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Sex differences in mobility and spatial cognition

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

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Abstract The fertility and parental care hypothesis interprets sex differences in some spatial-cognitive tasks as an adaptive mechanism to suppress women's travel. In particular, the hypothesis argues that estrogens constrain travel during key reproductive periods by depressing women's spatial-cognitive ability. Limiting travel reduces exposure to the dangers and caloric costs of navigating long distances into unfamiliar environments. Our study evaluates a collection of predictions drawn from the fertility and parental care hypothesis among the Twe and Himba people living in a remote region of Namibia. We find that nursing mothers travel more than women at any other stage of their reproductive career. This challenges the assumption that women limit travel during vulnerable and energetically demanding reproductive periods. In addition, we join previous studies in identifying a relationship between spatial ability and traveling among men, but not women. If spatial ability does not influence travel, hormonally induced changes in spatial ability cannot be used as a mechanism to reduce travel. Instead, it appears the fitness consequences of men's travel is a more likely target for adaptive explanations of the sex differences in spatial ability, navigation, and range size.

Keywords Mobility · Spatial cognition · Parental care

1 Introduction

Evolutionary psychologists have proposed several distinct theories that use assumed sex differences in ancestral travel to explain men's advantage in certain spatial-cognitive tasks. Most of these theories argue that past selection favored

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males who could travel more safely and efficiently long distances and into unfamiliar environments. This would have required superior navigation ability and the spatial-cognitive traits that facilitate it (Jones et al, 2003). 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 turns the focus on the fitness ramifications of women's long-distance mobility. This "fertility and parental care hypothesis" proposed by Sherry and Hampson (1997) argues that the observed sex differences in spatial ability can be explained in terms of the potential costs to women traveling, particularly during key periods of reproduction (Ecuyer-Dab and Robert, 2004a).

1.1 Fertility and parental care

The fertility and parental care hypothesis argues that ancestral women who avoided the risks and caloric costs of travel during key reproductive periods may have outcompeted those who did not, and that reduced spatial ability during those key periods facilitated the reduction in travel. Sherry and Hampson (1997) highlight the role of reproductive hormones as proximate mediators between reproductive status and performance on spatial tasks. Female spatial ability declines in the middle of the menstrual cycle, possibly due to the concurrent peak in estrogen levels (Hampson and Kimura, 1988; Hampson, 1990; McCormick and Teillon, 2001; Komnenich et al, 1978; Hausmann et al, 2000). This interpretation is consistent with studies linking estrogen to spatial ability in several non-human mammals (Lacreuse et al, 1999; Frye, 1995), but not postmenopausal women's improved performance in a mental rotation task after receiving estrogen replacement therapy (Duka et al, 2000).

Risky strategies tend to pay higher fitness dividends when variance in reproductive success among competitors is high (Clutton-Brock and Vincent, 1991; Clutton-Brock, 2007; Wilson and Daly, 1985). As is the case in many mammalian species, reproductive variance is higher among men than women (Betzig, 2012). In addition, human mothers are burdened by highly altricial infants. 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 can be risky. 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).

Travel is energetically costly as well as risky. Decreasing travel may be an efficient way for women to balance their energy budget during expensive reproductive periods (Dufour and Sauther, 2002). The fertility and parental care hypothesis presents an appealing evolutionary narrative. However, the logical thread hangs on several assumptions about the relationship between women's reproductive life-history, cognition, and mobility that are yet to be demonstrated. This paper sets out to test a series of predictions drawn from the fertility and parental care hypothesis, using data from a natural fertility population living a subsistence lifestyle in the remote Kunene Region of Namibia.

1.2 Hypotheses

We will test the following predictions:

1. Women will demonstrate lower spatial and navigational ability, report lower spatial anxiety, and travel less broadly.

Men outperform women in some 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 found in 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 contexts finds that men occupy larger ranges than women (Ecuyer-Dab and Robert, 2004a; Gaulin et al, 1988; MacDonald and Hewlett, 1999).

Our previous work among the Twe and Tjimba found that men travel farther than women in this population and have better spatial ability. These groups do indeed conform to this expected sex difference in spatial cognition, navigation, and ranging (Vashro and Cashdan, 2014). The current study amplifies our earlier results by adding an improved measure of spatial ability, a measure of spatial anxiety, and mobility data from GPS tracking.

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

Unlike most mammals, women may live an additional third of their lives following the cessation of fertility. Postmenopausal women are no longer primary care-providers, and thus should value risk aversion and energy conservation in a manner similar to that of 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 not demonstrated any postmenopausal decrease in the sex difference in performance on a mental rotation task, spatial memory task, or navigating virtual environments in humans (Willis and Schaie, 1988; Driscoll et al, 2005; Moffat et al, 2001), but one study does find the expected reduced sex difference with age in performance on a spatial memory task in rhesus monkeys, *Macaca mulatta* (Lacreuse et al, 1999). We will compare postmenopausal and reproductive-aged women in measures of spatial ability, navigational ability, spatial anxiety, and mobility. However, due to a limited sample of older participants, we offer only preliminary tests of these predictions.

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

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

Women's energy use increases by approximately 8-10% during pregnancy, and 26% during lactation. Women manage this elevated demand through reduced movement, as well as increased caloric intake, and in the case of lactation, by catabolizing fat stored during pregnancy (Dufour and Sauther, 2002). In addition to facing 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 at the time necessarily extend to the dependent offspring. Furthermore, threats like spiders, scorpions, small mammalian predators, and exposure pose uniquely deadly threats to infants. Among some of our closest primate relatives, including chimpanzees, gorillas, and baboons 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 today (Gregor, 1987).

Assuming women's mobility and associated cognitive traits respond facultatively to risk and energetic needs, pregnant and nursing women should be at the extreme in terms of limited mobility, spatial ability, and navigational ability, while also feeling elevated levels of spatial anxiety. These predictions flow from the logic of the fertility and parental care hypothesis; however, in the case of lactation they are at odds with the proposed hormonal mechanism. Women's estrogen levels are particularly low postpartum, which should instead confer an advantage to spatial ability and, correspondingly, navigational ability and mobility. A postpartum increase in spatial ability was previously demonstrated using an embedded figures task (Woodfield, 1984). Our 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 about 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.

Two studies have investigated this relationship in humans, one among urban Canadians and another among the Twe and Tjimba of northwestern Namibia. Both studies found a relationship between performance on the mental rotation task and range size for men but not women (Ecuyer-Dab and Robert, 2004b; 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 hitchhiking to the town, all travel is on foot (or sometimes by donkey). Most participants report having become lost at some point in their 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 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 on the western and eastern-most ends. 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 among the Himba, at least for economic purposes, than is seen among the Twe. Our sample captures a similar demographic range of participants from both the Twe and Himba. In order to bolster the study's sample-size, we pool both tribes together into a single population representing the people of 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 of age. Most of the reproductive-aged women included in this study (56%) reported that they were currently nursing. Unweaned children are almost always in contact with their mother, either actively feeding, strapped to her back while she works, or lying with her 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, $n = 48$), and then further subdivide the reproductive-aged women into "pregnant" ($n = 3$), "nursing" ($n = 27$), 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. As a result, sample sizes vary by task as noted in the results below.

2.1.1 Spatial cognition

Mental rotation: This task is a computer-based adaptation of the Mental Rotation Test developed by Shepard and Metzler (1971). Participants are shown two computer generated bodies rotated at 0, 60, 120, 180, 240, or 300 degrees on a two-dimensional axis. One of the bodies has a left hand out-stretched while the other has a right hand out-stretched. Participants are then asked to identify which of the two images matches a third body at the top of the screen with either a left or right hand out-stretched. The task was designed using gaming software (Unity, 2014) and presented to participants on a Toshiba

15.6" Touch-Screen laptop. Measures of task performance include both accuracy across 24 trials and the average amount of time needed to respond to each trial.

Initial analyses showed that response time increased with the degree of rotation up to 180 degrees, as is typical for object-based mental rotation tasks. This indicates that the person is mentally rotating the object, and that our task is measuring what it was designed to measure. While most participants understood the task, it was clear that some did not. Before beginning the task, participants worked through a set of training stimuli consistent with the images used in the actual experiment. Participants who failed to demonstrate understanding during this training were not asked to move on to the recorded trials. In addition, we removed any participants who proceeded to the recorded trials but scored below chance (50%). Because people seemed confused by the zero degree rotation, we did not include those in our analyses. We also dropped the first trial in each block, since times for the first trial were highly variable, probably because not everyone was ready at the first presentation. Extreme outlier trials (Reaction time > 5 times the interquartile range) were also dropped.

2.1.2 Navigation

Real-world pointing: We used accuracy pointing to distant locations as a measure of navigation ability. The task uses ten well-known locations with distances ranging from 10 to 130 kilometers. Viewers were asked if they had visited each location. If they had, they were then asked to use the sight on a Brunton Pocket Transit International Compass to indicate the bearing to that location. This estimated bearing was then compared to the actual bearing to the location, and the absolute difference between them was recorded as the participant's error. Measurements were taken in locations that were free of objects that visually occluded participants' views (e.g. dense foliage and mountains). Because most participants had never visited three of the locations, we removed points to these three locations and averaged across all of the remaining points for each participant.

2.1.3 Anxiety

Spatial anxiety questionnaire: This questionnaire included four questions in the native Twe and Himba language of *Otjiherero*. These questions were adapted from items in the spatial anxiety scale developed by Carol Lawton (Lawton, 1994). These questions ask about anxiety in situations that require spatial and navigation skills, such as trying a new shortcut. Participants were presented with navigationally challenging scenarios then asked 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 away from their home village that they spent the night in the past year. In addition, for each location 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 reflects 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: Participants were given an i-gotU GT-600 GPS decive to wear for three days. In order to ensure recovery of the devices, participants were asked to return them before leaving the village for more than one night. This makes the daily mobility tracks a poor measure of travel into less familiar and thus risky areas, but does allow for a precise measure of daily movement as it relates to the energetic costs of local travel. The analyses below use the total distance in meters traveled by each participant on an average day.

3 Results

3.1 Sex differences

Hypothesis 1: Women will demonstrate lower spatial and navigational ability, report lower spatial anxiety, and travel less broadly.

Men responded more accurately, though not more quickly, than women to the mental rotation stimuli (see Table 1). The real magnitude of this difference may be 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.

Table 1 Sex differences

		Men		Women	
Measure	*N*	*M(SD)*	*N*	*M(SD)*	*p*
Mental rotation (accuracy)	55	89.3% (2.7%)	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

Means and standard deviations for men and women in each of the listed measures. Final column gives the *p-value* for a Chi-squared test comparing the two groups.

Men also made smaller errors in the pointing accuracy task, 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).

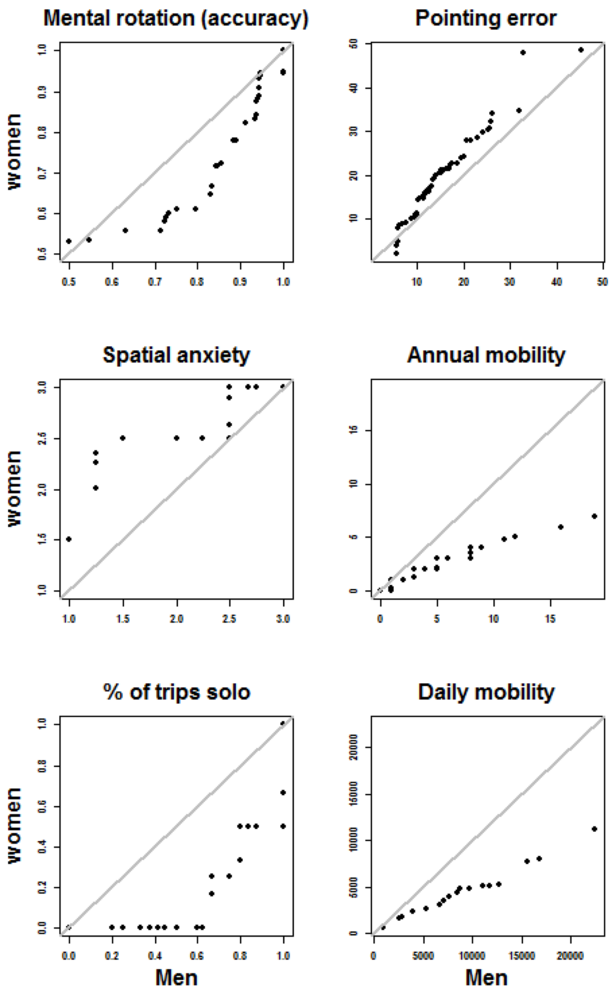

Fig. 1 Quantile-quantile plots showing the difference between the distribution of men's and women's scores in each measure. Where points fall below the grey line, men at that quantile score higher.

3.2 Menopausal effects

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

Postmenopausal women responded more slowly to the mental rotation task than reproductive-aged women, and were slightly less accurate (see Table 2). Postmenopausal women were also much less likely than reproductive-aged women to demonstrate sufficient understanding (61.4% compared to 21.4%), and thus a smaller fraction were included in the analysis. The fertility and parental care hypothesis does not necessarily predict that postmenopausal women will outperform younger reproductive-aged women, but it does predict a smaller sex difference among older participants. Men older than 50 performed worse than younger men, but the 3.2% decline (89.6% correct to 86.7% correct) is smaller than the 7.6% decline seen among women (see Table 2). These results suggest women's spatial ability does not improve after menopause even accounting for general age-based decline shared with men.

Unlike spatial ability, there is no meaningful difference between pre and postmenopausal women in pointing accuracy, nor is there a difference between older and younger men.

Table 2 Postmenopause

	Postmenopausal		Reproductive-aged		
Measure	*N*	*M(SD)*	*N*	*M(SD)*	*p*
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

Means and standard deviations for postmenopausal women and reproductive-aged women in each of the listed measures. Final column gives the *p-value* for a Chi-squared test comparing the two groups.

We find several interesting trends in the spatial anxiety and mobility measures, but the small sample of postmenopausal women limits statistical power. Postmenopausal women 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 expectations drawn from the fertility and parental care hypothesis.

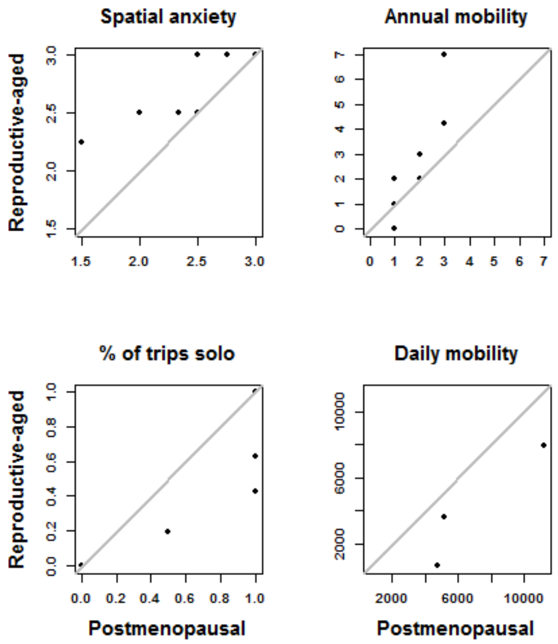

Fig. 2 Quantile-quantile plots showing the difference between the distribution of reproductive-aged and postmenopausal women's scores in each measure. Where points fall below the grey line, postmenopausal women at that quantile score higher.

3.3 Lactation and gestation effects

Hypothesis 3: Reproductive-aged women's mobility and associated cognitive traits will decrease when they are pregnant or nursing

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). 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 three pregnant women's advantage over other women in response time is statistically significant despite the weak power of the study (see Table 4).

Nursing women also 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. The three pregnant women were less accurate than the set of reproductive-aged women who were neither pregnant nor nursing.

Consistent with the fertility and parental care hypothesis, nursing women reported higher spatial anxiety than other reproductive-aged women. Only two of the pregnant women responded to the spatial anxiety questionnaire. These women reported lower spatial anxiety than the average of reproductive-aged women who were neither pregnant nor nursing.

Table 3 Nursing

Measure	*N*	Nursing *M(SD)*	*N*	Cycling *M(SD)*	*p*
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

Means and standard deviations for nursing mothers and reproductive-aged women who are neither nursing nor pregnant in each of the listed measures. Final column gives the *p-value* for a Chi-squared test comparing the two groups. "Cycling" refers to reproductive-aged women in any stage other than lactation or gestation.

The fertility and parental care hypothesis predicts that women will curtail mobility due to the risks and caloric costs of travel. Surprisingly, Twe and Himba women with unweaned children had visited more than twice as many locations in the past year as women who were neither pregnant nor nursing. Unlike the highly mobile nursing mothers, the four pregnant women remained home most of the past year, and none of them made a trip unaccompanied.[1]

3.4 Spatial ability, ranging, and the interaction with sex

Hypothesis 4: Spatial cognition predicts women's range size.

[1] One complication with the annual mobility data is that 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 nursing mothers 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.

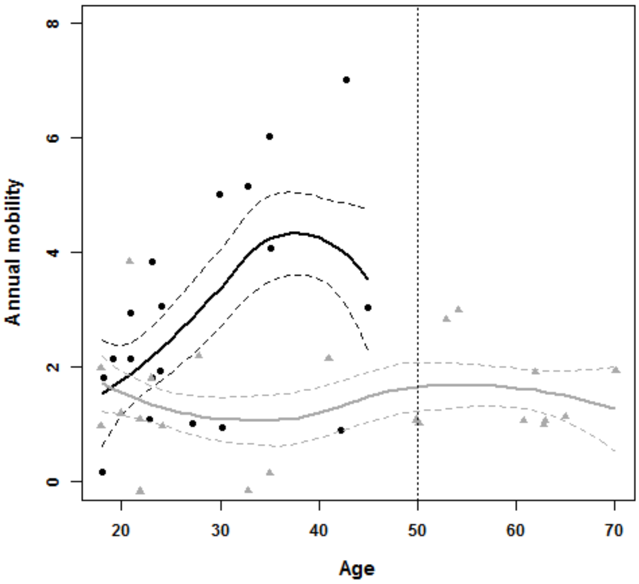

Fig. 3 The grey triangles and corresponding grey loess lines plot the number of unique annual visits reported by women who were neither pregnant nor nursing at all ages. The black circles and corresponding loess lines plot the number of unique annual visits reported by women who were breastfeeding. The dashed lines show one standard deviation on either side of the respective loess lines. The dotted line notes 50 years, after which all women are expected to be postmenopausal.

Table 4 Gestation

Measure	*N*	Pregnant *M(SD)*	*N*	Cycling *M(SD)*	*p*
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

Means and standard deviations for pregnant women and reproductive-aged women who are neither nursing nor pregnant in each of the listed measures. Final column gives the *p-value* for a Chi-squared test comparing the two groups. “Cycling” refers to reproductive-aged women in any stage other than lactation or gestation.

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

Table 5 Annual mobility and Spatial Cognition

	Independent Variables						
	MR		Male(1|0)		Male(1|0):MR		R^2
	Std.β	*Std.Err*	*Std.β*	*Std.Err*	*Std.β*	*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

Coefficient for a linear model with mental rotation accuracy as a lone predictor of annual visits ("Model 1"), and a binary sex variable included as an interaction term with mental rotation accuracy ("Model 2"). * $p < .05$; ** $p < .01$

effects, but the others focus on this relationship in men rather than women. Thus, looking at which sex travels more in response to variance in spatial ability may help discriminate between possible explanations.

Mental rotation performance as a lone predictor in a linear regression model 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 effect runs 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 4 and Table 5).

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 and navigational tasks, reported lower spatial anxiety, and traveled farther 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 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 might simply reflect 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

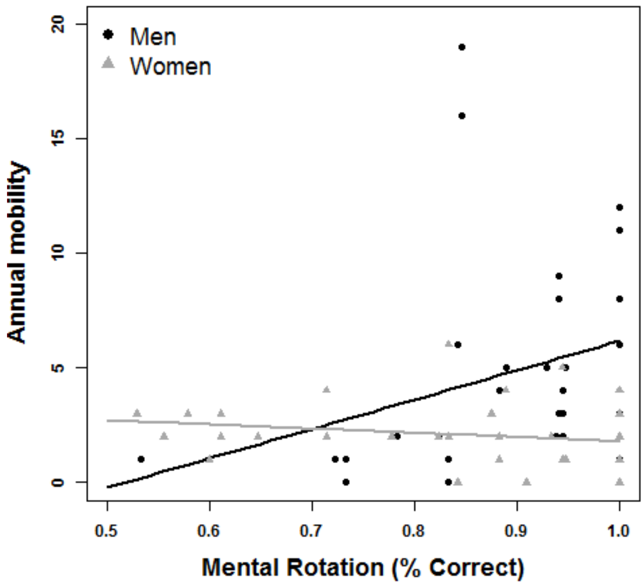

Fig. 4 Plot fitting the unstandardized coefficients for Model 2 described in 5. Grey triangles and corresponding line demonstrate the relationship between performance on the mental rotation task and annual range. Black triangles and corresponding line show the same relationship for men.

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 mothers, these women traveled to more than twice as many unique locations as other reproductive-aged (and not pregnant) women in the past year. As noted in the introduction above (Section 1.2), the underlying logic and specified mechanism of the fertility and parental care hypothesis conflict on expectations for postpartum mothers. The increased travel and trend towards better navigational ability during the lactational period is consistent with the hormonal mechanisms of the fertility and parental care hypothesis, since estrogen levels are low at this time, and this is associated with better spatial ability. But is is surprising given that the costs and risks of travel are expected to be higher at this time.

We asked about the purpose of each trip reported in the annual mobility interviews. This information allows us to examine some potential explanations for the surprisingly high rate of nursing travel. One possibility we considered is that women could be returning to their natal community to seek the childcare assistance of their mothers. This explanation follows from recent findings 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 nursing 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 extra-nuclear kin, while only 5% (2 out of 40) of the visits reported by reproductive-aged 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 small-stock. 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 relative's pot as a guest, rather than spending the day laboring to produce your next meal.

The assumption that mental rotation ability affects range size is the lynchpin of the theories linking the suite of traits measured in this study. We observe this relationship among Twe and Himba men, but not among women. The other results presented above offer some findings consistent with the fertility and parental care hypothesis along with some contrary patterns. However, in replicating previous work which only found a relationship between spatial ability and ranging among men, our findings pose a challenge to the fertility and parental care hypothesis. This key relationship has now been demonstrated among men in two extremely different populations, as well as males in one rodent species (Spritzer et al, 2005). The consistency of this finding without observing a similar relationship in women makes it difficult to place the costs and benefits of women's travel at the center of an adaptive explanation for sex differences in spatial ability, navigation, and mobility.

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