative motion as an ecological mechanism
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ABSTRACT

Relative motion is an ecological mechanism with the power to change the stability and longevity of populations and predict large scale movement patterns in highly mobile species. This dissertation introduces relative motion as an ecological mechanism using simulations and experiments at varying levels of spatial complexity. Chapters 2 and 3 describe the interactions between population movement and one-dimensional habitat movement, while Chapters 4 and 5 focus on the interactions between individual movement and three-dimensional habitat movement. Chapters 2 and 4 lay out my model justification, model development, and simulation results, while the remaining two chapters describe case studies competing those models with data. In Chapter 2, I simulate populations chasing moving habitat using stochastic spatial spread models. Results from these simulations show that populations lose symmetry when the habitat begins to move and suggest that loss of symmetry increases extinction risk. Results also show that assisted migration can restore some of that lost symmetry, but the success of assisted migration is sensitive to the transplant location and habitat speed. In Chapter 3, I build on the simulations presented in Chapter 2 by investigating assisted migration as a method of restoring symmetry using *Tribolium* microcosm experiments. Experimental results show that assisted migration both restored symmetry to the moving populations under fast-moving habitat conditions and significantly reduced extinction risk compared to the controls. Chapter 4 describes a 3-dimensional Geographic Information System (GIS) to track multiple sources of relative motion in the environment at once, using rigid body mathematics to move individual components in their own direction. In Chapter 5, I apply this GIS to deconstruct the migratory paths of 22 Greater shearwater (*Puffinus gravis*) migrants and rank the relative contributions of solar, wind, temperature, humidity, and surface cues to the figure-8 shaped migratory paths observed in this species.

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CHAPTER 1

INTRODUCTION TO ECOLOGICAL RELATIVE MOTION

The natural world is a complex system where individual components, such as weather patterns, organisms, and atoms, move with their own speed and in their own directions.

Einstein's theory of relativity shows us that we fail to recognize much of this motion because we measure all motion relative to our own reference frame. This perception bias often leads us to collect deceiving measurements about the moving world around us. For example, both planets and electrons move extraordinarily fast when viewed at scales similar to their own, but they appear stationary when viewed from the scale of the human eye. This same perception bias makes it easy to forget that the stationary objects around us on Earth are actually moving with us at 1,000 miles per hour as Earth rotates around its axis.

In ecological systems, the motion of one component, such as climate, can cause the motion of other components, such as migrating individuals. When we fail to account for the movement of the first component, because of our perception bias, we run the risk of misunderstanding the true drivers of the second component's motion. In this example, the movement of the first component serves as the causal link (or "ecological mechanism") driving the movement of the second component. Throughout my dissertation, I present both theoretical and experimental results that demonstrate that relative motion provides ecological mechanisms for phenomena observed in natural systems.

Relative motion is when two objects move in different directions or at different speeds when compared with each other (Dawson 1991, Laube and Imfeld 2002, Laube et al. 2005). Relative motion is a known source of measurement bias because the observer inevitably views moving components from his/her own, unique perspective. There are many tractable examples of motion corrupting our perception, but a well-done optical illusion (Mathot 2012, designed by

Anstis and Kaneko 2014) stands out as a great demonstration of the power of motion to change our understanding of a scenario. In the animation in Figure 1.1, it appears as though Mario is jumping vertically and the Koopa shell is gliding horizontally. Surprisingly, when the background stops moving, it becomes clear that Mario and the shell have been moving in circles, not up and down or left and right, the entire time (Anstis and Kaneko 2014).

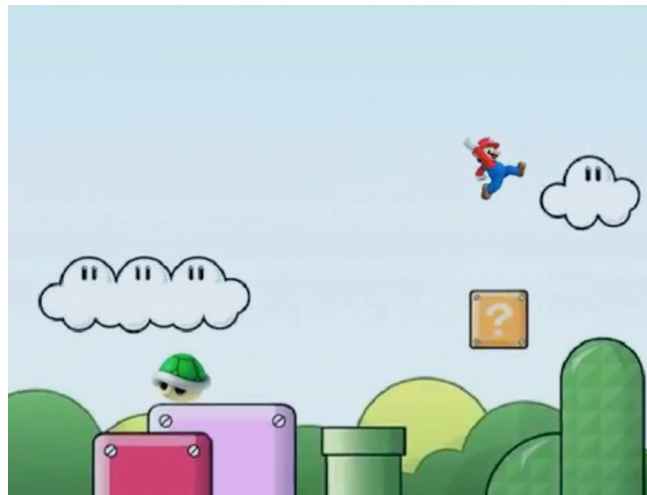


Figure 1.1 Marioland by COGSCI (Mathot 2012). Both Mario and the Koopa shell are moving in clockwise circular paths. However, Mario is traveling along the vertical side of his circular path while the Koopa shell is moving on the horizontal sides of its circular path. When in motion, the background travels in a circular path that is the same size as the characters' paths but in the counter-clockwise direction. When all three elements are moving, the horizontal movement between Mario and the background cancel each other out, and the observer only sees the remaining vertical movement. The same is true with the Koopa shell, except the observer only sees the remaining side-to-side movement. Link to video: <http://www.cogsci.nl/illusions/relative-motion-in-super-mario-land>.

The goals of my dissertation research are to (1) call attention to the application of relative motion in ecological research, (2) provide researchers with new tools that account for relative motion when measuring ecological phenomena, and (3) apply these tools and ideas to two case studies, avian migration and beetle persistence in a moving environment, to demonstrate their tractability. Throughout my dissertation, I show that relative motion provides an important, underestimated driver of ecological patterns and that accounting for motion provides novel

insight into the world around us—more specifically, novel insight into the pattern of species’ movement given moving environmental components.

Species are not omnipresent. They are typically absent from most places on Earth and restricted in occurrence to a few specific locations. These pockets of occurrences are the spatial expression of a species being confined to an ecological niche and an evolutionary history (Holt 2009, Wiens et al. 2010). Hutchinson describes an ecological niche as an N-dimensional hyper-volume encapsulating every interaction an individual can have between itself and its environment (G.E. Hutchinson 1957, Colwell and Rangel 2009). Grinnell focused his descriptions of a niche on the abiotic conditions limiting an individual’s survival and linked those conditions to a particular fixed location (Grinnell 1917). Elton, in contrast, focused his attention on the biotic dimensions (competition) of the hyper-volume and observed much more transient niche behavior (Elton and Miller 1954). While all perspectives are important, I focus on the Grinnellian niche, emphasizing the abiotic conditions that species require for persistence.

More recent advances in niche theory assign the niche description to the individual more than a location—for example, defining a niche according to an individual’s physiological constraints (Kearney and Porter 2004, 2009). Throughout my dissertation, I adopt the physiology-based definition of a niche as described by Kearney and Porter (2004), in order to explore niche-driven motion in an environment. This perspective defines a species’ niche mechanistically, using the energy/mass balance between an individual and the environment to define the “climate niche” that an individual must occupy to stay alive. Within this hyper-volume of climatic conditions, individuals can maintain survivable body temperatures. Outside of this hyper-volume, individuals can no longer balance their energy needs and eventually die.

In Chapter 2, I simulate populations chasing a moving climate niche in one-dimensional space, using stochastic models of spatial spread. I then simulate a treatment of assisted

migration, transplanting individuals from the trailing edge of the population to the leading edge of the population, to determine whether assisted migration can restore symmetry to the moving population and reduce the risk of stochastic local extinctions. These model results show that assisted migration was effective at restoring symmetry and reducing extinction risk in moving populations. However, the efficacy of assisted migration proved highly sensitive to the speed of the moving habitat—assisted migration was more useful when the habitat was moving slowly—and to the transplant location of individuals. In Chapter 3, I use microcosm experiments with *Tribolium castaneum*, the red flour beetle, to investigate assisted migration as a method of reducing extinction risk for moving populations in a live system. Experimental results show that assisted migration reduces extinction risk in moving populations while changing the population's spatial asymmetry from a negative to positive skew.

In Chapter 4, I develop a three-dimensional, Geographic Information System (GIS) model to explore the independent movement of different axes of a climate niche, using rigid body mathematics to move individual components in their own direction, focusing in particular on the movement of a solar niche component. In Chapter 5, I apply this three-dimensional, GIS model to the flight patterns of a pole-to-pole avian migrant, the Greater Shearwater (*Puffinus gravis*), to determine how the relative motion of multiple climate niche components might be driving migratory patterns. Results from this study show that highly mobile individuals follow a path most closely matching that of an object staying stationary relative to the sun, even though individuals appear to be moving when viewed from Earth's surface.

Broadly, each of my dissertation chapters begins by outlining a well-studied ecological phenomenon that is generally thought of as a stationary process and then explores how that phenomenon changes with the application of relative motion (Fig. 1.2). I constrain the scope of this dissertation to two scales of perspective: groups of individuals following a single moving

environmental factor in one dimension (as in the *Tribolium* populations chasing a moving habitat) and single individuals following multiple environmental factors in multiple dimensions (as in Greater Shearwater migration).

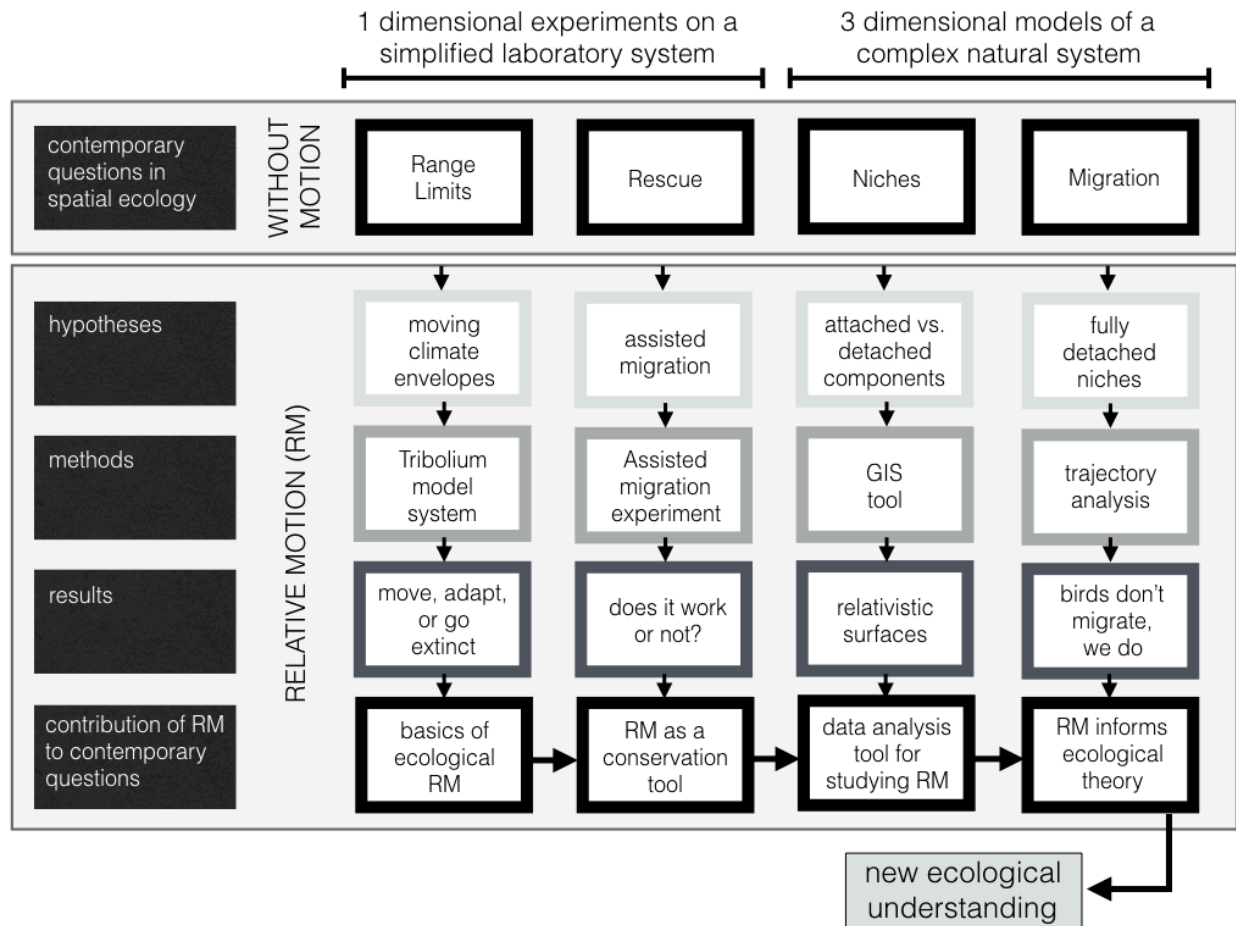


Figure 1.2 Dissertation outline. The four columns are the four content chapters and the rows show the progression through each chapter. These chapters build upon each other to develop better understanding of the role of relative motion in ecological systems. The first chapter models the movement of populations chasing a climate niche, and considers a model of rescue using assisted migration to help populations keep pace with the moving niche. The second chapter experimentally tests the ability of assisted migration to lower extinction risk in moving populations. The third chapter presents a 3-dimensional, GIS model to track moving climate niche components. The fourth chapter applies the 3-dimensional model to a highly mobile species (the Greater Shearwater) tracking a suite of moving climate niche dimensions.

Together, Chapters 2 through 5 highlight the impacts of relative motion on ecological systems and underscore the importance of considering biases in our perspective when measuring

and explaining ecological patterns. Results from Chapters 2 and 4 provide theoretical evidence of the insight gained by considering relative motion, while results from Chapters 3 and 5 provide empirical evidence supporting these ideas. Ultimately, this dissertation combines theoretical and experimental work to advance our understanding of the drivers of ecological patterns in a world of increasing climate niche motion. The expectation with climate change is that it drives climate conditions northward from the equator to the poles or upward from low altitudes to higher altitudes (Parmesan and Yohe 2003, Loarie et al. 2009, Parmesan et al. 2013, Burrows et al. 2014). Thus, we must develop a better understanding of the relationships between climate niche, individual, and population movement to better understand the fate of biodiversity under a shifting climate regime.

CHAPTER 2

ASSISTED MIGRATION AS A MEANS OF COMBATING NICHE MOVEMENT: A SIMULATION

2.1 Introduction

Climate change is expected to drive up to 35% of the world's species to extinction by the year 2054 (Thomas et al. 2004). While climate change affects biodiversity in a number of ways (Parmesan 2006, Barros et al. 2014), one of the leading mechanisms for this dramatic decline in biodiversity is that climate change spatially shifts local climates towards the Earth's poles and up elevational gradients (Walther et al. 2002, Parmesan 2006, Chen et al. 2011). Species that are sensitive to a particular suite of climatic conditions, known as a climate niche, are left with three possible outcomes when their climate niche moves away from their location: 1) they can spread spatially to keep pace with the shifting niche, 2) they can adapt to the niche moving in to replace the outgoing niche, or 3) they can go extinct (Sinervo et al. 2010). Some species will likely adapt to the incoming climate, but it is projected that 22-52% of Earth's species will need to relocate to survive (Joly and Fuller 2009). Indeed, populations of more than 1,500 species of birds, mammals, reptiles, insects, and plants (see figure SPM.5 in IPCC 2014) have shifted their geographic range to higher elevations or towards the Earth's poles over the last forty years, shifting an average of 12 m higher in elevation and/or 16.5 km closer to the poles per decade (Chen et al. 2011).

Assisted migration is a human intervention to help populations "keep up" with their shifting climate niche through physical transplantation (Griffith et al. 1989, McLachlan et al. 2007, Hewitt et al. 2011). Assisted migration can be implemented in multiple ways and has thus been difficult to define (Hewitt et al. 2011). Equivalent terms for assisted migration include facilitated migration, assisted colonization, managed relocation, assisted range expansion, and species translocation (reviewed in Hewitt et al. 2011). Several reviews have attempted to clarify

this terminology (McLachlan et al. 2007, Hewitt et al. 2011, Lawler and Olden 2011, Williams and Dumroese 2013, Lazarus and McGill 2014). Broadly, assisted migration can be defined as the movement of individuals either within or outside of the natural species range in order to mitigate the impacts of climate change (Aitken and Whitlock 2013).

As previously stated, assisted migration can be implemented in diverse ways to meet differing objectives. In species-centered assisted migration, individuals from a population are transplanted to a new location in order to save that species from extinction in its climatically altered historic range (Aubin et al. 2011, Pedlar et al. 2012, Ferrarini et al. 2016). In community-centered assisted migration, individuals are also transplanted to a new location but not to avoid extinction in a historic range. Instead, individuals are transplanted to construct a new ecological community adapted for the encroaching climatic conditions. Whereas species-centered approaches attempt to “rescue” populations from extinction through spatial transplantation (Kreyling et al. 2011), community-centered approaches attempt to “rescue” ecosystems by importing desirable genetic diversity into the community to build resilience through hybridization (Kreyling et al. 2011, Moir et al. 2012). In this study, I use simulations to explore the conditions within which species-centered assisted migration can effectively rescue a population, with implications for the conservation of endangered species dealing with shifting climate niches.

Seddon (2010) proposed a ‘translocation spectrum’ to describe the number of different ways that assisted migration can be applied across a gradient of both population connectivity and the proportion of the population transplanted. Along these spectrums, a few benchmark scenarios stand out for comparison. For example, “assisted population migration” maintains connectivity within the population by transplanting individuals either within or only just beyond the current species range. “Assisted range expansion” breaks connectivity within the population, when

individuals are transplanted outside of the current range in an attempt to find areas outside of the species' current range where they are able to survive. "Assisted relocation" maintains connectivity within the population but breaks that population's connectivity with its underlying habitat by moving the entire population from their current location to a new location because it is believed to contain more suitable habitat (reviewed in McLachlan et al. 2007, Hewitt et al. 2011, Lawler and Olden 2011, Wadgymar et al. 2015). In this study, I focus on assisted population migration because gene flow and genetic connectivity have been shown to have lasting benefits for populations facing extinction (Hampe and Petit 2005, Chevin et al. 2010, Ferriere and Legendre 2013).

Regardless of the implementation, species-centered assisted migration has seen mixed to poor success when applied to natural populations (McLane and Aitken 2012, Benito-Garzón and Fernández-Manjarrés 2015, Castellanos-Acuna et al. 2015). Castellano-Acuna (2015) moved twelve populations of 3 species of Mexican pine (*Pinus devoniana*, *P. leiophylla* and *P. pseudostrobus*) to three different elevations and found that populations could persist, but growth rates among transplants were very low and success among individuals was highly variable. Liu et al. (2012) tried a similar elevational transplant using 20 species of orchids whose populations were about to be destroyed by a new reservoir and found species success at higher elevations was again highly variable.

Assisted migration is a fairly new approach to conserving populations in the face of shifting climate niches (McLachlan et al. 2007, Hewitt et al. 2011), and it remains relatively untested in both experimental and natural systems (Zhou and Kot 2010, Leech et al. 2011, McLane and Aitken 2012, Benito-Garzón and Fernández-Manjarrés 2015). Here I simulate populations tracking a shifting suitable climate niche and apply transplantations to those moving populations along a continuum between assisted population migration and assisted range

expansion. In my simulation treatments, individuals are removed from the trailing edge of the population and transplanted to recipient locations ranging from far behind the suitable climate niche to well in front of the suitable climate niche; hence, the encompassing scenarios range from assisted population migration to assisted range expansion. The goal of this study is to determine whether and what kind of assisted migration can reduce the risk of local extinction events and, thus, provide a viable conservation strategy for endangered populations. I hypothesize that (**h1**) assisted migration is capable of rescuing moving populations from extinction but that (**h2**) the success of assisted migration is dependent on the transplant recipient location relative to habitat speed.

2.2 Methods

I simulated population abundance and distribution in a landscape comprised of both good and bad habitat patches. Good habitat patches had positive population growth rates to simulate a suitable (i.e. historic) climate niche, while bad habitat patches had negative population growth rates to simulate an altered (i.e. novel) climate niche. Throughout the simulation, good habitat patches were moved across the landscape to mimic a shifting climate niche, and the populations tracked the moving habitat. I then applied an assisted migration treatment by transplanting individuals from the trailing edge of the population to a new spatial location, ranging from far behind the good habitat patches too far in front of the good habitat patches. This series of simulated treatments ranges from assisted population migration to assisted range expansion, in order to test the contribution of transplant location to assisted migration success. To evaluate the success of the assisted migration treatment, I measured population abundance, population symmetry, and time to extinction as indicators of population viability (Brown 1984, South 1999). Details for each of these steps are provided below.

2.2.1 The stochastic spatial Ricker model

To model the spatial spread of a population over time, I used the stochastic spatial Ricker model described by Melbourne and Hastings (2009). This model separates population growth (births and deaths) from dispersal (immigration and emigration), alternating between the two each generation. Spatial spread refers to the inter-generational movement of populations across space, as individuals are born and disperse to raise their own offspring in a new location. In this model, population growth takes a Ricker form, while dispersal is modeled as a diffusion process (Melbourne and Hastings 2009).

Briefly, the Ricker model is a first-order difference equation that describes how population abundance changes over discrete periods of time (Ricker 1954, Bjorkstedt 2012). This model satisfies the births minus deaths component of the fundamental law of populations, but it is enriched by an ability to attribute different sources of births and deaths to different components of the environment or different stages of growth and development. The Ricker equation can take several forms but can always be reduced to $f(N) = aNe^{-bN}$, where a is a positive slope representing the maximum per capita productivity, and b determines how strongly a density-dependent mechanism reduces per capita productivity with increasing abundance, N (Bjorkstedt 2012).

In this study, I apply a fully stochastic implementation of the Ricker model, meaning that it has been redesigned using statistical distributions to account for the inherent variability in the environment, number of offspring per female, mortality, and sex ratios (Melbourne and Hastings 2008). This stochastic version of the Ricker model allows for variance to be contributed by the sources just mentioned, which is particularly helpful when modeling a population not at equilibrium and, thus, experiencing greater stochasticity.

The dispersal component of the model describes the movement of individuals away from their natal location to their location of reproduction. Most individuals travel only short distances from their natal location, but others travel long distances before reproducing. The frequency distribution of distances traveled by different members of the population defines a dispersal kernel. The diffusion model used here is a Poisson-diffusion kernel combined with a Dirichlet-multinomial variance component to create a composite stochastic diffusion model, in which the probability of moving each distance varies each generation, but the probability of all distances within a generation will always sum to one (Melbourne and Hastings 2009). The model is a one-dimensional, discrete-space version of Brownian motion, allowing for extra variability in distance traveled.

2.2.2 Modeling spatial distribution in a landscape of good and bad patches

The basic components of the stochastic model are the growth and dispersal processes described above acting in a one-dimensional array of good and bad habitat patches. Good patches have positive growth rates to simulate a suitable (historic) climate niche, while bad habitat patches have negative growth rates to simulate an altered (novel) climate niche. One full iteration of the model describes one generation of a semelparous lifecycle. The iteration starts with a certain abundance of adult individuals in each habitat patch across the landscape. This is the spatial abundance distribution (or “abundance profile” as described in more detail in section 2.2.4) at the beginning of a generation. Adults breed and produce offspring, after which the adults immediately die, while the offspring grow to adulthood in a single habitat patch. The type of patch (good or bad) and the density of individuals in the patch determine the birth and death rates of individuals in the patch and, hence, the growth rate of the population in the patch. Once all individuals have reached adulthood, individuals then disperse between habitat patches for a

limited amount of time. Dispersal occurs by the diffusion process described above and redistributes adults across the landscape. This is the end of one model iteration and the end of one biological generation. The spatial abundance distribution at this time is the distribution for the beginning of the next generation.

To simulate a moving climate niche with this model, the location of good quality habitat was shifted to the right either one patch (slow-moving habitat) or two patches (fast-moving habitat) each generation (Figs. 2.3 and 2.4, respectively). The shift occurred at the end of one model iteration (i.e. after dispersal was completed) before the next iteration began. In this way, the model takes into account changes in habitat quality and habitat location when it simulates population growth rates. This model is optimal for this application because it is a dynamic model that can account for the relative motion between the moving habitat and spreading population.

2.2.3 Applying assisted migration

An assisted migration treatment could vary in three ways: 1) the number of individuals that are transplanted, 2) the recipient location in the landscape to which those individuals are transplanted, and 3) the frequency of assisted migration transplants (Seddon 2010, Dumroese et al. 2015). For this experiment, I varied only the second parameter, transplant location, while holding the other two constant. For each replicate, the simulation performed one assisted migration transplant per growth-dispersal iteration (i.e. once per generation). In each transplant, 100 individuals were collected (16.7% of the equilibrium population at the beginning of the experiment) from the trailing edge of the population and transplanted to single patches at a new transplant location in the landscape. If fewer than 100 individuals remained in the population, all individuals were transplanted to the new location. The specific location that individuals were transplanted to did not change within simulation treatment but did vary between treatments,

ranging from 8 patches behind the good habitat to 13 patches ahead of the good habitat, for a total of 22 different locations in both slow and fast moving habitat scenarios (Figs. 2.3 and 2.4).

There is one notable difference in the initial conditions between the slow and fast moving habitat scenarios. In the slow-moving habitat scenario (one patch per generation), simulations started with 10 individuals in the leading good patch. In the fast-moving habitat scenario (two patches per generation), simulations instead started with 600 individuals in the leading good patch. These initial conditions needed to differ because preliminary simulations with the same initial population size showed that fast moving habitat quickly resulted in extinction and obscured the dynamics leading up to extinction. Populations experiencing one-patch movement were able to grow over time to build up high abundances, whereas populations experiencing two-patch movement declined to extinction very quickly. Starting the slow-moving treatments at low abundances and letting them grow to carrying capacity shows a detailed picture of the growth behavior of these populations under moving conditions. Starting fast-moving populations at the same low abundances drives them to extinction too quickly to see a clear signal of their extinction dynamics. By starting the fast-moving populations at higher abundances, their decline to extinction took more generations to achieve and it was therefore possible to observe the dynamics of extinction in more detail.

2.2.4 Measuring population symmetry

Individuals within an ecological population are distributed across space, such that the majority of individuals are found in high-quality habitat (e.g. areas within the climate niche) and a minority of individuals persist in the low-quality habitat surrounding the high-quality habitat (e.g. areas immediately outside of the climate niche) (Gaston 2009). A population at equilibrium and spatially constrained consists of two parts: a core population (individuals living in the high-

quality habitat) and a periphery population (individuals living in the surrounding low-quality habitat) (Gaston 2009). Core populations experience positive growth rates, whereas periphery populations experience negative growth rates (Gaston 2009). Periphery populations persist despite local negative growth rates because the core population produces a continuous flow of immigrants into periphery areas. A transect across the population from the absence of individuals, across the core and periphery populations, until absence again creates an “abundance profile” of the population (Fig. 2.1).

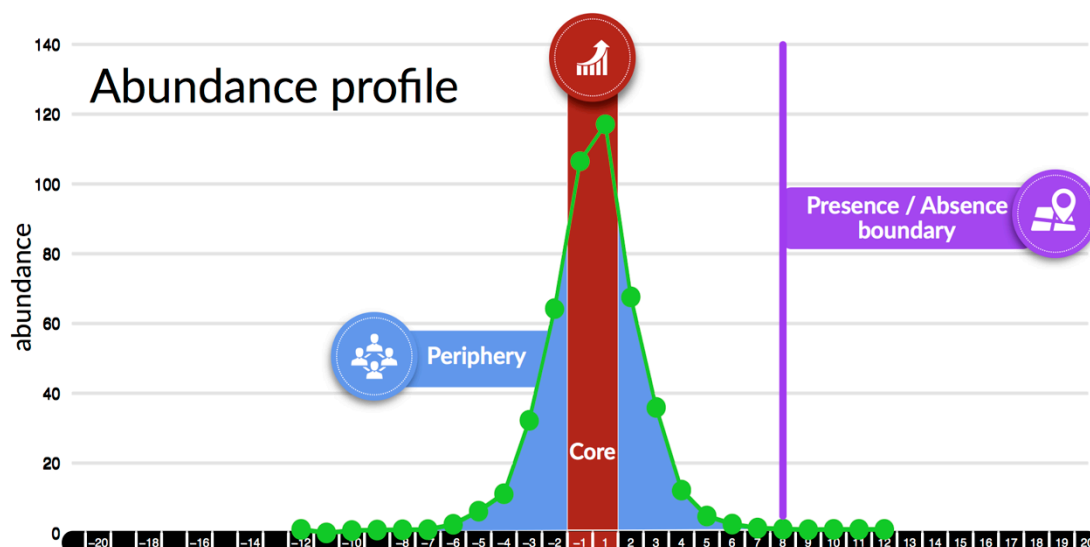


Figure 2.1 The anatomy of an abundance profile. An abundance profile is the number of individuals at each location along a one-dimensional transect. The result is the spatial distribution of individuals within a population. At each location (“habitat patch”), there is either good (red) or bad (black) habitat available. Populations have negative growth rates in bad habitat and positive growth rates in good habitat. The abundance profile typically maintains a symmetrical spatial distribution, centered on good habitat, as surplus individuals born in the core area disperse into the surrounding periphery area. The location of the last individual is the presence/absence boundary for the population.

Abundance profiles provide insight into population health by displaying the overall abundance and symmetry of the spatial distribution of individuals in the population (Gaston 2009, Urli et al. 2014). With a non-moving habitat, at equilibrium, populations should be spatially symmetrical and stable over time, which translates to a low risk of extinction under

normal stochastic conditions (Melbourne et al. *in prep*). Theoretical studies show changing the amount of available habitat or the dispersal rate of the population can alter the height and breadth of the abundance profile, but the distribution will remain symmetrical (Melbourne et al. *in prep*). Studies also show that when the spatial location of the high-quality habitat is shifted each generation, to simulate shifting climate niches, the symmetry of the distribution is reduced, leading to high risk of stochastic extinction (Roques et al. 2008, Berestycki et al. 2009, Berestycki and Nadin 2012, Melbourne et al. *in prep*). This shift from symmetric to asymmetric distributions when motion is added to the environment has been validated by both simulations and microcosm experiments (Berestycki and Chapuisat 2012, Urli et al. 2014). Figure 2.2 provides an example of the asymmetry that develops in abundance profiles following a moving habitat. This figure shows how asymmetry in the abundance profile develops under three movement conditions: stationary, one-patch movement, and two-patch movement. The moving populations show more asymmetry than the stationary populations and, notably, the mode of the population distribution with two-patch movement has shifted outside of the good habitat so the majority of the population is in bad habitat (Melbourne et al. *in prep*).

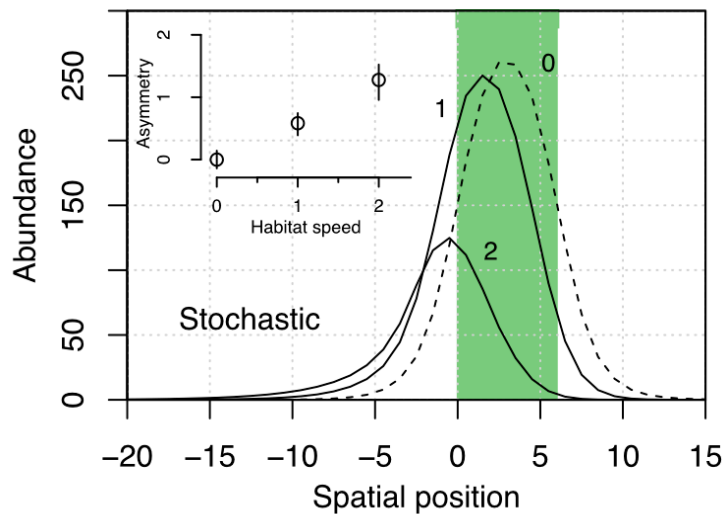


Figure 2.2 Movement makes abundance profiles asymmetric. The abundance profile of a population becomes more skewed as the habitat moves at faster rates. These results are for the model described in the text in the absence of assisted migration. Abundances are means over 10,000 replicate simulations of the model. Numbers above the curves indicate habitat speed (patches per generation). Asymmetry is measured as weighted skew. With zero patch movement, the population is both symmetrical and aligned with the high-quality habitat (green bar). As habitat movement increases to one patch per generation, the population becomes slightly asymmetrical, but the mode of the population is still within the high-quality habitat. At two patches of habitat movement per generation, the population becomes more asymmetrical and the mode of the abundance profile falls out of alignment with the high-quality habitat. This loss of alignment between the population and the high-quality habitat means that most of the population is experiencing negative growth rates, and the population as a whole declines over only a few generations. This movement-induced asymmetry causes instability that increases extinction risk for moving populations.

I measured the asymmetry of populations by measuring the third central moment of the abundance profile using a Pearson's first-moment coefficient of skewness (Equations 1-4). Skew is a measure of the degree of asymmetry in a distribution and is usually standardized by the standard deviation. Here, the skew is calculated using a weighted mean to better characterize the non-normal distribution of abundance profiles. A positive weighted skew value signifies a distribution with an asymmetric tail extending out towards more positive x , while a negative value signifies a distribution whose tail extends out towards more negative x .

Calculating a weighted skew involves first calculating the weighted mean position of the abundance profile

$$m_w = \frac{\sum_{x=1}^n (x \times w_x)}{\sum_{x=1}^n w_x} \quad (2.1)$$

where m_w is the weighted mean, x is the spatial position of a patch, w_x is the abundance in patch x , and n is the number of patches.

The second and third moments of the distribution are then

$$\mu_2 = \frac{\sum_{x=1}^n w_x \times (x - m_w)^2}{\sum_{x=1}^n w_x} \quad (2.2)$$

$$\mu_3 = \frac{\sum_{x=1}^n w_x \times (x - m_w)^3}{\sum_{x=1}^n w_x} \quad (2.3)$$

and the weighted skew is

$$\gamma_1 = \frac{\mu_3}{(\sqrt{\mu_2})^3} \quad (2.4)$$

2.3 Results

Simulations showed that the speed of the habitat movement was an important consideration for restoring symmetry to moving populations through assisted migration (weighted skew in Figs. 2.2- 2.4). With no movement and no assisted migration, the population was symmetrical and centered on the good habitat (Fig. 2.2). With one-patch movement, the population became slightly asymmetric and the mode of the abundance profile shifted left, although it was still within the good habitat (Fig. 2.2). With two-patch movement, the population became more asymmetric and the mode of the abundance profile was no longer within the good habitat, suggesting the majority of the population was experiencing unfavorable environmental conditions (negative growth rates) (Fig. 2.2).

Transplant location in assisted migration proved very important for restoring symmetry to moving populations, but the strength of the effect depended on the speed of habitat movement. With one-patch movement, symmetry was fully restored when individuals were transplanted to the leading good patch or within three patches ahead of the good habitat (Fig. 2.3). However, with two-patch movement, symmetry was fully restored only when individuals were transplanted to one or two patches ahead of the good habitat (Fig. 2.4). The speed of habitat movement and the transplant location for assisted migrants had noticeable effects on time to population extinction. Across the spectrum of transplant locations, only 4 locations (leading patch to 3 patches in front) in the one-patch movement scenario and 2 locations (leading good patch and 1 patch in front) in the 2-patch movement scenario were able to achieve long-term stability and increase population abundances over the control (Figs 2.3 and 2.4).

For populations experiencing only one-patch movement, time to extinction for assisted migration scenarios ranged from 170 generations for a transplant location 12 patches ahead to 700 generations for a transplant location 4 patches behind the good habitat (see generation time in total abundance column, Fig. 2.3). The controls (no assisted migration) for one-patch movement scenarios showed long term persistence (Fig. 2.3, first row), so any transplant locations that went extinct performed worse than the controls. Interestingly, this means that assisted migration was detrimental to the persistence of populations unless transplants were placed within a particular spatial window. The transplant locations that resulted in increased abundances over the control saw stable equilibrium abundance increases up to 500 and 600 individuals respectively compared to the control's abundances of 450 (Fig. 2.3).

In contrast, populations that went extinct in the two-patch movement scenarios only persisted for 22-34 generations (see generation time in total abundance column, Fig. 2.4). Transplant locations one or two patches in front of the good habitat showed long-term

persistence and increased abundance over the controls (no assisted migration), which went extinct in 23 generations (Fig. 2.4, controls in first row). Three to eight patches in front of the good habitat showed improvements over the controls but still went extinct after 40-100 generations without reaching long-term stability (Fig. 2.4). Most transplant locations maintained or improved conditions over the controls, but only two locations actually restored long-term persistence. Of these two, the transplant location one patch ahead maintained a stable population of 400 individuals and two patches ahead maintained a stable population of 450 individuals (Fig. 2.4).

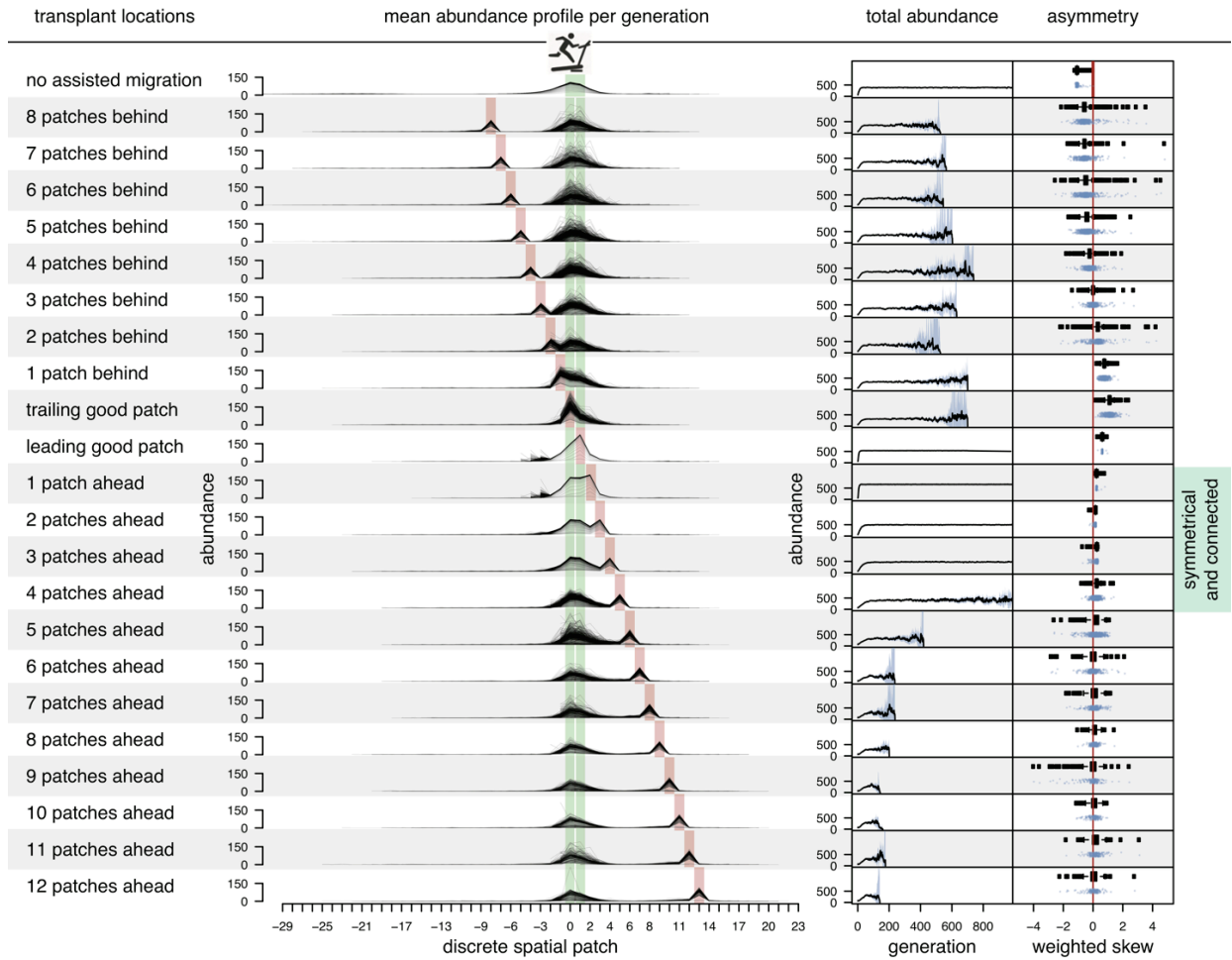


Figure 2.3 Simulation results testing the importance of transplant location when applying an assisted migration treatment, given one-patch habitat movement. Each generation, assisted migration was applied by collecting 100 individuals from the trailing (left) edge of the population and transplanting those individuals to the patch marked in pink. Patches of good habitat are marked in green. The top row shows the control population. The main column shows the mean abundance profile per generation, for 1,000 generations or until the population went extinct. Each mean abundance profile represents 3,000 replicate landscapes. The next column shows the mean number of individuals in the population per generation, with the blue polygon showing the 95% confidence interval for the mean. The far right column is the weighted skew value of each mean abundance profile.

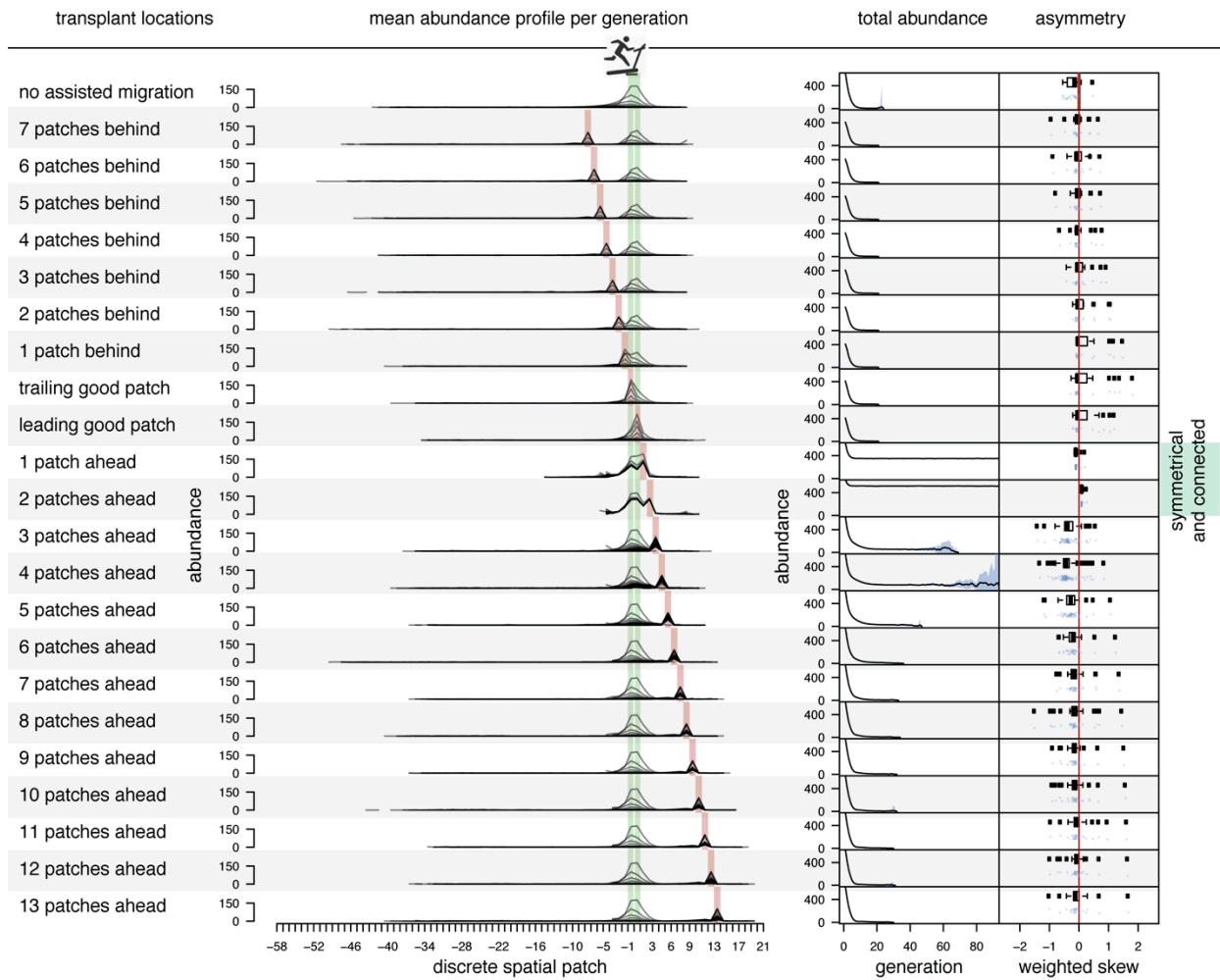


Figure 2.4 Simulation results testing the importance of transplant location when applying an assisted migration treatment, given two-patch habitat movement. Each generation, assisted migration was applied by collecting 100 individuals from the trailing (left) edge of the population and transplanting those individuals to the patch marked in pink. Patches of good habitat are marked in green. The top row shows the control population. The main column shows the mean abundance profile per generation, for 1,000 generations or until the population went extinct. Each mean abundance profile represents 3,000 replicate landscapes. The next column shows the mean number of individuals in the population per generation, with the blue polygon showing the 95% confidence interval for the mean. The far right column is the weighted skew value of each mean abundance profile.

2.4 Discussion

The purpose of this study was to test the potential for assisted migration to reduce extinction in populations chasing a suitable climate niche. I simulated assisted migration in 22 transplant recipient locations, ranging from behind the tail of the moving abundance profile to the front of the leading edge of the moving populations across two different speeds of habitat movement, one-patch per generation (Fig. 2.3) and two-patch per generation (Fig. 2.4). I hypothesized that (**h1**) assisted migration is capable of rescuing moving populations from extinction but that (**h2**) the success of assisted migration is dependent on the transplant recipient location relative to habitat speed.

Results from this study suggest that assisted migration can rescue moving populations from extinction, confirming **h1**, and that the success of assisted migration is sensitive to the speed at which the habitat is moving and the location to which individuals are transplanted, confirming **h2**. The most successful transplant locations were those that matched the speed of the good habitat—that is, transplanting individuals to one patch ahead of the good habitat when the good habitat was shifting one patch per generation or transplanting individuals to two patches ahead of the good habitat when the good habitat was shifting two patches per generation. When these transplant location conditions were met, assisted migration boosted the overall abundance of the population compared with the control group (Figs. 2.3 and 2.4). When these transplant location conditions were not met, assisted migration was detrimental to the population and shortened the time to extinction for all replicate populations. This sensitivity to transplant location makes the success of assisted migration very dependent on first identifying the proper habitat that the population is responding to and then transplanting individuals to the proper location relative to that habitat. Both of these conditions are likely to be very difficult to identify

in natural systems, which will likely mean assisted migration will see mixed success in management applications.

Overall, results showed assisted migration was more likely to be successful when individuals were placed in front of the optimal transplant location rather than behind it. Transplanting individuals was more effective and less sensitive to transplant location when the habitat was moving slower (one patch per generation) compared to faster (two patches per generation). In both fast and slow habitat scenarios, there was an optimal transplant location that increased equilibrium abundance compared to the control group (Figs. 2.3 and 2.4). However, the location of the optimal transplant location varied depending on the speed of the habitat movement. Under the two-patch movement scenario, transplanting individuals to the first or second patch in front of the good habitat showed the greatest long-term stability with the highest population abundances (Fig. 2.4). Under the one-patch movement scenario, the range of acceptable transplant locations increased so that any patch from one patch in front to four patches in front showed stability and improvement over the controls.

These findings supported my hypotheses, in that assisted migration was capable of rescuing moving populations from extinction but that the success of assisted migration is indeed dependent on the transplant location relative to habitat speed. Assisted migration rescued populations from extinction in both fast and slow moving habits, and those rescued populations were stable long-term when assisted migration was continually applied. When individuals were transplanted to the optimal location for their specific habitat speed, populations maintained spatial symmetry and connectivity. When individuals were transplanted to areas outside of the optimal location, populations lost both symmetry and connectivity, which decreased the total abundance and demographic stability of the population.

These results support findings from other studies that show asymmetry is symptomatic of a population chasing a moving climate niche (Berestycki and Rossi 2008, Berestycki et al. 2009) and connectivity is important for population persistence (Taylor and Norris 2010, Villard and Metzger 2014). These results also suggest that assisted migration might require more effort than expected. Here, assisted migration required transplanting individuals for many generations, which may not be feasible in natural systems.

One possible factor underlying this sensitivity to transplant location is the effect of removing individuals from their source location. In this study, assisted migration was applied by aggregating 100 individuals from the trailing edge of the population and transplanting those individuals to a recipient location. In effect, individuals were removed from the population according to their location in the abundance profile, but they were transplanted to a location relative to good habitat. Thus, as the location of the good habitat and the population became more spatially separated, the assisted migration treatment became more disruptive.

Assisted migration could be disruptive for two reasons: 1) loss of population connectivity, which can impact gene flow and encounter rates in natural populations, and 2) transferring individuals from areas of population growth (good habitat) to areas of population decline (bad habitat). In many instances throughout this study, individuals were removed from good habitat and transplanted to bad habitat, which lowered the overall population abundance. In some extreme cases, the assisted migration treatment transplanted all remaining individuals in the population to unsuitable habitat, effectively making extinction inevitable.

A current gap in our understanding of assisted migration—though not addressed in this study—is where best to draw transplants from. Individuals from the center of the historic range come from conditions where population densities are high and habitat is good. Under these conditions, individuals experience high densities but low environmental stress. Individuals from

the periphery of the historic range are under greater environmental stress because they are in poorer-quality environments but live at lower population densities. Transplanting from the core of the population to the periphery of the population means that transplanted individuals go from areas of low environmental selection and high density to areas of high environmental selection and low density (Kreyling et al. 2011). Sourcing transplants from the trailing edge of a population may be a more stable strategy, as individuals in the tail have already gone through multiple generations of living in a poor-quality environment. These individuals could be higher-quality transplants for the task of adapting to the poor-quality habitat on the leading edge.

The greatest limitation of this study is that it uses simulations rather than experiments in natural systems to draw conclusions about conservation best practices. Even though this model captures a great deal of the complexity observed in the beetle microcosm system (Melbourne and Hastings 2009, Melbourne et al. *in prep*), it misses some nuances observable with microcosm experiments (Melbourne and Hastings 2008, 2009; Hufbauer et al. 2015). For example, one of the major limitations of the Ricker model is that it doesn't account for the genetic adaptation of populations to novel environmental conditions.

These simulations are also limited in their imposition of symmetry for abundance profiles in stationary habitat. In these simulations, the poor-quality habitat is equally poor on either side of the good habitat, so the population is symmetrical across the good habitat when the habitat is stationary. The reason for this was to explicitly measure the increase in asymmetry as habitat speeds increased and to compare that asymmetry against a symmetrical stationary control. However, this symmetrical design does not match the current consensus on range boundaries, which says that northern and southern range boundaries are limited by different ecological mechanisms and, therefore, have differing degrees of suitability (Darwin 1859, Dobzhansky 1950, MacArthur 1972, Brown et al. 1996, Gaston 2003, Schemske et al. 2009, Cunningham et

al. 2016). Under this standard model, a stationary population would already be asymmetrical because the poor-quality habitat on one side of the suitable habitat will be better or worse than the poor-quality habitat on the other side. Thus, differences in quality between the two sides already impose asymmetry on a stationary population. Despite these limitations, this study provides insight into when, how, and if assisted migration can be effective at reducing extinction risk in moving populations. Future studies should address situations with asymmetrical habitat gradients.

This study provides the first rigorous test of the effectiveness of assisted migration in lowering extinction risk in moving populations but more work is needed before we can confidently apply assisted migration in natural populations. The assisted migration treatment can vary in three ways: 1) the number of individuals that are transplanted, 2) the location in the landscape to which those individuals are transplanted, and 3) the frequency of assisted migration transplants. Here I varied only the second parameter—transplant location. Future studies should vary the remaining two variables—size and frequency of transplants—to improve our understanding of assisted migration as a conservation strategy. Given the ubiquity of slow-moving climate niches in the world (Burrows et al. 2014), there is great potential for assisted migration to help conserve biodiversity in the face of climate change, but simulations also suggest that getting it wrong carries large consequences for the populations involved.

Efforts to better understand assisted migration should also focus on species' ability to adapt to novel environmental conditions (Szucs et al. 2014, Hufbauer et al. 2015a). A demographics-based approach to assisted migration, as used here, requires transplanting individuals every generation to sustain a population unable to keep up with its moving habitat, whereas a genetics-based approach, to allow for adaptation, would involve directing selection towards high dispersal rates and more generalist tendencies (Aitken and Whitlock

2013, Hufbauer et al. 2015a). Models combining both demography and genetics are greatly needed to fully understand the effects of assisted migration.

CHAPTER 3

ASSISTED MIGRATION AS A MEANS OF COMBATING NICHE MOVEMENT: AN EXPERIMENT

3.1 Introduction

Assisted migration describes the deliberate transplantation of individuals from their current spatial location to a new location within or outside of their current range (Griffith et al. 1989, McLachlan et al. 2007, Hewitt et al. 2011). One application of assisted migration is to help populations “keep up” with a climate niche that is moving in space due to anthropogenic climate change (Hoegh-Guldberg et al. 2008). Climate change can cause extinction through a number of different mechanisms (reviewed in Cahill et al. 2012) but one of the primary projected causes of extinction is that climate niches, and therefore range limits (Hoegh-Guldberg et al. 2008, La Sorte and Jetz 2012), are moving towards Earth’s poles through time (Loarie et al. 2009, Chen et al. 2011).

Studies on species’ range dynamics show strong correlations between changes in range boundaries and changes in climatic conditions (reviewed in Gaston 2009), suggesting that populations move in space in response to shifting climate niches (Parmesan and Yohe 2003, Walther 2004). Recent projections suggest that up to 35% of species worldwide will be driven to extinction by 2054 (Barnosky et al. 2012) because the climate niches on which they depend are moving (Loarie et al. 2009, Hamann et al. 2015). The best historical comparison available for this change is the last glacial retreat, which traveled at 5 km per year (Lazarus and McGill 2014) and resulted in widespread extinctions (Pearson 2006). Recent projections suggest that climate niches are moving at 0.1 km per year (Hamann et al. 2015), 1 km per year (Loarie et al. 2009), or 3.25 ± 1.36 km per year (Leroux et al. 2013), depending on the study system and algorithm used. Studies show that this habitat movement is acting as a

unique ecological mechanism driving extinctions across many taxa (Thomas et al. 2004, Cahill et al. 2012).

Assisted migration aims to artificially increase dispersal speed in species that cannot keep up with their moving climate niche (McLachlan et al. 2007). According to theory (Bellard et al. 2012, Lazarus and McGill 2014, Benito-Garzón and Fernández-Manjarrés 2015), and my modeling results in Chapter 2, assisted migration has the potential to save species from climate change-driven extinctions. However, the potential for negative impacts resulting from assisted migration (e.g. facilitating the spread of invasive species, genetic impacts, species biases) has made assisted migration a controversial intervention strategy (McLachlan et al. 2007, Hewitt et al. 2011) and has kept it from being tested extensively in field systems. Thus, most of the consideration given to assisted migration has been through models (Fordham et al. 2012, Regan et al. 2012, Lunt et al. 2013) and rhetorical arguments (Hewitt et al. 2011, Kreyling et al. 2011, Kabaz-Gomez 2012, Klenk and Larson 2013), with little experimental evidence to determine where, when, and how to be successful in applying assisted migration to populations at risk of extinction due to moving climate niches.

Broadly, there are two types of field experiments being used to test the application of assisted migration in natural systems. The first involves transplanting individuals to outside of their current range to see if they can persist in novel environmental conditions (Neilson and Wullstein 1983, Levin and Clay 1984, Asselin et al. 2003, Geber and Eckhart 2005, Griffith and Watson 2006, Van der Veken et al. 2012). This approach can reveal the shape and location of suitable habitat because individuals will persist in areas with suitable habitat and perish in areas with unsuitable habitat (Collyer et al. 2011, McLane and Aitken 2012 and Chapter 2). For example, McLane and Aitken (2012) transplanted whitebark pine trees on both side of the species' northern range boundary and found that the new location of the

range boundary was where snowfall shortened the growing season and increased mortality. Fewer transplant experiments have been conducted with animal species than plant species. Collyer et al. (2011) transplanted pupfish (*Cyprinodon tularosa*) throughout a landscape to show that individuals could adapt to the local environment. Other animal studies have examined butterflies (Crozier 2004), marine crustaceans (Sanford et al. 2006, Green et al. 2010), and hemipteran insects (Bird and Hodkinson 2005).

The second type of field experiment involves using species distribution models to predict the location of suitable habitat and then transplanting individuals to locations deemed viable (Willis et al. 2009). Species distribution models use the climate conditions of a species' historic range to predict its future range under different climate warming scenarios (Kearney and Porter 2009). For example, Willis et al. (2009) used a species distribution model for the marbled white butterfly (*Melanargia galathea*) and small skipper butterfly (*Thymelicus sylvestris*) to predict locations with suitable thermal conditions for the butterfly species under different warming scenarios. They then transplanted individuals from the core of their current populations to the new locations and found that transplanted populations increased in abundance and expanded spatially over the course of six years (Willis et al. 2009).

Studies have revealed varying degrees of success when applying assisted migration. Several studies showed no evidence of success (Woodward 1975, Bird and Hodkinson 2005), while other studies found that individuals could survive in novel environments but not reproduce successfully (Gilbert 1980, Woodward 1990, Hummel 2000, Asselin et al. 2003, Griffith and Watson 2006). Still other studies found that transplanted populations only persisted for a generation or two (Angert and Schemske 2005). One study tried to disentangle the effects of losing the resources available within a range limit and the effects of losing the

climate conditions available within a range limit by transplanting both dung beetles and their primary resource, dung, to a new location. However, they found no evidence that the supplementation of resources could help the beetles survive in the new climate (Qie et al. 2012).

Existing assisted migration experiments have focused on the common garden experiments described above, while only models (Leroux et al. 2013, Ferrarini et al. 2016) and discussion (Klenk and Larson 2013) have begun to consider the mechanisms and logistics of implementation. The experiment I present here addresses two critical gaps in our understanding of assisted migration as a conservation strategy: 1) many field experiments have not followed the fate of populations over time, and 2) many field experiments do not include contrasts between populations with assisted migration and populations without assisted migration (i.e. there were no controls). Here I provide a controlled experiment that tracks the success of assisted migration over the course of 10 generations to evaluate whether assisted migration is, indeed, an effective strategy for conserving populations in the face of climate change.

Here, in addition to examining persistence, I use abundance profiles as a quantitative tool for studying the demographic behavior and extinction risk of populations responding to a moving habitat. Abundance profiles provide insight into population longevity by providing a measureable expression of the interaction between growth rate, dispersal, and available suitable habitat across an environmental gradient (Brown 1984, Berestycki and Rossi 2008, Berestycki et al. 2009). At equilibrium and in a stationary environmental gradient, populations should be spatially symmetrical and stable over time, which translates to low risk of extinction under normal stochastic conditions (Berestycki et al. 2009, Melbourne et al. *in prep*). Studies show that a population's abundance profile becomes asymmetric when its

habitat begins to move in space, particularly if the speed of the habitat is close to a critical speed for extinction (Berestycki et al. 2009, Melbourne et al. *in prep*).

In Chapter 2, I used simulations to show that assisted migration is capable of rescuing moving populations from extinction but that the success of assisted migration depends on the location that individuals are transplanted to relative to habitat speed. Assisted migration interacted with habitat speed in such a way that when habitats were moving quickly, assisted migration had the potential to entirely rescue populations from extinction but when habitats were moving slowly, assisted migration had the potential to directly cause extinction. This sensitivity to transplant conditions adds more uncertainty to ongoing discussions about applying assisted migration (Benito-Garzón and Fernández-Manjarrés 2015, Castellanos-Acuna et al. 2015, Dumroese et al. 2015, Lopez 2015, Sansilvestri et al. 2015, Ferrarini et al. 2016). In this chapter, I use these simulations to inform the design of a microcosm experiment using *Tribolium castaneum* (the red flour beetle) to test the success of the assisted migration strategy in a living system with a fast-moving habitat.

I hypothesize that the assisted migration treatment will lengthen time to extinction and restore the symmetry of the abundance profile of beetle populations in a moving-habitat scenario. Unlike in Chapter 2, I do not vary transplant location in this study. Instead, all individuals are moved from the trailing edge of the population to one-generation ahead of good habitat, which was identified as a good strategy in the simulation study. In addition, I only move the habitat at a single speed (fast, two-patch movement). Past experimental studies with the *Tribolium* system show that populations are almost certain to go extinct when provided only two patches of good habitat when that habitat is moving at a speed of two-patches-per-generation. In a recent study, Melbourne et al. (*in prep*) found that only two of twelve populations survived for 12 generations under these conditions. Thus, my intention

with this study is to focus more directly on the potential for assisted migration to “rescue” a population when extinction seems certain.

Here I use experimental populations of *T. castaneum* in a landscape comprised of “good” (positive population growth) and “bad” (negative population growth) habitat to explore the application of assisted migration in a moving climate scenario. As in the simulation study, the good habitat gets shifted in space over time, which serves as a proxy for shifting climate niches in natural systems. I then apply assisted migration to help *T. castaneum* populations “keep up” with the moving good habitat, providing insight into the use of assisted migration as a strategy to help natural populations keep up with their shifting climate niches. Excitingly, assisted migration markedly reduced extinction risk in moving populations. By generation eleven, 27 out of 30 populations went extinct in the landscapes without assisted migration while only 6 out of 30 populations went extinct in the landscapes with assisted migration. Assisted migration also shifted the symmetry of the population’s abundance profiles to a positive skew rather than a negative skew. This change in skew value is believed to be a key mechanism for countering the negative effects of habitat movement and rescuing fast-moving populations from extinction.

3.2 Methods

This experiment was designed to mimic populations chasing shifting climate niches in natural systems using populations of *T. castaneum* chasing moving patches of “good” habitat across a landscape of “bad” habitat. Experimental landscapes consisted of plastic boxes connected together to allow dispersal between boxes while habitat was controlled by using different types of flour. Good habitat was moved each generation. The experiment compared two treatments: assisted migration versus no assisted migration. Assisted migration was conducted

each generation by transplanting beetles from the trailing edge of the population to the leading edge.

T. castaneum is a small (2mm long) beetle species that lives in stored grain and is generally considered a pest. This species has long been used as an experimental model species for studying population dynamics in laboratory microcosms (Costantino and Desharnais 1991, Desharnais 2005). *T. castaneum* beetles are ideal for testing the question of assisted migration because they are sexually reproducing, can be counted by hand, live at high densities so many large populations can be studied at once, and they have a short generation time so an experiment can run for multiple generations.

Beetles were housed in 4 x 4 x 6-cm acrylic boxes (hereafter called patches) with 2 tablespoons of flour medium for beetles to both live in and eat. These individual patches were connected in a linear array via holes drilled in the sides of each patch, forming a landscape of individual patches linked by dispersal. Each landscape comprised thirty-two patches. Dispersal was controlled by sliding acetate sheets between patches to block the holes. The medium in each patch consisted of either 95% wheat flour and 5% brewer's yeast (good habitat) or 96% corn flour, 3.5% wheat flour, and 0.5 % brewer's yeast (bad habitat). Good habitat provided the nutrients necessary to maintain positive population growth rates, whereas bad habitat lacked the necessary nutrients and maintained negative population growth rates.

Sixty experimental landscapes were used: thirty received the shifting habitat plus assisted migration treatment, while thirty received the shifting habitat treatment without assisted migration. Each landscape had two contiguous patches of good habitat and 30 patches of bad habitat. Between removing individuals to census the population and returning individuals to habitat patches, the two good habitat patches were shifted to the right two patches each generation to provide unidirectional, fast-paced habitat movement. Past studies with the *T.*

castaneum system show that populations were almost certain to go extinct when provided only two patches of good habitat with habitat movement set at two-patches-per-generation (Melbourne et al. in prep). Landscapes were started with the distribution of a stable, moving population as observed in a previous experiment (Fig. 3.1). In generation zero, patches 10 and 11 had good habitat, while all other patches had bad habitat. I controlled the lifecycle of *T. castaneum* by dividing it into a growth phase and a dispersal phase (Melbourne and Hastings 2009):

Growth phase: At the start of each generation, adults were placed in patches with fresh medium and allowed to lay eggs for 24 hours. Adults were then removed and discarded, and eggs were allowed to develop through larval and pupal stages to adulthood over 35 days.

Dispersal phase: Acetate sheets covered the holes between patches during much of the life cycle to ensure dispersal was a controlled, discrete event. These sheets were removed for 24 hours on day 34 in the life cycle to allow individuals to disperse for 24 hours between patches. After the 24-hour dispersal period, the medium was sieved to remove and census adults, which were then used to initiate the following generation (Fig. 3.2).

<i>Patch</i>	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
<i>Abundance</i>	0	0	6	12	20	40	70	125	150	90	75	20	6	0	0	0	0

Figure 3.1 Starting distribution of *T. castaneum* individuals in experimental landscapes. Patch describes the individual patch number. Abundance refers to the number of beetles in each patch. Only patches 1-17 are shown because patches 18-32 had zero beetles initially. Patches 10 and 11 contained good medium and the rest of the patches contained poor medium.



Figure 3.2 Acrylic boxes (patches) containing flour medium. These patches housed *T. castaneum* beetles during the growth phase of the experiment. Individual patches were linked together into landscapes so beetles could disperse between patches. Dispersal was controlled by sliding acetate sheets between patches to block the dispersal holes.

The abundance of beetles in each patch was counted by sieving the contents of each patch to separate the beetles from the flour medium. The flour that fell through the sieve was discarded and all the material that didn't fall through was transferred to a smooth and high walled cafeteria plate for sorting. Live adults were separated out and transferred to a clean container for censusing. Live adults were counted by hand if the total abundance from a patch was less than 75 individuals. If there were more than 75 individuals, then 50 individuals were weighed first and then the total population was weighed. The total abundance was estimated by dividing the total weight by the 50-individuals weight and multiplying by 50.

Landscapes were housed in temperature controlled incubators at 30 °C and $34 \pm 14\%$ relative humidity (Melbourne and Hastings 2008, 2009). Five total incubators were used for this study, and landscapes were randomized among and within incubators once each week to prevent any systematic effects of individual incubators or location within incubators. Raw data consisted of abundance per patch for each time point (i.e. each generation). When taken together, these individual spatial abundance points create an abundance profile that can be used as a diagnostic tool for understanding the persistence of a moving population.

I used two metrics to test for differences in success between landscapes with and without assisted migration. To compare the proportion of landscapes that went extinct between different treatments, I used a chi-square test with Yates' continuity correction to test for differences in the proportion of landscapes that went extinct in each of the treatments. To compare differences in the spatial symmetry of abundance profiles, I first calculated a weighted skew measure for each landscape to produce a weighted Pearson's first moment coefficient of skewness (See equations 2.1-2.4 in Chapter 2) and then compared coefficients between assisted migration treatments using a Student's t-test.

3.3 Results

This experiment showed that assisted migration can rescue populations from extinction when applied over several generations (Fig. 3.3). Landscapes without assisted migration all went extinct before generation 9, while only 6 of 28 (2 of the original 30 lost to laboratory error rather than extinction) went extinct in the assisted migration landscapes (Fig. 3.4). Extant landscapes in the assisted migration landscapes showed stability over multiple generations (Fig. 3.3), signaling that assisted migration may be a long-term solution to rescuing species threatened by shifting climate niches. The spatial symmetry of abundance profiles also differed between treatments, showing a consistent negative skew in populations without assisted migration and a consistent positive skew in populations with assisted migration applied (Fig. 3.5).

Figure 3.3 shows all landscapes throughout the full course of the experiment. This figure clearly shows that assisted migration treatments performed better over the course of 8 generations than the controls with no assisted migration. While the control group (no assisted migration) reached full extinction before generation nine, 22 of the original 28 assisted

migration landscapes were still extant and their population abundance profiles were starting to show signs of long-term persistence.

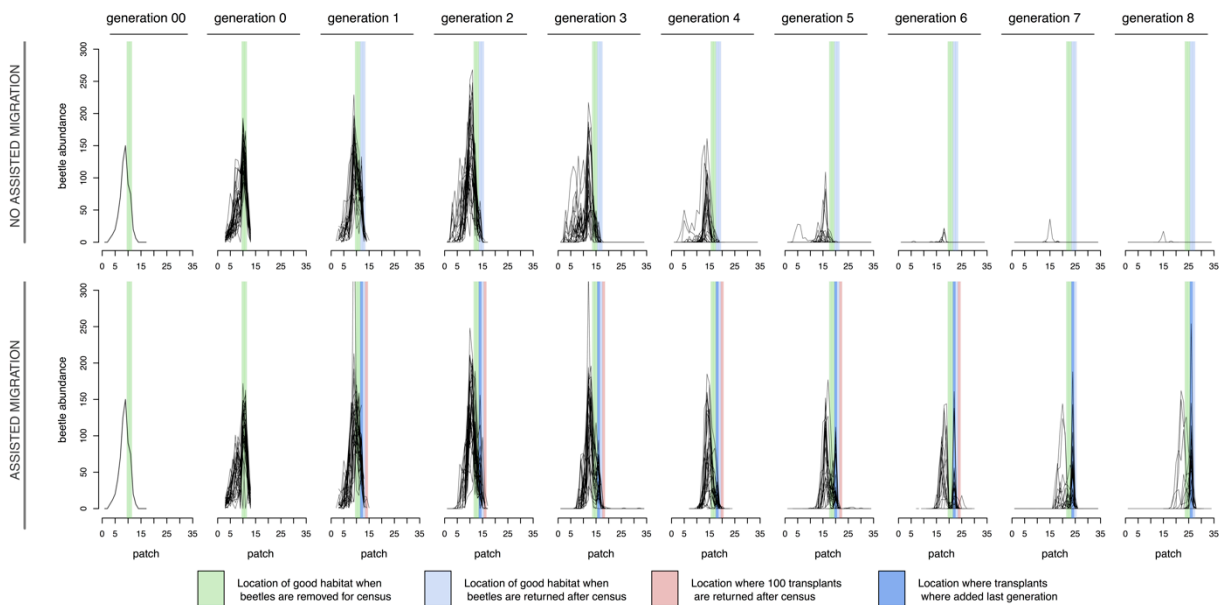


Figure 3.3 Experimental results of assisted migration in landscapes with moving good habitat. All of the landscapes in the control group (no assisted migration) went extinct by generation nine but the majority of assisted migration landscapes showed stability by that same generation. The top panel shows the 30 control landscapes from generation 00 (starting conditions), to generation 0 (growth phase with no dispersal), and then follows generations 1-8 as the 2-patch movement treatment was applied. The bottom row shows the same time sequence for the 30 replicates where assisted migration was applied in addition to patch movement. The green lines highlight the patches individuals were removed from during the census, i.e. the environment that individuals grew from egg to adulthood in. The blue lines highlight the patches that those individuals were placed back into after the census and habitat movement. The red line shows where the 100 individuals were transplanted to during each assisted migration cycle. The dark blue line shows the patches from which the 100 individuals were sourced.

Figure 3.4 shows the accumulation of extinctions throughout the experiment. These values represent a proportion of the total number of landscapes started, and so they are compared as proportions rather than rates of increase. A chi-square test with Yates' continuity correction showed a highly significant difference ($X^2 = 33$, $df = 1$, $p\text{-value} = 9e^{-9}$) between the proportion that went extinct in the no-assisted-migration treatment (28/28) and the proportion that went extinct in the assisted-migration treatment (6/28) by the end of the

experiment. A follow-up Fisher's exact test for count data corroborates the results of the chi-squared test ($p\text{-value} = 3.5e^{-10}$, odds ratio = 0, 95% confidence interval = 0, 0.057) in saying that there is a significant difference between the treatments.

Figure 3.5 shows the differences in skew coefficients between the treatments. Landscapes following a moving habitat without the application of the assisted migration treatment consistently showed a negative skew across all generations. Landscapes in the assisted migration treatment started with a similar negative skew according to the experiment's initial conditions, then became more symmetrical through the first few applications of assisted migration, and then stabilized on a positive skew for the majority of the remaining generations. The t-statistics, p-values, and degrees of freedom for each of these pairwise comparisons are shown next to each generation panel in Figure 3.5 and show that there was a significant difference in symmetry between treatments for most of the first five generations.

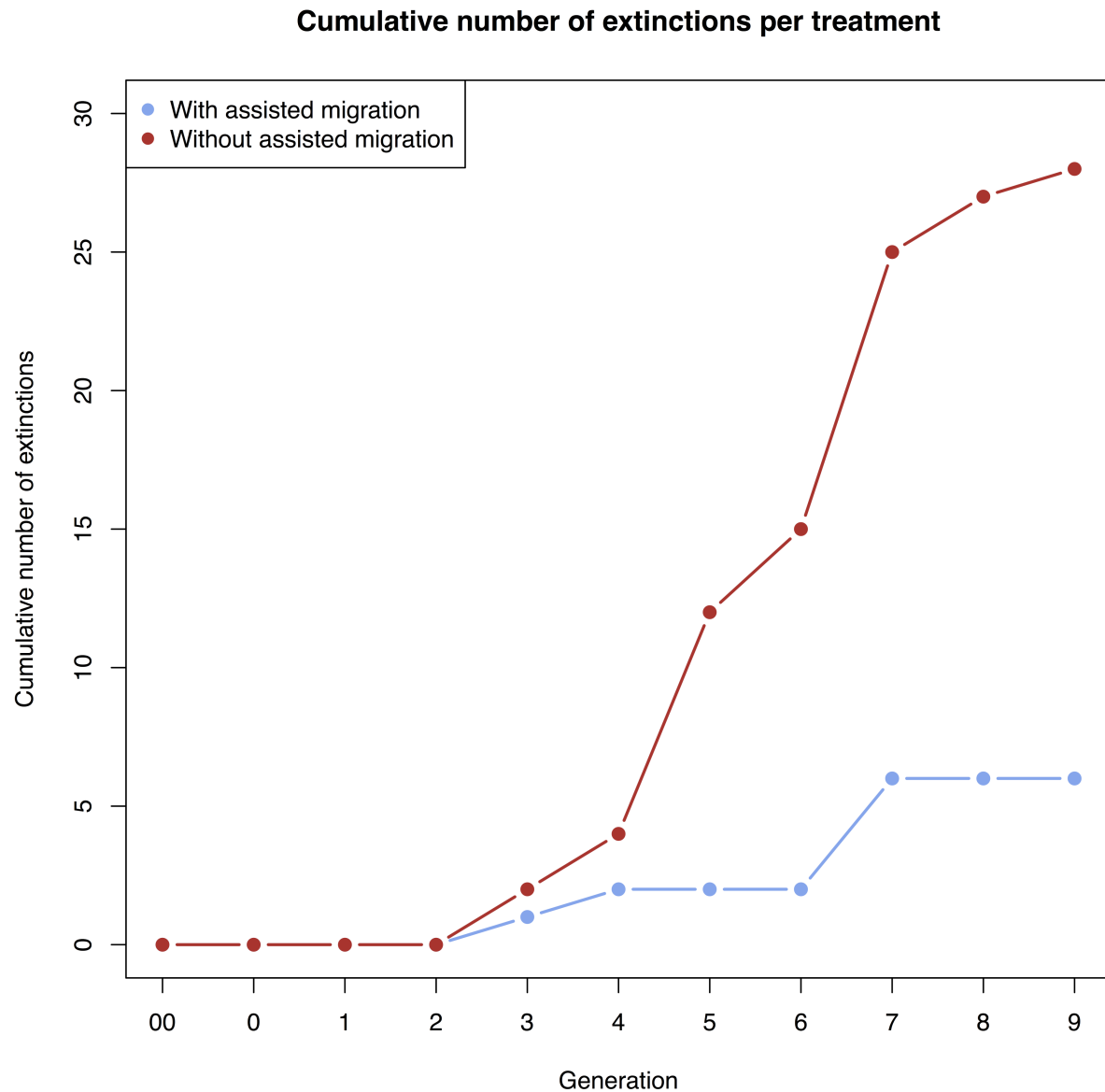


Figure 3.4 The cumulative extinctions between the two treatments. Extinctions began in generation 3 for both treatments: with assisted migration and without assisted migration. Even though both treatments started experiencing extinctions during the same generation, the proportion of extinct landscapes per treatment quickly diverged as the no assisted migration treatments continued to quickly accumulate extinctions until all treatments were extinct by the beginning of generation 9.

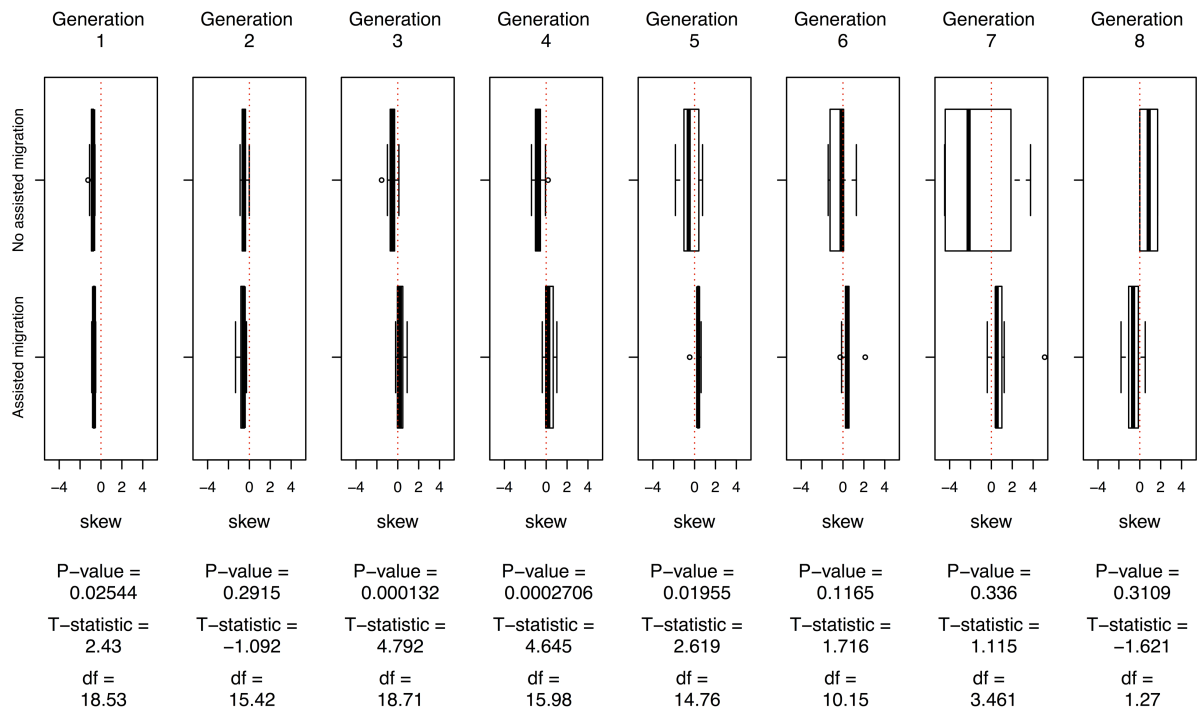


Figure 3.5 The weighted skew values for each treatment across generations. These panels show that a moving population without assisted migration maintained an abundance profile with a negative skew trailing behind the moving habitat. Applying assisted migration to half of those populations first shifted the skew to a symmetrical shape for one generation and then shifted the skew in the positive direction until generation 8 when the skew shifted back slightly. Generations 3-6 showed the strongest difference between skew because there were sufficient samples left in both treatments for comparison. In generation 6-8, the no assisted migration landscapes had mostly gone extinct and the sample size between treatments was thus very uneven. Generation 1 and 2 were when assisted migration was first being applied and there had not yet been time for spatial symmetry to be altered. Boxplots show the median weighted skew value and 25% quantiles for weighted skew values across all replicates with each treatment. The p-values, t-statistics, and degrees of freedom reported for each graph is the output of a Student's t-test comparing the skew coefficients from the two treatments.

3.4 Discussion

Here I provided a controlled, highly replicated laboratory microcosm experiment tracking the success of assisted migration over 10 generations. The purpose of this experiment was to test the ability of assisted migration to rescue moving populations from extinction and to address two critical gaps in our understanding of assisted migration: 1) most field experiments do not follow the fate of populations over time, and 2) most field

experiments do not include contrasts between populations with assisted migration and populations without assisted migration (i.e. no control group). In doing so, this study is better able to report on the ability of assisted migration to foster multi-generational persistence, as opposed to studies that only report on the recruitment success of transplanted individuals (Levin and Clay 1984, Prince et al. 1985, Geber and Eckhart 2005, Marsico and Hellmann 2009, Hancock and Gallagher 2014).

In this study, I hypothesized that assisted migration would lengthen time to extinction and restore the symmetry of the abundance profile of beetle populations in a moving-habitat scenario when compared with a control group. Excitingly, results show that assisted migration did significantly reduce extinction risk for moving populations (Fig. 3.4), providing the first experimental demonstration that assisted migration can work to reduce extinction risk and combat the effects of climate change. Assisted migration also reversed, rather than restored, spatial symmetry. The assisted migration treatments first matched the negative skew of the control landscapes, then became symmetrical for a single generation, and then maintained a positive skew for the rest of the experiment. There was a significant difference in both the proportion of landscapes going extinct and abundance profile asymmetry between assisted migration and no assisted migration treatments (Figs. 3.4 and 3.5, respectively).

Abundance profiles provide insight into population health by displaying the number and the symmetry of the spatial distribution of individuals in the population. Both models (Berestycki et al. 2009) and experiments (Melbourne et al. *in prep*) show that a population's abundance profile becomes asymmetrical when movement is applied to the habitat, and this experiment confirmed those findings. Transplanting individuals from the trailing edge of a

moving population to the leading edge of a moving population restored the symmetry of populations, but a positive (rather than symmetrical) skew was associated with persistence.

These results suggest that assisted migration can rescue populations from extinction in scenarios where their habitat is moving. Other studies have shown individuals transplanted outside of their current range can successfully colonize the transplant location (Willis et al. 2009), but the mechanisms attributed to colonization success remain idiosyncratic (Gaston 2009) and new methods have yet to emerge that produce a cohesive answer as to why assisted migration works in some species and not in others. A good example of the variation in success of assisted migration is presented in Liu et al. (2012), in which they transplanted 20 species of orchid up a mountain to escape the construction of a new reservoir. The authors found a diversity of responses across species, where 9.3% of the 462 individual plants died within the first year due to the stress of transplantation, 21.0% of the plants died due to herbivory by insects and/or small mammals, and 60.4% survived for the entire, 5-year study. Additionally, an extreme cold event led to mortality in four of the 20 species, one of which (*Vandopsis gigantean*) was fully extirpated.

The primary limitation of my study is that the data were produced in a microcosm and suffer from the lack of complexity that field systems provide (e.g. lack of community dynamics and environmental variability). However, microcosms avoid the ethical and logistical complications of conducting field experiments of assisted migration and are, thus, critical to advancing our understanding of its success as a conservation strategy. A second limitation is that this experiment only studied the demographic responses to assisted migration and not the genetic responses. One aspect often neglected in assisted migration studies is that the success of assisted migration will depend on the ability of the focal species to adapt to climate niche movement by increasing dispersal speed and developing more

tolerance to variable conditions. Without this adaptation, assisted migration would need to be carried out every generation in perpetuity. Future studies addressing the potential for adaptation and heightened dispersal ability to enhance the success of assisted migration in natural systems will be helpful. Studies that tease apart the relative contributions of genetic and demographic responses to the success of assisted migration will be particularly valuable.

Additionally, future studies should strive for large-scale, long-term experiments that incorporate biological dynamics (competition and predation) for a more comprehensive understanding of assisted migration as a conservation strategy for endangered populations. These studies should focus on applying assisted migration before populations face imminent extinction. Studies where the few remaining individuals in a population are transplanted to a new location offer little value in the pursuit of generality. These studies are rarely reproducible, and the success of assisted migration becomes tightly linked to the natural history of the particular focal species.

CHAPTER 4

NOT ALL NICHE'S ARE ATTACHED TO EARTH'S SURFACE

4.1 Introduction

Over the last several decades, we have seen an emerging interest across disciplines in the analysis of moving objects (Laube and Imfeld 2002, Alfriend and Yan 2005, Laube et al. 2005, Chang et al. 2016, Mishra and Saroha 2016). In ecology, movement can be considered in the context of multiple niche components (Hutchinson 1957, Kearney and Porter 2004, 2009, Colwell and Rangel 2009, Holt 2009). For example, researchers interpreting patterns of bird migration can consider solar angle (Matthews 1953, Pennycuick 1960, Walcott and Michener 1971), wind (Liechti 2006, Felicísimo et al. 2008, Mateos-Rodríguez and Bruderer 2012), and local temperature regimes (Jenni and Kéry 2003, Schmaljohann et al. 2008, Lazarus and McGill 2014), which are functions of both Earth's rotation and seasonal solar energy variation (Brock 1981, Nikolov and Zeller 1992, Meeus 1998, Hesslerová et al. 2013).

In this chapter, I demonstrate the ways that we can improve the analysis of moving objects on or near the surface of Earth by linking coordinate systems for Earth and coordinate systems for the sun. The model I present in this chapter describes the relativistic motion between Earth and the sun at two different time scales: yearly and hourly. This model describes large-scale movement that links a fixed point in one system with the movement of a sister point in the opposing coordinate system for one year. I seek to show that a stationary observer on planet Earth will see a single point in the atmosphere as moving in an analemma pattern, with the shape of the analemma (Fig. 4.1) determined by the location from which the point is being observed, the time of day at which the point is being observed, and the duration of time over which the point is being tracked (Yeow 2001, Sidoli 2005, Bull 2011,

Lynch 2012). In contrast, a stationary observer on the sun will see a point on Earth's surface passing below, in a vector field that has the shape of two opposing parabolas. These parabolas represent the time-dependent, mirror image of the analemma. In Chapter 5, I use the framework developed here to consider the motion of individuals on Earth's surface as well as the motion of individuals detached from Earth's surface, using the example of avian migration. Broadly, I seek to show that mapping ecological components from an external observational coordinate system standardizes their relative motion, allowing us to directly compare the movement of ecological components even if they are traveling in different directions or are observable at different scales. In doing so, I hope to demonstrate the influence relative motion can have on our measurement and understanding of ecological systems.

I begin by defining the context for this relative motion tool and by highlighting two key ecological components that are constantly moving in space: Earth's surface and the contact zone where solar radiation hits the Earth's surface. These two components provide a case study of how controlling for motion-biased measurement can lead to new understanding of ecological patterns. I then describe a set of coordinate systems (Earth coordinate system, solar coordinate system, and observational coordinate system) and sync transformations that allow for mapping the relative motion between Earth and the solar contact zone to correct for human-scale motion bias. I then provide results for two scenarios: 1) a year-scale analemma scenario that describes how one ecological component will measure another component as they pass each other in space over the course of a year, and 2) a day-scale scenario that describes the relative contributions of different ecological components to the realized movement patterns of an individual over the course of an hour or a day.

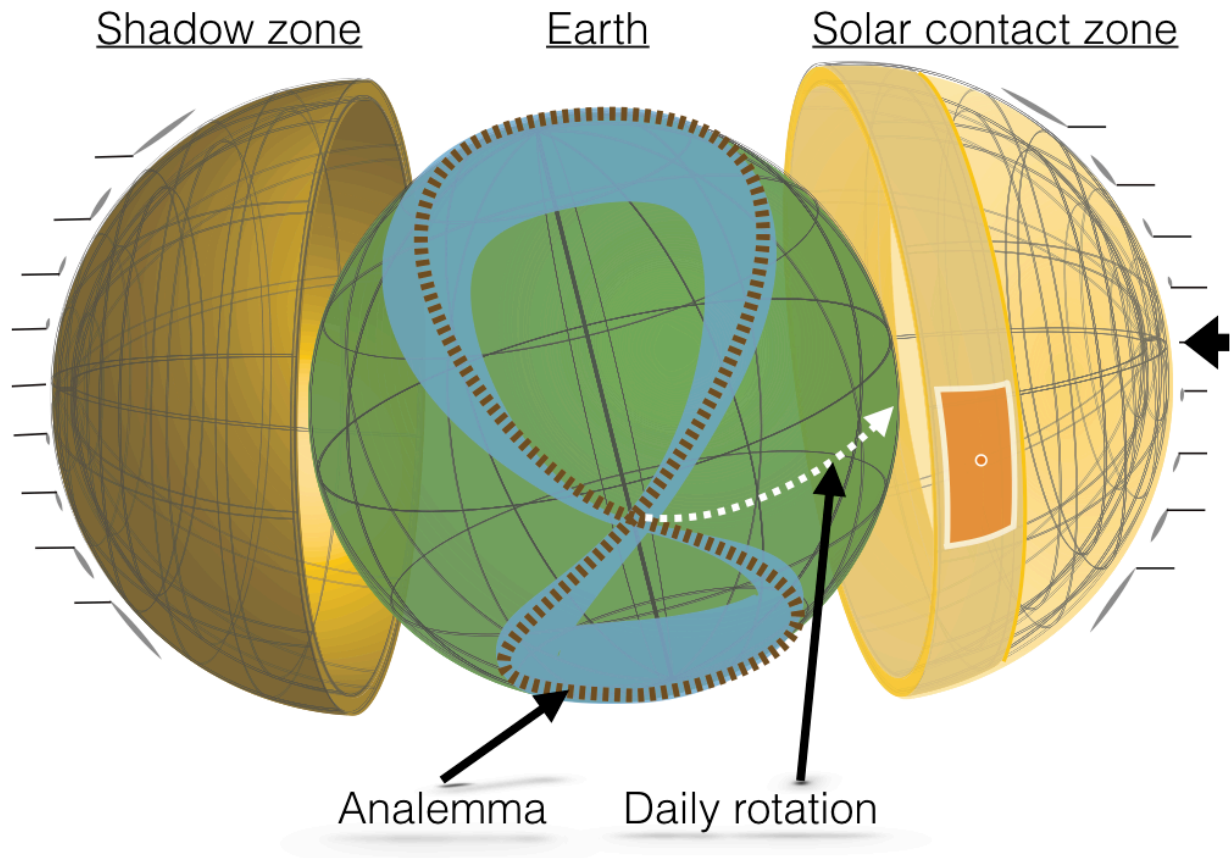


Figure 4.1 Earth suspended in a sunbeam. Components of the nested coordinate systems including a spinning Earth (Earth coordinate system), a containing sphere of solar energy (solar coordinate system), a rectangle showing the home range of a hypothetical individual in the solar coordinate system, and the analemma shape indicating where that individual might be located throughout the course of a year's travel in the Earth coordinate system. The green sphere represents Earth as it spins within the stream of photons coming from the sun. The yellow sphere represents the contact of those photons with the surface of Earth. To base the model on a solar reference, the solar contact sphere (i.e. the solar coordinate system) stays stationary through time, while Earth moves within it. In this figure, the sun is located to the right so the solar energy is flowing from right to left. The right hemisphere experiences daytime, while the left hemisphere experiences nighttime. The orange box on the yellow sphere is a home range of an individual in the solar coordinate system. The point at the center of the box is the current location of an individual detached from Earth's surface. The brown dotted line shows the locations on Earth where the detached individual would be seen throughout the year, and the blue buffer around the line shows how the solar home range changes shape as it translates to the Earth coordinate system. The figure-8 shape represents a generalized analemma. The observational coordinate system (not shown) is a sphere surrounding the Earth coordinate system and the solar coordinate system.

4.1.1 Defining attached and detached niches

When Hutchinson defined a niche as a multi-dimensional hyper-volume (Hutchinson 1957), it sparked discourse about how to measure such a phenomenon in nature and how to use those measurements to refine the theory over time. Elton (1927) and Grinnell (1917) had previously realized that organisms respond differently to the biotic and abiotic components of their habitat. Thus, theory was developed around measuring and interpreting a species' interactions and sustainable growth rates using the surrounding biotic and abiotic environment as a measure of niche size and shape (reviewed in Holt 2009).

Within this paradigm, the “fundamental niche” is considered the maximum spatial extent an individual can occupy, while the “realized niche” is considered the subset of that fundamental niche that species do occupy. The size of a species' realized niche, that is, the space occupied, is largely determined by the biotic interactions that limit the species' ability to exploit the full fundamental niche (Connell 1961, Kearney and Porter 2004, McNerny and Etienne 2012). These definitions focus on spatial occupancy. More recent work has shifted the focus from defining a species' niche by the spatial extent of the suitable abiotic environment to defining a species' fundamental niche by the physiological traits of individuals (Clarke and Gaston 2006, Kearney and Porter 2009, Chown and Gaston 2015). This physiological perspective defines the fundamental niche as a property of the organism while the realized niche is the spatial pattern of occupancy that is an outcome of the interaction of the organism with its environment.

This latest, physiological, iteration of the fundamental and realized niche adds flexibility, as niches no longer need to be attached to Earth's surface. Fundamental niches are defined by the physiology of the individual and not the habitat that they live in, although of course they are connected by the interaction of the fundamental niche with the abiotic environment, thus determining the realized niche. Thus, a flying bird will “take its fundamental niche with it”, so to

speaking, as it travels, and its realized niche will change constantly as the individual shuttles between hot and cold areas to meet its physiological needs. The process of measuring a niche changes when the niche dimensions are detached from Earth's surface. Rather than measuring interactions between an individual and its surrounding environment to define niche dimensions (McInerney and Etienne 2012), an individualized niche perspective calls for first defining the physiological needs of an individual and then mapping those physiological conditions across the landscape to identify the locations where individuals can meet those needs (Kearney and Porter 2004, 2009).

There are five climate dimensions to the physiological niche of an above-ground terrestrial organism: solar radiation, air temperature, relative humidity, air pressure, and wind speed (Gates 1980, Kearney and Porter 2004, 2009). Henceforth, I will refer to this 5-dimensional physiological niche as the climate niche. This suite of climate variables controls the rate at which an individual can release metabolic heat waste from its body to the surrounding environment (Porter and Gates 1969, Porter and Tracy 1983). If climate conditions are unsuitable, the individual will release too much or too little metabolic heat and lose performance as a result (Porter and Gates 1969, Spotila et al. 1973, Bakken et al. 1974, Gates 1980). If climate conditions are suitable, the individual establishes an equilibrium with the environment where it can exhaust enough heat waste to be active and still maintain a stable body temperature. Highly mobile individuals need to metabolize more energy and, consequently, produce more heat waste than sedentary individuals (Pennycuik 2003, Bishop 2005, Klaassen et al. 2012). Thus, highly mobile individuals should occupy cooler environments than sedentary ones to exhaust this extra heat.

It takes all five dimensions of the climate niche to fully define the relationship between an individual and its environment, but those five dimensions are not equal in their

influence on the outcome (reviewed in Gates 1980). Solar radiation has a disproportionately large influence on the climate niche because it supplies the energy to the environment (Clarke and Gaston 2006, Angel 2006), while the remaining dimensions determine how easily that energy can dissipate from the individual (Gates 1980, Kearney and Porter 2009). Solar radiation is supplied directly from the sun, so trends in solar movement through time are translated into trends in ecological distribution (Williamson and Neale 2001, Clusella-Trullas et al. 2008, Gaston et al. 2009, Bozinovic et al. 2011, Victor III et al. 2012, Chown and Gaston 2015). Here I focus on this solar dimension and present a tool for tracking the movement of the sun as a way of defining climate niches for ecological investigation. This tool can be expanded to accommodate the relative motion of multiple, detached dimensions of a species' climate niche, but here I focus on solar radiation because it is the most important dimension of the climate niche (Porter and Tracy 1983, Porter and Sabo 2002, Jackson 2010).

4.1.2 Solar energy is the primary detached niche component

Terrestrial coordinate systems reference locations either to Earth's center of gravity, to a point on its surface, or to its polar axis using latitude and longitude (Meeus 1998). Thus, terrestrial coordinate systems require a nonlinear association between 'clock time' and a location to track Earth's rotation (Meeus 1998). Clock time has served as an important tool throughout science and history (Landes 2000), but clock time is not the most relevant measure of time for many ecological questions. More relevant measures of space and time, such as the location of the sun, can provide insight into the connection between planetary dynamics and the movement patterns of organisms that travel across the Earth (Laube and Imfeld 2002, Laube et al. 2005).

Here I develop a tool to map the relativistic relationship between Earth and the sun because spatial patterns on Earth's surface and energy inputs from the sun are two central organizing forces of life on Earth (reviewed in Roderick 2006, Jackson 2011), but they are moving in different directions from each other through time. Thus, disentangling their relative contributions to the movement of an organism can be difficult, especially for highly mobile species, but is important. The interconnections between Earth and the sun drive stationary surface processes, such as photosynthesis, as well as non-stationary surface processes, such as the movement of plants, animals, and water through time (Chown 2004, Chown and Gaston 2015). Beyond providing energy for plants to make sugar, the sun moves material around the surface of Earth by powering currents in the ocean and in the atmosphere (Makarieva et al. 2013). Many aspects of life on Earth are organized around these sun-driven processes, so fluctuations in the amount of energy coming from the sun will change the outcomes of sun-driven processes. This mapping tool can improve visualization and measurement in these moving systems by controlling for motion of the sun to isolate the motion of organisms relative to the sun (Fig. 4.1).

4.2 Methods

Here I mathematically describe the relative motion between Earth and the sun. It takes three objects to simulate this interaction and those three objects are called the "Earth coordinate system," the "solar coordinate system," and the "observational coordinate system." I will define each of these terms below but then refer to them by these names throughout. It takes three mathematical objects to describe Earth and the sun because the solar coordinate system and the Earth coordinate system are nested within the observational coordinate system to allow their joint movement to be tracked through time. Each of these

coordinate systems is built using a mathematical structure called a rigid body, which is defined as a set of points arranged in space, whose locations relative to each other are assumed to stay constant over time (Kosenko 1998, Arribas et al. 2006, Carron 2013, Pagnozzi and Biggs 2014). When the rigid body takes on a specific coordinate form, it becomes a coordinate system (Schwab and Meijaard 2006) and the term rigid body and coordinate system become interchangeable. Thus, I define a coordinate system as the orientation of points within a rigid body.

Earth moves a lot over the course of a year and this movement follows a complicated trajectory (Meeus 1998). The sun is a moving object relative to a surface observer, but the position of the sun changes by only small increments day-to-day. However, over the year these small increments ultimately form a figure-8 shape called the Analemma (Figure 4.1) (Yeow 2001, Bull 2011, Lynch 2012). The north-south movements creating the vertical components of the analemma are due to changes in the sun's declination (distance above the horizon) (Meeus 1998). The horizontal components of the analemma are due to the *equation of time*, which maps the relationship between Earth's daily spin and Earth's location in its orbit around the sun (Meeus 1998, Lynch 2012). The analemma is an important part of the model because the inner rigid body, Earth, moves along this path.

In the following sections I convert the mathematical and logical abstractions of relativity into a model that forms the basis of an approachable spatial mapping tool for data visualization. I begin by outlining the mathematical structure of the rigid body model and defining the parameters used to move each rigid body in such a way that the model will mimic Earth's movements. I then formalize this mathematical structure into a Geographic Information System (GIS) that includes an external observational coordinate system for measuring relative motion.

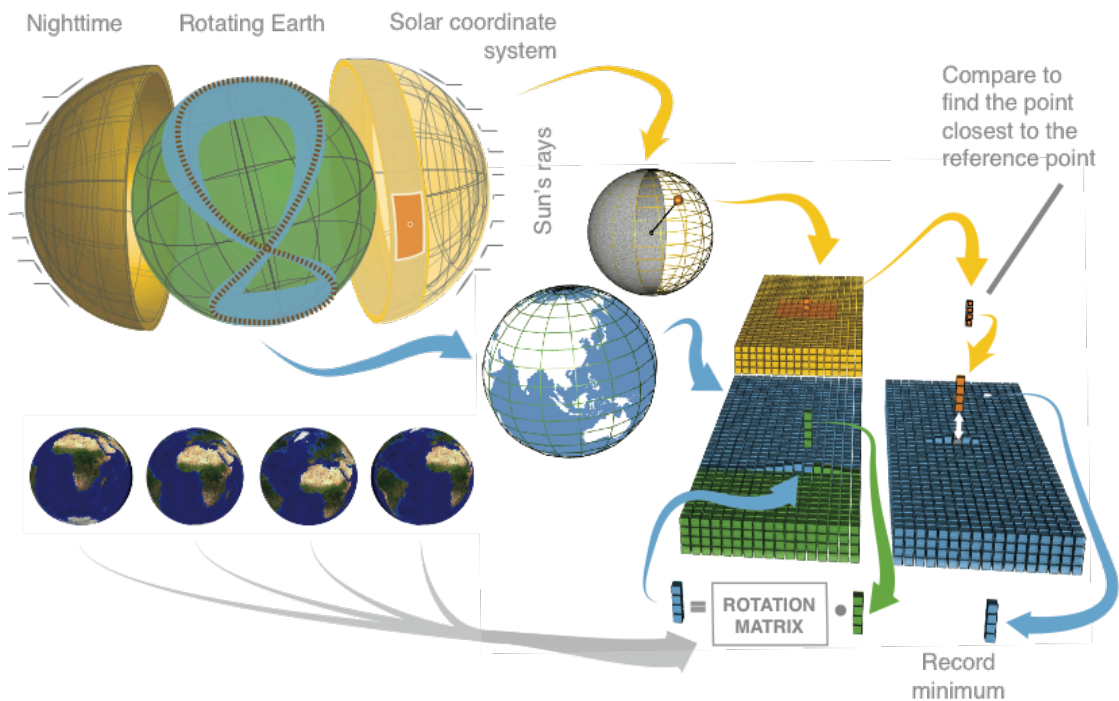


Figure 4.2 Relativistic Geographic Information System summary. Starting from the familiar figure of the two rigid bodies on the top-left, the location of the detached individual is identified as a cell located at a row and column defined by the detached individual's latitude and longitude. A buffer of cells around that point define the larger home range of that individual in the detached environment. At each iterative time step, the earth matrix is rotated through an element-by-element operation that pulls a stack of x, y, and z coordinates, multiplies them by a composite rotation matrix defining the three rotations needed to mimic Earth's rotation, and then returned to the array. When each stack of the array has been processed to represent its new location, then the solar array and earth surface array can be compared for similarities. When compared, the points of interest in the solar storage array are measured against each stack in the earth surface array as a straight line distance between points in Cartesian space. The point is the earth surface array with the shortest distance to the solar reference point is pulled as the 'nearest neighbor' and those two points are stored as time specific co-locations. The four globes on the lower left of the figure represent 4 reference orientations throughout the year (from left to right): winter solstice, spring equinox, summer solstice, and fall equinox.

4.2.1 Defining Earth and the sun as rigid body coordinate systems

The rigid body model operates using three spheres, each a rigid body with the same origin and radius, representing the three coordinate systems. While each sphere occupies exactly the same space, we can conceptually think of these spheres as being arranged so that the Earth coordinate system, E, is on the inside; the solar coordinate system, S, is wrapped around E; and

the observational coordinate system, O, is on the outside of both E and S (corresponding with the conceptual model of Fig. 4.1). The observational coordinate system is crucial for tracking relative motion between the Earth and solar coordinate systems. Since the objects are rigid bodies, they can be represented either in spherical or Cartesian coordinates and rotated using standard math.

All movements of a rigid body can be decomposed into rotational components defined as rotations around an axis (Carron 2013). The magnitude and direction of these rotations are measured with reference to an external coordinate system (the observational coordinate system), which is also a rigid body. Here we simplify the rigid body problem to its least-complex form (no translations are necessary) by modeling Earth as one rigid body, modeling the solar coordinate system as another rigid body, constraining these rigid bodies to the origin, and only rotating them around primary axes of the observational coordinate system. As a consequence, only the most elementary forms of rigid body equations are needed to model the sun-Earth relationship through time.

This simple form of moving a single point of a rigid body around the axis of rotation uses the orthogonal matrix R as a rotation matrix to transform the coordinates of a point r from the observational coordinate system to the time-specific rotated coordinate system r' , according to $r' = Rr$, where r' and r are 3x1 matrices containing the x , y , and z coordinates of the point in Cartesian space. Rotating the entire rigid body requires independently rotating each point in the body according to the same R .

To model the interactions of the sun and Earth over time, I first establish the observational coordinate system, O, which is the external reference frame for measuring movement between the other two rigid bodies. The rigid body spheres E and S representing Earth and the solar coordinate system respectively are first constructed as surfaces of hollow spheres

using a spherical coordinate system and are thus in $\mathbb{S}^2$. I then convert $\mathbb{S}^2 \rightarrow \mathbb{R}^3$ to directly compare E and S in $\mathbb{R}^3$. The points of a rigid body maintain their positions relative to each other when undergoing rotation, so the spherical coordinates embedded in the original $\mathbb{S}^2$ bodies maintain their spatial structure, regardless of how they are rotated. By storing both the $\mathbb{S}^2$ and $\mathbb{R}^3$ coordinates for each point the model can accept both spherical coordinates and Cartesian coordinates.

4.2.2 Making the model move

All three of the rigid body spheres in this model can be moved independently of one another, but when implemented as a connection between solar contact zone and Earth's surface, only the sphere representing Earth, E , needs to rotate at each time step. Under normal operation, the observational coordinate system, O , remains stationary as a uniform reference for motion between the other two spheres, and the solar sphere, S , is initially moved into place to represent solar angle in a ring arrangement and then left stationary for model runs.

The rotational angle, speed, and distance of a rigid body rotation can be described by a series of vectors describing the magnitude and direction of that rotation (method reviewed in Kosenko 1998, Arribas et al. 2006, Carron 2013). In 2D, the velocity or acceleration of a flat plane (e.g. flat rigid body) can be represented with the following equations:

$$\vec{v} = (\vec{\omega} \times \vec{r}) \quad (1)$$

$$\vec{a} = (\vec{v} \times \vec{r}) + (\vec{\omega} \times \vec{v}) \vec{a} = (\vec{a} \times \vec{r}) + (\vec{\omega} \times \vec{v}) \quad (2)$$

$\vec{a} = \vec{a} \times \vec{r} + \vec{\omega} \times \vec{v}$ where $\vec{r}$ represents a single element of the larger rigid body to be rotated, $\vec{\omega}$ represents an angular velocity vector, and $\vec{a}$ represents an angular acceleration for the surface of the rigid body sphere. When rigid bodies interact under complex rotation, the location of one body's orientation becomes conditional on the other's orientation. This means that the

movement of reference point $d\vec{r}_B$ depends on the initial location of $d\vec{r}_A$ and the conditional relationship $d\vec{r}_{B/A}$, according to $d\vec{r}_B = d\vec{r}_A + d\vec{r}_{B/A}$. The time derivative of this equation gives

$$\frac{d\vec{r}_B}{dt} = \frac{d\vec{r}_A}{dt} + \frac{d\vec{r}_{B/A}}{dt} \quad (3)$$

to produce the conditional velocity equation

$$\vec{v}_B = \vec{v}_A + \vec{v}_{B/A} \quad (4)$$

The second derivative gives

$$\frac{d^2\vec{r}_B}{dt^2} = \frac{d^2\vec{r}_A}{dt^2} + \frac{d^2\vec{r}_{B/A}}{dt^2} \quad (5)$$

to produce the conditional acceleration equation

$$\vec{a}_B = \vec{a}_A + \vec{a}_{B/A} \quad (6)$$

where $\vec{v}_{B/A} = \vec{\omega} \times \vec{r}_{B/A}$ and $\vec{a}_{B/A} = \alpha \times \vec{r}_{B/A} - \omega^2 \vec{r}_{B/A}$.

Extending this example into spherical three dimensions provides a mechanism to relate the two rigid bodies E and S to the 3D observational coordinate system. To track relative movement between elements within the observational coordinate system, the observational coordinate system needs a standard reference point to measure that movement from. The reference vector $\vec{m}$ establishes that reference point for measuring motion in O by running from the origin of O and along the positive x axis to define the point where Earth's prime meridian and equator lie in Earth's surface coordinate system, E . I have arranged the rigid bodies in the observational coordinate system so that the solar coordinate system (a.k.a. a formal spatial object describing the solar contact zone) can remain stationary through time and the Earth coordinate system can express all of the motion in the system without causing gimbal lock. Gimbal lock is a problem that arises when two axes of multiple coordinate systems become parallel so there is no way to know which direction is positive and which is negative along those parallel axes: this forces the rotation into a two dimensional degenerate space, thus losing important rotational

properties in the third dimension (Hoag 1963). The observation reference point $\vec{m}_A$ remains fixed through time so all motion is expressed in terms of $\vec{m}_B$ across the $\mathbb{S}^2$ surface, E . Euler's rotational theorem shows that the combination of three independent vectors produces one resultant vector (Euler 1776, Meyer 1966, Palais and Palais 2007), which will be called $\vec{p}$. As point $\vec{m}_B$ moves from $\vec{m}_{B_t} \Rightarrow \vec{m}_{B_{t+1}}$, $\vec{m}_B$ travels along $\vec{p}$. Vector $\vec{p}$ thus models the spatial trajectory of rigid body E through time based on the composite of three rotations, negative *local hour angle*, negative *solar declination*, and negative *right ascension* at each time step. These rotations will be described in section 4.2.3.

A 2-hour discrete time interval is implemented as a standard unit of time. This time interval matches the resolution of available movement data that I will use in Chapter 5 and available computing power. For each 2-hour time step, the S coordinate system remains stationary and the E coordinate system rotates along vector $\vec{p}$. These are the basic dynamics of this model and only explain the dynamics of stationary points on a moving rigid body. Creating an ecologically relevant model requires another degree of movement to describe non-stationary points in each of the rigid bodies so we can model individuals traveling across Earth's surface or navigating relative to the sun.

This model allows movement across a rotating raster at the same time that the raster is rotating within the observational coordinate system. An individual moving from point g to point h on rigid body E will travel distance d in 2 hours to produce a curved distance vector $\vec{d} = \vec{g} \times \vec{h}$. An individual moving from point i to j on rigid body S will travel a distance l in 2 hours to produce a curved distance vector $\vec{l} = \vec{i} \times \vec{j}$. The vector resulting from the product of baseline movement along with surface movement and solar movement is the composite vector $\vec{T} = \vec{d} \times \vec{l} \times \vec{p}$, where $\vec{T}$ is the total distance traveled in the observational coordinate system O , d and l are the distances traveled in each reference frame and $\vec{p}$ is the starting location of the

measurement and is referenced to the reference vector $\vec{m}$ in the coordinate system O . The benefit of rasterizing this set of movements is that the $\vec{p}$ vector drops out of the model fitting procedures so model fitting (described later in Chapter 5), is reduced to determining the relative contributions $\vec{d}$ and $\vec{l}$ make to the observed conditional vector $\vec{T}$.

4.2.3 Modeling the movement of Earth throughout the year

I have fixed the orientation of S to define the sun as the fixed reference point for measuring ecological interactions, and so all remaining motion must be translated into rotations of the rigid body, E , to express the full dynamics of Earth's rotation. The initial position of E is the position it would take relative to the sun during the spring equinox. At the moment of the equinox, the pole of E is aligned with the y-axis of O and the prime meridian of E is aligned with the x-axis of O to match the alignment of S relative to O . This is the only moment when E and S both align with each other and also align with the y-axis of O . From the initial position, I begin to rotate E to simulate the passage of time using a sequence of 3 rotations to simulate the rotation, tilt, and orientation of Earth relative to the sun. The composite of these rotations takes the form $E_{t+1} = E_t * R_\theta R_\delta R_\alpha$ where R_θ , R_δ , and R_α are orthogonal matrices rotating the rigid body E by the angles θ , δ , and α respectively (Fig. 4.3). These rotations are non-transitive so they must be applied in sequence to get the proper final orientation for each time step. This ordering produces the correct final orientation and defines the singularities where gimbal lock occurs to be out of the field of rotation for the model.

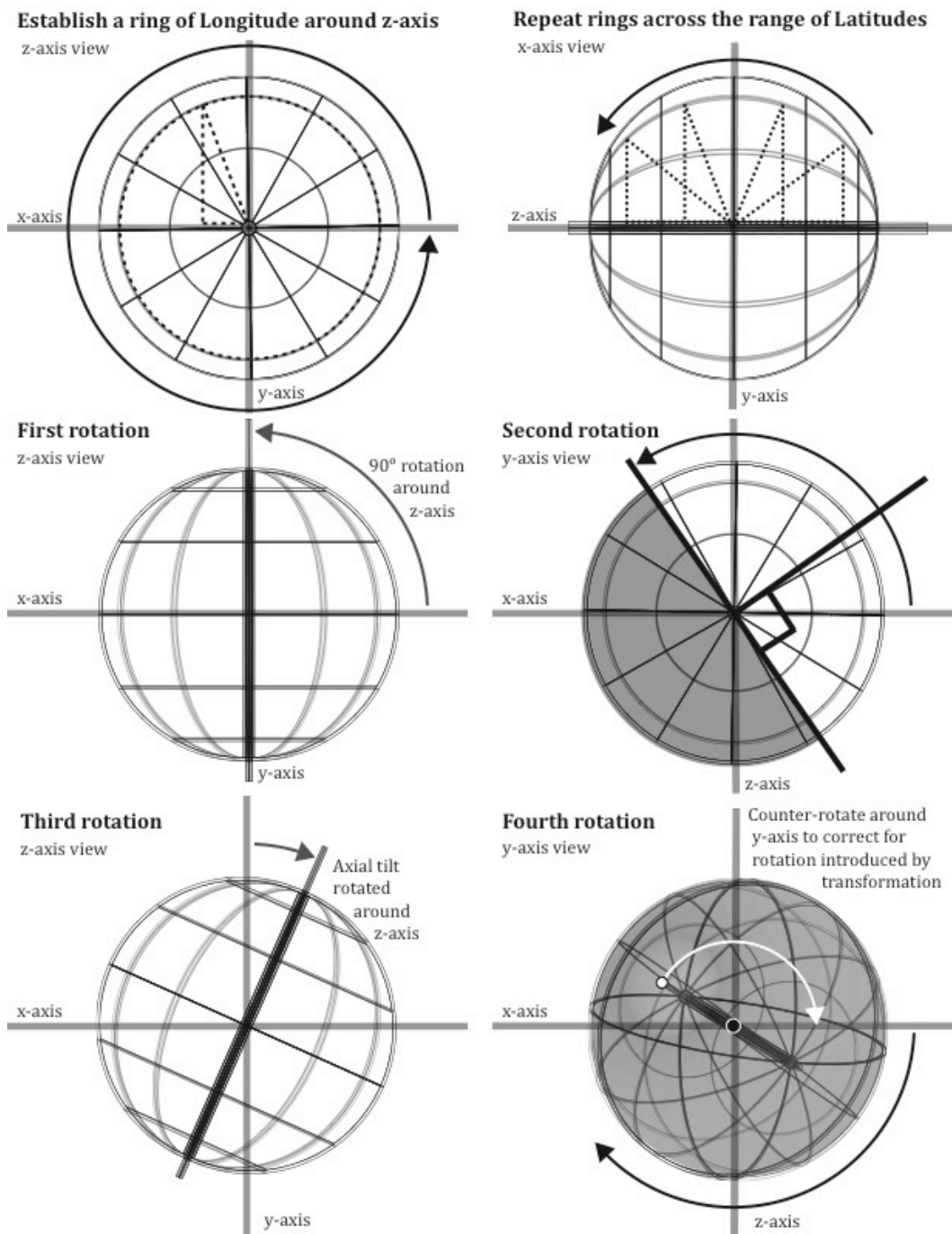


Figure 4.3 Order of operations for establishing and rotating the rigid body E. The first row describes establishing the rigid body. The remaining rows show the sequence of four rotations imposed on the rigid body E to mimic the rotations of Earth throughout the year.

I will here discuss the rotation angles θ , δ , and α (Fig. 4.3). These rotations must be applied in the correct order, otherwise they will produce the wrong final orientation, even if the

individual angles stay the same (Schwab and Meijaard 2006, Arribas et al. 2006). For the final orientation to be aligned correctly, the first in the rotation sequence for E is a rotation around the y-axis of O by the angle θ to align the equatorial prime meridian and the Greenwich mean time (GMT) of S with the appropriate longitudinal time and time zone of E . The angle θ is defined as $\theta = (-H_{\text{sunrise}} - H + 12) * 15$ where $H = \text{local hour angle}$ measured westwards from the prime meridian when viewed from the south, the addition of 12 is the hour equivalent of a 180 degree rotation and is done to reference the time zone of any generic surface location rather than just the prime meridian or GMT, and multiplying the subtotal by 15 is to convert from hours to degrees. After this rotation, the polar axis of E is still aligned with the y-axis of O but the prime meridian of E is no longer aligned with the x-axis of O or the prime meridian of S . The second rotation of E is a rotation around the z-axis by the angle δ to impose the tilt of Earth's polar axis on E . The angle δ is defined as $\delta = -\text{solar declination}$, measured as 0 to ± 90 degrees from the equator, positive to the north, negative to the south. The third rotation of E is a rotation around the y-axis by the angle α to impose the rotation of Earth around the sun. The angle α is defined as $\alpha = -\text{right ascension}$, measured as hour degrees from the vernal equinox, positive to the east, along the celestial equator. The full derivation for calculating *local hour angle*, *solar declination*, and *right ascension* from first principles is given in Meeus (1998) and summarized in the next section.

4.2.4 Angles for each rigid body rotation

The Meeus (1998) algorithm (Figure 4.4) was adopted by the National Institute of Standards and Technology, USA (NIST) for calculating solar declination and angle, the time of sunset and sunrise for an observer, and the shape of the analemma. NIST monitors the accuracy of the angles through time using confirmatory ground measurements to add correction factors to the model. A geometrical derivation of Meeus's algorithm is given in Figure 4.4. In this figure,

the process of calculating solar angles begins by recording A and P , which are the aphelion (summer solstice) and perihelion (winter solstice) of Earth's orbit respectively. From those two points it is possible to calculate the center of Earth's orbit and an auxiliary circle around that center point with a radius equal to the distance between the center and A or P . Tracking the difference in trajectory between Q and Earth over time describes the eccentricity (how oval it is) of the ellipse and the mean anomaly (oval misshape). The mean anomaly increases linearly over time as the orbit rotates around the sun. The true anomaly is the instantaneous anomaly of Earth at any given time. Kepler's laws of orbital motion tell us that (1) Earth travels in an ellipse around the sun and the sun is located at one of the focal points of that ellipse and (2) that Earth will speed up when it is closer to the main focal point. Calculating the location of the sun relative to the orbital ellipses then involves two steps, first calculating the two focal points of the ellipse and then measuring the rate of change in the angle between Earth and the sun as Earth travels past P and A respectively. Once the location of the sun is defined by the orbit, the orbital parameters are given as constants and all measurements are taken in reference to the sun rather than directly from P and A . P' is the primary reference point for relating the sun's location with Earth's orbit and is defined as the angle between Earth and the sun when Earth is at P . This angle is set to zero to make it the rotational reference point for other angular measurements. Angles M and V are the angle of Earth relative to the sun at two different time points and both referenced from P' . These angles, along with a measurement of the distance between the sun and Earth, r , can define the orbital position of Earth at any specified time (Fig. 4.4).

Once the orbital position of Earth is known, the rotational dynamics of Earth can be calculated according to the track the sun takes across Earth's surface (Fig. 4.4). The universal reference point for measuring Earth's rotation is an arbitrarily defined line running from pole to pole through Greenwich, England and named Greenwich Mean Time (GMT). Earth is divided

into 24 equal angular segments wrapping from GMT back to GMT. When the sun is directly overhead on the GMT line, that location is experiencing noon and the location directly on the other side of Earth is experiencing midnight. The sun's rays only shine on half of the planet at a time, and the line between light and dark is called the solar terminator. The solar terminator line is 90° in any direction from the center of solar contact and is calculated as such. Passing across the terminator from the surface of a rotating Earth is defined as sunrise when GMT passes from the dark to light of Earth and sunset when GMT passes from light to dark. If Earth traveled in a circular orbit around the center point rather than focal point, then GMT would measure solar noon at the same angle each day. However, the elliptical orbit of Earth and the off center location of Earth within that orbit mean that there is a lateral shift in the alignment of GMT and solar noon throughout the year. One complete rotation of Earth is called a sidereal day and one rotation from noon to noon is called a solar day. These two diverge according to a function called the equation of time, which describes the divergence between solar and sidereal time throughout the year. These measurements are equal during the equinoxes and solstices, but diverge from each other the rest of the year (Meeus 1998). The equation of time defines the shape of the analemma (Yeow 2001, Sidoli 2005, Lynch 2012).

4.2.5 Defining rigid bodies using computer storage arrays

To expand the vector solutions of the Meeus (1998) model to work with raster data, I adopt a data structure that can hold the coordinate values for the observational coordinate system O , hold the associated coordinate values for the rigid bodies E and S , and accommodate available National Aeronautics and Space Administration (NASA) and National Oceanic and Atmospheric Administration (NOAA) data (e.g. MODIS, NoMAD, Science on a sphere) in spherical coordinates with the dimensions 360 by 180 to match the 1-degree resolution of their published data. These three constraints best fit a data storage array with the dimensions of 180 rows, 360 columns, and 3 stacks (Figure 4.6). In this array, the 180 rows correspond to 1-degree resolution of the ring defining latitude and the 360 columns correspond to 1-degree resolution of the ring defining longitude. The index location on the row-column axis of this array defines the location of a point on the rigid body defined by this array. The stack position of a specific location defines the x , y , and z coordinates, in the coordinate system O , of that point within the rigid bodies E or S . This set-up means that a single point within a rigid body is defined here in two coordinate systems simultaneously; coordinates of E or S defined by a row and column location and the stacks below that location storing the x , y , and z coordinate of that same point in O .

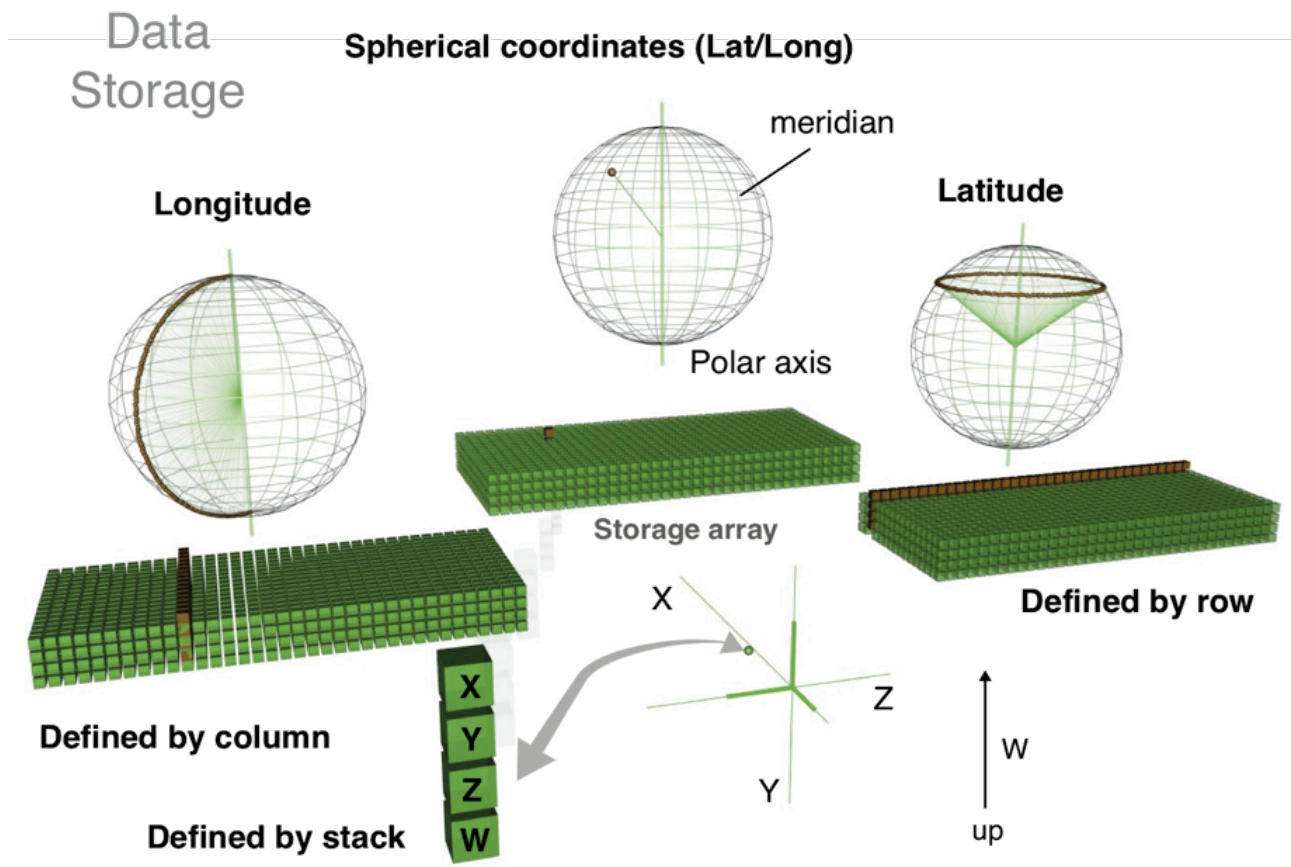


Figure 4.5 Array structure for comparing relative motion using raster data. The data storage array structure for simultaneously storing S^2 coordinates of E or S defined by a row and column location and the stacks below that location storing the x , y , and z coordinate of that same point in O . The w in this figure is an optional additional parameter that marks the direction “up” vs. “down” for x , y , and z to reference to as they rotate in space. This additional parameter is the cure for gimble lock if it occurs.

We will often need to know when a point in one coordinate system, say E , is in the same location as a point in another coordinate system, say S . Since locations are represented by discrete space, locations are not exact and we need a way to determine when two locations are in the same place. I will call locations in two coordinate systems that are in the same place with respect to the observational coordinate system a “co-location”. At a given timestep, when the two rigid bodies E and S are stationary and aligned in an orientation unique to that time point, each point on one rigid body has a sister point on the other body that is closer than all the rest. This set

of two points is determined by measuring the minimum straight-line distance between a point in one rigid body and all of the points in the opposing rigid body. A set of two nearest neighbor points marks a co-location between the two rigid bodies (Fig. 4.2).

4.2.6 Yearly time scale scenario: how movement in one coordinate system translates to movement in another coordinate system

To simulate motion, the rigid body model is iterated through time using an appropriate discrete time scale. Here, I use iterations of two hours. That is, for each iteration, the rigid bodies are rotated according to rotation angles that correspond to two hours. By marking co-locations at each 2-hour time point, the path of movement can be recorded. Motion for a full year is in this way made up of 2-hourly iterations.

Opposing vectors are a natural product of tracking motion between stationary and moving objects and so they are a natural product of the rigid body model. Iterating the rigid body model to simulate one year, results in the individual time step vectors p_t , joining end-to-end in a continuously spiraling resultant vector $p_{t_{sum}}$. Applying $p_{t_{sum}}$ to any point on the rigid body will direct that point into continuous rotation around the origin and following a path that smoothly winds up and down the rigid body sphere as Earth experiences a full year's rotation. A stationary observer in the rigid body S will observe Earth moving below according to the $p_{t_{sum}}$ vector, but if that observer were to start pouring paint onto the ground moving below it, that paint would produce a vector in direct opposition to $p_{t_{sum}}$. The vector $o_{t_{sum}}$ will share an origin and magnitude with $p_{t_{sum}}$ but they oppose each other in direction. One vector will travel north while the other travels south and one will travel west while the other travels east, both winding up and down the sphere as the year goes by. This full deterministic model shows a nice holistic

representation of Earth's movements but needs to be broken down into ecologically relevant parts to add explanatory power to questions at ecological scales.

Sub-setting $p_{t_{sum}}$ into smaller time segments helps bring the scale of the analysis down to a more ecologically relevant scale. For example, if a bird is only flying for 2 hours a day, from 5 AM to 7 AM, then they would only need to reference the sun for navigation to experience relative motion for 2 of the day's 24 hours and the model should reflect that limitation. Sub-setting $p_{t_{sum}}$ using these parameters will produce a set of $p_{t_{5-7\ AM}}$ that do not connect with each other but stack in sequence next to each other to form an analemma through time.

4.2.7 Hourly time scale scenario: disentangling the relative contributions that Earth-based and solar-based niche components make to the spatial trajectory of an individual

When an object moves from one location to another in a small increment of time, for example, 2 hours, they express a realized vector from their initial location to their final location. If the object we are considering is an individual, and the individual is attached to Earth's surface and is stationary on Earth's surface, then they are only occupying the Earth coordinate system and so they will track the same course through the observational coordinate system as a fixed point in the Earth coordinate system does. If an object is instead stationary in the solar coordinate system, it will track a course identical to a fixed point in the solar coordinate system during this time. In both these cases, the object was stationary relative to its own coordinate system but movement relative to the observational coordinate system was imposed on the object by moving the entire coordinate system. If an object in the Earth coordinate system starts to move around, that movement is relative to the Earth coordinate system and is added to the rotation of the entire Earth coordinate system. The realized spatial path of an object is likely the result of influences from the Earth coordinate system, the solar coordinate system, and the object. Disentangling the

motion contributed by two independent coordinate systems and by the object being tracked is done by assigning a component vector to each element independently and then comparing the relative contribution of each component vector to the final resultant vector.

4.2.8 Fitting data: appropriate measures of variance and preservation of variance in different coordinate systems.

Observational data can describe the timing and direction of an object's movement through space at a number of different scales and each of those scales has its own error characteristics. The two scenarios described above describe the same process of Earth rotating relative to the sun, but at different temporal scales. Those scale differences affect the way data describing the movement of individual objects interact with models described above and therefore, limit the types of data that can be confronted with each model. The mechanism presented here is the relative motion between Earth and the sun and the spatial model for representing that relative motion is a vector field in the shape of the analemma, a figure-8 (Fig. 4.6).

There are three primary mechanisms by which variation can arise in this model. First is that there can be spatial variation around a point to define a home range for an object. Second, independently there can be stochastic variation around each spatial position that the individual occupies. Third, the process of measuring spatial locations through time introduces measurement/observer error that can amplify or hide the other two sources of error.

In the year scale scenario, variance is described relative to the analemma shape and orientation. The analemma changes both shape and orientation depending on the time, latitude, and longitude of the reference location used in the solar coordinate system. The precise shape of this vector field is defined by the clock time and solar location from which it is observed.

Changing the observation location in the solar coordinate system changes both the symmetry of the figure-8 and the location of the center point of the figure-8 pattern.

In the hour scale scenario, motion is described as a set of component vectors that equate to a realized resultant vector. Comparing the trajectory of a point through a phase plane produces an analytical solution and does not include any estimates of measurement or system error. There are two levels of error modeling that can be added to trajectory measurements depending on the normality and the symmetry of particular phenomena. The Von Mises distribution is the angular S^2 equivalent to the normal distribution so it is frequently used when the assumptions of normality are met (Fernández-Durán 2007, Méndez et al. 2014, Agostinelli and Agostinelli 2015).

The specific location of a reference point in the solar stationary reference frame is important because that location determines the energy intensity experienced by that point (Meeus 1998). In a system where energy intensity determines spatial patterns (Clarke and Gaston 2006, Shepard et al. 2013), the pattern of energy distribution across the solar coordinate system becomes important (Gates 1966). The fact that energy organizes itself in rings radiating out from the center of contact means that individuals should organize themselves in rings radiating out from the center of contact (Reda and Nrel 2003, Lisovski et al. 2012). An individual's abiotic niche must be constrained to one of those energy rings and then further constriction of range within that ring will eventually define an individual's home range in the solar stationary reference frame (see Chapter 5). Movement of the center of this home range produces the baseline analemma vector field and then the partial ring shaped home range is translated to produce the boundary vector fields around the baseline vector field (Fig. 4.1).

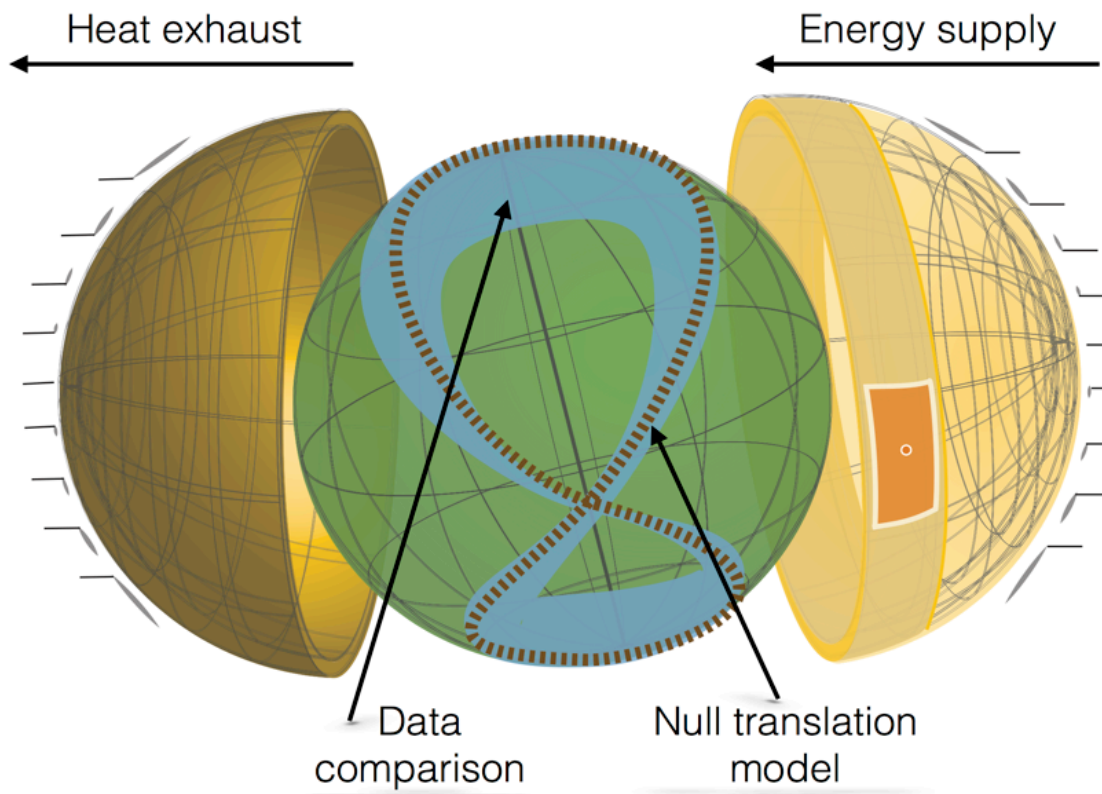


Figure 4.6 Analemma as a model for relative motion between Earth and the sun. This figure highlights the way an analemma can be used to model the interaction between solar-referenced natural phenomena and surface-referenced Earth phenomena. If an individual is stationary in the yellow solar region on the right, then an observer on the green surface would observe the individual as moving in an analemma path over the course of a year. This relationship establishes the null model for an individual staying completely stationary relative to the sun. Different stationary locations will produce differently shaped analemmas. Movement within the solar zone will produce a composite analemma path assembled from the different solar locations that an individual travels through. Individuals responding to surface phenomena, like encountering land or water obstruction, will create variation around the analemma rather than modify the overall shape.

4.3 Results

I present three results from the development and operation of this relativistic model: 1) demonstrating the way attached individuals measure the solar contact coordinate system (Fig. 4.8a); 2) the way detached individuals measure the surface of Earth passing beneath them (Fig. 4.7b); and 3) showing the different shapes that result from translating a home range in one coordinate system to a home range in another coordinate system (Fig. 4.8).

4.3.1 Measuring the solar contact zone: Earth perspective

I demonstrate that the shape of the Earth vector field's outline is defined by the shape of the analemma and therefore the shape of the vector field changes depending on the location of the reference point defining the shape of the analemma (Fig. 4.8). The classic analemma shape is the analemma seen from the equatorial prime meridian noon using the distant sun as a reference point. This basic analemma then distorts as the reference point moves from the center of solar flow to the edge of solar flow (Yeow 2001, Lynch 2012). Moving the reference point north-south in the solar reference frame, then crossing the intersection point at the center of the analemma will move up and down to make the two loops of the analemma more symmetrical the more centered the reference point is and more asymmetrical the more north or south the reference point gets. Moving left or right in the solar reference frame adjusts the time component of the analemma and so the analemma tilts as the reference point moves left or right in the solar coordinate system (Yeow 2001, Bull 2011, Lynch 2012).

The blue polygon in Figure 4.8a describes the shape that a deviation from the mean Analemma will take. Variance in the N-S axis of the solar coordinate system is expressed as uncertainty in the N-S location of the center point of the analemma. Variance on the east-west axis of the solar coordinate system produces uncertainty in both the length and angle of each time-specific trajectory angle making up the vector field. So, the overall shape of the vector changes relative to the individual's location in the solar coordinate system, the breadth of the vector field is determined by the clock time when individuals are active, and spatial variance around a point in solar stationary space are expressed as both a change in analemma shape and adds uncertainty to the width of the vector field.

4.3.2 Measuring the solar contact zone: Solar perspective

From the perspective of the solar reference frame, the analemma is deconstructed into a set of four parabolas arranged in two opposing sets (Fig. 4.7b). These parabola shapes are vector fields made of the opposition vectors for p_t and they represent the land surface that will travel underneath an individual staying at one point at the center of the solar flow. In this scenario, an individual responding to the sun instead of Earth's surface will exhibit these particular relativistic paths.

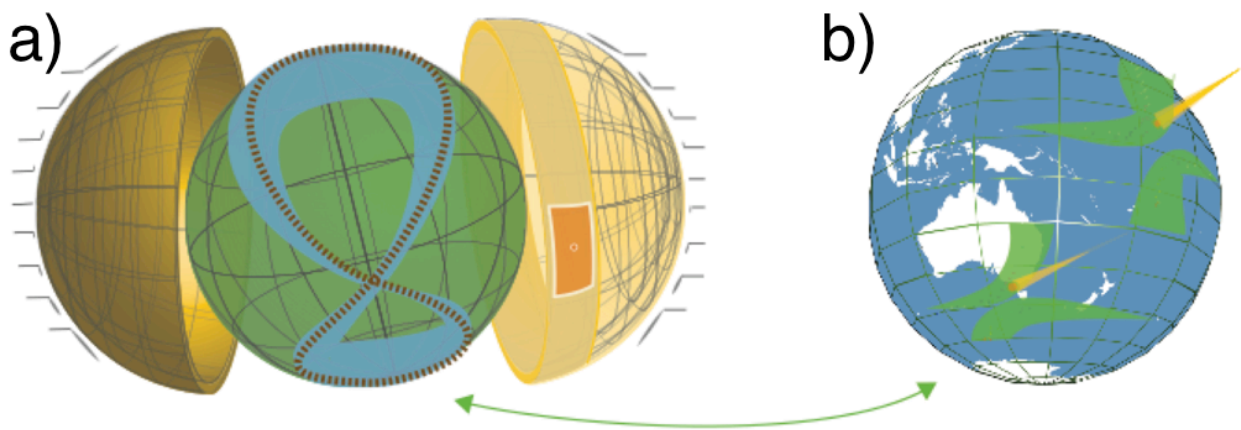


Figure 4.7 Translated relative paths between Earth and the sun. Demonstration of the way each coordinate system measures the other's trajectory over the course of a year. The left globe describes the relationship between the two interacting rigid body coordinate systems by slitting the solar contact coordinate system in two and pulling it away from the earth surface coordinate system to show the full dynamics of the two rigid bodies' interactions. The green sphere is spinning within the yellow sphere and the brown dotted line shows the place where a green-sphere observer will witness the orange reference point on the yellow sphere throughout the year. The blue buffer around the brown line shows the way variance is translated between the two coordinate systems. Specifically, the blue band widens as the location of tracking in the yellow sphere grows larger than a single point. The brown dotted line describes the generic shape of an analemma and the blue shaded region around that line shows the expected pattern of variability around that line. The exact shape of the analemma depends on the location of the surface observer and the location in the solar coordinate system they are tracking. The right figure describes the way a stationary observer in the solar coordinate system will measure the movement of the spinning globe below it. The figure-8 shape of the analemma is deconstructed into a set of 4 opposing parabolas describing the path that Earth's surface will take underneath a stationary solar observer.

4.3.3 The shape of the home range in two coordinate systems

Most of this chapter has dealt with comparing single points between moving coordinate systems. This final result considers the translation of a group of interacting points rather than a single point and shows that interactions between points change according to where they are located in different coordinate systems. Figure 4.8 shows the difference in interaction shape between a solar location hitting the center (a) versus the side (b) of the solar contact zone. A square cluster of points in the solar coordinate system project a shape onto the underlying Earth coordinate system that closely resembles the original shape and retains the original orientation (Fig. 4.8a). As that cluster of points moves away from the center of contact and towards the terminator, the original cluster shape is rotated outward and elongated along the center-to-terminator axis of the solar coordinate system. This location dependent change in shape has important consequences for the measurement and analyses of trends across these coordinate systems. A small cluster of locations in the solar coordinate system can translate to a large area on the Earth coordinate system if the location in the solar coordinate system is toward the terminator rather than the center of solar contact. This is notable because the intensity of solar energy decreases toward the terminator as the same amount of energy is dispersed over a larger surface area. This wider dispersion of sunlight also means greater variance in the spatial patterns of individuals tracking that light. Individuals tracking a solar angle near the center will have a small area where they can find the solar angle they need, while individuals near the terminator can find a wide diversity of locations where the solar angle doesn't change and the energetics stay the same.

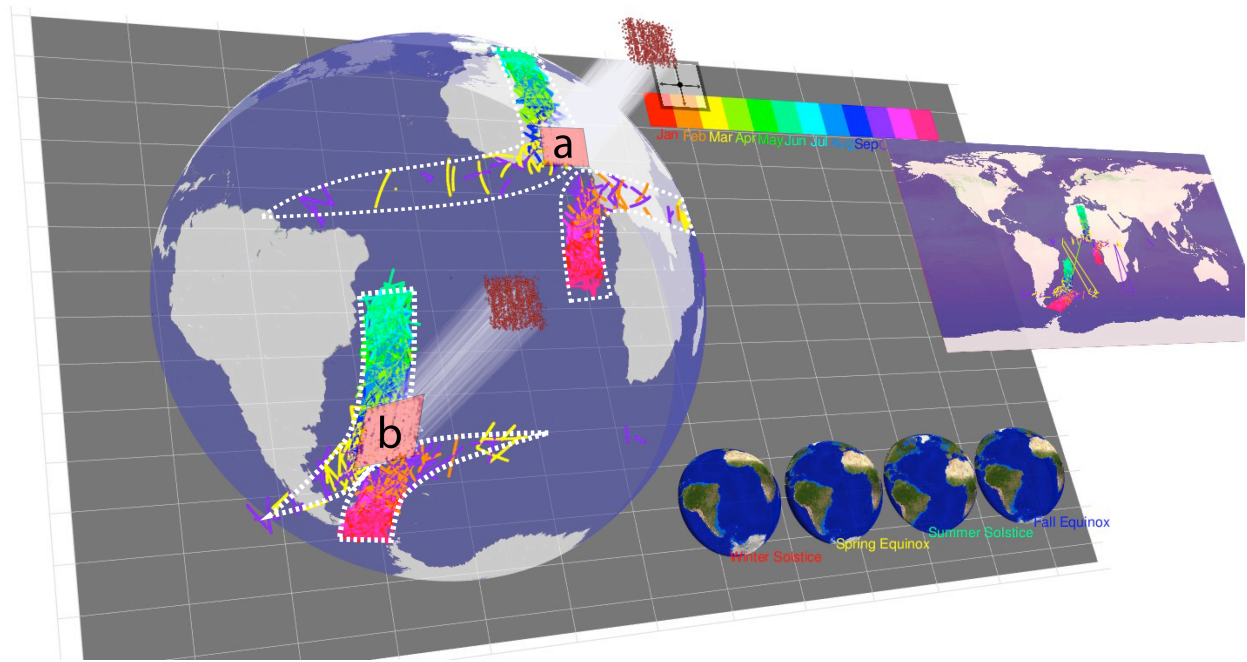


Figure 4.8 Different solar angles create different home range shapes. This figure demonstrates two example home range shape translations. The cluster of red dots represents a zone of locations in the solar contact zone making up the home range of an individual in that coordinate system. Those red dots are linked to a set of white dots using a set of white lines. The white lines linking these dots represent solar rays and the white dots represent the location where those rays hit the surface of Earth. The result demonstrated here is that the shape of the red dot cluster is different than the white dot cluster and so the shape of home ranges in one coordinate system will translate into a different shape in a different coordinate system.

4.4 Discussion

In this chapter, I present a new model for mapping the relative motion between Earth and the sun. This model deconstructs relative motion between Earth and the sun by treating each as a rigid body moving within a fixed spatial coordinate system and comparing movement between those coordinate systems as an external observer. I examined two scenarios, one at the yearly scale and the other at the hourly scale. The first explicitly described the spatial relationship between Earth's surface and energy from the sun, and the second built upon that foundation to describe a method for disentangling the relative contributions made by different sources of relative motion to create a realized hourly path.

The first scenario described the full spatial extent, over the course of one year, of interactions between points in one coordinate system and points in an opposing coordinate system. This process showed that a stationary individual on Earth's surface will observe the sun traveling in a figure-8 throughout the year (as described in Meeus 1998, Yeow 2002, Lynch 2012) and a stationary individual in the solar coordinate system will see Earth's surface move below it in a set of two opposing parabola shapes (Figs. 4.7b and 4.8).

The second scenario weighed the relative contribution of attached and detached niche components over an hourly scale (two hours in this particular case), based on how much an individual diverts away from the trajectory of Earth's surface. In this sense, the scenario of the individual that is stationary in the Earth coordinate system can act as a null model against which hypotheses of detached niche components can be contrasted. I will call this the surface null model. An individual attached to Earth's surface (i.e. stationary) will experience the same view of the sun as described above in the yearly scenario, except on the hourly scale the view will be a short segment of the analemma. An individual's trajectory hour-by-hour throughout the year can, therefore, indicate the amount of influence that attached versus detached niche components have on a particular individual. The more time an individual has spent responding to detached niche components instead of attached (surface) niche components, the more they will diverge from the surface null model. If the detached niche components are solar-based, that is, an individual moves across Earth's surface to keep solar cues consistent, the individual will instead tend to assume the trajectory of a stationary point in the solar coordinate system.

It is unrealistic to assume that an individual will stay precisely in one location for the entire year but might instead stay in a general location that it moves about within, such as a home range. If that individual moves with small random movements on Earth's surface, they will

observe the sun traveling in a widened analemma path due to the increased variance in their location.

These results speak to a growing interest in analyzing the movement of niche components to understand ecological phenomena and spatial patterns through time (Morales et al. 2004, Jonsen et al. 2005, Holyoak and Casagrandi 2008, Shepard et al. 2013, Méndez et al. 2014). Much of this growing interest in movement analysis comes from the increasing availability of time-stamped location data for individuals like those obtained from geolocators (Stutchbury et al. 2009, Lisovski et al. 2012), GPS trackers (Morales et al. 2004, Guilford et al. 2008, Méndez et al. 2014) and Doppler weather radars (Tobalske and Dial 1996, Safi et al. 2013, Dokter et al. 2013). As these data become more available, there is a growing need for analysis tools and ecological theory to guide investigation (Morales et al. 2004). The tools already in circulation are predominantly statistical and not mechanistic, meaning that they usually compare realized paths in the data against a series of random walk models (e.g. Brownian motion or Levy motion) to test divergence away from random (Morales et al. 2004, Jonsen et al. 2005, Méndez et al. 2014). As I have shown here, there are important links between organism movement and celestial movement that cannot be captured by merely comparing realized movement patterns against random walk models.

This platform also contributes to a large community of developers working on advancing 3D- and 4D-mapping systems. Google Earth (Google development team 2016) and NASA's community-developed, open-source "World Wind" (Bell et al. 2007) are among the most advanced of these technologies, but there are many platforms including QGIS (QGIS development team 2016), Science on a sphere (National Oceanic and Atmospheric Administration 2016), ossimPlanet (ossim development team 2016), gvSIG 3D (gvSIG association 2016), Earth3D (Gunia 2016), and Marble (Marble development team 2016) to

name a few. These platforms extend GIS functionality into 3 dimensions, but they still cannot account for relative motion between interacting parts. Since these platforms cannot track relative motion between map components, they cannot disentangle the relative contributions of attached and detached niche components.

There are several existing methods for mapping solar angle onto Earth's surface for both scientific and industrial applications (Reda and Nrel 2003, Perpignan Lmigueiro 2010, Reda 2010, Lisovski et al. 2012). Solar angle and solar energetics are important to the photovoltaic industry, landscape designers, city planners, and ecologists studying the interaction of spatial processes with solar-energy dynamics (Reda 2010). These models calculate the changing energy dynamics between a single surface location with the changing solar angle over that location (e.g. Perpignan Lmigueiro 2010). However, many of these models cannot generate the surface path that an individual would take if the organism was maintaining a constant position in the solar coordinate system rather than a constant surface location on Earth.

The model described here is assembled differently than other 3D, GIS systems in that the surface of Earth is rotated and the solar angle is held constant, as opposed to the Earth's surface being held stationary while the sun's influence is modelled around it. The sun is one detached (or moving) niche component but we can introduce new rigid bodies to keep track of the motion of other niche components. For example, rigid bodies could be added to this model to represent continental drift, magnetic declination, glacial movement, or lunar forces. Equipping this GIS with a greater diversity of moving elements allows for more complex hypotheses to be tested.

The main limitation of this rigid body model is that it is computationally intensive to rotate multiple bodies and track their interactions. As implemented here, all the points for a

rigid body are stored in a single array and each array is transformed for each time step. It is possible to reduce the memory requirements by instead storing each rigid body as a data tree, but the complexity added by the non-intuitive structure of data trees makes it more difficult to explain or organize data easily.

A rigid body model makes it possible to measure and describe spatial and temporal interactions between ecological phenomena on Earth's surface and the solar radiation that powers those ecological systems. These results collectively show there are multiple ways to measure a single phenomenon in nature and the perspective of measurement can lead to different results. Here I use the Earth's surface and the solar contact zone as examples of surface-driven and solar-driven movement patterns because they are both known drivers of ecological patterns. This tool should provide the resources necessary for broader and more comprehensive studies of the relative motion between Earth and the sun.

Future use of this model should focus on describing mechanistic links between various surface processes and solar radiation. There are broad-ranging ecological implications for relative motion between Earth's surface and solar radiation but it is an underdeveloped scientific field. Chapter 5 provides an example of this type of analysis that incorporates more moving niche components by including new rigid bodies to represent those components.

CHAPTER 5

RELATIVE MOTION BETWEEN DETACHED INDIVIDUALS AND DETACHED NICHES

5.1 Introduction

Migratory birds travel great distances along circuitous paths. Many decades of research and theory have correlated a long list of avian traits with migratory status (reviewed in Greenberg and Marra 2005) to explore the links between biological mechanisms and migration (Budzynski, Dyer, and Bingman 2000; Papi 2001; Susanne Åkesson et al. 2005; S Åkesson and Hedenström 2007). In the hunt for better understanding of why species migrate, studies have dissected the spatial paths taken by migrating individuals and attributed different components of the route to different ecological drivers (Ristow et al. 2000, Liechti 2006, Shaffer et al. 2006, Nathan et al. 2008, Safi et al. 2013). I adopt this method of deriving ecological process from spatial patterns to suggest a new framework for understanding avian migration in the context of solar cues.

I contest that one migratory pattern that shows up in many migratory species is the tendency to follow part or all of a figure-8 path throughout the year. Such a pattern is apparent in many records of migratory paths. Some species trace a full figure-8 course (e.g. shearwaters, Shaffer et al. 2006, Guilford et al. 2008, Dias et al. 2012; and terns, Egevang et al. 2010), while others only trace an ‘S’ (e.g. falcons, Fuller et al. 1998) or ‘U’ (e.g. Albatross, Jouventin and Weimerskirch 1990, Lecomte et al. 2010), which, as I argue below, are likely subsets of the full figure-8 path. This figure-8 path taken by birds qualitatively matches both the shape and timing of the path the sun takes across Earth’s surface throughout the year (Chapter 4). Since solar angle is known to influence avian migration, it is likely that the figure-8 path taken by individual migrants is related to solar angle.

In this chapter, I first explore the links between solar angle and migratory patterns with a brief review of the literature. I then show how the observed figure-8 migratory patterns may be linked to climate niche components, including solar angle, wind speed and bearing, temperature, and humidity.

Annual, seasonal avian migration is defined as a heritable trait that obligates individuals to travel away from their birth location to mature but then later compels them to return to their birth location to reproduce (Greenberg and Marra 2005, Vardanis 2011). In contrast, one-way journeys or continuous movement (without returning to the same locations) are referred to as dispersal and nomadism respectively (Shaw and Couzin 2013). Dispersal and nomadism are both common in bird species and often display seasonal trends that mimic migration (Greenberg and Marra 2005). However, dispersal and nomadism are not migration because individuals don't return to the same location year after year.

Migratory species exhibit important differences in flight behaviors. There are some species, like the Greater Shearwater (*Puffinus gravis*), that almost never touch the surface of Earth and other species, like the Cedar Waxwing (*Bombycilla cedrorum*), that migrate only short distances each spring and fall (Morris et al. 1996). Species from open habitats are more likely to migrate than forest species (Greenberg and Marra 2005; originally from M.S.L. Mills and P.A.R. Hockey, unpublished data); and species with flying or seasonally growing food preferences are more likely to migrate than seed eaters (Greenberg and Marra 2005; originally from G. Balme and P.A.R. Hockey, unpublished data). The location of the breeding ground also influences the likelihood of migration. The farther away from the equator the breeding ground is, the more likely a species is to be migratory (Newton and Dale 1996a, 1996b, Greenberg and Marra 2005).

While all avian migrants are highly mobile species, pole-to-pole migrants are the most extreme (Alerstam et al. 2003). These species maintain little connection to the terrestrial environment (i.e. “attached niche components”, see Chapter 4) beyond short-term nesting needs during the breeding season and hunting requirements throughout the year (Liechti et al. 2013, Gavrilov 2014). Instead, studies show pole-to-pole migrant species respond to a variety of climate conditions, including wind direction and intensity (Felicísimo et al. 2008, Weimerskirch et al. 2012, Grönroos et al. 2012), air and water upwelling (Rykaczewski and Checkley 2008, Ákos et al. 2008, Van Loon and Shamoun-Baranes 2011), and seasonality (Wikelski et al. 2000, Dawson and King 2001, Shaw and Couzin 2013). These climate conditions all vary spatio-temporally in such a way that they effectively move across the Earth’s surface, so I consider them to be detached niche components. Pole-to-pole migrant species have also been shown to respond to non-climatic cues that I consider to be detached, including visual solar cues (Pennycuick 1960, Pennycuick et al. 1999, Liboff and Jenrow 2000), magnetic declination cues (Wiltschko and Wiltschko 1988, Liboff and Jenrow 2000, Sanders 2005, Wiltschko and Munro 2006), and circadian rhythms (Gwinner 1996, Taghert 2011).

The path that Greater Shearwater migrants take during migration is likely a direct result of the cues they use for navigation. The sun has proven an important direct and indirect cue guiding migratory patterns across all avian migrant species (Wiltschko and Wiltschko 1988, Gwinner 1996) and there is no indication that shearwaters should deviate from that general trend. When the sun shines on a surface location, the location becomes more energetic due to the addition of solar radiation. Avian migrants have long been known to have the ability and inclination to hold solar elevation and azimuth constant over time (Wiltschko and Wiltschko 1988, Wiltschko and Munro 2006) by tracking the angle of polarized light (Kramer 1950, Åkesson and Hedenström 2007, Kishkinev et al. 2010).

The idea that birds use the sun to navigate is not novel. The concept was heavily debated in the 1950s and 1960s (Matthews 1955, Rawson and Rawson 1955, Kramer 1957, Kramer 1959, Pennycuick 1960, Hoffman 1965, Schmidt-Koenig 1965, Matthews 1968), when several mechanisms for navigation had been proposed and there was little experimental evidence to support one mechanism over another (reviewed in: Wiltschko and Wiltschko 1988, Wiltschko 2003, Wiltschko and Munro 2006). Solar navigation was originally the leading hypothesis (Matthews 1951, Pennycuick 1960, Tunmore 1960), but this was only a few years before the discovery that birds could measure magnetic declination (Keeton 1970). Eventually, magnetic navigation hypotheses gained popularity over solar navigation hypotheses (Wiltschko and Wiltschko 1988, Liboff and Jenrow 2000, Wiltschko and Munro 2006).

Outside of these leading hypotheses, some thought that birds navigated by recording their acceleration and displacement through time (reviewed in Matthews 1952), others invoked a ‘double clock’ or ‘bi-coordinate’ mechanism where birds used a combination of time and space to judge their location (Kramer 1953, Koenig 1965, Wallraff 1967), while still others proposed a ‘map-and-compass’ system where birds first picked a compass bearing to track, and then tracked that bearing with an internal compass (Walcott and Michener 1970, Mouritsen and Mouritsen 2000, Kishkinev et al. 2010). Even though many of these hypotheses explicitly considered anatomical and physiological explanations for navigation (Pennycuick 1960), many of them suggested that visual and biological cues were important navigation supplements for returning to precise locations (reviewed in Greenberg and Marra 2005).

What was revealed through these discussions, and the experiments that followed, was that birds can accurately and precisely measure the angle of the sun relative to the horizon, but they cannot accurately or precisely measure *changes* in angle of the sun relative to the horizon (Pennycuick 1961). This seems like a minor distinction, but the hypothesis being debated in the

1960s was that birds were integrating the movement of the sun across the horizon rather than holding a solar angle constant (Mathews 1954). By showing that birds could not integrate solar angles over time or remember angles between days (Pennycuik 1960, Pennycuik 1961), consensus grew that solar angle could not fully explain navigation and that magnetic declination must be a stronger navigational signal than the sun (Liboff and Jenrow 2000, Freake et al. 2006, Wiltschko and Munro 2006). This argument has more recently come full circle with the discovery of a small organ in the avian eye that enables visualization of magnetic fields (Mouritsen et al. 2004, Mouritsen and Ritz 2005), but this organ is light activated so it only works in direct sunlight (Wiltschko et al. 2002, Wiltschko et al. 2003). Solar angle, magnetic signals, and circadian rhythms are all detached niche components that birds use for navigation. Here I focus on solar angle, showing that migratory flight patterns can be accurately recreated if individuals hold a constant solar angle while hovering about Earth's surface.

Migration is a well-studied phenomenon, and the list of attached and detached niche components influencing migratory pathways is extensive (Bowlin et al. 2010, McKinnon et al. 2010). In this chapter, I explore the relationship between the annual flight patterns of a pole-to-pole migrant species and the movement patterns of detached, climate niche components. Specifically, I compare the annual, migratory flight patterns of Greater Shearwaters (data from Halpin et al. 2009; Viet 2010) to the annual movement patterns of various detached niche components (solar angle, wind speed, wind bearing, temperature, and humidity) to better understand the factors driving the analemma flight patterns of pole-to-pole migrants.

The analemma model described in Chapter 4 predicts that objects staying stationary relative to the sun will be viewed from Earth's surface as travelling in a figure-8 pattern over the course of a year. The annual path of several shearwater species has been described as a figure-8

pattern (Shaffer et al. 2006, Felicísimo et al. 2008, Guilford et al. 2009, Dias et al. 2012), much like the one predicted by the analemma model. This suggests that Greater Shearwater individuals could be acting like stationary objects relative to the sun. More importantly, it suggests a more parsimonious explanation for why migration happens: that individuals are trying to minimize energy expenditure by seeking stability in their climate niche. In this study, I show that migrating individuals work to stay within the parts of the solar-stationary climate niche that meet their physiological needs. I test three hypotheses to rank the relative contributions of climate niche components to the figure-8 pattern observed in Greater Shearwater migratory paths: **(h1)** solar angle is the strongest driver of migratory pathways, **(h2)** wind speed and wind direction are the strongest drivers of migratory pathways, and **(h3)** temperature and humidity are the strongest drivers of migratory pathways. In testing the contribution of these three detached niche components, this study contributes enhanced understanding to the long-term debate over the drivers of avian migration behaviors.

5.2 Methods

5.2.1. *Greater Shearwater ecology*

The Greater Shearwater is the largest member of the *Puffinus* genus and among the largest members of the *Procellariidae* family (Penhallurick and Wink 2004). They are one of the few species to breed in the southern hemisphere and winter in the northern hemisphere. They are pelagic birds that live and hunt over the open ocean (Ronconi et al. 2010), so they can stay in flight nearly all of the time and migrate from one pole to the other. Individuals alternate between short bouts of vigorous wing flapping to accelerate to appropriate flight speeds and then lock their wings to glide for long stretches (Cuthbert 2005). When in a glide, individuals use a process called ‘wave recharge’ where they exploit the burst of air thrust

upward when a wave breaks to increase lift and lengthen glide time (process described in Felicísimo et al. 2008). The most common method of rest for this species is to float in large groups on calm water.

Individuals primarily feed on fish, squid, and crustaceans, which they catch by plunge-diving into open marine water (Ronconi et al. 2010). They are often seen following ships because they can recharge their flight off the boat's wake and they can exploit food that has been pulverized by the ship's propulsion system (Lee 2009, Ronconi et al. 2010).

The Greater Shearwater spends most of its time at sea and only comes to land to breed. When they do come to land for breeding, they seek out remote volcanic islands with small landings and steep slopes covered with tussock grass or *Phylica* woodland (Cuthbert 2005). Dense colonies will assemble on these islands, engage in courtship rituals, and then form pair bonds. Pairs mate in October or November and then the females lay a single egg in a burrow that they have excavated under the grass or in the woodland (Cuthbert 2005). Both parents provide care to the young by leaving all day to forage and then return to the nest each night to feed and protect the young (Cuthbert 2005, Ronconi et al. 2010). The adults leave for migration after their young have fledged but before the young are prepared to migrate. Adults abandon their nest to start migration in April and the young remain in the burrow until they are mature enough to start their own migration in May (Cuthbert 2005). This means that migration is innate: parents do not teach their young how to migrate, the young find their own way after leaving the burrow.

5.2.2. Defining the avian migrant's climate niche

All species have a niche but measuring or defining that niche can be difficult. Hutchinson offered a set of tools for measuring the niche (Hutchinson 1957, reviewed in Holt

2009), but these tools rely on mapping the population dynamics of a species onto environmental gradients to judge where populations can persist. Such measurements can be difficult to obtain in natural avian systems where the high mobility of individuals blurs the link between population abundance and the resources individuals are responding to in the environment. An alternative measure of the abiotic components of the niche can be done using a climate niche calculation that is based on the physiology of the individual. This is a mechanistic definition of a species niche where the physiology of individual birds dictates the abiotic conditions where they are able to survive and reproduce (Kearney and Porter 2004, 2009). This method predicts the abiotic conditions that a species is trying to achieve based on their physiology rather than measuring population dynamics as a response to environmental gradients.

Defining the avian migrant's climate niche starts with the standard five dimensions of the climate niche introduced in Chapter 4: solar radiation, wind speed, air pressure, air temperature, and relative humidity (Porter and Gates 1969, Spotila et al. 1973, Bakken and Gates 1975, Gates 1980). The five dimensions of the climate niche can be reduced into three dimensions in avian species (air temperature, wind speed, and direct solar radiation) because individual birds can only stay in flight at particular air speeds, based on their aerodynamics and physiology.

Climate niche dimensions set physiological constraints for individuals. Birds use their pectoral muscles to pull the wing down and resist the wind (Pennycuick 2006, Hedenström 2009). If the wind is too slow, the bird cannot pull its wings any farther forward and the individual falls out of the air. If the wind is too fast, the muscles are overpowered by the wind and the bird must collapse its wings and hence fall out of flight (Pennycuick 2006, 2008a). Pennycuick (2008a) describes an algorithm for calculating the wind speed and air

pressure limits for avian flight based on the flight physics of a bird, using the mass of the bird and shape parameters (length and area) of the wing to determine the bird's aerodynamic parameters (specifically lift to drag ratio, chemical power use, and mechanical power use, see Fig. 5.3). These physical limits constrain individuals to a specific wind speed and air pressure, which means that the five-dimensional climate niche can now only vary on the remaining three climate dimensions, solar radiation, air temperature, and relative humidity. These three remaining dimensions can be further collapsed into two, heat input (solar radiation) and heat limitations (combining air temperature and relative humidity). The workflow for this reduction is outlined in Figure 5.1.

As described in Figure 5.2, solar radiation is the most stable and the most predictable of all the climate niche dimensions. Photons emanating from the sun collide with the spherical Earth from only one direction. The energy from this contact is most intense in the center where photons are hitting Earth's surface at a 90-degree angle. At angles away from that center of contact, photons spread across a greater area and become more diffuse as a result. Energy density is determined by the angular distance from the center of contact, which is radially symmetric, so areas of equal energy manifest as rings around that center point. Rings near the center are the most energetically intense and rings near the terminator are the most diffuse.

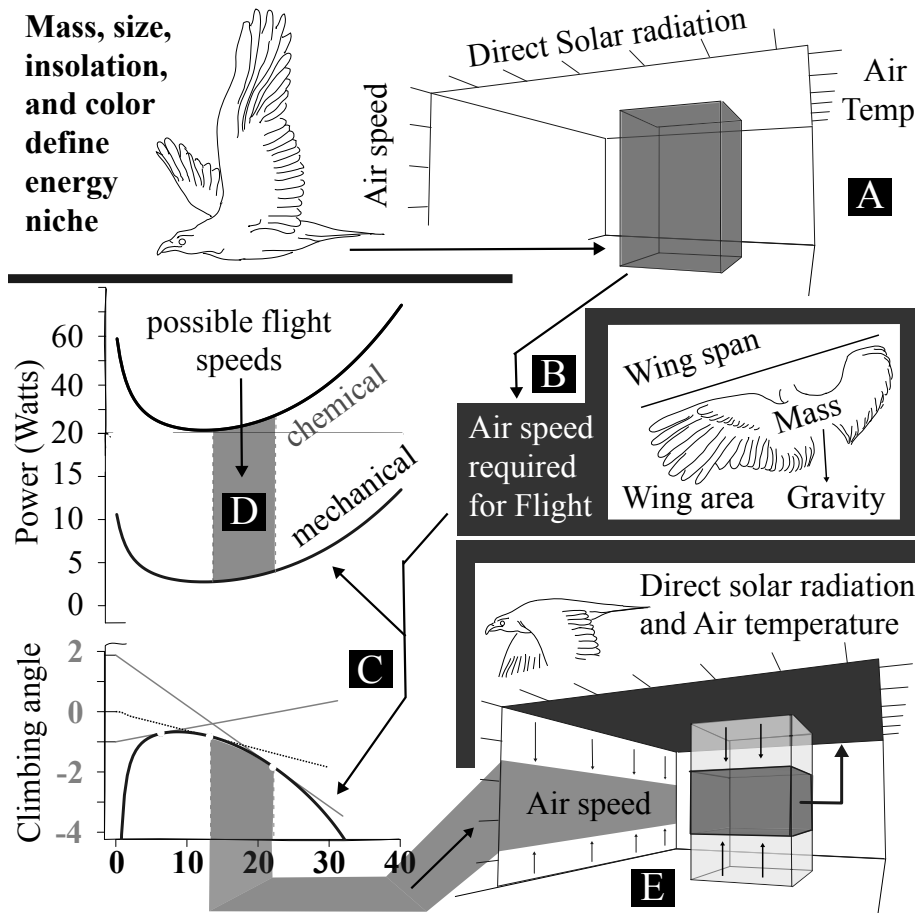


Figure 5.1 Workflow for reducing 5 climate niche dimensions into 3 dimensions. **A:** According to Gates's (1980) equations, an individual bird's energy niche is defined by air speed, air pressure, direct solar radiation, air temperature, and relative humidity. An individual is physiologically constrained to a limited range of values on each one of these axes and these constraints define the limits of an individual's energy niche. I calculate these physiological constraints using the individual's mass, size, insolation, and color. **B:** The physiological constraints limiting the range of values for each niche dimension are structural and aerodynamic. Adding aerodynamic determinants to the physiological model constrains its range of values to the velocities that individuals must sustain to stay in flight. **C:** Pennycuick's (2008) functions translate the shape of an individual bird (defined by wing span, wing area, mass, and gravity) into two curves relating the individual's velocity to its ability to stay in the air and relating its velocity to mechanical power consumption. Mechanical power consumption can be converted directly to chemical energy using an individual's metabolic efficiency. Chemical energy consumption is directly proportional to heat waste production according to heat efficiency. **D:** A combination of physiological, mechanical, and aerodynamic constraints limit the range of velocities physically available to individuals maintaining flight. **E:** Defining the velocity necessary for maintaining flight collapses the air speed axes in Gates's (1980) original equations down to only the remaining axes, direct solar radiation and air temperature.

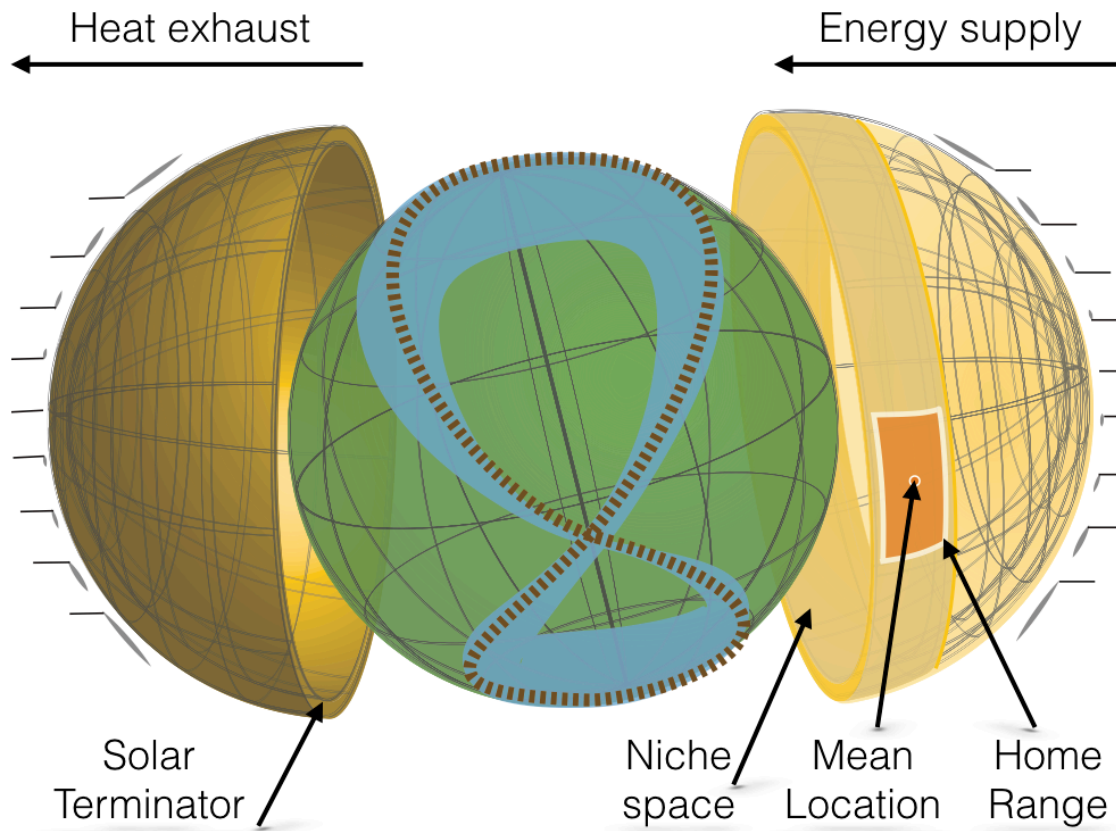


Figure 5.2 The two halves of the outer sphere are split along the solar terminator to show Earth within. The right hemisphere of this split sphere is the area where the sun's rays hit Earth's surface. The left hemisphere is the area shaded from the sun and experienced from Earth as night time. A solar niche is a ring and a solar home range is a subset of that ring. This figure highlights the niche ring and the restricted home range within that ring. The yellow area on the right of this figure represents the zone where solar photons hit Earth's surface and becomes usable energy for the organisms encountering it. The shaded yellow ring is an area where the energy from the sun is equivalent because everywhere in this ring shares the same solar elevation angle, which determines the intensity of energy that area receives. The energy coming from the sun is most intense in the center of the solar contact hemisphere (far right of the figure). Energy is diffused by the curvature of the earth for locations away from the center of contact facing directly at the sun. The radial nature of this energy gradient means that the spatial location where a species' energy requirements are met is a circular ring symmetrical about the center of solar contact. The most intense rings of energy are near the center of the right hemisphere above and the least intense near the solar terminator, where the two hemispheres are split apart above. An individual anywhere in an energetic ring will measure the same solar elevation at the same hour each day. An observer moving around the niche ring will measure a change in solar azimuth angle, but maintain a consistent solar elevation angle throughout. The orange square within the ring is a solar home range. An individual may be able to meet its solar needs anywhere in the niche ring but they are likely restricted to only part of that ring because of other ecological restrictions like wind, water, temperature, and habitat. The restricted area within the niche ring where the individual migrant is able to maintain positive fitness is then the realized niche, or home range.

An observer close to Earth's surface, in this case a bird, can triangulate their location relative to the sun using the angle from the horizon to the sun (elevation) and the side-to-side angle along the horizon (azimuth) (Pennycuick 1960, Meeus 1998). If an individual moves on the surface of a stationary sphere while holding these two angles constant during motion, that individual will trace out an 'energy niche ring' as defined here around the center of contact with the sun (blue zone, Fig. 5.2). When the sphere is not stationary, as is the case with Earth, relative motion obscures the line between the ring and the moving surface below.

In the case of the Greater Shearwater, I expect them to maintain a solar elevation that is low to the horizon, which is where their energy ring is near the solar terminator because of their need to cool their high metabolic heat (for heat exhaust requirements see: Pennycuick 1996, 1998, 2003, Spedding and Pennycuick 2001). On a stationary sphere, all areas of this ring would be equivalent and the individual could move about its energy niche ring freely. In the case of the rotating Earth, not all areas of the ring are equal. A bird will receive the same amount of solar radiation input at any location within the ring, but some locations require more energy output by the flying bird to stay within the ring because Earth is moving faster in some places than others (Fig. 5.3).

The reason not all locations within the energy niche ring are the same is that Earth is rotating across the ring rather than around the ring. Earth is a sphere and so there is more surface area around the equator than near the poles. When Earth makes a single revolution around its axis, a point on the equator moves a greater distance at a faster speed than a point near the pole during the same revolution. A bird working to stay in one solar location near the poles can fly at a slower speed relative to Earth's surface because there is less surface passing under them each day. A bird working to stay in one solar location near the equator must let the entire circumference of Earth pass under them each day. This added amount of

Earth's surface traveling below equatorial solar locations means that birds working to stay in those locations need to fly faster relative to Earth's surface and will encounter more land with more ecological interactions along the way.

There is more available ocean and more overlap between ocean and climate niche in the southern hemisphere, and so shearwaters should favor locations in the southern half of their niche energy ring, here defined as the primary zone (Fig. 5.3a), where they can most easily and consistently meet their climate niche requirement. If individuals get driven from their primary zone in the energy niche ring, the most energy efficient course is to transition as quickly as possible from the primary zone to the northern peak of the energy niche ring here defined as the secondary zone (Fig. 5.3d). The northern hemisphere has less high latitude ocean than the southern hemisphere so there are fewer locations where shearwater individuals can meet their climate niche needs. The primary and secondary zones are likely reversed in terrestrial species because there is more available terrestrial surface in the northern hemisphere and, therefore the northern hemisphere provides more opportunities for individuals to meet their attached terrestrial needs at the same time as their climate niche needs.

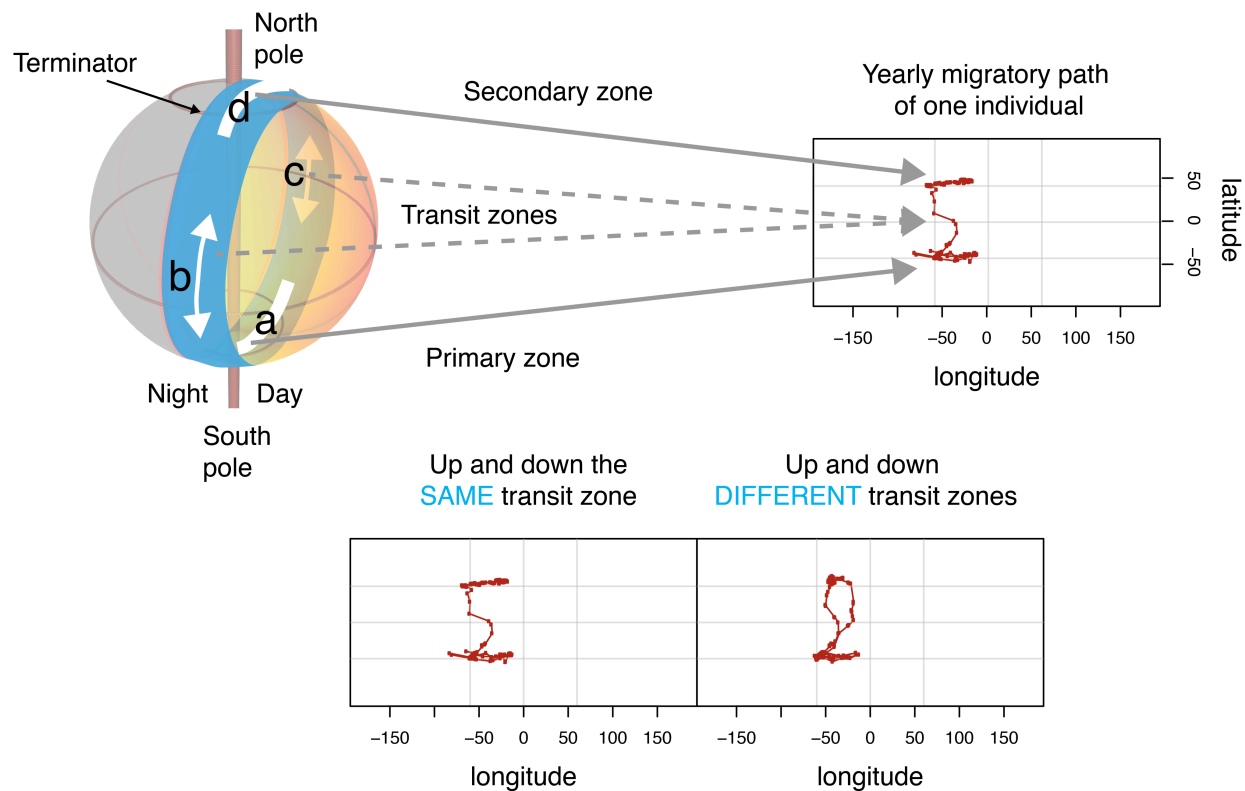


Figure 5.3 Model for predicting migratory paths based on solar angle. This model builds a connection between the energy niche ring defined by a constant solar angle and the path that an individual would take if it were responding to that energy niche ring. The Greater Shearwaters individuals in this study usually occupied the ‘primary zone’ (a). If individuals are pushed out of the primary zone for any reason, the niche ring will direct them through an unstable ‘transit zone’ (b and c) to an alternative equilibrium point called the ‘secondary zone’ (d). Individuals can move through one of two “transit zones” (b and c) while shuttling between the north and south equilibria. Transit zones are less stable than equilibrium zones because Earth is moving more quickly under these zones and its angle of movement is changing over time. Travelling through these zones can push an individual north or south depending on the season and the time of day that the individual encounters them. Accordingly, individuals can shuttle between equilibrium zones using any combination of same (b and b) or different (b and c) transit zones to achieve the desired movement. Different outcomes in an individual’s transit zone choice are expressed in the path the individual takes. If an individual shuttles up and down the same transit zone (b and b), then they will produce an “S” shaped path. If they travel up one side and down the other side (b and c), then they will produce an “8” shaped path.

The sides of the energy niche ring, here defined as transit zones (Fig. 5.3), require more energy to maintain than the primary or secondary zones. The most efficient course of action for an individual forced out of the primary or secondary zone is to move across the

transit zone as quickly as possible to get to the next stable location within the energy niche ring. If individuals use the same side of the ring as a transit zone for up migration as they use for down migration, a surface observer will record them making an “S” shaped path over the course of the year (Figs. 5.3 and 5.8, same transit zone). If individuals travel up one side of the ring during up migration and the other side during down migration, a surface observer will record them making an “8” shape (Figs. 5.3 and 5.8, different transit zones). Individuals who avoid being pushed out of the primary zone will stay in the southern hemisphere all year and a surface observer will record them making a “U” shape as individuals get pushed toward the equator but not pushed through the transit zone (Fig. 5.8, individuals 1-12 that stayed in the primary zone only). The most likely phenomenon to push an individual out of the primary or secondary zone is the intrusion of either inhospitable surface types (e.g. terrestrial land masses are unsuitable for pelagic sea birds) or polar circles. Polar circles interfere with the energetic niche ring because they are the latitudes in the north and south where the sun’s elevation falls to the horizon and loses its usefulness for navigation.

Birds in flight are free to make a number of choices about the wind speed and wind bearing that they occupy (Alerstam et al. 2007, Pennycuick 2008b, Ainley et al. 2015). However, individuals are constrained to a limited range of possible flight speeds because of the physiological constraints of flight (see above and Fig. 5.1). Within that range they can still choose slower wind speeds to fly more efficiently or faster speeds to travel farther at a higher energetic cost (Pennycuick 2008a). There are no physiological constraints to an individual bird’s choice of wind bearing, but an individual trying to stay in their energy niche ring will need to behaviorally constrain their wind bearing to counteract the movement of the planet below. At every point in the energy niche ring, Earth’s surface is moving underneath from west to east. An individual trying to stay in the energy niche ring will need to fly west

at the same speed that the planet is moving east for the two to cancel out. Birds face head-on into the wind to maintain flight, so a bird trying to hold a consistent flight bearing to the west will seek a consistent wind bearing to the east (Liechti 2006, Alerstam et al. 2007).

An individual maximizes its total efficiency when it can find a location in the energy niche ring where the planet and wind are moving in the same direction and near the minimum flight speed of the individual. The primary and secondary zones are locations within the energy niche ring where Earth's surface is moving relatively slowly, allowing birds to fly at efficient speeds while still keeping pace with Earth's surface below. The primary and secondary zones are made even more stable by the alignment of orientation between the ring and the spin direction of Earth's surface. In these zones, the orientation of the energy niche ring runs east-west so a point on the east-west spinning Earth will stay within the ring for several hours at a time, even if individuals have landed and are temporarily attached to the surface. This is in contrast to the transit zones, which are oriented perpendicular to the movement of Earth's surface.

Earth's surface moves more than twice as fast in the transit zones as it does in the primary or secondary zones and that difference in speed disrupts the balance between the energy niche ring, wind speed relative to flight speed, and flight bearing angle. In the primary zone, these three elements are often nicely aligned and efficient to track. In the transit zone, the increase in surface speed means that the wind speed necessary for countering Earth's rotation is also faster and requires more metabolic energy from the individual to track it. The margin for error is tighter because, in a sense, gravity is pulling individuals out of the energy ring rather than down the energy ring, as it does in the primary and secondary zones. As the wind speed increases across the transit zone, the bird may be inclined to adopt a port or starboard tack rather than a head-on flight angle, orienting its head 30° to 60° away from

head-on. This decreases the force on the bird's body but transfers that kinetic energy into sideways propulsion so the bird traverses across the wind like it is sailing on a tack angle rather than staying stationary relative to the sun. The bird must sail its way across the transit zone to transition between the primary and secondary zones where the spatial interactions between the energy niche ring and Earth surface are more stable and require the least amount of energy to maintain a position within the energy niche ring.

Temperature and relative humidity interact with each other to determine the air's affinity for absorbing metabolic heat waste from an individual. If the air's affinity for heat is too high, it will draw too much heat from the individual and drop the individual's body temperature. If the air's affinity for heat is too low, it will fail to accept heat waste from the individual and the bird's body temperature will increase. Body temperatures that are too high or too low will disrupt metabolic function to lower fitness and eventually lead to mortality. These fundamental limits are linked to the location and size of the energy niche ring but they are also the mechanism for fine scale pattern formation within the ring and a mechanism for stopping and starting flying behavior. As with the other climate niche dimensions, individuals should strive to keep these parameters as consistent as possible and all members of the same species should share the same temperature and humidity needs (Huey and Kingsolver 1989, Chown and Gaston 2015).

5.2.3. Analyses

I used Greater Shearwater (*Puffinus gravis*, family *Procellariiforme*) movement data acquired from the OBIS SEAMAP data repository (data deposited by Roncini et al. 2010). These movement data were collected using satellite microwave telemetry tags (5g) from 30 September 2009 until 25 November 2010 as part of a study titled 'Migration and foraging

ecology of Greater Shearwater' by Veit et al. (2010). Greater Shearwaters complete one transatlantic migration each year, travelling to the Northern Hemisphere from their breeding grounds in the southern Atlantic Ocean (Lee 2009, Ronconi et al. 2010).

The global population of Greater Shearwaters uses the same small chain of islands, the Tristan de Cunha Islands, halfway between South Africa and South America as their primary wintering ground where they nest in volcanic islands where nests are guarded from predators (Cuthbert 2005). Individuals travel on long foraging bouts for days at a time (Ronconi et al. 2010) where they maintain a low flight elevation and catch wind updrafts from the tops of waves to efficiently stay in flight (Pennycuik 2002). The 22 individuals analyzed here were bred in captivity on Gough Island and Inaccessible Island, which are both in the Tristan de Cunha Island group and under the legal jurisdiction of the United Kingdom (Veit M. 2010).

When a connection was available between the satellite tag on the bird and the satellite receiving the data, data were collected every two hours. However, a satellite connection was often unavailable and so there were only 8,842 unique data points between all 22 individuals for more than a year, which is an average of one or two datum per day, per individual. The dispersion of missing data through time was rather clumped, with reliable satellite connections for a day or two and then connections failing for several days before regaining a connection and resuming data collection.

Solar elevation and azimuth angles were calculated using the Meeus (1998) solar calculator algorithm as described in Chapter 4. I calculated one elevation angle and one azimuth angle from the latitude, longitude, and time signature data at each time point. The unique combination of these two angles and the Earth's surface horizon triangulate the location of an individual relative to the sun.

Wind, temperature, and relative humidity data were downloaded from the National Oceanic and Atmospheric Administration's (NOAA) National Operational Model Archive and Distribution System (NOMADS) using the R library rNOMADS (Bowman 2014, 2016) to manage data downloads, data parsing, and map re-projection. These data are the output from the Global Forecast System (GFS), which is a weather forecast model produced by the National Centers for Environmental Prediction (NCEP). This model analyzes historical meteorological data to build a reconstruction of the atmospheric conditions for a location at a particular time. This model covers the entire globe with a spatial resolution of 28 km (0.5°) and a temporal resolution of 4 day intervals at 4 time points (00, 06, 12, 18 hours) per interval. Data layers were delivered in 259,920-point (720x361) global Longitude/Latitude grids centered on 0° E and 90° N and without the prime meridian duplicated. Data were parsed after download to extract the fields of interest and then assigned to an equal-area projection for spatial analysis.

Wind data were vector quantities described by an angular bearing and a scalar magnitude. Wind data were delivered from NOMADS in a set of two layers with the wind vector divided into its x and y-components so that one layer contained the magnitude of the length of the x-component and the other layer contained the magnitude of the length of the y-component. Greater Shearwaters fly at a maximum of 1600m, and so I restricted the scope of wind data to the five data layers at relevant scales: 10 m above sea level, 850 mb, 900 mb, 950 mb, 1000 mb, and 1829 m above sea level. Vertical profiles of the atmospheric conditions at a specific point were compiled using a spatial averaging basis spline (B-spline) provided in the rNOMADS package (Bowman 2014, 2016) to interpolate point estimates from each raster grid. The bearing and magnitude of the wind vector were calculated from the values of the x and y vector component provide by rNOMADS using the Pythagorean

theorem at the point estimate location. I plotted these data in a radial plot with the spatial point at sea level as the origin and the elevation above that point radiating out from the origin. The lines plotted on the radial graph are bearing and magnitude per elevation at each time step.

I restricted the wind speeds displayed to speeds that are biologically relevant for shearwater flight according to the flight energetics calculated from an algorithm called ‘Flight’ (Pennycuick 2008a). Temperature and humidity data were processed at the same time and using the same process as the wind data except temperature and humidity data were scalars rather than vectors so they did not require calculations to merge layers. Converting latitude, longitude, and time points into their location in the solar niche ring (solar coordinate system) was done according to the model outlined in Chapter 4.

Minimum and maximum wind speeds for flight were calculated using the Pennycuick flight model that I coded in R so that it could interface with the rest of the analysis (Figure 5.1). This model was built directly from the book ‘Modeling the flying bird’ (Pennycuick 2008a) and the output values from my R code were validated against Pennycuick’s C language version of the model (accessed from [http://research-information.bristol.ac.uk/en/persons/colin-j-pennycuick\(30ae7955-a03b-4eae-a692-f71f812b2e58\).html](http://research-information.bristol.ac.uk/en/persons/colin-j-pennycuick(30ae7955-a03b-4eae-a692-f71f812b2e58).html) on 1 July 2012). Pennycuick’s model is a biological analogy to the models used to calculate the fuel range of airplanes, where jet fuel consumption has been replaced by metabolic energy production based on size, shape, and fat intake. Flight energetics in this model depend on three parameters that are characteristics of the bird: mass, wing span, and wing area. The values of these parameters for Greater Shearwaters were approximated from the literature as follows: all up mass = 819 g; wing span = 1.148 m; wing area = 7.068 m (Warham 1977).

The final parameter for the model was air density, for which I used 0.909 kg/m^3 at 3 km above sea level (Yahya 2003). This model calculates mechanical power and lift to drag ratio as a function of wind speed, which in turn translates into the chemical (fuel) power requirements to maintain flight. The slowest wind speed upon which an individual bird can maintain horizontal flight is the speed at which it maximizes aerodynamic efficiency. Birds don't immediately drop from flight below these speeds, but they can't maintain horizontal glide and start to descend back to the surface.

Shearwaters rarely land on Earth's surface and are known to glide for most of their flight, indicating that they rarely adopt a negative flight angle. The maximum flight range is achieved at the speed where an individual can achieve the greatest lift-to-drag ratio, calculated from the mechanical power curve as a function of mass, gravity, and air pressure. Birds don't immediately drop from flight when they exceed the maximum speed, but they pass a threshold where they can't keep their head down to maintain horizontal flight and they are forced into a positive flight angle. Depending on the severity of that angle, a positive flight angle either slows them down by gaining altitude or blows them backwards out of flight (Pennycuick 2008a).

5.3 Results

Results show that solar angle was a strong predictor of migratory paths (Fig. 5.5), that the environmental wind speeds used by shearwater migrants matched the physically achievable wind speeds predicted by the Pennycuick model (Figs. 5.4 and 5.6), that individuals maintained consistent wind bearings that countered Earth's rotation (Fig. 5.6), and that individuals maintained consistent temperature and humidity locations (Fig. 5.7).

Figure 5.4 shows a series of curves that describe the amount of power (power = force*velocity) required to maintain horizontal flight as a function of true air speed for the Greater Shearwater. The total mechanical power needed to maintain flight is the sum of three different power measurements: parasite power (needed to overcome body drag), induced power (needed to support weight), and profile power (needed to overcome wing drag). At low speeds, the mechanical power required to overcome drag is greater than an individual is able to produce and so they are not able to maintain flight. This relationship of low efficiency at high and low speeds is expressed as an upward facing concave curve with high power requirements at low and high speeds and a minimum value at the most efficient wind speed. The minimum, and most efficient, flight speed for Greater Shearwaters was calculated to be 12 m/s at the location of the minimum value on the mechanical power curve (minimum power line in Fig. 5.4). The lift-to-drag ratio for Greater Shearwaters at sea level reached its maximum level of 13:1 at a true air speed of 22 m/s, thus setting the maximum flight speed (maximum range line in Fig. 5.4). This calculated lift-to-drag ratio is comparable with recorded ratios for a similar species, the Great Knot, that achieves a ratio of 12:1 (Pennycuick 2008a). The chemical power curve in the upper half of Figure 5.4 is exactly the same shape as the mechanical power curve, but it has been scaled according to the metabolic efficiency of these birds. This curve shows that there is a three-fold increase in energy requirements for flight between the minimum power velocity and zero.

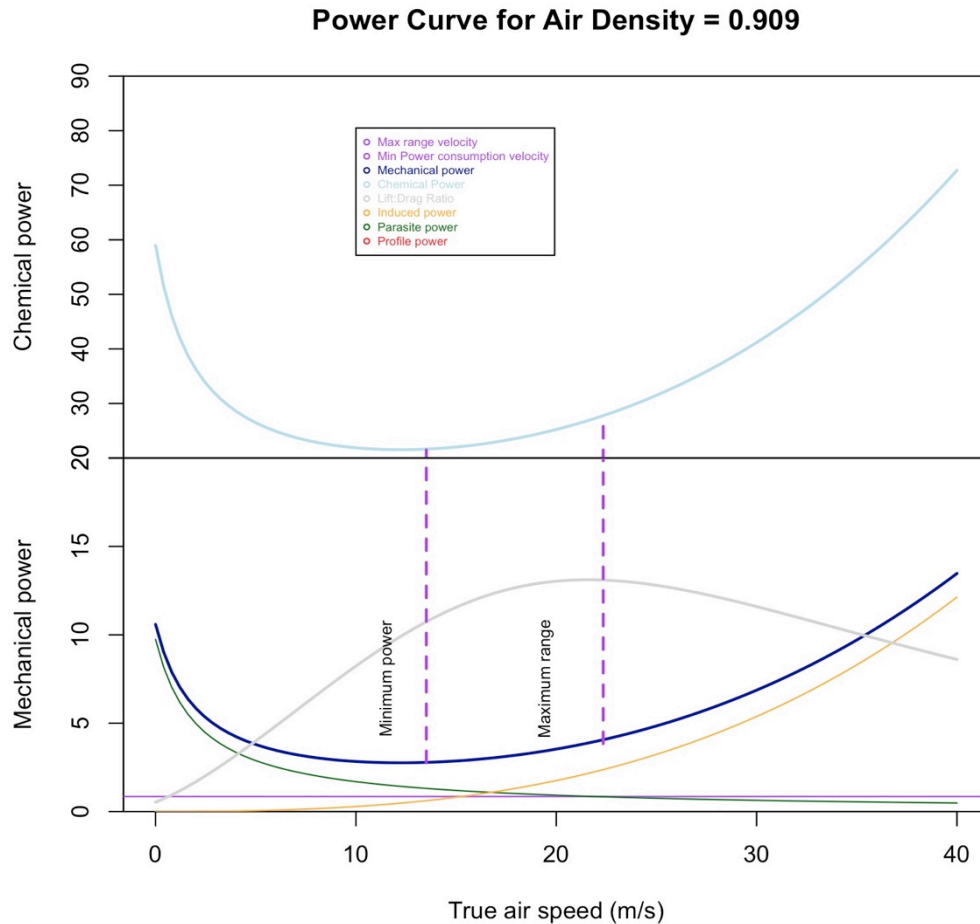


Figure 5.4 Calculating wind speed performance for the Greater Shearwater. This is a set of power (power = force * velocity) curves describing the flight dynamics of individual birds. The induced power, parasite power, and profile power curves are at the bottom of the figure and they sum to the mechanical power curve in blue. The chemical power curve is the same shape as the mechanical power curve but it is adjusted to reflect the efficiency rate of transferring fuel into flight. The minimum power value on that curve is the minimum speed for maintaining flight and the most efficient speed to fly at. The lift:drag ratio uses the same scale as mechanical power (watts generated per kg) and is drawn as a grey line to represents how efficiently an individual can fly based on how much weight they are carrying and how efficient their body shape is. The maximum lift:drag ratio of 13:1 determines the maximum speed an individual can fly and the speed at which they will travel the farthest given a fixed amount of fuel. Minimum power is more efficient to maintain metabolically but it requires slower flight. Maximum range speed covers more ground at the cost of burning more energy overall.

The results presented in Figure 5.5 show the close coherence between the observed locations of Greater Shearwaters and the solar-angle model predicting a stationary-relative

orientation between individual birds and the sun. The figure shows that individuals that move out of the energy ring shift above or below the model (e.g. individual 22 around the summer solstice). Transitions through the transit zone translate to lateral shifts between analemmas in the southern hemisphere to analemmas in the northern hemisphere. Individual 12 is a good example of an individual that stayed in the southern hemisphere the entire year, and individual 21 is a good example of an individual that spent time in both the primary and secondary zone by traveling through the transit zone (Fig. 5.5).

The top left of Figure 5.5 shows a globe with the shearwater's solar niche ring highlighted in blue. Each location on this ring shares the same solar elevation angle but differs in azimuth angle around the ring. The blue niche ring is represented in two dimensions by a set of analemmas arranged into sine and cosine curves with a resolution of one analemma for each hour degree angle around the ring. A single one of these analemmas shows the relative trajectory between one point on the ring and Earth's surface moving below that point over the course of one year. The full suite of analemmas broadly shows the relationship between the entire niche ring and the Earth moving under it. The analemma model (mean solar elevation) is centered on the southern-most point of the ring because that is the primary zone of occupation for Greater Shearwaters.

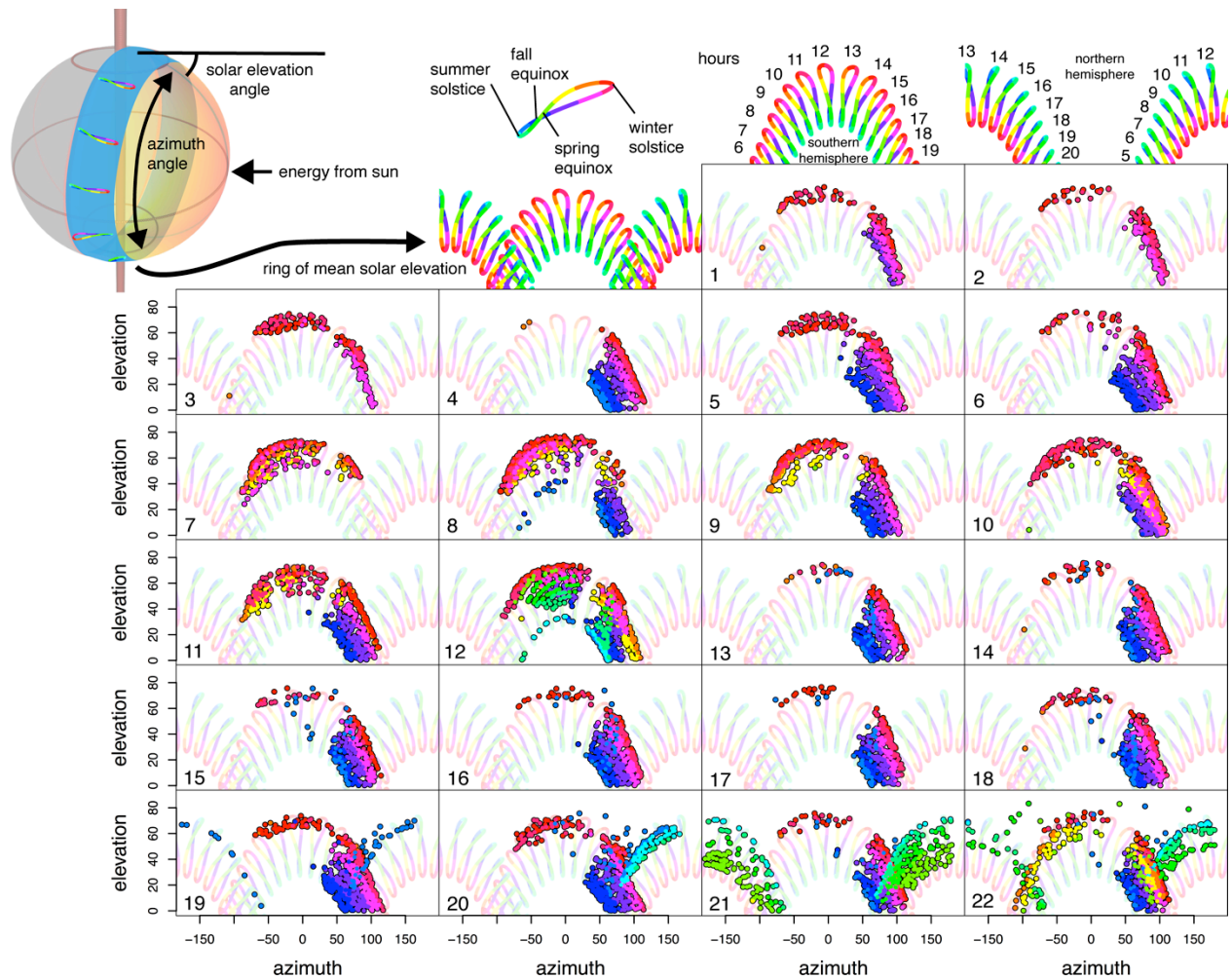


Figure 5.5 Solar position of 22 individual migrants throughout the year. Each point is a location of an individual migrant at a particular time and the series of analemmas behind the points are the predictive model for an individual maintaining a constant solar angle to stay in an energy niche ring. Each of the 22 panels with black frames presents the solar elevation and azimuth angles for one individual throughout the year. Lines are model predictions. Points are observations. The color indicates the time of year, from January (red) to December (violet). Birds were tagged and released during the fall equinox, so the first data points are violet and then red. Top right shows the full model broken into two parts to show which components describe the southern hemisphere and which describe the northern hemisphere. Those two components are each a series of 12 analemmas that each describe the path that section of the energy ring follows throughout the year. To the left of those two hemispheres, is a single analemma showing the progression of colors throughout the year and the major landmarks for Earth and sun interactions. Below the single analemma is the full model for avian migrants following an energy niche ring. This full model is 24 individual analemmas from each hour of the energy ring. Individuals moving laterally within the ring will move laterally between analemmas. The individuals presented here are numbered for comparison with Figures 5.6, 5.7, and 5.8.

Individuals occupied a consistent wind speed and wind bearing throughout the year (Fig. 5.6) that in general would tend to maximize their flight efficiency. A wind speed of 12 m/s and an easterly wind bearing matching Earth's rotational bearing are predicted to maximize flight efficiency, given that shearwaters must occupy a specific range of wind speeds between 12 and 22 m/s (as determined in Fig. 5.4) and the Earth's surface below these flying birds (as they are detached in their energy niche ring) is always traveling from west to east as a result of Earth's rotation. In agreement with this prediction, Shearwaters were most frequently recorded in areas with wind speeds that optimize their flight efficiency, that is, at lower speeds near 12 m/s (Fig. 5.5). On average, individuals were found in locations with a wind bearing of east to southeast throughout the year (Fig. 5.6).

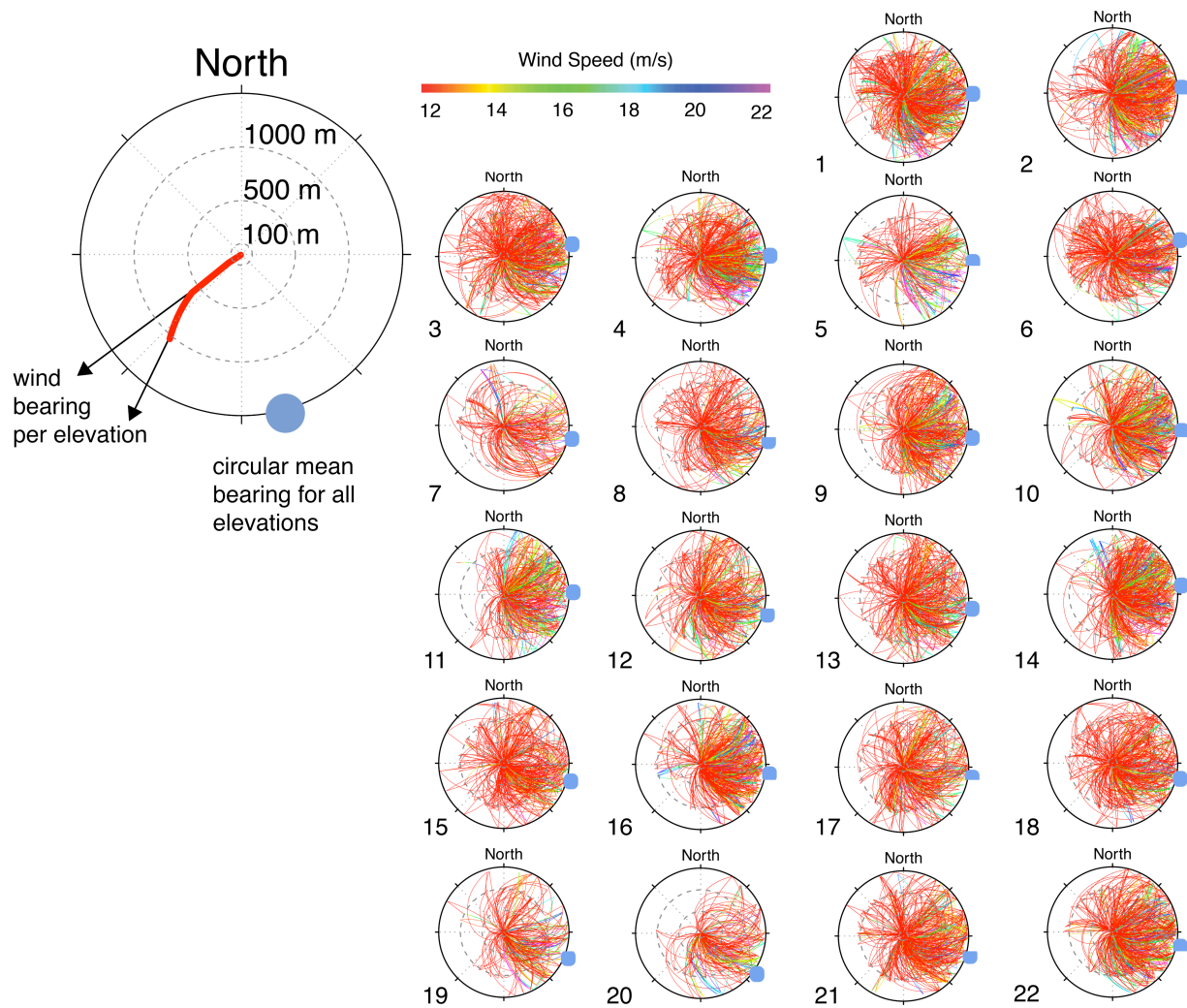


Figure 5.6 Wind position of individual migrants. Individual migrants tended to maintain a wind speed and wind bearing that would maximize flight efficiency. This figure shows radial plots of wind bearing and speed per elevation for 22 Greater Shearwater individuals from release date (September 2009) to the end of data transmission (January 2010 - March 2011). Each of the 22 graphs shows the wind history of a single individual. Each line in the plot is a single time point. Low elevations are at the center of the radial plot and high elevations are on the outside of the circle. The bearing of the line at each radial distance indicates the wind bearing at that elevation. The color of the line at each radial distance indicates the wind speed at that elevation. Wind speed values are restricted to 12-22 m/s because that is the full range of speeds at which a Greater Shearwater can stay in flight. Blue dots are the circular mean bearing across all elevations. Elevation is capped at 1000 m, which is the maximum recorded flight height for this species.

Individuals occupied similar environmental temperature and humidity ranges to each other (Fig. 5.7). Fifty percent of observations across individuals (quantile 25-75%) were

within 10-20°C, and no individual ever experienced temperatures below -15°C or above 30°C (Fig. 5.7). Individuals showed more tolerance for changes in humidity levels than they did to temperature. Fifty percent of observations across individuals (quantile 25-75%) were within 45 to 85 percent relative humidity, although occasionally humidity levels were as low as 10% and as high as 100% (Fig. 5.7). The averages for temperature and humidity were very similar across individuals. The yearly average temperature experienced by an individual was always between 6°C and 16°C, while the yearly average humidity level experienced by an individual was always between 59 and 79 percent (Fig. 5.7).

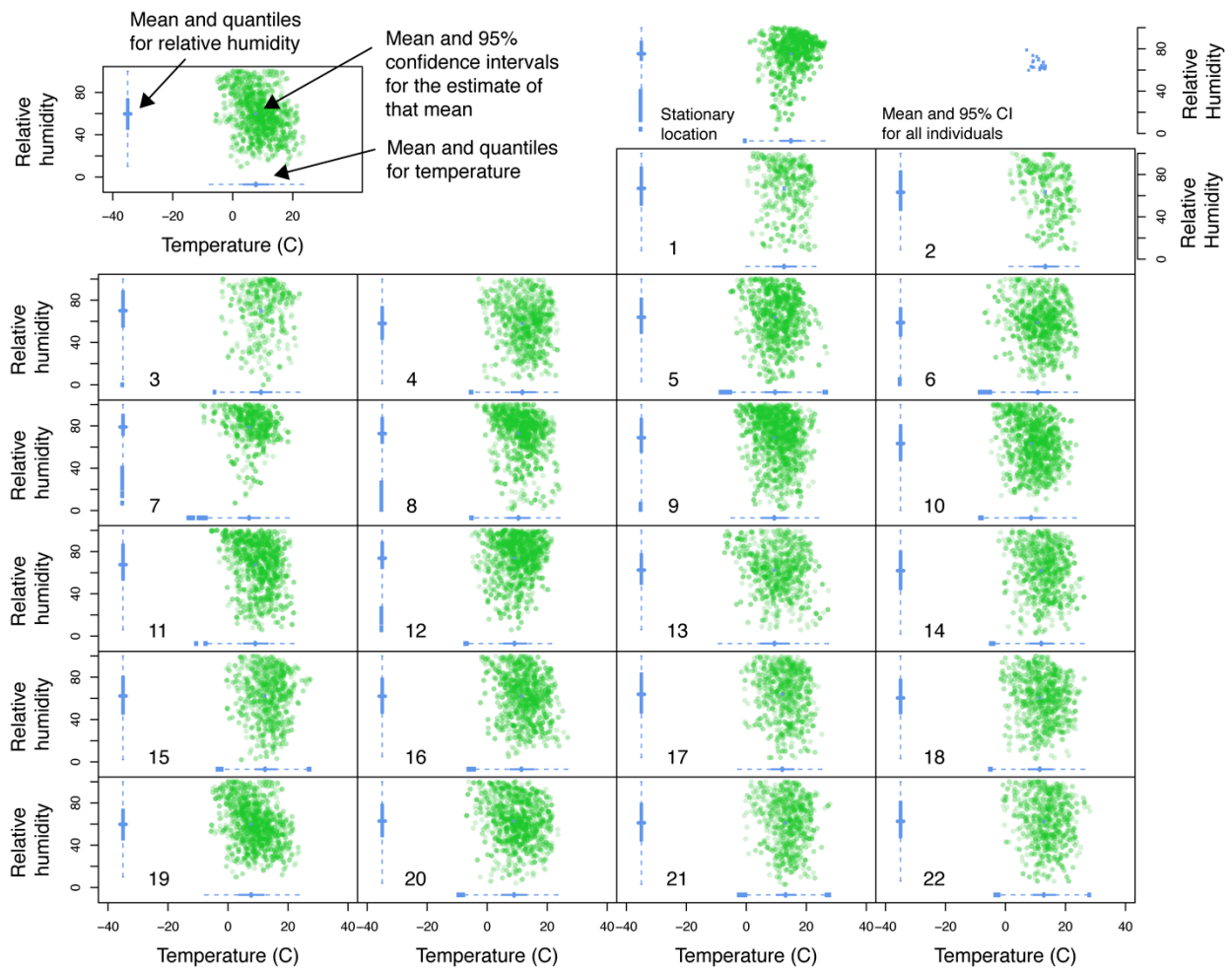


Figure 5.7 Temperature and humidity position of individual migrants. This figure shows the temperature and humidity range experienced by 22 individual Greater Shearwater migrants throughout the year. Each of the 22 graphs shows the data for a single individual. The points in green are the temperature and humidity for an individual's location at a single time point. In whole, the points show the full range of temperature and humidity conditions experienced by an individual over that period of time as it traveled from place to place. These data are summarized by three metrics in blue. Along the y-axis, on the left side, a bar plot summarizes all of the relative humidity data by quantile. Along the x-axis, on the bottom side, a bar plot summarizes all of the temperature data by quantile. The hash in the middle of these boxplots is the mean value. The box extending from the mean contains 50% of the data. The dashed lines that fall outside the box show the remaining 50% of the data. Plotted on top of the green point clouds is the mean temperature and humidity combination. Those mean values are plotted together in the top-right panel for comparing individuals against each other. For comparison, to the left of the summary plot of all statistical means is a plot of a surface location through the same time series as the avian migrants, but remaining attached to Earth's surface. The arrangement of the 22 panels matches those in Figures 5.5, 5.6, and 5.8 for comparison.

Individual shearwaters showed a variety of movement patterns, including partial and full traversals of a figure-8 path (Fig. 5.8). The following results pertain to Figure 5.8: a majority of individuals (1-12) stayed in the lower hemisphere of their solar niche ring and slid back and forth on the bottom of a figure-8 to make a long, slightly U-shaped surface path. These individuals did not travel out of the southern hemisphere but instead stayed in the primary zone the entire time. Six individuals (13-18) spent some time in the transit zone near the equator but never traveled all the way to the secondary zone and overall traversed a small part of a figure-8 path. Individuals 19-22 spent time in both the primary and secondary zones and they traveled through the transit zone during that transition. Within the individuals that made it to the secondary zone, individuals 19 and 20 traveled to the secondary zone but we do not have record of them returning, individual 21 traveled between the primary and secondary zone using the same transit zone for both trips, and individual 22 traveled between the primary and secondary zone using opposing transit zones for the trip up and the trip back. Accordingly, individuals 19-21 formed an S-shaped path (i.e. most of a figure-8 except one section) over the course of the year, while individual 22 formed a full figure-8 over the course of the year.

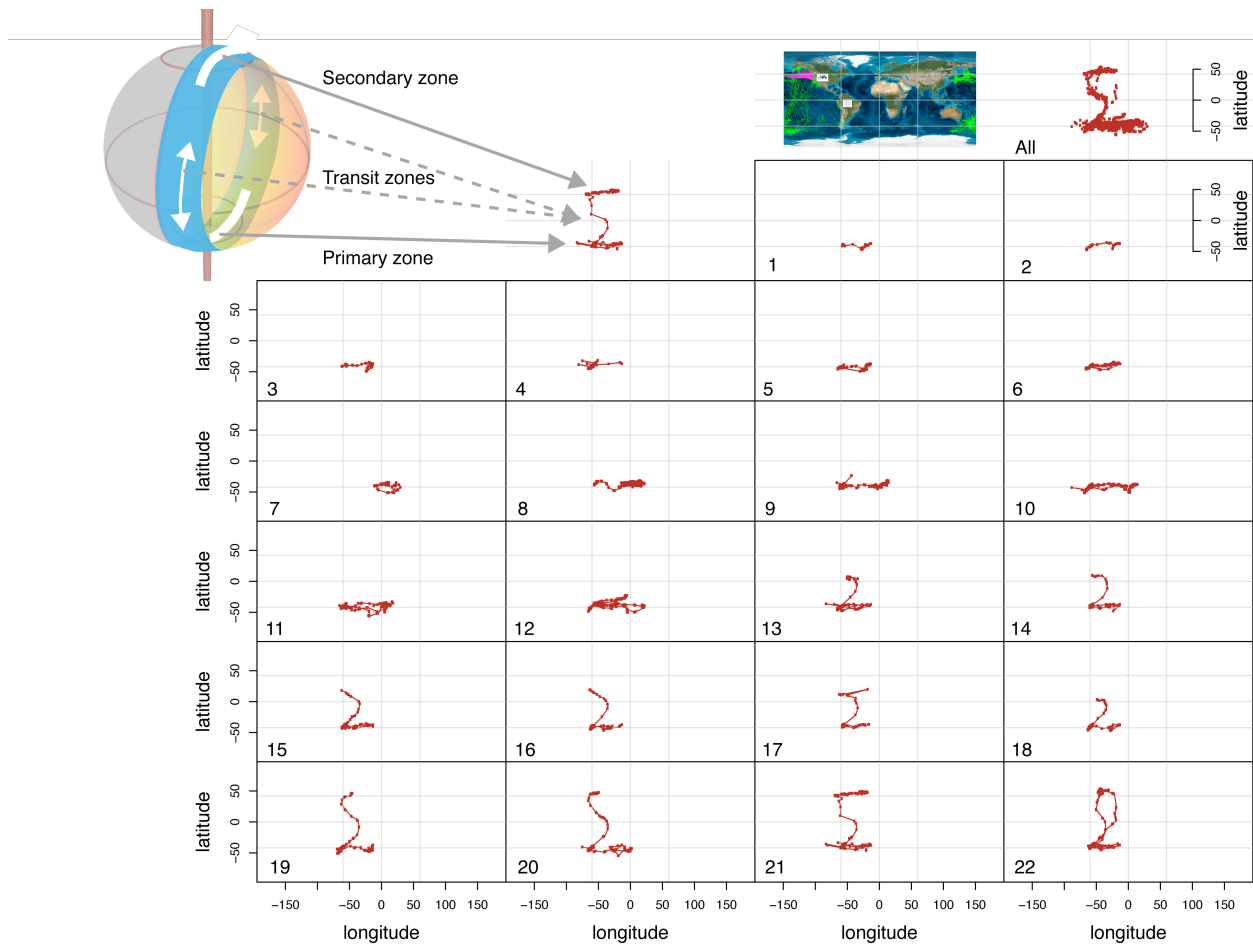


Figure 5.8 Spatial paths of individual migrants. This figure is an equal-area projection of the migration path of 22 Greater Shearwater individuals from their release date (September 2009) to the end of data transmission (January 2010 - September 2010). The yearly path is plotted on a geo-referenced projection. If a species lives in a fully detached niche, its yearly movement path will look like a figure-8 when plotted on a geo-referenced map projection. Responding to terrestrial niche dimensions will restrict individuals to part of that figure-8. The panel in the top right shows the paths of all individuals overlaid.

Plotting the same location data in 3D and in the solar coordinate system instead of the Earth coordinate system, reveals that most observed locations were within a well-defined but not fully complete ring centered on solar noon (Fig. 5.3), as expected if individuals were staying within a solar-niche ring. The greatest density of points was in the southern hemisphere of the ring (Fig. 5.3a), while fewer points were located above the equator in the northern hemisphere of the ring (Fig. 5.3 b, c, and d), giving a pronounced “U” shape (Fig. 5.8). This “U” shape is plotted in a solar coordinate system (method described in Chapter 4)

and is distinct from the “U” described as a subset of the analemma shape when analyzing movement patterns in the Earth coordinate system.

This solar-referenced spatial distribution reveals the preference of individuals to stay within the primary zone (Fig. 5.3a) of the southern hemisphere throughout the year. However, individuals that stayed in the primary zone the entire year were temporarily pushed out of their energy niche ring as a consequence for doing so. This is evident in the red, yellow, and orange dots on the left planet of Figure 5.9. These individuals shifted laterally within the primary zone, out of the niche ring entirely, and then back into the niche ring, instead of staying in the ring the entire time but covering more area within the ring. It is unclear which strategy is more efficient overall, but it is clear that strategies can differ between individuals.

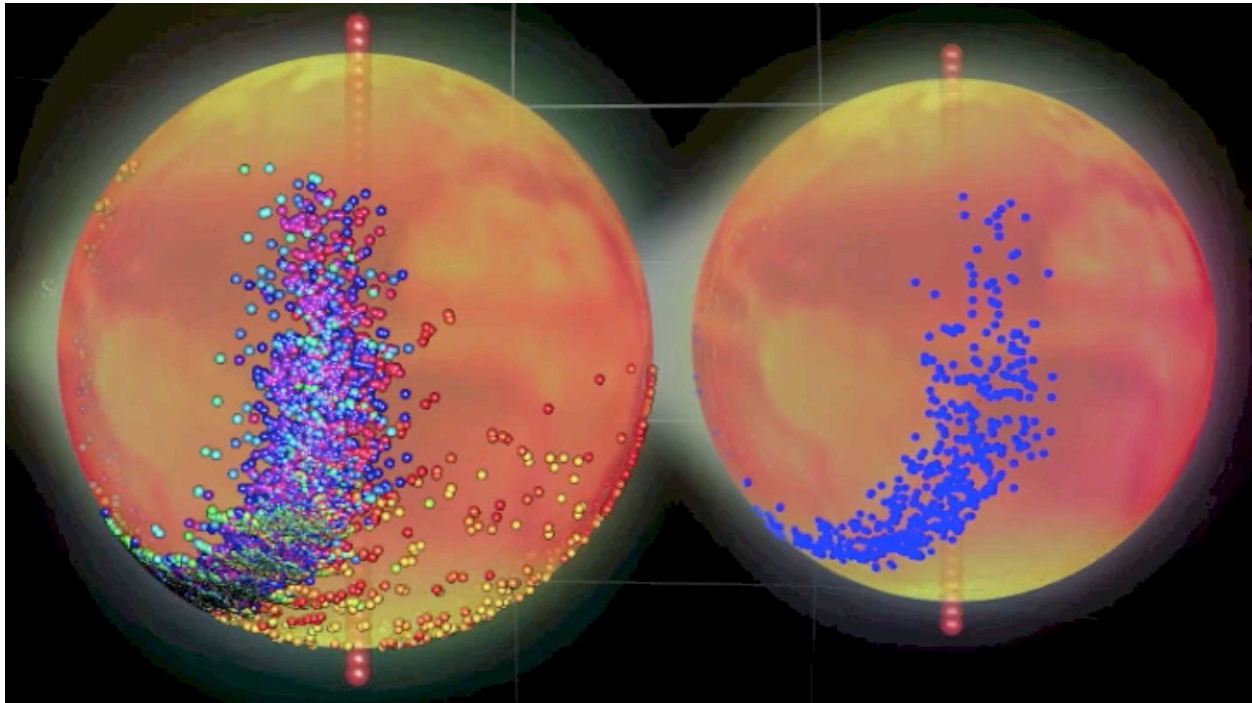


Figure 5.9 The location of individual migrants in the solar coordinate system throughout the year. These data began as latitude, longitude, and time data and then they were converted using the relativistic Geographic Information System described in Chapter 4 into the solar coordinate system. In this figure, energy from the sun is coming from the left side of the figure. The left planet shows all individuals plotted together. The right planet shows the path of one individual (#20). The colors of points on the left planet indicate the individual migrants being tracked and the planet on the right uses a single point color to show the spatial pattern of a single individual. The poles are the axial poles of Earth and they are arranged so north is up.

5.5 Discussion

The purpose of this study was to rank the relative contribution of climate niche components to the figure-8 pattern observed in Greater Shearwater migratory paths, with the broader goal of achieving a better understanding of why and how avian species migrate. I have shown that (1) solar angle is the primary driver of the observed figure-8 pattern, (2) wind contributes to the efficiency an individual bird is able to achieve as they stabilize solar angle, and (3) temperature crossed with humidity contributes the least to long-term movement patterns, even though populations clearly made an attempt to stabilize these variables through time.

Shearwater migrants displayed the expected behavior of individuals tracking a solar niche

by maintaining a constant solar angle throughout the year (Figs. 5.3, 5.8, 5.9) and seeking out solar angles that are low to the horizon (Fig. 5.5). Individuals selected wind speeds matching their most efficient flight speeds and maintained wind bearings that countered the rotation of Earth (Fig. 5.6). Additionally, individuals in the population occupied the same temperature and humidity ranges throughout the year (Fig. 5.7). These findings best support the first proposed alternative hypothesis (**h1**) by showing that solar angle was the strongest determinant of migratory path, followed by wind, and lastly by temperature and humidity.

Here I propose a specific mechanism for the interaction between solar cues and the migratory paths taken by long-distance avian migrants on the Earth's surface. An energy niche ring defines the total area on Earth's surface experiencing the same instantaneous solar declination. An observer can occupy any part of this ring and measure the same solar angle at that moment, but a surface observer fixed at a single point on Earth usually sees this ring at a particular time of day as Earth rotates under the sun and carries the observer past the ring. A bird that is able to fly and maintain a constant solar angle will experience the ring independently of Earth's movements and will be able to move freely about the ring. Earth takes an analemma path under the energy niche ring each year, and so any observer on Earth's surface will observe the individual in the energy niche ring as traveling along some section of a figure-8 path over the course of the year. An avian migrant can only consistently follow a figure-8 path if they are maintaining a constant solar angle. Greater Shearwater migrants consistently demonstrate such a figure-8 migratory path (or part of a figure-8), which is the primary support for solar angle being the main driver of individual realized migratory paths.

The energy niche ring model also offers an explanation for the difference in “8”, “S”, and “U” shaped migratory paths by offering a distinction between primary, secondary, and transit zones of the energy niche ring. The “U” shaped pattern is when an individual stays in the bottom

of the “8” (analemma) pattern all year and never crosses the equator, it is a subset of the larger figure-8 pattern. Individuals that get bumped from the primary zone will travel as quickly as possible to the more-stable secondary zone. A surface observer will record any individual that moves through the transit zone as migrating north and south, while time spent in the primary or secondary zones will be observed as moving east and west. This “U” shape should not be confused with the partially completed ring shape in Figure 5.9. The ring in Figure 5.9 is the solar niche ring and could be fully filled by data points to look like the ring that it is. Instead, individuals are mostly absent from the top of the ring and so the remaining points look like a “U”. The “U” shape, described in reference to the “8” and “S” shapes, is part of an analemma rather than a ring. They are different in that one is plotted in the Earth coordinate system and the other in the solar coordinate system.

The distinction between an “8” shape and an “S” shape is determined by the combination of transit zones that an individual uses when shuttling between primary and secondary zones of the energy niche ring. If an individual moves up and down the same transit zone, they will make a figure-8 path throughout the year. If an individual moves up one transit zone and down another, they will form an “S” path throughout the year. The contrast between the “8” and “S” paths is demonstrated in Figure 5.3. In the same figure, you can see the difference in path shape between two individuals that took different transit zones to shuttle between the primary and secondary zone. These two individuals were noteworthy for their migration (individuals 21 and 22 in Figs. 5.5 and 5.8) because they did a full shuttle from the primary zone, into the secondary zone, and back to the primary zone again.

There was strong coherence between the solar angle model defining the energy niche ring (Fig. 5.5) and time-specific location data of Greater Shearwater migrants. This means that individual birds *did* maintain constant solar angles throughout the year as their figure-8 path

would suggest. Individuals 21 and 22 diverged slightly from the model during spring migration, suggesting that they had a difficult time maintaining their solar angle during these periods where Earth's dynamic movements intensified underneath them, and that they temporarily shifted to a different solar angle before shifting back to their normal angle with the following month.

Wind data support the energy niche ring model rather than a wind-dominant hypothesis (**h2**) because individual birds held a constant wind bearing that countered Earth's rotation rather than following a shifting wind bearing to create a figure-8 pattern from wind cues only. If wind was the primary driver of the figure-8 pattern, then the wind bearing would shift through a full 360-degree rotation to achieve every angle necessary for creating a figure-8 pattern out of wind. Instead, individuals maintained a constant solar bearing as the energy niche model predicts. The reason the energy niche model predicts this is that individuals trying to stay in a constant location relative to the solar niche will need to counter the rotation of Earth's surface below them to achieve that stability in the niche ring. The energy niche ring model is further supported by individual migrants consistently choosing flight locations with wind speeds matching their minimum, and most efficient, flight speeds. This indicates that staying in the stability of a well-defined-but-small energy niche can be an efficient life history strategy, if species have few surface requirements.

Temperature data supported the energy niche ring model rather than a temperature-driven hypothesis (**h3**) because the entire population maintained similar temperature and humidity combinations throughout the year, rather than moving in response to changing temperatures. Individuals responding to temperature as a movement cue are expected to experience temperature stress before being motivated to travel and none of the temperature data suggest that individuals were under thermal stress at any point during the year. The population of shearwaters also showed remarkable consistency in the temperature and humidity range that individuals in

the population were maintaining, regardless of where individuals were located relative to one another or relative to the energy ring. Individuals could be spatially separated and still maintain consistent temperatures with their conspecifics. Thus, temperature offers little explanation for why individuals would move in a figure-8 pattern throughout the year.

Past studies have also shown that solar cues are a primary driver of migratory patterns (Matthews 1953, Pennycuik 1960, Wiltschko 2003, Åkesson et al. 2005, Wiltschko and Munro 2006, Boström et al. 2012, Armstrong et al. 2013), but they lacked a unifying mechanism for defining the interrelatedness of solar, magnetic, wind, and temperature cues. What was left unresolved in these discussions was the relative contribution of each component or a synthesis of these cues into a single unified framework. Here I have taken the first step to unifying these cues into a single framework by building a model to explore the link between climate niche cues and the migratory path that individual migrants take throughout the year.

One of the limitations of this study was the low availability of movement data relative to the spatial and temporal scope of the research question. While there were more than 8000 data points over the course of 6-18 months in the Greater Shearwater dataset, these included only 22 individuals and many periods lacked data as individuals moved in and out of the satellite signal. Additionally, many of the geolocators stopped reporting before the full journey could be completed.

A second limitation of this study is that I only looked at a single species. Shearwaters are not alone in demonstrating a figure-8 shaped migration pattern. Arctic terns (Egevang et al. 2010), Sooty shearwaters (Shaffer et al. 2006), Cory's shearwaters (Felicísimo et al. 2008, Dias et al. 2012), and bar-tailed godwits (Battley et al. 2012) are all equally striking examples. Species that are less efficient fliers, species with more reliance on surface resources, and species that migrate shorter distances may be responding to different environmental cues than these pole-

to-pole migrants. Such species, including the Arctic peregrine falcon (*Falco peregrinus tundrius*) (The southern cross Peregrine project 2016), Osprey (*Pandion haliaetus*) (Hake and Kjellén 2001, Martell et al. 2001, Alerstam et al. 2006), Great snipes (*Gallinago media*) (Klaassen et al. 2011), and storks (*Ciconiidae*) (Liechti et al. 1996, Shamoun-Baranes et al. 2003, Berthold et al. 2004), often have an S-shaped migration pathway. La Sorte et al. (2016) recently mapped the flight patterns of 118 terrestrial, new world avian migrants, including a number of warblers (*Sylviidae* sp.), orioles (*Icterus* sp.), flycatches (*Muscicapidae* sp.), sparrows (*Emberizidae* sp.), and hummingbirds (*Trochilidae* sp.). La Sorte et al. (2016) showed that all 118 species converged on the same tendency to move north and south at the same time and east and west along an “S” path rather than straight line.

Future studies should explore the relative contribution of solar, wind, and temperature cues in the migration paths of other species, using the solar niche ring model. Terrestrial ungulates display the same analemma path as these shearwaters, but they run into terrestrial barriers and track environmental cues using different physiological mechanisms, which changes the local dynamics they encounter en route (Sawyer and Kauffman 2011, Sawyer et al. 2016). Marine turtles also demonstrate similar migratory patterns (Luschi et al. 1996, Nichols et al. 2000, Mansfield et al. 2014), but they migrate more slowly than their avian counterparts, so their figure-8 patterns would be expected to change orientation accordingly. To date, these ideas remain relatively unexplored, but I believe applying these solar stationary models to other species will reveal a broader and more generalizable connection between solar movement patterns and patterns of organismal organization.

CHAPTER 6

CONCLUSIONS ABOUT RELATIVE MOTION AS AN ECOLOGICAL MECHANISM

6.1 Overview

Relative motion becomes an ecological mechanism when it alters the functionality of natural systems. Throughout this dissertation, I provided individual and population-level case studies that showed how ecological systems operate differently when motion is applied. In Chapters 2 and 3, I used simulated and living populations of *Tribolium* beetles to track changes in population dynamics and extinction risk following the application of motion. Relative motion in these chapters referred to the movement of suitable habitat conditions and the movement of beetle populations tracking that moving habitat through spatial spread. In Chapters 4 and 5, I used advanced modeling approaches to study how planetary movements can influence migratory pathways. Relative motion in these chapters referred to the movement of a spinning planet and the movement of birds maintaining their preferred climatic conditions throughout the year. When taken together, Chapters 2 through 5 demonstrate the influence relative motion can have on our measurement and understanding of ecological systems.

This dissertation offers ideas, theories, and empirical results to guide the ecological community in thinking more deeply about relative motion. The contributions of this work center on (1) providing a quantitative and theoretical framework to explicitly consider relative motion as an ecological mechanism underlying ecological patterns (Chapters 2 and 4), and (2) testing the empirical support for the theories presented to determine their tractability (Chapters 3 and 5). Ultimately, this dissertation provides evidence that relative motion is an important and underestimated driver of ecological patterns.

6.2 Summary of key findings

Relative motion between individuals, populations, and their environment is common in natural systems. Historically, researchers have considered the movement of habitat and ecosystems over long time scales, following events like the recession of a continental ice sheet or tectonic shifts (Parmesan et al. 2005, Barve et al. 2011). Over the last decade, research has expanded to include habitat movement over shorter time scales (Ewers and Didham 2006, Pearman and Guisan 2008), largely due to improved understanding of how global climate warming is shifting the location of climate niches and the impacts of those shifts on species, communities, and ecosystems (Thomas et al. 2004, Joly and Fuller 2009). My research has taken this understanding a step further by explicitly considering the relative motion of individuals, populations, and climatic conditions as a mechanism driving ecological phenomena. I showed that relative motion is a primary mechanism determining a) the shape of a population's spatial abundance profile, b) the extinction risk of populations experiencing ecological relative motion, and c) the route and timing of long-distance avian migration.

In Chapters 2 and 3, I explored the application of assisted migration to populations experiencing shifting climate niches. Assisted migration is a unique conservation method because it uses relative motion to rescue populations under threat from relative motion. It is a technique that reduces the degree to which two ecological components, populations and their habitat, are moving relative to each other. My research showed that, in reducing the relative motion of populations and their habitat, assisted migration can extend the time to extinction and reshape the population's spatial abundance profile to be more symmetrical and stable.

In Chapter 2, I simulated the dynamics of populations tracking a moving climate niche using stochastic spatial spread models (adapted from Melbourne and Hastings 2008, 2009). Data from these simulations showed that assisted migration reduced the risk of extinction in moving

populations, but the success of assisted migration was sensitive to the speed at which the habitat was moving and the location to which individuals were transplanted. For example, with one-patch movement, time to extinction was greatly reduced by transplanting individuals far ahead of the good habitat. With two-patch movement, time to extinction was greatly reduced by transplanting individuals far ahead or far behind the good habitat (see generation time in total abundance column, Fig. 2.4). Simulations also showed that transplanting individuals the same distance ahead of their good habitat as the per-generational speed of that habitat (i.e. the relative speeds match each other) maximized the success of assisted migration. Thus, data from Chapter 2 suggest that an “equal motion” strategy may be the most effective way to maintain healthy populations in the face of climate change.

In Chapter 3, I experimentally manipulated relative motion in a *Tribolium* (red flour beetle) microcosm experiment to test whether assisted migration could reduce extinction risk in living populations experiencing shifting climate niches. Assisted migration studies are rarely conducted in living systems because of the large potential for negative impacts (e.g. facilitating the spread of invasive species, genetic impacts, and species biases) (McLachlan et al. 2007, Hewitt et al. 2011). In fact, this study provides the first controlled experiment tracking the success of assisted migration over multiple generations in a living system.

Excitingly, results from Chapter 3 showed that assisted migration significantly reduced extinction risk in moving populations (Fig. 3.5), providing evidence that assisted migration can work to combat the effects of climate change. By generation eleven, 27 out of 30 populations went extinct in the landscapes without assisted migration while only 6 out of 30 populations went extinct in the landscapes with assisted migration. Assisted migration also changed the symmetry of the abundance profiles of moving populations from a negative to positive skew, suggesting that population skew may be an effective indicator of extinction risk in populations

tracking a shifting climate niche. Ultimately, findings from Chapter 3 provide hope that populations under threat from moving climate niches may be successfully rescued through strategies that reduce the relative motion between populations and their climate niche.

The influence of relative motion on ecological processes extends beyond the scale of regional movement patterns to movement at the global scale. However, measuring relative motion at the global scale requires a special set of mathematical tools and models. In Chapter 4, I described my modeling platform for tracking multiple sources of relative motion on a global scale. I used the relationship between Earth and the sun as a test case for demonstrating the platform's functionality. Specifically, I considered scenarios for the interaction between Earth and the sun at two different time scales: hourly and yearly. The first scenario described the full spatial extent, over the course of one year, of relative interactions between points in one coordinate system and points in an opposing coordinate system. The second scenario weighed the relative contribution of various detached niche components over an hourly scale, based on how much one moving object (an individual bird) diverts away from a second moving object (the trajectory of Earth's surface).

Data from Chapters 4 and 5 showed that the interaction between Earth and the sun can be summarized using distinctive shapes. An observer on Earth's surface will measure the sun as traveling in a figure-8 pattern throughout the year. In contrast, an observer detached from Earth's surface will observe Earth moving under them along a trajectory of two opposing parabolas. These shapes, the Analemma vs. the two parabolas, outline the area of Earth's surface that individuals will pass over throughout the course of a year and, therefore, outline the surface resources available to them throughout the year.

The modeling platform described in Chapter 4 was designed specifically to deconstruct and track relative motion between ecological components. I have not yet conceived many of the

applications of the modeling platform, but I hope it can be used to inform a number of questions about the relationship between the relative motion and relativistic relationship between Earth and the sun.

The first application for my modeling platform was to deconstruct the relative motion between detached migratory birds using the shape of their yearly migration routes and daily movement trajectories. In Chapter 5, I used this platform to rank the relative contribution of climate niche components to the figure-8 pattern observed in Greater Shearwater migratory paths. My data suggest that solar angle is the primary driver of the observed figure-8 pattern in shearwater migration paths and that wind and temperature primarily contribute to the efficiency an individual achieves when responding to solar cues. Shearwater migrants preferentially chose solar angles that were low to the horizon where the temperature was cool and selected wind bearings that countered the rotation of Earth at efficient speeds. The methods used in this study provide a first step to developing a unifying framework for understanding the relative interrelatedness of solar, wind, and temperature cues in the spatial paths of migratory species. In total, these conclusions show that shearwater migration is an emergent property of relative motion between the stable but limited energetic niche that birds primarily respond to and the more dynamic surface resources that they rely on for some needs.

6.3 Future directions

As is often the case, this research has led to more questions than answers about relative motion in natural systems. Simulations and experiments showed that assisted migration was sensitive to where individuals were transplanted relative to their suitable habitat, but there is currently no way of measuring moving habitat in the field. In ecological systems, the environmental conditions defining a species range boundary can be difficult or impossible to

detect when stationary and is likely even more difficult to detect when the habitat is moving. There is currently no reliable method for tracking moving habitat through time and across space, but population abundance profiles have been a useful tool for detecting stationary range limits and may be a useful diagnostic for defining where moving habitats are located and how fast those habitats are moving across a landscape. Melbourne et al. (*in prep*) were able to show that symmetric abundance profiles indicate a stationary habitat, and abundance profiles become more asymmetric as habitats gain speed. This feature of abundance profiles may prove useful for finding and tracking moving habitats in natural systems but it is so far untested in ecological systems. Until these methods are developed more fully, the advancement of these ideas must be limited to laboratory and modeling experiments.

Even more questions remain about the role of relative motion in avian migration, particularly the role of physiology and energetics during flight, as well as shuttling behavior between Earth's surface and a detached solar niche. The shearwater case study focused on the migration dynamics of a single species, but analyses on a variety of avian and non-avian migratory species are necessary to better understand the dynamics of organisms tracking a detached climate niche. There remain many questions surrounding the compromise between an individual's need to be aligned with their climate niche and biological interactions between those individuals and surface species. For example, shearwaters feed on oceanic fishes, so they must regularly leave their detached niche and return to the surface to forage and feed. It is unclear how they balance these needs or which resource they track if prey and climate do not align in space.

I was constantly surprised throughout my dissertation research, as relative motion provided a much more powerful ecological mechanism than I had even imagined. Results show that adding motion to a population's habitat can drive that population to extinction but intervening with more motion in the form of assisted migration can reverse those consequences

and stabilize the population. I found that adding motion to the interactions between Earth's surface and the atmosphere above it means that small individuals can travel very long distances along very complicated paths by following a few simple rules. Consequently, a major question to address in the future is what else is moving in the environment and how strong are the effects of that movement on ecological patterns and processes?

6.4 Conclusions

Relative motion is an ecological mechanism with the power to alter population survivorship and to direct individual movement patterns. There is a long history of studying environmental and individual motion, but I present several new ways to conceptualize and measure the movement of multiple ecological components as they travel in different directions or different speeds relative to each other. This extra movement complexity changes the way populations operate and where individuals move throughout the year. I hope that this work stirs the imagination of future researches as they seek to identify, measure, and predict the full extent of the influence that relative motion has on shaping ecological phenomena.

Bibliography

- Agostinelli, C., and M. C. Agostinelli. 2015. Package “CircStats.” R Package Documentation.
<https://cran.r-project.org/web/packages/CircStats/CircStats.pdf>
- Ainley, D. G., E. Porzig, D. Zajanc, and L. B. Spear. 2015. Seabird flight behavior and height in response to altered wind strength and direction. *Marine Ornithology* 43:25–36.
- Aitken, S. N., and M. C. Whitlock. 2013. Assisted gene flow to facilitate local adaptation to climate change. *Annual Review of Ecology, Evolution, and Systematics* 44:367–388.
- Åkesson, S., and A. Hedenström. 2007. How migrants get there: migratory performance and orientation. *BioScience* 57:123–133.
- Åkesson, S., J. Morin, R. Muheim, and U. Ottosson. 2005. Dramatic orientation shift of white-crowned sparrows displaced across longitudes in the high arctic. *Current Biology* 15:1591–1597.
- Ákos, Z., M. Nagy, and T. Vicsek. 2008. Comparing bird and human soaring strategies. *Proceedings of the National Academy of Sciences of the United States of America* 105:4139–4143.
- Alerstam, T., M. Hake, and N. Kjellen. 2006. Temporal and spatial patterns of repeated migratory journeys by Ospreys. *Animal Behavior* 71:555–566.
- Alerstam, T., A. Hedenstrom, and S. Akesson. 2003. Long-distance migration: evolution and determinants. *Oikos* 103:247–260.
- Alerstam, T., M. Rosén, J. Bäckman, G. P. Ericson, and O. Hellgren. 2007. Flight speeds among bird species: allometric and phylogenetic effects. *PLoS Biology* 5:e197 1656–1662.
- Alfriend, K. T., and H. Yan. 2005. Evaluation and comparison of relative motion theories. *Journal of Guidance, Control, and Dynamics* 28:254–261.
- Angel, R. 2006. Feasibility of cooling the Earth with a cloud of small spacecraft near the inner

- Lagrange point (L1). Proceedings of the National Academy of Sciences of the United States of America 103:17184–17189.
- Angert, A. L., and D. W. Schemske. 2005. The evolution of species' distributions: reciprocal transplants across the elevation ranges of *Mimulus cardinalis* and *M. lewisii*. Evolution 59:1671–1684.
- Anstis, S., and S. Kaneko. 2014. Illusory drifting within a window that moves across a flickering background. i-Perception 5:585–588.
- Armstrong, C., H. Wilkinson, J. Meade, D. Biro, R. Freeman, and T. Guilford. 2013. Homing pigeons respond to time-compensated solar cues even in sight of the loft. PloS One 8:e63130 1–6.
- Arribas, M., A. Elipe, and M. Palacios. 2006. Quaternions and the rotation of a rigid body. Celestial Mechanics and Dynamical Astronomy 96:239–251.
- Asselin, H., S. Payette, M. J. Fortin, and S. Vallee. 2003. The northern limit of *Pinus banksiana* Lamb. in Canada: Explaining the difference between the eastern and western distributions. Journal of Biogeography 30:1709–1718.
- Aubin, I., C. M. Garbe, S. Colombo, C. R. Drever, D. W. Mckenney, C. Messier, J. Pedlar, and M. A. Saner. 2011. Why we disagree about assisted migration 1: Ethical implications of a key debate regarding the future of Canada's forests. The Forestry Chronicle 87:755–765.
- Bakken, G. S., and D. M. Gates. 1975. Heat-transfer analysis of animals: some implications for field ecology, physiology, and evolution. Perspectives of biophysical ecology. 12:255–290.
- Bakken, G. S., D. M. Gates, T. H. Strunk, and M. Kleiber. 1974. Linearized heat transfer relations in biology. Science 183:976–978.
- Barnosky, A. D., E. A. Hadly, and J. Bascompte. 2012. Approaching a state shift in Earth's biosphere. Nature 486:52–58.

- Barros, V. R., D. J. Dokken, K. J. Mach, M. D. Mastrandrea, T. E. Bilir, M. Chatterjee, K. L. Ebi, Y. O. Estrada, B. Genova, B. Girma, E. S. Kissel, A. N. Levy, S. MacCracken, P. R. Mastrandrea, and L. L. White. 2014. Summary for policymakers. *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, New York, United States..
- Barve, N., V. Barve, A. Jiménez-Valverde, A. Lira-Noriega, S. P. Maher, T. Peterson, J. Soberón, and F. Villalobos. 2011. The crucial role of the accessible area in ecological niche modeling and species distribution modeling. *Ecological Modelling* 222:1810–1819.
- Battley, P. F., N. Warnock, T. L. Tibbitts, R. E. Gill, T. Piersma, C. J. Hassell, D. C. Douglas, D. M. Mulcahy, B. D. Gartrell, R. Schuckard, D. S. Melville, and A. C. Riegen. 2012. Contrasting extreme long-distance migration patterns in bar-tailed godwits *Limosa lapponica*. *Journal of Avian Biology* 43:21–32.
- Bell, D. G., F. Kuehnel, C. Maxwell, R. Kim, K. Kasraie, T. Gaskins, P. Hogan, and J. Coughlan. 2007. NASA world wind: Open source GIS for mission operations. 2007 IEEE Aerospace Conference IEEE:1–9.
- Bellard, C., C. Bertelsmeier, and P. Leadley. 2012. Impacts of climate change on the future of biodiversity. *Ecology Letters* 15:365–377.
- Benito-Garzón, M., and J. F. Fernández-Manjarrés. 2015. Testing scenarios for assisted migration of forest trees in Europe. *New Forests* 48:979–994.
- Berestycki, H., and G. Chapuisat. 2013. Traveling fronts guided by the environment for reaction-diffusion equations. *Networks and Heterogeneous Media* 8:79–114.
- Berestycki, H., O. Diekmann, C. J. Nagelkerke, and P. A. Zegeling. 2009. Can a species keep

- pace with a shifting climate? *Bulletin of Mathematical Biology* 71:399–429.
- Berestycki, H., and G. Nadin. 2012. Spreading speeds for one-dimensional monostable reaction-diffusion equations. *Journal of Mathematical Physics* 53:1–23.
- Berestycki, H., and L. Rossi. 2008. Reaction-diffusion equations for population dynamics with forced speed I - The case of the whole space. *Discrete and Continuous Dynamical Systems* 21:41-67.
- Berthold, P., M. Kaatz, and U. Querner. 2004. Long-term satellite tracking of white stork (*Ciconia ciconia*) migration: constancy versus variability. *Journal of Ornithology* 145:356–359.
- Bird, J. M., and I. D. Hodkinson. 2005. What limits the altitudinal distribution of *Craspedolepta* species (*Sternorrhyncha: Psylloidea*) on fireweed? *Ecological Entomology* 30:510–520.
- Bishop, C. M. 2005. Circulatory variables and the flight performance of birds. *The Journal of Experimental Biology* 208:1695–16708.
- Bjorkstedt, E. P. 2012. Ricker model. *Encyclopedia of Theoretical Ecology* (eds Hastings, A., and L. Gross). pp. 632–636. University of California Press, Berkeley and Los Angeles, California, United States.
- Boström, J. E., S. Åkesson, and T. Alerstam. 2012. Where on earth can animals use a geomagnetic bi-coordinate map for navigation? *Ecography* 35:1039–1047.
- Bowlin, M. S., I. A. Bisson, J. Shamoun-Baranes, J. D. Reichard, N. Sapir, P. P. Marra, T. H. Kunz, D. S. Wilcove, A. Hedenström, C. G. Guglielmo, S. Åkesson, M. Ramenofsky, and M. Wikelski. 2010. Grand challenges in migration biology. *Integrative and Comparative Biology*. Oxford University Press, Oxford, United Kingdom.
- Bowman, D. 2014. Downloading and Analyzing Weather Forecast Data with rNOMADS using the GrADS-DODS system.

http://www.unc.edu/~haksaeng/rNOMADS/rNOMADS_dods_examples.pdf

- Bowman, D. 2016. Package “rNOMADS.” R Package Documentation. <https://cran.r-project.org/web/packages/rNOMADS/rNOMADS.pdf>
- Bozinovic, F., P. Calosi, and J. I. Spicer. 2011. Physiological correlates of geographic range in animals. *Annual Review of Ecology, Evolution, and Systematics* 42:155–179.
- Brock, T. D. 1981. Calculating solar radiation for ecological studies. *Ecological Modelling* 14:1–19.
- Brown, J. H. 1984. On the relationship between abundance and distribution of species. *The American Naturalist* 124:255–279.
- Brown, J. H., G. C. Stevens, D. M. Kaufman, D. M. Kaufmann, and H. Brown. 1996. The Geographic Range: Size, Shape, Boundaries, Structure, and Internal. *Annual Review of Ecology and Systematics* 27:597–623.
- Buckley, L. B., and J. G. Kingsolver. 2012. Functional and phylogenetic approaches to forecasting species’ responses to climate change. *Annual Review of Ecology, Evolution, and Systematics* 43:205–226.
- Budzynski, C. A., F. C. Dyer, and V. P. Bingman. 2000. Partial experience with the arc of the sun is sufficient for all-day sun compass orientation in homing pigeons, *Columba livia*. *The Journal of Experimental Biology* 203:2341–2348.
- Bull, H. 2011. The analemma dilemma solving visualization issues in astronomy using 3D graphics. <http://www.math.nus.edu.sg/aslaksen/projects/Hannalemma.pdf>
- Burrows, M. T., D. S. Schoeman, A. J. Richardson, J. G. Molinos, A. Hoffmann, L. B. Buckley, P. J. Moore, C. J. Brown, J. F. Bruno, C. M. Duarte, B. S. Halpern, O. Hoegh-Guldberg, C. V. Kappel, W. Kiessling, M. L. O’Connor, J. M. Pandolfi, C. Parmesan, W. J. Sydeman, S. Ferrier, K. J. Williams, and E. S. Poloczanska. 2014. Geographical limits to species-range

- shifts are suggested by climate velocity. *Nature* 507:492–495.
- Cahill, A. E., M. E. Aiello-Lammens, M. C. Fisher-Reid, X. Hua, C. J. Karanewsky, H. Yeong Ryu, G. C. Sbeglia, F. Spagnolo, J. B. Waldron, O. Warsi, and J. J. Wiens. 2012. How does climate change cause extinction? *Proceedings of the Royal Society B: Biological Sciences* 280:1–9.
- Carron, N. J. 2013. Rotating frame analysis of rigid body dynamics in space phasor variables. *American Journal of Physics* 81:518–526.
- Castellanos-Acuna, D., R. Lindig-Cisneros, and C. Saenz-Romero. 2015. Altitudinal assisted migration of Mexican pines as an adaptation to climate change. *Ecosphere* 6:1–16.
- Chang, C. H., S. C. Wang, and C. C. Wang. 2016. Exploiting moving objects: Multi-robot simultaneous localization and tracking. *IEEE Transactions on Automation Science and Engineering* 13:810–827.
- Chen, I. C., J. K. Hill, R. Ohlemüller, D. Roy, and C. D. Thomas. 2011. Rapid range shifts of species associated with high levels of climate warming. *Science* 333:1024–1026.
- Chevin, L. M., R. Lande, and G. M. Mace. 2010. Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. *PLoS Biology* 8:e1000357 1–8.
- Chown, S. L. 2004. Macrophysiology: large-scale patterns in physiological traits and their ecological implications. *Functional Ecology* 18:159–167.
- Chown, S. L., and K. J. Gaston. 2015. Macrophysiology - progress and prospects. *Functional Ecology* 30:2–15.
- Clarke, A., and K. J. Gaston. 2006. Climate, energy and diversity. *Proceedings of the Royal Society B: Biological Sciences* 273:2257–2266.
- Clusella-Trullas, S., J. S. Terblanche, T. M. Blackburn, and S. L. Chown. 2008. Testing the thermal melanism hypothesis: a macrophysiological approach. *Functional Ecology* 22:232–

- Collyer, M. L., J. S. Heilveil, and C. A. Stockwell. 2011. Contemporary evolutionary divergence for a protected species following assisted colonization. *PLoS One* 6:e22310 1–7.
- Colwell, R. K., and T. F. Rangel. 2009. Hutchinson’s duality: the once and future niche. *Proceedings of the National Academy of Sciences of the United States of America* 106:19651–19658.
- Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Cthalamus stellatus*. *Ecology* 42:710–723.
- Costantino, R. F., and R. A. Desharnais. 1991. Dynamics and the *Tribolium* model. Pages 214–237 *Population Dynamics and the Tribolium Model: Genetics and Demography*. Springer-Verlag, New York, New York, United States.
- Crozier, L. 2004. Warmer winters drive butterfly range expansion by increasing survivorship. *Ecology* 85:231–241.
- Cunningham, H. R., L. J. Rissler, L. B. Buckley, and M. C. Urban. 2016. Abiotic and biotic constraints across reptile and amphibian ranges. *Ecography* 39:1–8.
- Darwin, C. 1859. *On the origin of species by means of natural selection*. John Murray, London, United Kingdom.
- Dawson, A., and V. M. King. 2001. Photoperiodic control of seasonality in birds. *Journal of Biological Rhythms* 16:365–380.
- Dawson, M. R. 1991. The how and why of what went where in apparent motion: modeling solutions to the motion correspondence problem. *Psychological Review* 98:569–603.
- Desharnais, R. A. 2005. Population dynamics of *Tribolium*. *Structured-Population Models in Marine, Terrestrial, and Freshwater Systems* (eds Tuljapurkar, S., and H. Caswell). Pages 303–328. Springer US, New York, New York, United States.

- Dias, M. P., J. P. Granadeiro, and P. Catry. 2012. Do seabirds differ from other migrants in their travel arrangements? On route strategies of Cory's shearwater during its trans-equatorial journey. *PloS One* 7:e49376 1–7.
- Dobzhansky, T. 1950. Evolution in the tropics. *American Scientist* 38:209–221.
- Dokter, A. M., J. Shamoun-Baranes, M. U. Kemp, S. Tijm, and I. Holleman. 2013. High altitude bird migration at temperate latitudes: a synoptic perspective on wind assistance. *PloS One* 8:e52300 1–7.
- Dumroese, R. K., M. I. Williams, J. A. Stanturf, and J. B. S. Clair. 2015. Considerations for restoring temperate forests of tomorrow: forest restoration, assisted migration, and bioengineering. *New Forests* 46:947–964.
- Egevang, C., I. J. Stenhouse, R. A. Phillips, A. Petersen, J. W. Fox, and J. R. D. Silk. 2010. Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration. *Proceedings of the National Academy of Sciences of the United States of America* 107:2078–2081.
- Elton, C. S., and R. S. Miller. 1954. The ecological survey of animal communities: with a practical system of classifying habitats by structural characters. *The Journal of Ecology* 42:460–496.
- Ewers, R. M., and R. K. Didham. 2006. Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews of the Cambridge Philosophical Society* 81:117–142.
- Felícíσιμο, A. M., J. Muñoz, and J. González-Solis. 2008. Ocean surface winds drive dynamics of transoceanic aerial movements. *PloS One* 3:e2928 1–7.
- Fernández-Durán, J. J. 2007. Models for circular-linear and circular-circular data constructed from circular distributions based on nonnegative trigonometric sums. *Biometrics* 63:579–585.

- Ferrarini, A., A. Selvaggi, T. Abeli, J. M. Alatalo, S. Orsenigo, R. Gentili, and G. Rossi. 2016. Planning for assisted colonization of plants in a warming world. *Scientific Reports* 6:1–6.
- Ferriere, R., and S. Legendre. 2013. Eco-evolutionary feedbacks, adaptive dynamics and evolutionary rescue theory. *Philosophical Transactions of the Royal Society B: Biological Sciences* 368:1–14.
- Fordham, D. A., M. J. Watts, S. Delean, B. W. Brook, L. M. B. Heard, and C. M. Bull. 2012. Managed relocation as an adaptation strategy for mitigating climate change threats to the persistence of an endangered lizard. *Global Change Biology* 18:2743–2755.
- Freake, M. J., R. Muheim, and J. B. Phillips. 2006. Magnetic maps in animals: a theory comes of age? *The Quarterly Review of Biology* 81:327–347.
- Fuller, M. R., W. S. Seegar, and L. S. Schueck. 1998. Routes and travel rates of migrating Peregrine falcons *Falco peregrinus* and Swainson's hawks *Buteo swainsoni* in the western hemisphere. *Journal of Avian Biology* 29:433–440.
- Gaston, K. J. 2003. The structure and dynamics of geographic ranges. Oxford University Press, Oxford, United Kingdom.
- Gaston, K. J. 2009. Geographic range limits: achieving synthesis. *Proceedings of the Royal Society B: Biological Sciences* 276:1395–1406.
- Gaston, K. J., S. L. Chown, P. Calosi, J. Bernardo, D. T. Bilton, A. Clarke, S. Clusella-Trullas, C. K. Ghalambor, M. Konarzewski, L. S. Peck, W. P. Porter, H. O. Pörtner, E. L. Rezende, P. M. Schulte, J. I. Spicer, J. H. Stillman, J. S. Terblanche, and M. van Kleunen. 2009. Macrophysiology: a conceptual reunification. *The American Naturalist* 174:595–612.
- Gates, D. M. 1966. Spectral distribution of solar radiation at the Earth's surface. *Science* 151:523–529.
- Gates, D. M. 1980. Biophysical ecology. Springer-Verlag, New York, New York, United States.

- Gavrilov, V. M. 2014. Ecological and scaling analysis of the energy expenditure of rest, activity, flight, and evaporative water loss in Passeriformes and Non-Passeriformes in relation to seasonal migrations and to the occupation of boreal stations in high and moderate Latitude. *The Quarterly Review of Biology* 89:107–150.
- Geber, M. A., and V. M. Eckhart. 2005. Experimental studies of adaptation in *Clarkia xantiana*. II. Fitness variation across a subspecies border. *Evolution* 59:521–531.
- Gilbert, N. 1980. Comparative dynamics of a single-host aphid. I. The evidence. *The Journal of Animal Ecology* 49:351–369.
- Google development team. 2016. Google earth. <https://www.google.com/earth/>
- Green, B. S., C. Gardner, A. Linnane, and P. J. Hawthorne. 2010. The good, the bad and the recovery in an assisted migration. *PLoS One* 5:e14160 1–8.
- Greenberg, R., and P. P. Marra. 2005. Birds of two worlds: the ecology and evolution of migration. (R. Greenberg and P. P. Marra, Eds.). The Johns Hopkins University Press, Baltimore, Maryland, United States.
- Griffith, B., J. M. Scott, J. W. Carpenter, and C. Reed. 1989. Translocation as a species conservation tool: status and strategy. *Science* 245:477–480.
- Griffith, T. M., and M. A. Watson. 2006. Is evolution necessary for range expansion? Manipulating reproductive timing of a weedy annual transplanted beyond its range. *The American Naturalist* 167:153–164.
- Grinnell, J. 1917. The niche-relationship of the California Thrasher. *The Auk* 34:427–433.
- Grönroos, J., M. Green, and T. Alerstam. 2012. To fly or not to fly depending on winds: Shorebird migration in different seasonal wind regimes. *Animal Behavior* 83:1449–1457.
- Guilford, T. C., J. Meade, R. Freeman, D. Biro, T. Evans, F. Bonadonna, D. Boyle, S. Roberts, and C. M. Perrins. 2008. GPS tracking of the foraging movements of Manx Shearwaters

- Puffinus puffinus* breeding on Skomer Island, Wales. *Ibis* 150:462–473.
- Guilford, T., J. Meade, J. Willis, R. A. Phillips, D. Boyle, S. Roberts, M. Collett, R. Freeman, and C. M. Perrins. 2009. Migration and stopover in a small pelagic seabird, the Manx shearwater *Puffinus puffinus*: insights from machine learning. *Proceedings of the Royal Society B: Biological Sciences* 276:1215–1223.
- Gunia, D. A. 2016. Earth3d. <http://www.earth3d.org>
- gvSIG association. 2016. gvSIG. <http://www.gvsig.com/en>
- Gwinner, E. 1996. Circadian and circannual programs in avian migration. *Journal of Experimental Biology* 48:39–48.
- Hake, M., and N. Kjellén. 2001. Satellite Tracking of Swedish Ospreys *Pandion haliaetus*: Autumn Migration Routes and Orientation. *Journal of Avian Biology*. 32:47-56.
- Halpin, P. N., A. J. Read, E. Fujioka, and D. D. Best. 2009. OBIS-SEAMAP: the world data center for marine mammal, sea bird, and sea turtle distributions. *Oceanography* 22:104–115.
- Hamann, A., D. R. Roberts, Q. E. Barber, C. Carroll, and S. E. Nielsen. 2015. Velocity of climate change algorithms for guiding conservation and management. *Global Change Biology* 21:997–1004.
- Hampe, A., and R. J. Petit. 2005. Conserving biodiversity under climate change: the rear edge matters. *Ecology Letters* 8:461–467.
- Hancock, N., and R. Gallagher. 2014. How ready are we to move species threatened from climate change? Insights into the assisted colonization debate from Australia. *Austral Ecology* 39:830–838.
- Hedenström, A. 2009. Mechanics of bird flight: the power curve of a pigeon by CJ Pennycuik. *Journal of Experimental Biology* 212:1421–1422.
- Hesslerová, P., J. Pokorný, J. Brom, and A. Rejšková-Procházková. 2013. Daily dynamics of

- radiation surface temperature of different land cover types in a temperate cultural landscape: Consequences for the local climate. *Ecological Engineering* 54:145–154.
- Hewitt, N., N. Klenk, A. L. Smith, D. R. Bazely, N. Yan, S. Wood, J. I. MacLellan, C. Lipsig-Mumme, and I. Henriques. 2011. Taking stock of the assisted migration debate. *Biological Conservation* 144:2560–2572.
- Hoag, D. 1963. Apollo guidance and navigation - considerations of Apollo IMU gimbal lock. MIT Instrumentation Laboratory E-1344:1–64.
- Hoegh-Guldberg, O., L. Hughes, S. McIntyre, D. B. Lindenmayer, C. Parmesan, H. P. Possingham, and C. D. Thomas. 2008. Assisted colonization and rapid climate change. *Science* 321:345–346.
- Holt, R. D. 2009. Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. *Proceedings of the National Academy of Sciences of the United States of America* 106:19659–19659.
- Holyoak, M., and R. Casagrandi. 2008. Trends and missing parts in the study of movement ecology. *Proceedings of the National Academy of Sciences of the United States of America* 105:19060–19065.
- Huey, R. B., and J. G. Kingsolver. 1989. Evolution of thermal sensitivity of ectotherm performance. *Trends in Ecology & Evolution* 4:131–135.
- Hufbauer, R. A., M. Szucs, E. Kasyon, C. Youngberg, M. J. Koontz, C. Richards, T. Tuff, and B. A. Melbourne. 2015a. Three types of rescue can avert extinction in a changing environment. *Proceedings of the National Academy of Sciences of the United States of America* 112:10557–10562.
- Hufbauer, R. A., M. Szűcs, E. Kasyon, C. Youngberg, M. J. Koontz, C. Richards, T. Tuff, and B. A. Melbourne. 2015b. Reply to Wootton and Pfister: The search for general context should

- include synthesis with laboratory model systems. *Proceedings of the National Academy of Sciences of the United States of America* 12:E5904–E5904.
- Hummel, S. 2000. Height, diameter, and crown dimensions of *Cordia alliodora* associated with tree density. *Forest Ecology and Management* 127:31–40.
- Hutchinson, G. E. 1957. Concluding remarks. *Cold Spring Harbor Symposia* 22:415–427.
- Jackson, S. 2010. *Photoperiodism: The biological calendar*. Oxford University Press, Oxford, United Kingdom.
- Jenni, L., and M. Kéry. 2003. Timing of autumn bird migration under climate change: Advances in long-distance migrants, delays in short-distance migrants. *Proceedings of the Royal Society B: Biological Sciences* 270:1467–1471.
- Joly, J. L., and N. Fuller. 2009. Advising Noah: A legal analysis of assisted migration. *Environmental Law Reporter* 297:10413–10425.
- Jonsen, I. D., J. M. Flemmings, and R. A. Myers. 2005. Robust state – space modeling of animal movement data. *Ecology* 86:2874–2880.
- Jouventin, P., and H. Weimerskirch. 1990. Satellite-tracking of wandering albatrosses. *Nature* 343:746–748.
- Kabaz-Gomez, J. 2012. Rules for playing God: the need for assisted migration and new regulation. *Animal law* 19:111–149.
- Kearney, M., and W. P. Porter. 2004. Mapping the fundamental niche: physiology, climate, and the distribution of a nocturnal lizard. *Ecology* 85:3119–3131.
- Kearney, M., and W. P. Porter. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters* 12:1–17.
- Kishkinev, D., N. Chernetsov, and H. Mouritsen. 2010. A double-clock or jetlag mechanism is unlikely to be involved in detection of east–west displacements in a long-distance avian

- migrant. *The Auk* 127:773–780.
- Klaassen, M., B. J. Hoyer, B. A. Nolet, and W. A. Buttemer. 2012. Ecophysiology of avian migration in the face of current global hazards. *Philosophical Transactions of the Royal Society B: Biological Sciences* 367:1719–1732.
- Klaassen, R. H. G., T. Alerstam, P. Carlsson, J. W. Fox, and A. Lindström. 2011. Great flights by great snipes: long and fast non-stop migration over benign habitats. *Biology Letters* 7:833–5.
- Klenk, N. L., and B. M. H. Larson. 2013. A rhetorical analysis of the scientific debate over assisted colonization. *Environmental Science and Policy* 33:9–18.
- Kosenko, I. I. 1998. Integration of the equations of a rotational motion of a rigid body in quaternion algebra: The Euler case. *Journal of Applied Mathematics and Mechanics* 62:193–200.
- Kreyling, J., T. Bittner, A. Jaeschke, A. Jentsch, M. J. Steinbauer, D. Thiel, and C. Beierkuhnlein. 2011. Assisted colonization: A question of focal units and recipient localities. *Restoration Ecology* 19:433–440.
- La Sorte, F. A., and W. Jetz. 2012. Tracking of climatic niche boundaries under recent climate change. *Journal of Animal Ecology* 81:914–925.
- Landes, D. 2000. *Revolution in time: clocks and the making of the modern world*. The Belknap Press of Harvard University Press, Cambridge, Massachusetts, United States.
- Laube, P., and S. Imfeld. 2002. Analyzing relative motion within groups of trackable moving point objects. *International Conference on Geographic Information Science*:132–144.
- Laube, P., S. Imfeld, and R. Weibel. 2005. Discovering relative motion patterns in groups of moving point objects. *International Journal of Geographical Information Science* 19:639–668.

- Lawler, J. J., and J. D. Olden. 2011. Reframing the debate over assisted colonization. *Frontiers in Ecology and the Environment* 9:569–574.
- Lazarus, E. D., and B. J. McGill. 2014. Pushing the pace of tree species migration. *PloS One* 9:e105380 1–7.
- Lecomte, V. J., G. Sorci, S. Cornet, A. Jaeger, B. Faivre, E. Arnoux, M. Gaillard, C. Trouvé, D. Besson, O. Chastel, and H. Weimerskirch. 2010. Patterns of aging in the long-lived wandering albatross. *Proceedings of the National Academy of Sciences of the United States of America* 107:6370–6375.
- Lee, D. S. 2009. Mass die-offs of Greater Shearwaters in the western north Atlantic: Effects of weather patterns on mortality of a trans-equatorial migrant. *The Chat* 73:37–47.
- Leech, S. M., P. L. Almuedo, and G. O. Neill. 2011. Assisted migration: Adapting forest management to a changing climate. *BC Journal of Ecosystems and Management* 12:18–34.
- Leroux, S. J., M. Larrivée, V. Boucher-Ladonde, A. Hurford, J. Zuloaga, J. T. Keer, and F. Lutscher. 2013. Mechanistic models for the spatial spread of species under climate change. *Ecological Applications* 23:815–828.
- Levin, D. A., and K. Clay. 1984. Dynamics of synthetic *Phlox drummondii* populations at the species margin. *American Journal of Botany* 71:1040–1050.
- Liboff, A. R., and K. A. Jenrow. 2000. New model for the avian magnetic compass. *Bioelectromagnetics* 21:555–565.
- Liechti, F. 2006. Birds: blowin’ by the wind? *Journal of Ornithology* 147:202–211.
- Liechti, F., D. Ehrich, and B. Bruderer. 1996. Flight Behaviour of White Storks *ciconia ciconia* on their migration over southern israel. *Ardea* 84:3–13.
- Lisovski, S., C. M. Hewson, R. H. G. Klaassen, F. Korner-Nievergelt, M. W. Kristensen, and S. Hahn. 2012. Geolocation by light: Accuracy and precision affected by environmental

- factors. *Methods in Ecology and Evolution* 3:603–612.
- Loarie, S. R., P. B. Duffy, H. Hamilton, and G. P. Asner. 2009. The velocity of climate change. *Nature* 462:1052–1055.
- Lopez, J. 2015. Biodiversity on the brink: the role of “assisted migration” in managing endangered species threatened by rising. *Harvard Environmental Law Review* 39:157–190.
- Lunt, I. D., M. Byrne, J. J. Hellmann, N. J. Mitchell, S. T. Garnett, M. W. Hayward, T. G. Martin, E. McDonald-Maddden, S. E. Williams, and K. K. Zander. 2013. Using assisted colonization to conserve biodiversity and restore ecosystem function under climate change. *Biological Conservation* 157:172–177.
- Luschi, P., F. Papi, H. Liew, and E. Chan. 1996. Long-distance migration and homing after displacement in the green turtle (*Chelonia mydas*): a satellite tracking study. *Journal of Comparative Physiology* 178:447–452.
- Lynch, P. 2012. The equation of time and the analemma. *Bulletin of the Irish Mathematical Society* 69:47–56.
- MacArthur, R. H. 1972. *Geographical ecology: patterns in the distribution of species*. Princeton University Press, Princeton, New Jersey, United States.
- Makarieva, A. M., V. G. Gorshkov, D. Sheil, A. D. Nobre, and B. L. Li. 2013. Where do winds come from? A new theory on how water vapor condensation influences atmospheric pressure and dynamics. *Atmospheric Chemistry and Physics* 13:1039–1056.
- Mansfield, K. L., J. Wyneken, W. P. Porter, and J. Luo. 2014. First satellite tracks of neonate sea turtles redefine the “lost years” oceanic niche. *Proceedings of the Royal Society B: Biological Sciences* 281:20133039.
- Marble development team. 2016. Marble geographical information system.
- Marsico, T. D., and J. J. Hellmann. 2009. Dispersal limitation inferred from an experimental

- translocation of *Lomatium* (*Apiaceae*) species outside their geographic ranges. *Oikos* 118:1783–1792.
- Martell, M., C. Henny, P. Nye, and M. J. Solensky. 2001. Fall migration routes, timing, and wintering sites of North American Ospreys as determined by satellite telemetry. *The Condor* 103:715–724.
- Mateos-Rodríguez, M., and B. Bruderer. 2012. Flight speeds of migrating seabirds in the Strait of Gibraltar and their relation to wind. *Journal of Ornithology* 153:881–889.
- Mathot, S. 2012. Relative motion in Super Mario land. <http://www.cogsci.nl/illusions/relative-motion-in-super-mario-land>
- Matthews, G. V. T. 1953. Sun navigation in homing pigeons. *Journal of Experimental Biology* 243-267.
- McInerny, G. J., and R. S. Etienne. 2012. Stitch the niche - a practical philosophy and visual schematic for the niche concept. *Journal of Biogeography* 39:2103–2111.
- McKinnon, L., P. A. Smith, E. Nol, J. L. Martin, F. I. Doyle, K. F. Abraham, H. G. Gilchrist, R. I. G. Morrison, and J. Bêty. 2010. Lower predation risk for migratory birds at high latitudes. *Science* 327:326–327.
- McLachlan, J. S., J. J. Hellmann, and M. W. Schwartz. 2007. A framework for debate of assisted migration in an era of climate change. *Conservation Biology* 21:297–302.
- McLane, S. C., and S. N. Aitken. 2012. Whitebark pine (*Pinus albicaulis*) assisted migration potential: Testing establishment north of the species range. *Ecological Applications* 22:142–153.
- Meeus, J. H. 1998. *Astronomical algorithms*. 1st English. Willmann-Bell Inc., Richmond, Virginia, United States.
- Melbourne, B. A., and A. Hastings. 2008. Extinction risk depends strongly on factors

- contributing to stochasticity. *Nature* 454:100–103.
- Melbourne, B. A., and A. Hastings. 2009. Highly variable spread rates in replicated biological invasions: fundamental limits to predictability. *Science* 325:1536–1539.
- Méndez, V., D. Campos, and F. Bartumeus. 2014. *Stochastic foundations in movement ecology*. Springer, Berlin and Heidelberg, Germany.
- Meyer, G. 1966. On use of Euler's theorem on rotations for the synthesis of attitude control systems. NASA Technical Note.
<http://ntrs.nasa.gov/archive/nasa/casi.ntrs.nasa.gov/19660027747.pdf>
- Mishra, P. K., and G. P. Saroha. 2016. A study on classification for static and moving object in video surveillance system. *International Journal of Image, Graphics and Signal Processing* 5:76–82.
- Moir, M. L., P. A. Vesk, K. E. C. Brennan, R. Poulin, L. Hughes, D. A. Keith, M. A. . McCarthy, and D. J. Coates. 2012. Considering extinction of dependent species during translocation, ex situ conservation, and assisted migration of threatened hosts. *Conservation Biology* 26:199–207.
- Morales, J. M., D. T. Haydon, J. Frair, K. E. Holsinger, and J. M. Fryxell. 2004. Extracting more out of relocation data: Building movement models as mixtures of random walks. *Ecology* 85:2436–2445.
- Morris, S. R., D. W. Holmes, and M. E. Richmond. 1996. A ten-year study of the stopover patterns of migratory passerines during fall migration on Appledore Island, Maine. *The Condor* 98:395–409.
- Mouritsen, H., and O. Mouritsen. 2000. A mathematical expectation model for bird navigation based on the clock-and-compass strategy. *Journal of Theoretical Biology* 207:283–291.
- Nathan, R., W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, and P. E. Smouse. 2008.

- A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences of the United States of America* 105:19052–19059.
- National Oceanic and Atmospheric Administration. 2016. Science on a sphere.
- Neilson, R. P., and L. H. Wullstein. 1983. Biogeography of two southwest American Oaks in relation to atmospheric dynamics. *Journal of Biogeography* 10:275–297.
- Newton, I., and L. Dale. 1996a. Relationship between migration and latitude among west European birds. *Journal of Animal Ecology* 65:137–146.
- Newton, I., and L. C. Dale. 1996b. Bird migration at different latitudes in eastern North America. *The Auk* 113:626–635.
- Nichols, W. J., A. Resendiz, J. A. Seminoff, and B. Resendiz. 2000. Transpacific migration of a loggerhead turtle monitored by satellite telemetry. *Bulletin of Marine Science* 67:937–947.
- Nikolov, N. T., and K. F. Zeller. 1992. A solar radiation algorithm for ecosystem dynamic models. *Ecological Modelling* 61:149–168.
- OSSIM development team. 2016. OSSIM Planet: advanced image processing and geospatial data fusion. <https://trac.osgeo.org/ossim/>
- Pagnozzi, D., and J. D. Biggs. 2014. Dynamical analysis of an orbiting three-rigid-body system. 10th International Conference on Mathematical Problems in Engineering, Aerospace, and Sciences: ICNPAA 1637:786-795.
- Palais, B., and R. Palais. 2007. Euler's fixed point theorem: The axis of a rotation. *Journal of Fixed Point Theory and Applications* 2:1661–7738.
- Papi, F. 2001. Animal navigation at the end of the century: A retrospect and a look forward. *Italian Journal of Zoology* 63:171–180.
- Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology and Systematics* 37:637–669.

- Parmesan, C., M. T. Burrows, C. M. Duarte, E. S. Poloczanska, A. J. Richardson, D. S. Schoeman, and M. C. Singer. 2013. Beyond climate change attribution in conservation and ecological research. *Ecology Letters* 16:58–71.
- Parmesan, C., S. Gaines, L. Gonzalez, D. M. Kaufman, J. Kingsolver, T. A. Peterson, and R. Sagarin. 2005. Empirical perspectives on species borders: from traditional biogeography to global change. *Oikos* 108:58–75.
- Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42.
- Pearman, P. B., and A. Guisan. 2008. Niche dynamics in space and time. *Trends in Ecology & Evolution* 23:149–158.
- Pearson, R. G. 2006. Climate change and the migration capacity of species. *Trends in Ecology & Evolution* 21:111–113.
- Pedlar, J. H., D. W. Kenney, I. Aubin, T. Beardmore, J. Beaulieu, L. Iverson, G. A. O. Neill, R. S. Winder, and C. Ste-Marie. 2012. Placing forestry in the assisted migration debate. *BioScience* 62:835–842.
- Penhallurick, J., and M. Wink. 2004. Analysis of the taxonomy and nomenclature of the *Procellariiformes* based on complete nucleotide sequences of the mitochondrial cytochrome b gene. *Emu* 104:125–147.
- Pennycuik, C. J. 1960. The physical basis of astronavigation in birds: theoretical considerations. *Journal of Experimental Biology* 37:573–593.
- Pennycuik, C. J. 1996. Stress and strain in the flight muscles as constraints on the evolution of flying animals. *Journal of Biomechanics* 29:577–581.
- Pennycuik, C. J. 1998. Computer simulation of fat and muscle burn in long-distance bird migration. *Journal of Theoretical Biology* 191:47–61.

- Pennycuick, C. J. 2002. Gust soaring as a basis for the flight of petrels and albatrosses (*Procellariiformes*). *Avian Science* 2:1–12.
- Pennycuick, C. J. 2003. The concept of energy height in animal locomotion: Separating mechanics from physiology. *Journal of Theoretical Biology* 224:189–203.
- Pennycuick, C. J. 2006. In search of a biological constant: the maximum isometric stress of vertebrate skeletal muscle deduced from the flight performance of a Whooper swan. Supplement to *Modelling the Flying Bird*. pp. 1–23. Elsevier, London, United Kingdom.
- Pennycuick, C. J. 2008a. *Modelling the flying bird*. Theoretical Ecology Series. Elsevier, London, United Kingdom.
- Pennycuick, C. J. 2008b. Fuel economy in cross-country soaring flight. Supplement to *Modelling the Flying Bird* 5:1–13. Elsevier, London, United Kingdom.
- Pennycuick, C. J., T. Bradbury, Ó. Einarsson, and M. Owen. 1999. Response to weather and light conditions of migrating Whooper Swans *Cygnus cygnus* and flying height profiles, observed with the Argos satellite system. *Ibis* 141:434–443.
- Perpinan Lmigueiro, O. 2010. Package “solaR.” R Package Documentation. <https://cran.r-project.org/web/packages/solaR/solaR.pdf>
- Porter, W. P., and D. M. Gates. 1969. Thermodynamic equilibria of animals with environment. *Ecological Monographs* 39:227–244.
- Porter, W. P., and J. L. Sabo. 2002. Physiology on a landscape scale: plant-animal interactions. *Integrative and Comparative Biology* 42:431–453.
- Porter, W. P., and C. R. Tracy. 1983. Biophysical analyses of energetics, time-space utilization, and distributional limits. *Lizard Ecology: Studies of a model organism* 55–83.
- Prince, S. D., R. N. Carter, and K. J. Dancy. 1985. The geographical distribution of Prickly Lettuce (*Lactuca Serriola*): II. Characteristics of populations near its distribution limit in

- Britain. *Journal of Ecology* 73:39–48.
- QGIS development team. 2016. QGIS geographic information system. Open Source Geospatial Foundation Project. <http://www.qgis.org/en/site/>
- Qie, L., S. D. Howard, S. L. H. Lim, and N. S. Sodhi. 2012. Assisted dispersal of tropical dung beetles. *The Raffles Bulletin of Zoology* 25:155–160.
- Reda, I. 2010. Solar eclipse monitoring for solar energy applications using the solar and moon position algorithms. http://digitalscholarship.unlv.edu/renew_pubs/17/?utm_source=digitalscholarship.unlv.edu%2Fnew_pubs%2F17&utm_medium=PDF&utm_campaign=PDFCoverPages
- Reda, I., and A. A. Nrel. 2003. Solar position algorithm for solar radiation applications. *Solar Energy* 76:577–589.
- Regan, H. M., A. D. Syphard, J. Franklin, R. M. Swab, L. Markovchick, A. L. Flint, L. E. Flint, and P. H. Zedler. 2012. Evaluation of assisted colonization strategies under global change for a rare, fire-dependent plant. *Global Change Biology* 18:936–947.
- Ricker, W. E. 1954. Stock and recruitment. *Journal of Fisheries* 11.5:559–623.
- Ristow, D., P. Berthold, and D. Hashmi. 2000. Satellite tracking of Cory's shearwater migration. *Condor* 102:696–699.
- Roderick, M. L. 2006. The ever-flickering light. *Trends in Ecology and Evolution* 21:3–5.
- Ronconi, R. A., P. G. Ryan, and Y. Ropert-Coudert. 2010. Diving of great shearwaters (*Puffinus gravis*) in cold and warm water regions of the South Atlantic Ocean. *PloS One* 5:e15508 1–7.
- Roques, L., A. Roques, H. Berestycki, and A. Kretzschmar. 2008. A population facing climate change: joint influences of Allee effects and environmental boundary geometry. *Population Ecology* 50:215–225.

- Rykaczewski, R. R., and D. M. Checkley. 2008. Influence of ocean winds on the pelagic ecosystem in upwelling regions. *Proceedings of the National Academy of Sciences of the United States of America* 105:1965–1970.
- Safi, K., B. Kranstauber, R. Weinzierl, and L. Griffin. 2013. Flying with the wind: Scale dependency of speed and direction measurements in the modelling of wind support in avian flight. *Movement Ecology* 1:1–13.
- Sanders, R. 2005. Static magnetic fields: animal studies. *Progress in Biophysics and Molecular Biology* 87:225–239.
- Sanford, E., S. B. Holzman, R. A. Haney, D. M. Rand, D. Mark, and B. Holzman. 2006. Larval tolerance, gene flow, and the northern geographic range limit of Fiddler Crabs. *Ecology* 87:2882–2894.
- Sansilvestri, R., N. Frascaria-Lacoste, and J. F. Fernández-Manjarrés. 2015. Reconstructing a deconstructed concept: Policy tools for implementing assisted migration for species and ecosystem management. *Environmental Science and Policy* 51:192–201.
- Sawyer, H., and M. J. Kauffman. 2011. Stopover ecology of a migratory ungulate. *Journal of Animal Ecology* 80:1078–1087.
- Sawyer, H., M. J. Kauffman, R. M. Nielson, and J. S. Horne. 2016. Identifying and Prioritizing Ungulate Migration Routes for Landscape-Level Conservation. *Ecological Applications* 19:2016–2025.
- Schemske, D. W., G. G. Mittelbach, H. V. Cornell, J. M. Sobel, and K. Roy. 2009. Is there a latitudinal gradient in the Importance of biotic interactions? *Annual Review of Ecology, Evolution, and Systematics* 40:245–269.
- Schmaljohann, H., B. Bruderer, and F. Liechti. 2008. Sustained bird flights occur at temperatures far beyond expected limits. *Animal Behavior* 76:1133–1138.

- Schwab, A. L., and J. P. Meijaard. 2006. How to draw Euler angles and utilize Euler parameters. Proceedings of IDETC/CIE 2006 ASME 2006 International Design Engineering Technical Conferences & Computers and Information in Engineering Conference DETC2006-9:1–7.
- Seddon, P. J. 2010. From reintroduction to assisted colonization: moving along the conservation translocation spectrum. *Restoration Ecology* 18:796–802.
- Shaffer, S. A., Y. Tremblay, H. Weimerskirch, D. Scott, D. R. Thompson, P. M. Sagar, H. Moller, G. a Taylor, D. G. Foley, B. a Block, and D. P. Costa. 2006. Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. *Proceedings of the National Academy of Sciences of the United States of America* 103:12799–12802.
- Shamoun-Baranes, J., A. Baharad, P. Alpert, P. Berthold, Y. Yom-Tov, Y. Dvir, and Y. Leshem. 2003. The effect of wind, season, and latitude on the migration speed of white storks *Ciconia ciconia*, along the eastern migration route. *Journal of Avian Biology* 34:97–104.
- Shaw, A. K., and I. D. Couzin. 2013. Migration or residency? The evolution of movement behavior and information usage in seasonal environments. *The American Naturalist* 181:114–124.
- Shepard, E. L., R. P. Wilson, W. G. Rees, E. Grundy, S. A. Lambertucci, and S. B. Vosper. 2013. Energy landscapes shape animal movement ecology. *The American Naturalist* 182:298–312.
- Sidoli, N. 2005. Heron’s Dioptra 35 and analemma methods: An astronomical determination of the distance between two cities. *Centaurus* 47:236–258.
- Sinervo, B., F. Mendez-de-la-Cruz, D. B. Miles, B. Heulin, E. Bastiaans, M. Villagran-Santa Cruz, R. Lara-Resendiz, N. Martinez-Mendez, M. L. Calderon-Espinosa, R. N. Meza-Lazaro, H. Gadsden, L. J. Avila, M. Morando, I. J. De la Riva, P. V. Sepulveda, C. F. D. Rocha, N. Ibarguengoytia, C. A. Puntriano, M. Massot, V. Lepetz, T. A. Oksanen, D. G.

- Chapple, A. M. Bauer, W. R. Branch, J. Clobert, and J. W. Sites. 2010. Erosion of lizard diversity by climate change and altered thermal niches. *Science* 328:894–899.
- South, A. 1999. Dispersal in spatially explicit population models. *Conservation Biology* 13:1039–1046.
- Spedding, G. R., and C. J. Pennycuik. 2001. Uncertainty calculations for theoretical flight power curves. *Journal of Theoretical Biology* 208:127–139.
- Spotila, J. R., P. W. Lommen, G. S. Bakken, and D. M. Gates. 1973. A mathematical model for body temperatures of large reptiles: Implications for dinosaur ecology. *The American Naturalist* 107:391–404.
- Stutchbury, B. J. M., S. A. Tarof, T. Done, E. Gow, P. M. Kramer, J. Tautin, J. W. Fox, and V. Afanasyev. 2009. Tracking long-distance Songbird Migration by Using Geolocators. *Science* 323:896–896.
- Szucs, M., B. A. Melbourne, T. Tuff, and R. A. Hufbauer. 2014. The roles of demography and genetics in the early stages of colonization. *Proceedings of the Royal Society B: Biological Sciences* 281:1–8.
- Taghert, P. H. 2011. Circadian pacemakers: how clock properties relate to their cellular properties. *Current biology* 21:R894–R896.
- Taylor, C. M., and D. R. Norris. 2010. Population dynamics in migratory networks. *Theoretical Ecology* 3:65–73.
- The southern cross Peregrine project. 2016. Island Girl. http://www.frg.org/track_pefa12.html
- Thomas, C. D., A. Cameron, and R. E. Green. 2004. Extinction risk from climate change. *Nature* 427:145–148.
- Tobalske, B., and K. Dial. 1996. Flight kinematics of black-billed magpies and pigeons over a wide range of speeds. *The Journal of Experimental Biology* 199:263–280.

- Urli, M., S. Delzon, A. Eyermann, V. Couallier, R. Garcia-Valdes, M. A. Zavala, and A. J. Porte. 2014. Inferring shifts in tree species distribution using asymmetric distribution curves: A case study in the Iberian mountains. *Journal of Vegetation Science* 25:147–159.
- Van Loon, E. E., and J. Shamoun-Baranes. 2011. Understanding soaring bird migration through interactions and decisions at the individual level. *Journal of Theoretical Biology* 270:112–126.
- Vardanis, Y. 2011. Individuality in bird migration: routes and timing. *Biology letters* 7:502–505.
- Van der Veken, S., P. De Frenne, L. Baeten, E. Van Beek, K. Verheyen, and M. Hermy. 2012. Experimental assessment of the survival and performance of forest herbs transplanted beyond their range limit. *Basic and Applied Ecology* 13:10–19.
- Victor III, B., E. C. Hellgren, M. W. Sears, and R. W. Moody. 2012. High-resolution niche models via a correlative approach: Comparing and combining correlative and process-based information. *Ecological Modelling* 237-238:63–73.
- Viet, M. 2010. Migration and foraging ecology of Greater Shearwater. OBIS-SEAMAP. <http://seamap.env.duke.edu/dataset/550/html>
- Villard, M. A., and J. P. Metzger. 2014. Beyond the fragmentation debate: A conceptual model to predict when habitat configuration really matters. *Journal of Applied Ecology* 51:309–318.
- Wadgymar, S. M., M. N. Cumming, and A. E. Weis. 2015. The success of assisted colonization and assisted gene flow depends on phenology. *Global Change Biology* 21:3786–3799.
- Walcott, C., and M. C. Michener. 1971. Sun navigation in homing pigeons—attempts to shift sun coordinates. *Journal of Experimental Biology* 54:291–316.
- Walther, G. 2004. Plants in a warmer world. *Perspectives in Plant Ecology Evolution and Systematics* 6:169–185.

- Walther, G. R., E. Post, P. Convey, and A. Menzel. 2002. Ecological responses to recent climate change. *Nature* 416:389–395.
- Warham, J. 1977. Wing loadings, wing shapes, and flight capabilities of *procellariiformes*. *New Zealand Journal of Zoology* 4:73–83.
- Weimerskirch, H., M. Louzao, S. De Grissac, and K. Delord. 2012. Changes in wind pattern alter albatross distribution and life-history traits. *Science* 335:211–214.
- Wiens, J. J., D. D. Ackerly, A. P. Allen, B. L. Anacker, L. B. Buckley, H. V. Cornell, E. I. Damschen, J. T. Davies, J. A. Grytnes, S. P. Harrison, B. A. Hawkins, R. D. Holt, C. M. McCain, and P. R. Stephens. 2010. Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters* 13:1310–1324.
- Wikelski, M., M. Hau, and J. C. Wingfield. 2000. Seasonality of reproduction in a neotropical rain forest bird. *Ecology* 81:2458–2472.
- Williams, M., and K. Dumroese. 2013. Preparing for climate change: Forestry and assisted migration. *Journal of Forestry* 111:287–297.
- Williamson, C. E., and P. J. Neale. 2001. Beneficial and detrimental effects of UV on aquatic organisms: implications of spectral variation. *Ecological Applications* 11:1843–1857.
- Willis, S. G., J. K. Hill, C. D. Thomas, D. B. Roy, R. Fox, D. S. Blakeley, and B. Huntley. 2009. Assisted colonization in a changing climate: a test-study using two UK butterflies. *Conservation Letters* 2:45–51.
- Wiltschko, R. 2003. Avian navigation: from historical to modern concepts. *Animal Behavior* 65:257–272.
- Wiltschko, W., and U. Munro. 2006. Bird navigation: what type of information does the magnetite-based receptor provide? *Proceedings of the Royal Society B: Biological Sciences* 273:2815–2820.

- Wiltschko, W., and R. Wiltschko. 1988. Magnetic versus celestial orientation in migrating birds. *Trends in Ecology and Evolution* 3:13-15.
- Woodward, F. I. 1975. Climatic control of the altitudinal distribution of *Sedum rosea* (L.) Scop. and *Sedum telephium* L. II. The analysis for plant growth in controlled environments. *New Phytologist* 74:335–348.
- Woodward, F. I. 1990. Global change: Translating plant ecophysiological responses to ecosystems. *Trends in Ecology and Evolution* 5:308–311.
- Yahya, S. M. 2003. Fundamentals of compressible flow: SI units with aircraft and rocket propulsion. New Age International (P) Limited Publishers, New Delhi, India.
- Yeow, T. S. 2001. The analemma for latitudinally-challenged people. National University of Singapore Publication 2. <http://www.math.nus.edu.sg/aslaksen/projects/tsy.pdf>
- Zhou, Y., and M. Kot. 2010. Discrete-time growth-dispersal models with shifting species ranges. *Theoretical Ecology* 4:13–25.