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Original Article

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.

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1. Introduction

Men occupy larger ranges than women across a broad spectrum of geographical and subsistence contexts (Ecuyer-Dab & Robert, 2004b; Gaulin & Hoffman, 1988; MacDonald & Hewlett, 1999), 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, 1992; Gaulin & FitzGerald, 1986) 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 (Carazo, Noble, Chandrasoma, & Whiting, 2014; Gaulin & FitzGerald, 1986; Gaulin & Fitzgerald, 1989; Jasarevica, Williams, Roberts, Geary, & Rosenfeld, 2012; Perdue, Snyder, Zhihe, Marr, & Maple, 2011).

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

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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 (Jahoda, 1980; Linn & Petersen, 1985; Silverman, Choi, & Peters, 2007; Voyer, Voyer, & Bryden, 1995). Spatial visualization helps with encoding, maintaining, and using spatial information during navigation (Allen, 1999; Hegarty, Montello, Richardson, Ishikawa, & Lovelace, 2006). This relationship is seen in the link between mental rotation performance and successful maze navigation (Moffat, Hampson, & Hatzipantelis, 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, Aron, Nelson, & Poole, 1997) but see (Burke, Kandler, & Good, 2012; Evans, 1980; Gilmartin & Patton, 1984; Golledge, 1995; Montello, Richardson, Hegarty, & Provenza, 1999) and to feel less confident in their navigational ability regardless of skill level (Devlin & Bernstein, 1995; Kolakowski & Malina, 1974; Lawton & Kallai, 2002; Picucci, Caffo, & Bosco, 2011; Schmitz, 1997). When navigating, women are also less likely than men to rely on geocentric cues like celestial markers, exact distances, and cardinal directions (Choi & Silverman, 1996; Galea & Kimura, 1993; Lawton, 1994; Sandstrom, Kaufman, & Huettel, 1998). Geocentric cues generalize to novel

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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 (Ecuyer-Dab & Robert, 2004b; Gaulin & Hoffman, 1988; MacDonald & Hewlett, 1999). 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 (Galea, Kavaliers, Ossenkopp, Innes, & Hargreaves, 1994; Gaulin & FitzGerald, 1986; Gray & Buffery, 1971), children in both suburban United States and African herding-agricultural societies (Matthews, 1987; Munroe & Munroe, 1971; Nerlove, Munroe, & Munroe, 1971), 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 (Bollig, 2004, 2006; Malan, 1974). 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.

2.2.1. 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 tenquestion trial period before proceeding to the recorded task. We collected mental rotation data from 68 men and 52 women.

2.2.2. Water-level task

The water-level task, which asks participants to indicate the waterline 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, McKillop, Ward, & L'Hirondelle, 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 waterlevel data from 67 men and 55 women.

2.2.3. 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, Marlowe, Crittenden, Porter, & Wood, 2012). Our object location memory task was a version of the "memory game" and followed the procedure used by McBurney, Gaulin, Devineni, and Adams (1997) and Cashdan et al. (2012). Six 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.

2.2.4. Pointing task

The logic connecting spatial cognition to range size assumes that spatial cognition facilitates navigation, which in turn allows individuals

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