Spatial cognition, mobility, and reproductive success in northwestern Namibia

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Abstract

Males occupy a larger range than females in many mammal populations including humans, and show an advantage in certain spatial-cognitive laboratory tasks. Evolutionary psychologists have explained these patterns by arguing that an increase in spatial ability facilitated navigation, which allowed range expansion in pursuit of additional mating and hunting opportunities. This study evaluates this hypothesis in a population with navigational demands similar to those that faced many of our ancestors, the Twe and Tjimba of northwestern Namibia. Twe and Tjimba men have larger visiting ranges than women and are more accurate in both spatial (mental rotations) and navigational (accuracy pointing to distant locations) tasks. Men who perform better on the spatial task not only travel farther than other men, but also have children with more women. These findings offer strong support for the relationship between sex differences in spatial ability and ranging behavior, and identify male mating competition as a possible selective pressure shaping this pattern.

1 Introduction

Men occupy larger ranges than women across a broad spectrum of geographical and subsistence contexts (MacDonald & Hewlett, 1999; Ecuyer-Dab & Robert, 2004b; Gaulin & Hoffman, 1988), and they also outperform women in some spatial and navigational tasks (Eals & Silverman, 1994; Lawton, 2010). One prominent explanation for the dimorphism in range size is that ancestral men with superior spatial-cognitive ability were also better at navigating across long distances and into unfamiliar environments, and that these skills allowed them to outcompete other men by ranging farther in search of mates (Gaulin & FitzGerald, 1986; Gaulin, 1992) and game animals (Silverman et al., 2000). A male advantage in spatial ability associated with larger range size is also found in several other polygynous species, where males gain a reproductive advantage from patrolling multiple female ranges (Gaulin & FitzGerald, 1986; Gaulin & Fitzgerald, 1989; Perdue et al., 2011; Jašarević et al., 2012; Carazo et al., 2014).

Support for this explanation among humans has been indirect, and comes predominantly from studies in urban industrialized societies, where the motives and modes of travel differ markedly from those of ancestral populations. Our study was conducted among the Twe and Tjimba of northwestern Namibia. These part-time foragers travel long distances on foot through a natural environment, and thus face navigational challenges similar to those that faced many human ancestors. This study combines data on range size, spatial ability, and reproductive success to test the hypothesis that larger ranges have selected for better spatial ability in human males.

Men perform better than women in several spatial tests, particularly the ability to mentally rotate objects in order to determine how they would look in different orientations (a test of spatial visualization) (Shepard & Metzler, 1971). On average, men complete these mental rotation tasks more quickly and accurately than women, both in Western laboratory experiments and cross-culturally (Linn & Petersen, 1985; Voyer et al., 1995; Silverman et al., 2007; Jahoda, 1980). Spatial visualization helps with encoding, maintaining, and using spatial information during navigation (Allen, 1999; Hegarty et al., 2006). This relationship is seen in the link between mental rotation performance and successful maze navigation (Moffat et al., 1998), map learning proficiency (Galea & Kimura, 1993), accuracy pointing to distant locations (Bryant, 1982), and wayfinding (Silverman et al., 2000). Women also tend to do less well at many of these navigational tasks (Bryant, 1982; Galea & Kimura, 1993; Henrie et al., 1997) but see (Evans, 1980; Gilmartin & Patton, 1984; Golledge, 1995; Montello et al., 1999; Burke et al., 2012) and to feel less confident in their navigational ability regardless of skill level (Kolakowski & Malina, 1974; Devlin & Bernstein, 1995; Schmitz, 1997; Lawton & Kallai, 2002; Picucci et al., 2011). When navigating, women are also less likely than men to rely on geocentric cues like celestial markers, exact distances, and cardinal directions (Galea & Kimura, 1993; Lawton, 1994; Choi & Silverman, 1996; Sandstrom et al., 1998). Geocentric cues generalize to novel environments, and are thus preferred when navigating long distances and into unfamiliar terrain.

Greater navigational skill and confidence among males may facilitate their larger ranges. The sex difference in range size is robust, with men occupying larger ranges in societies practicing forager, farmer, horticultural, pastoral, and market modes of subsistence, and those living in arid, arctic, jungle, island, and urban environments (MacDonald & Hewlett, 1999; Gaulin & Hoffman, 1988; Ecuyer-Dab & Robert, 2004b). Among foragers, larger male ranges result from both tracking game animals across long distances (Marlowe, 2010) and social visiting in the interest of maintaining political networks and seeking mating opportunities (MacDonald & Hewlett, 1999). Women in foraging societies are also mobile, but their mobility tends to be concentrated in a smaller geographical area than men's. For example among the G//ana of the Kalahari Desert, more women were observed visiting other residence camps than men in the local region, but more men than women were observed visiting distant regions (Cashdan, 1984). This is consistent with our assessment of mobility among the Twe and Tjimba. Both men and women regularly travel between the interconnected residence camps in their home region, but men are more likely to expand their visits into more distant locations.

A relationship between range size and spatial ability has been documented for several non-human species (Gray & Buffery, 1971; Gaulin & FitzGerald, 1986; Galea et al., 1994), children in both suburban United States and African herding-agricultural societies (Munroe & Munroe, 1971; Nerlove et al., 1971; Matthews, 1987), as well as urban Canadian men (Ecuyer-Dab & Robert, 2004b). Our study tests for a relationship between spatial-cognitive ability and range size in a population that faces navigational challenges similar to those that faced many ancestral humans, and tests the hypothesis that increased range size and better spatial ability confers fitness benefits (more mates and more children) for men.

2 Materials and methods

2.1 Population

The Twe and Tjimba live in the dry and mountainous region surrounding the Kunene River in northwestern Namibia and southwestern Angola. Their material and ritual cultures mirror that of the well-studied Himba (Malan, 1974; Bollig, 2004, 2006). The most significant distinction between the Twe and Tjimba is the local perception of their ethnic history. People in the Kunene region view the Tjimba as an impoverished branch of the politically dominant Himba and Herero line of Bantu people, but view the Twe as an outsider ethnic group.

The Twe and Tjimba practice a mixed subsistence that includes seasonal horticulture, foraging, animal husbandry, and the sale of craft goods. Families often shift between a rainy season camp near their garden and dry season camps near the mountains for foraging, or, as of late 2007, near a government camp where they receive a monthly food subsidy. Most men own no livestock, although about 15% control enough cattle to provide a stable source of calories in fermented milk, and these men move between cattle posts throughout the dry season. Both men and women travel into nearby mountains to forage for wild fruits and tubers, while men go on regular trips to find honey. Craft goods are either exchanged with visiting traders or men and women take them about twenty kilometers to the nearest town. Twe and Tjimba men still hunt wild game, but only elderly individuals remember a time when hunting was centrally important. Devastation of the local game populations and strict conservancy regulations have reduced hunting's role in Twe and Tjimba subsistence (Estermann, 1979).

Twe and Tjimba families live in stable residence groups, but are highly mobile within their broader political region. Many households spend the dry season at one or more seasonal camps. These camps are typically within the same ten square kilometer region as their wet season camp, but sometimes extend farther. Travel outside the local region is safe and relatively common. Most travel is on foot. The biggest exception is any travel to Opuwo, a small town more than 140 kilometers away which is typically reached by hitch-hiking. This study includes participants from two distinct but interacting regions each spanning roughly ten square kilometers.

In addition to food subsidy, the Namibian government also provides education for Twe and Tjimba children. However, because this is a new arrangement, very few of the participants in this study have ever attended school.

2.2 Procedure

A trained Otjiherero/English interpreter assisted in all of the following tasks. Otjiherero is the native language of the Twe and Tjimba.

Mental rotation task The mental rotation task used a self-directed computer program. The screen displayed a series of hands facing either palm up or down and oriented in different directions in three dimensions. The participant was asked to identify whether the pictured hand was a left or right hand, and then press the associated button. This process was repeated for twenty-four images, each with a unique hand orientation. Each image was displayed for 7.5 seconds. Failure to respond in the allotted time or pressing the wrong button counted as an incorrect response for that image. The percent of correct responses was used to assess performance on this task. Participants in this study worked through a ten-question trial period before proceeding to the recorded task. We collected mental rotation data from 68 men and 52 women.

Water-level task The water-level task, which asks participants to indicate the water-line in a tipped vessel, was included as a measure of spatial perception. This is another spatial factor that shows a robust sex difference (Voyer et al., 1995), and it has been associated with wayfinding (Choi et al., 2006), vestibular navigation (Sholl, 1989), and use of geocentric navigational cues (Lawton, 1994). The task reflects the ability to identify horizontal and vertical accurately in spite of competing cues. In our version, participants studied a picture of a glass of water with a horizontal water-line in the middle of the glass and another horizontal line beneath the glass, which in this context was likely interpreted as the ground. The experimenter then showed participants a single item with four similar images of that same glass tipped relative to the ground-line. The correct image had a water-line parallel to the ground-line, another had a water-line parallel to the base of the glass, and the other two had intermediate water-lines. We collected water-level data from 67 men and 55 women.

Object location memory task Memory for the relative location of objects has received attention because it usually shows a female advantage where a sex difference exists (Silverman et al., 2007). Performance on this task is not expected to correlate with geocentric navigation ability or distant ranging, but was included in an attempt to replicate the surprising male advantage found among the Hadza of Tanzania (Cashdan et al., 2012). Our object location memory task was a version of the "memory game" and followed the procedure used by McBurney et al. (1997) and Cashdan et al. (2012). Pairs of food-plant and animal cards were placed face down on a table, and participants flipped them over in pairs, trying to find a match. Matched cards were removed, unmatched cards were replaced face down. Fewer card flips indicated better location memory. We collected object location memory data from 68 men and 55 women.

Pointing task The logic connecting spatial cognition to range size assumes that spatial cognition facilitates navigation, which in turn allows individuals to travel long distances more safely and efficiently. We measured participants' ability to accurately point to distant locations in order to capture one particular form of navigation that might mediate the relationship between spatial cognition and ranging. In particular, pointing accuracy measures geocentric navigation ability and survey knowledge of the region (Allen, 2003).

Participants pointed to nine locations elsewhere in the Kunene region. The farthest location was 125 kilometers away, and the nearest was 12 kilometers away. The experimenter measured the bearing indicated by participants' points using the compass on a Garmin eTrex hand-held GPS, and compared the pointed bearing to the actual bearing given by the GPS device. We collected pointing accuracy data from 37 men and 36 women.

Range size measures During the pointing task, we also asked participants whether they had ever visited each location, whether they had visited it more than once, and whether they had visited that place "many times". We then used the percentage of locations a participant reported visiting many times as an approximation of *lifetime mobility*. We collected lifetime mobility data from 67 men and 54 women.

Nearly all Twe and Tjimba regularly visit the residence camps in their approximately ten square kilometer "home region." We asked participants to name all of the locations outside of their home region in which they spent the night during the past year. Since travel outside the home region is less common, participants appeared to have no difficulty recalling all of the locations they had visited. This provided two correlated measures of *annual range size*: (1) the total number of places visited and (2) the minimum distance required to visit each of those places. The latter was calculated by summing the distance traveled from home to each of the named locations using GPS coordinates and known walking paths. Most of these trips were made exclusively on foot, however long distance trips to the south typically involve hitch-hiking. Because being a passenger does not pose the same navigational demands as walking, we did not include the part of these trips that would involve car travel, only the distance to the road where the person would find a ride. We collected this annual range data during a second trip to the field approximately two years following the other measures. Because of this, even though we collected annual range data for 68 participants only 20 (12 men and 8 women) of those cases overlap with the previously collected measures.

Reproductive history Participants listed all of their children and the partner with whom they had each child. This data gives the total number of children each participant has, and the number of different partners each participant has had a child with. We have reproductive history data for 49 men and 51 women.

2.3 Analyses

The data were analyzed using regression models and data visualization techniques to test assumptions of normality. We conducted all data analysis using R 2.15.1 statistical software (Team, 2012).

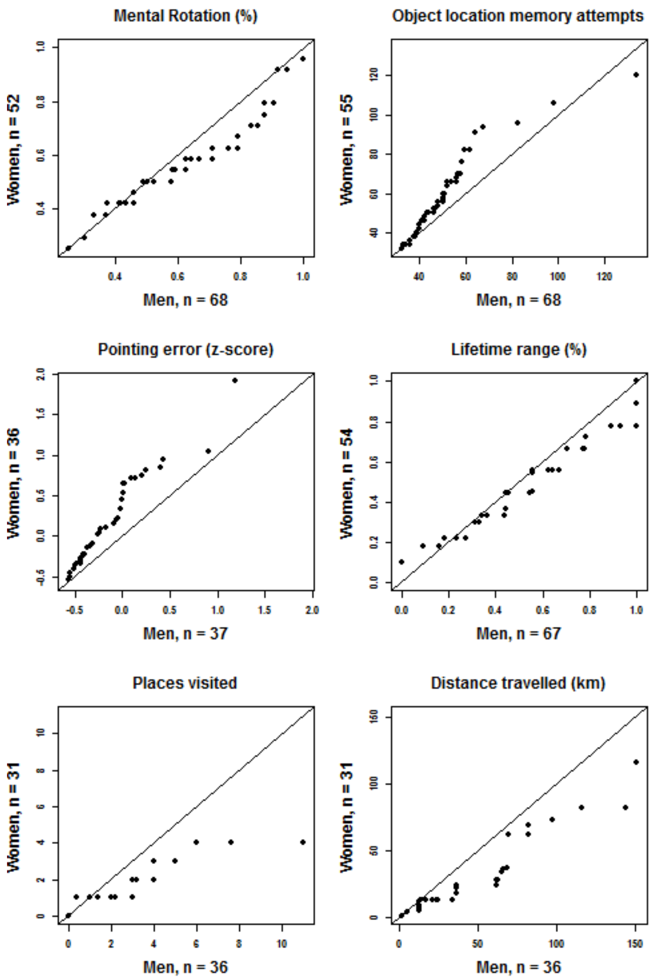
3 Results

3.1 Sex Differences

Mental rotation task On average, men responded correctly to one more of the twenty-four stimuli than women but this difference is not statistically significant. Both men and women performed significantly better than chance. However, many individual scores fell at or below chance. The bottom end of men's and women's distributions are indistinguishable, implying the sex difference may be masked by participants who did not fully understand the task (see Figure 1). Restricting the sample to only the top-half of performers among both men and women, there is a statistically significant sex difference in response accuracy ($t(59.8) = 2.48, p = .02$) and no significant difference in reaction time. All analysis looking at mental rotation performance throughout the rest of this paper only uses the top half of performers under the assumption that variance in the lower half of the distribution does not reflect the targeted cognitive abilities.

Water-level task The water level task included one correct response and three incorrect responses. Sixty percent of men chose the correct response, which is significantly above chance ($p < 0.001$), while only forty percent of women gave the correct response, which is only a marginally significant improvement over chance ($p = .067$). This sex difference is statistically significant ($t(115.1) = 2.36, p = .02$).

Figure 1: Sex differences in task performance



Quantile-quantile plots comparing the distributions for men and women in the mental rotation task, object location memory task, pointing task, lifetime mobility measure, and a composite score of both annual range size measures. This method compares male and female scores at each quantile of the respective distributions such that when the male scores are higher the points fall to the right of the diagonal line and when female scores are higher they fall to the left.

Object location memory The fewer attempts participants needed to finish the object location memory task, the better their performance. The average man required fifty attempts to complete the memory task. The average woman required fifty-eight attempts. This sex difference is statistically significant ($t(104.8) = -2.45, p = .02$). It is in the opposite direction of expectations based on research in Western societies (Tottenham et al., 2003; McBurney et al., 1997; Voyer et al., 2007), but is consistent with the results found in another foraging population, the Hadza (Cashdan et al., 2012).

Pointing task Participants were tested in two different residence locations and many participants did not attempt pointing to all of the nine locations. This meant that not all participants experienced the same task. In order to compare individual performance we used z-scores to standardize pointing error across all participants who attempted each unique pointing event (*i.e.* from the same location to the same target), and used the mean of an individual's standardized scores across all points to obtain an average pointing error. Men made 0.3 standard deviations less error across their points than women. This difference is statistically significant($t(63.3) = -2.61, p = .01$).

Range size Men reported visiting a higher percentage of distant locations "many times", but this sex difference in our measure of lifetime mobility is not statistically significant ($t(119) = 1.67, p = .1$).

Twe and Tjimba men reported visiting more unique locations spanning a greater distance outside of their home region than women in the past year. The mean male participant reported visiting 3.4 locations across 47 kilometers while the mean female participant reported visiting only 2 locations covering 30 kilometers. The sex difference in both of these correlated annual range measures is statistically significant (places: $t(56.4) = 3.11, p = .003$; distance: $t(63.3) = 2.02, p = .048$). We also combined the annual range measure into a single composite measure by standardizing them with z-scores and taking their mean. The sex difference remains in this composite measure ($t(57.9) = 2.7, p = .009$).

3.2 Cognition, navigation, and range size

Mental rotations and pointing accuracy Participants who performed better on the mental rotation task also pointed more accurately to distant locations, but the effect is not statistically significant ($n = 46, Std.\beta = -0.22, p = .12, R^2 = 0.06$). This relationship was more pronounced in men ($n = 24, Std.\beta = -0.27, p = .21, R^2 = 0.07$). There was no relationship between pointing accuracy and performance on the water-level task.

Mental rotations and Range Size Twe and Tjimba men who correctly responded to a higher percentage of stimuli in the mental rotation task visited a higher percentage of distant locations "many times" throughout their lives (see Table 1). Men who responded more accurately in the mental rotation task also visited more locations in the past year and covered more distance in doing so (see Table 1, and Figure 2). A man who correctly responded to 75% of the mental rotation stimuli is predicted to visit four locations covering 75 kilometers while a man with a perfect score in the mental rotation task is expected to visit nearly eight location spanning 175 kilometers.

Table 1: Mental rotation and range size regression models (Men)

	Intercept	Mental rotation		Age		
	B	*B*	*SE B*	*B*	*SE B*	R^2
Lifetime mobility	-0.22	0.8 *	0.35	0.008 *	0.03	0.18
Without age						
Places visited	-6.5	14.2 *	4.8			0.55
Distance Visited	-221.1	395.4 **	79.8			0.78
Composite	-4.4	6.19 **	1.9			0.44
With age						
Places visited	-1.32	9.7	7.0	-0.05	0.06	0.61
Distance Visited	-136.6	321.1 *	115.3	-0.85	0.94	0.80
Composite	-4.9	6.67 *	2.53	0.006	0.02	0.45

* $p < .05$; ** $p < .01$

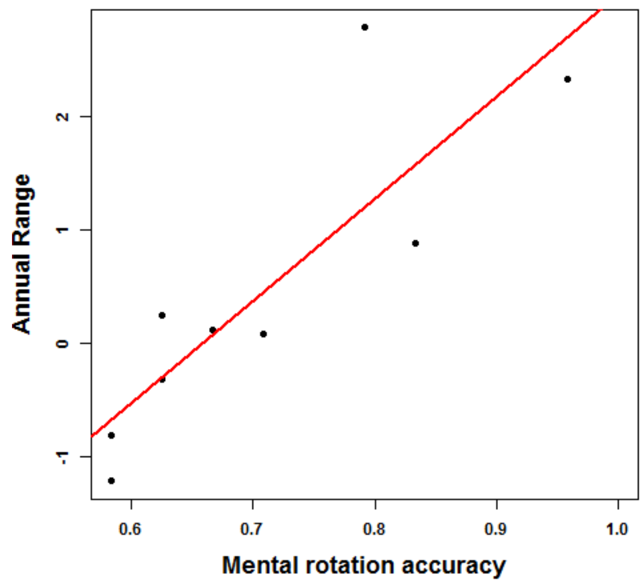
Independent variables include mental rotation (% correct, range = 0.58 to 1) and age (range = 18 to 69) as a control variable. Dependent variables include lifetime mobility (% of locations visited), places visited in the past year (range = 0 to 8), distance traveled in the past year (range = 1 to 151), and the composite annual range measure (range = -1.2 to 2.8). Sample size of 39 for relationship with lifetime mobility and sample size of 9 for annual range size.

There are only nine men in both the truncated mental rotation sample and the annual mobility sample. However, even with that small sample size the relationships between mental rotation accuracy and both distance traveled and the composite annual range measure are significant after controlling for age (see Table 1). These findings remain if we reintroduce the four participants removed due to the concern regarding poor performance on the mental rotation task.

There is no relationship between mental rotation accuracy and our measures of lifetime mobility among women, nor is there a relationship between mental rotation accuracy and unique distance traveled for women. Mental rotation is a marginally significant predictor of the number of places women visited in the past year, but the number of women included in both the mental rotation and annual range size samples is even smaller than that for men ($n = 6, Std.\beta = 0.73, p = .08, R^2 = 0.59$).

There was no relationship between annual range size and performance in the water-level task.

Figure 2: Mental rotation and range size (Men)



Best fit line for accuracy in the mental rotation task predicting the composite annual range measure (see Table 1)

Mental rotations, range size, and reproductive success The hypothesized relationship between range size and reproductive success received mixed support. Men who visited more unique locations in the past year have fathered children with more women after controlling for age (see Table 2), indicating that yearly range size is related to number of mates, although these men did not father more children in total. This pattern was not found with lifetime mobility, which was unrelated to either measure of reproductive success in men. Range size measures were not related to reproductive success among women, nor was there a relationship between mental rotation performance and range size for either sex.

Table 2: Annual range and reproductive success regression models (Men)

	Intercept	Range size		Age		
	B	*B*	*SE B*	*B*	*SE B*	R^2
		Places visited				
# Partners	0.01	0.15 *	0.07	0.02 *	0.01	0.24
# Children	-1.02	0.38 .	0.21	0.10 ***	0.03	0.35
		Distance Visited				
# Partners	0.30	0.006	0.005	0.02 *	0.01	0.16
# Children	-0.42	0.015	0.013	0.10 **	0.03	0.30

* $p < .05$; ** $p < .01$

Regression models with the number of places visited and the distance traveled in the past year as independent variables, and the number of women with whom a man has had a child and his total number of children as dependent variables. Age is added as a control variable in each model. Sample size of 31.

4 Discussion and Conclusions

Twe and Tjimba men responded more accurately in the mental rotation task, were more likely to choose the correct response in the water-level task, and made more accurate points to distant locations than women. Men also reported visiting more locations in their lifetimes and occupied a larger range in the past year. These results add to the cross-cultural support for some of the strongest and best-replicated sex differences in human cognition and behavior. In addition, they allow us to test whether these traits are related. The link between spatial cognition, navigation, and range size is intuitive, but previous research offers limited support.

Evolutionary theorists posit a variety of different explanations for the male advantage in mental rotation tasks (Jones et al., 2003). One explanation argues that spatial visualization helps hunters return home from hunting trips (Eals & Silverman, 1994). Another explanation argues that spatial visualization allows travel in search of mating opportunities (Gaulin, 1992; Ecuyer-Dab & Robert, 2004a). Another explanation argues that spatial visualization helps men execute raids against distant camps (Geary, 1995). Another explanation focuses instead on how distant ranging may be more costly to women than men, and thus increased spatial visualization was not selected for in women (Sherry & Hampson, 1997). All of these explanations share the assumption that men's superior spatial visualization is linked to long distance mobility. Our results offer support for this relationship by showing that mental rotation performance predicts men's lifetime and annual mobility.

Navigation ability is the likely mediator between spatial cognition and range size, but we failed to find support for this model using pointing accuracy as our measure of navigation ability. The direct link between any one spatial-cognitive task and any one navigation task is weak, especially when the navigation task does not use a novel environment (Wolbers & Hegarty, 2010; Pearson & Ialongo, 1986; Allen et al., 1996; Montello et al., 2004). This study asked participants to point to familiar locations. The task may have been so easy that any variance due to spatial visualization ability was overwhelmed by other sources of error. Future efforts to identify the mediator between spatial cognition and mobility should use a broad collection of difficult navigational tasks set in unfamiliar environments.

In addition to the relationship between spatial cognition and ranging, we find some preliminary evidence that increased range size has direct fitness consequences for Twe and Tjimba men. Men who had visited more places in the past year have fathered children with more women, although relationships between our other measures of reproductive success and annual range were weak. Our other range size measure (number of places out of 9 visited "many times"), which we are calling "lifetime mobility," was not related to male reproductive success. Lifetime mobility should be a better predictor of reproductive success than annual range size given that both are lifetime measures, but our ability to measure it in this study was limited and indirect.

One possible alternative explanation for the correlation between ranging and reproductive success is that men are traveling to visit their children rather than searching for mates. While we did not systematically collect data on the purpose of all trips away from home, we did receive this information for many visits (80 for men and 33 for women), and were able to identify visits to kin as well as social visits generally. Men's visits were more likely than women's to be for social purposes (53% vs. 42%), and men's social visits were more likely to involve visiting friends or extended family (e.g. uncles or cousins) rather than primary kin. Women, in contrast, were more likely to be traveling for the purpose of visiting primary kin (e.g. children, parents, or siblings) or attending large ceremonial gatherings. In only one case was a man explicitly visiting one of his children. This pattern implies that some of men's greater mobility is a function of increased casual visits to camps where they are more likely to find possible sexual partners.

Although we found some support for a relationship between male reproductive success and range size, we did not find a relationship between reproductive success and spatial ability. This may not be surprising. Spritzer et al. (2005) found that polygamous male voles with superior spatial ability visit more female nests and that voles that visit more nests sire more litters, however their study also failed to find a direct relationship between spatial ability and reproductive success. In both cases a larger sample may be necessary to appropriately test this relationship.

Our findings offer tentative support for the theory that men occupy larger ranges than women in pursuit of additional mating opportunities. This explanation for men's advantage in spatial-cognitive and navigational tasks is appealing, because it is consistent with findings in other mammal species (Jones et al., 2003; Gaulin, 1992; Perdue et al., 2011; Jašarević et al., 2012). Our results support the current evolutionary explanations of men's superior spatial ability. There is now research demonstrating a relationship between men's spatial visualization and range size in populations as diverse as rural Namibia and urban Canada. While this study identifies mate searching as an incentive for men to expand their ranges, this and the other evolutionary explanations noted above are not mutually exclusive. The benefits of increased mating range, increased hunting range, increased raiding ability, and women's preference to limit their range size may all have added to the selective pressure favoring sex differences in range size, navigation, and spatial cognition.

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Data accessibility

Data used in these analyses are available from Vashro by request.

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