

# Mathematical Models of Decision Processes for Dispersing Animals

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*Academic*

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## Preface

Each chapter in this expository paper considers a mathematical model of an aspect of animal behavior, and how it affects the patterns of movement across and within a landscape. These models are all directly or indirectly related to questions in either Behavioral Ecology or Landscape Ecology, or both. I first learned about Ecologists' efforts to connect Landscape Ecology with Behavioral Ecology when Dr. Judy Stamps, Emerita of the University of California, Davis, visited the IGERT colloquium at OSU in the Fall of 2008.

Landscape Ecology focuses on neighborhoods, groups, and populations of animals and plants, which are all linked together by the process of dispersal. By contrast, Behavioral Ecology focuses on decisions made by individual dispersers – how they forage for food, select mates, and settle in habitat. Stamps ([27], [18], [26]) argues that this last process – the process of habitat selection – was one way to bridge the gap between Landscape Ecology and Behavioral Ecology. To this end, we introduce and develop three individual-based models of dispersal.

Most of our efforts have gone into Chapter 1, where we develop a Stochastic Dynamic Programming model of habitat selection in natively-dispersing brush mice. The individual choices that brush mice make to investigate, return to, and eventually settle in different habitat sites across the landscape are shown to affect their overall patterns of dispersal: the average time spent on this process, the quality of the site achieved by the process, and the length of the refractory period – the time during which an individual will not settle in response to cues from a habitat.

In Chapter 2, we consider a challenge offered by Brillinger [3], regarding the simulation of animal movement constrained to a bounded landscape. As an example model of constrained animal motion, we consider a diffusion model constrained to an interval and study its properties and the conditions on them, for example the conditions for ergodicity and the existence of a stationary distribution. Determining these conditions is an important first step if one wants to make any statistical comparison to data from animal movement.

Seeley, Visscher, & Passino [22] document a fascinating example of democratic animal behavior. This example is in the swarming behavior of honeybees selecting a new site for a colony which has split off from its home. The process by which they make their decision is highly democratic, and Seeley himself has started employing a version of it in departmental meetings. In Chapter 3, we consider a model to study the efficacy of swarms using a range of methods to distribute and deploy their scouts for search, and with different memory capacities. We are aware of one other simulation model of this behavior [15], which we introduce for the purposes of comparing and contrasting with our own. We present preliminary results, but note that this chapter is included more as a reference point for future work rather than for the presented, preliminary results.



# Chapter 1

## Predation risk drives habitat selection behaviors

### 1.1 Introduction

The habitat that an individual animal selects impacts its ability to find food, stay safe, and choose a suitable mate. Species as diverse as brush mice [18], flying squirrels [23], birds [16], planktonic larvae [28], [20], and fruit flies [27] have demonstrated properties of dispersal that seem to indicate some level of sophistication in the methods they employ to find suitable habitat. The refractory period, the time during which a natively dispersing animal does not settle in response to cues from potential habitats (though it may respond in other ways), is just one such example.

Variations in the patterns of dispersal have been observed empirically for brush mice [18] and flying squirrels [23], by comparing their behavior to that of simulated decision processes, which were originally developed to model mate selection. In this context, Luttbeg [17] has provided several arguments for why individual behaviors may differ, based on the total amount of time for search, the cost of searching, the number of options available, etc.

The current swell of research interest in animal personality (see [25], [5], and [24]) may also improve our understanding of why there is so much variation within species in their selection behavior. In this paper, we summarize the modeling approaches researchers have taken to model uncertainty and stochasticity in the landscape, as well as an individual's decision processes, and the functional relationships that connect them. We develop a Stochastic Dynamic Programming (SDP) model of natively-dispersing brush mice prospecting for habitat, in order to suggest how differences in animal personality may influence variation in search behavior.

#### 1.1.1 Optimal Stopping Theory

Optimal stopping theory may offer insights into the questions of how animals should optimally search for habitats. This was first pointed out by Dombrovsky and Perrin [7], who explained how mate search was a problem that could be approached by reformulating it in terms of the Best-Choice Problem. In this subsection, we explain what the Best-Choice Problem is and its solution, and then summarize the many extensions that have been made to the original Best-Choice problem. The extensions we offer are those particular examples with different assumptions that may be more applicable to questions regarding habitat selection.

In the Best Choice Problem, an individual must select the best of  $T$  options and views each online, meaning options are viewed one-at-a-time (equivalently they have total time for search  $T$ ),

and at each moment the selector must decide whether to select or discard the option. Discarded options cannot be retrieved. It can be shown, in [8] for instance, that the manager's optimal strategy is to wait until the  $\lceil T/e^{th} \rceil$  interview, and then select the next candidate who is better than all those interviewed so far. This strategy is called the *optimal stopping rule* or *optimal stopping time*. We will call it the *optimal stopping rule*.

We also introduce some standard notation to coordinate our discussion below. Let  $x_t$  be the relative rank of the site viewed at time  $t$ ,  $t = 1, \dots, T$ . Let  $a_t$  be the absolute rank of the site viewed at time  $t$ . Note that  $x_t$  can be calculated by anyone who has viewed the first  $n$  sites, but  $a_t$  requires full knowledge of the set of sites. For example, if  $T = 3$ , if the individual observes sites in the order  $(a_t)_{t=1}^3 = (2, 1, 3)$ , then the relative ordering is  $(x_t)_{t=1}^3 = (1, 1, 3)$ .

Kubicki [14] generalizes the best-choice problem from the assumed linear ordering to a partial ordering. He defines this through a nearest-neighbor ordering, such that a set  $P$  is to be examined, and is now equipped with a partial order,  $\prec$  and at a moment  $t$  the selector only knows candidates  $x_{\pi_1}, \dots, x_{\pi_t}$ , and their relative ranks from the induced order  $\prec \cap \{x_{\pi_1}, \dots, x_{\pi_t}\}^2$ . And, if two candidates are separated by a value greater than 1, they cannot be compared until the selector observes all candidates of intermediate rank. This could relate to species or groups within a species that have difficulty comparing very disparate types of habitats.

However, the goal of Kubicki's model is still to pick the single best site. It is possible that a habitat selection strategy which optimizes the probability of finding a habitat with minimal rank (e.g. first to last) could perform better than the Best-Choice problem under some conditions. To this effect, we introduce two extensions to the Best-Choice Problem.

Let  $a_t^T$  be the absolute rank of the site selected at some time,  $t$ , from a set of  $T$  sites. Chow, Moriguti, Robbins, & Samuels [4] derive a selection strategy for the goal of minimizing the expected absolute rank of the site selected by the process. This is solved, with the limiting absolute rank as the number of sites grows asymptotically,

$$\lim_{T \rightarrow \infty} \mathbb{E}(a_{\tau_T}^T) = \prod_{j=1}^{\infty} \left(1 + \frac{2}{j}\right)^{1/(j+1)} = 3.869,$$

where  $a_{\tau_T}^T$  is the absolute rank (1st, 2nd, 3rd, ...) of the site achieved by optimal search (and therefore stopping at the optimal stopping time,  $\tau^T$ ). Therefore, as the number of sites grows large, the expected rank of the selected site is just better than 4<sup>th</sup> place. This means that even with an incredibly large number of sites to choose from, if one follows this optimal stopping rule then they can expect to get about the 4th best site. To explore how this can be so, we consider their optimal stopping rule.

Chow et. al. construct the sequence  $s_t$  of stopping times, such that if  $t \geq s_i$ , one settles in a site if it is at least the  $i^{th}$  best site of those seen so far. We consider the sequence  $c_1, \dots, c_T$ , where  $c_i$  is the minimal possible expected absolute rank of the quality of the site selected if the individual settles after  $s_i$ , which they derive by backward induction:

$$\begin{aligned} c_T &= \mathbb{E}[a_T | x_T = j] = x_T \\ c_{T-1} &= \mathbb{E}[a_T | x_T = j] = \frac{1}{T} \sum_{j=1}^T j = \frac{T+1}{2} \\ c_{T-2} &= \mathbb{E}[\min \{ \mathbb{E}[a_{T-1} | x_{T-1} = j], c_{T-1} \}] = \mathbb{E} \left[ \min \left\{ \frac{T+1}{i+1} y_i, c_i \right\} \right] \\ &\vdots = \vdots \end{aligned}$$

This forms an increasing sequence (in decreasing  $t$ ). Therefore as  $t$  increases, the minimal possible expected absolute rank decreases, so the selector is rewarded more for waiting more.

The Gusein-Zade problem [11] also addresses our concerns regarding the unrealistic goal of selecting the best element. This problem is identical to the Best-Choice problem, except the choice is successful if the selected site is one of the  $r$  best, not just the best. They consider a general utility function  $g_t(x)$  which may depend on time. Note that if  $g_t(x_t) = 1$  for  $x_t = 1$  and zero otherwise, we recover the classical Secretary Problem.

Gusein-Zade derived the optimal stopping time for the special case where  $g_t(x) = 1$  if  $x$  is one of the  $r$  best sites, and  $g_t(x) = 0$  otherwise. As in Chow, et. al., Gusein-Zade constructs a monotonically decreasing function  $c_t$  such that the individual stops at the first  $t$  such that  $c_t \leq g_t(x_t)$ . He then shows that there exists a sequence of stopping times,  $s_t$ , such that  $c_{s_t} \leq g_{s_t}(x_{s_t})$ . This prescribes the optimal stopping rule.

Denote the probability of success of an individual using the optimal stopping rule by  $p_T^r$  and  $\varepsilon_t^r = \lim_{T \rightarrow \infty} s_t(T, r)/T$ , which compares the asymptotic growth of the optimal stopping rule with linear growth. We note that only the first  $r$  terms of the  $\varepsilon_t^r$  sequence (in  $t$ , that is) are of interest. This is because only the top  $r$  sites are wanted, and it can be shown [11] that the stopping times regarding these undesirable sites satisfy  $s_t(T, r) = T$  for  $t > r$ .

Gusein-Zade shows also that  $\lim_{r, T \rightarrow \infty} p_T^r = 1$  and that if the individual wants one of the top  $r$  sites, the optimal stopping rule grows asymptotically like,

$$\varepsilon_r(r) = \begin{cases} e^{-1} & \text{for } r = 1, \\ r^{-1} \sqrt{\frac{r}{2r-1}} & \text{for } r > 1. \end{cases}$$

In 1966, Gilbert & Mosteller [10] generalized Gusein-Zade's utility function results to include weights,  $w_1 \geq w_2 \geq \dots \geq w_k$ , that represent the payoffs for the  $k$  best sites. The optimal stopping rules and the probabilities of success are known exactly for  $r$  up to 3 with  $w_1 = w_2 = w_3 = 1$  [10], [21]. The optimal selection strategy has been derived (in multiple ways) for  $T$  asymptotically large, [9], [30]. A method has been derived for calculating the optimal stopping rule for general  $r$  and general weights,  $w_a$ , [30]. The distribution of the stopping time  $T$  is known exactly for general  $r$  [31].

Now that we have a large collection of extensions to consider, it is unclear which extension is most applicable to the system at hand, or what remains in terms of open questions. We now turn to the progress made in Ecology towards understanding and motivating the decision processes used by dispersing individuals.

### 1.1.2 Decision Processes: A History

The threshold, best-of- $n$ , and comparative Bayes decision processes were developed in the context of mate search, but have been used recently to describe habitat selection in natively-dispersing brush mice [18]. The threshold model and best-of- $n$  model, introduced by Janetos in [13], assume that:

- H1 females mate only once,
- H2 males may mate more than once,
- H3 male fitness is heritable and assigned a random variable,
- H4 males are dispersed randomly in space with respect to fitness,
- H5 and males can only influence female choice through their fitness.

Translated into the language of habitat selection, these models assume that:

H'1 an individual can select only one habitat,

H'2 habitats can be occupied by more than one individual,

H'3 a habitat confers a certain fitness or reproductive benefit on the individual who selects it based on its quality, which is assigned a random variable,

H'4 habitats are dispersed randomly in space with respect to quality,

H'5 and a habitat cannot influence whether an individual selects it.

Obviously, some of these assumptions fit better than others. In particular, populations of territorial animals would probably not allow habitats to be occupied by multiple individuals, and quality of habitats is most likely spatially auto-correlated.

A finer collection of decision processes may be needed. For example, the threshold rule provides only one possible explanation for the sequential search pattern associated with it. It is similar to the classical Secretary Problem described by Chow et al. [4] where the goal is to minimize the expected rank, but in the classical Secretary Problem, the qualities of habitat sites are given by their ranking: a permutation of the numbers 1 to  $n$ . These could correspond to the ordinals of a continuous distribution, but we can show that the introduction of search costs affect the classical Best-Choice Problem and the problem of minimizing expected rank differently. One can easily construct examples where labeling sites by rank,  $\{1, 2, 3, 4\}$ , versus by quality (especially if some are closer in quality than others) for example  $\{3, 3.05, 3.1, 4\}$ , yields different decision behavior, even though the search cost is the same in both labeling systems. However, both yield the same sequential search behavior, and in both cases optimal solutions have been derived ([17], [4]). With specific knowledge of the species of interest, it is possible to discern between these two models: for instance it may be unrealistic for an animal to keep close track of fine differences and thus a realistic model would rank sites.

The best-of- $n$  rule requires frequent resampling (assuming an individual requires many visits to a site for accurate estimation of its quality), and thus high average total assessment cost. Luttbegg compares these decision rules in [17] and shows that when costs are high the best-of- $n$  rule is handily outperformed in simulations by the threshold rule. However, this conflicts with Mabry & Stamps' [18] empirical observations of individuals using a best-of- $n$  or related rule in habitat selection, which is assumed to have high assessment costs. Could this be explained with another decision process or optimal stopping problem that yields best-of- $n$  behavior in a high-cost regime?

### 1.1.3 Brush Mice

We recognize that the usefulness of a model is predicated upon its ability to reflect the behavior we aim to study. Therefore we discuss here some relevant life history traits of brush mice (*Peromyscus boylii*), the particular animal to which we would like to apply our model.

Brush mice are small, nocturnal mammals that live in a variety of habitats in western North America. Their dispersal behavior has been studied using radio telemetry. As nocturnal creatures, they are inactive during the day and make their initial forays out from the natal nest at night. This is especially convenient for studies of the process of habitat selection, as it partitions the foray phase into disjoint events. Thus, even if one's movement data is coarse, one can track where individuals chose to visit a nest during the day. Brush mice are known to be both socially and genetically promiscuous, yet no significant difference in patterns of dispersal between male and female brush mice has been shown, in the literature of which we are aware.

We assume that phenotypic variation in personality will already be expressed at this point and remains relatively fixed during the selection process. Of particular emphasis in our models is the large amount of uncertainty the individual is required to manage. When the search process begins, natively dispersing mice leave the natal nest for the first time, so a visit or multiple visits are required for accurate measurement of a site's quality. Natal habitat preference induction, which occurs when experience in a natal habitat increases a dispersing individual's preference for sites with similar cues to the natal nest [26], may explain how animals can exhibit appropriate functional responses to cues it has never been exposed to in a non-natal setting.

It is also unclear how well the individual has interpreted the quality of the site: If the individual is interested in many different properties of the site (safety, food supply, availability of mates, etc.) then it may be the case that only a few of those properties are measurable at the time the individual encounters the site, or that an individual's measurement of one or all of these qualities is itself unreliable and requires refinement over multiple visits.

The safety of a site depends on the predation risk there, which in turn depends on the abundance of predators in the area, and structural features of the habitat that may enhance or hinder the animal's ability to hide or evade the predator. Predation risk can be measured in different ways. Suppose an individual returns repeatedly to a habitat site and observes occurrences of predation there. These repeated observations could be used to determine the expected rate of predation at that site. But this would take a long time, and it is unclear whether a brush mouse is capable of the cognition required for such a measurement.

Instead, we suppose that when an individual visits a site, it looks for cues of a predator. Examples of these cues include scent cues, physical cues like droppings, or audible cues like alarm calls made by conspecifics (though on the other hand, the presence of a competitor might be a concern in its own right). An individual may visit a site and observe no such cues, or cues that indicate low risk or predation, such as a conspecific's productive nest (again, we are ignoring the effect of competitors here) or plentiful hiding spots.

Mice may vary in their ability to evade predators, as a function of several factors which we will lump into one category termed athleticism. An athletic individual is one that can run faster, jump higher, has greater stamina, etc. than the average brush mouse. We refer to those unfortunate individuals in a population that do *not* run faster, jump higher, or have greater stamina than the average as sedentary individuals. We assume that an animal is perfectly aware of their own degree of athleticism or sedentarism. In our model, an animal's personal predation risk at a given site will depend on the predation risk there and its athleticism.

## 1.2 The Model

Our goal in this section is the development of a Stochastic Dynamic Programming model that represents the process of selecting habitat for an individual, natively-dispersing brush mouse (*Peromyscus boylii*). We will identify the assumptions required for application of our model, introduce the model itself, and then show how to solve for the optimal strategy. Our model for selection is based on sampling for information about predation risk, balancing increased certainty against the cost of sampling in How a given animal reacts to this information is reflected in their individual utility of risk. In Section 1.3 we identify how the optimal strategy varies with respect to the parameters of the model. Of particular interest is the difference in optimal search behavior between bold and shy individuals.

### 1.2.1 Predation Risk $p_j$ and Perceived Predation Risk Level, $R_j$

As our model for selection is based on sampling for information about predation risk, we begin by defining what we mean when we say predation risk. Let  $H$  be the set of potential habitat sites,  $H = \{1, 2, \dots, n\}$

**Definition 1.** *The predation risk,  $p_j$ , ( $j \in H$ ) of a habitat site is the probability that the individual will be predated at that site within the given season.*

But an individual's perception of the predation risk at a site is just as important to our model. The individual animal must decide between sites by visiting each site, some maybe multiple times, while others may be ignored entirely. We assume the animal has the capacity to keep track of the distribution of belief it has regarding the predation risk level it perceives at site  $j$  at time  $t$ , which we define now.

**Definition 2.** *The perceived predation risk level,  $R_j$ , is an estimate of  $p_j$  based on information gained from visiting the site. In other words, it is a function of the data obtained from sampling. We model  $R_j$  as a stochastic process such that for each  $t$ ,  $R_j(t)$  is a continuous random variable on  $[0, 1]$  (with density function denoted by  $f_{R_j(t)}$  absolutely continuous with respect to Lebesgue measure) representing the distribution of belief an individual brush mouse has regarding the perceived predation risk level at site  $j \in H$  at time  $t$ .*

Note that the predation risk at a site is connected to the physical landscape of the model, whereas the perceived predation risk level depends implicitly on the physical landscape and explicitly on the animal's ability to interpret the signal given by the landscape.

We model habitat selection as a process in discrete time, with distinct "turns." For example, each turn can take one day and the individual has  $T$  days for the entire process, since we suppose settlement must occur before an individual's energy reserves run out. We impose this condition by fixing a total time allotment for search,  $T$ , of which the individual is aware. The individual makes its first decision at time  $t = 1$  and may visit only one site per time step. If  $T = 1$ , then the individual must settle immediately. As such he or she can only visit either site at most  $T$  times, including the time that it settles in the site.

Though Dall & Cuthill [6] argue that the optimal time an individual should spend investigating any one option may vary over the search process, for instance in the context of foraging behavior of specialists versus generalists, we suppose the amount of time required to properly investigate a site is one time step, and that an optimal time allocation of multiple days can be effectively approximated in our simulation by multiple sequential revisits to the same site. Thus, we let  $t \in \{1, \dots, T\}$ .

Specifically, this means that at some time  $t$ , for an estimate  $\hat{p} \in d\hat{p} \subset [0, 1]$ ,  $R_j(t)$  has probability density given by  $P(R_j \in d\hat{p})$ . For example, we could say that the animal perceives that the risk level is above 0.5 with probability  $P(R_j > 0.5)$ .

**Definition 3.** *A Beta random variable has two parameters,  $\alpha_j(t)$  and  $\beta_j(t)$ , and density function given by,*

$$P(R_j(t) \in dp) = \frac{\Gamma(\alpha_j(t) + \beta_j(t))}{\Gamma(\alpha_j(t))\Gamma(\beta_j(t))} p^{\alpha_j(t)-1} (1-p)^{\beta_j(t)-1} dp, \quad \text{for } p \in [0, 1].$$

*A Beta random variable has mean and variance given by,*

$$\mathbb{E}[R_j(t)] = \frac{\alpha_j(t)}{\alpha_j(t) + \beta_j(t)} \quad \text{and} \quad \text{Var}[R_j(t)] = \frac{\alpha_j(t)\beta_j(t)}{(\alpha_j(t) + \beta_j(t))^2(\alpha_j(t) + \beta_j(t) + 1)}.$$

This describes a family of probability densities on  $[0, 1]$  which includes, in particular, the Uniform density ( $\alpha_j(t)$  and  $\beta_j(t) = 1$ ).

If an individual has no information regarding the predation risk at a site, then in the Bayesian sense of the belief regarding a parameter, this is modeled by a Uniform random variable; we write this as  $P(R_j \in d\hat{p}) = d\hat{p}$  for all estimates  $\hat{p} \in [0, 1]$ ; equivalently  $R_j(0)$  is equal in distribution to  $\text{Unif}([0, 1])$ .

### 1.2.2 Sensing Cues from Predators

As it is unlikely the individual will actually see an act of predation at any given site at any given time, we suppose the individual instead relies on cues or social information regarding predator presence, for example droppings or other scent cues. An individual also may find hints of predator absence, for instance the discovery of a productive, nearby nest. Therefore, we define the following random variable:

**Definition 4.** We define the cue-sensing event to be the event that an individual visits a site,  $j$ , and senses cues of a predator, or not. For each site  $j \in H$ , we model this by defining an independent, identically distributed (i.i.d) sequence of Bernoulli random variables,  $S_j(t)$  for  $t = 1, 2, \dots, T$ , with parameter  $p_j$ , where  $S_j = 1$  if a predator is sensed, and  $S_j = 0$  otherwise, when it revisits site  $j$  at time  $t$ . The density function for  $S_j(t)$  is denoted by  $g_{S_j(t)}$ , which is absolutely continuous with respect to counting measure. Note that each  $S_j$  is defined to be independent of time,  $t$ , which assumes both that the predator does not get any worse or better over time at masking its cues, and the individual does not get any worse or better at perceiving the predator.

### 1.2.3 Updating $R_j$ with Bayesian Inference

At time  $t$ , suppose the individual decides to revisit site 1, and observes evidence of predation, ( $S_1(t) = 1$ ). What is a reasonable model for the method by which the individual incorporates this information?

The Bayesian decision theory approach has been used with some success in studying foraging behavior and mate search behaviors of animals [19]. This approach asks whether animals make decisions that are optimal given the appropriate posterior probabilities. The application of Bayesian decision theory to habitat selection is not without precedent either [26].

Under the following assumptions on the species of interest: they are habitat generalists, they live in a landscape where potentially suitable habitats produce distinctive habitat-specific cues, and the expected quality of habitats can take on different values as a result of spatial and temporal variation, Stamps, Luttbeg, & Krishnan use Bayesian statistics to demonstrate a relationship between an individual's survival to dispersal age and its preference for habitat similar to the natal habitat.

More specifically, in their model, the prior estimate of the quality of a specific type of natural habitat is indicated by the attractiveness of cues from that type of habitat to naive individuals, while the posterior estimate of habitat quality is indicated by the attractiveness of cues from that same type of habitat to individuals born and raised in that type of habitat, where naive individuals are those only recently born.

Thus, we suggest that the effects of evidence regarding predation risk, gathered in the process of visiting habitat sites, can also be analyzed from a Bayesian perspective.

Bayesian statistics consists of (some say entirely) this result: the posterior density of the random variable  $R_j(t + 1)$  can be calculated by multiplying the prior density,  $R_j(t)$ , with the likelihood function of the evidence – in particular for the random variable  $S_j(t)$  (likelihood function provided

below) – and normalizing (so that the resulting distribution integrates to 1), for each  $j \in H$  and  $t = 1, 2, \dots, T$ .

The posterior density (for each site  $j$ ) in our model is the conditional distribution of  $R_j(t+1)$  given  $S_j(t)$ . As  $R_j(t+1)$  is a random variable with density absolutely continuous with respect to Lebesgue measure, and  $S_j(t)$  is a random variable with density absolutely continuous with respect to counting measure (for all  $j \in H$  and  $t = 1 \dots T$ ) we denote the conditional density function,

$$f_{[R_j(t+1)|S_j(t)]}(p)$$

which we can calculate for some particular  $s \in \{0, 1\}$ . The conditional probability density function is just the normalization of the joint density function to a probability density by dividing by the marginal density function of  $S_j(t)$ . So for any  $A \subset [0, 1]$ ,

$$P(R_j(t+1) \in A | S_j(t)) = \int_A \left( \frac{f(p, s)}{\int_0^1 f(p, s)} \right) dp$$

where  $s$  is fixed.

The posterior density provides a description of the degree of belief the animal has regarding the true value of the predation risk,  $p_j$ , after the “experiment” is performed with result  $s$ , where in our model the “experiment” is a visit to a habitat site with outcomes described in Subsection 1.2.2. One can also interpret the prior density in our model,  $P(R_j(t) \in A)$ , as expressing the individual’s degree of belief that the true value of the predation risk,  $p_j$ , is in some interval  $A$  prior to the experiment being performed.

The choice of the prior is subjective: no restrictions (at least, not by Bayesian statistics itself) are made on the prior distribution of a natively-dispersing animal. Initially, we set  $f_{R_j(0)}(dp) = P(R_j(0) \in dp) = 1$  on  $[0, 1]$ , which is the Uniform distribution, though some literature suggests dispersing individuals develop distinct posterior distributions merely by surviving to dispersal age [26] and that brush mice specifically are capable of a rough estimation of habitat quality from a distance, and thus before assuming the risk of visitation [18].

We can also calculate the likelihood of the evidence given the prior belief, which is given by another conditional density function, denoted

$$f_{[S_j(t)|R_j(t)]}(s)$$

which is written by normalizing the joint density function to be a probability density function by dividing by the marginal density function of  $R_j(t)$ . Fix  $p \in [0, 1]$ . Whereas the density of  $R_j(t)$  is absolutely continuous with respect to Lebesgue measure, meaning  $P(R_j(t) = p) = 0$  for all points  $p$ ,  $S_j(t)$  is absolutely continuous with respect to counting measure, so  $P(S_j(t) = s)$  makes sense as the probability of the outcome  $s$ . So we can write,

$$P(S_j(t) = s | R_j(t)) = \frac{f(p, s)}{\int_{\{0,1\}} f(p, s) ds}$$

But, of course, the left hand side is the probability that the animal observes cues of a predator, which is independent of its belief  $R_j(t)$ . And, the marginal density function of  $R_j(t)$  is just the prior. Therefore, we can express the joint density, for fixed  $p$ ,

$$\begin{aligned} f(p, s) &= P(S_j(t) = s | R_j(t)) \int_{\{0,1\}} f(p, s) ds \\ &= p^s (1-p)^{1-s} \frac{\Gamma(\alpha_j(t) + \beta_j(t))}{\Gamma(\alpha_j(t))\Gamma(\beta_j(t))} p^{\alpha_j(t)-1} (1-p)^{\beta_j(t)-1} \\ &= \frac{\Gamma(\alpha_j(t) + \beta_j(t))}{\Gamma(\alpha_j(t))\Gamma(\beta_j(t))} p^{\alpha_j(t)+s-1} (1-p)^{\beta_j(t)-s}. \end{aligned}$$

So the conditional density we get is

$$P(R_j(t+1) \in A | S_j(t)) = \int_A \left( \frac{f(p, s)}{\int_0^1 f(p, s)} \right) dp.$$

Calculating the denominator,

$$\begin{aligned} \int_0^1 f(p, s) dp &= \int_0^1 \frac{\Gamma(\alpha_j(t) + \beta_j(t))}{\Gamma(\alpha_j(t))\Gamma(\beta_j(t))} p^{\alpha_j(t)-1+s} (1-p)^{\beta_j(t)-s} dp \\ &= \frac{\Gamma(\alpha_j(t) + s)\Gamma(\beta_j(t) + 1 - s)}{\Gamma(\alpha_j(t) + \beta_j(t) + 1)} \\ &\quad \cdot \int_0^1 \frac{\Gamma(\alpha_j(t) + \beta_j(t) + 1)}{\Gamma(\alpha_j(t) + s)\Gamma(\beta_j(t) + 1 - s)} p^{\alpha_j(t)+s-1} (1-p)^{\beta_j(t)-s} dp \\ &= \frac{\Gamma(\alpha_j(t) + s)\Gamma(\beta_j(t) + 1 - s)}{\Gamma(\alpha_j(t) + \beta_j(t) + 1)}, \end{aligned}$$

since the integral sums to 1.

Therefore,

$$P(R_j(t+1) \in A | S_j(t)) = \int_A \frac{\Gamma(\alpha_j(t) + \beta_j(t) + 1)}{\Gamma(\alpha_j(t) + s)\Gamma(\beta_j(t) + 1 - s)} p^{\alpha_j(t)-1+s} (1-p)^{\beta_j(t)-s} dp. \quad (1.1)$$

Note that the posterior probability density function after one experiment ( $R_j(t+1)$  for example) can become the prior for a second experiment (where  $R_j(t+1)$  is then used to calculate  $R_j(t+2)$ ), and so on. Also, the Beta and Binomial distributions form what is called a conjugate-prior relationship, since by setting a Beta random variable to describe an individual's prior distribution, and giving evidence by a Binomial random variable, we observe that the posterior distribution is also a Beta random variable. This provides closed-form expressions that are more readily understood than the complicated approximations we would have to calculate if conjugate-priors were unavailable.

Note that  $(\alpha_j(t), \beta_j(t))$  denote the parameters of the Beta random variable,  $R_j(t)$ . Therefore, if the animal revisits site  $j$  and senses cues from a predator, or not, it updates its parameters according to,

$$\alpha_j(t+1) = \alpha_j(t) + s \quad \text{and} \quad \beta_j(t+1) = \beta_j(t) + (1-s), \quad (1.2)$$

and the new mean and variance can be calculated,

$$\mathbb{E}[R_j(t+1)] = \frac{\alpha_j(t) + s}{\alpha_j(t) + \beta_j(t) + 1} \quad \text{and} \quad \text{Var}(R_j(t+1)) = \frac{(\alpha_j(t) + s)(\beta_j(t) + (1-s))}{(\alpha_j(t) + \beta_j(t) + 1)^2(\alpha_j(t) + \beta_j(t) + 2)}.$$

We note that  $\mathbb{E}R_j$  and  $\text{Var}(R_j)$  are themselves stochastic processes.

### Example: Update Perceived Predation Risk Level at Site 1

Let  $t = 0$  and consider site 1. Let the individual's perceived predation risk level at this site be  $R_1(0) \sim \text{Beta}(1, 1)$ , which we recall means  $P(R_1(0) \in dp) = dp$  for  $p \in [0, 1]$ . If the individual chooses to visit site 1 and senses cues left by a predator at the site ( $S_1(0) = 1$ ), we can calculate its updated perceived predation risk level at site 1,  $R_1(1)$ , (the posterior density) by applying Bayes'

Theorem.

$$\begin{aligned} P(R_1(1) \in dp \mid S_1(0) = 1) &= \frac{P(S_1(0) = 1, R_1(0) \in dp)}{\int_0^1 P(S_1(0) = 1, R_1(0) \in dp)} \\ &= \frac{p \frac{\Gamma(2)}{\Gamma(1)\Gamma(1)} p^0 (1-p)^0}{\int_0^1 \frac{\Gamma(2)}{\Gamma(1)\Gamma(1)} p'^1 (1-p')^0 dp'} dp, \end{aligned}$$

where  $p'$  is just a dummy variable for the integration. Computing the integral in the denominator,

$$\int_0^1 \frac{\Gamma(2)}{\Gamma(1)\Gamma(1)} p' dp' = \frac{1}{2} \int_0^1 2p' dp' = \frac{1}{2}.$$

since the integral integrates to 1 (notice that the integrand is a Beta distribution with parameters (2,1)). Continuing,

$$P(R_1(1) \in dp \mid S_1(0) = 1) = 2p dp$$

so our posterior belief  $R_1(1)$  is distributed according to Beta(2,1). Similarly, if the individual receives evidence  $S_1(0) = 0$ , one can show its posterior is distributed according to Beta(1,2).

### Connection to Polya's Urn Models

It may be helpful to understand our model by pointing out its similarity to a well-known model: the Polya's Urn model of reinforced sampling. Consider an urn with one red ball and one blue ball and the following rule: Every time you take out a red ball, put another red one back in (along with the original ball), and every time you take out a blue ball, put another blue ball back in (again, along with the original ball). The proportion of red balls in the urn evolves exactly the same way the process,  $R_j$ , does, (in the mean) that is, if the individual just keeps guessing what will happen when it repeatedly visits site  $j$ . For example, starting with one red ball and one blue ball in the urn, you could pull out one red ball, then one blue ball, and then one red ball again, so the proportion of red balls goes: 1/2, 2/3, 2/4, 3/5. In our model, an individual may guess that visiting site 1 repeatedly will first yield a cue from a predator, then no cues, then another cue. Applying Bayes' Rule each time, we see that if  $S_j(t) = \{1, 0, 1\}$  for  $t = 0, 1, 2$ , then  $(\alpha_j(t), \beta_j(t)) = \{(1, 1), (2, 1), (2, 2), (3, 2)\}$  and thus  $\mathbb{E}R_j(t) = \{1/2, 2/3, 1/2, 3/5\}$  for  $t = 0, 1, 2, 3$ .

Now, suppose we have an urn with one red ball and one blue ball in it, and a coin which comes up heads with some probability,  $p_j$ . Every time the coin comes up heads, we put another red ball in the urn, and every time the coin comes up tails, we put a blue ball in. The proportion of red balls in the urn evolves exactly the same way the process,  $R_j$  does, (in the mean) that is, if the individual repeatedly visits site  $j$ . For example, starting with one red ball and one blue ball in the urn, the coin could come up heads three times in a row, so the proportion of red balls goes: 1/2, 2/3, 3/4, 4/5 – after three heads in a row it is not unreasonable to start estimating a high chance of heads. In our model, if an individual visits site 1 three times and senses cues of a predator each time, then Bayes' Rule will show  $\mathbb{E}R_j$  also evolves according to 1/2, 2/3, 3/4, 4/5. In our model as well, the individual can reasonably start to suspect the odds are loaded towards predation risk.

#### 1.2.4 Search Costs

Since an animal must sometimes travel quickly through matrix areas which are between habitat sites and have significantly less cover, therefore expending a significant amount of energy, it is reasonable to suppose there is a cost,  $c_j(t)$ , associated with sampling. For the sake of simplicity,

this cost is accrued every time the individual samples a site, even if the individual was previously at that site and thus may not actually need to move through matrix. Some dispersing brush mice sometimes return to the natal site between every excursion to a site, even two sequential visits to the same site, so this cost structure might not be too unreasonable.

It is important to explicitly incorporate both finite time for search and search costs, at least when comparing performances of the decision processes described in Subsection 1.1.2. The best-of- $n$  decision process was found to outperform the threshold model (in terms of the average fitness of the mate yielded by the process) when time constraints exceeded a certain value and costs were fixed, whereas the threshold model yields a mate of higher average fitness over a range of costs when time for search is assumed infinite [17].

### 1.2.5 Background: Utility Theory

We begin by introducing some notation. Given an individual's perceived predation risk level at two sites,  $j$  and  $k$ , which are given by two probability distributions,  $R_j(t)$  and  $R_k(t)$ , we write,

$$R_j(t) \preceq R_k(t)$$

which is intended to mean choosing site  $j$  is at least as preferable as choosing site  $k$ . If  $R_j(t) \preceq R_k(t)$  and  $R_k(t) \preceq R_j(t)$  we say that the two sites are equally preferred and write  $R_j(t) \sim R_k(t)$ . Also, if  $R_j(t) \preceq R_k(t)$  but it is not true that they are equally preferred, then  $R_j(t) \prec R_k(t)$ . We also define  $R_k(t) \succeq R_j(t)$ ,  $R_k(t) \succ R_j(t)$  to mean  $R_j(t) \preceq R_k(t)$ ,  $R_j(t) \prec R_k(t)$  respectively.

Given distributions of belief,  $\{R_j(t)\}$  for  $j \in H$ , it is unclear how a brush mouse would rank them, as we can see in the following example. Suppose, for example, that an individual has been sampling for a while, and now its belief can be described by  $R_1(t)$  and  $R_2(t)$ , where  $R_1(t)$  is distributed according to Beta(9, 8) and  $R_2(t)$  is Beta(2, 2). Which should the mouse prefer?

An immediate answer is that  $R_2(t)$  is preferable to  $R_1(t)$  because it has a lower expected perceived predation risk level (0.5 versus .529). Implicit in this answer are the notions that preferences can order probability distributions, and that there is some numerical ordering that corresponds to this preference ordering. And also, the somewhat natural ordering of the expected values of the two sites' distributions could be this numerical ordering. This is termed the *principle of expected value*, and in many cases it provides a satisfactory means of numerically ordering preferences, but in general it leads to paradoxes like the St. Petersburg paradox.

In the St. Petersburg paradox, it costs  $D$  dollars to toss a coin until it comes up heads. You then win  $2^t$  dollars, where  $t$  is the number of tosses it took. One can show the expectation of the winnings is infinite, and therefore larger than any number  $D$ , so the principle of expected value says one should always play. But as the game becomes more and more expensive, say  $D = 256 = 2^7$ , your probability of just breaking even decreases and decreases, to 0.0156 if  $D = 256$  for example. The paradox is that the principle of expected value says one should always play, but for large costs  $D$ , one should really probably just keep their money.

Instead of considering the expected value, von Neumann and Morgenstern [29] (Section 3.3: Probability and Numerical Utilities) permit a decision-maker not only to state a preference among any two alternative events, but also to be able to compare alternative sets of events, each with some probability of occurring, if he or she knows these probabilities.

We model this comparison with utility functions. Before we introduce these, we must mention a basic theorem in utility theory which guarantees these utility functions satisfy the properties we require.

**Theorem 1.** Bernoulli's Utility Postulate states that, at time  $t$ , an individual's preferences among perceived predation risk levels at sites  $j$  and  $k$ , given by probability distributions  $R_j(t)$  and  $R_k(t)$

with densities  $f_{R_j(t)}$  and  $f_{R_k(t)}$ , are ordered according to the numerical ordering of ones expected utilities, denoted  $b(p)$ . That is,

$$R_j(t) \preceq R_k(t) \quad \text{if and only if} \quad \int_0^1 b(\hat{p}) f_{R_j(t)}(\hat{p}) d\hat{p} \geq \int_0^1 b(\hat{p}) f_{R_k(t)}(\hat{p}) d\hat{p}$$

and for simplified notation, we can write  $b(R_j(t)) = \int_0^1 b(\hat{p}) f_{R_j(t)}(\hat{p}) d\hat{p}$ , which represents the value that an individual assigns to the perceived predation risk level given its current distribution of belief,  $R_j(t)$ . For a predation risk level known with certainty (meaning the predation risk is  $\hat{p}$  with probability 1), we evaluate  $b(\hat{p})$ .

In our model, a brush mouse must consider a continuum of possible values: its estimate,  $\hat{p}$ , can take on any value in  $[0, 1]$ . Beginning with a Uniform distribution and applying Bayesian Updating to its risk assessments (with evidence given by a Bernoulli random variable), will *never* yield a probability distribution, for any time  $t$ , that assigns zero density to the occurrence of some value of  $\hat{p}$  in  $(0, 1)$ .

We recall the definition of athleticism, as applied to brush mice, given in Subsection 1.1.3. Fix a predation risk level,  $\hat{p}$  in  $(0, 1)$ . We introduce the concept of an individual animal's personal predation risk level.

**Definition 5.** *The personal predation risk level of an individual is the predation risk level at a site, for a specific individual, as a function of the predation risk level observed, and the individual's own athleticism. We model this quantity with the function,  $z(\hat{p}) : [0, 1] \rightarrow [0, 1]$  which is assumed to be monotone increasing, with the properties  $z(0) = 0$  and  $z(1) = 1$ . The shape of the function varies with the degree of athleticism or sedentarism in the individual; three examples are given below.*

But first, we explain why we assume  $z(0) = 0$  and  $z(1) = 1$ . Consider the special case that  $\hat{p} = 0$ . Then, empirically, if the mouse could run an experiment where a finite number of mice repeatedly settled this site, none of the mice would be predated. Therefore, for the purposes of the model, we assume that any mouse, regardless of athleticism, would assign personal predation risk equal to zero. In other words, we assume,  $z(0) = 0$ .

On the other hand, if  $\hat{p} = 1$ , then empirically the mouse estimates that, as in the experiment above, every mouse would be killed by a predator. For the purposes of the model, we assume that any animal would assign personal predation risk equal to 1. In other words, we assume  $z(1) = 1$ .

In our model, we choose to consider utility functions, in order to model the positive benefit gained from choosing a site with lesser predation risk, so we define  $b(\hat{p}) = 1 - z(\hat{p})$ . The function  $z$  is monotone increasing, so the utility function  $b$  is monotone decreasing. If the utility function is decreasing, then the preferences follow a “*less is better*” principle with regards to predation risk. As far as we are aware, there is no evidence that an animal would not identify a higher risk site as less preferable. This is why in this paper we only consider decreasing utility functions.

The athletic individual knows it can run faster, has higher stamina, jump higher, etc. than the average naturally-dispersing brush mouse, and so it decides its personal predation risk level should be less than the predation risk level:  $z(\hat{p}) \leq \hat{p}$ . For an athletic individual this yields a utility function,  $b_a(\hat{p})$  (shortened from  $b_{\text{athletic}}(\hat{p})$ ) such that,

$$b_a(\hat{p}) \geq \hat{p} \quad \text{for all } \hat{p} \in [0, 1].$$

The sedentary individual, as opposed to the athletic individual, knows that it runs more slowly, has lower stamina, cannot jump as high, etc. than the average. So it would assign a higher personal

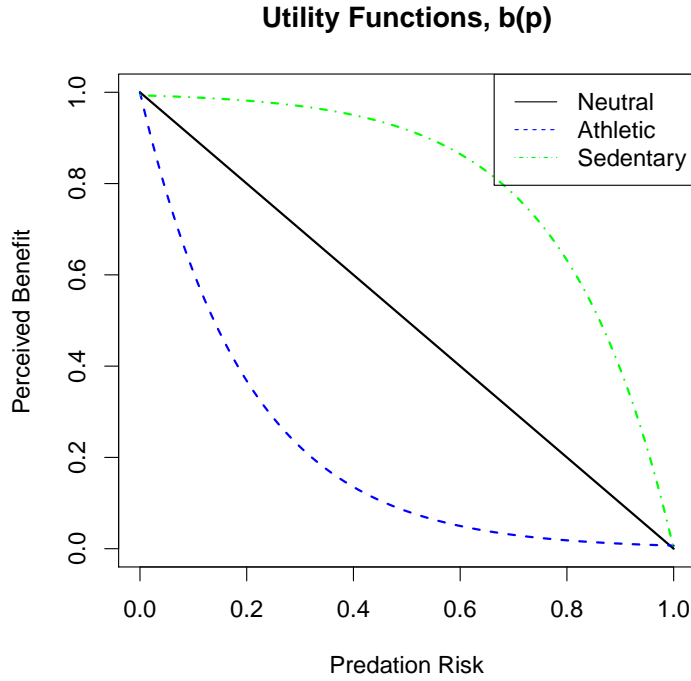


Figure 1.1: The utility functions for individuals which vary in their personal predation risk, as determined by their ability to handle predation risk, and described by Equations 1.3-1.5.

predation risk level to each predation risk level, and as above we prescribe the utility function,  $b_s(\hat{p})$  (shortened from  $b_{\text{sedentary}}(\hat{p})$ ) satisfying,

$$b_s(\hat{p}) \leq \hat{p} \quad \text{for all } \hat{p} \in [0, 1].$$

We also model an individual who is, at least with respect to the athleticism in brush mice, exactly average. This mouse would assign a personal predation risk level equal to its estimate of the predation risk level. Therefore its utility function,  $b_n(\hat{p})$  (shortened from  $b_{\text{neutral}}(\hat{p})$ ) satisfies,

$$b_n(\hat{p}) = \hat{p} \quad \text{for all } \hat{p} \in [0, 1].$$

Note that the principle of expected value is maintained by taking  $b_n$  here.

We consider a linear utility function,  $b_n(x)$ , which models neutrality towards predation risk under the principle of expected value, a concave utility function,  $b_a(x)$ , and a convex utility function,  $b_s(x)$ , which model the relationship between an individual's athleticism and whether this determines a positive or negative change in the resulting, personal predation risk. The example functions we use are given below:

$$b_n(x) = 1 - x, \tag{1.3}$$

$$b_a(x) = 1 - e^{\gamma(x-a_b)} \tag{1.4}$$

$$b_s(x) = e^{-\gamma x} \tag{1.5}$$

where  $a_b$  is the  $x$ -intercept (we set  $a_b = 1$  in all computer simulations) of the athletic individual's utility function. Notice that the value of  $\gamma$  determines the curvature of the function, meaning that the greater  $\gamma$  is, the greater the deviation of the function from the line given by the neutral utility function.

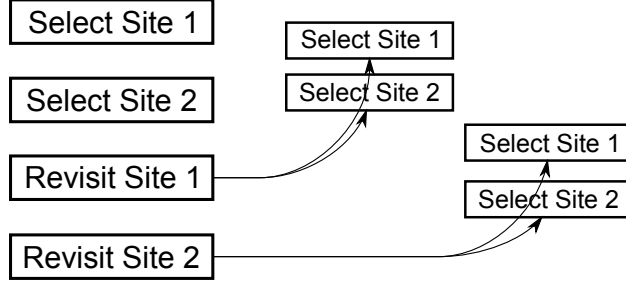


Figure 1.2: A diagram of the decisions available to an individual in the process of habitat selection, assuming they must settle on the next turn and with  $n = 2$ . The decision to revisit a site at the current turn depends on the outcomes of visiting Site 1 or Site 2 at the next turn.

### 1.2.6 Solving for the Optimal Strategy with Backwards Induction

We suppose that at each time,  $t$ , the brush mouse may choose from the following  $2n$  actions: visit one of the  $n$  sites in  $H$ , or settle immediately in one of the  $n$  sites in  $H$  and stop the process there, as in Figure 1.2. At the final time,  $T$ , the brush mouse must settle immediately in one of the sites in  $H$  and stop the process there.

The model we have described thus far is a *finite-horizon optimization problem* and as such, an optimal policy can be derived by applying the Dynamic Programming Equation, [1].

**Theorem 2.** *Let  $\mathcal{S}$  be a finite set of states, and let  $\mathcal{A}$  be a finite set of actions, with rewards given by the utility function,  $u(x)$ . The state of the model is given by the current time and the individual's perceived predation risk level at each site  $j \in H$ , so  $\mathcal{S}$  is all  $n + 1$ -tuples of form  $(t, (R_j(t))_{j \in H})$ . If  $t = T$  then the only available actions are to select one of the sites in  $H$  and the Dynamic Programming Equation is given by,*

$$V(T) = \max_{j \in H} \{ \mathbb{E}b(R_j(T)) \}.$$

*At the second-to-last time step,  $t = T - 1$ , there are more actions available. The individual can stop and settle in one of the sites in  $H$ , taking the site with the greatest expected utility,  $\mathbb{E}[b(R_j(T - 1))]$ , or it can visit one of the sites in  $H$  and update its perceived predation risk level at that site. Then it will compare the utility of the updated site against the utilities of the other, non-updated sites.*

**Definition 6.** *We define the animal's estimate of the cue-sensing event,  $\hat{S}_j(t) = \hat{s}$  as an i.i.d. sequence of Bernoulli random variables in  $t$ , with parameter  $\mathbb{E}[R_j(t)]$ .*

*Therefore at  $t = T - 1$  the Dynamic Programming Equation is given by*

$$V(T - 1) = \max_{j \in H} \left\{ \mathbb{E}b(R_j(T - 1)), \sum_{\hat{s}} P(\hat{S}_j(T - 1) = \hat{s}) V_{j, \hat{s}}(T) - c \right\}$$

where

$$V_{j, \hat{s}}(T) = \max \left\{ \mathbb{E}b(R_1(T - 1)), \dots, \mathbb{E} \left[ b(R_j(T) | \hat{S}_j(t) = \hat{s}) \right], \dots, \mathbb{E}b(R_j(T - 1)) \right\}$$

*We assume as a modeling hypothesis that the animal's estimate of the cue-sensing event can be incorporated to calculate the conditional expectation of the animal's updated distribution of belief,*

$\mathbb{E}[b(R_j(t+1))|\hat{S}_j(t) = \hat{s}]$ , with Bayes' Theorem, exactly as was done for the cue-sensing event ( $[S_j(t) = s]$ ) in Subsection 1.2.3.

Note that the set of actions available at an arbitrary time  $t$  ( $t \neq T$ ) is the same as the set of actions available at  $t = T - 1$ . The Dynamic Programming Equation for  $0 \leq t < T$  is given by

$$V(t) = \max_{j \in H} \left\{ \mathbb{E}b(R_j(t)), \sum_{\hat{s}} P(\hat{S}_j(t) = \hat{s}) V_{j,\hat{s}}(t+1) - c \right\}, \quad (1.6)$$

where

$$V_{j,\hat{s}}(t+1) = \max \left\{ \mathbb{E}b(R_1(t)), \dots, \mathbb{E} \left[ b(R_j(t+1)|\hat{S}_j(t) = \hat{s}) \right], \dots, \mathbb{E}b(R_j(t)) \right\}$$

so informally we can say that the Dynamic Programming Equation calculates the maximal possible expected utility at time  $t$ .

For each state of the model in  $\mathcal{S}$ , one way to write out the optimal policy is by taking the argmax of the right-hand side, instead of the max, of the above equations.

In [16], Luttbeg develops a model of mate selection in which mate fitnesses are represented by Normal random variables. Because of the incredibly large number of cases one has to deal with, the authors use a ‘‘myopic rule’’ which says that an individual only compares the benefits of selecting an option at the current time with the benefits of choosing an option at the next time step, even though there may be more time remaining for search. In this case,  $V(t)$  is calculated the same as  $V(T-1)$  for each  $t$ . Because the possible values for  $\alpha_j(t+1)$  and  $\beta_j(t+1)$  are restricted to  $\alpha_j(t)$  or  $\alpha_j(t)+1$  and  $\beta_j(t)$  or  $\beta_j(t)+1$ , we do not need to use a myopic rule and solve for fully optimal behavior.

**Example:**  $T = 0$

If  $T = 0$ , then the individual must settle immediately. We suppose the individual has utility function,  $b(x)$ , and a perceived predation risk level,  $R_j(t)$ , for each site  $j \in H$ . Therefore to choose the site with maximal utility, the individual applies the Dynamic Programming Equation and chooses site  $j^*$ , where

$$\text{site } j^* : \quad b(R_{j^*}(0)) = \max_{j \in H} \{ \mathbb{E}b(R_j(0)) \}$$

and if we suppose each site's perceived predation risk level is Uniform on  $[0, 1]$ , then for each  $j$ ,

$$\int_0^1 b(x) f_X(x) dx = \int_0^1 b(x) dx = \int_0^1 1-x dx = \frac{1}{2}.$$

where we substitute in the neutral utility function (for illustration more than anything else) and end up calculating the expectation exactly. One can also calculate the integral above for the other utility functions. Also note that no search cost is accrued if the individual settles immediately. But, if for all  $j \in H$  all the  $R_j(0)$  are the same, then no site is preferable to another (regardless of utility function), and so every site is equally preferred.

**Example:**  $T = 1$

If  $T = 1$ , then the individual may either settle immediately or visit one site, update its perceived predation risk level at that site, and then settle in a site. As in Theorem 2, we write out the

Dynamic Programming Equations,

$$\begin{aligned}
V(0) &= \max_{j \in H} \left\{ \mathbb{E}b(R_j(0)), \sum_{\hat{s}} V_{j,\hat{s}}(1) P(\hat{S}_j(0) = \hat{s}) - c \right\} \\
V_{j,1}(1) &= \max\{\mathbb{E}[b(\text{Beta}(1, 1))], \mathbb{E}[b(\text{Beta}(2, 1))]\} = \max\left\{\frac{1}{2}, \frac{1}{3}\right\} = \frac{1}{2}, \\
V_{j,0}(1) &= \max\{\mathbb{E}[b(\text{Beta}(1, 1))], \mathbb{E}[b(\text{Beta}(1, 2))]\} = \max\left\{\frac{1}{2}, \frac{2}{3}\right\} = \frac{2}{3}, \\
P(\hat{S}_1(0) = 0) &= P(\hat{S}_1(0) = 1) = \frac{1}{2}
\end{aligned}$$

yielding,

$$V(0) = \max\left\{\frac{1}{2}, \frac{1}{2} \cdot \frac{2}{3} + \frac{1}{2} \cdot \frac{1}{2} - c\right\} = \max\left\{\frac{1}{2}, \frac{7}{12} - c\right\}$$

where we obtain utility  $1/2$  if we settle in any of the  $j$  sites, but we obtain utility  $7/12 - c$  if we re-sample any of the  $j$  sites. Therefore, we should re-sample if and only if  $c < 1/12$ .

Note that  $V_{j,s=\hat{s}}(1)$  provides the maximal possible expected utility at time 1, given that the individual visited site  $j$  and observed  $S_j(t) = s$ , and therefore taking the argmax will give us the optimal rule. We call this process backwards induction since we must calculate  $V_{j,s=\hat{s}}(1)$  in order to calculate  $V(0)$ . For larger values of  $T$ , the process is similar, but one can see how it grows in complexity.

### 1.2.7 The Simulation

We wrote a program to simulate our model of habitat selection by solving the Dynamic Programming Equation to calculate the optimal stopping rule, and then simulated an individual using this optimal stopping rule. We let  $H = \{1, 2\}$ , meaning we run the model for the special case where the landscape consists entirely of two sites. The individual is initially ignorant of the predation risk at each site, which we model by setting initial condition:  $(R_1(0), R_2(0)) = (\text{Beta}(1, 1), \text{Beta}(1, 1))$ .

First, the program solves Equation 1.6 for some finite  $T$ , search cost  $c$ , and one of the utility functions,  $b(x)$ , from Equations 1.3-1.5, which all together yield the optimal stopping rule. The simulation then runs forward in time. We fix values for  $p_1$  and  $p_2$ , without loss of generality setting  $p_1 < p_2$ . At time  $t = 0$ , the individual chooses its action according to the optimal stopping rule derived from Equation 1.6. When the individual chooses to settle, the simulation records the true predation risk at the site chosen, whether it is the better site, and how long it took to settle. If two sites are identical (for instance, at the outset, for both sites  $j$  it is true that  $(\alpha_j(t), \beta_j(t)) = (1, 1)$  so they are indistinguishable) then we suppose the individual cannot tell them apart and arrives at site 1 or site 2 with probability 0.5 each.

For example, if the animal decides to settle immediately, and it has distributions of belief  $R_1(0) = R_2(0)$  distributed like a Beta random variable with  $\alpha = \beta = 1$ , then with probability 0.5 the animal settles in site 1, and the simulation records: that it chose the better site, a stopping time of 0, and that the predation risk there is  $p_1$ . However, with probability 0.5, the animal settles in site 2 and in this case the simulation records: it chose the worse site, a stopping time of 0, and that the predation risk there is  $p_2$ .

If the animal visits site  $j$  then we simulate the cue-sensing event with a Bernoulli random variable with parameter  $p_j$  and the individual updates its perceived predtion risk level at site  $j$  according to Bayesian Updating, as described in Subsection 1.2.3. We assume as a modeling hypothesis that  $p_1$  and  $p_2$  are properties of the habitat sites independent of the observer and can

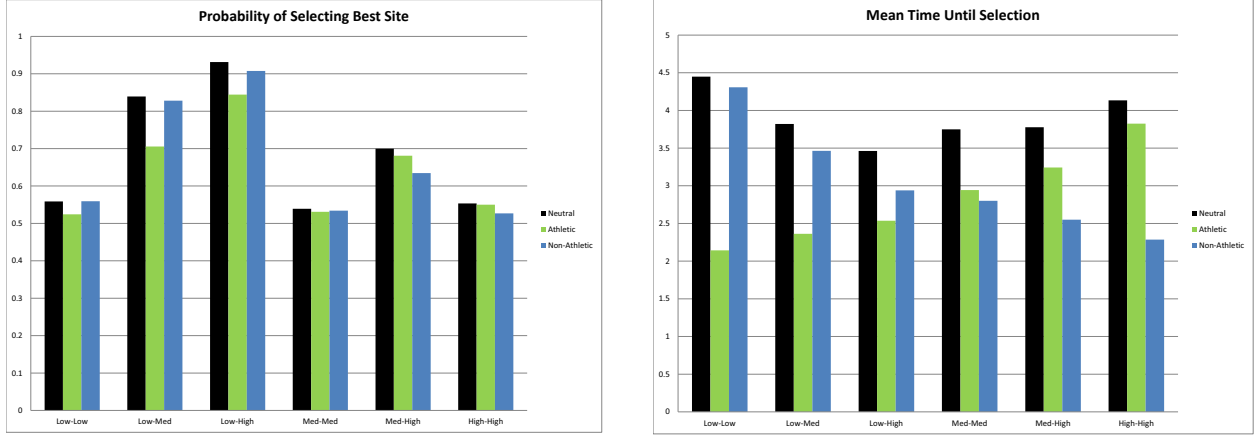


Figure 1.3: The graph on the left plots the probability that an individual employing the optimal stopping rule derived in Equation 1.6 chooses the site with least predation risk, in a range of landscape types, with search cost,  $c = 0.01$ , and finite total time for search,  $T = 5$ , by simulating 10,000 individuals and recording which site they chose. In the graph on the right, we plot the mean time taken by 10,000 simulated individuals to settle in either habitat site.

be empirically measured, and that they represent the probabilities of observing cues of predation risk in site 1 and site 2 respectively, so in simulating the cue-sensing event it suffices to sample a random variable.

## 1.3 Results

In this section we calculate statistics of the simulation discussed in Subsection 1.2.7 to study the effects of varying the search cost,  $c$ , and the total search time,  $T$ , and compare among the different utility functions.

### 1.3.1 Comparison of Performances

The probability of selecting the best site is calculated by running the simulation described in Subsection 1.2.7 10,000 times and calculating the proportion of successes. The average stopping time is calculated at the same time, as well as the mean predation risk, which is calculated by taking the average of the predation risks of the sites selected in each run of the model. We repeat this across a range of landscape values for every combination of low, medium, and high predation risk at each of the two sites.

Low predation risk is defined as  $p = 0.1$ , medium predation risk is defined as  $p = 0.5$  and high predation risk is defined as  $p = 0.75$ . In comparisons of two sites of the same predation risk level, we set one site as having predation risk less than the other by 0.05. For instance, this means that in the “low-low” landscape, the landscape with two sites of low predation risk, we set  $p_1 = 0.1$  and  $p_2 = p_1 + 0.05 = 0.15$ .

We observe in Figure 1.3 that when the search cost is low ( $c = 0.01$ ) and the predation risk at at least one of the habitat sites is low, that the non-athletic individual has a higher probability of selecting the best habitat site than the athletic individual. However, this relationship switches when at least one habitat site has high predation risk (with the exception of the “low-high” landscape). Curiously, when both sites have medium predation risk,  $(p_1, p_2) = (0.5, 0.55)$ , no individual clearly

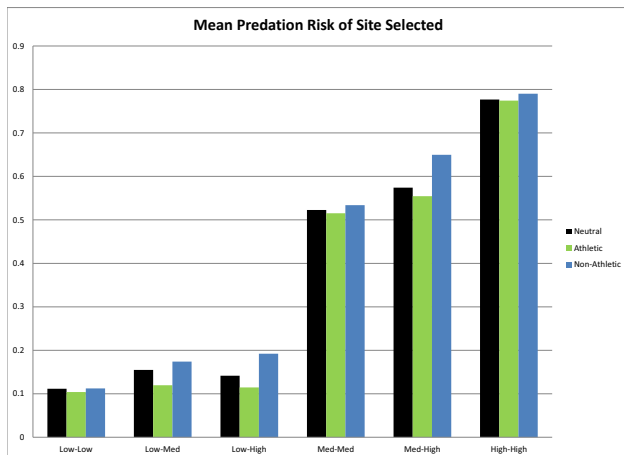


Figure 1.4: The mean predation risk of the site chosen by 10,000 simulated individuals employing the optimal stopping rule derived in Equation 1.6 with search cost  $c = 0.01$  and finite total time for search  $T = 5$ , plotted against a range of landscapes with varying predation risk.

outperforms the other.

As the landscape transitions from sites of low predation risk to sites of high predation risk, the mean time until the athletic and non-athletic individuals make their selection evinces a clear trend. As we see in Figure 1.3, the non-athletic individual responds to increasing predation risk in the landscape by decreasing the mean time it takes to make its selection from 4.25 to 2.25. The athletic individual responds to increasing predation risk by spending more time until selecting a habitat site, in the mean.

The mean predation risk of the site obtained by an individual using the optimal stopping rule depends on the difference between the predation risk levels at the two sites and the probability with which the individual selects the best site. This is shown in Figure 1.4 for the same range of landscapes we consider in Figure 1.3.

Indeed, one of the things the figure suggests is that even though there may be a significant difference in the probability of one individual selecting the best site over another, if the two sites are very similar (as in Figure 1.4; the “low-low,” “medium-medium,” and “high-high” landscapes), then the difference in the mean predation risk of the sites chosen by either individual will decrease. Given that other properties of a habitat site that may be of interest to an animal, and the difficulty seen in discerning between them, it may be that in these cases predation risk would be completely ignored in a comparison.

Now, we consider the statistics above (the probability of selecting the best site, the average stopping time, and the mean predation risk at the site selected) for 10,000 runs of the simulation, but with search cost  $c = 0.02$  instead of  $c = 0.01$ .

To investigate the effect of the total search time on an individual’s probability of success and its mean time until settling, we run the simulation in Subsection 1.2.7 for  $c = 0.01$  and  $T = 10$ , over the same range of landscapes, with 10,000 runs. The results are reported in Figure 1.6.

The ordering among the athletic, non-athletic, and neutral individuals (in terms of the probability of choosing the site with least predation risk) is maintained by increasing  $T = 5$  to  $T = 10$ , though we note that the probabilities increase somewhat for each individual.

We see that when predation risk is low at both sites, the mean time until selection by the non-athletic individual exceeds that of the neutral individual when  $T = 10$ , whereas the order was reversed when  $T = 5$ . Elsewhere the ordering is maintained, with the neutral individual taking the

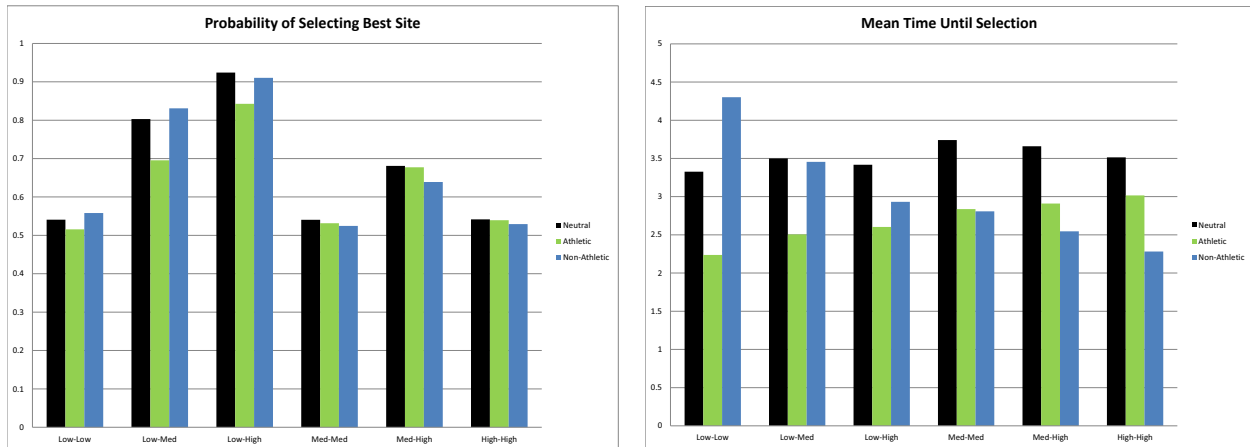


Figure 1.5: Plots of the probability that an individual employing the optimal stopping rule derived in Equation 1.6 chooses the site with least predation risk, and the mean time it takes to settle in either habitat site, over a range of landscape types, with medium search cost,  $c = 0.02$ , and finite total time for search,  $T = 5$ , calculated by simulating 10,000 individuals.

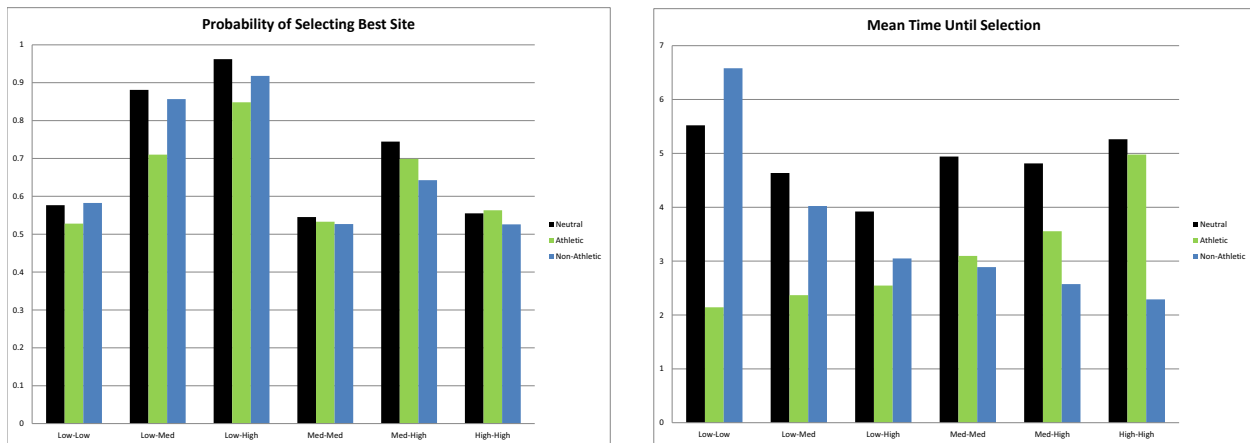


Figure 1.6: Plots of the probability that an individual employing the optimal stopping rule derived in Equation 1.6 chooses the site with least predation risk, and the mean time it takes to settle in either habitat site, over a range of landscape types, with search cost  $c = 0.01$  and larger, finite total time for search,  $T = 10$ , calculated by simulating 10,000 individuals.

longest mean time until selection, and the athletic individual exceeding the non-athletic individual for landscapes with predation risk higher than “medium-medium.”

It is also worth noting that we see a fairly linear relationship between increasing risk at the landscape level, and the mean time until selection of the athletic and non-athletic individuals when  $T = 5$ . But when  $T = 10$ , we see a nonlinear relationship, especially when both sites have low predation risk (for the non-athletic individual), and when both sites have high predation risk (for the athletic individual).

### 1.3.2 Analysis of Some Simulation Results

In our simulations, we observe that athletic individuals tend to spend a greater amount of time on the process of habitat selection when predation risk in the landscape is high, than the amount of time they spend when predation risk in the landscape is low, and than the amount of time spent by sedentary individuals in the same landscape. Conversely, sedentary individuals tend to spend a greater amount of time on the process of habitat selection when predation risk is low, than when predation risk is high, and than the amount of time spent by athletic individuals in the same landscape. We analyze this mathematically by deriving sufficient conditions under which we can determine that if a neutral individual chooses to revisit a site, then an athletic individual certainly will (and vice versa), and conditions under which if a neutral individual chooses to settle then a sedentary individual certainly will. We also analyze the opposing responses of sedentary and athletic individuals to low or high predation risk.

Let  $X_1(t)$  and  $X_2(t)$  be the perceived predation risk levels of site 1 and site 2 (the only habitat sites available in the landscape). We consider the Bellman equation,  $V(t)$ , which determines the maximal possible expected utility from choosing the optimal strategy,

$$V(t) = \max \left\{ \mathbb{E}[b(X_1(t))], \mathbb{E}[b(X_2(t))], \sum_{\hat{s}} V_{1,\hat{s}}(t+1)P(\hat{S}_1(t) = \hat{s}) - c, \sum_{\hat{s}} V_{2,\hat{s}}(t+1)P(\hat{S}_2(t) = \hat{s}) - c \right\}$$

and observe that an individual will decide that it is better to visit another site than to settle at one of the previously visited sites if at least one of the  $\sum_{\hat{s}} V_{j,\hat{s}}(t+1)P(\hat{S}_j(t) = \hat{s}) - c$  values exceeds both of the  $\mathbb{E}[b(X_j(t))]$  values. Since the  $P(\hat{S}_j(t) = \hat{s})$  sum to 1, this sum is a convex combination of the  $V_{j,\hat{s}}(t+1)$ .

We consider  $V_{2,1}(t+1)$ , or the case where positive evidence of predation risk is found at site 2,

$$V_{2,1}(t+1) = \max \left\{ \mathbb{E}[b(X_1(t))], \mathbb{E} \left[ b(X_2(t+1)) | \hat{S}_2(t) = 1 \right], \sum_{\hat{s}} V_{1,\hat{s}}(t+2)P(\hat{S}_1(t) = \hat{s}) - c, \sum_{\hat{s}} V_{2,\hat{s}}(t+2)P(\hat{S}_2(t) = \hat{s}) - c \right\}$$

We ignore the contributions from the  $V(t+2)$  terms. Instead, we focus on the event that the maximum of  $V_{2,1}(t+1)$  comes from the second term, when

$$\mathbb{E} \left[ b(X_2(t+1)) - \mathbb{E}b(X_1(t)) | \hat{S}_2(t) = 1 \right] \geq 0.$$

We note that if the  $V(t+2)$  terms do in fact exceed the other two terms, then they will do so by the above inequality holding, but with  $t+2$  substituted in for  $t+1$  and  $t+1$  for  $t$ , so essentially we are considering the  $V(t+2)$  terms as well.

Applying the utility function of the athletic individual,

$$\mathbb{E} \left[ b_a(X_2(t+1)) - \mathbb{E} [b_a(X_1(t))] | \hat{S}_2(t) = 1 \right] \geq \mathbb{E} \left[ b_a(X_2(t+1)) - b_a(\mathbb{E}X_1(t)) | \hat{S}_2(t) = 1 \right]$$

by Jensen's Inequality. Now, applying the Mean Value Theorem inside the expected value, there exists  $\xi(t) \in [\mathbb{E}X_1(t), \mathbb{E}[X_2(t+1)|\hat{S}_2(t) = 1]]$  such that

$$\mathbb{E} \left[ b_a(X_2(t+1)) - b_a(\mathbb{E}X_1(t)) | \hat{S}_2(t) = 1 \right] = \mathbb{E} \left[ b'_a(\xi(t)) (X_2(t+1) - \mathbb{E}X_1(t)) | \hat{S}_2(t) = 1 \right].$$

If we apply the utility function of the neutral individual,

$$\mathbb{E} \left[ b_n(X_2(t+1)) - \mathbb{E}b_n(X_1(t)) | \hat{S}_2(t) = 1 \right] = -\mathbb{E} \left[ X_2(t+1) - \mathbb{E}X_1(t) | \hat{S}_2(t) = 1 \right].$$

We can make a comparison between the difference of the expected utilities according to the athletic or the neutral utility function, by finding  $\xi(t)$  such that,

$$\begin{aligned} \mathbb{E}[b'_a(\xi(t))] &= -1 \\ -\gamma e^{-\gamma\xi(t)} &= -1 \\ \xi(t) &= \frac{1}{\gamma} \left( \gamma + \ln \left( \frac{1}{\gamma} \right) \right) = 1 - \frac{\ln(\gamma)}{\gamma}. \end{aligned}$$

Therefore, when  $\mathbb{E}X_1(t)$  and  $\mathbb{E}[X_2(t+1)|\hat{S}_2(t) = 1] \geq 1 - \ln(\gamma)/\gamma$ , we have  $b'_a(\xi(t)) \leq -1$  for  $\xi \in [\mathbb{E}X_1(t), \mathbb{E}[X_2(t+1)|\hat{S}_2(t) = 1]]$  and we obtain the comparison,

$$\mathbb{E} \left[ b_a(X_2(t+1)) - \mathbb{E}b_a(X_1(t)) | \hat{S}_2(t) = 1 \right] \geq \mathbb{E} \left[ b_n(X_2(t+1)) - \mathbb{E}b_n(X_1(t)) | \hat{S}_2(t) = 1 \right] \quad (1.7)$$

which means that when the right-hand side is greater than zero, the neutral individual will decide to revisit site 2, and therefore the left-hand side must be greater than zero, and the athletic individual will decide to revisit site 2 as well. We note that there may also be times when the neutral individual decides not to revisit site 2 (when the right hand side is negative), but the athletic individual may settle (the left hand side may be positive).

In the program we run, the curvature parameter for the athletic utility function,  $\gamma$  in  $b_a$ , is set  $\gamma = 5$ , so the critical point derived above works out to,

$$\xi(t) = 1 - \frac{\ln(\gamma)}{\gamma} \approx 0.678$$

which is between 0.55 and 0.75, the highest “medium” predation risk and lowest “high” predation risk values we use in our simulation. This may explain why the athletic individual begins to behave similarly (in terms of the mean time until selection) to the neutral individual when predation risk gets higher – more and more decisions in the optimal stopping rule come down to a comparison where the elements,  $\mathbb{E}X_1(t)$  and  $\mathbb{E}[X_2(t+1)|\hat{S}_2(t) = 1]$  exceed this critical value.

The actual computation of the critical point,  $\xi(t)$ , above was straightforward. So we repeat this computation to compare the stopping time behaviors of the athletic individual with the sedentary individual, and the neutral individual with the sedentary individual. First, the comparison of the athletic individual with the sedentary individual:

$$\begin{aligned} b'_a(\xi(t)) &= b'_s(\xi(t)) \\ -\gamma e^{\gamma(x-1)} &= -\gamma e^{-\gamma x} \\ \gamma(x-1) &= -\gamma x \\ x &= \frac{1}{2}. \end{aligned}$$

This helps explain the qualitatively different simulated behaviors of the athletic and sedentary individuals on the interval  $[0, 1/2]$  and  $[1/2, 1]$ . For comparisons of values of  $\mathbb{E}X_1(t)$  and  $\mathbb{E}[X_2(t+1)|\hat{S}_2(t) = 1]$  above  $1/2$ , the athletic individual is more likely to re-sample than the sedentary individual, and these values are more frequently above  $1/2$  in landscapes where predation risk ranges from medium to high, and therefore an individual's estimates will more likely be higher.

Now, the comparison of the sedentary individual with the neutral individual:

$$\begin{aligned} b'_s(\xi(t)) &= b'_n(\xi(t)) \\ -\gamma e^{-\gamma x} &= -1 \\ x &= -\frac{1}{\gamma} \ln\left(\frac{1}{\gamma}\right) = \frac{\ln(\gamma)}{\gamma} \end{aligned}$$

In the program we run, the curvature parameter for the sedentary utility function,  $\gamma$  in  $b_s$ , is set  $\gamma = 5$  (just as for the athletic individual), so the critical point works out to,

$$\xi(t) = 1 - \frac{\ln(\gamma)}{\gamma} \approx 0.322$$

which is between 0.15 and 0.5, the highest “low” predation risk and lowest “medium” predation risk values we use in our simulation. This may explain why the sedentary individual begins to behave similarly (in terms of the mean time until selection) to the neutral individual when predation risk in the landscape is low – more and more decisions in the optimal stopping rule come down to a comparison where the elements,  $\mathbb{E}X_1(t)$  and  $\mathbb{E}[X_2(t+1)|\hat{S}_2(t) = 1]$  are below this critical value.

Therefore, the average stopping time behavior of an individual, relative to other individuals, depends on there being a critical point at which the slope of its decreasing preference for increasing predation risk exceeds that of another individual. The average stopping time behavior also depends on the concavity or convexity of this function, in order to ensure that the ordering of the comparison of the slopes of the two individual's utility functions is maintained over the interval of all predation risk values greater than or less than (in the case of the athletic individual or the sedentary individual, respectively) this critical value.

## 1.4 Conclusion

In this chapter, we motivated, developed, simulated, and analyzed a mathematical model of the process of habitat selection in natively-dispersing brush mice. To motivate our model, we detailed the history of Best-Choice models in mathematics, and decision processes in ecology. We developed a model which included Bayesian Updating of belief, so that the individual could update its beliefs regarding predation risk at each potential habitat site from cues found while moving about the landscape. We derived the optimal strategy for the model by solving the associated Stochastic Dynamic Program which maximizes the possible expected benefit of eventually settling in one of a set of habitat sites, with respect to a utility function representing the individual's perception of how predation risk affected them personally.

We then programmed a simulation of this model which measured the probability of an individual selecting the best site, the mean predation risk at the obtained site, and the average stopping time (specifically, the mean amount of time spent until settling). In our analysis of our model, we compared the probabilities of an individual achieving the best site, over all types of individuals in landscapes of varying predation risk. In addition, we also compared the mean predation risk at the achieved site, and we compared the average amount of time spent on the process of habitat selection, for the range of individuals and landscape types.

Athletic individuals have the greatest average stopping times when predation risk in the landscape is high, and sedentary individuals have the greatest average stopping times when predation risk in the landscape is low. The relationship looks almost linear when  $T = 5$ , but becomes nonlinear when  $T = 10$ . The probability of selecting the best site is greater for sedentary individuals than athletic individuals when predation risk in the landscape is low, and increases with the difference in the predation risk levels at each site. The probability of selecting the best site is greater for athletic individuals than sedentary individuals when predation risk is high, and increases with the difference in the predation risk levels at each site.

From analyzing the average stopping times mathematically, we determined that an individual stops sooner or later than a neutral individual depending on the concavity of the individual's utility function, and the value of the individual's estimates of the predation risk at each site relative to the critical values,  $\ln(\gamma)/\gamma$ ,  $1/2$ , and  $1 - \ln(\gamma)/\gamma$ , which depend on the curvature of the utility function,  $\gamma$ .

Ecological studies have demonstrated variation in patterns of dispersal, relating to habitat selection, but it is often hard to determine the individual decisions being made by the subjects of the experiment. By developing our model, we attempted to provide a framework of simple, mathematical objects and relationships which connect animal behavior to empirically measurable properties of the landscape and habitat sites. We consider only one parameter of interest at each habitat site: predation risk. However, we were able to connect behaviors, such as the means by which an individual updates its beliefs, its perception of the predation risk at the site, the utility it assigns to a value of predation risk, the total time it has for search, and the cost it associates with visiting a potential habitat site, etc. to quantities that could potentially be measured in the field.



## Chapter 2

# A Diffusion Model of Constrained Animal Motion

### 2.1 Introduction

Though deterministic processes like migration may influence animal movement on a broad scale, on a fine scale the movement of an animal across a landscape looks much more random. Brillinger cites examples of a ringed seal constrained within an ice covered lake, an elephant seal sojourning from an island off Santa Barbara, and an elk living in the Starkey Reserve of Eastern Oregon [3].

In each of these examples, we observe that in order to model realistic animal motion across a landscape, it is necessary to model natural boundaries that the animal cannot cross. Real-life examples of this are roads, fences, rivers, climate boundaries, ice sheets, elevations, etc. To this end, we consider a simple example of a diffusion on a finite interval.

We determine that the diffusion is positive recurrent or ergodic (henceforth referred to as ergodic) if and only if it is recurrent (Theorem 4), which occurs when the range size,  $L$  exceeds or equals the critical domain size,  $L_c = \pi\sigma^2/(2\mu)$  (Theorem 3). In this case the diffusion has an invariant probability density, which we provide in Theorem 5. When  $L$  is strictly less than the critical domain size, the diffusion is transient (Theorem 3), and we show that in this case explosion occurs in finite time with positive probability (Theorem 6), whereas when the diffusion is recurrent explosion occurs in finite time with probability zero.

### 2.2 The Diffusion

We consider the process defined by

$$dX_t = -\mu \tan\left(\frac{\pi}{2L}X_t\right) dt + \sigma dB_t, \quad X(0) = x \in (-L, L). \quad (2.1)$$

This process has drift function given by  $f_X(x) = -\mu \tan(\pi/(2L)x)$  and diffusion function given by  $g_X(x) = \sigma$ , and we note that  $g_X^2(x) = \sigma^2$ , the diffusion coefficient. If  $\sigma^2 = 0$ , then the process is deterministic and as we see in Figure 2.1 the drift function attracts the process towards  $X_t = 0$ , a stable state. The process converges faster if  $\mu$  is large. It is especially important to note that as the process gets close to  $-L$  or  $L$ , the opposing drift becomes asymptotically large:

$$\lim_{x \rightarrow L} -\mu \tan\left(\frac{\pi}{2L}L\right) = \lim_{x \rightarrow L} -\mu \tan\left(\frac{\pi}{2}\right) = -\infty$$

and similarly the limit as  $x$  goes to  $-L$  is  $+\infty$ . Therefore it is impossible that  $|X_t|$  should ever exceed  $L$ , if  $X_0 \in (-L, L)$ , though as we will demonstrate later the process may diverge to the boundary depending on the relationship between  $\mu$ ,  $\sigma^2$ , and  $L$ .

We can solve for a closed form expression under different conditions on the parameters of  $X_t$ .

### 2.2.1 Case: $\sigma = 0$

If  $\sigma = 0$  then

$$dX_t = -\mu \tan\left(\frac{\pi}{2L}X_t\right) dt.$$

If  $\mu = 0$ , then the process is trivial:  $X_t = X_0$  for all  $t$ . So we suppose that  $\mu \neq 0$ .

Separating variables and integrating both sides,

$$\int_0^t -\frac{1}{\mu} \frac{\cos\left(\frac{\pi}{2L}X_s\right)}{\sin\left(\frac{\pi}{2L}X_s\right)} dX_t = \int_0^t ds$$

and we recall that, for any nonzero function  $f$  differentiable on  $[0, t]$ ,

$$\int_0^t \frac{f'(s)}{f(s)} ds = \ln(f(t)) - \ln(f(0))$$

so we have

$$-\frac{1}{\mu} \left[ \ln\left(\sin\left(\frac{\pi}{2L}X_t\right)\right) - \ln\left(\sin\left(\frac{\pi}{2L}X_0\right)\right) \right] = t.$$

Solving for  $X_t$ ,

$$\begin{aligned} \ln\left(\sin\left(\frac{\pi}{2L}X_t\right)\right) &= \ln\left(\frac{\pi}{2L}X_0\right) - \mu t \\ \sin\left(\frac{\pi}{2L}X_t\right) &= \sin\left(\frac{\pi}{2L}X_0\right) e^{-\mu t}. \end{aligned}$$

Letting  $c_1 = \sin(\pi/(2L)X_0)$ ,

$$X_t = \frac{2L}{\pi} \sin^{-1}(c_1 e^{-\mu t}). \quad (2.2)$$

We can notice immediately that if  $X_0 = 0$ , then  $X_t = 0$  and if  $t = 0$ ,  $X_t = 2L/\pi \sin^{-1}(\sin(\pi/(2L)X_0)) = X_0$ .

If  $\mu < 0$ , then  $e^{-\mu t} > 1$  and for all  $X_0$  there exists  $t$  such that  $c_1 e^{-\mu t} > 1$ . But,  $\sin^{-1}(x)$  is only defined for  $|x| < 1$ . Therefore we only ever consider  $\mu \geq 0$ .  $\square$

### 2.2.2 Case: $\mu = 0$

If  $\mu = 0$  then

$$dX_t = \sigma dB_t.$$

If  $\sigma = 0$  then for all  $t$ ,  $X_t = X_0$ . We suppose  $\sigma \neq 0$ . Integrating,

$$X_t = X_0 + \int_0^t \sigma dB_s = X_0 + \sigma B_t.$$

so, unsurprisingly, the process is purely Brownian motion with diffusion coefficient  $\sigma^2$ .  $\square$

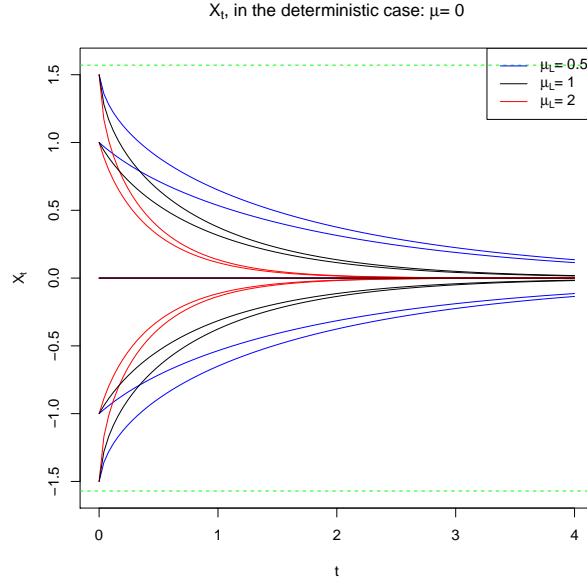


Figure 2.1: We plot the process,  $X_t$ , with  $\sigma^2 = 0$ , across the following values for the drift,  $\mu = (0.5, 1, 2)$ , given the following initial values,  $X_0 = (-1.5, -1, 0, 1, 1.5)$ .

### 2.2.3 Transforming $X_t$ to a process on all of $\mathbb{R}$

The tangent function has asymptotes at  $-\pi/2$  and  $\pi/2$ , so that the closer the process tries to get to the asymptote, the greater the velocity of the particle in the opposite direction. This keeps the process in this interval for all time,  $t$ . However, if we are to discuss transience, recurrence, and positive recurrence, we need to transform  $X_t$  into a process on the whole real line. We do so by defining,

$$Y_t = \tan\left(\frac{\pi}{2L}X_t\right) = \phi\left(\frac{\pi}{2L}X_t\right).$$

Ito's Lemma provides the following expression for  $dY_t$ ,

$$dY(t) = A\phi(\zeta)dt + \phi'(\zeta)g(t)dB_t\Big|_{\zeta=\pi/(2L)X_t},$$

where

$$A\phi = \phi'(\zeta)f(\zeta) + \frac{g^2(\zeta)}{2}\phi''(\zeta)\Big|_{\zeta=\pi/(2L)X_t}.$$

Calculating the derivatives,

$$\begin{aligned} \phi'\left(\frac{\pi}{2L}X_t\right) &= \frac{d}{dx}\tan(x)\Big|_{x=\pi/(2L)X_t} = \frac{\pi}{2L}\sec^2\left(\frac{\pi}{2L}X_t\right). \\ \phi''\left(\frac{\pi}{2L}X_t\right) &= \frac{\pi}{2L}\frac{d}{dx}(\sec^2(x))\Big|_{x=\pi/(2L)X_t} = \frac{\pi}{2L}2\sec(x)\frac{d}{dx}\left(\frac{1}{\cos(x)}\right)\Big|_{x=\pi/(2L)X_t} \\ &= \left(\frac{\pi}{2L}\right)^2 2\sec(x)\frac{\sin(x)}{\cos^2(x)}\Big|_{x=\pi/(2L)X_t} = \left(\frac{\sqrt{2}\pi}{2L}\right)^2 \sec^2\left(\frac{\pi}{2L}X_t\right)\tan\left(\frac{\pi}{2L}X_t\right). \end{aligned}$$

Therefore,

$$\begin{aligned} A\phi &= -\frac{\mu\pi}{2L} \sec^2\left(\frac{\pi}{2L}X_t\right) \tan\left(\frac{\pi}{2L}X_t\right) + \frac{\sigma^2}{2} \left(\frac{\sqrt{2}\pi}{2L}\right)^2 \sec^2\left(\frac{\pi}{2L}X_t\right) \tan\left(\frac{\pi}{2L}X_t\right) \\ &= -\left(\frac{\mu\pi}{2L} - \left(\frac{\sigma\pi}{2L}\right)^2\right) \sec^2\left(\frac{\pi}{2L}X_t\right) \tan\left(\frac{\pi}{2L}X_t\right). \end{aligned}$$

yielding,

$$dY_t = -\left(\frac{\mu\pi}{2L} - \left(\frac{\sigma\pi}{2L}\right)^2\right) \sec^2\left(\frac{\pi}{2L}X_t\right) \tan\left(\frac{\pi}{2L}X_t\right) dt + \frac{\sigma\pi}{2L} \sec^2\left(\frac{\pi}{2L}X_t\right) dB_t.$$

Let  $\mu_L = \mu\pi/(2L)$  and  $\sigma_L = \sigma\pi/(2L)$ . With the substitutions  $\pi/(2L)X_t = \tan^{-1}(Y_t)$  and  $\sec^2(\tan^{-1}(Y_t)) = (1 + Y_t^2)$ , we have

$$dY_t = -(\mu_L - \sigma_L^2)(1 + Y_t^2)Y_t dt + \sigma_L(1 + Y_t^2) dB_t. \quad (2.3)$$

so our drift function is  $f_Y(y) = -(\mu_L - \sigma_L^2)y(1 + y^2)$  and our diffusion function is  $g_Y(y) = \sigma_L(1 + y^2)$ .

In order to understand our new process,  $Y_t$ , we consider some simplifying cases in which we can derive closed-form solutions to the corresponding SDE.

#### 2.2.4 Case: $\sigma_L^2 = \mu_L$

We note that if  $\sigma_L^2 = \mu_L$ , then

$$dY_t = \sigma_L(1 + Y_t^2)dB_t,$$

and the process is exclusively diffusion. However, we cannot give a closed form expression for  $Y_t$ .

#### 2.2.5 Case: $\sigma_L^2 = 0$

If  $\sigma_L^2 = 0$ , then the process is exclusively deterministic, and we can solve for a closed form expression for  $Y_t$ . Considering  $dY_t$ ,

$$dY_t = -\mu_L(1 + Y_t^2)Y_t dt.$$

Integrating,

$$\int_0^t -\frac{1}{\mu_L} \frac{dY_s}{(1 + Y_s^2)Y_s} = \int_0^t ds = t.$$

To solve the integral, we use partial fractions, obtaining,

$$\frac{1}{(1 + x^2)x} = -\frac{x}{1 + x^2} + \frac{1}{x}.$$

Returning to the integral,

$$\begin{aligned} -\frac{1}{\mu_L} \left( \frac{1}{2} \int_0^t -\frac{2Y_s}{1 + Y_s^2} dY_s + \int_0^t \frac{1}{Y_s} dY_s \right) &= t \\ -\frac{1}{\mu_L} \left( \frac{1}{2} (\ln(1 + Y_s^2) - \ln(1 + Y_0^2)) \right) &= -t \\ \ln \left( \frac{Y_t}{1 + Y_t^2} \frac{1 + Y_0^2}{Y_0^2} \right) &= -\frac{\mu_L}{2} t \\ \frac{Y_t^2}{1 + Y_t^2} &= \frac{Y_0^2}{1 + Y_0^2} e^{-\mu_L t/2}. \end{aligned}$$

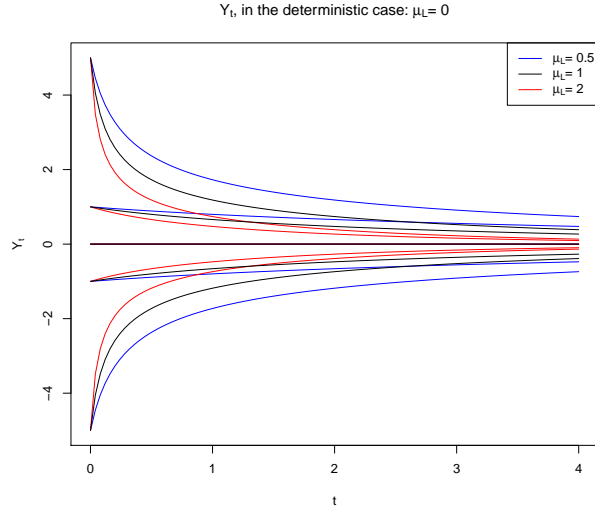


Figure 2.2: We plot the transformed process,  $Y_t$ , with  $\sigma^2 = 0$ , across the following values for the (transformed) drift,  $\mu_L = (0.5, 1, 2)$ , given the following initial values,  $Y_0 = (-5, -1, 0, 1, 5)$ .

Solving for  $Y_t^2$  and taking the square root yields,

$$Y_t = \frac{Y_0 e^{-\mu_L t/4}}{\sqrt{1 + Y_0^2 (1 - e^{-\mu_L t/2})}}.$$

We immediately note that if  $Y_0 = 0$ ,  $Y_t = 0$  for all  $t \in \mathbb{R}^+$  and that if  $t = 0$ ,  $Y_t = Y_0$ .

We plot this function in Figure 2.2 for different values of  $Y_0$ , noting that it has an attractive stable state at  $Y_t = 0$ . The (transformed) drift,  $\mu_L$ , affects the convergence to the stable state; increasing  $\mu_L$  increases the rate of convergence of the process.

## 2.3 Results

In this section, we use the diffusion,  $Y_t$ , to derive conditions on the diffusion,  $X_t$ , for transience and ergodicity. A diffusion on  $\mathbb{R}$  is recurrent if the diffusion reaches every point in  $\mathbb{R}$  with probability 1. More precisely, recurrence requires that for all  $x$  and  $a$  in  $\mathbb{R}$ , with  $X_0 = x$ ,  $P(X_t \text{ reaches } a) = 1$ . On the other hand, a diffusion is transient if it returns to every arbitrary point,  $a$ , at most finitely often. More precisely, a diffusion is transient if, for all  $x, a \in \mathbb{R}$ ,  $P(\sup\{t : X_t = a\} = \infty) = 0$ .

**Theorem 3** (Recurrence). *The process  $X_t$  with drift function  $f_X(x) = -\mu \tan(\pi/(2L)x)$  and diffusion function,  $g_X^2(x) = \sigma^2$ , is recurrent if  $L \geq \pi\sigma^2/(2\mu)$  and transient if  $L < \pi\sigma^2/(2\mu)$ .*

*Proof.* We derive results for the diffusion  $Y_t$  with drift function  $f_Y(y)$  and diffusion function  $g_Y^2(y)$  as in Equation 2.3. Theorem 4.4. of [1] states that if  $f_Y(y)$  and  $g_Y^2(y)$  are locally Lipschitzian, and that  $g_Y^2(y)$  does not vanish anywhere, then the diffusion is either recurrent or transient, and that the diffusion is recurrent if and only if

$$\int_{-\infty}^0 \exp\{I(y, 0)\} dy = \infty \quad \text{and} \quad \int_0^{\infty} \exp\{-I(0, y)\} dy = \infty,$$

where,

$$I(0, y) = \int_0^y \frac{2f(z)}{g^2(z)} dz.$$

We prove the statement for  $L = \pi/2$  and  $\mu = 1$  and provide relevant results for general  $L$  and  $\mu$  as necessary. We consider the second integral first and begin by calculating  $I(0, y)$ ,

$$\begin{aligned} I(0, y) &= \int_0^y \frac{2f(z)}{g^2(z)} dz = \int_0^y \frac{-2(1-\sigma^2)z(1+z^2)}{\sigma^2(1+z^2)^2} dz \\ &= (1-1/\sigma^2) \int_0^y \frac{2z}{1+z^2} dz \end{aligned}$$

and, with the substitution,  $u = z^2$ , (and therefore  $du = 2z dz$ ),

$$= (1-1/\sigma^2) \int_0^{y^2} \frac{du}{1+u} = (1-1/\sigma^2) \log(1+y^2).$$

Therefore the exponential,  $\exp\{-I(0, y)\}$ , is of form,

$$\begin{aligned} \exp\{-I(0, y)\} &= \exp\{-(1-1/\sigma^2) \log(1+y^2)\} \\ &= \exp\left\{\log\left((1+y^2)^{-(1-1/\sigma^2)}\right)\right\} \\ &= (1+y^2)^{-(1-1/\sigma^2)} = (1+y^2)^{(1/\sigma^2-1)}. \end{aligned}$$

As it turns out, we can compute the integral directly if we restrict the values of  $\sigma^2$ . Considering the integral,

$$\begin{aligned} \int_0^\infty \exp\{-I(0, y)\} dy &= \int_0^\infty (1+y^2)^{(1/\sigma^2-1)} dy \\ \text{(letting } u = y^2) &= \int_0^\infty \frac{(1/2)u^{-1/2}}{(1+u)^{1-1/\sigma^2}} du. \end{aligned}$$

Observe the integral form of the Beta function:

$$\int_0^\infty \frac{u^{a-1}}{(1+u)^{a+b}} du = \frac{\Gamma(a)\Gamma(b)}{\Gamma(a+b)} \quad \text{if } \operatorname{Re}(a) > 0, \operatorname{Re}(b) > 0.$$

In our case,  $a = 1/2$  and  $b = 1/2 - 1/\sigma^2$ , but the stronger condition on  $\sigma^2$  comes from  $a + b > 0$ :

$$1 - 1/\sigma^2 > 0 \quad \text{requiring} \quad \sigma^2 > 1.$$

The integral form of the Beta function holds exactly when the integral converges, so if  $\sigma^2 \leq 1$ , the integral diverges. Therefore if  $\sigma^2 \leq 1$  the diffusion is recurrent, and if  $\sigma^2 > 1$  the diffusion is transient.

Considering the first integral, we note that

$$I(y, 0) = \int_y^0 \frac{2f(z)}{g^2(z)} dz = - \int_0^y \frac{2f(z)}{g^2(z)} dz = -I(0, y).$$

Therefore,

$$\begin{aligned} \int_{-\infty}^0 \exp\{-I(0, y)\} dy &= \int_{-\infty}^0 (1 + y^2)^{(1/\sigma^2 - 1)} dy \\ &= \int_0^{\infty} (1 + y^2)^{(1/\sigma^2 - 1)} dy \end{aligned}$$

by even-ness of the integrand. But then that's equal to the second integral, and we find that they pose the same condition on  $\sigma^2$ .

Before we move on, let's finish computing that integral, noting that  $\Gamma(1/2) = \sqrt{\pi}$ ,

$$\int_0^{\infty} \exp\{-I(0, y)\} dy = \frac{\sqrt{\pi} \Gamma(1/2 - 1/\sigma^2)}{2 \Gamma(1 - 1/\sigma^2)}.$$

For general  $L$ , it is easy to work back through the proof to find that

$$\int_0^{\infty} \exp\{-I(0, y)\} dy = \frac{\sqrt{\pi} \Gamma(1/2 - \mu_L/\sigma_L^2)}{2 \Gamma(1 - \mu_L/\sigma_L^2)}$$

and if  $1 - \mu_L/\sigma_L^2 \geq 0$ , equivalently  $L \geq \pi\sigma^2/(2\mu)$ , the diffusion is recurrent and if  $L < \pi\sigma^2/(2\mu)$  the diffusion is transient.  $\square$

A recurrent diffusion is said to be ergodic if it reaches every arbitrary point in finite time, e.g. for a diffusion  $X_t$  and  $x$  and  $a \in \mathbb{R}$ , with  $X_0 = x$ ,  $\mathbb{E}\tau_a^x < \infty$ , where  $\tau = \inf\{t \geq 0 : X_t = a\}$ .

**Theorem 4** (Ergodicity). *The process  $X_t$  with drift function  $f_X(x) = -\mu \tan(\pi/(2L)x)$  and diffusion function,  $g_X^2(x) = \sigma^2$ , is ergodic if  $L \geq \pi\sigma^2/(2\mu)$ , exactly when the process is recurrent.*

*Proof.* We derive results for the diffusion  $Y_t$  with drift function  $f_Y(y)$  and diffusion function  $g_Y^2(y)$  as in Equation 2.3. We recall that  $f_Y(y)$  and  $g_Y^2(y)$  are locally Lipschitzian, and  $g_Y^2(y)$  does not vanish anywhere. By Theorem 7.1 in [1], the diffusion is ergodic if it is recurrent (requiring  $L \geq \pi\sigma^2/(2\mu)$ ) and one has

$$\int_{-\infty}^0 \frac{2}{g^2(y)} \exp\{-I(y, 0)\} dy < \infty \quad \text{and} \quad \int_0^{\infty} \frac{2}{g^2(y)} \exp\{I(0, y)\} dy < \infty.$$

Again, let  $L = \pi/2$  and  $\mu = 1$ . We set about computing the second integral. We have already computed  $\exp\{I(0, y)\}$  in the proof of Theorem 3 so immediately we have,

$$\begin{aligned} \int_0^{\infty} \frac{2}{g^2(y)} \exp\{I(0, y)\} dy &= \int_0^{\infty} \frac{2}{\sigma^2(1 + y^2)^2} (1 + y^2)^{(1 - 1/\sigma^2)} dy \\ &= \frac{2}{\sigma^2} \int_0^{\infty} (1 + y^2)^{(-1 - 1/\sigma^2)} dy \\ &= \frac{2}{\sigma^2} \int_0^{\infty} \frac{(1/2)u^{-1/2}}{(1 + u)^{(1 + 1/\sigma^2)}} du \\ &= \frac{\sqrt{\pi} \Gamma(1/2 + 1/\sigma^2)}{\sigma^2 \Gamma(1 + 1/\sigma^2)} \end{aligned}$$

using, again, the integral form of the Beta function, which is defined if and only if  $(1/2)$ ,  $(1/2 + 1/\sigma^2)$  and  $(1 + 1/\sigma^2) > 0$ . All these requirements are trivially satisfied since we only consider  $\sigma^2 \geq 0$ . The same holds for general  $L$ .

Considering the first integral (with  $L = \pi/2$ ),

$$\begin{aligned} \int_{-\infty}^0 \frac{2}{g^2(y)} \exp\{-I(y, 0)\} dy &= \int_{-\infty}^0 \frac{2}{\sigma^2(1+y^2)^2} (1+y^2)^{(-1-1/\sigma^2)} dy \\ &= \frac{2}{\sigma^2} \int_0^{\infty} (1+y^2)^{(-1-1/\sigma^2)} dy, \end{aligned}$$

where we switch the limits of integration by the even-ness of the integrand. Note that this is equal to the second integral, which we already computed. It is not hard to see that the integrals are also equal for general  $L$ .

Thus, the conditions for ergodicity are given by either integral condition and are trivial. Therefore, if the diffusion is recurrent, then it is ergodic.  $\square$

**Theorem 5** (Invariant Density of  $X_t$ ). *The process  $X_t$  with drift function  $f_X(x) = -\mu \tan(\pi/(2L)x)$  and  $g_X^2(x) = \sigma^2$  has a unique invariant probability density if  $L \geq \pi\sigma^2/(2\mu)$ , and it is given by,*

$$\pi_X(x) = \frac{1}{\sqrt{\pi}} \frac{\Gamma(1 + \mu_L/\sigma_L^2)}{\Gamma(1/2 + \mu_L/\sigma_L^2)} (\cos(x))^{2/\sigma_L^2}. \quad (2.4)$$

*Proof.* We begin by finding the invariant density of the diffusion  $Y_t$ . We recall that  $f_Y(y)$  and  $g_Y^2(y)$  are locally Lipschitz, and  $g_Y^2(y)$  does not vanish anywhere. Corollary V.9.3 in [1] states that our diffusion,  $Y_t$ , admits a unique invariant probability if it is ergodic, and the invariant probability is absolutely continuous with respect to Lebesgue measure (meaning  $\pi_Y(dy) = \pi_Y(y) dy$ ), where the density  $\pi_Y(y)$  is given by, for  $y \in (-\infty, \infty)$ ,

$$\pi_Y(y) = \frac{c}{g^2(y)} e^{I(0,y)}$$

where  $c$  is the normalizing constant. We've calculated  $\exp\{I(0, y)\}$  before, so we have directly that

$$\pi_Y(y) = \frac{c}{\sigma_L^2(1+y^2)^2} (1+y^2)^{(1-\mu_L/\sigma_L^2)} = \frac{c}{\sigma_L^2} (1+y^2)^{-(1+\mu_L/\sigma_L^2)}.$$

We integrate to find  $c$ , noting

$$\int_{-\infty}^{\infty} \frac{c}{\sigma_L^2} (1+y^2)^{-(1+\mu_L/\sigma_L^2)} dy = 1 \iff \frac{1}{c} = \frac{2}{\sigma_L^2} \int_0^{\infty} (1+y^2)^{-(1+\mu_L/\sigma_L^2)} dy.$$

Having already calculated this integral in the previous proof, we obtain

$$\frac{1}{c} = \frac{\sqrt{\pi} \Gamma(1/2 + \mu_L/\sigma_L^2)}{\sigma_L^2 \Gamma(1 + \mu_L/\sigma_L^2)}$$

yielding our desired result,

$$\pi_Y(y) = \frac{1}{\sqrt{\pi}} \frac{\Gamma(1 + \mu_L/\sigma_L^2)}{\Gamma(1/2 + \mu_L/\sigma_L^2)} (1+y^2)^{-(1+\mu_L/\sigma_L^2)}. \quad (2.5)$$

Now that we have these results for  $Y_t$ , the transformed process, we can derive the invariant density for  $X_t$  on the interval  $(-L, L)$ .

We recall that the process  $Y_t = \tan(\pi/(2L)X_t)$ . If  $Y_t$  is ergodic on  $\mathbb{R}$  then  $X_t$  is ergodic on  $(-L, L)$ . Therefore, if  $L \geq \pi\sigma^2/(2\mu)$ ,  $X_t$  has an invariant probability density, this density is absolutely continuous with respect to Lebesgue measure, and additionally, we can find it from the

derived density for  $Y_t$ . As these are invariant probabilities, their distribution is independent of  $t$  and so we need only refer to the processes as  $X$  and  $Y$ . Indeed, denoting by  $F_X(x)$  and  $F_Y(y)$  the invariant distribution functions of  $X$  and  $Y$ , we have that

$$F_X(x) = P(X \leq x) = P(Y \leq y) = P\left(Y \leq \tan\left(\frac{\pi}{2L}x\right)\right) = F_Y\left(\tan\left(\frac{\pi}{2L}x\right)\right).$$

Taking derivatives,

$$\begin{aligned} \pi_X(x) &= \frac{d}{dx}F_X(x) = \frac{d}{dx}F_Y\left(\tan\left(\frac{\pi}{2L}x\right)\right) \\ &= \frac{\pi}{2L}f_Y\left(\tan\left(\frac{\pi}{2L}x\right)\right)\sec^2\left(\frac{\pi}{2L}x\right) \\ &= \frac{c}{\sigma_L^2}\frac{\pi}{2L}\left(1 + \tan^2\left(\frac{\pi}{2L}x\right)\right)^{-(1+\mu_L/\sigma_L^2)}\sec^2\left(\frac{\pi}{2L}x\right) \\ &= \frac{c}{\sigma_L^2}\frac{\pi}{2L}(\sec^2(x))^{-1/\sigma_L^2} = \frac{c}{\sigma_L^2}\frac{\pi}{2L}(\cos(x))^{2/\sigma_L^2} \end{aligned}$$

and inputting the normalization constant derived in the previous proof,

$$\pi_X(x) = \frac{1}{\sqrt{\pi}}\frac{\Gamma(1 + \mu_L/\sigma_L^2)}{\Gamma(1/2 + \mu_L/\sigma_L^2)}(\cos(x))^{2/\sigma_L^2}.$$

□

If a diffusion  $Y_t$  is transient on  $\mathbb{R}$ , then it approaches an infinite limit,  $+\infty$  or  $-\infty$  as  $t$  increases. We set  $Y_t = \infty$  for  $t \geq \tau$  if  $Y_t \rightarrow \infty$  as  $t \uparrow \tau < \infty$ , where  $\tau$  is the explosion time. Similarly, we set  $Y_t = -\infty$  for  $t \geq \tau$  if  $Y_t \rightarrow -\infty$  as  $t \uparrow \tau < \infty$ .

Therefore, for  $X_t$  which is constrained to  $(-\pi/2, \pi/2)$ , we set  $X_t = \infty$  for  $t \geq \tau$  if  $X_t \rightarrow \pi/2$  as  $t \uparrow \tau < \infty$ , where  $\tau$  is the explosion time (to the boundary,  $\pi/2$ ). Similarly,  $X_t = -\pi/2$  for  $t \geq \tau$  if  $X_t \rightarrow -\pi/2$  as  $t \uparrow \tau < \infty$ .

**Theorem 6** (Explosion Time of  $X_t$ ). *The probability that explosion occurs for the process  $X_t$  in finite time is zero, i.e.  $P(\tau < \infty) = 0$ , if and only if the process is ergodic, requiring  $L \geq \pi\sigma^2/(2\mu)$ .*

*Proof.* We consider the process  $Y_t$ . By Feller's Criterion for Explosion [2],  $P(\tau_{+\infty} < \infty) = 0$  if and only if

$$\int_0^\infty e^{-I(y)}\left(\int_0^y \frac{1}{g^2(z)}e^{I(z)}dz\right)dy = \infty. \quad (2.6)$$

We can show that the integral converges if  $L \geq \pi\sigma^2/(2\mu)$  by bounding the integral in Equation 2.6 by one that converges.

The inner integrand can be written as,

$$\frac{1}{g^2(z)}e^{I(z)} = \frac{1}{\sigma_L^2}(1+z^2)^{-(1+\mu_L/\sigma_L^2)}$$

so the inner integral can be bounded by,

$$\begin{aligned} \int_0^y \frac{1}{\sigma_L^2}(1+z^2)^{-(1+\mu_L/\sigma_L^2)}dz &\leq \int_0^\infty \frac{1}{\sigma_L^2}(1+z^2)^{-(1+\mu_L/\sigma_L^2)}dz \\ &= \frac{\sqrt{\pi}}{2\sigma_L^2}\frac{\Gamma(1/2 + \mu_L/\sigma_L^2)}{\Gamma(1 + \mu_L/\sigma_L^2)} = c \end{aligned}$$

for all  $\sigma_L^2 \geq 0$ . Now,

$$\begin{aligned} c \int_0^\infty e^{-I(y)} dy &= c \int_0^\infty \frac{1}{\sigma^2} (1+y^2)^{-(1-\mu_L/\sigma_L^2)} \\ &= c \frac{\pi \Gamma(1/2 - \mu_L/\sigma_L^2)}{2 \Gamma(1 - \mu_L/\sigma_L^2)} < \infty \end{aligned}$$

$$\begin{aligned} c \int_0^\infty e^{-I(y)} dy &= c \int_0^\infty \frac{1}{\sigma_L^2} (1+y^2)^{-(1-\mu_L/\sigma_L^2)} \\ &= c \frac{\pi \Gamma(1/2 - \mu_L/\sigma_L^2)}{2 \Gamma(1 - \mu_L/\sigma_L^2)} < \infty \end{aligned}$$

so long as  $1 - \mu_L/\sigma_L^2 > 0$ , which requires  $L < \pi\sigma^2/(2\mu)$ . Therefore, if this condition on  $L$  is satisfied, the process is transient and the integral in the Feller condition is finite, implying  $P(\tau_{+\infty} < \infty) > 0$ .

We can show that the integral in Equation 2.6 diverges by bounding it from below by a divergent integral. Let  $m \in \mathbb{R}^+$ . Then,

$$\int_0^\infty e^{-I(y)} \left( \int_0^y \frac{1}{g^2(z)} e^{I(z)} dz \right) dy \geq \int_0^\infty e^{-I(y)} \left( \int_0^m \frac{1}{g^2(z)} e^{I(z)} dz \right) dy$$

and define

$$M = \int_0^m \frac{1}{g^2(z)} e^{I(z)} dz < \infty.$$

Then,

$$\int_0^\infty e^{-I(y)} \left( \int_0^y \frac{1}{g^2(z)} e^{I(z)} dz \right) dy \geq M \int_0^\infty e^{-I(y)} dy$$

which as we saw above diverges if  $L \geq \pi\sigma^2/(2\mu)$ . Therefore the Feller criterion yields that  $P(\tau_{+\infty} < \infty) = 0$ .  $\square$

## 2.4 Simulation

We would like to verify our results with a simulation, and in particular understand the behavioral differences between the diffusion we model when it is transient and ergodic.

We use the open-source programming and statistics language, ‘‘R-Project’’ to simulate the diffusion described in Equation 2.1. We discretize time and simulate paths of the auxiliary process,  $Y_t$ , with  $L = \pi/2$  for simplicity. When we display the positions of the diffusion, we do so by transforming the positions back with the arctan function. The process,  $Y_t$ , is simulated by calculating displacements according to

$$\Delta y = -(1 - \sigma^2)y(1 + y^2)\Delta t + \sqrt{\sigma^2(1 + y^2)}\Delta B_t,$$

The term  $\Delta B_t$  measures the displacement of the increment  $B_{t_2} - B_{t_1}$ , for two times  $t_1$  and  $t_2$  (assuming  $t_1 \leq t_2$ ). The increments of Brownian Motion are independent Gaussian random variables with mean 0 and variance  $t_2 - t_1$ , so  $\Delta B_t$  is simulated by sampling from a Normal distribution at each time  $t$ , with mean 0 and variance given by the step size. Therefore we call the R function,

```
> rnorm(num.animals, 0, sqrt(dispatchsize))
```

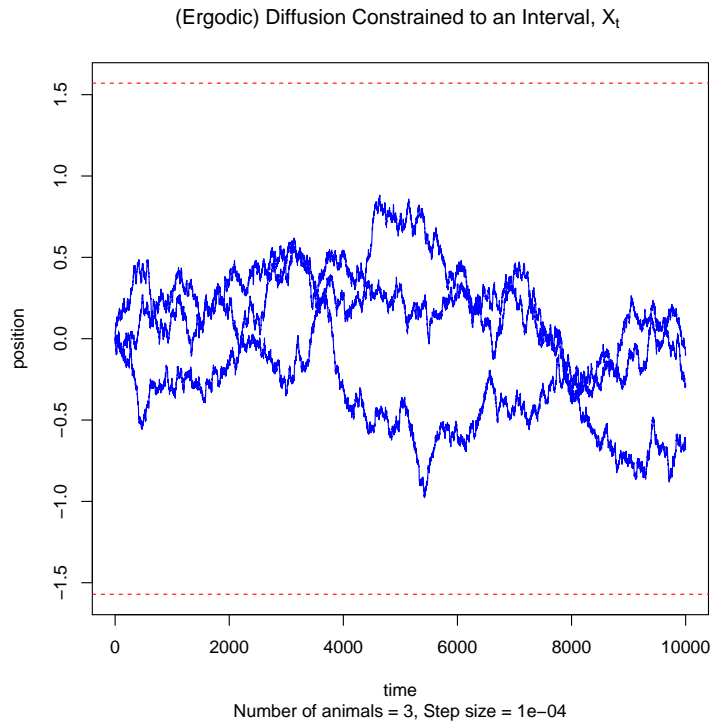


Figure 2.3: Three realizations of the constrained diffusion,  $X_t$ , with  $\mu = 1$  and  $\sigma^2 = 1$ , under ergodic conditions:  $L = \pi/2$ .

as `rnorm` takes the standard deviation instead of the variance in its third argument.

We calculate the frequency distribution of the states of the diffusion after a long time,  $t$ . More specifically, the total number of time steps,  $T$ , and the step size,  $s$  seem to require  $Ts \gg 1$ . We use  $Ts > 10$  with  $s = 1e - 05$  sufficient to model Brownian motion and therefore  $T = 1e06$ .

We use the `hist` function (`h <- hist(pos[,num.steps+1], breaks='FD')`) to obtain a list containing the densities (`h$density`) of the position data at the last time step (henceforth referred to as the terminal positions) and the endpoints of the intervals that contain them (`h$breaks`). We evaluate the density function at the right endpoints by appending a zero to the front (`append(0, h$density)`) when we take the total variation distance below.

Figure 2.4 is a graphical comparison of the densities of the terminal positions of 1,000 realizations of the constrained diffusion with the theoretical invariant probability density function we compute in Theorem 2.5. The bin width is calculated by the “Freedman-Diaconis” R method. We use the total-variation distance to compare the two distributions, where total-variation distance, for two distributions  $\mu$  and  $\nu$  on a common space,  $\Omega$ , is defined as,

$$d_{TV}(\mu, \nu) = \frac{1}{2} \sum_{x \in \Omega} |\mu(x) - \nu(x)|.$$

We compute the total-variation distance between the simulated densities and the theoretical distribution with the following command, yielding,

```
> error = (1/2)*sum(abs(append(0, h$density) - disp.limit(h$breaks)))
+ *(h$breaks[2]-h$breaks[1]);
> error
```

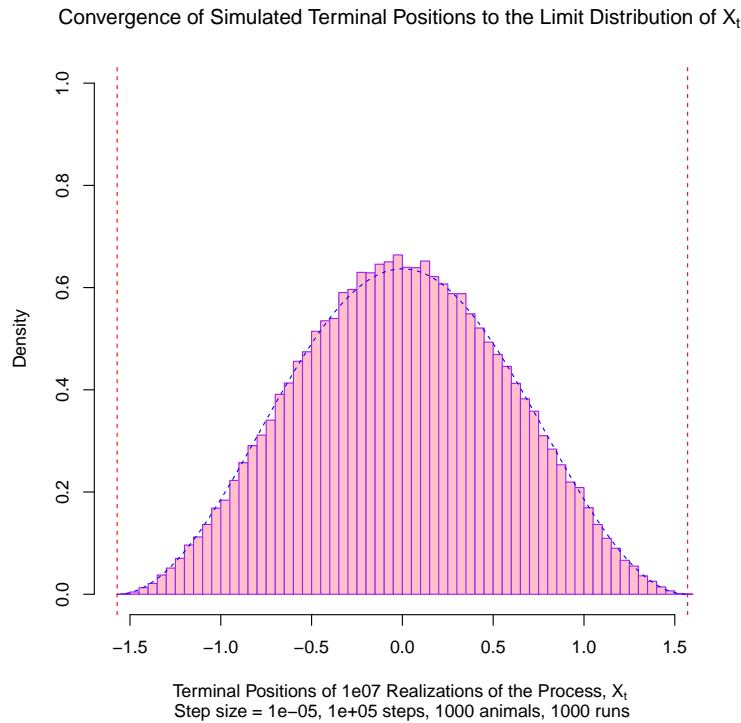


Figure 2.4: A histogram displaying the relative frequencies of terminal positions of  $1e07$  sampled paths of the constrained diffusion,  $X_t$ , after  $1e06$  steps, with step size  $1e-05$ , plotted against the invariant probability density function of the constrained diffusion,  $X_t$ .

[1] 0.018

It is also interesting to compare the invariant density of the diffusion to the results of the simulation under the transient condition. We observe in Figure 2.5 that all the mass is now at a narrow band at the boundaries. The simulation lets each realization of the process run for  $1e+05$  time steps, giving each realization sufficient time for explosion. In terms of the simulation, this means that the positions of the realizations overflow the machine precision. To account for this in the simulation, without tampering with the actual positions of the realizations at any time, we set a variable to record the sign of each realization and once the position of the realization overflows the machine precision, the simulation instead reports  $\pi/2$  or  $-\pi/2$ , depending on the value of the recorded sign.

To investigate further, we simulate three realizations of the constrained diffusion,  $X_t$ , in Figure 2.6. As predicted by the transience of the diffusion, it appears that it will not return infinitely often to each state in the interval, as compared to the ergodic diffusion which frequently returns to states in the interval, even on the small time interval we simulate. Additionally, we note the simulation indicates that the transient diffusion can diverge to one of the two boundaries and get stuck there. In fact, the diffusion's distance from the origin exceeds the machine precision of the computer, which is on the order of  $10^{15}$ . This demonstrates that under the transient condition, the diffusion explodes in finite time.

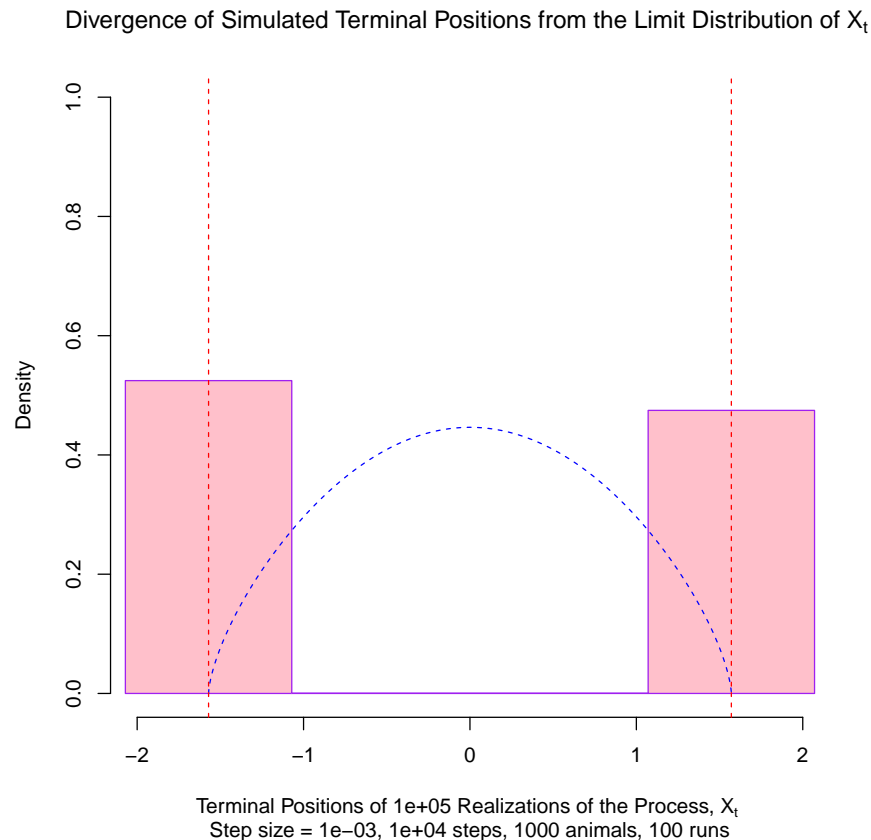


Figure 2.5: A histogram displaying the relative frequencies of positions of  $1e+05$  sampled paths of the constrained diffusion under transient conditions,  $X_t$ , after  $1e+05$  steps, with step size  $1e-05$ , plotted against the invariant probability density function of the constrained diffusion,  $X_t$ .

## 2.5 Conclusion

We have shown that the diffusion can be transient or ergodic, depending on  $L$  as in the following table:

Condition	Status
$L \geq \pi\sigma^2/(2\mu)$	Ergodic
$L < \pi\sigma^2/(2\mu)$	Transient

Since  $Y_t$  serves as a 1-1 transformation of the state space of the diffusion,  $X_t$ , on the interval  $(-L, L)$ , the same conditions on  $L$  apply to the status of  $X_t$  – whether it is transient or ergodic. We originally considered  $X_t$  because of its potential usefulness in modeling the motion of an animal within a region bounded by impassable obstacles, and considered  $Y_t$  for its usefulness in being able to apply known theorems to determine its properties.

The conditions and statuses above tell us that the kind of behavior the animal demonstrates depends on the relationship between any drift in the system, how diffusive its movement is, and whether the size of the range to which the animal is constrained is greater than or less than the critical domain size. For instance, if the animal’s movement is highly diffusive and the range is small, our model says that the animal will move to the boundary of the domain in finite time and

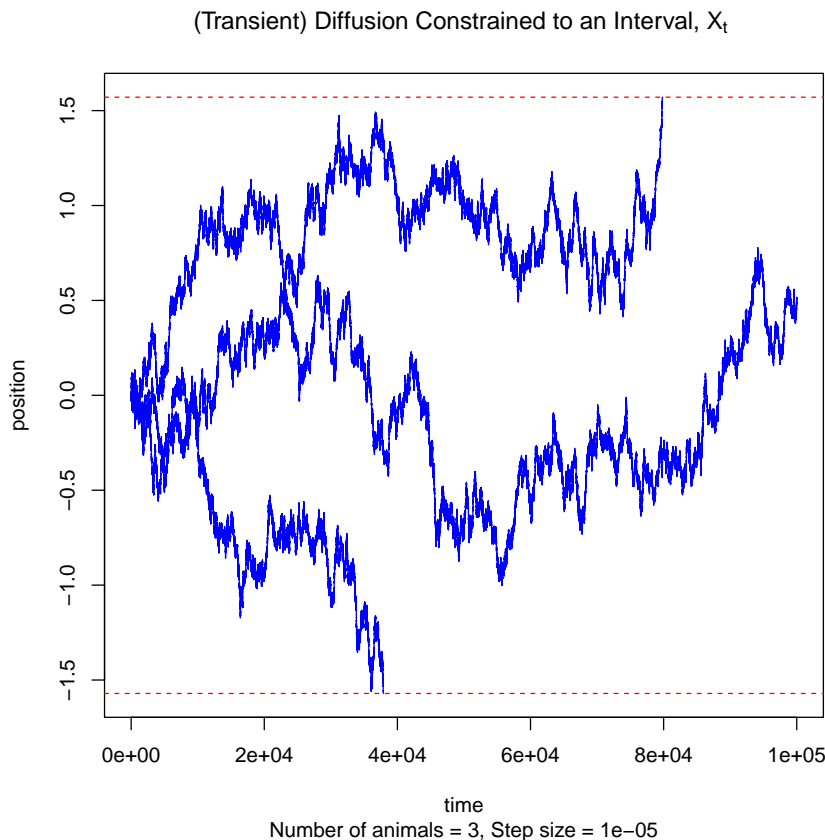


Figure 2.6: Three realizations of the constrained diffusion,  $X_t$ , under transient conditions ( $\sigma^2 = 3$ ) with  $L = \pi/2$ .

stay there forever. A nice metaphor for this is that of an energetic monkey in a small cage at the zoo, who spends all of his time rattling at the windows and climbing the walls. However, if the drift term is large enough, then the diffusion is ergodic. We extend our metaphor a little bit by putting a magical pile of bananas in the center of the cage, which never go bad and which never run out. If the monkey has this kind of treat in the center of his cage, then he will return to the center many, many times, and only approach the very edge, without getting “stuck” there. An important note to point out here is that as silly as this example might seem, the reason for the animal’s motion could be behavioral, and this behavior can be captured by a diffusion model just as well as the familiar physical concepts of pressure, forces, and drift.

In the analysis of a species’ movement across the landscape, the data may indicate a qualitative “type” of movement, specifically whether its motion is transient, point-recurrent, null-recurrent, or ergodic. The diffusion we study cannot discriminate between point-recurrence and recurrence or null-recurrence and ergodicity. However, there are species whose community is distributed across “islands” with limited connectivity. Examples of these include those species of birds and insects studied by metapopulations or island biogeography [12]. To study these animals, it would be important to develop a model in which the diffusion was point-recurrent among all points in one region, but not another. Our original diffusion,  $X_t$ , could fit this purpose by a periodic extension to the whole real line. However, this only yields one type of connectivity – no connectivity – and identical regions.

Brillinger identifies important biological questions: “how do we allocate resources?”, “how do different species co-exist?”, “how do we measure changes in the landscape?” [3]. These questions can be addressed by determining an appropriate stochastic differential equation model given data. In order to determine how well the model does at describing and predicting the animal behaviors which inform its movement, one would like to compare statistics of the species distribution (mean, variance, expected crossing times, etc.). But to do that, one must first establish the conditions under which a diffusion indeed has a stationary distribution in the first place. We have presented such a preliminary analysis.



## Chapter 3

# Models of Group Decision Making in Bees

### 3.1 Introduction

We model the process of a hive dividing and swarming, during which a new nesting site must be found, usually a tree cavity. Martin Lindauer, a German zoologist, first decoded two aspects of the waggle dance by which bees communicate information regarding a nest site. The waggle dance is performed by a female scout (all scouts are females, in fact) by running straight forward some distance and then looping back around and doing the run again. He determined that the length of the straight run part of the waggle dance communicates the distance to a nesting site, and the angle of the dance indicates direction.

Seeley, Visscher, & Passino [22] repeated this experiment, but instead of using painted dots to keep the bees straight as Lindauer had done, they used video recordings and numbered labels on all bees. In one case, they determined that the entire decision process took about 16 hours of dance activity, over the course of three days. The process seemed to have two qualitatively different stages, each taking up about half the time: in the first stage all sites were considered and danced for uniformly, and in the second stage one site emerged as the site being danced for by a majority of bees; towards the end of the process, a majority turned into nearly all of the bees dancing for this site.

To assess the accuracy of the swarm in finding the best nest site, Seeley, Visscher, & Passino [22] set up five nest boxes, four mediocre ones and one excellent one (based on the size of the living space). They determined that the quality of the site, as perceived by each individual scout, determines the number of circuits done in the waggle dance. Also, the greater the strength of dancing for a particular site, the larger the number of scouts who decide to visit that site next. Even though these scouts were motivated to visit this site based on the waggle dance they viewed, the amount of time they dance for this site is independent of the length of the viewed waggle dance. The quorum-sensing method, which determines when a nest site has the support of a majority of the scouts, balances the demands of accuracy and limited time for search, by lasting just long enough to gather diverse, independent opinions, but only lasting the time required to minimize decision error.

We are aware of only one other model of decision making in bees, which we introduce here briefly in order to compare and contrast with our own model. List, Elsholtz, & Seeley [15] developed a state-based individual model of scouts in a swarm. Let  $x_{i,t} = (s_{i,t}, d_{i,t})$  be the state of bee  $i$  at time  $t$ , where  $s_{i,t} \in \{0, 1, \dots, b\}$  is the site for which bee  $i$  is dancing at time  $t$  and  $d_{i,t}$  is the amount of

time remaining for its dance. Initially (at time  $t = 1$ ), all scouts are assumed not to be dancing for a site, and thus  $x_{i,1} = (0, 0)$ .

If  $s_{i,t} = 0$ , then a scout is not dancing for a site at time  $t$ , and thus must decide what site it will dance for in the next time step, at  $t + 1$ . Denote by  $p_{j,t+1}$  the probability that a scout finds site  $j$  and dances for this site at time  $t + 1$ , (and  $p_{0,t+1}$  the probability that a scout gets lost and finds no site). We require  $\sum_{j=0}^b p_{j,t+1} = 1$ . Then,

$$s_{i,t+1} = \left\{ \begin{array}{ll} 0 & \text{with probability } p_{0,t+1} \\ 1 & \text{with probability } p_{1,t+1} \\ \vdots & \vdots \\ b & \text{with probability } p_{b,t+1} \end{array} \right\}$$

where

$$p_{j,t+1} = (1 - \lambda)\pi_j + \lambda f_{j,t},$$

with these definitions:

- $\lambda$  is the amount of interdependence among scouts, represented by a value in  $[0, 1]$ ,
- $\pi_j$  is the *a priori* probability of finding the  $j^{\text{th}}$  site,
- $f_{j,t}$  is the proportion of scouts dancing for site  $j$  at time  $t$ .

We note that if  $\lambda = 0$ , then all scouts ignore all others, and if  $\lambda = 1$  the probability of finding a site is completely determined by the proportion of scouts dancing for it.

Then, they define  $d_{i,t+1}$ ,

$$d_{i,t+1} = \left\{ \begin{array}{ll} q_j e^{T_\sigma} & \text{with probability } 1 - \mu \\ K e^{T_\sigma} & \text{with probability } \mu \end{array} \right\}$$

where  $T_\sigma$  is a Normally distributed random variable with mean  $\mu$  and variance  $\sigma^2$ , and  $K \geq 0$ . We note that if  $\mu = 0$  then each individual makes a completely independent assessment, and if  $\mu = 1$ , then every scout mimics each other and the dance duration fluctuates around the quality-independent constant,  $K$ .

If  $s_{i,t} \neq 0$ , then

$$x_{i,t+1} = \left\{ \begin{array}{ll} (s_{i,t}, d_{i,t} - 1) & \text{if } d_{i,t} > 1 \\ (0, 0) & \text{else.} \end{array} \right\},$$

so while a scout is dancing for a site, the duration of its dance reduces by one second per second and goes back to the case described above when it finishes dancing.

They consider two different criteria for selection according to the concept of a “quorum” outlined by Seeley, [22]. The first (weak) criterion is that site  $j$  is selected if at time  $t$  the number of scouts dancing for site  $j$  exceeds the number of scouts dancing for any other site:  $n_{j,t} \geq n_{k,t}$  for all  $k \neq j$  and  $k \neq 0$  in their notation. Under the second (strong) criterion, site  $j$  is selected if the number of scouts dancing for it exceeds twice the number of scouts dancing for any other site:  $n_{j,t} \geq 2n_{k,t}$  for all  $k \neq j$ ,  $k \neq 0$ , and more than 20% of the scouts are dancing at time  $t$ :  $n_{0,t} < 0.8n$ , where  $n$  is the total number of scouts.

## 3.2 The Model

We now introduce our model of site selection in a swarm. Let  $b$  equal the number of habitable nest boxes. We consider the possibility that some nesting sites will not be considered habitable, and that some scout bees may get lost and not find a site. We lump these two cases together and say that the set of all possible sites is  $B^{(0)} = \{\emptyset, 1, 2, \dots, b\}$ , where  $\emptyset$  represents the case where a scout finds an uninhabitable or no box. Also, let  $B = \{1, 2, \dots, b\}$  be the set of all habitable nest boxes.

Let  $m$  be the number of scout bees. It seems reasonable to assume  $m \gg b$ .

### 3.2.1 Initializing the Model

We initialize the model by assuming the  $m$  bees distribute themselves uniformly across the  $b + 1$  possible nest boxes. Let  $N_i(0)$  be the random variable for the number of scouts at box  $i$  at time  $t$ .

Bees return from each box and perform a “waggle dance” for an amount of time corresponding how much they like that box. Let  $D_{ij}(0)$  be the amount of time that the  $j^{\text{th}}$  scout dances for site  $i$ . For each box  $i$ , there are  $N_i(0)$  scouts dancing, so  $j \in \{1, \dots, N_i(0)\}$ .

Let us also suppose that there is some uncertainty in the measurement a scout makes of a nest box, and define the  $D_{ij}(0)$  as independent, identically distributed random draws from the random variable  $D_i(0)$ .

Looking across all sites, we require additionally that

$$D_1(0) \prec D_2(0) \prec \dots \prec D_b(0)$$

where  $\prec$  refers to first-order stochastic dominance. If we suppose the  $D_i(0)$  are exponentially distributed, this is done easily enough by setting  $\mathbb{E}D_i(0) = i$ .

By convention, we always assume  $D_\emptyset(0) = 0$  as the unfound sites are not habitable or not sites and thus not worth dancing for.

After all scouts return to the swarm and dance for their location, nest boxes are given scores according to the maximum amount of time danced for a site,  $M_i(0)$ , where,

$$M_i(0) = \max_{j \in \{1 \dots N_i(0)\}} \{D_{ij}(0)\},$$

or by the average amount of time,  $A_i(0)$ , where,

$$A_i(0) = \frac{1}{N_i(0)} \sum_{j=1}^{N_i(0)} \{D_{ij}(0)\}.$$

And of course by convention,  $M_\emptyset(0) = 0$ .

A swarm of bees using a score derived from the maximum time over all the waggle dances for a box may have improved performance over a swarm that scores boxes based on the sum of all waggle dance times for a box. We see this by considering a swarm where, by initial dumb luck, many bees have visited the worst habitable site and only a few have visited the best. The scores for the worst site easily overwhelm those of the best site just by number, and it is possible that the best site will be ignored.

However, the score of a box measured by a swarm using the maximum time increases only slightly with increasing numbers of scouts dancing for a site, leading us to believe that the better site will be more accurately scored higher a greater percentage of the time.

### 3.2.2 Redistributing the Scouts

The scouts now need to decide what boxes they will visit at time  $t = 1$  based on the scores they have seen at time  $t = 0$ .

#### The “Maximum” condition

We suppose that no scout will knowingly visit a nest box with a poorer score than the box it last visited. Therefore, each of the  $N_i(0)$  scouts that visited box  $i$  at time 0 may not visit site any site  $j \in \{1, \dots, b\}$  satisfying the condition,

$$M_j(0) < M_i(0). \quad (3.1)$$

Let  $F_i(0) = \{j : M_j(0) < M_i(0)\}$ . Then, each of the  $N_i(0)$  scouts *may* visit all boxes in the set  $B^{(0)} \setminus F_i(0)$  and scouts are assumed to distribute themselves uniformly across these options.

Note that  $B^{(0)}$  includes any boxes that have not yet been visited, as they have not received a score, and cannot satisfy the condition. This is important to ensure that scouts do not ignore good, but yet undiscovered boxes.

Once the scouts return from their newly selected boxes, we will be able to calculate scores for each box  $i$ ,

$$M_i(1) = \max_{j \in \{1 \dots N_i(1)\}} \{D_{ij}(1)\}.$$

#### The “Average” condition

Alternatively, we can define a method of redistributing the scouts that involves the average (instead of the maximum) dance time. In this method, we require

$$A_j(0) < A_i(0), \quad (3.2)$$

instead of the condition given in Equation 3.1. Let  $G_i(0) = \{j : A_j(0) < A_i(0)\}$ . Then, each of the  $N_i(0)$  scouts *may* visit all boxes in the set  $B^{(0)} \setminus G_i(0)$  and scouts are assumed to distribute themselves uniformly across these options.

We would also like to introduce a discount rate,  $\alpha \in [0, 1]$ , which accounts for the scouts’ depleting energy reserves as time goes on. We implement  $\alpha$  by defining  $D_i(1) \stackrel{d}{=} \alpha D_i(0)$ .

### 3.2.3 General $t$

The model proceeds for general time  $t$  just as it proceeds from time 0 to time 1 in the previous subsections. Specifically, given a number of scouts at each nest box  $i$ ,  $N_i(t-1)$ , we have waggle dance times given by  $D_{ij}(t-1)$  which are independent and identically drawn from  $D_i(t-1) \stackrel{d}{=} \alpha^t D_i(0)$ , which preserves the first-order stochastic dominance, yielding  $D_1(t-1) < \dots < D_b(t-1)$ .

Sites are scored according to the maximum over all waggle times danced for a site, meaning

$$M_i(t-1) = \max_{j \in \{1 \dots N_i(t-1)\}} \{D_{ij}(t-1)\},$$

or according to the average of all waggle times danced for a site,

$$A_i(t-1) = \frac{1}{N_i(t-1)} \sum_{j=1}^{N_i(t-1)} D_{ij}(t-1).$$

Scouts redistribute themselves uniformly over all sites according to the “Maximum” condition that the  $N_i(t-1)$  scouts that visited site  $i$  at time  $t-1$  must visit only those boxes included in the set  $B^{(0)} \setminus F_i(t-1)$ , where  $F_i(t-1) = \{j : M_j(t-1) < M_i(t-1)\}$ , or according to the “Average” condition that a scout may visit only those boxes in the set  $B^{(0)} \setminus G_i(t-1)$ , where  $G_i(t-1) = \{j : A_j(t-1) < A_i(t-1)\}$ .

We suppose that each hive’s scouts only use one of the “Maximum” or “Average” conditions throughout the entire process of dancing for sites and redistributing.

### 3.2.4 Final Stage

We suppose that the swarm has only a finite amount of time, denoted  $n$ , to scout out possible nest cavities.

At time  $t = n$ , after all scouts have returned and finished their waggle dances, the  $M_i(n)$  are evaluated, and the swarm can make its decision. There are a couple of ways this could happen.

#### Sum Method

The swarm may compare the sum over all scores for each site. Specifically, denote the final value of site  $i$ ,  $V_i$ , so that

$$V_i = \sum_{t=0}^n M_i(t), \quad i = 1, \dots, b.$$

#### Last Method

The swarm may compare only the last score for each site. Specifically,

$$V_i = M_i(n), \quad i = 1, \dots, b.$$

In each case, the swarm picks  $j^*$  such that  $V_{j^*} = \max\{V_1, \dots, V_b\}$ .

### 3.2.5 Further Work

If this were not a preliminary attempt to write down and record a model, we would consider the probability that the site selected by the scouts at the final time  $n$  was the best site,  $P(V_{j_n^*} = b)$ , and attempt to prove that as  $n \rightarrow \infty$ , this probability goes to 1.

Similar, we would like to show that as the number of scouts,  $b \rightarrow \infty$ , this probability likewise goes to 1, for sufficiently large  $n$ .

## 3.3 Simulation Results

We develop a simulation in the open-source programming and statistics language, “R-Project.” The simulation assumes the scouts initially distribute themselves uniformly across the available sites, and that the waggle dance times,  $D_i(0)$ , are exponentially distributed with mean  $i$ . The simulation compares the performance of swarms using the “average” and “maximum” redistribution conditions, and the “Sum” and “Last” Final Decision methods.

We study the sensitivity of of the swarm’s success to the rate of decay of the individual’s dance times by comparing the performances of swarms using the “Maximum” condition, and the “Sum” or “Last” final decision methods as we vary the discount rate,  $\alpha$ , from 0.1 to 1, as shown in Figure 3.1.

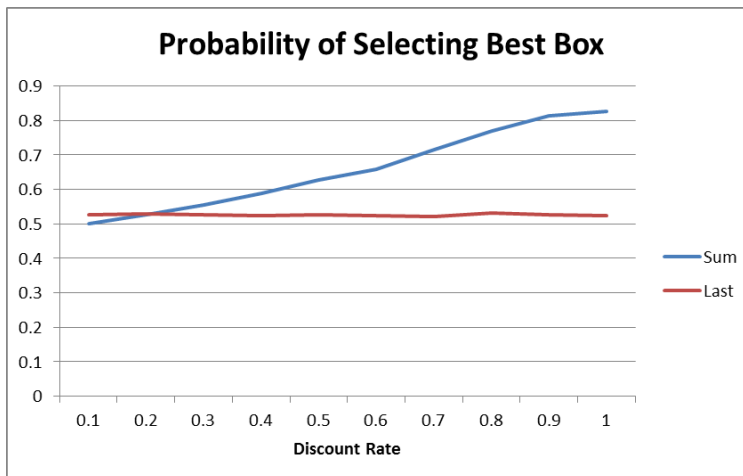


Figure 3.1: The probability of success in finding the best site, as a function of the discount rate  $\alpha$ , for swarms using the “Maximum” condition for redistribution, and either the “Sum” or “Last” Final Decision methods. We simulate 20,000 swarms and compute the average probability of success.

We are interested in determining the conditions required for the “Last” memory method to become sufficiently successful, 95% successful or above. We simulate swarms using the “average” and “maximum” redistribution conditions and the “Sum” and “Last” Final Decision methods, over swarm sizes ranging from 50 scouts to 1000 scouts, with 100 replicates of each. The discount rate is set at  $\alpha = 0.75$  and the number of times for redistribution set to  $n = 10$ . There are 5 boxes to choose from, with box 5 being the superior box. The results are provided in Figure 3.2.

Swarms which use the “Sum” method to make their final decision benefit immediately from slight increases in the swarm size. For swarms of greater than 100 individuals, their probability of success, regardless of whether scouts redistribute according to the “Maximum” or “Average” condition, is very close to 1.

The performance of swarms using the “Last” method to make their final decision is a little more interesting, as their probability of success increases gradually as the number of scouts in the swarm increases. Swarms that redistribute scouts to sites according to the “Average” condition, as described in Subsection 3.2.2, see their probability of success increase to 0.95 when the swarm size exceeds 800 scouts. Those that redistribute according to the “Maximum” condition see an increase, but the probability of success seems to level off at 0.8 for swarms of 500 scouts or more.

In order to explore the apparent asymptote in the probability of success for the swarm using the “Maximum” condition for redistribution, and the “Last” method to make their final decision, we simulate the performance of this hive across a range of values of some model parameters. Specifically, we double the amount of time for search and increase the discount rate from 0.75 to 1. If the discount rate is 1, then no scout gets tired and the waggle dance time of each individual at each site remains unchanged throughout the process. Neither change seems to make a significant difference for swarms including greater than 250 scouts.

### 3.4 Discussion

The limits of the cognitive and memory capacities of honeybees are unclear to us, and so it is not necessarily safe to assume cognitive ability where there may be none. We modeled a swarm’s Final Decision process two ways: with the “Sum” method – a full memory that allowed the swarm to

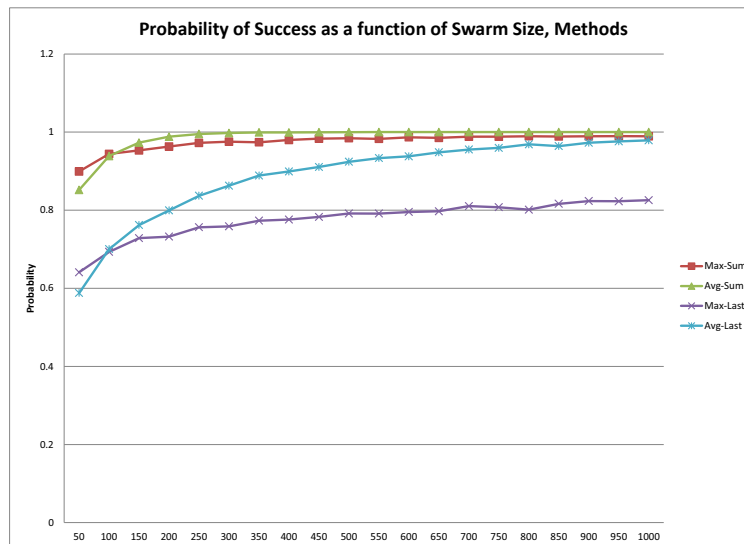


Figure 3.2: Probabilities of success in finding the best site, for each of the four combinations of conditions and methods, for swarm sizes ranging from 50 to 1000 scouts, with discount rate  $\alpha = 0.75$  and  $T = 5$ .

compute the sum of all waggle dance times, over the entire process spent dancing and redistributing to sites – and with the “Last” method – no memory, which required the swarm to depend entirely on the proportion of scouts dancing for each site at that moment to make its decision. The “Sum” method assumed that honeybees have explicit memory of all dance times at each site going back to the start of the process.

A simpler assumption is that scouts can only observe what is happening currently in the swarm, and make their decisions based entirely on this “persistent memory,” as in the “Last” method. Our simulations suggest that a swarm only capable of the “Last” memory condition will perform at 80% capacity of a swarm using full memory, if it also uses the “Average” condition for redistribution. However, if this swarm also uses the “Maximum” condition for redistribution, it obtains 100% capacity of a swarm using full memory, but only with a swarm at least twice the size required for the swarm with full memory. If we assume there is no other mechanism by which the hive can improve its accuracy, then this result would suggest adaptive benefit to full memory, though it is possible that partial memory may have benefits that we did not explore.

Again, all of our results are preliminary. We would also like to know the proportion of scouts dancing for the winning site at the final time, to define the success rate as a function of this proportion. Assuming monotonicity, by taking the inverse of this function, one could find the minimum proportion of scouts required to ensure the probability of success remain above some threshold. This result would suggest quantitative “quorum” conditions, as put forth by Seeley, Visscher, & Passino [22] and would test the conditions modeled by List, Elsholtz and Seeley [15].

Our simulation compared the performance of swarms using two different conditions for redistribution and two different memory methods. This varies from the only other model of which we are aware, which includes a comparison of the probability of choosing the best site (then 2nd best, then 3rd best, etc.) for swarms using weak or strong quorum criteria, and with varying values of independence and interdependence,  $\lambda$  and  $\mu$  in their notation, respectively. Both models, however, are interested in understanding the incredible success formed from the dynamic balance found by these swarms of bees between independent measurement, intelligent conditions for interdependent

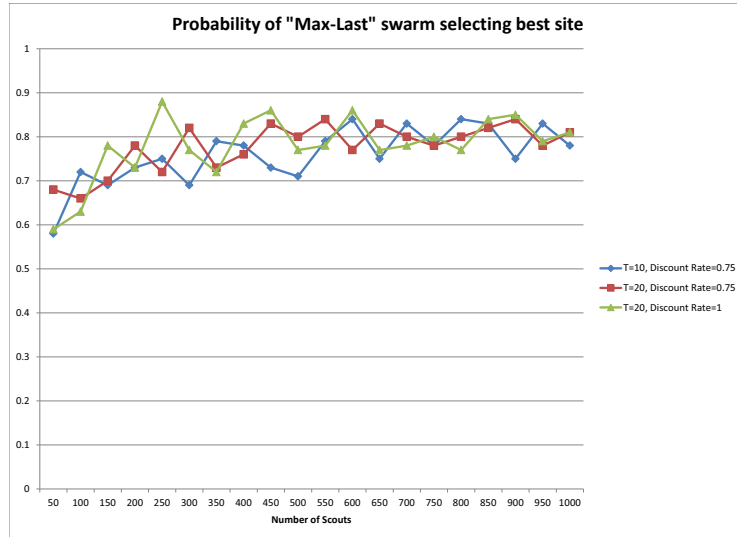


Figure 3.3: The probability of success for the swarm using the “Maximum” condition for redistribution and the “Last” method for its final decision, over swarm sizes ranging from 50 to 1000 scouts, and under three different sets of value for the parameters, where  $T$  is the total number of turns allowed for redistribution and the discount rate,  $\alpha$ , is the multiplicative decrease of the bees’ waggle dance time for each site over time.

learning, and simple yet robust methods of voting.

# Appendix A

## Provided Simulation Code

### A.1 Habitat Selection Simulation

```
# This program calculates the expected utility of pursuing any choice,
# using the V(t) recursion, given (Beta) parameters for the distribution
# of belief regarding predation risk at both sites, and the present time.
# Probability of evidence, Y_j, given by most current belief: a1 -> a1 + 1
# with probability a1/(a1+b1). The program only uses one utility function
# at a time: those provided include a linear, convex, and concave utility function,
# written as either an exponential or a polynomial expansion.
rm(list=ls(all=TRUE));
# The program then simulates an individual beginning with a uniform prior
# regarding the perceived predation risk level at each site and uses the
# optimal strategy. We calculate statistics: chosen site, predation risk
# at chosen site, stop time, and their distributions and means.

sim.pred.lst <- list(site.selected=c(), p=c(), stop.time=c());
num.runs = 25000;
cost.range = 0.01;
p = c(0.1, 0.75);
T = 10;
mesh = 0.01;
x <- seq(0,1,by=mesh);

# Linear utility function
ben.l = 1 - x;

# Risk-averse
# Convex utility functions
g=5; a=0.5;
ben.sed = exp(-g*x);
# ben = exp(-g*a)
- g*exp(-g*a)*(x-a)
+ g^2/2*exp(-g*a)*(x-a)^2
- g^3/6*exp(-g*a)*(x-a)^3;
```

```

# Risk-prone
# Concave utility functions
g = 5; a = 1; #High g means high curvature, a = x-int, close to 1
# x0=0.5; #Necessary to center the polynomial expansion away from the x-intercept
ben.ath = 1 - exp(g*(x-a));
# ben = 1 - exp(g*(x0-a))
- g*exp(g*(x0-a))*(x-x0)
- g^2*exp(g*(x0-a))*(x-x0)^2/2
- g^3*exp(g*(x0-a))*(x-x0)^3/6;

ben=ben.l

for (cost in 1:length(cost.range)) {

#Data: utility of optimal choice stored in optimal.utility,
#Choice of optimal choice in optimal.choice
optimal.utility <- array(c(0), dim=c(T,T,T,T,T));
optimal.choice <- array(c(0), dim=c(T,T,T,T,T));
a1=1; b1=1; a2=1; b2=1;

# Final Time Stage
# Site 1 can be sampled T times, so a1 can be T+1 at maximum, likewise for the others
for (a1 in 1:T) {
for (b1 in 1:(T+1-a1)) {
for (a2 in 1:(T+2-a1-b1)) {
b2 = T+3-(a1+b1+a2);
optimal.utility[a1,b1,a2,b2,T] = max(
c(mesh*ben%%dbeta(x,a1,b1),
mesh*ben%%dbeta(x,a2,b2)
)
);
optimal.choice[a1,b1,a2,b2,T] = 2 + which.max(
c(ben%%dbeta(x,a1,b1),
ben%%dbeta(x,a2,b2)
)
);
}
}
}

#Iterating backwards...
for (stage in (T-1):1) {
for (a1 in 1:stage) {
for (b1 in 1:(stage+1-a1)) {
for (a2 in 1:(stage+2-a1-b1)) {
b2 = stage+3-(a1+b1+a2);
bUpd1 = a1/(a1+b1)*optimal.utility[a1+1,b1,a2,b2,(stage+1)]
}
}
}
}
}

```

```

+ b1/(a1+b1)*optimal.utility[a1,b1+1,a2,b2,(stage+1)]
- cost.range[cost];
bUpd2 = a2/(a2+b2)*optimal.utility[a1,b1,a2+1,b2,(stage+1)]
+ b2/(a2+b2)*optimal.utility[a1,b1,a2,b2+1,(stage+1)]
- cost.range[cost];
optimal.utility[a1,b1,a2,b2,stage] = max(
c(bUpd1,
bUpd2,
mesh*ben%*%dbeta(x,a1,b1),
mesh*ben%*%dbeta(x,a2,b2)
)
);
optimal.choice[a1,b1,a2,b2,stage] = which.max(
c(bUpd1,
bUpd2,
mesh*ben%*%dbeta(x,a1,b1),
mesh*ben%*%dbeta(x,a2,b2)
)
);
}
}
}
}

# Step 2: Now simulate individual comparison search using optimal behavior
#stored in optimal.choice
for (i in 1:num.runs) {
site.selected = 0;
stage = 0;
a1=1; b1=1; a2=1; b2=1;

while (site.selected == 0) {
stage = stage+1;
choice = optimal.choice[a1,b1,a2,b2,stage];

#If sites look identical, one is selected randomly.
if (a1/(a1+b1)==a2/(a2+b2) && (choice == 1 || choice == 2)) {
choice = 1 + round(runif(1,0,1));
}

if (choice == 1) {
#Visit Site 1
if (runif(1,0,1) <= p[1]) {
a1=a1+1;
}
else {
b1=b1+1;
}
}
}
}

```

```
}

if (choice == 2) {
#Visit Site 1
if (runif(1,0,1) <= p[2]) {
a2=a2+1;
}
else {
b2=b2+1;
}
}

if (choice == 3) {
site.selected = 1;
}

if (choice == 4) {
site.selected = 2;
}
}

sim.pred.lst$site.selected = c(sim.pred.lst$site.selected, site.selected);
sim.pred.lst$p = c(sim.pred.lst$p, p[site.selected]);
sim.pred.lst$stop.time = c(sim.pred.lst$stop.time, stage);

} #End num.runs loop
} #End cost.range loop

avg.stop.time = mean(sim.pred.lst$stop.time)
prob.best.choice = length(which(sim.pred.lst$site.selected==1))/num.runs
mean.pred.risk.selected = mean(sim.pred.lst$p);

c(avg.stop.time, prob.best.choice, mean.pred.risk.selected)
hist(
sim.pred.lst$stop.time,
freq=FALSE,
breaks=seq(0,10,by=1),
xlab="Stopping Time",
main="Distribution of Stopping Times"
)
```

## A.2 Constrained Animal Movement Simulation

```

#This program simulates the movement of some number of individuals according to
# the diffusion  $Y_t$  for some number of steps, and then takes the arctan of the
# positions, to put them in the interval from  $-\pi/2$  to  $\pi/2$ .
#For  $L = \pi/2$ , the diffusion is recurrent if  $\sigma^2 \leq 1$  and transient if  $\sigma^2 > 1$ 
#The histogram of the final positions is then compared to the invariant
# distribution derived in the paper.
rm(list=ls(all=TRUE));

#Simulation parameters
sigma2 = 3;
disp.stepsize = .001;
num.animals = 10;
num.steps = 100;
num.runs = 100;
#Total simulation time = disp.stepsize*num.steps
pos.Y = array(c(0), dim=c(num.animals));
pos.Y.data = array(c(0), dim=c(num.animals, num.runs));

disp.f <- function(x) {
-(1-sigma2)*x*(1+x^2)*disp.stepsize;
}
disp.g2 <- function(x) {
sqrt(sigma2)*(1+x^2)*rnorm(length(x),0,sqrt(disp.stepsize));
}
disp.limit <- function(x) {
1/sqrt(pi)*gamma(1+1/sigma2)/gamma(1/2+1/sigma2)*(cos(x))^(2/sigma2);
}

for (j in 1:num.runs) {
#Generate sample paths
for (i in 1:num.steps) {
disp = disp.f(pos.Y) + disp.g2(pos.Y);
pos.Y = pos.Y + disp;
pos.Y.sign = ifelse(
is.na(pos.Y) == FALSE,
sign(pos.Y),
pos.Y.sign
);
pos.X.explosion = ifelse(
is.na(pos.Y) == TRUE,
pi/2*pos.Y.sign,
0
);
}
pos.Y.data[,j]=pos.Y;
pos.Y = array(c(0), dim=c(num.animals));

```

```

}

#Arrange data as an array: each column is an animal's trajectory,
# each row is the position of all animals at that time

pos.X = ifelse(is.na(pos.Y.data) == TRUE, pos.X.explosion, atan(pos.Y.data));
pos.min = min(pos.X); pos.max = max(pos.X);

h <- hist(pos.X,
breaks=c(-pi/2-.5, -pi/2+.5, pi/2-.5, pi/2+.5),
freq=FALSE,
border='purple',
col='pink',
xlim=c(-2,2),
ylim=c(0,1),
main=expression(
paste(
"Divergence of Simulated Terminal Positions from the Limit Distribution of ",
X[t],
sep=" "
)
),
xlab=expression(
paste(
"Terminal Positions of 1e+05 Realizations of the Process, ",
X[t],
sep=" "
)
),
sub="Step size = 1e-03, 1e+04 steps, 1000 animals, 100 runs"
);
lines(x <- seq(-pi/2, pi/2, by=.001),
disp.limit(x),
lty=2,
col='blue'
)
abline(v=c(-pi/2, pi/2),
lty=2,
col='red'
)

error = (1/2)*sum(abs(append(0, h$density) - disp.limit(h$breaks)))*(h$breaks[2]-h$breaks[1]);
error

```

### A.3 Group Decision Making Simulation

```

#This program simulates a swarm of some number of scouts distributing itself
# across potential habitat sites according to the max or avg criterion, and
# then selecting a site based on either the sum or last memory method. We
# compare the results of each combination of criterion and method by calculating
# the probability with which the swarm selects the best site.

rm(list=ls())

num.runs = 10000;
# total.time.range = seq(2, 10, length=9);
total.time.range = 10;
# discount.rate = seq(0.1, 1, length = 10)
discount.rate = 0.75;
num.scouts.val = seq(50,1000,by=50);
num.boxes = 5; #num.scouts should be larger than num.boxes
boxes = seq(0,num.boxes);
#meaning there are (num.boxes) real boxes and one "unfound" position
# representing lost scouts or unacceptable boxes
history = list();
success.data = array(c(0), dim=c(length(num.scouts.val), 4));

for (n in 1:length(num.scouts.val)) {
for (total.time in 1:length(total.time.range)) {
for (r in 1:length(discount.rate)) {
success.max.sum = 0;
success.avg.sum = 0;
success.max.last = 0;
success.avg.last = 0;

## Simulation begins here
for (run in 1:num.runs) {
## Initialize
# dist.scouts.lst = list();
dist.boxes.array = array(c(0), dim=c(total.time.range[total.time], num.boxes+1));
max.dance.time.array = array(c(0), dim=c(total.time.range[total.time], num.boxes+1));
avg.dance.time.array = max.dance.time.array;
## Initial, uniform distribution of scouts on sites
dist.scouts = floor(runif(num.scouts.val[n], 0, num.boxes+1));
# dist.scouts.lst[1] = list(dist.scouts);

dist.boxes = c();
for (i in 0:num.boxes) {
dist.boxes = c(dist.boxes, length(dist.scouts[dist.scouts==i]))
}
dist.boxes.array[1,] = dist.boxes;

```

```

max.dance.time = array(c(NA), dim=c(num.bboxes));
max.dance.time[1] = 0;
for (i in 1:num.bboxes) {
max.dance.time[i+1] = {
if(dist.bboxes[i+1] > 0) {
max(c(rexp(dist.bboxes[i+1], 1/i)))
}
else {
if (sum(dist.bboxes.array[,i+1]) > 0) {
0
}
else {
NA
}
}
}
}
max.dance.time.array[1,] = max.dance.time;

avg.dance.time = array(c(NA), dim=c(num.bboxes));
avg.dance.time[1] = 0;
for (i in 1:num.bboxes) {
avg.dance.time[i+1] = {
if(dist.bboxes[i+1] > 0) {
mean(c(rexp(dist.bboxes[i+1], 1/i)))
}
else {
if (sum(dist.bboxes.array[,i+1]) > 0) {
0
}
else {
NA
}
}
}
}
avg.dance.time.array[1,] = avg.dance.time;

## Redistribute
for (t in 2:total.time.range[total.time]) {
for (j in 1:num.scouts.val[n]) {
#cond.bboxes includes only sites j such that max.dance.time[j] not less
#than max.dance.time[i] where i is current site
not.cond.bboxes = which(max.dance.time < max.dance.time[dist.scouts[j]+1]);
cond.bboxes = setdiff(bboxes, not.cond.bboxes);
#Distribute uniformly across cond.bboxes
dist.scouts[j] = cond.bboxes[

```

```

floor(runif(1,
1,
length(cond.bboxes)+1)
)
]
}
# dist.scouts.lst[t] = list(dist.scouts);

dist.bboxes = c();
for (i in 0:num.bboxes) {
dist.bboxes = c(dist.bboxes, length(dist.scouts[dist.scouts==i]))
}
dist.bboxes.array[t,] = dist.bboxes;

max.dance.time = array(c(NA), dim=c(num.bboxes));
max.dance.time[1] = 0;
for (i in 1:num.bboxes) {
max.dance.time[i+1] = {
if(dist.bboxes[i+1] > 0) {
max(c(discount.rate[r]^(t-1)*rexp(dist.bboxes[i+1], 1/i)))
}
else {
if (sum(dist.bboxes.array[,i+1]) > 0) {
0
}
else {
NA
}
}
}
}
max.dance.time.array[t,] = max.dance.time;

avg.dance.time = array(c(NA), dim=c(num.bboxes));
avg.dance.time[1] = 0;
for (i in 1:num.bboxes) {
avg.dance.time[i+1] = {
if(dist.bboxes[i+1] > 0) {
mean(c(discount.rate[r]^(t-1)*rexp(dist.bboxes[i+1], 1/i)))
}
else {
if (sum(dist.bboxes.array[,i+1]) > 0) {
0
}
else {
NA
}
}
}
}

```

```

}
}
avg.dance.time.array[t,] = avg.dance.time;

}

selected.max.sum = which.max(colSums(max.dance.time.array, na.rm=TRUE));
success.max.sum = success.max.sum + as.numeric(selected.max.sum == num.bboxes+1);

selected.avg.sum = which.max(colSums(avg.dance.time.array, na.rm=TRUE));
success.avg.sum = success.avg.sum + as.numeric(selected.avg.sum == num.bboxes+1);

selected.max.last = which.max(max.dance.time);
success.max.last = success.max.last + as.numeric(selected.max.last == num.bboxes+1);

selected.avg.last = which.max(avg.dance.time);
success.avg.last = success.avg.last + as.numeric(selected.avg.last == num.bboxes+1);

} #End number of runs loop

} #End discount.rate loop
} #End num.scouts.val loop
## Print history
history[[total.time]] <- list(
# "distribution of scouts at time"=dist.scouts.lst,
"distribution of boxes"=dist.bboxes.array,
"maximum dance time"=max.dance.time.array,
"average dance time"=avg.dance.time.array
)

success.data[n,] = c(success.max.sum/num.runs,
success.avg.sum/num.runs,
success.max.last/num.runs,
success.avg.last/num.runs
);

} #End total time range loop

success.data
write.csv(success.data, 'success.data.csv', row.names=num.scouts.val)

```

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