Sex differences in mobility and spatial cognition

A test or the fertility and parental care hypothesis in northwestern Namibia

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1 Introduction

Researchers consistently find that men perform better than women in certain spatial-cognitive and navigational tasks. These differences are well-documented in Western industrialized societies and have increasingly been replicated crossculturally. Evolutionary psychologists have put forward several distinct theories that link these sex differences to further differences in traveling long distances and into unfamiliar environments. In most of these theories, past selection favored the males who could travel more safely and efficiently which required superior navigation ability and the spatial-cognitive traits that facilitate it (Gray and Buffery, 1971). The key point of disagreement among these arguments is simply the presumed payoff of that travel, whether it is mates (Gaulin, 1992), hunting (Eals and Silverman, 1994), or warfare (Geary, 1995). However, one explanation for the sex differences in ranging, spatial cognition, and navigation ignores the payoffs to males and instead turns the focus on the fitness ramifications of women's long-distance mobility. This "fertility and parental care hypothesis" put forward by Sherry and Hampson (1997) argues that the observed sex differences can be explained in terms of the potential costs to women traveling, particularly during key periods of reproduction.

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1.1 Fertility and parental care

The fertility and parental care hypothesis highlights the relationship between women's performance on spatial tasks and hormonal changes related to developmental and cyclical stages of reproduction (Hampson and Kimura, 1988; McCormick and Teillon, 2001). In particular, the negative correlation between estradiol levels and spatial ability (Hausmann et al, 2000). Assuming spatial ability is a necessary component of successful navigation, hormonal shifts that decease spatial ability should also inhibit travel. The fertility and parental care hypothesis notes that ancestral women who avoided the risks and caloric costs of travel during key reproductive periods may have outcompeted those who did not (Sherry and Hampson, 1997).

Risky strategies tend to pay higher fitness dividends when variance in reproductive success among competitors is high (Darwin, 1871; Bateman, 1948; Clutton-Brock, 2007). As is the case in many species, men's reproduction skews higher than women's (Trivers, 1972; Wilson and Daly, 1985). The constraints of women's extensive prepartum investment in offspring places a ceiling on potential reproduction, and in doing so limits the prospective bounty paid to risky strategies relative to men. In addition to this common mammalian pattern, humans are a particularly altricial species (Montagu, 1961). Infants have an extended period of dependence, the burden of which falls predominantly on the mother in most societies. Fitness calculations for men need to account for the potential loss of future offspring due to risky behavior, but at least in the subsistence societies that have been investigated, fathers' deaths do not endanger living children (Sear and Mace, 2008). This is not the case for women, since the passing of a mother dramatically reduces any dependent children's likelihood of survival (Hill and Hurtado, 1996; Sear and Mace, 2008).

Travel away from home is risky behavior. Large predators, snakes, interpersonal violence, inclement weather, exposure, falling rocks, and many other dangers are real concerns when navigating wild natural environments (Treves and Naughton-Treves, 1999; Pugh and Theakston, 1980; Walker, 2001). The nature of the risk has changed for many of us in today's world, but travel remains one of the riskier activities. Travel related "road injury" is the seventh most common cause of death worldwide (Krug et al, 2000), and even in the United States traffic accidents are the second largest external cause of death (Murphy et al, 2010).

In addition to the risks associated with travel, the fertility and parental care hypothesis also highlights the energetic costs and how these trade-off against the need to divert as many calories as possible towards reproduction. With these concerns about the risks and energetic costs of travel in mind, the link between hormonal patterns associated with women's reproduction and the tools and desire to travel broadly presents an appealing evolutionary narrative. However, the logical thread hangs on several assumptions about the relationship between women's reproductive life-history and cognition and mobility that need to be demonstrated.

1.2 Predictions

This paper sets out to test a series of predictions drawn from the fertility and parental care hypothesis. In some cases this means replicating well-established patterns in a population that faces navigational challenges more similar to those faced by ancestral humans. In other cases, we offer the first test of predictions that underpin the fertility and parental care hypothesis and/or help distinguish it from alternative evolutionary theories explaining human sex differences across these traits.

1. Men will demonstrate higher spatial-cognitive and navigational ability, report lower spatial anxiety, and travel more broadly.

Men outperform women in specific measures of cognitive spatial ability (Sanders et al, 1982; Shepard and Metzler, 1971; Eals and Silverman, 1994; Lawton, 2010). This difference begins in infancy (Quinn and Liben, 2008; Moore and Johnson, 2008; Levine et al, 1999), and is corroborated by several non-human mammals (Jašarević et al, 2012; Perdue et al, 2011; Gaulin and FitzGerald, 1986). Measures of navigational skill, especially those that tap into cues used in long-distance travel into unfamiliar environments also tend to favor men (Moffat et al, 1998; Bryant, 1982; Galea and Kimura, 1993; Henrie et al, 1997), though this difference is not as robust (Burke et al, 2012; Gilmartin and Patton, 1984; Montello et al, 1999). Women also report higher levels of spatial anxiety than men and are less confident in their navigational ability (Devlin and Bernstein, 1995; Lawton, 1994; Picucci et al, 2011). Finally, research across a broad spectrum of environmental and subsistence context finds that men occupy larger ranges than women (Ecuyer-Dab and Robert, 2004a; Gaulin et al, 1988; MacDonald and Hewlett, 1999).

This collection of sex-differences captures the empirical pattern that led researchers to posit the fertility and parental care hypothesis, as well as the other competing hypotheses noted above. Previous work among the Twe and Tjimba found that these groups do indeed conform to this expected sex-difference in spatial cognition, navigation, and ranging. This study adds an improved measure of spatial-cognitive ability and a measure of spatial anxiety.

2. Women's mobility and associated cognitive traits will increase (at least relative to men) following menopause.

Unlike most mammals, human women may live an additional third of their lives following the cessation of fertility (Hawkes, 2003). Women in this postmenopausal period are no longer primary care-providers, and thus should value risk aversion and energy conservation more similar to their male age-mates. Following from the fertility and parental care hypothesis, this means postmenopausal women should be more mobile, less anxious, and perform better in spatial-cognitive tasks than reproductive-aged women, at least relative to same-aged men. Previous research has failed to demonstrate this expected

pattern in spatial ability and navigation in humans (Willis and Schaie, 1988; Driscoll et al, 2005; Moffat et al, 2001), but one study does find the expected reduction in the sex difference with age in rhesus monkeys, *Macaca mulatta* Lacreuse et al (1999). This study compares postmenopausal and reproductive-aged women across spatial and navigational ability, spatial anxiety, and mobility.

The fertility and parental care hypothesis makes a similar prediction about the comparison of reproductive-aged women and prepubescent girls, but we only included adult participants in this study.

3. Reproductive-aged women's mobility and associated cognitive traits will decrease when they are pregnant or lactating

Women cycle through a series of reproductive stages: mating (courtship, estrous), gestation, parturition, lactation, post-lactational parental care, and maternal recovery during their reproductive career (Gittleman and Thompson, 1988). In a review of the fertility and parental care hypothesis, Jones et al (2003) highlight gestation and lactation as particularly important periods for women to limit exposure to risk and caloric expenditure.

Women's energy budgets increase by approximately 8-10% during pregnancy, and 26% postpartum. Women manage this elevated demand through a combination of increased caloric intake, reduced movement, and in the case of lactation, by catabolizing fat stored during pregnancy (Dufour and Sauther, 2002). In addition to increased energetic demands, pregnant and postpartum women often report higher levels of anxiety (Heron et al, 2004; Wenzel et al, 2003). This is not a surprising pattern since any threats now necessarily extend to the dependent offspring as well. Furthermore, environmental threats like spiders, scorpions, small mammalian predators, and exposure pose uniquely deadly threats to infants. Among some of our closest primate relatives, including chimpanzees, Chimpanzee chimpanzee, gorillas, Gorilla gorilla gorilla, and baboons, Papio cynocephalus, the threat of infanticidal non-paternal males constrains the movement of mothers with unweaned infants in a variety of ways (Collins et al, 1984; Watts, 1989; Smuts, 1992; Stokes et al, 2003; Watts and Mitani, 2000). Male infanticide is rare in contemporary human societies, but may have been a realistic threat in our ancestral past, and other forms of sexual violence threaten women traveling alone in some societies Gregor

Assuming women's mobility and the cognitive traits that facilitate it respond facultatively to risk and energetic needs, pregnant and lactating women should be at the extreme in terms of limiting mobility and thus performance on spatial-cognitive and navigational tasks. These women should also report higher levels of spatial anxiety than other women. This study tests these predictions by comparing pregnant and postpartum Twe women to other Twe women of reproductive age.

4. Spatial cognition predicts women's range size.

The fertility and parental care hypothesis predicts a positive correlation between *women's* spatial ability and range size. Competing explanations for the male advantage in spatial cognition predict a positive correlation between *men's* spatial ability and range size. In each case, these arguments are agnostic to the relationship within the other sex; however, if spatial ability only predicts male range size it poses a challenge to the fertility and parental care hypothesis.

One study demonstrated a positive correlation between spatial ability (measured using the Morris water maze task) and range size among male meadow voles, *Microtus pennsylvanicus*, but did not look for a similar relationship among females (Spritzer et al, 2005). Two studies investigating this relationship in humans, one among urban Canadians and another among the Twe and Tjimba of northwestern Namibia, found a relationship between performance on the mental rotation task and range size for men but not women (Vashro and Cashdan, 2014). However, the sample for the Namibian study was small and thus the lack of a relationship among women may be the result of Type II error. This study attempts to replicate this finding among a similar population using an improved mental rotation task and a larger sample of participants.

2 Methods

2.1 Population

Participants in this study live in the dry mountainous region near the Kunene River which separates northwestern Namibia and southwestern Angola. This is a wild environment free of paved roads and large artificial structures. None of the participants in the study own an automotive vehicle, and with the exception of occasionally hitch-hiking to the town, all travel is on foot (or sometimes by donkey). Most participants report having become lost at some point in there lives. The field researcher was present during two instances of a search party being called for a missing person. In one case, an adolescent boy wandered too far during the day and could not find his way home by nightfall. In the other case, an elderly man became lost traveling between two villages. Many of the traditionally dangerous species of wildlife no longer live in the region Viljoen (1982), but people still list leopards and snakes as real threats to travelers, especially when passing through the mountains. State police rarely patrol the region, but inter-personal violence is suppressed through tribal law and the threat of involving the Namibian authorities. That said, violence is of some concern to people traveling outside their home region. As an example, the field researcher visited one remote mountain village where a rapist had been targeting women who traveled unaccompanied to their gardens.

This study included all of the people living in the *Ovizorowe* mountain valley in northwestern Namibia. This valley is known as the home of the Twe ethnic group, but 32% of the sample (41 participants) is drawn from Himba

villages positioned at the outlets on either end of the valley. For the purposes of this study, the most meaningful difference between these groups is that Himba men tend to own considerably more livestock than Twe men. Men are responsible for bringing cattle to pasture in distant locations once the local supply of grass is depleted. This results in a greater sex difference in mobility, at least for economic purposes, than is seen among the Twe. The analyses do not distinguish tribe membership and speak to the population of "people living in the *Ovizorowe* valley".

Twe and Himba women do not have access to birth-control and a large proportion of their lives are spent either pregnant or breastfeeding. Children are typically weaned at somewhere between 18 and 30 months old. Most of the reproductive-aged women included in this study (56%) were currently in the lactation stage of reproduction. Unweaned children are almost always in contact with their mother, either actively feeding, strapped to her back while she works, or laying together in the shade while she rests. Mothers are granted a brief reprieve from work immediately surrounding parturition, but afterwards are expected to continue their role in domestic production.

We recruited a total of 129 participants, including 65 men and 64 women for this study. Intake interviews asked participants' age and reproductive status. This allowed us to separate the participants into groups of "postmenopausal" (all women over 50 years of age, n=16) and "reproductive-aged" (all women under 50 years of age, n=48), then further subdivide the reproductive-aged women into "pregnant" (n=3), "lactating" (n=27), or "other" (n=18). The experimental items were split into two sessions, but we were not successful in recovering all of the participants for the second session. Due to this, sample sizes vary by task as noted in the results below.

2.1.1 Spatial cognition

Mental rotation: The mental rotation task was based on the Mental Rotation Test (MRT) developed by (Shepard and Metzler, 1971). In the traditional task, objects created by configurations of cubes are presented to the viewer. These cubes are either rotated versions of the same cube or an entirely different cube. The viewer is then asked to decide if the cubes are the same or different. Both accuracy and response time are recorded. We designed an adapted computerbased version of the MRT using gaming software (Unity, 2014) and conducted the experiment on a Toshiba 15.6" Touch-Screen laptop. Due to the novel nature of rectilinear objects, for the Twe, we adapted the Mental Rotation Test by having the viewers make judgments about computer generated images of human bodies with one out stretched arm, which were rotated on a twodimensional axis. Additionally, instead of showing the viewers two objects and asking them to make a same or different decision, we chose to show one target image at the top of the screen and have the viewer select one of two images that matched the target. This configuration was designed to avoid linguistic issues around having a button or icon that indicated same or different. Instead, the viewer simply used the touched screen interface to touch the body that matched the target object. 12 trials were presented to the viewers showing the bodies from the front and back, rotated twice at 0, 60, 120, 180, 240, and 300 degrees, making a total of 24 trials. This task was readily understood by most participants. However, it was unclear if some participants understood the task, as a few adopted a strategy where they only selected the left or right responses or alternated between the two. For this reason, only participants that scored above chance were used in the analyses.

2.1.2 Navigation

Real-world pointing: We used Real-world distant pointing accuracy as a measure of navigation abilities. Previous work has suggested that the ability to point to a location is a skill that is uniquely develop by mobility Bell and Saucier (2004). In our task we selected ten locations well-known locations with distances ranging from 10 to 130 kilometers. We used a Brunton Pocket Transit International Compass with 0-360 Degree Scale mounted on a tripod to record the pointing data. Viewers were first asked if they had visited one of the locations. If they had, they were then asked to use the sight on the compass to point to the location. Degree measurements were then taken from the compass. Accuracy was measured by taking the GPS coordinates that the compass was located at and the coordinates of the location pointed to, then calculating the degree of error from were the viewer pointed and the actual location. This resulted in errors ranging from 0 degrees (perfectly accurate) to 180 degrees (completely in the wrong direction). Measurements were taken in locations that were free of objects that visually occluded participants' views (e.g. dense foliage and mountains).

2.1.3 Anxiety

Spatial anxiety questionnaire: Adapted from Lawton (Lawton, 1994) we used a questionnaire that tested spatial anxiety in situations that required spatial and navigation skills, such as trying a new shortcut. Participants were presented with navigationally challenging scenarios then ask to indicate if they were concerned, sometimes concerned, or not concerned by the scenario.

2.2 Mobility

Annual visiting interviews: Participants were asked to name each place they traveled to and spent the night in the past year. In addition, they were asked who they traveled with, who they stayed with, and why they made the trip. These data were used to calculate the number of unique locations visited by each participant in the past year. In addition to this measure of "annual range", we also calculated the percentage of trips on which the participant was unaccompanied. This additional measure is designed to account for the fact that solo traveling presents a unique navigational challenge, in that a person is unable to free-ride on the navigational skills of others.

Daily GPS tracking: For each of the three days that the participants wore the trackers, we asked a series of questions that were intended to identify the nature and extent of their daily mobility. Data was collected on the purpose and mode of their travel, as well as whom they traveled with, including the relationship, age and sex of their travel companion. We also asked if they had any problems on their route, to determine the risks as well as navigational challenges that they may have encountered. Further, we inquired about their familiarity with the route and if they went off the trail, in order to assess a need for route or survey knowledge of the terrain.

3 Results

3.1 Sex differences

Men responded more accurately, though not more quickly, than women to the mental rotation stimuli (see Table 1). The real magnitude of this difference is likely larger than these results show, due to bias in the patterning of missing data. Only 18.8% of men were omitted from the analysis due to failure to demonstrate understanding compared to 28.3% of women. Assuming some correlation between spatial ability and ease of comprehending a spatial task, these analyses understate the sex difference.

Table 1 Sex differences

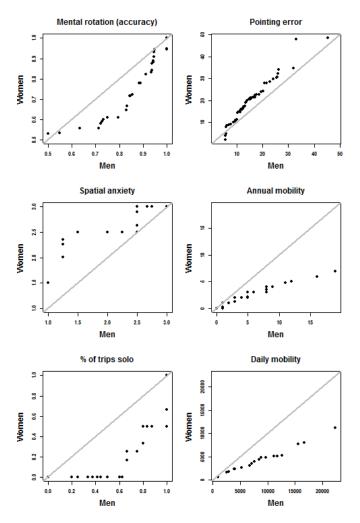
	Men			Women				
Measure	n1	$\mu 1$	$\sigma 1$	n1	$\mu 2$	$\sigma 2$	p-value	
Mental rotation (accuracy)	55	89.3%	12.7%	43	82.7%	16.4%	.033	
Mental rotation (time)	55	5.91	1.95	43	5.64	1.73	.459	
Pointing error	61	15.18°	7.51°	57	19.22°	9.26°	.011	
Spatial anxiety	27	2.29	0.57	27	2.64	0.37	.010	
Annual visits	42	4.29	4.18	45	2.02	1.59	.002	
Solo visit %	40	46.4%	38.7%	40	24.2%	37.1%	.011	
Daily mobility (km)	20	8.75	5.49	18	4.38	2.59	.004	

say something here

Men also made smaller errors in the pointing accuracy task, self-reported lower spatial anxiety, visited more unique locations in the past year, traveled alone to a higher percentage of those locations, and traveled more than twice as far on a daily basis. All of these differences are statistically significant (see Table 1).

3.2 Menopausal effects

Postmenopausal women responded more slowly to the mental rotation task than reproductive-aged women, and were slightly less accurate (see Table 2).



 ${f Fig.~1}$ Please write your figure caption here

Postmenopausal women were also much more likely than reproductive-aged women to fail to demonstrate sufficient understanding (61.4% compared to 21.4%), and thus not be included in the analysis. The fertility and parental care hypothesis does not necessarily predict postmenopausal women will outperform younger reproductive-aged women, but it does expect the sex difference to be smaller among older participants. However, comparing men split into analogous age groups the differences look similar but with a slightly weaker decline (Accuracy decrease from 89.6% to 86.7% and reaction time increase from 5.7 to 7.6). It does not look like women's spatial ability improves after menopause even accounting for general age-based decline shared with men. There do not appear to be any meaningful differences between postmenopausal

and younger women in pointing accuracy, which mirrors the pattern among men.

Table 2 Postmenopause

	Postmenopausal			Reproductive-aged				
Measure	n1	$\mu 1$	$\sigma 1$	n1	$\mu 2$	$\sigma 2$	p-value	
Mental rotation (accuracy)	5	77.1%	19.7%	38	83.4%	16.1%	.524	
Mental rotation (time)	5	7.46	2.08	38	5.40	1.55	.090	
Pointing error	14	20.54°	6.31°	43	18.79°	10.06°	.449	
Spatial anxiety	8	2.45	0.51	19	2.72	0.28	.183	
Annual visits	10	1.60	0.84	35	2.14	1.73	.180	
Solo visit %	10	35.0%	47.4%	30	20.6%	33.2%	.389	
Daily mobility (km)	3	7.05	3.62	15	3.85	2.11	.262	

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We find several interesting trends in the spatial anxiety and mobility measures, but the small sample of postmenopausal women limits statistical power. Postmenopausal reported lower spatial anxiety than reproductive-aged women, which is consistent with the fertility and parental care hypothesis. Postmenopausal women did not travel to as many unique locations in the past year as reproductive-aged women, which runs against our expectations. However, a higher percentage of those trips were made unaccompanied, which is consistent with the expectation of diminished risk-aversion. Among the three post-menopausal women to participate in the daily task, one recorded the highest average travel of all eighteen women included in the study (11.22 km), while the other two older women averaged a kilometer more daily travel than the average of the reproductive-aged women (4.97 km compared to 3.85 km). A larger sample is clearly needed, but these initial findings are intriguing and generally consistent with expectation drawn from the fertility and parental care hypothesis.

3.3 Postpartum and gestation effects

Women with an unweaned child at the time of testing responded slightly more quickly and accurately to the mental rotation task than other women of reproductive age, but the differences are small enough to easily be explained by random chance (see Table 3). These postpartum women performed considerably better than other reproductive-aged women on the pointing accuracy measure of navigational skill. However, the difference is not statistically significant, and a larger sample may be needed to assess the relationship between navigation ability and lactation. Consistent with the fertility and parental care hypothesis, postpartum women self-reported higher spatial anxiety than other reproductive-aged women.

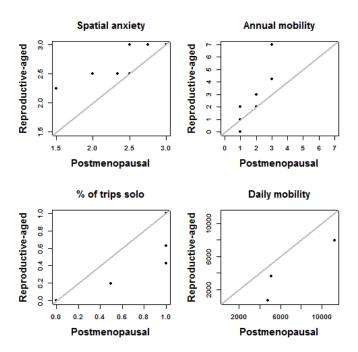


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Table 3 Postpartum

		Lactating		Mating or post-lactation				
Measure	n1	$\mu 1$	$\sigma 1$	n1	$\mu 2$	$\sigma 2$	p-value	
Mental rotation (accuracy)	21	83.7%	17.5%	14	81.0%	14.6%	.627	
Mental rotation (time)	21	5.38	1.68	14	5.80	1.27	.404	
Pointing error	24	16.73°	8.02°	17	20.97°	12.37°	.227	
Spatial anxiety	12	2.83	0.25	5	2.60	0.22	.092	
Annual visits	19	2.84	1.89	12	1.33	1.15	.01	
Solo visit %	19	22.0%	33.7%	9	22.2%	36.3%	.984	
Daily mobility (km)	19	3.78	1.36	5	3.71	2.82	.960	

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The fertility and parental care hypothesis predicts that women will curtail mobility due to the risks and caloric costs of travel. However, Twe women with unweaned children visited more than twice as many locations as other reproductive-aged women in the past year. One complication with the annual mobility data is that women women may have moved through more than one of the relevant reproductive stages in the past year. One woman who was breastfeeding at the time of her interview reported two visits away from home, both of which took place while she was pregnant. None of the other lactating women reported a unique visit that occurred prepartum. Similarly, none of

the pregnant women reported unique visits that took place before they were pregnant, and none of the other women reported unique visits that took place before their youngest child was weaned. For this measure, we moved the one problematic case from the "lactating" to the "gestating" group.

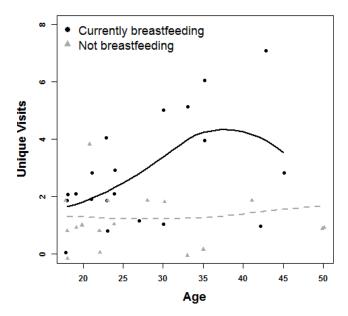


Fig. 3 Please write your figure caption here

The sample includes only three pregnant women, but two of them were among the eleven women to obtain a perfect score on the mental rotation task. This difference in accuracy is not statistically significant, but the speed with which they responded is despite the weak power of the study (see Table 4). The three pregnant women had remained home most of the past year, and none of them made a single trip unaccompanied.

3.4 Spatial ability, ranging, and the interaction with sex

The fertility and parental care hypothesis predicts a positive relationship between spatial-cognitive ability and mobility. This expectation is shared with the other prominent theories linking spatial cognition to travel-based fitness effects, however, the others focus on this relationship in men rather than women. Thus, looking at which sexes travel more in response to variance in spatial ability may help discriminate between possible explanations.

Table 4 Gestation

		Pregnant		Mating or post-lactation				
Measure	n1	$\mu 1$	$\sigma 1$	n1	$\mu 2$	$\sigma 2$	p-value	
Mental rotation (accuracy)	3	92.6%	12.8%	14	81.0%	14.6%	.255	
Mental rotation (time)	3	3.7	0.51	14	5.80	1.27	.001	
Pointing error	3	24.98°	8.09°	17	20.97°	12.37°	.611	
Spatial anxiety	2	2.38	0.18	5	2.60	0.22	.274	
Annual visits	4	1.25	0.96	12	1.33	1.15	.891	
Solo visit %	2	0%	0%	9	22.2%	36.3%	.104	
Daily mobility (km)	3	4.24	3.06	5	3.71	2.82	.820	

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Table 5 Annual mobility and Spatial Cognition

Independent Variables								
		MR	Male	e(1 0)	Male(R^2		
	$Std.\beta$	Std.Err	Std.eta	Std.Err	$Std.\beta$	Std.Err		
Model 1	0.207	0.134					0.036	
Model 2	0.262.	0.137	0.331**	0.114	.300*	0.131	0.222	

Mental rotation performance alone is only weakly predictive of travel in the past year and is not a statistically significant improvement over a null model $(M_{null}|M_1, \chi^2(1,98) = 2.348, p = 0.121)$. However, including sex as an interaction effect dramatically improves model performance $(M_1|M_2, \chi^2(2,98) = 12.091, p = 0.0006)$. Interestingly, the direction of the effect is in the opposite direction of expectations drawn from the fertility and parental care hypothesis. Men, but not women, with higher spatial ability appear to travel more broadly (see Figure ?? and Table 5). This is consistent with findings in a previous study using a different measure of mental rotation (cite me).

4 Discussion

The observed sex differences across spatial cognition, navigation, spatial anxiety, annual mobility and daily mobility are all consistent with the fertility and parental care hypothesis. Men outperformed women in the spatial-cognitive and navigational tasks, reported lower spatial anxiety, and traveled further at both scales. However, all of these predictions apply equally well to the other prominent theories linking these traits in an evolutionary framework.

The only area of this study that consistently fits expectations uniquely drawn from the fertility and parental care hypothesis is the spatial anxiety measure. Postmenopausal women reported lower spatial anxiety than reproductive-aged women, and among the latter group, women with an unweaned infant reported higher spatial anxiety. Unfortunately, both of these tests lack statistical power. We may expect increased anxiety during key periods of reproduction to be adaptive even if limiting travel is not the function. In addition to concerns about travel, anxiety should promote hyper-vigilance to threats like children

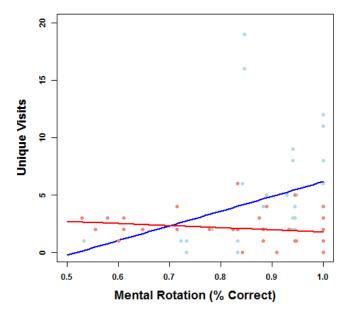


Fig. 4 Please write your figure caption here

being bitten by scorpions, consuming harmful substances, or falling into fires (a common source of injury for Twe and Himba children). This study specifically used a measure targeting the dangers of travel, but the results could simply be picking up on general anxiety.

The mobility data also shows intriguing trends in the difference between postmenopausal and reproductive-aged women, with the older women moving much more on a daily basis and making a higher percentage of their annual visits abroad without accompaniment. These trends are consistent with the fertility and parental care hypothesis but again are observed in a very small sample.

Interestingly, one of the strongest findings of the study actually runs in the opposite direction of the fertility and parental care hypothesis. Despite the postpartum period being the most vulnerable time in a woman's life, and higher self-reported spatial anxiety among nursing Twe mothers, these women traveled to more than twice as many unique locations as other reproductiveaged (and not pregnant) women in the past year.

We asked about the purpose of each trip reported in the annual mobility interviews. This information helps examine some potential explanations for the surprisingly high rate of postpartum travel. The data may be capturing women returning to their natal community to seek the childcare assistance of their mothers. This explanation follows from recent work showing exactly that pattern among a nearby Himba community (Scelza, 2011). However, none of

the cases in our data are consistent with this explanation. This may not be surprising, since the majority of Twe women already live with their mothers and other close kin (Vashro, 2014).

Instead of traveling to visit parents and siblings, the stated reason for many of the postpartum women's travel was to visit extended kin. For example, two sisters, each with an unweaned child, traveled together approximately 160 kilometers through an unfamiliar region to visit a maternal aunt they had not seen since childhood. Overall, 38.2% (21 out of 55 trips) of the visits reported by women with unweaned children were targeted social visits to extranuclear kin, while only 5% (2 out of 40) of the visits reported by reproductiveaged women at other reproductive stages were of that nature. Extended kin networks are the primary safety net among the Twe. Women with infants may be more successful in soliciting immediate assistance from relatives, and in several cases the explicit purpose of the trip was to beg for food or smallstock. In addition, mothers may want to introduce their new infants to relatives to begin forming a strong kinship bond that will prove useful in the future. If these incentives are strong enough, they could outweigh the risks of travel (though they may not have in a more dangerous past). In addition, traveling long distances on foot to visit family may not be an energetic cost if you are ultimately eating from a relatives pot as a guest, rather than spending the day laboring to produce your next meal.

Another finding that poses a challenge to the fertility and parental care hypothesis was that there is a positive relationship between spatial ability and travel in the past year among men but not women. This is consistent with previous work in the same population (Vashro and Cashdan, 2014). Furthermore, a study among urban Canadians found a positive correlation between homerange size and mental rotation among men and not women (Ecuyer-Dab and Robert, 2004b). The consistency of this finding makes it difficult to highlight the importance of this relationship for women.

References

Bateman AJ (1948) Intra-sexual selection in drosophila. Heredity 2(Pt. 3):349–368

Bell S, Saucier D (2004) Relationship among environmental pointing accuracy, mental rotation, sex, and hormones. Environment and Behavior 36(2):251–265

Bryant K (1982) Personality correlates of sense of direction and geographic orientation. Journal of Personality and Social Psychology 43(6):1318

Burke A, Kandler A, Good D (2012) Women who know their place. Human Nature 23(2):133-148

Clutton-Brock T (2007) Sexual selection in males and females. Science 318(5858):1882-1885

Collins D, Busse C, Goodall J (1984) Infanticide in two populations of savanna baboons.

- Darwin C (1871) Sexual selection and the descent of man. Murray, London Devlin AS, Bernstein J (1995) Interactive wayfinding: Use of cues by men and
- women. Journal of environmental psychology 15(1):23–38
- Driscoll I, Hamilton DA, Yeo RA, Brooks WM, Sutherland RJ (2005) Virtual navigation in humans: the impact of age, sex, and hormones on place learning. Hormones and behavior 47(3):326–335
- Dufour DL, Sauther ML (2002) Comparative and evolutionary dimensions of the energetics of human pregnancy and lactation. American Journal of Human Biology 14(5):584–602
- Eals M, Silverman I (1994) The hunter-gatherer theory of spatial sex differences: Proximate factors mediating the female advantage in recall of object arrays. Ethology and Sociobiology 15(2):95–105
- Ecuyer-Dab I, Robert M (2004a) Have sex differences in spatial ability evolved from male competition for mating and female concern for survival? Cognition 91(3):221–257
- Ecuyer-Dab I, Robert M (2004b) Spatial ability and home-range size: examining the relationship in western men and women (homo sapiens). Journal of Comparative Psychology 118(2):217
- Galea L, Kimura D (1993) Sex differences in route-learning. Personality and individual differences 14(1):53–65
- Gaulin SJ (1992) Evolution of sex difference in spatial ability. American Journal of Physical Anthropology 35(S15):125-151
- Gaulin SJ, FitzGerald RW (1986) Sex differences in spatial ability: an evolutionary hypothesis and test. American Naturalist pp 74–88
- Gaulin SJ, Hoffman HA, et al (1988) Evolution and development of sex differences in spatial ability. In: Betzig LL, Mulder MB, Turke P (eds) Human reproductive behaviour: A Darwinian perspective, Cambridge: Cambridge University Press, pp 129–152
- Geary DC (1995) Sexual selection and sex differences in spatial cognition. Learning and Individual Differences 7(4):289–301
- Gilmartin PP, Patton JC (1984) Comparing the sexes on spatial abilities: Mapuse skills. Annals of the Association of American Geographers 74(4):605–619
- Gittleman JL, Thompson SD (1988) Energy allocation in mammalian reproduction. American zoologist 28(3):863-875
- Gray JA, Buffery AW (1971) Sex differences in emotional and cognitive behaviour in mammals including man: adaptive and neural bases. Acta Psychologica 35(2):89–111
- Gregor T (1987) Anxious pleasures: The sexual lives of an Amazonian people. University of Chicago Press
- Hampson E, Kimura D (1988) Reciprocal effects of hormonal fluctuations on human motor and perceptual-spatial skills. Behavioral neuroscience 102(3):456
- Hausmann M, Slabbekoorn D, Van Goozen SH, Cohen-Kettenis PT, Güntürkün O (2000) Sex hormones affect spatial abilities during the menstrual cycle. Behavioral neuroscience 114(6):1245

- Hawkes K (2003) Grandmothers and the evolution of human longevity. American Journal of Human Biology 15(3):380–400
- Henrie RL, Aron RH, Nelson BD, Poole DA (1997) Gender-related knowledge variations within geography. Sex Roles 36(9-10):605–623
- Heron J, O'Connor TG, Evans J, Golding J, Glover V, Team AS, et al (2004) The course of anxiety and depression through pregnancy and the postpartum in a community sample. Journal of affective disorders 80(1):65–73
- Hill KR, Hurtado AM (1996) Ache life history: The ecology and demography of a foraging people. Transaction Publishers
- Jašarević E, Williams SA, Roberts RM, Geary DC, Rosenfeld CS (2012) Spatial navigation strategies in peromyscus: a comparative study. Animal behaviour 84(5):1141–1149
- Jones CM, Braithwaite VA, Healy SD (2003) The evolution of sex differences in spatial ability. Behavioral neuroscience 117(3):403
- Krug EG, Sharma GK, Lozano R (2000) The global burden of injuries. American journal of public health 90(4):523
- Lacreuse A, Herndon JG, Killiany RJ, Rosene DL, Moss MB (1999) Spatial cognition in rhesus monkeys: male superiority declines with age. Hormones and Behavior 36(1):70–76
- Lawton CA (1994) Gender differences in way-finding strategies: Relationship to spatial ability and spatial anxiety. Sex roles 30(11-12):765-779
- Lawton CA (2010) Gender, spatial abilities, and wayfinding. In: Handbook of gender research in psychology, Springer, pp 317–341
- Levine SC, Huttenlocher J, Taylor A, Langrock A (1999) Early sex differences in spatial skill. Developmental psychology 35(4):940
- MacDonald DH, Hewlett BS (1999) Reproductive interests and forager mobility 1. Current Anthropology 40(4):501–524
- McCormick CM, Teillon SM (2001) Menstrual cycle variation in spatial ability: relation to salivary cortisol levels. Hormones and Behavior 39(1):29–38
- Moffat SD, Hampson E, Hatzipantelis M (1998) Navigation in a virtual maze: Sex differences and correlation with psychometric measures of spatial ability in humans. Evolution and Human Behavior 19(2):73–87
- Moffat SD, Zonderman AB, Resnick SM (2001) Age differences in spatial memory in a virtual environment navigation task. Neurobiology of aging 22(5):787–796
- Montagu A (1961) Neonatal and infant immaturity in man. JAMA 178(1):56–57
- Montello DR, Richardson AE, Hegarty M, Provenza M (1999) A comparison of methods for estimating directions in egocentric space. PERCEPTION-LONDON- 28:981–1000
- Moore DS, Johnson SP (2008) Mental rotation in human infants a sex difference. Psychological Science 19(11):1063–1066
- Murphy SL, Xu J, Kochanek KD (2010) National vital statistics reports. National Vital Statistics Reports 61(4)
- Perdue BM, Snyder RJ, Zhihe Z, Marr MJ, Maple TL (2011) Sex differences in spatial ability: a test of the range size hypothesis in the order carnivora.

- Biology Letters 7(3):380–383
- Picucci L, Caffò AO, Bosco A (2011) Besides navigation accuracy: Gender differences in strategy selection and level of spatial confidence. Journal of environmental psychology 31(4):430–438
- Pugh R, Theakston R (1980) Incidence and mortality of snake bite in savanna nigeria. The Lancet 316(8205):1181–1183
- Quinn PC, Liben LS (2008) A sex difference in mental rotation in young infants. Psychological Science 19(11):1067–1070
- Sanders B, Soares MP, D'Aquila JM (1982) The sex difference on one test of spatial visualization: A nontrivial difference. Child Development pp 1106–1110
- Scelza BA (2011) Female mobility and postmarital kin access in a patrilocal society. Human Nature 22(4):377–393
- Sear R, Mace R (2008) Who keeps children alive? a review of the effects of kin on child survival. Evolution and human behavior 29(1):1–18
- Shepard RN, Metzler J (1971) Mental rotation of three-dimensional objects Sherry DF, Hampson E (1997) Evolution and the hormonal control of sexually-dimorphic spatial abilities in humans. Trends in Cognitive Sciences 1(2):50–56
- Smuts B (1992) Male aggression against women. Human Nature 3(1):1–44 Spritzer MD, Solomon NG, Meikle DB (2005) Influence of scramble competition for mates upon the spatial ability of male meadow voles. Animal Behaviour 69(2):375–386
- Stokes EJ, Parnell RJ, Olejniczak C (2003) Female dispersal and reproductive success in wild western lowland gorillas (gorilla gorilla gorilla). Behavioral Ecology and Sociobiology 54(4):329–339
- Treves A, Naughton-Treves L (1999) Risk and opportunity for humans coexisting with large carnivores. Journal of Human Evolution 36(3):275–282
- Trivers R (1972) Parental investment and sexual selection

Unity (2014) Unity 3D

- Vashro L, Cashdan E (2014) Spatial cognition, mobility, and reproductive success in northwestern namibia. Evolution and Human Behavior
- Vashro LJ (2014) Residence and childcare assistance among the twe. PhD thesis, THE UNIVERSITY OF UTAH
- Viljoen P (1982) The distribution and population status of the larger mammals in Kaokoland, South West Africa/Namibia. Staatsmuseum
- Walker PL (2001) A bioarchaeological perspective on the history of violence. Annual Review of Anthropology pp 573–596
- Watts DP (1989) Infanticide in mountain gorillas: new cases and a reconsideration of the evidence. Ethology 81(1):1–18
- Watts DP, Mitani JC (2000) Infanticide and cannibalism by male chimpanzees at ngogo, kibale national park, uganda. Primates 41(4):357–365
- Wenzel A, Haugen E, Jackson L, Robinson K (2003) Prevalence of generalized anxiety at eight weeks postpartum. Archives of women's mental health 6(1):43–49

Willis SL, Schaie KW (1988) Gender differences in spatial ability in old age: Longitudinal and intervention findings. Sex Roles 18(3-4):189–203 Wilson M, Daly M (1985) Competitiveness, risk taking, and violence: The young male syndrome. Ethology and sociobiology 6(1):59–73