Sex Differences in Mobility and Spatial Cognition

A Test of the Fertility and Parental Care Hypothesis in Northwestern Namibia

Layne Vashro[1] · **Lace Padilla**[2] · **Elizabeth Cashdan**[1]

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 · Namibia · Fertility · Sex differences

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 males who could travel more safely and efficiently for long distances and into unfamiliar environments. This would have

✉ Layne Vashro
layne.vashro@anthro.utah.edu

1   University of Utah, 270 South 1400 East, Salt Lake City, UT 84112, USA

2   Department of Psychology, University of Utah, 380 S 1530 E Beh S 502, Salt Lake City, UT 84112, USA

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).

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 this selected for a reduction in spatial ability during those key periods. 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 because of the concurrent peak in estrogen levels (Hampson 1990; Hampson and Kimura 1988; Hausmann et al. 2000; Komnenich et al. 1978; McCormick and Teillon 2001). This interpretation is consistent with studies linking estrogen to spatial ability in several non-human mammals (Frye 1995; Lacreuse et al. 1999), but not with 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 2007; Clutton-Brock and Vincent 1991; Wilson and Daly 1985). As is the case in many mammalian species, reproductive variance is higher among men than women (Betzig 2012; Brown et al. 2009). In addition, human mothers are burdened by highly altricial infants. Fitness calculations for men need to account for the potential loss of future offspring resulting from 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 death 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 (Pugh and Theakston 1980; Treves and Naughton-Treves 1999; 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 relationships among 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.

Hypotheses

We will test the following predictions.

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

Men outperform women in some measures of cognitive spatial ability (Eals and Silverman 1994; Lawton 2010; Sanders et al. 1982; Shepard and Metzler 1971). This difference begins in infancy (Levine et al. 1999; Moore and Johnson 2008; Quinn and Liben 2008) and is found in several nonhuman mammals (Gaulin and FitzGerald 1986; Jašarević et al. 2012; Perdue et al. 2011). Measures of navigational skill or spatial orientation, especially those that tap into cues used in long-distance travel into unfamiliar environments, also tend to favor men (Bryant 1982; Galea and Kimura 1993; Henrie et al. 1997; Moffat et al. 1998), though this difference is not as robust (Burke et al. 2012; Coluccia and Louse 2004; 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 2015). 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 (Driscoll et al. 2005; Moffat et al. 2001; Willis and Schaie 1988), 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, because of our limited sample of older participants, we offer only preliminary tests of these predictions. Since we are comparing women separated by many years of age, this is the aspect of the study most likely impacted by our reliance on cross-sectional data. This study works with a population that, similar to most societies around the world, has experienced considerable change over the past few decades. This means that any differences between postmenopausal and reproductive-aged women may represent cohort effects rather than generalizable patterns. However, we do not have any specific initial expectations for how lifestyle changes might impact our findings.

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, postlactational 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 such as 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. 2008; Smuts 1992; Stokes et al. 2003; Watts 1989; 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).

If we assume 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 experiencing 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 women with other 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 2015). 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.

Methods

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 interpersonal 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 afterward they are expected to continue their role in domestic production.

We recruited 129 participants (65 men and 64 women) for this study. Intake interviews asked participants' age and reproductive status. This allowed us to separate the female 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 "cycling" ($n = 18$). 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.

Spatial Cognition: Mental Rotation Researchers sometimes refer to a strong sex difference in spatial ability generally, but the observed difference in features within that broad construct range considerably. Studies working with populations outside of a laboratory setting tend to emphasize ease of administration when selecting measures. However, in spatial cognitive research this might result in using measures that show only a weak sex difference or have not been linked to navigation and mobility (Bailey et al. 2012). This study uses a field-adapted version of the classic mental rotation task (Shepard and Metzler 1971). Experiments that ask participants to mentally rotate figures and identify how they would look in different orientations produce some of the largest sex differences observed in the cognitive literature (Linn and Petersen 1985; Voyer et al. 1995). This ability may help with the encoding, maintenance, and trans-formation of large-scale spatial information during navigation (Hegarty et al. 2006), which is substantiated by the positive correlation between performance on mental rotation tasks and a variety of navigational tasks (Bryant 1982; Galea and Kimura 1993; Moffat et al. 1998; Silverman et al. 2000).

In our version of this task, participants are shown two computer-generated images of human bodies rotated at 0, 60, 120, 180, 240, or 300° on a two-dimensional axis. One of the bodies has a left arm outstretched and the other has a right arm outstretched. Participants are then asked to identify which of the two images matches a third body at the top of the screen with either left or right hand outstretched. 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°, 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. Although 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.

Navigation: Real-World Pointing We used accuracy of pointing to distant locations as a measure of navigation ability. The task uses ten well-known locations with distances ranging from 10 to 130 km. 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 with 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 the data for these three locations and averaged across all of the remaining points for each participant.

Anxiety: Spatial Anxiety Questionnaire This questionnaire included four questions in the native Twe and Himba language of Otjiherero. The questions were adapted from items in the spatial anxiety scale developed by Carol 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 and then asked to indicate whether they were concerned, sometimes concerned, or not concerned by the scenario.

Mobility

Annual Visiting Interviews Participants were asked to name each place away from their home village where they had spent the night in the past year. In addition, for each location they were asked with whom they traveled, with whom they stayed, 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 device 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 it 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.

Results

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 (Table 1, Fig. 1). The real magnitude of this difference may be larger than these results show owing to bias in the patterning of missing data. Only 18.8% of men were omitted from the analysis because they failed to demonstrate understanding compared with 28.3% of women.

Men also made smaller errors in the pointing accuracy task, reported lower spatial anxiety, had 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 (Table 1).

Menopausal Effects

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

Table 1 Spatial performance, anxiety, and mobility in men and women

Measure	Men			Women			*p*
	N	*M*	*SD*	*N*	*M*	*SD*	
Mental rotation (accuracy)	55	89.3%	13%	43	82.7%	16.4%	0.033
Mental rotation (time)	55	5.91	1.95	43	5.64	1.73	0.459
Pointing error	61	15.18	7.51	57	19.22	9.26	0.011
Spatial anxiety	27	2.29	0.57	27	2.64	0.37	0.010
Annual visits	42	4.29	4.18	45	2.02	1.59	0.002
Solo visit %	40	46.4%	38.7%	40	24.2%	37.1%	0.011
Daily mobility (km)	19	9.16	5.31	18	4.38	2.59	0.002

Means and standard deviations for all men and women in each of the listed measures. Final column gives the *p* value for a chi-square test comparing the two groups
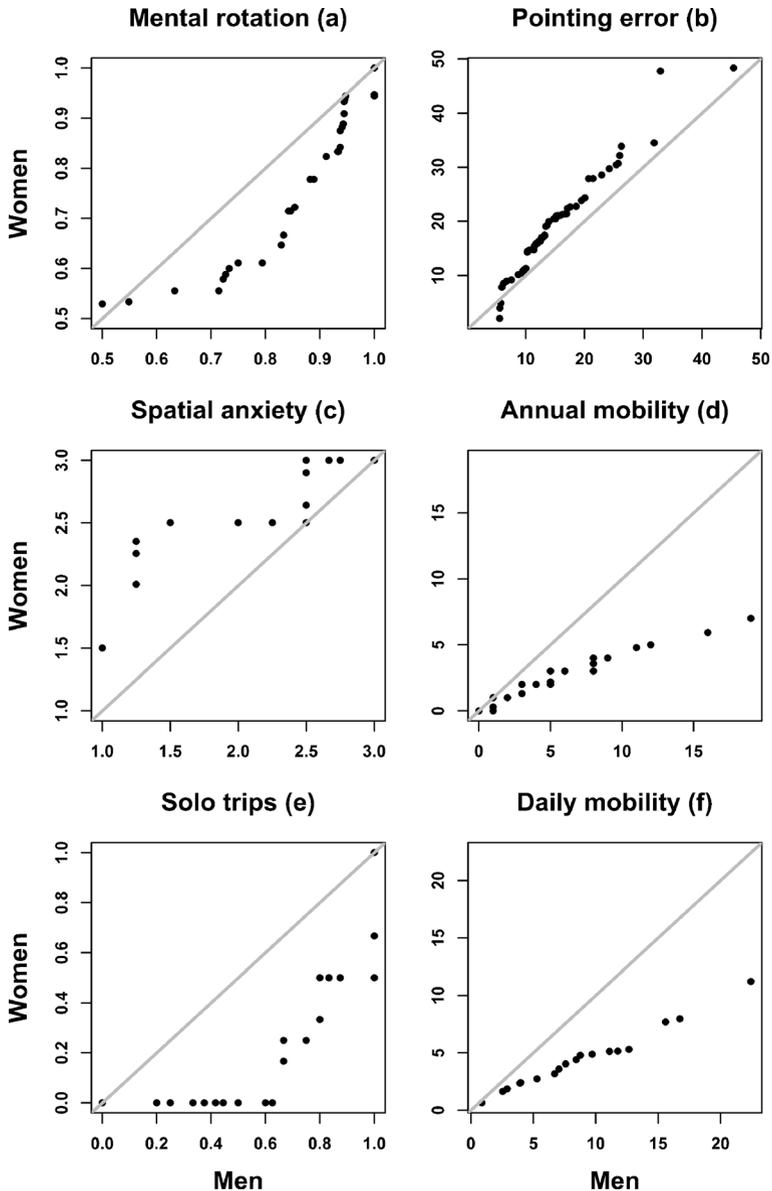
Fig. 1 Quantile-quantile plots showing the difference between the distribution of men's and women's scores in each measure. When points fall below the *gray line*, men at that quantile score higher. **a** The proportion of correct responses in the mental rotation task. **b** Pointing error in degrees. **c** Ordinal score in spatial anxiety questionnaire, with higher scores indicating greater anxiety. **d** Unique visits in the past year. **e** Proportion of visits in the past year that were made without accompaniment. **f** Total distance traveled (in kilometers) during an average day

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

Table 2 Spatial performance, anxiety, and mobility in reproductive-aged and postmenopausal women

Measure	Postmenopausal			Reproductive-Aged			p
	N	M	SD	N	M	SD	
Mental rotation (accuracy)	5	77.1%	19.7%	38	83.4%	16.1%	0.524
Mental rotation (time)	5	7.46	2.08	38	5.40	1.55	0.090
Pointing error	14	20.54	6.31	43	18.79	10.06	0.449
Spatial anxiety	8	2.45	0.51	19	2.72	0.28	0.183
Annual visits	10	1.60	0.84	35	2.14	1.73	0.180
Solo visit %	10	35.0%	47.4%	30	20.6%	33.2%	0.389
Daily mobility (km)	3	7.05	3.62	15	3.85	2.11	0.262

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-square test comparing the two groups

demonstrate sufficient understanding (61.4% versus 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 2.9 percentage-point decline (89.6% correct versus 86.7% correct) is smaller than the 6.3 percentage-point decline seen among women (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 as seen for 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.

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 postmenopausal women to participate in the daily mobility 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

---

[0] 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.
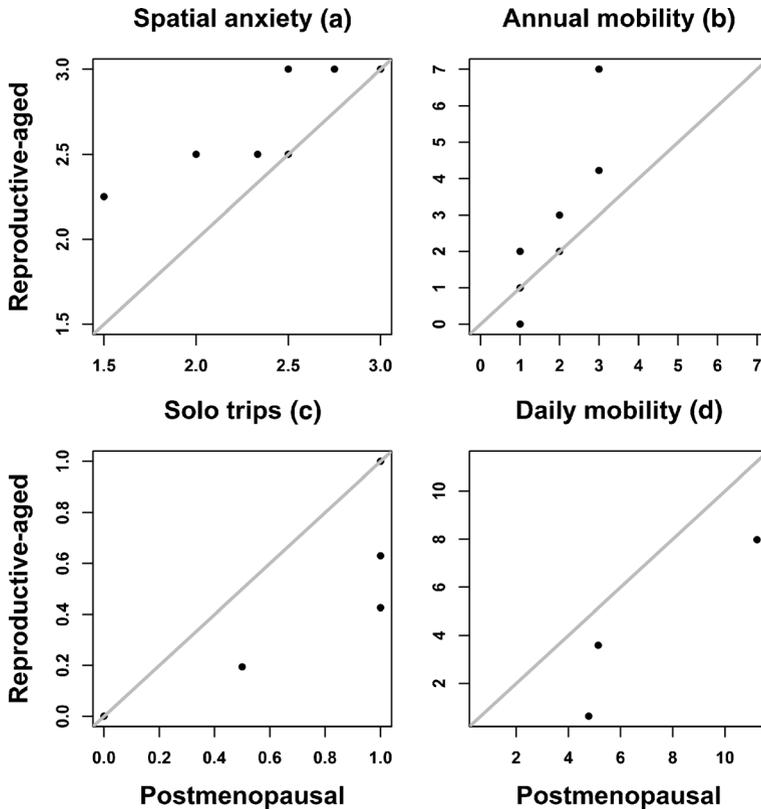
Fig. 2 Quantile-quantile plots showing the difference between the distribution of reproductive-aged and postmenopausal women's scores in each measure. When points fall below the *gray line*, postmenopausal women at that quantile score higher. **a** Ordinal score in spatial anxiety scale, with higher scores indicating greater anxiety. **b** Unique visits in the past year. **c** Proportion of visits in the past year that were made without accompaniment. **d** Total distance traveled (kilometers) during an average day

women (4.97 km versus 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.

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 be explained by chance (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

Table 3 Spatial performance, anxiety, and mobility in nursing and cycling women

Measure	Nursing			Cycling			p
	N	M	SD	N	M	SD	
Mental rotation (accuracy)	21	83.7%	17.5%	14	81.0%	14.6%	0.627
Mental rotation (time)	21	5.38	1.68	14	5.80	1.27	0.404
Pointing error	24	16.73	8.02	17	20.97	12.37	0.227
Spatial anxiety	12	2.83	0.25	5	2.60	0.22	0.092
Annual visits	19	2.84	1.89	12	1.33	1.15	0.01
Solo visit %	19	22.0%	33.7%	9	22.2%	36.3%	0.984
Daily mobility (km)	7	3.78	1.36	5	3.71	2.82	0.960

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-square test comparing the two groups. "Cycling" refers to reproductive-aged women in any stage other than lactation or gestation

women in response time is statistically significant despite the weak power of the study (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 4 Spatial performance, anxiety, and mobility in pregnant and cycling women

Measure	Pregnant			Cycling			p
	N	M	SD	N	M	SD	
Mental rotation (accuracy)	3	92.6%	12.8%	14	81.0%	14.6%	0.255
Mental rotation (time)	3	3.7	0.51	14	5.80	1.27	0.001
Pointing error	3	24.98	8.09	17	20.97	12.37	0.611
Spatial anxiety	2	2.38	0.18	5	2.60	0.22	0.274
Annual visits	4	1.25	0.96	12	1.33	1.15	0.891
Solo visit %	2	0%	0%	9	22.2%	36.3%	0.104
Daily mobility (km)	3	4.24	3.06	5	3.71	2.82	0.820

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-square 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 because of 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 (Fig. 3). 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]

Spatial Ability, Ranging, and the Interaction with Sex

Hypothesis 4 Spatial cognition predicts women's range size.

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, 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 it 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 (Table 5, Fig. 4).
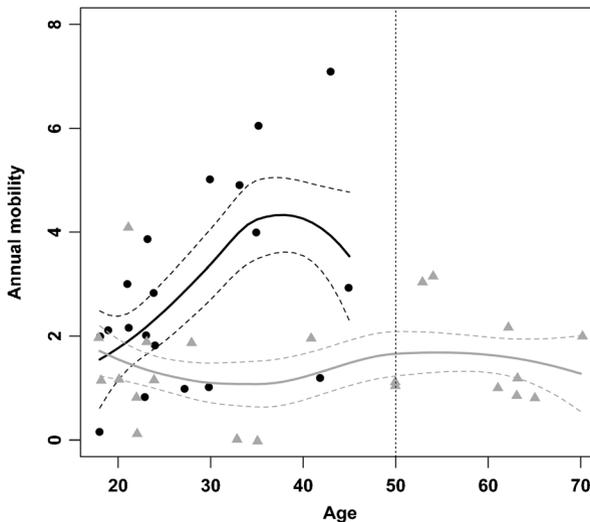

Fig. 3 The *gray triangles* and corresponding gray loess lines plot the number of unique annual visits reported by women who were neither pregnant nor nursing at all ages. The *black circles* and corresponding loess lines plot the number of unique annual visits reported by women who were breastfeeding. 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 5 Relationship between spatial cognition and annual mobility among men and women

	Independent Variables						
	MR		Male(1|0)		Male(1|0):MR		
	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**	0.300*	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). * $p < 0.05$; ** $p < 0.01$

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
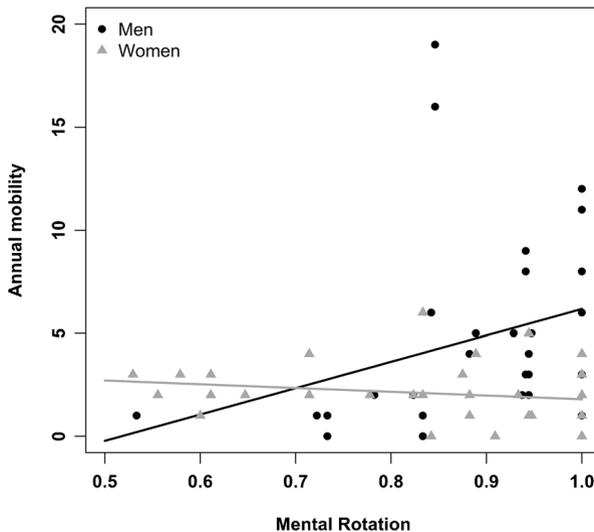

Fig. 4 Plot fitting the unstandardized coefficients for Model 2 described in Table 5. *Gray triangles* and corresponding line demonstrate the relationship between the proportion of correct responses in the mental rotation task and annual range for women. *Black triangles* and corresponding line show the same relationship for men

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 hypervigilance to threats such as children falling into fires (a common source of household 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 show 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 self-reported spatial anxiety being higher 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 above ("Hypotheses"), the underlying logic and specified mechanism of the fertility and parental care hypothesis conflict in terms of expectations for postpartum mothers. The increased travel and trend toward 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. However, the increased travel 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 travel by nursing mothers. One possibility we considered is that women could be returning to their natal community to seek assistance in childcare from their mothers. This explanation follows from findings among a nearby Himba community (Scelza 2011). However, none of the cases in our data is 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 much of the nursing women's travel was to visit extended kin. For example, two sisters, each with an unweaned child, traveled together approximately 160 km through an unfamiliar region to visit a maternal aunt they had not seen since childhood. Overall, 38.2% (21 of 55) of the visits reported by women with unweaned children were targeted social visits to extra-nuclear kin, and only 5% (2 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 livestock. 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 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.

References

Bailey, D. A., Lippa, R. A., Del Giudice, M., Hames, R., & Geary, D. C. (2012). Sex differences in spatial abilities: methodological problems in Hoffman et al. *Proceedings of the National Academy of Sciences*, *109*(10), E583.

Betzig, L. (2012). Means, variances, and ranges in reproductive success: comparative evidence. *Evolution and Human Behavior*, *33*(4), 309–317.

Brown, G. R., Laland, K. N., & Mulder, M. B. (2009). Bateman's principles and human sex roles. *Trends in Ecology & Evolution*, *24*(6), 297–304.

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.

Clutton-Brock, T., & Vincent, A. (1991). Sexual selection and the potential reproductive rates of males and females. *Nature*, *351*(6321), 58–60.

Collins, D., Busse, C., & Goodall, J. (2008). Infanticide in two populations of savanna baboons. In G. Hausfater, & M. S. B. B. Hrdy (Eds.), *Infanticide: comparative and evolutionary perspectives* (pp. 193–216). Piscataway: Aldine/Transaction (Originally published in 1984).

Coluccia, E., & Louse, G. (2004). Gender differences in spatial orientation: a review. *Journal of Environmental Psychology*, *24*(3), 329–340.

Devlin, A. S., & Bernstein, J. (1995). Interactive wayfinding: use of cues by men and women. *Journal of Environmental Psychology*, *15*(1), 23–38.

Driscoll, I., Hamilton, D., Yeo, R., Brooks, W., & Sutherland, R. (2005). Virtual navigation in humans: the impact of age, sex, and hormones on place learning. *Hormones and Behavior*, *47*(3), 326–335.

Dufour, D., & Sauther, M. (2002). Comparative and evolutionary dimensions of the energetics of human pregnancy and lactation. *American Journal of Human Biology*, *14*(5), 584–602.

Duka, T., Tasker, R., & McGowan, J. (2000). The effects of 3-week estrogen hormone replacement on cognition in elderly healthy females. *Psychopharmacology*, *149*(2), 129–139.

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.

Frye, C. (1995). Estrus-associated decrements in a water maze task are limited to acquisition. *Physiology & Behavior*, *57*(1), 5–14.

Galea, L., & Kimura, D. (1993). Sex differences in route-learning. *Personality and Individual Differences*, *14*(1), 53–65.

Gaulin, S. (1992). Evolution of sex difference in spatial ability. *American Journal of Physical Anthropology*, *35*(S15), 125–151.

Gaulin, S., & FitzGerald, R. (1986). Sex differences in spatial ability: an evolutionary hypothesis and test. *American Naturalist*, *127*(1), 74–88.

Gaulin, S., Hoffman, H., et al. (1988). Evolution and development of sex differences in spatial ability. In L. L. Betzig, M. B. Mulder, & P. Turke (Eds.), *Human reproductive behaviour: A Darwinian perspective* (pp. 129–152). Cambridge: Cambridge University Press.

Geary, D. (1995). Sexual selection and sex differences in spatial cognition. *Learning and Individual Differences*, *7*(4), 289–301.

Gilmartin, P., & Patton, J. (1984). Comparing the sexes on spatial abilities: map-use skills. *Annals of the Association of American Geographers*, *74*(4), 605–619.

Gittleman, J., & Thompson, S. (1988). Energy allocation in mammalian reproduction. *American Zoologist*, *28*(3), 863–875.

Gregor, T. (1987). *Anxious pleasures: The sexual lives of an Amazonian people*. Chicago: University of Chicago Press.

Hampson, E. (1990). Estrogen-related variations in human spatial and articulatory-motor skills. *Psychoneuroendocrinology*, *15*(2), 97–111.

Hampson, E., & Kimura, D. (1988). Reciprocal effects of hormonal fluctuations on human motor and perceptual-spatial skills. *Behavioral Neuroscience*, *102*(3), 456–459.

Hausmann, M., Slabbekoorn, D., Van Goozen, S. H., Cohen-Kettenis, P. T., & Güntürkün, O. (2000). Sex hormones affect spatial abilities during the menstrual cycle. *Behavioral Neuroscience*, *114*(6), 1245–1250.

Hegarty, M., Montello, D. R., Richardson, A. E., Ishikawa, T., & Lovelace, K. (2006). Spatial abilities at different scales: individual differences in aptitude-test performance and spatial-layout learning. *Intelligence*, *34*(2), 151–176.

Henrie, R., Aron, R., Nelson, B., & Poole, D. (1997). Gender-related knowledge variations within geography. *Sex Roles*, *36*(9–10), 605–623.

Heron, J., O'Connor, T., Evans, J., Golding, J., & Glover, V. (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, K., & Hurtado, M. (1996). *Ache life history: The ecology and demography of a foraging people*. Hawthorne: Aldine.

Jašarević, E., Williams, S., Roberts, M., Geary, D., & Rosenfeld, C. (2012). Spatial navigation strategies in *Peromyscus*: a comparative study. *Animal Behaviour*, *84*(5), 1141–1149.

Jones, C., Braithwaite, V., & Healy, S. (2003). The evolution of sex differences in spatial ability. *Behavioral Neuroscience*, *117*(3), 403–411.

Komnenich, P., Lane, D. M., Dickey, R. P., & Stone, S. C. (1978). Gonadal hormones and cognitive performance. *Physiological Psychology*, *6*(1), 115–120.

Krug, E., Sharma, G., & Lozano, R. (2000). The global burden of injuries. *American Journal of Public Health*, *90*(4), 523–526.

Lacreuse, A., Herndon, J., Killiany, R., Rosene, D., & Moss, M. (1999). Spatial cognition in rhesus monkeys: male superiority declines with age. *Hormones and Behavior*, *36*(1), 70–76.

Lawton, C. (1994). Gender differences in way-finding strategies: relationship to spatial ability and spatial anxiety. *Sex Roles*, *30*(11–12), 765–779.

Lawton, C. (2010). Gender, spatial abilities, and wayfinding. In J. C. Chrisler, & D. R. McCreary (Eds.), *Handbook of gender research in psychology* (pp. 317–341). New York: Springer.

Levine, S., Huttenlocher, J., Taylor, A., & Langrock, A. (1999). Early sex differences in spatial skill. *Developmental Psychology*, *35*(4), 940–949.

Linn, M. C., & Petersen, A. C. (1985). Emergence and characterization of sex differences in spatial ability: a meta-analysis. *Child Development*, *56*(6), 1479–1498.

MacDonald, D., & Hewlett, B. (1999). Reproductive interests and forager mobility. *Current Anthropology*, *40*(4), 501–524.

McCormick, C., & Teillon, S. (2001). Menstrual cycle variation in spatial ability: relation to salivary cortisol levels. *Hormones and Behavior*, *39*(1), 29–38.

Moffat, S., 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, S., Zonderman, A., & Resnick, S. (2001). Age differences in spatial memory in a virtual environment navigation task. *Neurobiology of Aging*, *22*(5), 787–796.

Montello, D. R., Richardson, A. E., Hegarty, M., & Provenza, M. (1999). A comparison of methods for estimating directions in egocentric space. *Perception*, *28*, 981–1000.

Moore, D., & Johnson, S. (2008). Mental rotation in human infants a sex difference. *Psychological Science*, *19*(11), 1063–1066.

Murphy S, Xu J, Kochanek K (2010) Deaths: Final data for 2007. National Vital Statistics Reports 61(4). Centers for Disease Control and Prevention. Available at http://www.cdc.gov/nchs/data/nvsr/nvsr61/nvsr61_04.pdf.

Perdue, B., Snyder, R., Zhihe, Z., Marr, J., & Maple, T. (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, A. O., & 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, P., & Liben, L. (2008). A sex difference in mental rotation in young infants. *Psychological Science*, *19*(11), 1067–1070.

Sanders, B., Soares, M. P., & D'Aquila, J. (1982). The sex difference on one test of spatial visualization: a nontrivial difference. *Child Development*, *53*(4), 1106–1110.

Scelza, B. (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, R. N., & Metzler, J. (1971). Mental rotation of three-dimensional objects. *Science*, *171*(1), 701–703.

Sherry, D., & Hampson, E. (1997). Evolution and the hormonal control of sexually-dimorphic spatial abilities in humans. *Trends in Cognitive Sciences*, *1*(2), 50–56.

Silverman, I., Choi, J., Mackewn, A., Fisher, M., Moro, J., & Olshansky, E. (2000). Evolved mechanisms underlying wayfinding: further studies on the hunter-gatherer theory of spatial sex differences. *Evolution and Human Behavior*, *21*(3), 201–213.

Smuts, B. (1992). Male aggression against women. *Human Nature*, *3*(1), 1–44.

Spritzer, M., Solomon, N. G., & Meikle, D. (2005). Influence of scramble competition for mates upon the spatial ability of male meadow voles. *Animal Behaviour*, *69*(2), 375–386.

Stokes, E., Parnell, R., & 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.

Unity (2014) Unity 3D. Available at www.Unity3D.com.

Vashro L (2014) *Residence and childcare assistance among the Twe.* PhD thesis, Department of Anthropology, University of Utah, Salt Lake City.

Vashro, L., & Cashdan, E. (2015). Spatial cognition, mobility, and reproductive success in northwestern Namibia. *Evolution and Human Behavior*, *36*(2), 123–129.

Viljoen P (1982) The distribution and population status of the larger mammals in Kaokoland, South West Africa/Namibia. *Cimbebasia* (A) 7(2):5–33 Windhoek Staatsmuseum.

Voyer, D., Voyer, S., & Bryden, M. P. (1995). Magnitude of sex differences in spatial abilities: a meta-analysis and consideration of critical variables. *Psychological Bulletin*, *117*(2), 250–270.

Walker, P. (2001). A bioarchaeological perspective on the history of violence. *Annual Review of Anthropology*, *30*(1), 573–596.

Watts, D. (1989). Infanticide in mountain gorillas: new cases and a reconsideration of the evidence. *Ethology*, *81*(1), 1–18.

Watts, D., & Mitani, J. (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, S., & Schaie, W. (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.

Woodfield, R. (1984). Embedded figures test performance before and after childbirth. *British Journal of Psychology*, 75(1), 81–88.

Layne Vashro is a postdoctoral researcher on the SCAN project at the University of Utah's Department of Anthropology. Vashro is interested in the costs and benefits of travel as well as the cognitive mechanisms underlying long-distance navigation.

Lace Padilla is a PhD student at the University of Utah in the Cognitive Neural Science department. Padilla is a member of the Visual Perception Spatial Cognition Research Group directed by Sarah Creem-Regehr, Jeanine Stefanucci, and William Thompson. Her work focuses on individual differences in visual perception. In 2014, she was awarded the Martin Harris Hiatt Memorial Graduate Fellowship for Underrepresented Populations and the Clayton Fellowship for Excellence in Research with Underrepresented Populations.

Elizabeth Cashdan is a professor of anthropology at the University of Utah. She is currently principal investigator on an interdisciplinary project that aims to understand how navigational demands affect spatial cognition, and how these differ for men and women through the lifespan and cross-culturally.