

NOT ALL THOSE WHO WANDER ARE LOST: CHARACTERIZING
SEX DIFFERENCES IN SPATIAL EXPLORATION
AND THEIR RELATIONSHIP TO
NAVIGATION ABILITY

by

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ABSTRACT

Sex differences in spatial ability and navigation are well documented. Although several theories explain a subset of these findings, a comprehensive theory has yet to be offered and tested. As such, we provide evidence that co-occurring evolutionary pressures shaping male and female range sizes lead to the use of different navigation strategies, which produce differences in self-reported spatial anxiety and sense of direction. Next, we provide experimental evidence testing two important implications of our model. First, if the co-occurring evolutionary pressures producing differences in range size are functional, then they ought to shape how males and females explore a novel environment. In our experiment, males demonstrated a higher rate of diffusion than females (e.g., spreading throughout the space more quickly), and females demonstrated more caution while exploring a novel, large-scale virtual environment. Second, maintaining a larger range size places greater demands on male navigation, which not only leads to the use of a different navigation strategy, but also to better navigation performance. At first glance, there is inconclusive evidence in support of superior male navigation ability. A closer look reveals that sex differences in navigation often emerge when individuals are allowed to freely explore the environment prior to testing. Given the expected sex differences in exploration behavior predicted by our model, we provide evidence that features characteristic of male exploration also offer the individual a wealth of spatial information that may lead to better navigation performance.

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CHAPTER 1

INTRODUCTION

Jones, Braithwaite, and Healy (2003) reviewed several explanations for the wealth of sex differences observed in human spatial ability and navigation. The most well-supported hypothesis suggests that males have evolved superior spatial abilities to help them maintain a large range size that encompasses many female ranges, leading to more offspring with more mates (e.g., Gaulin, 1989; Jones et al., 2003). Another plausible hypothesis purports that female range sizes are constrained so as to avoid predation, especially considering their higher rate of parental investment (Ecuyer-Dab & Robert, 2004). These proposed evolutionary pressures are not mutually exclusive, leading to a two-fold evolutionary pressure model as an explanation for differences in range size (Ecuyer-Dab & Robert, 2004). One implication of maintaining a larger range size, however, is the need to accurately navigate over longer distances, leading males to rely more heavily on a survey-based strategy¹ as opposed to a route-based strategy. A survey-based strategy (e.g., bird's eye view) involves understanding the layout of an environment independent of one's location, whereas a route-based strategy involves remembering when to turn left or right and is tied to one's first-person perspective. Based on experimental evidence, a survey-based strategy tends to lead to better

¹ Sometimes known as orientation, geocentric, or an allocentric strategy.

navigation performance (Rieser, Lockman, & Pick, 1980), which should lead to a better sense of direction and a reduction in spatial anxiety. We will provide a comprehensive test of these hypotheses using self-report measures collected from 514 individuals, and propose a model explaining sex differences in spatial navigation.

Our model leads to two important assumptions we wish to experimentally test. First, differences in range size are thought to be a product of the male motivation to venture farther from home in search of mates and the female motivation to remain in safe locations, suggesting a functional role for wanderlust in males and cautious exploration in females. If this is the case, then one functionally crucial situation that ought to elicit these characteristics in males and females is the exploration of a novel environment due to the uncertainty of the costs and benefits. The current study will test if males explore a novel large-scale virtual environment in a more diffusive manner than females. While measuring diffusion may test the functional nature of male wanderlust behavior, it only indicates *relative* caution in female exploration. Therefore, we will also test if females have a greater tendency than males to revisit previously occupied locations.

A second important assumption underlying our model is that large range sizes encourage males to adopt a survey-based navigation strategy that actually enhances their navigation ability. This is important because the fitness benefits associated with a large range size could be undermined by routinely getting lost, especially in novel terrain where the risks of predation are higher. Coluccia and Louse (2004) reviewed the extant navigation literature from 1993 to 2003, concluding that in some cases, less than 60% of the studies examined found a male advantage in navigation performance. They also reported that in simulated (virtual) environments, when participants are in control of their

exploration, approximately 85% of the studies examined found a male advantage in navigation performance (Coluccia & Louse, 2004). It might be the case that the way in which males explore novel terrain provides them access to spatial information that enhances their navigation ability and allowing them to realize the fitness benefits associated with a large range size. Unfortunately, none of the experiments allowing free exploration actually measured how individuals explore (e.g., where they go and how they get there). Our study will test whether the difference between male and female exploration uniquely provides males with spatial information enhancing navigation performance.

1.1 Specific Aims

Previous research has established that males and females self report different navigation strategies, levels of spatial anxiety (Lawton, 1994), sense of direction (Hegarty, Montello, Richardson, Ishikawa, & Lovelace, 2006), and harm avoidance tendencies (Ryan, 2009). Theoretically, these sex differences may be a result of the different navigation demands placed on males and females. In particular, males tend to have a larger home range size than females (Ecuyer-Dab & Robert, 2004). It has been proposed that fitness benefits were conferred upon males and costs imposed upon females when traveling far from home (Ecuyer-Dab & Robert, 2004). The difference in fitness costs and benefits are thought to generate differences in range size, which lead to differences in navigation strategies, sense of direction, and spatial anxiety. The current work will be the first comprehensive test of the two-fold evolutionary pressure model.

The evolutionary pressures explaining sex differences in range size imply that males ought to be more motivated to venture into unknown environments than females,

and females ought to be more cautious when exploring novel environments. We expect that if large range sizes benefited males more than females, then when males are placed in a novel environment, they should explore with more wanderlust than females.

Similarly, if large range sizes placed females at a greater risk of predation, then they should explore a novel environment with more caution, reducing their risk of predation.

The current work will characterize sex differences in the exploration of a novel environment, with the expectation that males will show more wanderlust than females, and females will show more caution than males.

Ultimately, the two-fold evolutionary pressure model holds the promise of explaining sex differences in navigation ability. While a number of studies have reported a male navigation advantage, roughly 45% studies find no sex difference in navigation ability. Interestingly, if participants are free to move around in the environment, almost 85% of navigation studies report a male advantage in performance (Coluccia & Louse, 2004). Although human spatial navigation has been extensively researched, very little work has thoroughly examined how people encode spatial information in a novel large-scale environment. Previous work has constrained the encoding process by forcing participants along a preplanned route (Silverman, Choi, Mackewn, Fisher, Moro, & Olshansky, 2000), or neglected to quantify the behavior during free exploration (Castelli, Corazzini, & Geminiani, 2008). Spatial memory research shows how important one's encoding is to their development of layout knowledge, a form of knowledge important for navigation (Shelton & McNamara, 1997). If we expect sex differences in the exploration of a novel environment, could these differences lead to a different spatial encoding and account for differences in navigation performance? The current proposal will test if the

sex differences in exploration account for differences in navigation performance.

Finally, the two-fold evolutionary pressure model accounts for the sex differences in navigation strategy and spatial anxiety. Other work has suggested a relationship between these self-report measures and navigation ability. Therefore, we will include these measures as mediators between participant sex, exploration behaviors, and navigation ability.

Aim 1: Provide a comprehensive test of an evolutionary model explaining sex differences in spatial cognition and navigation. The navigation literature has identified a number of sex differences related to navigation. First, females report higher levels of spatial anxiety than males (Lawton, 1994). The spatial anxiety measure used asks specifically about how anxious an individual feels while navigating, often in unfamiliar places. Second, males tend to report using a survey-based strategy while navigating, while females tend to report using a route-based strategy (Lawton, 1994). The self-reported navigation strategies have also been shown to correlate with spatial anxiety, such that those who report the use of a survey-based strategy often report lower spatial anxiety than those who report the use of a route-based strategy (Lawton, 1994). Third, self-reports of one's sense of direction also show sex differences, with males reporting a better sense of direction than females (Hegarty, Montello, Richardson, Ishikawa, & Lovelace, 2006). Theoretically, there is good reason to predict an association between spatial anxiety, navigation strategy, sense of direction, and biological sex.

There are several evolutionary hypotheses that may account for functional differences between males and females in navigation, due to the fact that males have larger range sizes than females. First, it has been proposed that males (of many species

including humans) travelled farther from home on a regular basis in order to find genetically unrelated mates (Gaulin, 1992), and defend a “territory” that potentially encompasses many mates and subsequently resources (Krebs & Davies, 1993). Second, it has been proposed that traveling far from home is associated with greater fitness costs for females than for males. Specifically, females were the primary caregivers of offspring and would be putting themselves and their offspring at risk when traveling far from home and in unfamiliar territory (Ecuyer-Dab & Robert, 2004). This last hypothesis has not been tested as extensively as the first two, although it has been demonstrated that females report higher levels of harm avoidance (Ryan, 2009). The harm avoidance questionnaire is a well-established individual difference that attempts to assess the degree to which an individual is motivated to avoid physically harmful situations, but is not specific to spatial navigation situations. These two evolutionary pressures are not mutually exclusive, leading Ecuyer-Dab and Robert (2004) to suggest that both evolutionary pressures shape range sizes, which places different demands on male and female navigation, explaining many sex differences in spatial ability and navigation.

From the two-fold evolutionary pressures model, several predictions are made. First, females should have a smaller range size than males. Second, higher levels of harm avoidance should reduce overall range size. Third, larger range sizes should lead to the use of a survey-based navigation strategy, allowing one to effectively navigate over longer distances. Third, a survey-based navigation strategy should lead to a better sense of direction and less spatial anxiety as it is often considered a better navigation strategy than route-based navigation. Evidence exists supporting all of these relationships, but they have yet to be assessed comprehensively within the same individuals. In the current

study, participants will self report their spatial anxiety, harm avoidance tendencies, navigation strategy, sense of direction, and range size. Structural equation modeling will be used to comprehensively test the two-fold evolutionary pressure model proposed by Ecuier-Dab and Roberts (2004), and the models ability to account for sex differences in spatial ability and navigation.

Aim 2: Characterize sex differences in the exploration of a novel environment and relate these differences to navigation ability. The two evolutionary pressures contributing to sex differences in range size lead to the prediction that males and females will explore a novel environment differently. First, sexual selection pressures are thought to encourage males to establish larger ranges in order to encompass many potential mates (Gaulin & Fitzgerald, 1989). This leads to the prediction that males should show more wanderlust than females, encouraging larger range sizes for males. Range sizes can only become so large until defending against sexual competition becomes unmanageable. Therefore, we might expect males to show wanderlust in novel environments where they have yet to establish a range size and where the potential fitness benefits are unknown. Second, it has been suggested that the risk of predation is much greater as one increases his or her range size. Given that females show more parental investment than males (spending more time raising offspring), predation is more costly to females than to males. This leads to the prediction that females will show more caution than males, thereby constraining female range sizes. However, females ought to establish a range with a relatively low risk of predation reducing the need for cautious exploration in known environments. Therefore, we might expect that females will show more caution than males when exploring a novel environment where the risk of predation is unknown.

Finally, females tend to report higher levels of spatial anxiety than males, so we expect self-reported spatial anxiety to mediate the relationship between participant sex and the degree of wanderlust or caution during exploration. The current work will ask men and women to explore a novel large-scale environment, allowing us to test if males show more wanderlust and females show more caution while exploring. Participants will also report their typical level of spatial anxiety, so we can test whether this mediates the relationship between biological sex and wanderlust/caution during exploration.

Next, the two-fold evolutionary pressure model is supposed to explain sex differences in spatial navigation. Spatial navigation is the ability to locomote to a desired location that is currently undetected by one's senses, inherently relying on one's ability to infer or remember properties about the environment to guide the direction of travel. A review of the spatial navigation literature suggests that males are more likely to outperform females when the participants are allowed to freely move around in the environment (Coluccia & Louse, 2004). We already suspect that males and females will explore a novel environment differently, so perhaps the differences in exploration lead to a different encoding experience accounting for the male advantage in navigation performance. Strikingly, none of the previous work has examined how people encode the spatial information in a large-scale space, a presumable precursor to developing spatial memories of the environment. Instead, past research has either constrained the participant's encoding process by leading them along a preplanned route (Silverman et al., 2000), or neglected to quantify behavior during encoding (Castelli, Corazzini, & Geminiani, 2008).

Previous work has revealed that males rely on a different navigation strategy than

females. Females tend to rely more heavily on a strategy as route-based navigation, which primarily involves remembering when or where to make a specific turn (e.g., turn right at the museum) and is considered to be inflexible when the desired route must be altered (Lawton, 1994). In contrast, males rely more heavily on survey-based navigation, which primarily involves remembering or inferring the spatial configuration of several locations (e.g., imagining a bird's eye view), and is considered to be flexible enough to allow the navigator to take short-cuts or detours when necessary (Lawton, 1994).

One of the main distinctions between survey and route navigation is that survey navigation relies on layout knowledge (Rieser, Lockman, & Pick, 1980). Layout knowledge requires spatial information indicating the relative distance between fixed spatial features in the environment, and one source of relative distance information comes from motion parallax (Braunstein & Tittle, 1988; Rogers & Graham, 1979). Motion parallax refers to the phenomenon where objects closer to an observer move more in her visual field than objects farther from her when translating through a space, revealing the relative distance between the objects. In fact, research shows that when individuals are provided multiple different views of a single space, the accuracy of their layout knowledge increases (Shelton & McNamara, 1997). In fact, some have suggested that complete layout knowledge can be achieved if one is allowed to freely explore the space, presumably creating enough motion parallax to observe the relative distance between all spatial features. However, much of this work has been conducted on room-sized spaces or smaller.

Spatial memory research on larger spatial scales suggests that spatial memory is also hierarchically structured, such that knowledge of smaller scale spaces are nested

within larger scale spaces (e.g., neighborhoods nested within a city) (McNamara, 1986). For example, participants judged the distance between cities in different states to be larger than distances between equally spaced cities that exist in the same state (Stevens & Coupe, 1978). Theoretically, this should allow someone the ability to begin their navigation by orienting accurately in the general direction of the goal location, and subsequently use spatial information at smaller and smaller scales to hone in on the goal location. This is important because spatial information on large spatial scales is often too coarse to fine tune navigation in small spaces, and spatial information on small spatial scales is rarely visible at the beginning of the journey. Therefore, we should expect one to explore a novel large-scale space in a pattern that exposes them to multiple different views at multiple nested spaces. Overall, this suggests that the key to generating accurate layout knowledge for navigation in large-scale spaces, one must obtain relative distance information on multiple spatial scales (i.e., layout knowledge of distant landmarks and layout knowledge of local landmarks).

In the current study, participants will be asked to explore a novel large-scale virtual environment for several objects. Afterwards, participants will navigate back to each object and then complete a pointing task. Exploration behavior will be recorded with the hypothesis that those who expose themselves to relative distance information on multiple spatial scales will be better at navigating back to each object. Furthermore, if obtaining relative distance information on multiple spatial scales is required to use a survey-based navigation strategy, then we should see a positive relationship between this feature of exploration and reliance on survey navigation. Finally, research shows that using a survey-based strategy relates to better navigation performance. Therefore, we will test if

obtaining relative distance information on multiple spatial scales during exploration mediates the relationship between survey strategy use and navigation performance. This research will simultaneously inform theories of spatial memory and animal movement, a cross-disciplinary integration that has been recently encouraged (Fagan et al., 2013).

1.2 Significance and Innovation

This dissertation takes an interdisciplinary approach to understanding sex differences in spatial navigation, and offers both theoretical contributions and innovative methods. Animal movements in natural settings have been extensively studied (Bartumeus & Levin, 2008; Benhamou, 2004; Dickinson et al., 2000; Turchin, 1998; Vishwanathan et al., 2008). Recently, anthropologists examined human hunter-gatherer mobility, showing that they paralleled many of the mobility patterns found in other species (Raichlen et al., 2014). Other work has found similar mobility patterns in a western sample of humans (Gonzalez et al., 2008; Rhee et al., 2011). Simultaneously, the psychological literature has studied spatial learning and memory by either providing static views of a room-sized layout of objects (Shelton & McNamara, 1997), or neglected to quantify the mobility of people as they learn the layout of a novel space (Malinowski & Gillespie, 2001). Behavioral ecologists and geographers have acknowledged that spatial memory is an important factor in understanding mobility (Fagan et al., 2013), and psychologists have suggested that allowing individuals to actively explore a novel space may be important for developing an accurate spatial memory (Coluccia & Louse, 2004; Presson et al., 1987; Shelton & McNamara, 1997). However, very few studies have attempted to relate mobility patterns, spatial learning, and navigation ability. The current

work will quantify human exploration patterns using similar methods employed in behavioral ecology, geography, and physics and relate these patterns to spatial memory and navigation performances. Overall, this work should serve as one way in which to integrate theories and findings of spatial mobility and memory across disciplines.

The current work will inform theories of sex-related differences in spatial cognition and theories of spatial learning. First, several theories have been proposed in an attempt to explain sex differences in spatial cognition, range size, and navigation (Jones et al., 2004). Recently, Ecuver-Dab and Roberts (2004) have suggested the combination of two evolutionary pressures as an explanation for such sex differences; however, this model has yet to be tested comprehensively. The current work will use a structural equation modeling approach to assess the plausibility of the Ecuver-Dab and Robert model. Second, the psychological literature has provided a wealth of findings regarding the structure (Shelton & McNamara, 1997; Zhang, Mou, McNamara, & Wang, 2014) and neuroanatomical underpinnings of spatial memory (Moser, Kropff, & Moser, 2008). Other work has suggested a process by which an individual develops spatial knowledge starting with knowledge of locations, to routes, to layout knowledge (Golledge et al., 1995). It is still unclear how an individual generates and develops spatial knowledge, especially in natural settings where mobility patterns are complex and scale-free (Gonzalez et al., 2008). The current work proposes a potential psychological mechanism that may allow an individual to develop spatial knowledge, namely motion parallax information through scale-free directional persistence during encoding.

Finally, the current work allows individuals to freely explore a large-scale environment and relates their exploration to their navigation performance. Previous work

has not always found a male advantage in navigation performance, but some have suggested that active movement in the environment tends to coincide with a male navigation advantage (Coluccia & Louse, 2004). The current work will not only test the presence of sex differences when active control of movement is provided to participants, but it will attempt to relate this active movement to navigation performance. This has the potential to speak to why a male navigation advantage is often found in studies that allow active control of movement through the environment. Secondly, this work provides three innovative methods that allow for the study of exploration behavior. We use the mean-squared displacement (MSD) as a way to characterize wanderlust and a measure of revisiting behavior as a way to characterize caution in exploration behavior. In addition, we use a fractal analysis (i.e., windowed periodogram) to characterize the degree to which an individual experienced motion parallax information on multiple different spatial scales. Traditionally, psychologists measure the path length of an individual's exploration (Moffat et al., 2007), but this has two drawbacks. First, it is not clear how the length of one's path during exploration is related to encoding and spatial memory. One might assume that a longer path length would provide more exposure to the space, yielding better navigation performance, but this is often the opposite of what is found (Moffat et al., 2007). Second, it has been demonstrated that human (and other animal) movements are scale-free and complex (Gonzalez et al., 2008; Boyer et al., 2006). Scale-free patterns do not have a single path length, but a scaling relationship between the measured path length and the resolution at which one chooses to measure that path (Liebovitch, 1998; Turchin, 1998). In addition, knowing that human movement in a large-scale space is very complex, suggests that we should at least consider quantifying exploration using

techniques that capture the spatial-temporal complexity. While there are many ways to characterize a complex time-series, the current work provides three different measures that may prove fruitful for understanding how humans develop spatial knowledge through complex scale-free exploration.

CHAPTER 2

SEX DIFFERENCES IN SPATIAL ABILITY

Research has consistently reported a variety of sex differences in spatial abilities and navigation. For example, females self-report higher levels of spatial anxiety when navigating in unfamiliar environments (Lawton, 1994; Malinowski & Gillespie, 2001), and males self-report having a better sense of direction (Hegarty et al., 2006). Males are more likely to report the use of a survey-based strategy while navigating, while females tend to report using a route-based strategy (Lawton, 1994). A survey-based strategy (e.g., bird's eye view) involves understanding the layout of an environment independent of one's location, whereas a route-based strategy involves remembering when to turn left or right and is tied to one's first-person perspective. The self-reported navigation strategies have been shown to correlate with spatial anxiety, such that those who report the use of a survey-based strategy often report lower spatial anxiety than those who report the use of a route-based strategy (Lawton, 1994). In general, females tend to report more spatial anxiety when navigating (Lawton, 1994; Schmitz, 1997). The self-reported sex differences parallel the sex differences observed in navigation behavior, as males often outperform females when asked to point in the direction of a distant location or find their way back to a starting location; however, these findings are less consistent across the literature (Coluccia & Louse, 2004). Several explanations for these sex differences have been offered, but the majority of the explanations only account for a fraction of the

findings (Jones et al., 2003), and those that hold more promise as a comprehensive model have yet to be tested in a single large sample.

2.1 Theoretical Accounts

Several theoretical explanations have been put forth in an attempt to explain sex differences in spatial ability and navigation. These explanations have been extensively reviewed elsewhere (see for review Ecuyer-Dab & Roberts, 2004; Jones et al., 2003), so we wish to highlight the explanation supported by the most evidence, which can account for a wider range of findings and can be appropriately applied to the vast array of species demonstrating similar sex differences. Jones and colleagues (2003) provide an extensive review of the existing hypotheses, but conclude that the two promising explanations involve sexual selection pressures expanding male range sizes, and natural selection pressures constraining female range sizes. Interestingly, Ecuyer-Dab and Roberts (2004) propose that these two evolutionary pressures likely combined to produce the plethora of sex differences in spatial abilities today. We will summarize these evolutionary pressures next.

The first evolutionary pressure is concerned with the fact that males of many species (including humans) maintain a larger range size than females. The existing evidence suggests that this is due to sexual selection pressures pushing males to travel greater distances in search of genetically unrelated mates (Carazo, Noble, Chandrasoma, & Whiting, 2014; Gaulin & Fitzgerald, 1989; Miner, Gurven, Kaplan, & Gaulin, 2014; Vashro & Cashdan, 2015). In fact, in a human forager population, Vashro and Cashdan (2015) found a positive relationship between the amount of places visited in a year and the number of offspring produced by males. While larger range sizes may have provided

fitness benefits to males, they likely came with increased fitness costs to females. The second evolutionary pressure to consider is the increased risk of predation associated with traveling far from home (Gaulin & Fitzgerald, 1989). While these risks are present for males, the risks are potentially more severe to the fitness of females, largely due to their higher rate of parental investment. That is, a female is usually the primary caregiver of her offspring, so threats to her survival are often threats to her offspring's survival. Even if the offspring survive a threat, the death of their mother (in comparison to their father) reduces their chances of survival in the future (Sears & Mace, 2008). These differences in fitness costs and benefits may help explain why females are typically more avoidant of physically harmful situations (i.e., Campbell, 1999), while males typically take more physically dangerous risks (Croson & Gneezy, 2009; Cross, Cyrenne, & Brown, 2013). The differences in risk-taking and caution may modulate range sizes by constraining and propelling female and male mobility, respectively, consistent with Ecuier-Dab and Robert's (2004) proposal.

From this evolutionary framework, one can derive a more comprehensive model explaining the wealth of sex differences related to spatial navigation (see Ecuier-Dab & Robert, 2004). First, females are expected to have smaller range sizes than males, and this relationship should be partially explained by the increased tendency of females to avoid physically harmful situations. Next, larger range sizes place different demands on male navigation, as they have to traverse longer distances, and explore novel terrain in search of mates. As a result, males may develop a different navigation strategy that allows them to establish and maintain a large range size. More specifically, males tend to utilize a survey-based navigation strategy more so than females. Survey-based navigation relies

on knowledge about the layout of fixed spatial features and exists independent of the navigator's location (Golledge, 1995), making it possible to take novel shortcuts, or accurately determine a direction of travel when in a new area. Taking shortcuts can conserve both time and energy over long distance travels, but are rather frivolous for short excursions, suggesting that females actually benefit less from a survey-based strategy if they maintain a smaller range size. On the other hand, females tend to rely on a route-based navigation strategy, which only requires spatial information indicating the sequences of turns along a known (or suggested) route. Traveling primarily by well-known routes does decrease the amount of unknown risk involved in one's excursion, especially if the route is close to home. The downside is that relying solely on route knowledge leaves one at risk of being lost when deviating from the expected route. We might expect that those who rely more heavily on a route-based strategy to be less confident in their navigation ability, leading to more anxiety when navigating in novel environments (see Figure 2.1 for proposed model). Although previous research has amassed findings in support of the proposed model, and similar explanations have been offered before (Ecuyer-Dab & Roberts, 2004), the plausibility of this model has not been tested within a single, large sample.

2.2 Summary of Hypotheses

Given evolutionary theory proposed by Ecuyer-Dab and Robert (2004), along with several of the reported sex differences found in spatial ability and navigation, we will test a number of predictions within one model. First, we expect that males will have a larger range size than females, so we will calculate the proportion of places an individual has visited in the surrounding area with a higher proportion indicating a larger

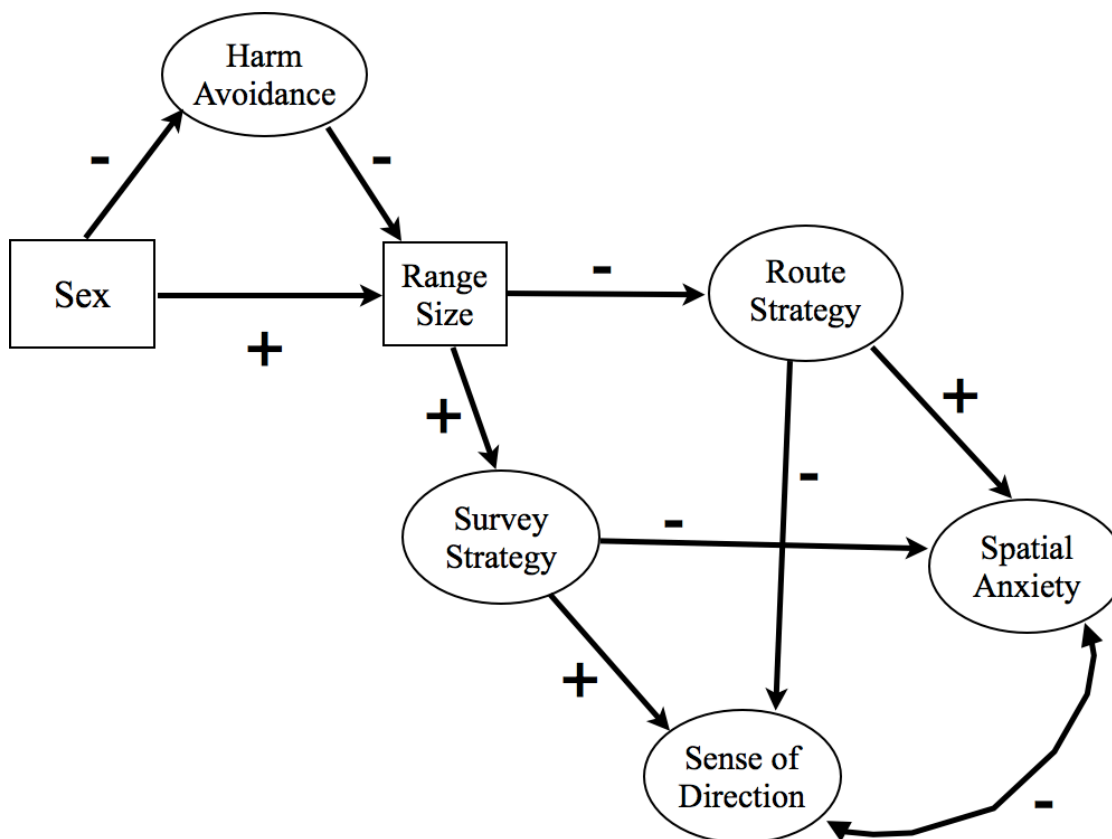


Figure 2.1. Proposed model. Ellipses represent latent variables and rectangles represent observed variables. Questionnaire items are not presented, but assumed to load onto their respective latent variable. For the “Sex” variable, Females = 0 and Males = 1. Plus signs indicate a positive relationship and negative signs indicate a negative relationship.

range size. Next, we expect that part of the sex difference in range size can be accounted for by the fact that females have evolved a stronger motivation to avoid physically harmful scenarios (e.g., situations with known predators). As such, we will also administer a harm avoidance questionnaire that asks participants to choose one of two situations that are either indicative of physical harm or equally unpleasant, but not life-threatening. Next, we expect that larger range sizes will lead to a greater reliance on a survey-based strategy and possibly less reliance on a route-based strategy. Therefore, we

will also administer a navigation style questionnaire used in previous research (Lawton, 1994). Finally, we expect that relying on a survey-based navigation strategy will lead to better navigation performance, increasing one's confidence in their sense of direction and decreasing their spatial anxiety. As such, we will administer both a questionnaire asking one to self-report their sense of direction and a questionnaire asking participants to rate their level of anxiety in a variety of situations, typically involving navigating in a novel environment.

2.3 Method

2.3.1 Participants

Five hundred fourteen (287 Females, 227 Males) undergraduates completed the questionnaire for course credit.

2.3.2 Materials

The following questionnaires were administered online via Survey Monkey: 15-item Santa Barbara Sense of Direction (SBSOD) (Hegarty et al., 2006), the 14-item Navigation Strategy Scale (Lawton, 1994), the 8-item Spatial Anxiety Scale (Lawton, 1994), the 26-item Harm Avoidance subscale from the Tridimensional Personality Questionnaire (Tellegen & Waller, 2008), and a 79-item list of local, national, and worldwide locations and regions to assess range size. The list of local locations was developed such that the locations were distributed throughout the state (i.e., some far away, some nearby), and provided a mixture of well-known locations, somewhat familiar locations, and locations that were more or less off the beaten path. This would allow us to infer that more locations visited indicate travel to farther and more remote locations.

2.3.3 Data Manipulation

The proportion of locations visited for local, national, and worldwide locations were calculated separately by dividing the number of locations visited by the total possible locations. Due to the possibility that worldwide travel is constrained by one's economic circumstances, only the proportion of local and national locations visited were averaged together to create a "range size" score for each individual.

2.3.4 Model Estimation Procedure

Mplus Version 7.11 (Muthén & Muthén, 1998-2012) was used for all structural equation modeling procedures. Missing data were observed for 65 items across all measures for all participants. The 26-item harm avoidance scale was treated as a categorical variable because of the forced-choice dichotomous response. This required the use of the robust mean-variance adjusted weighted least squares estimator (WLSMV). The WLSMV estimator does not assume multivariate normality, and was developed to test models that involve a combination of categorical and continuous variables (Kline, 2011).

2.4 Results

2.4.1 Overall Model Fit

To assess the overall ability of the model to explain the relationships (i.e., covariances) in these data, two measures of model fit are reported. First, the root mean square error of approximation (RMSEA) suggests acceptable model fit, estimate = 0.034, 95% CI [0.032, 0.036]. The comparative fit index (CFI) and Tucker-Lewis index (TLI) showed poor model fit, $CFI = 0.745$, $TLI = 0.736$. CFI and TLI values of 0.95 or

higher are often considered acceptable.

2.4.2 Measurement Model

The main purpose for utilizing latent variables to test the proposed model is to reduce error in the measurement of each construct prior to testing the theorized relationships between them. The items for each questionnaire were forced to load onto their respective factors. The only exception was the Navigation Style questionnaire developed by Lawton (1994). Based on previous work by Lawton (1994), items indicative of survey-based navigation and items indicative of route-based navigation were forced to load onto their own respective factors (i.e., survey and route navigation).

All five factors exhibited significant loadings with their respective items, suggesting that the questions for each questionnaire are indeed measuring the latent construct they were intended to measure. This is not surprising given that these scales have been developed and tested quite extensively.

2.4.3 Structural Model

To assess the plausibility of the Ecuyer-Dab and Robert (2004) proposed two-fold evolutionary pressure model, we look first at the ability of harm avoidance to mediate the relationship between sex and range size. First, males reported having visited 14.1% more locations than females, $b_1 = 0.141$, $SE = 0.03$, $p < 0.001$, but this was partially mediated by one's level of harm avoidance. That is, males reported lower levels of harm avoidance, $b_2 = -0.37$, $SE = 0.06$, $p < 0.001$, and higher levels of harm avoidance led to a further decrease in range size, $b_3 = -0.09$, $SE = 0.02$, $p < 0.001$. Next, to test whether range sizes place different navigation demands on males and females, leading to the

development of different navigation strategies, we examine the ability of range size to predict survey and route navigation. We find that larger range sizes predict more reliance on a survey-based navigation strategy, $b_4 = 4.14$, $SE = 0.85$, $p < 0.001$, but the extent to which one uses a route-based navigation strategy was not predicted by range size, $b_5 = -0.02$, $SE = 0.11$, $p = 0.898$. Finally, to test the hypothesis that survey-based navigation leads to better navigation outcomes, reducing spatial anxiety and increasing one's self-reported sense of direction, we examine the ability of survey navigation to predict both spatial anxiety and sense of direction. We find that more reliance on survey navigation yields lower levels of spatial anxiety, $b_6 = -0.37$, $SE = 0.06$, $p < 0.001$, and a higher self-reported sense of direction, $b_7 = 0.95$, $SE = 0.12$, $p < 0.001$. Interestingly, we also found that those who rely more heavily on route-based navigation show higher levels of spatial anxiety, $b_8 = 0.47$, $SE = 0.22$, $p = 0.036$, but did not emerge as a significant predictor of one's sense of direction, $b_9 = -0.47$, $SE = 0.28$, $p = 0.095$. Finally, higher levels of spatial anxiety negatively correlate with one's sense of direction, $b_{10} = -0.18$, $SE = 0.04$, $p < 0.001$ (see Figure 2.2 for model results).

2.5 Discussion

First, we provide evidence in support of the Ecuycer-Dab and Robert (2004) proposal that the sex differences found in spatial ability and navigation are a result of the fitness benefits conferred upon males and the fitness costs conferred upon females to travel far from home. In particular, we found that males reported visiting significantly more locations than females, and this was partially mediated by harm avoidance. To the extent that harm avoidance is reflecting one's tendency to avoid physical threats (e.g.,

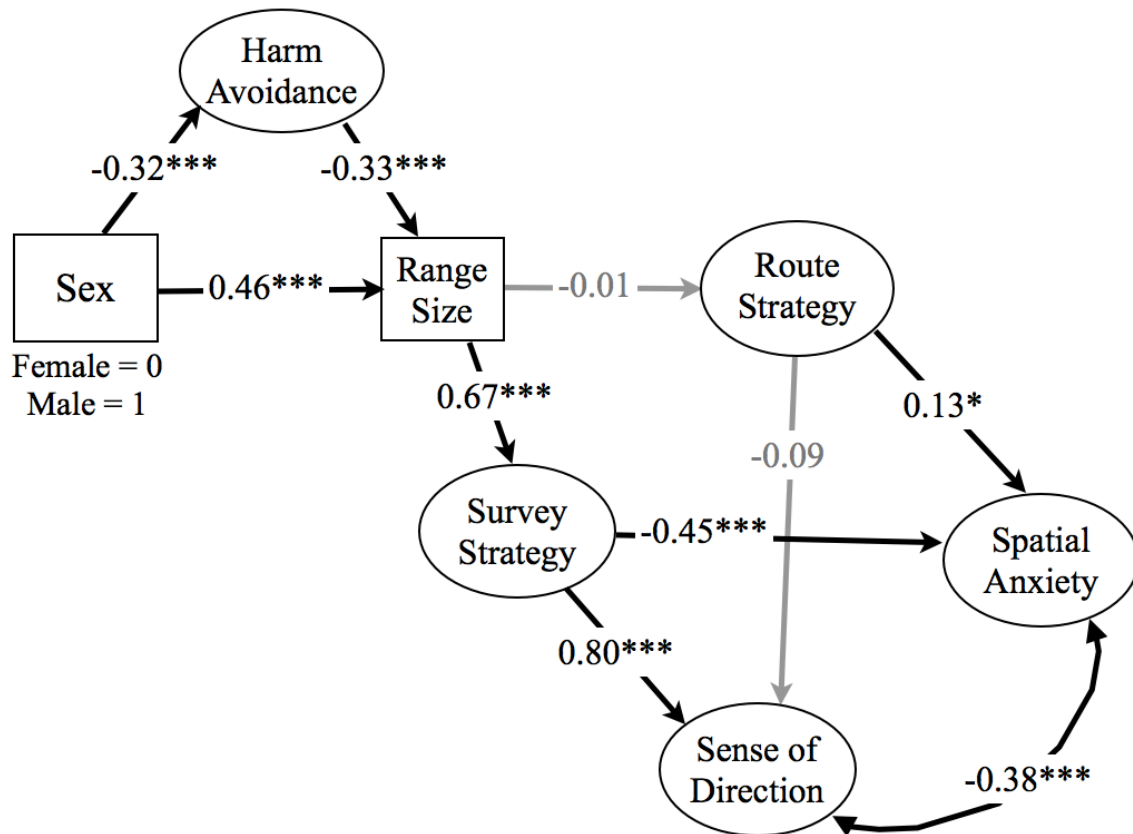


Figure 2.2. Structural model results. Path coefficients are in standardized metric. Ellipses represent latent variables and rectangles represent observed variables. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Grey path arrows and coefficients represent non-significant paths (at a 0.05 level).

predation), we find that more avoidance leads to an even smaller range size, above and beyond any other effect related to biological sex (e.g., male mating benefits with large range size). Therefore, we interpret the partial mediation as support for the two-fold evolutionary pressure model proposed by Ecuyer-Dab and Robert (2004).

In support of our hypothesis that larger range sizes change the demands on male navigation, we find that larger range sizes predict more reliance on a survey-based navigation strategy. To our knowledge, this is the first study to test whether the use of a survey strategy is related to range size. While previous research has found that males

report a greater reliance on a survey strategy than females (Lawton, 1994; Prestopnik & Roskos-Ewoldsen, 2000), our model shows that this relationship still holds even when forcing the effect to be completely mediated by one's range size. We believe that this result further supports the Ecuier-Dab and Robert (2004) model because larger range sizes require navigating over longer distances, at which point remembering all of the turns one must take to navigate back home would be nearly impossible. Furthermore, survey-based strategies allow one to take shortcuts, and when traveling over long distances, shortcuts have the potential to save time and metabolic resources. Interestingly, smaller range sizes did not predict the use of a route-based strategy. This is consistent with some literature showing that males and females both use a route-based strategy at least some of the time they navigate (Castelli et al., 2008). In addition, Saucier et al. (2002) found that males outperformed females in a navigation task when participants were forced to take a survey strategy, but that there was no sex difference in navigation performance when participants were forced to take a route-based strategy. Overall, this finding supports previous literature, suggesting that the difference between male and female navigation strategies is that males tend to utilize both survey- and route-based strategies (Saucier et al., 2002).

Next, our model shows that the more one uses a survey-based strategy, the greater their sense of direction, and the lower their spatial anxiety. This is consistent with literature showing that the use of a survey-based strategy is positively related to spatial perception ability (Lawton, 1994), mental rotation (Pazzaglia & Beni, 2001), one's sense of direction (Prestopnik & Roskos-Ewoldsen, 2000) and negatively related to spatial anxiety (Lawton, 1994; Lawton & Kallai, 2002). In addition, it has been suggested that a

survey-based strategy is more robust to navigation error (Saucier et al., 2002), which may reduce the frequency with which one gets lost, increasing their sense of direction and decreasing their spatial anxiety. Again, previous research has reported sex differences in both sense of direction and spatial anxiety (Lawton, 1994; Lawton & Kallai, 2002; Schmitz, 1997), but this is the first study to report that these sex differences still emerge after forcing them to be completely mediated by range size. This provides additional support for the proposal that many of the sex differences in spatial cognition and navigation may be due to differences in range size. Alternatively, it has been suggested that the ability to flexibly switch between navigation strategies given the available information in the environment is a better predictor of navigation ability (Wolbers & Hegarty, 2010).

Finally, we found that those who rely heavily on a route-based strategy tend to have higher levels of spatial anxiety. Although Lawton (1994) found a negative relationship between the use of a survey strategy and spatial anxiety, we show that relying too much on a route-based strategy (above and beyond one's use of a survey strategy) can lead to more spatial anxiety. We believe this relationship could result from the fact that a route-based strategy requires following a known route, but when in a novel environment, there are no known routes, so the risk of getting lost is rather high, leading to more spatial anxiety when navigating in novel environments. Overall, previous research has found sex differences in navigation strategy, sense of direction, spatial anxiety, and range size. Other works has found a relationship between range size and spatial ability (Ecuyer-Dab & Robert, 2004), and between navigation strategy and spatial anxiety (Lawton, 1994). This is the first study to show in a comprehensive test that sex

differences in a variety of navigation-related self-reports can be completely mediated by a person's range size. Finally, we are the first to show that one's level of physical harm avoidance actually reduces their range size above and beyond the typical sex differences found in range size.

There are several limitations with the current findings. First, we used the harm avoidance subscale as a proxy for a motivation to avoid predation or any life-threatening situation. Certainly harm avoidance does measure one's tendency to avoid life-threatening situations, but we did not measure actual behaviors consistent with the avoidance of harm. Furthermore, our model assumes that females are more motivated to avoid physically harmful situations due to their larger investment in parenting. Future work might consider assessing the relationship between harm avoidance and the number of reproductive aged children one has, with the expectation that more harm avoidance leads to more children.

Another limitation involves our measure of range size. We calculated the proportion of places participants had visited within a single state as a proxy for range size. First, some participants may have recently moved to this state, reducing our estimate of their range size, regardless of the range size they had established prior to their migration. In addition, visiting more locations does not necessarily mean you travel farther from home. In fact, Stephan, Jäschke, Oberzaucher, and Grammer (2014) measured the Euclidean distance of a participant's sketch of their range size and found no significant difference between males and females. A better measure would be GPS tracks showing the distance someone typically travels from home, rather than a proportion of places visited.

Finally, our model does not involve two important performance measures for which the theory supposedly accounts. The model does not involve a true measure of navigation ability, nor does it measure spatial ability (mental rotation as an example). Originally, the whole motivation for the theories discussed was to account for sex differences in spatial and navigation ability. Future work should consider adding measures of these abilities. However, we do believe that sense of direction is a decent reflection of one's navigation ability as has been shown in the past (Hegarty, Richardson, Montello, Lovelace, & Subbiah, 2002).

CHAPTER 3

SEX DIFFERENCES IN SPATIAL EXPLORATION

According to the proposed model, males gain more fitness benefits and females incur more fitness costs for maintaining a large range size. As a result, we expect females to be more cautious in their mobility, while males should exhibit more wanderlust tendencies. Furthermore, the model suggests that the sex differences in cautious versus wanderlust mobility served an important functional role in human evolution, namely, that more wanderlust in males led to more offspring, and more caution in females increased the chances their offspring would survive (at least long enough to reproductive age). One test of this functional hypothesis would be to place males and females in a novel environment where the potential costs and benefits are unknown, and see if their exploration behavior is consistent with more caution or wanderlust. Exploring a novel environment is a critical moment where men can take advantage of the potential benefits, and females are at risk of incurring the costs associated with a new terrain. Another reason a novel environment should be used to test this functional hypothesis is because individuals likely know the costs and benefits inherent in environments they know well. Furthermore, we would expect females to occupy safe environments, so their mobility in known environments is likely not influenced by their cautious tendencies (Ecuyer-Dab & Robert, 2004). The first hypothesis for Study 2 is that males and females will explore a novel environment differently, such that males will diffuse more quickly throughout the

space (in a wanderlust fashion), and females will tend to revisit previously explored locations (reflecting cautious exploration).

3.1 Does Exploration Relate To Navigation?

Wanderlust in a novel environment may lead males to discover the benefits associated with long distance travel, but it also places greater demands on their navigation. Our model implies that males develop the use of a survey-based strategy to deal with navigation over longer distances. Otherwise, the fitness benefits associated with maintaining a larger range size could be negated by getting lost in unfamiliar environments, or reducing their ability to effectively defend their territory.

Do males outperform females in navigation tasks? The vast majority of empirical findings reporting a male navigation advantage have utilized paper and pencil tasks of visual-spatial ability, or evaluated map-use ability (Coluccia & Louse, 2004). More recently, experimental tests that are more similar to real-world navigation show a male advantage in navigation performance (Castelli, Corazzini, & Geminiani, 2008; Galea & Kimura, 1993; Moffat, Hampson, & Hatzipantelis, 1998). Furthermore, Lawton (1996) demonstrated that individuals who reported relying more on survey-based navigation strategy had lower pointing errors than those who relied less heavily on this strategy. Other work found similar relationships between sex, navigation strategy, and navigation ability (Prestopnik & Roskos-Ewoldsen, 2000).

Spatial ability and navigation tasks are often cited as showing reliable sex differences (Astur et al., 1998; Castelli et al., 2008; Moffat et al., 1998). Despite these claims, a review of the spatial cognition and navigation literature from 1993 to 2003 found less conclusive evidence for a male advantage in actual navigation tasks (Coluccia

& Louse, 2004). In fact it was reported that approximately 58% of real-world and virtual-world experiments found a significant male advantage in spatial orientation tasks. It is worth noting that this review did not employ meta-analytical statistical tools, so a systematic view of effect sizes across these experiments was not reported.

Interestingly, Coluccia and Louse (2004) found that 85% of virtual-world experiments found a male navigation advantage when participants were allowed to actively control their movement in the world, but only 28% of “passive” experiments found such a difference. For example, Rossano and Moak (1998) had participants either study a map of a campus or observe a video tour of the campus (i.e., passive spatial encoding). While their main question was not about sex differences, they reported no difference between male and female performance on a spatial orientation or configuration test. Likewise, Sadalla and Montello (1989) asked participants to walk a path through a hallway with a variety of different angled turns. Afterwards, participants estimated the angle of their turn, pointed to their original direction of travel and their starting location, finding no difference between male and female performance. Although this experiment involved active movement through the space, participants were not allowed to freely explore, nor was there much to explore in that environment. Finally, this experiment, like many other navigation tasks, was conducted in a room-sized space, which may contribute to the lack of sex differences found (Coluccia & Louse, 2004).

In contrast, there is more evidence that free-exploration tasks lead to sex differences in navigation. Malinowski and Gillespie (2001) asked 978 military personnel to explore a 6 km outdoor area for 10 targets using a map and compass. They found that men found more targets and took less time to complete the task than women, while

women reported more anxiety about the task than men. Unfortunately, they did not directly measure navigation ability, but presumably finding one's way out of a 6 km outdoor environment requires some degree of navigation. More pertinent to the current study, Waller, Knapp, and Hunt (2001) allowed participants to freely explore virtual and real world mazes. Their main objective was to test the ability to transfer spatial knowledge from a virtual world to a real world, but interestingly, they did find that men pointed more accurately to landmarks than females. One well-known task that tends to show reliable sex differences in navigation performance is the Morris water maze. In a typical water maze task, participants explore a small arena in search of a hidden platform. After participants find the platform, they are repositioned at some other location within the arena and asked to navigate back to the platform. While the task is conducted in a small space, participants are required to freely explore and males typically outperform females (Astur, Ortiz, & Sutherland, 1998).

Finally, there are certainly some experiments that report a male navigation advantage even when exploration is constrained (Devlin & Bernstein, 1995; Lawton, 1994). For example, Lawton (1994) led participants along a tortuous path through a wooded outdoor area, and had participants stop four different times and point from each stop to their starting location. Near the end of the route, they asked participants to lead the experimenter to the starting location as another measure of navigation ability. They found that males pointed more accurately than females, but only for one of the four responses, but they could navigate more accurately to the starting location than females.

To our knowledge, no one has provided an explanation for why sex differences are often found in navigation tasks when exploration is unconstrained. Given that our

model predicts sex differences in exploration, it seems plausible that there is something about the typical male exploration pattern that facilitates their acquisition of spatial knowledge. One potential reason why this question has yet to be addressed is due to the complexity involved in quantifying human mobility (or the movement of any biological organism). Research in geography has found that humans move in a complex, scale-free pattern (Rhee et al., 2011). In fact, there is an entire swath of research in behavioral ecology devoted to the study and quantification of animal movements (Turchin, 1998). Therefore, if we expect to find a unique signature in male exploration that enhances their navigation ability, we should begin with a plausible theory that can narrow our focus to specific spatial-temporal dynamics in exploration behavior.

3.2 What Aspects of Exploration Might Relate to Navigation Ability?

One of the hallmark distinctions between male and female navigation is that males tend to rely more heavily on survey-based navigation. Survey-based navigation relies on information specifying the relative distance between fixed spatial features (e.g., landmarks) in order to maintain a cohesive “mental map” independent of a navigator’s current location (i.e., geocentric perspective). This is often referred to as layout knowledge (Rieser, Lockman, & Pick, 1980) because the combined relative distance information between all objects theoretically allows one to reconstruct the layout of the space. Shelton and McNamara (1997) examined the learning of spatial layouts by asking participants to encode a room-sized layout of objects from a single viewpoint, and then recall this configuration from different viewpoints around the room. They found that the accuracy of layout knowledge (smaller pointing errors) was greatest when recalling the layout from their originally encoded view. Later, Shelton and McNamara (1997)

provided participants with two distinct encoding views and found that the accuracy of layout knowledge was greatest for both of the encoded views. Even when individuals encode a layout from a top-down view, they show more accurate layout knowledge when recalling the layout from that same view (Shelton & McNamara, 1997). Other research suggests that when people receive many different views of the space, their layout knowledge is accurate regardless of the view from which they are to recall the layout from (Evans & Pezdek, 1980; Thorndyke Hayes-Roth, 1982). In other words, if you can view the same space from multiple perspectives, you can generate more accurate layout knowledge.

Furthermore, successful navigation with a survey strategy requires layout knowledge on multiple spatial scales. If you only have layout knowledge of room-sized spaces, then navigating several miles would require you to recall the layout of a large number of small spaces. This might look more like route-based navigation as you use layout knowledge of one local area to guide your navigation to the next local area and so on, until you reach your destination. With layout knowledge on a single small scale, you would not be able to reliably take shortcuts. However, if you obtain layout knowledge on a larger scale, you can use fixed spatial features that are visible from many locations within the environment, allowing you to guide your overall direction of travel. Layout knowledge on only a single large scale, though (e.g., only knowing how distal cues are configured), would preclude you from being able to pinpoint your destination, as distant cues are not precise enough. Therefore, a survey-based strategy likely involves the acquisition of layout knowledge on multiple spatial scales. In fact, research shows that spatial memory, in part, is hierarchically structured (Zhou, Mou, Wang, & McNamara,

2014). For example, your layout knowledge for a smaller space is partially dependent upon your layout knowledge for larger spaces (campus to city) (McNamara, 1986). Given the spatial information that is important to encode in order to effectively use a survey strategy, we expect that males will explore a novel environment in ways that allow them to gain layout knowledge on multiple spatial scales.

It is worth discussing in more detail how one might go about encoding layout knowledge on multiple spatial scales to understand the use of our quantitative approach. The spatial information central to layout knowledge is determining the relative distance between all pairs of the features that make up the layout (Rieser, Lockman, & Pick, 1980). The more accurate one's relative distance information, the less distorted the overall layout. Distortions in layout knowledge may appear as error in pointing, or in more indirect navigation paths to locations within the layout.

The question then becomes, how does a person extract relative distance information from a layout of spatial features? One source of relative distance information (or depth cue) is motion parallax (Braunstein & Tittle, 1988; Rogers & Graham, 1979). Motion parallax describes the rate at which objects in your visual field move as you translate through the environment. Movements of translation simply refer to a change in your position, regardless of a change in your direction (i.e., rotation). The reason why motion parallax provides relative distance information is because objects closer to you move more than objects far from you. Therefore, two objects that are close together should move at similar rates as you translate through the environment. The usefulness of motion parallax information depends upon your distance to the object and the length of your translation. For example, objects very far away may not appear to move in your

visual field, unless you translate over a larger distance. While motion parallax is concerned with how far you translate, regardless of your change in direction, it is worth noting that changing direction too often will reduce the overall length of your translation, so we cannot ignore the changes in one's direction when measuring the length of their translations. In fact, much of the animal movement literature uses the term "directional persistence" to identify the length of a translation prior to a significant change in heading, so to facilitate discussion, this term will be used throughout the rest of this paper.

Directional persistence, via motion parallax, offers a way to extract relative distance information from a spatial layout, but only on a scale proportional to the length of the directional persistence. Therefore, to obtain relative distance information regarding spatial features on multiple spatial scales, one must add variety to the length of their directional persistent movements. In other words, to obtain layout knowledge on multiple spatial scales, using motion parallax, one must have periods of long directional persistence mixed with periods of medium and short directional persistence.

3.3 Summary of Hypotheses

According to our model, females have a greater tendency to avoid physical harm, which restricts their range size, reducing incurred costs associated with traveling far from home. In contrast, males often take more physical risks, leading to larger range sizes and increasing the benefits associated with traveling far from home. If these relationships are functional, then males and females should explore a novel environment with more wanderlust and caution, respectively. To measure wanderlust and caution in exploration behavior, we will use a well-known measure of diffusion, called the mean squared displacement. Diffusion can be thought of as the rate at which something spreads

throughout an area over time. It has been demonstrated that many particles diffuse at a rate proportional to the square root of time (Einstein, 1905), known as normal diffusion. The consecutive movement of these particles is typically uncorrelated over time, and is known as Brownian motion. In contrast, when consecutive movements are correlated over time, the rate of displacement exceeds normal diffusion and is called super diffusion (Ben-Avraham & Havlin, 2000). Typically, the movement of an animal is consistent with super diffusion (Benahamou, 2004; Rhee, Shin, Hong, Lee, Kim, & Chong, 2011; Vishwanathan, Raposo, & da Luz, 2008), possibly due to an animal's ability to remember where they have been and a desire to move away from their previous spatial locations (Fagan et al., 2013). We expect that males will explore in a more super diffusive pattern than females, reflecting more wanderlust in male exploration and more caution in female exploration. Caution will be assessed by measuring the amount of revisiting behavior while exploring. Revisiting is defined here as an instance where a person travels back to a locale that they have already explored, and will be described in more detail in the methods.

The second hypothesis derived from our model is that the wanderlust- style of exploration should expose males to relative distance information on multiple spatial scales, allowing them to effectively use a survey-based navigation strategy. To measure the extent to which one's exploration exposed them to relative distance information on multiple spatial scales, we will focus on the time course of their directional persistence. An instance of directional persistence produces motion parallax that indicates the relative distance to fixed spatial features. The key, therefore, is to exhibit directional persistence on short, medium, and large spatial scales. However, instead of artificially categorizing

periods of directional persistence into long, medium, and short varieties, we can simplify the problem by assessing the scaling relationship in the time course of their directional persistence. More precisely, we should expect individuals to cycle between moments of high directional persistence (i.e., high speed in one direction) and low directional persistence (i.e., low speed or constant direction change, or both). Yet to achieve directional persistence on many spatial scales, one must change up the frequency with which they cycle between high and low directional persistence. In fact, expecting a scaling relationship in directional persistence is to say that we expect the distribution of frequencies to be consistent with a power law distribution. In contrast, a distribution of frequencies consistent with a normal distribution would be primarily comprised of a single frequency (i.e., the mean or fundamental frequency). In terms of layout knowledge, this would provide a wealth of relative distance information on a single spatial scale, and a lack of relative distance information at all other scales. Instead, a distribution of frequencies that follows a power law distribution would reveal a wealth of relative distance information on many spatial scales, theoretically supporting a survey-based strategy and leading to better navigation performance.

Finally, as reviewed above, research is mixed as to whether males do outperform females in navigation. First, the vast majority of these studies have not measured navigation behavior. Instead, many experiments rely on the ability to point accurately to the origin or destination, or the ability to provide accurate wayfinding directions. Second, of the studies that have measured navigation behavior (e.g., Astur, Ortiz, & Sutherland, 1998; Morris water maze), very few use a large-scale space (e.g., see Malinowski & Gillespie, 2001 for an exception). Finally, the majority of these experiments have

constrained the exploration, or spatial encoding, leading to a lack of ecological validity. Given these methodological limitations, the current study will also simply assess male and female navigation performance in a large-scale environment where participants are free to explore in any way they wish. In addition, we will ask participants to navigate to and from previously visited locations, as well as point to these locations. This will allow us to test the ability of pointing tasks to reflect actual navigation behavior.

3.4 Methods

3.4.1 Participants

One hundred six undergraduate students (60 Females, 46 Males; Mean Age = 21.7, $SD = 5.01$) participated for course credit. All participants had normal or corrected-to-normal vision. Unfortunately, 8 females and 2 males did not complete the experiment due to motion sickness, leaving 96 participants (52 Females, 44 Males) left in our sample.

3.4.2 Materials

The virtual world was developed using Unity 4.6, and consisted of a 1 km² rectangular world containing several subregions: a desert, swamp, deciduous forest, coniferous forest, grassland, and meadows. Each subregion contained unique vegetation and geological features (see Figure 3.1 for examples). There were two main geological features that were visible from nearly all locations in the world: a sandstone canyon and a mountain peak. A waterfall, large boulders, and an arch were visible from approximately 0.5 km away. Uniquely colored trees, rocks, and hills were visible within a subregion, and then unique bushes and ground cover (i.e., flowers, grass) were visible from only certain locations within a subregion. A large lake bordered one of the four sides of the

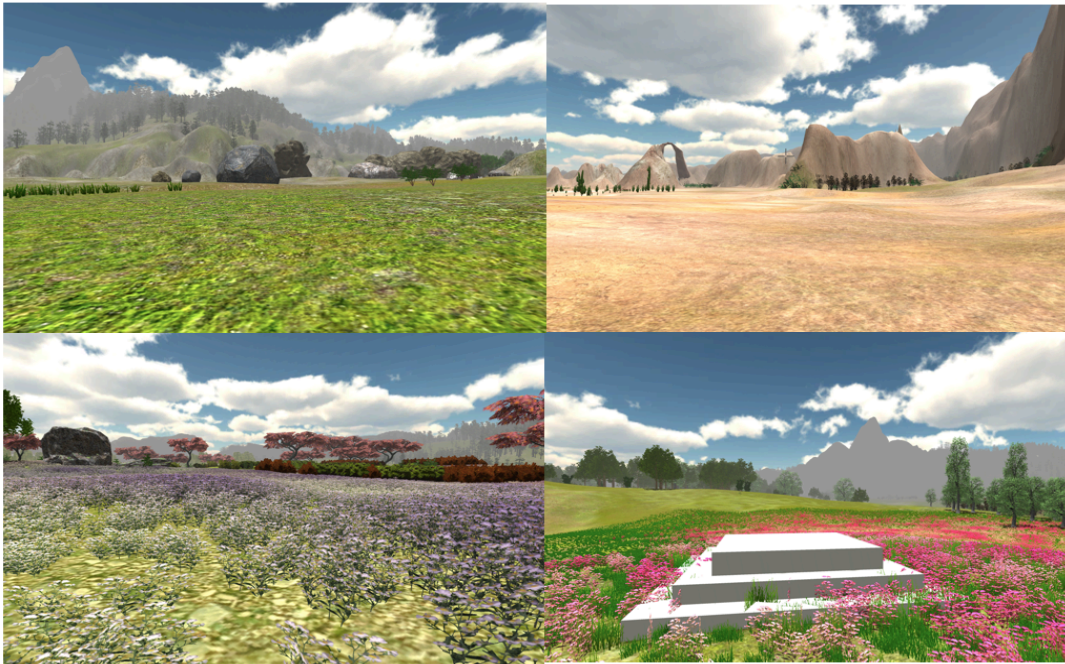


Figure 3.1. Screenshots of VE. Notice the variety of visual appearance throughout the virtual environment. Images were captured from the first-person camera used by participants during the experiment.

virtual world, a river separated the coniferous forest from the rest of the subregions, and a small pond was located between the meadow and the swamp. Finally, a square white platform indicated the participant's starting or home location, and a wooden cart, a treasure chest, and a water well were used as target objects. The starting location and the location of the target objects were identical for all participants.

Participants viewed the world from a first-person perspective (a virtual eye height of 1.8 m and a walking speed of 15 m/s) and controlled their movement using an Xbox 360 wired controller. The X, Y, Z position and camera orientation of the virtual camera was recorded at a sampling rate of 20 Hz, but was resampled to 1 Hz during data processing. The virtual world was displayed on a 60 cm display (resolution: 1920 x 1200,

rendered horizontal field of view: 60°).

The following questionnaires were administered online via Survey Monkey after the virtual exploration and navigation task: 15-item Santa Barbara Sense of Direction (SBSOD) (Hegarty et al., 2006), the 14-item Navigation Strategy Scale (Lawton, 1994), the 8-item Spatial Anxiety Scale (Lawton, 1994), the 26-item Harm Avoidance subscale from the Tridimensional Personality Questionnaire (Tellegen & Waller, 2008), and a 79-item list of local, national, and worldwide locations and regions to assess range size.

3.4.3 Procedure

Participants were seated at a computer in a quiet room. After finishing the consent process, the experimenter relayed the following instructions:

In this experiment you will be in a virtual world, similar to a first person video game. When you begin the task, you will see a white platform with an object hovering over it. This is your starting location, and the hovering object is your first target object. As soon as you press “A” on the controller, this object will be hidden somewhere in the world, and your task is to find it as quickly as possible. After you find the object, you will be asked to navigate back to the starting platform as quickly as possible. From there you will be asked to navigate back to the object as quickly as possible. The object will be located in the same location you originally found it, so do your best to remember its location when you first find it. Once you navigate back to the object, you’ll turn around and go back to the starting location and begin the next trial. From here, a new object will appear hovering over the starting platform. As soon as you press “A” on the controller, this object will then be hidden somewhere in the world, and you will repeat the entire process for this object, and then for the final object. Once you’ve finished exploring and navigating you will be at the starting location and asked to point, one at a time, in the direction you would travel if you were to return to each object. To do this, you will move the cross-hair on the screen such that it is pointing in the direction you would travel if you were to return to each object. Then, you will be teleported to an object and asked to point in the direction of the starting platform as well as the other two objects. You will repeat this process for all three objects. Finally, instructions will be provided at the bottom of the screen guiding you through the entire procedure.

The experimenter then explained how to use the controller, and informed the participant

that there was an online survey to take after they finished. Finally, participants were informed that if they began to feel sick, the experiment would be terminated and they would receive their full participation credit.

To ensure that more participants could finish the entire experiment, a procedure was implemented to provide hints if the participant exceeded a time limit. Participants were allowed 20 minutes to find each object, after which the experimenter would verbally guide them directly to the object. Participants were allowed 10 minutes to navigate between the object and the starting platform, after which the experimenter would verbally guide them to their destination. We recorded the part(s) of the procedure for which a participant was provided a hint. Participants were also administered the online questionnaires used in Study 1 after completing the virtual exploration task. Finally, we recorded the participant's video gaming experience, and the purpose of the study was revealed to them at this time.

3.4.4 Data Processing

We recorded the location (X, Y, and Z) and the camera orientation of the participant over the course of the entire virtual exploration and navigation task. These data were originally sampled at 20 Hz, but were then down-sampled to 1 Hz prior to performing any other processing or analysis. Next, we trimmed the beginning and end of each trajectory (i.e., three exploration bouts, and the nine navigation bouts), such that they began and ended when the participant was 15 m away from their starting location and destination (i.e., starting platform or target object). We chose to trim the data as such for two important reasons. First, at the very beginning of the experiment, some participants were confused about the task instructions, so they did not move for a period

of time, as the experimenter clarified the instructions for them. We did not want this data to be considered “cautious” behavior in our analysis. Second, once participants found the target object or navigated back to it, they were required to record this with a button press, but many participants were not able to do this successfully on their first attempt. As such, some participants wandered around the object attempting to successfully record that they had completed this portion of the experiment. We did not want this behavior to be considered in our calculations of caution or navigation performance, so it was removed. Finally, approximately 60% of the participants required a hint while searching for a target object. As such, we only analyzed the first 20 minutes of the exploration data for every participant, as any data after this point do not reflect the participant’s own behavior.

3.4.5 Mean Squared Displacement

To quantify wanderlust in the exploration trajectories, we used a measure of diffusion known as the mean squared displacement (MSD). To calculate the MSD, we compute the mean of all displacements (i.e., change in position) separated by a time lag, τ . We repeat this process for $\tau = 1, 2, 3 \dots N/4$, where N is the length of the time series. After taking the logarithm of all τ values and means, we fit a least squares regression where the slope is equal to the diffusion coefficient, D . The MSD was obtained for each individual three times, once from each of their three exploration trajectories.

3.4.6 Revisiting Behavior

As a way of measuring the level of caution in one’s exploration, we calculated was the extent to which the participant revisited locations throughout their trajectory. First, we established a 100 m radius around each location along a participant’s trajectory.

The decision of 100 m was based on the maximum distance one could reasonably visually identify one of the objects from within the virtual world. In other words, we believe that a participant could effectively search a circle with a radius of 100 m from each position in their trajectory. For each position in the participant's trajectory, the Euclidean distance between this position and all other previous positions (in time) was calculated, and all positions with a Euclidean distance equal to or less than 100 m were identified. Next, any positions that were within the 100 m radius that consecutively preceded the current position were ignored, as these do not indicate revisiting behavior per se. Then, revisiting positions were defined as any of the positions within the 100 m radius in which the participant left and then re-entered that same area (see Figure 3.2). Finally, we computed the average number of revisiting positions across all samples in the exploration trajectory.

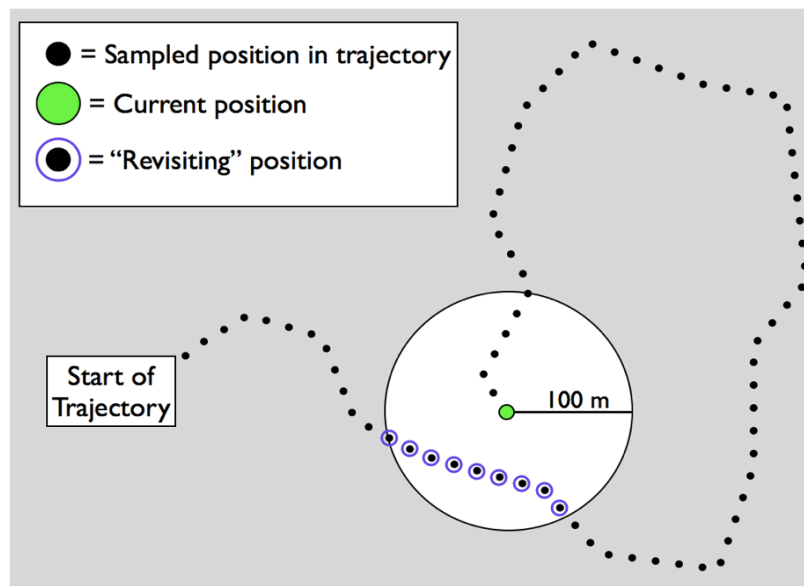


Figure 3.2. Revisiting diagram. Demonstrates how “revisiting” was calculated. Black dots encompassed by a blue circle indicate data points that would be counted as “revisits” for the current position indicated by the green dot.

3.4.7 Navigation Performance

To measure navigation performance, we compared the trajectory travelled by participants when navigating back to each object to a straight line connecting the starting platform and the target object. We quantified the deviation of the navigation trajectory from a straight line using the Fréchet distance (a measure of the similarity between two curves). Lower Fréchet distance estimates indicate more similarity between the navigation trajectory and a straight line to the target, suggesting better navigation performance.

3.4.8 Pointing Performance

Participants made 12 total pointing responses (3 responses from the starting platform and each of the three target object locations). For each pointing response, we calculated the absolute error in degrees. Then, we averaged the absolute errors for all the trials in which the participant pointed from one target object to another target object. This is a strong indication of the participant's layout knowledge because they were never required to travel to and from each target object, so to make an accurate pointing response, they had to infer the layout of the objects relative to each other. In addition, we averaged the absolute errors for all the trials in which the participant pointed from the starting platform, or from a target object to the starting platform. These pointing responses are less indicative of layout knowledge because participants had experience navigating between the starting platform and each target object.

3.5 Results

3.5.1 Sex Differences in Exploration

We wish to address our first hypothesis that males and females will explore a novel environment in ways consistent with the different selective pressures contribution to their range sizes (i.e., wanderlust in males, caution in females). To test this hypothesis, we will measure the rate of diffusion (i.e., how quickly one spreads throughout the environment over time), and the rate of revisiting (i.e., the amount of time spent in previously visited locations in the environment).

To test differences in diffusion rate, a 2 (Participant Sex) x 3 (Exploration Trial) mixed ANOVA showed a main effect of trial as diffusion rates increased over the course of the three exploration trials, $F(2,188) = 16.91, p < 0.001, \eta_p^2 = 0.15$. However, there was not a significant main effect of sex or a sex by trial interaction. Given that we expect males to show more wanderlust in a novel environment, we chose to compare males and females for only the first exploration trial because this is the time when the environment is the most novel. In fact, post-hoc comparisons showed that males ($M = 1.59, SE = 0.02$) explored with a higher rate of diffusion than females ($M = 1.51, SE = 0.02$), but only for the first exploration trial, $t(94) = -2.16, p = 0.03, d = 0.44$. By the second and third exploration trials, females increased their rate of diffusion to a level comparable to the male rate of diffusion (see Figure 3.3). This finding supports the idea that males show more wanderlust in their exploration of a novel environment than females. The sex difference in diffusion rate dissipated by the second trial, which may have been due to the environment being less novel, so females exhibited less caution in their exploration. However, we will turn to a more direct test of the female caution hypothesis next.

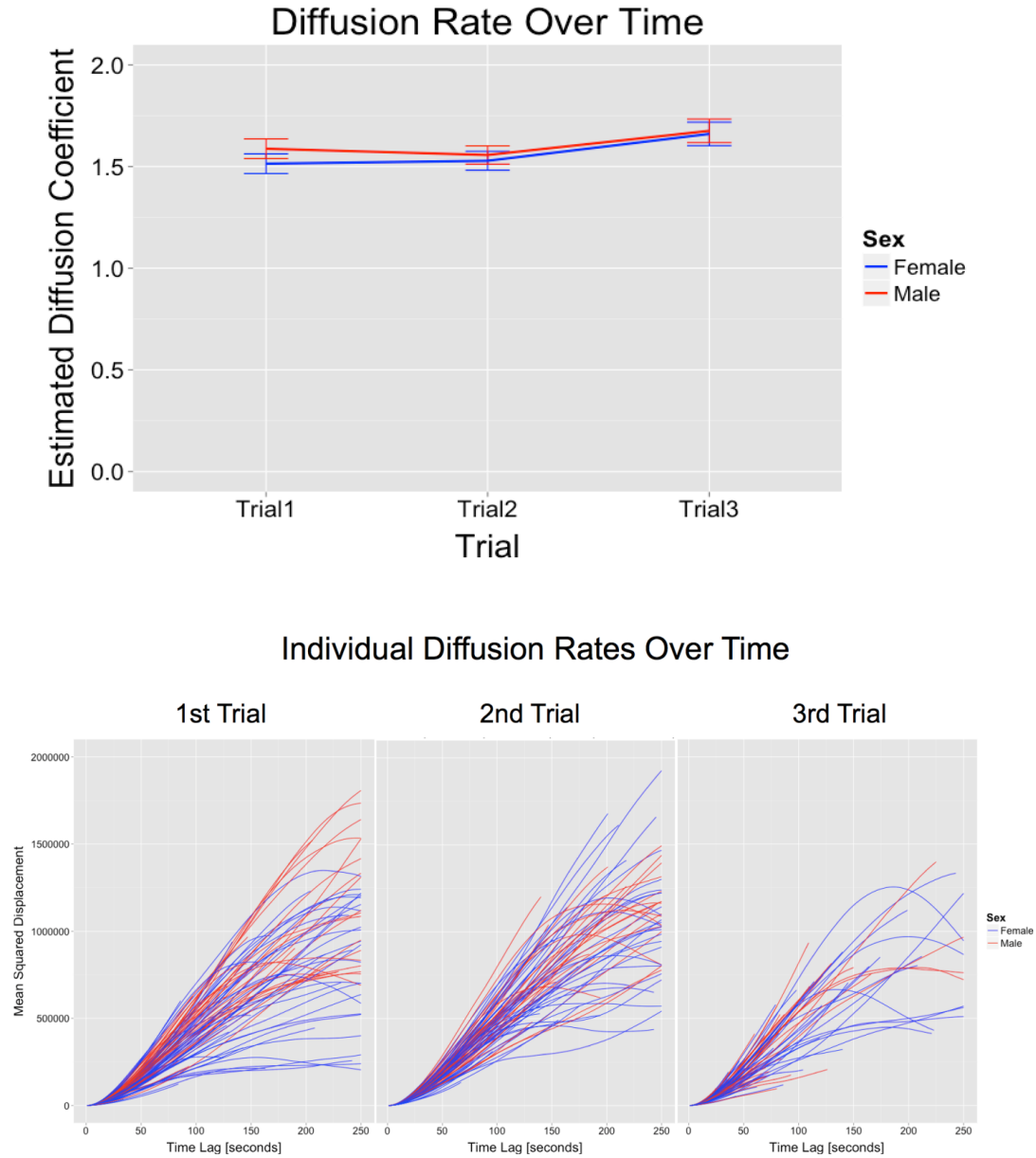


Figure 3.3. Diffusion rates over time. Top graph depicts the average diffusion rate for females (blue) and males (red) with 95% confidence intervals. Y-axis indicates the estimated diffusion coefficient and the x-axis indicates the trial. Bottom graph depicts individual diffusion rates separated by the three trials. Blue lines indicate female participants and red lines indicate male participants. Y-axis indicates the average squared displacement and the x-axis indicates the time lag in seconds. Importantly, these individual trajectories are depicted prior to taking the logarithm of both the y- and x-axes.

To examine the rate of cautious exploration, we used a 2 (Participant Sex) x 3 (Exploration Trial) mixed ANOVA with the average amount of revisiting behavior as the dependent variable. First, there was a significant main effect of trial, $F(2,188) = 11.7$, $p < 0.001$, $\eta_p^2 = 0.11$, suggesting that participants reduced their overall amount of revisiting over the course of the three exploration trials. Second, there was a significant main effect of participant sex, $F(1,94) = 9.55$, $p = 0.003$, $\eta_p^2 = 0.092$, with females showing a higher rate of revisiting behavior on average across the three exploration trials. No significant trial by participant sex interaction emerged. Post-hoc comparisons found that females ($M = 5.13$, $SE = 0.69$) only exhibited a higher amount of revisiting behavior than males ($M = 2.77$, $SE = 0.42$) for the first exploration trial, $t(94) = 2.67$, $p = 0.009$, $d = 0.56$. Paralleling the rate of diffusion results, males exhibited more cautious exploration for only the first exploration trial, possibly reflecting the fact that the environment was no longer novel after the first trial (see Figure 3.4).

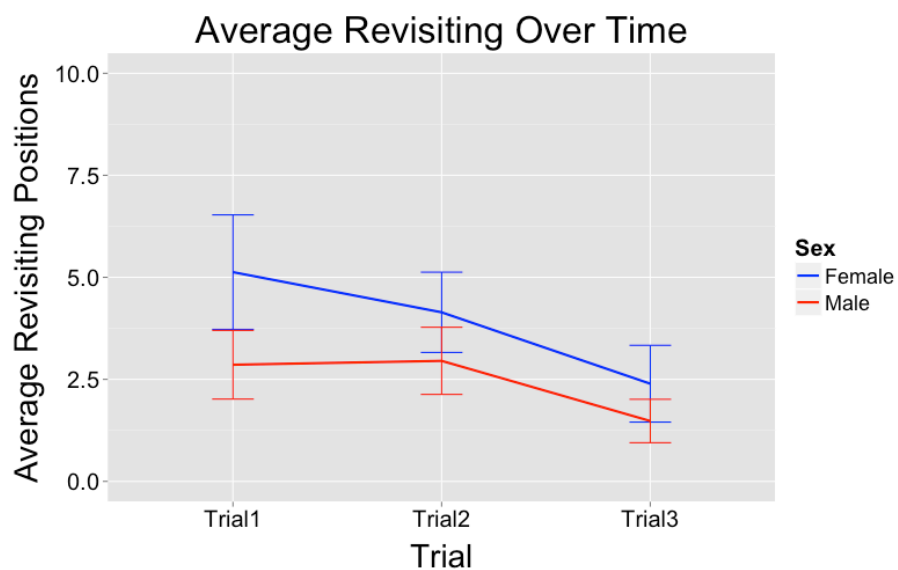


Figure 3.4. Revisiting results. Red line indicates the male average and blue line indicates the female average. Error bars indicate 95% confidence interval.

Thus far, we have interpreted higher levels of revisiting and lower rates of diffusion as reflecting caution during exploration. To provide further support for this interpretation, we tested the relationship between an individual's level of self-reported spatial anxiety and their average amount of revisiting and rate of diffusion for the first exploration trial. There is likely a statistical dependency between diffusion rate and revisiting behavior, as well as the potential for participant sex to serve as a better predictor than spatial anxiety for both exploration behaviors. As such, we ran a mediation model to provide a more rigorous test. In particular, we expected that females would report higher levels of spatial anxiety, and that more spatial anxiety would lead to more revisiting while exploring a novel environment. Simultaneously, we expected that more spatial anxiety would lead to a lower diffusion rate while exploring. Therefore, we tested the extent to which spatial anxiety mediated the relationship between participant sex and revisiting and diffusion rates during exploration² (see Figure 3.5). First, we found that males ($M = 2.40$, $SE = 0.12$) reported significantly less spatial anxiety than females ($M = 2.80$, $SE = 0.76$), $b_1 = -0.42$, $SE = 0.153$, $p = 0.006$, $r^2 = 0.07$. Next, participant sex predicted the amount of revisiting, with females exhibiting more revisiting than males, $b_2 = -1.46$, $SE = 0.70$, $p = 0.03$, partial $r^2 = 0.04$. Spatial anxiety did not significantly mediate the relationship between participant sex and the amount of revisiting behavior, $b_3 = 1.83$, $SE = 0.95$, $p = 0.053$. In contrast, levels of spatial anxiety completely mediated the relationship between participant sex and rates of diffusion, $b_4 = -0.06$, $SE = 0.03$, $p = 0.03$, $r^2 = 0.05$, with more spatial anxiety predicting a lower diffusion rate during

² Mediation models were estimated with maximum likelihood and bootstrapped to provide more robust estimates of standard errors.

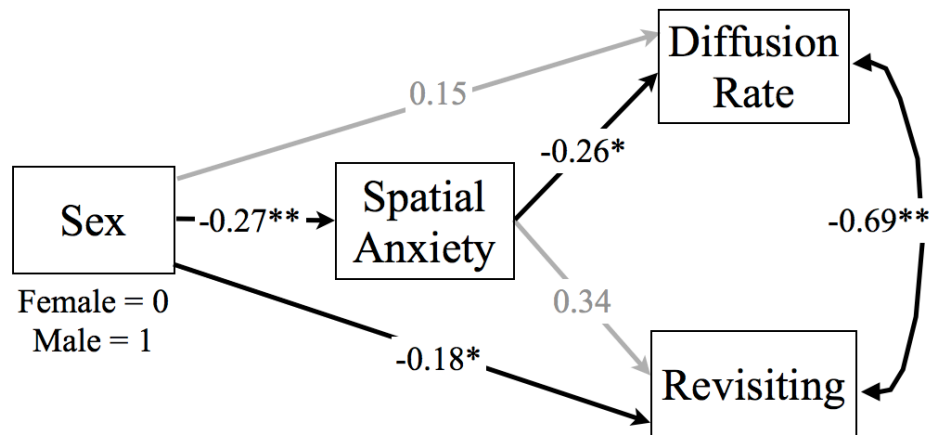


Figure 3.5. Exploration path model. Results showing spatial anxiety completely mediating the relationship between participant sex and diffusion rates, but no mediation between participant sex and revisiting. Path coefficients are estimated standardized results. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Grey path arrows and coefficients represent nonsignificant paths (at a 0.05 level).

exploration. Finally, a higher diffusion rate significantly correlated with lower amounts of revisiting, $r = -0.43$, $p < 0.001$. Overall, this model suggests that females exhibited more caution than males while exploring a novel environment, and that diffusion rates might serve as a better reflection of the caution vs. wanderlust distinction, given that spatial anxiety was not a significant mediator of the relationship between participant sex and our revisiting measure.

3.5.2 Exploration Relates to Navigation Ability.

Our second hypothesis was that males would explore in a way that would allow them to obtain relative distance information on multiple spatial scales, and that this would

account for their navigation ability. However, the research findings are mixed as to whether males actually outperform females in navigation tasks. As such, we need to observe a sex difference in navigation performance in order to test our second hypothesis. After finding a target object, participants were asked to navigate back to the starting location as quickly as possible. Once they arrived at the starting location, they were then asked to navigate back to the target object. This procedure was completed for three different target objects, providing six different measures of their navigation ability over time. We tested for a male advantage in navigation ability using a 2 (Participant Sex) x 6 (Trial) mixed ANOVA. There was a significant main effect of trial, $F(5,470) = 17.37, p < 0.001, \eta_p^2 = 0.16$, demonstrating that participants improved their navigation performance over time. Second, there was a significant main effect of time, $F(1,94) = 19.49, p < 0.001, \eta_p^2 = 0.17$, with males performing better than females on average. Post-hoc comparisons with a Bonferroni correction revealed that males outperformed females when navigating to and from the first and second target objects, but that there was no difference in navigation performance when navigating to and from the last target object (see Figure 3.6).

Previous research has often inferred navigation ability by measuring the accuracy with which an individual can point to unseen, but previously visited, locations. In this experiment, participants performed a pointing task after the exploration and navigation portion of the experiment. Participants made a total of 12 pointing responses, three while located at each target location and the starting location. While located at the starting location, participants were asked to point to the three target locations, assessing their spatial knowledge for a relationship with which they had much experience (i.e.,

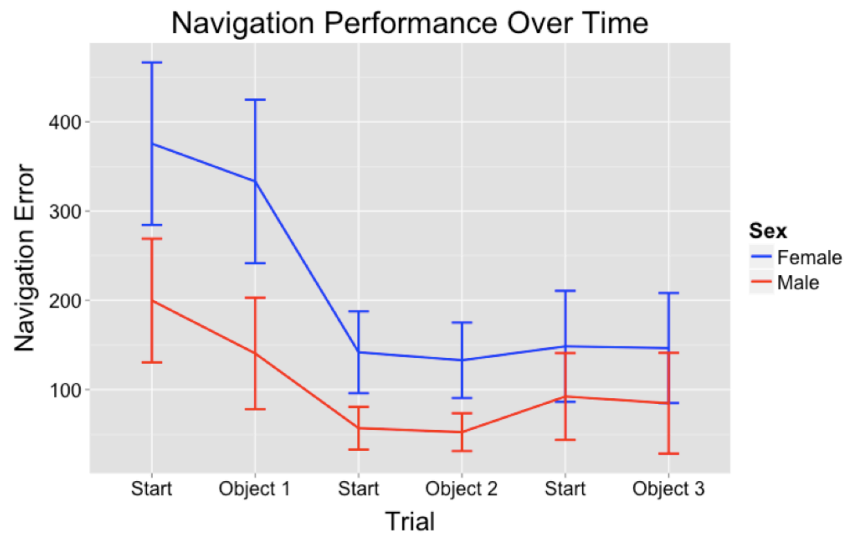


Figure 3.6. Navigation performance over time. Y-axis indicates estimated Fréchet distance with larger values indicating more deviation from a straight line (i.e., more navigation error). X-axis indicates the navigation goal. Blue line indicates the average for females and the red line indicates the average for males. Error bars represent 95% confidence intervals.

navigating to and from each target object). Similarly, while located at each target location, participants were asked to point to the starting location as one of their three pointing responses. These responses also assess their knowledge for a spatial relationship they had plenty of experience with. In contrast, while located at each target object, participants were asked to point to the other two target objects. These pointing responses should assess the participant's knowledge for spatial relationships they did not have experience with, because they never had to navigate between target objects. While we expect males to point more accurately than females based on similar previous findings, we expect this effect to be driven by the pointing responses from one target object to another target object. Therefore, we used a MANOVA to test for sex differences across the two different types of pointing responses. The model revealed that males were

significantly more accurate than females when pointing from one target object to another target object, $F(1,94) = 7.79, p = 0.006, \eta_p^2 = 0.08$, while there was no sex difference in pointing accuracy to or from the starting location, $F(1,96) = 2.27, p = 0.14$ (see Figure 3.7).

From a functional perspective, actual navigation performance is more important than pointing to unseen locations because failing to find one's way (i.e., navigation) has real fitness consequences, whereas failing to point accurately to a location has little impact on reproduction and survival. Therefore, to test our second hypothesis that the way males explore can account for their better navigation ability, we will simply use the

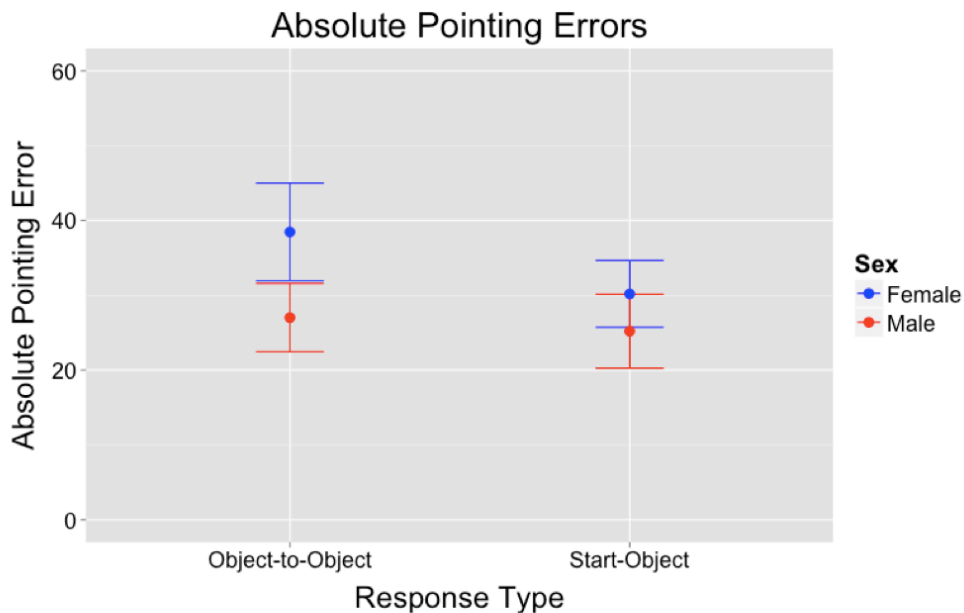


Figure 3.7. Pointing results. Pointing errors in degrees grouped by participant sex and type of pointing response. “Object-to-object” indicates pointing responses where participants were located at one of the three objects and were asked to point to the other two objects (a total of 6 pointing responses). “Start-Object” indicates pointing responses where the participants were either located at the start and pointed to the three objects, or located at an object and were asked to point back to the start (a total of 6 pointing responses). Blue dots indicate female average and red dots indicate male average. Error bars represent 95% confidence intervals.

average navigation performance across all six navigation trials.

To assess the extent to which an individual's exploration provided relative distance information on multiple spatial scales, we analyzed the time-course of their directional persistence using a windowed periodogram analysis. Directional persistence was calculated by multiplying the individual's speed (change in distance over change in time) by the cosine of their turning angle. Therefore, traveling at maximum speed (15 m/s) in a straight line would yield a directional persistence estimate of 15. Traveling at maximum speed, but making a 90 degree turn, would yield a directional persistence estimate of 0. We obtained an estimate of their directional persistence once every second for a single exploration bout. This produced a time-series of directional persistence such that the individual oscillated between moments of high directional persistence and moments of low directional persistence. This time-series can then be decomposed into a distribution of frequencies, where low frequencies indicate long moments of high directional persistence followed by long moments of low directional persistence. High frequencies then indicate rapid switching between high and low directional persistence. In order to obtain relative distance information on multiple spatial scales, one ought to have a variety of different frequency making up the time-course of their directional persistence. So, we estimated the distribution of frequencies (i.e., fractal dimension) in their directional persistence within a series of 50 s windows. Then, we averaged the estimated fractal dimension across all 50 s windows and repeated this process separately for all three exploration trials. Larger estimates of fractal dimension indicate more variety in their frequency distribution, potentially leading to more relative distance information at more spatial scales.

To test the hypothesis that male exploration exposes them to relative distance information at more spatial scales than females, we ran a 2 (Sex) x 3 (Trial) mixed ANOVA with the estimated fractal dimension of their direction persistence as the dependent variable. First, there was a main effect of trial, $F(2,186) = 15.38, p < 0.001, \eta_p^2 = 0.14$, and a main effect of participant sex, $F(1,93) = 27.89, p < 0.001, \eta_p^2 = 0.23$. There was also a significant interaction between trial and participant sex, $F(2,186) = 4.13, p = 0.02, \eta_p^2 = 0.04$. The interaction can be explained by a significant quadratic effect of trial interacting with participant sex, $F(1,93) = 8.97, p = 0.004, \eta_p^2 = 0.09$, such that the fractal dimension for male directional persistence increased from trial 1 to trial 2 and then leveled off, while the fractal dimension for female directional persistence remained low for trials 1 and 2 and only increased at trial 3 (see Figure 3.8). Overall, this indicates that male exploration provided relative distance information on more spatial scales than female exploration, but only for the first two trials.

Theoretically, if superior navigation performance relies on the use of a survey-based navigation strategy, and if obtaining relative distance information on multiple spatial scales allows one to effectively use a survey-based strategy, then we expect that individuals who adopt a survey-based strategy and then subsequently explore with a higher fractal dimension in their directional persistence will perform better in a navigation task. To test this hypothesis, we used the estimated fractal dimension of directional persistence for the first exploration trial because this was the participant's first chance to encode the environment providing them with layout knowledge to be used throughout the rest of the experiment. In other words, we believe that a person's first time in a novel environment will involve the most important portion of their encoding

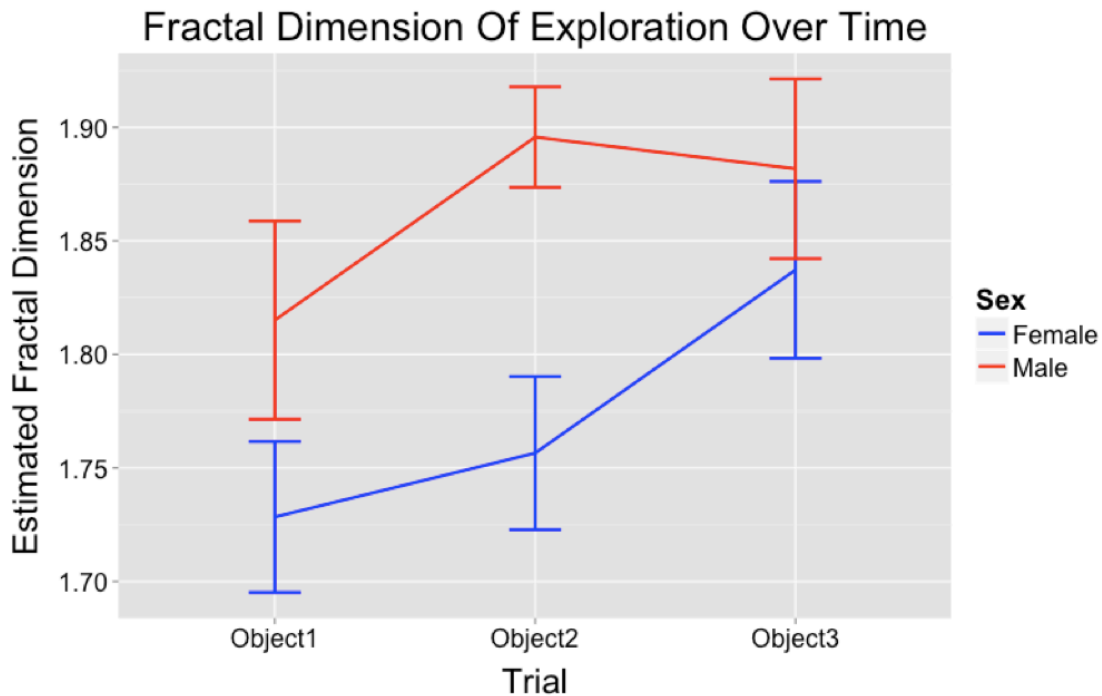


Figure 3.8. Average estimated fractal dimension over three exploration trials. Grouped by participant sex (Females = blue, Males = red). Error bars indicate 95% confidence intervals.

experience.

We then assessed whether participant sex predicted one's use of a survey strategy, if one's use of a survey strategy predicted navigation performance, and if the fractal dimension of their directional persistence while exploring was a significant mediator between survey strategy use and navigation performance (see Figure 3.9).

First, we found that males ($M = 3.24$, $SE = 0.10$) reported more use of a survey-based strategy than females ($M = 2.83$, $SE = 0.09$), $b_1 = 0.41$, $SE = 0.13$, $p = 0.002$, $r^2 = 0.10$, and that relying more on a survey-based strategy predicted significantly better navigation performance (i.e., lower navigation error), $b_2 = -59.7$, $SE = 18.1$, $p = 0.001$, r^2

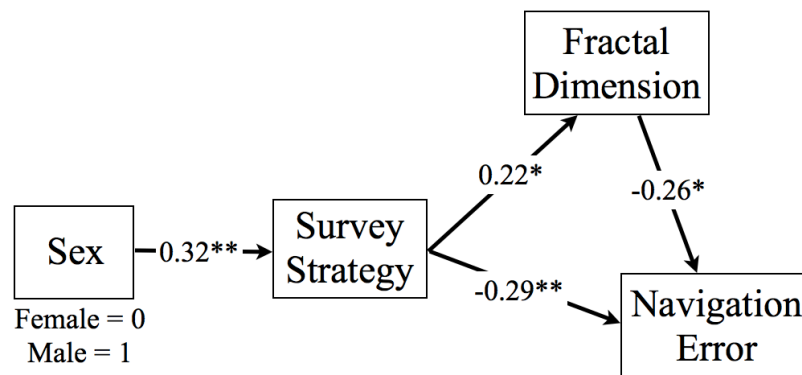


Figure 3.9. Navigation path model. Results demonstrating partial mediation between self-reported survey strategy and navigation error by one's fractal dimension during their first exploration trial. Path coefficients represent estimated standardized coefficients. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

= 0.09. Importantly, a higher fractal dimension in directional persistence while exploring was a significant mediator of the relationship between survey strategy use and navigation performance. That is, relying more on a survey-based strategy predicted a higher fractal dimension in directional persistence, $b_3 = 0.05$, $SE = 0.13$, $p = 0.002$, $r^2 = 0.05$, suggesting that individuals who use a survey-based navigation strategy might be seeking out relative distance information at multiple spatial scales. Finally, a higher fractal dimension in directional persistence predicted significantly better navigation performance (i.e., lower navigation error), $b_5 = -250.49$, $SE = 103.95$, $p = 0.02$, $r^2 = 0.06$. Overall, the results of this path model support our hypothesis that males rely more heavily on a survey-based strategy, and that this leads them to explore a novel environment ways that provide them access to spatial information at multiple spatial scales, which ultimately leads to better navigation performance (see Figure 3.9).

Finally, we provided hints to participants that were unable to find a target object within 20 minutes of exploration, or navigate back to the starting location or target within 10 minutes of exploration. Twenty-two of the 44 male participants and 35 of the 52 female participants required a hint at some point throughout the experiment. When only looking at the participants that did not receive a hint, the correlation between participant sex and average navigation performance approached significance, $r(37) = -0.29, p = 0.07$, with male participants almost showing better navigation performance than female participants. When only looking at the participants that did receive a hint, the correlation between participant sex and average navigation performance was significant, $r(55) = -0.44, p < 0.001$, with males outperforming females. However, there was only a sex difference in diffusion rate, $r(55) = 0.32, p = 0.01$, and revisiting behavior, $r(55) = -0.29, p = 0.03$, for the group of participants that received a hint, but not for the group that did not receive a hint. Finally, when examining the participants that did not receive a hint, participant sex and the fractal dimension of directional persistence approached significance, $r(37) = 0.28, p = 0.08$, with males almost having a higher fractal dimension than females. For the participants that did receive a hint, male participants exhibited a higher fractal dimension in their directional persistence than females, $r(55) = 0.32, p = 0.01$. We did not include the receiving of a hint as a covariate in our models due to the drastic reduction in statistical power we would have observed. Furthermore, our measurements of diffusion, revisiting, and the fractal dimension of directional persistence were computed on the data up to the 20-minute time limit. If the participant required a hint to navigate back to the starting location or an object, they would have had to exceed a 10-minute time limit. In this case, participants likely created a long tortuous path while

failing to find their destination. Our measure of navigation performance would have captured this long tortuous path deviating very far from a straight line. In fact, it is likely the case that if the participants who did need a hint while navigating were never offered any help from the experimenter, their navigation performance score would have been even worse. Therefore, we do not believe that receiving a hint could have accounted for our pattern of findings.

3.6 Discussion

We set out to test two hypotheses motivated by the theoretical model discussed in Study 1. First, we predicted that when placed in a novel environment, males would explore with more wanderlust than females and that females would show more caution in their exploration than males. Second, we predicted that male exploration patterns would contain certain spatial-temporal dynamics that lead to better navigation performance. In our experiment, participants freely explored a novel large-scale virtual environment in search of three objects, one at a time. After finding each object, participants were asked to navigate back to the starting location and then back to the object. Then, participants pointed in the direction of each target and the starting location. Afterwards, participants answered questions regarding their general spatial anxiety and navigation strategy. We provide evidence in support of our hypotheses, as well as other interesting results. Next, we will address how our findings relate to previous work, their implications for future directions, and limitations with our methods.

3.6.1 Sex Differences in Exploration

We found support for our first hypothesis by showing that males explored a novel environment with a higher diffusion rate than females, and females showed more revisiting behavior. Importantly, higher diffusion by males and more revisiting by females was only observed the first time that participants explored the virtual world. Theoretically, males have faced selection pressures encouraging them to venture farther from home in search of mates, while females have faced selection pressures encouraging them to be more cautious and stay closer to home (Ecuyer-Dab & Robert, 2004). Novel environments contain unknown costs and benefits, but once this environment has been explored, one presumably knows the costs and benefits very well. Therefore, if females explore cautiously to avoid the costs associated with traveling far from home, then we should expect their cautious behavior to dissipate as they learn the environment is safe.

Other work has found that females took longer to navigate a maze than males (Schmitz, 1997), and females took longer to find hidden objects in a large outdoor environment (Milanowski & Gillespie, 2001). In both cases, the authors attributed the slower completion times by females to poorer navigation ability. Our experiment measured caution and wanderlust during an explicit exploration phase separate from a navigation task. To our knowledge, this is the first experiment to show quantitatively different behaviors in males and females during free exploration. Furthermore, the differences we observed may be direct reflections of evolved motivations that generate different range sizes in males and females.

Not only is our finding novel, but the quantitative methods we used are also novel in the psychological literature. First, we created a measure of revisiting behavior as a

reflection of caution exploration. Revisiting was strictly defined as any instance in which a person left a general location and then returned to this location at a later point in time. We argue that this reflects caution because whether one is avoiding getting lost or predation, then a locale you previously occupied is safer than a new locale. However, there are several other reasons why an individual may revisit a location. First, retracing one's steps may aid in establishing a navigation route for later use. While Lawton (1994) found that females report a higher reliance on a route-based navigation strategy, our findings from Study 1, as well as work by Castelli et al. (2008), failed to find such a sex difference. The second reason a person may exhibit more revisiting behavior, especially when exploring while in search of targets, is if they struggle to keep track of where they have been. If the motivation for revisiting is due to caution or route establishment, then we are implying that it is an intended behavior. On the other hand, if an explorer cannot remember where they have previously searched, then they will inevitably search the same location more than once. In our study, we were able to show that individuals' levels of spatial anxiety positively related to the amount of revisiting behavior, although this relationship did not reach significance when spatial anxiety was allowed to simultaneously predict diffusion rates.

The second quantitative method we used to measure wanderlust was the mean squared displacement (MSD). The MSD is a very popular method used to measure the rate of diffusion of a system. For example, Einstein (1905) discovered that the random movement of a particle diffuses at a rate proportional to the square root of time. That means that if a system does not have a strong motivation to move in one particular direction, then it will undergo normal or subdiffusion. On the other hand, if a system

continues moving away from where it has been in the past, then it will undergo super-diffusion - diffuses at a rate greater than the square root of time. Recently, Rhee et al. (2011) analyzed GPS tracks of individuals while on a campus, at a state fair, or an amusement park. One of their findings was that human mobility in these contexts was super-diffusive. We also observed super-diffusion in both male and female participants, but the rate of super-diffusion was greater for males than females on the first trial. Over the course of the three trials, rates of diffusion increased for both men and women, presumably because participants were more familiar with the environment and “knew” where they wanted to search. Interestingly, greater diffusion rates were associated with less spatial anxiety even when spatial anxiety was allowed to simultaneously predict revisiting behavior. We suggest that MSD might be a better indication of cautious exploration than our measure of revisiting, but more work needs to be done to validate the use of these measures in this context. However, we would like to offer a word of caution in using the MSD on data collected in the real world because the MSD relies on computing the mean of spatial locations, outliers due to measurement error (e.g., GPS connection lost for a period of time) will drastically skew estimates of diffusion. In the present study, there was little to no measurement error in the virtual environment, so we are confident in our use of the MSD in these data. Future research that utilizes such a technique should first take steps to identify outliers or other extreme values prior to calculating diffusion rates.

3.6.2 Exploration Predicts Navigation

In support of our second hypothesis, we found that male exploration patterns tended to have a particular spatial-temporal dynamic that predicted better navigation performance. The spatial-temporal dynamic we quantified was the extent to which their directional persistence was observed on many different spatial scales. In other words, males tended to travel at full speed in one direction (i.e., high directional persistence) for long, medium, and short periods of time. In contrast, females tended to show directional persistence on fewer spatial scales (e.g., directional persistence for only medium and short periods of time). Theoretically, directional persistence creates motion parallax information, which provides relative distance information regarding spatial features. Obtaining relative distance information regarding spatial features at many spatial scales allows one to use distant landmarks to guide their overall direction of travel, less distant landmarks to guide their travel to a particular locale, and then very local landmarks to pinpoint their destination. Furthermore, we demonstrated that the more one reports relying on a survey-based strategy, the more spatial scaling we observed in their directional persistence. Finally, we found that the more spatial scaling in one's directional persistence, the better their navigation performance.

First, this finding is conceptually consistent with some spatial memory literature. For example, Chase (1983) found that what distinguished expert taxi drivers from novices was that experts conceptualized the city in terms of a hierarchy of spatial scales. That is, there are regions within a city, and within these regions are neighborhoods, and within these neighborhoods are specific locations. McNamara (1986) asked participants to learn a layout of objects that were divided into particular regions (i.e., a string on the

floor). Afterwards, participants were asked to make distance and direction judgments regarding these objects, finding that responses were sensitive to the regions the object was located within. Other behavioral research supports the idea that spatial memory is hierarchically structure such that our knowledge for local layouts is nested within our knowledge of global layouts (Zhang et al., 2014). Evidence even exists for the idea that hippocampal neurons encode spatial information hierarchically as some fire for local cues, distal cues, relationships between cues on the same spatial scale, and the relationship between local and distal cues (Shapiro, Tanila, & Eichenbaum, 1997). However, none of this work has measured the behavior of a person as they attempt to build a hierarchical structure to their spatial memory of a large-scale space. Here, we suggest that one possible way to develop a hierarchical structure to your spatial memory is to obtain information about the relative distance between spatial features at many different scales. For example, one might travel a long distance in a particular direction to get a sense for the layout of distant cues, but then at other times, they travel only short distances in a particular direction where the only useful motion parallax information they receive is informative of the layout of local cues.

We have placed emphasis on obtaining layout knowledge on multiple spatial scales, but there is another interesting connection between our use of a fractal analysis and theories of spatial learning. Kuiper (1978) suggested that route knowledge can be considered one-dimensional because it can be described using a single line, whereas survey knowledge is considered two-dimensional because it requires a plane in order to capture the relative distance between multiple spatial features. Later, Golledge (1999) suggested that our knowledge of a location or landmark can be thought of as the

knowledge of a point (0-dimensional), while routes are knowledge of lines (1-dimensional), and layouts are knowledge of planes (2-dimensional). Interestingly, to measure the extent to which directional persistence was present on multiple spatial scales, we utilized what is known as a fractal dimension, meaning fractional or part of a dimension. Often times we think of topological dimensions, or dimensions as whole numbers, but several aspects of our biology actually exhibit properties that exceed the topological dimension that they exist in. For example, the brachiation of the human lungs has a topological dimension of 3 (i.e., they have height, width, depth), but if one measures the surface area of the lungs at finer and finer scales, the estimate of the surface area continues to get larger and larger. In essence, the surface area of the lungs functions in more than three dimensions (West, Brown, & Enquist, 1999). Others have found that the time between heartbeats of healthy individuals is fractal, but not for those at risk of congestive heart failure (Peng, Havlin, Hausdorff, Mietus, Stanley, & Goldberger, 1995). In other words, healthy hearts do not have a single heartbeat interval, but a distribution of heartbeat intervals that follows a power law distribution, and is known as fractal scaling (i.e., many short heartbeat intervals with a few very long intervals). Likewise, in the current study, we found that exploration patterns with more fractal scaling in directional persistence predicted better navigation performance. Furthermore, the fractal dimensions reported in this study ranged from roughly 1.5 to 2.0, indicating that while the directional persistence exhibited by our participants has a topological dimension of a line (i.e., 1.0), it functioned in more than one dimension, and the closer one's directional persistence was to two dimensions, the better their navigation performance. It may be the case that when certain aspects of one's exploration (e.g., directional persistence) exceed a particular

fractal dimension, their spatial knowledge shifts from route (1-dimensional) to survey (2-dimensional) knowledge. However, this is speculative and much more work needs to be conducted to substantiate this claim.

One of the major limitations to the current finding is that we did not experimentally manipulate the directional persistence of exploration (i.e., the encoding process). We chose to allow participants to freely explore because it was unknown what people would do, and if there were any spatial-temporal dynamics that might relate to navigation performance. Given our findings, future work might consider creating multiple encoding conditions that vary the fractal scaling of the directional persistence in the movement, ultimately manipulating the number of spatial scales of spatial information one is exposed to.

Despite this limitation, we believe this finding provides a major contribution to the spatial memory and navigation literature. As of now, there is a gap in the literature between spatial memory and spatial exploration studies. Certainly the ability to navigate requires learning and remembering spatial layouts, but much of the spatial memory research has focused provided participants with a very static encoding process (Shelton & McNamara, 1997). Yet some of the navigation research allows participants to freely explore, but does not attempt to quantify or relate the exploration behavior to navigation performance. This study offers evidence to suggest that the way in which a person explores a novel environment may be important for spatial learning and ultimately navigation performance. We also are able to offer a measure of exploration that captures both spatial and temporal properties of the movement, such that our theories of spatial learning and memory can generalize to observed real-world human mobility, that also

shows fractal properties and complex spatial temporal dynamics.

In addition to finding support for our two main hypotheses, we also found a number of other interesting results relevant to the spatial navigation literature. First, we observed that males outperformed females when asked to navigate back to a starting location or a previously visited target location, but only for the first two trials. By the third trial, female navigation performance was comparable to male navigation performance. This is interesting in part because previous research has not always found a male advantage in navigation performance, and those that have often allowed participants to freely explore the environment (Coluccia & Louse, 2004). Our work supports the idea that the male advantage in navigation tends to emerge when participants are allowed to freely explore. In fact, our work goes one step further and identifies an aspect of typical male exploration that is predictive of better navigation performance.

We also asked participants to point in the direction of each target object while standing at the starting location, point in the direction of the starting location while standing at each target object, and point in the direction of the other two target objects while standing at each target. This is conceptually analogous to much of the spatial learning work (Shelton & McNamara, 1997) in which participants study an array of objects from a single viewpoint and then (from memory) are asked to point towards an object as if they were standing at the same location as their encoded view as well as from a number of locations different from their encoded view. It is often found that participants are much more accurate when pointing to objects when imagining standing at their originally encoded view. In our experiment, the pointing trials that required participants to point from the starting location to each target, or from each target to the

starting location, were viewpoints that they had experienced while exploring and navigating. Interestingly, participants were never asked to navigate between the targets, yet we asked them to point in the direction of each target while standing at another target. The only pointing trials where we observed a significant male advantage in pointing accuracy was when pointing from one target to another target. This may be reflecting better layout knowledge on the part of males because they would have had to infer the distance between targets in order to accurately point from one target to another target. In contrast, when pointing from the starting location to a target location, one may simply point in the direction of an observable spatial feature that they remember navigating towards when they successfully navigated to and from the given target. In other words, one may only have knowledge of a direct route to and from the targets and the starting location and still point accurately during these trials.

3.6.3 General Limitations

Some limitations specific to particular findings have been discussed, but now we wish to address other methodological limitations that may impact our findings more broadly. First, we asked participants to explore and navigate in a virtual environment because this would ensure that the environment was novel and consistent across participants. In relation to our first hypothesis, which involved sex differences in exploration, our virtual environment did not contain any fitness related costs or benefits. Certainly we do not believe that male participants explored with such wanderlust because they were mate seeking, nor do we believe that female participants explored with such caution because they were avoiding predation. However, we do believe that people likely establish a way of exploring a novel environment, which then carries over to virtual

environments as well. Future work may consider involving costs and benefits in a virtual environment, such as the metabolic costs of travel. Another reason why the use of a virtual environment to study navigation is a limitation is because navigation is a multi-sensory (Sholl, 1989) process and our virtual environment almost exclusively relies on visual information. It may be the case that sex differences are only found in navigation tasks that require individuals to rely solely on visual information. However, Malinowski and Gillespie (2001) did find a male navigation advantage in a large-scale real world setting where all sensory cues were available for use while navigating.

Previously, we discussed the limitation of allowing individuals to freely explore and relate their exploration to navigation performance, but here we would like to expand on that discussion as it pertains more broadly to our findings. First, we chose to allow free exploration because our primary concern was with characterizing what individuals do while exploring a novel environment. While we found one aspect of spatial exploration (i.e., fractal scaling or directional persistence) that relates to navigation performance, the effect size was rather small. It is very possible that a whole host of other patterns embedded in one's exploration might be important for later navigation. Future work will likely have to combine methods allowing free exploration with methods that constrain encoding, until we develop a better understanding of how one's exploration contributes to their spatial learning and subsequently navigation performance. However, even if encoding is control for, we cannot guarantee that the individual is paying attention to the spatial information a particular exploration pattern exposes them to.

CHAPTER 4

OVERVIEW AND SIGNIFICANCE

In Study 1, we provided support for the Ecuyer-Dab and Robert (2004) proposal that both the fitness benefits to males and the fitness costs to females contribute to sex differences in range size, which lead to sex differences in spatial ability and navigation. In Study 2, we demonstrate that males explore a novel environment with more wanderlust and females explore with more caution, consistent with the overarching model tested in Study 1. Finally, in Study 2, we demonstrate that male exploration tends to provide an explorer with spatial information on multiple spatial scales, which leads to better navigation performance.

The findings from Study 1 mainly contribute to providing a comprehensive explanation for the pattern of sex differences observed in spatial ability and navigation. Jones et al. (2003) provide a wonderful summary of explanations put forth to account for these sex differences, but conclude that more evidence needs to be gathered to support or refute these accounts. Ecuyer-Dab and Robert's (2004) propose that the sex differences in spatial ability are likely due to two simultaneous evolutionary pressures, one that propels males to travel long distance in search of mates, and one that encourages females to stay closer to home to avoid predation. First, we provide evidence that both evolutionary pressures shape one's range size. Second, these explanations are put forth to account for a number of observed sex differences related to spatial navigation, such as different

navigation strategy use, navigation confidence, and spatial anxiety. We provide evidence of range size predicting navigation strategy development, which in turn leads to differences in navigation confidence and spatial anxiety. Importantly, we are the first to test all of these proposed relationships within the same individuals.

In Study 2, we are the first to quantify exploration behavior in humans and relate this to navigation performance, spatial anxiety, and navigation strategies. In particular, based on the model tested in Study 1, we predicted that males would explore with more wanderlust and females would explore with more caution. We found evidence in support of both of these relationships, suggesting that caution and wanderlust tendencies in females and males may reflect the same evolved tendencies that have generated sex differences in range size. This is the first study to show sex differences in exploration behavior and relate them to an overarching explanation for the sex differences in spatial abilities.

Next, much of the spatial memory literature forces people to learn a layout of objects from one or a few static views, making it difficult to extrapolate those findings to large-scale navigation ability. Much of the spatial navigation literature either constrains the encoding process or does not quantify exploration behaviors. Interestingly, many of the studies that observe sex differences in navigation ability allowed participants to freely explore. In Study 2, we provide the first evidence that *how* an individual explores a novel space may be crucial to their navigation ability later.

Finally, we utilized three novel quantitative techniques to capture meaningful behaviors in individual exploration patterns: Mean squared displacement, revisiting, and fractal dimension of directional persistence. Considering the lack of research that has

attempted to characterize human spatial exploration, all three measures provide a significant contribution to the literature because they may be useful in quantifying exploration behaviors in the future. Certainly, future research should work to discover additional tools that can aid in our understanding of spatial learning in a large-scale environment, but we do believe that the techniques used herein are a great start.

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