Cognitive Development 52 (2019) 100800

Contents lists available at ScienceDirect

Cognitive Development

journal homepage: www.elsevier.com/locate/cogdev

Spatial cognition, navigation, and mobility among children in a forager-horticulturalist population, the Tsimané of Bolivia

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ARTICLE INFO

Keywords:
Spatial cognition
Navigation
Gender
Children
Learning
Tsimané

ABSTRACT

In many societies, males range farther than females, and this greater environmental experience may foster better spatial ability. Females are also reported to be more harm-avoidant, which may reduce spatial exploration. We evaluated these relationships among 6–18 year old Tsimané children, who live in a forager-horticulturalist society where both girls and boys have few constraints on spatial exploration compared to children in Western societies. Mobility was assessed through GPS tracking and interview, spatial ability through pointing accuracy, perspective-taking and mental rotation, and harm avoidance through interview. Few gender differences were found in mobility or spatial ability, although males pointed more accurately to challenging (high sinuosity) routes. Both girls and boys became more harm avoidant about travel risks as they got older, but there were few gender differences in harm avoidance. Schooling was associated with better performance on mental rotation but worse performance on regional pointing accuracy, probably because schooling limits outdoor spatial exploration.

1. Introduction

Gender differences in some spatial cognitive abilities are well-documented in Western studies (Halpern, 2013; Voyer, Voyer, & Bryden, 1995), as are gender differences in play preferences and spatial experiences that might foster those abilities (Baenninger & Newcombe, 1989; Geary, 2010). It is likely that these gender differences are shaped not solely by cultural expectations but also by sexually-dimorphic evolved propensities and preferences. A variety of evolutionary hypotheses have been proposed to explain gender differences in spatial ability (Geary, 1995), but common to many of them is that males gained greater evolutionary benefits from larger ranges. One hypothesis is that this arose from the division of labor during the Pleistocene era, where males functioned primarily as hunters (with increased mobility and navigational demands) and females as childcare providers and gatherers of plant food (low mobility and limited navigational demands (Silverman, Choi, & Peters, 2007). Another hypothesis, which has found support in a variety of non-monogamous species is that navigational challenges associated with mate search and male-male competition selected for better male spatial ability (Gaulin, 1992; Jones, Braithwaite, & Healy, 2003). Both hypotheses emphasize the role that mobility plays in spatial competence and suggest that these are evolved adaptations to the different navigational challenges that males and females faced over our evolutionary history (Cashdan & Gaulin, 2016; Ecuyer-Dab & Robert, 2004a, 2004b).

These evolutionary arguments are consistent with the finding that men occupy larger ranges than women across many different environments and cultures (Cashdan & Gaulin, 2016; Ecuyer-Dab & Robert, 2004a, 2004b; Vashro & Cashdan, 2015), a pattern that

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https://doi.org/10.1016/j.cogdev.2019.100800
Received 8 August 2018; Received in revised form 20 March 2019; Accepted 28 May 2019

begins in middle childhood (Hart, 1979; Matthews, 1992, 1987). However, most of what we know comes from industrialized societies, and as a consequence, biological, environmental, and cultural drivers are often conflated. Although gender differences in children's range size and spatial ability are not unique to Western societies, modern Western societies are highly unusual in matters affecting children's spatial experience. Both girls and boys in forager-horticultural societies are typically given far greater latitude for independent exploration spatially and with dangerous objects (Lancy, 2016), most of their time is spent outdoors, and their time is typically less structured than it is in industrial societies. All of these factors might enhance spatial exploration and training (Cashdan & Gaulin, 2016; Ecuyer-Dab & Robert, 2004a, 2004b).

In order to understand the implications of these cultural differences in spatial experience for the development of spatial cognition, this paper looks at age changes in mobility and spatial ability among the Tsimané, a population of forager-farmers in Bolivia. Like most such populations, Tsimané children (girls and boys) are allowed to roam with few restrictions from about the age of three. We want to see whether (and at what age) gender differences emerge in this population, and whether variation in mobility patterns is related to small and large scale spatial abilities.

In Western societies, boys' greater range size translates into improved spatial knowledge, as evidenced by more detailed and accurate sketch maps of their home ranges (Hart, 1979; Matthews, 1992, 1987; Prezza, 2007). Greater range size also appears to be supportive of female navigational ability in a virtual water maze (Padilla, Creem-Regehr, Stefanucci, & Cashdan, 2017). Coluccia and Louse (2004) have argued that a male advantage in navigation is most frequently found in studies where individuals are allowed to actively control their movements, which suggests that gender differences in natural mobility may also be relevant in understanding differences in navigational ability.

Mobility may also affect performance on tests of object-based spatial transformations such as mental rotation, although this relationship is less clear, and these spatial abilities may derive from different selection pressures. Many studies have found small or no direct relationships between large-scale and small-scale spatial abilities (Hegarty & Waller, 2005), although they may be indirectly related through other spatial skills (Allen, Kirasic, Dobson, Long, & Beck, 1996). In a comprehensive analysis, Hegarty et al. (2006) conclude that large and small-scale spatial abilities are correlated but also partially dissociated.

Because gender differences in mental rotation are widely reported, we are examining the relationship of mobility to mental rotation ability as well as to tasks reflective of navigation ability. Some studies have shown that larger range size is associated with better performance on a block design task in African children (Munroe & Munroe, 1971; Nerlove, Munroe, & Munroe, 1971) and with mental rotation ability in adult males (Ecuyer-Dab & Robert, 2004a, 2004b; Vashro & Cashdan, 2015). However, it would be reasonable to expect mobility patterns to affect navigation (a large-scale ecologically-relevant spatial task) more directly than more abstract small-scale spatial tasks like mental rotation, which may be more affected by formal education.

We are also examining the role harm avoidance may play in shaping gender differences in travel patterns and spatial performance. Females are more harm avoidant than males about physical risks (Byrnes, Miller, & Schafer, 1999) and have more wayfinding anxiety (Lawton & Kallai, 2002; Schmitz, 1997). These gender differences may have implications for mobility, because travel, particularly over large distances and novel terrain, carries risks. Gender differences in travel patterns may, in turn, affect navigation. In virtual environment studies, women have demonstrated more caution in exploring new environments (more pausing and revisiting previous locations), which led to poorer navigational performance (Gagnon, Cashdan, Stefanucci, & Creem-Regehr, 2016, 2018). We want to see whether the Tsimané children's environment and freedom to explore might reduce these gender differences.

Our focus is on middle childhood and adolescence. There remains disagreement about whether gender differences in spatial ability appear in younger children, with some studies reporting a male advantage in mental rotation in infants and preschoolers (Levine, Huttenlocher, Taylor, & Langrock, 1999; Moore & Johnson, 2011; Quinn & Liben, 2014), while others find none (Frick, Hansen, & Newcombe, 2013; Frick, Möhring, & Newcombe, 2014). However, there is broader agreement that gender differences in mental rotation ability appear reliably in middle childhood (Neuburger, Jansen, Heil, & Quaiser-Pohl, 2011; Voyer et al., 1995), in parallel with emerging gender differences in range size. Middle childhood (approximately age 6–11) is marked by both hormonal changes (adrenarche) and social ones, as the child engages with a wider social world (Hewlett, Fouts, Boyette, & Hewlett, 2011; Lancy & Grove, 2011) and spends time farther from home. Gender differences in range size emerge around this time and increase with age, both in Western populations (Hart, 1979; Matthews, 1992, 1987) and cross-culturally (Whiting & Edwards, 1988). Adolescence may increase these gender differences further. Schlegel (1995) has argued that adolescence in preindustrial societies is primarily "a time of preparation for adult reproductive life," which suggests that gender differences in behaviors related to mating and parenting would increase at this age. Adolescents also engage more fully in gendered adult work (Bock, 2005; Kramer & Greaves, 2011; Lew-Levy, Lavi, Reckin, Cristóbal-Azkarate, & Ellis-Davies, 2018) than younger children, including responsibilities associated with household production and allocare support (Bock, 2002; Kramer, 2005). For both of these reasons (reproductive maturity and task behavior) we expect gender differences to increase during adolescence.

Previous work highlights the importance of mate seeking in understanding gender differences in range size among the Tsimané. Miner, Gurven, Kaplan, and Gaulin (2014), using retrospective data on number of places visited during three life stages, found that Tsimané males had larger ranges than Tsimané females only during adolescence (the mate-seeking years). Our study attempts both to replicate their findings using complementary methods (including GPS tracking), and to investigate the implications for gender differences in spatial ability. If larger ranges require greater navigational competence and provide greater environmental experience, we may see gender differences in navigational performance emerge during Tsimané adolescence. On the other hand, if the greater freedom allowed girls and boys in the early years promotes similar spatial learning experiences through middle childhood, gender differences in spatial ability may be expected to remain small.

Further complicating expectations is the nature of the habitat itself, which obscures distal landmarks and sun position through dense tropical forest vegetation and frequent cloud cover. Males preferentially use such cues, which provide information useful for a survey (birds-eye-view) knowledge of the landscape, while females are more likely to use their position relative to local landmarks, which is more conducive to a route strategy (Choi & Silverman, 1996; Dabbs, Chang, Strong, & Milun, 1998; Galea & Kimura, 1993; Moffat, Hampson, & Hatzipantelis, 1998; Sandstrom, Kaufman, & Huettel, 1998; Ward, Newcombe, & Overton, 1986). Trumble, Gaulin, Dunbar, Kaplan, and Gurven (2016) found that Tsimané men and women were equally accurate in pointing to other villages in the region, which they suggest may be because the habitat does not provide the kind of cues that give males an advantage in navigation. It remains an open question; both because there are other gradient cues important in providing survey knowledge, such as river currents, and because pointing accuracy could reflect familiarity as well as ability. In order to better assess differences in navigational performance, we measured not only pointing accuracy, but also spatial perspective taking in real space over the landscape.

The analysis proceeds in two stages. We first document the pattern of age changes in harm avoidance, mobility, and spatial ability in girls and boys, looking separately at middle childhood and adolescence. Because our interest in mobility lies in its role in spatial experience and learning, we consider both daily distance traveled and the shape (sinuosity) of travel paths, as assessed by GPS, as well as regional mobility (annual and lifetime places visited) assessed through interview. We use two measures of large-scale spatial ability: accuracy in pointing to other places in the region, and the ability to imagine oneself in another location and point accurately to a third (spatial perspective-taking). Small-scale spatial transformation was assessed with a mental rotation task, and harm-avoidance through interview.

We then examine the following hypothesized relationships among these variables. We expected greater harm avoidance to reduce navigational experience, operationalized here as shorter daily travel distance and travel on straighter paths. We also expected more complex routes to be associated with better performance on the large-scale spatial tasks (pointing accuracy and perspective-taking), and mental rotation ability (an abstract task) to be more associated with performance on other abstract tasks (Raven's Progressive Matrices and reading) that are fostered by formal schooling.

1.1. *Study population*

Tsimané territory extends through the Andean foothills to the Moxos savanna in the Beni Department of the Bolivian Amazon. Approximately 500 Tsimané people inhabit the study village located along the Maniqui River, a tributary to the Amazon river, where the data were collected. The Tsimané described is this paper live between 60 and 70 km (crow's flight) from San Borja and Yucumo, two market towns with greater access to wage labor opportunities and commercial goods. Travel to and from the market towns is mostly conducted by boat and, depending on seasonality and river depth, can take between 13 to 20 h (using an outboard motor).

Daily life for Tsimané children depends largely on age (Stieglitz, Gurven, Kaplan, & Hooper, 2013). For both genders, common domestic and alloparenting tasks are delegated at young ages, particularly lower-skill and lower-strength tasks that young children can perform efficiently (Gurven & Kaplan, 2006). As children age, they continue assisting their families with foraging tasks and begin fishing and participating in higher skill-based activities. By 9 years old, Tsimané children are helping with gardening, foraging, and other domestic tasks (e.g. collecting water). Children are increasingly asked as they age to participate in tasks that require more skills and strength. Hunting, for example, encourages children (mostly boys) to accompany fathers in nonproductive "apprenticeship" roles in the forests; however, children of both genders often assist in carrying items home after a hunt. All these activities require both boys and girls to spend considerable time walking and working in the densely forested areas surrounding their villages.

Tsimané children attend school, but Tsimané formal education should be classified as performing at the lower end of a graded "educational continuum" relative to schools in industrialized countries (Davis, 2014). Classes in Tsimané elementary schools are conducted roughly four hours per day, and five days per week. Cumulatively, the total number of hours per year of schooling experienced at any age for Tsimané is well below levels in many other countries: Bolivian children between 1st and 5th grade attend over 50% fewer hours and days of school than their American peers (Davis, 2014). This allows for considerable time outside of school hours to engage in subsistence and foraging behaviors, as well as play (Stieglitz et al., 2013). Thus, even with the introduction of schools and settlements, Tsimané children are more independent, explore a broader physical environment at younger ages, and frequently participate in unsupervised subsistence activities. These behavioral differences provide navigational challenges during childhood and adolescence to both girls and boys that may lead to a reduction in gender differences in spatial cognitive differences.

2. Methods

The study was conducted with 121 children (6–18 years, 51% female, 56% literate) from one upriver Tsimané community. The village was chosen because of its larger population. However, like other Tsimané villages, much of the community is highly dispersed along a smaller tributary. Data collection required visiting individual households to conduct interviews and recruit subjects. The distance of homes from our project area (village center) ranged from 0.1 km to 8 km away (M = 2.3 km, Mdn = 2.9 km) and often requires river crossings with small canoes. Infrequent, but torrential rains can occur during the dry season (May through August). In some cases, visiting certain homes would be delayed for multiple days due to weather.

In all, this study collected data on 58% of the children listed on the census as alive in 2015 by the Tsimané Health and Life History Project (Gurven, Stieglitz et al., 2017). Though the census is updated by the project every few years, migration and mortality made determining the exact number of children in and around the villages difficult.

Table 1
Study sample characteristics.

	Total Sample		**Middle childhood (6-11)**		**Adolescence (12-19)**	
	N	Mean (SD)	N	Mean (SD)	N	Mean (SD)
Sex (1=boys, 0=girls)	121	50.4% girls	80	50% girls	41	51% girls
Age (yrs)	121	11.00(3.6)	80	8.90(2.1)	41	15.10(1.8)
Harm avoidance (0-3)*	121	1.19(0.5)	80	1.11(0.4)	41	0.31(0.3)
Mobility						
Average daily distance (km)	50	5.26(2.6)	26	5.21(2.6)	24	5.31(2.7)
Daily sinuosity	50	0.24(0.9)	26	0.24(0.2)	24	0.24(0.6)
Annual mobility (# unique visits)	114	1.4(0.7)	74	0.26(0.6)	40	0.68(0.9)
Lifetime mobility (0-90)	114	13.3(11.0)	74	12.9(12.3)	40	14.1(8.1)
Spatial ability						
Pointing accuracy (degree error)	95	40.02(21.5)	58	43.57(22.3)	37	34.46(19.0)
Perspective taking (degree error)	102	66.90(30.0)	65	69.36(28.4)	37	62.6(32.4)
Mental rotation (% correct)	63	0.75(0.1)	42	0.69(0.1)	21	0.85(0.2)
Other cognitive tasks						
Raven's (RCPM) (0-36)	59	14.47(.7)	29	11.6(1.9)	30	17.3(1.7)
Reading Comprehension (0-5)	59	1.8(.24)	29	0.59(.95)	30	2.9(1.8)

2.1. Age

Ages for every child were collected and cross-validated through three channels: individual interviews, parent interviews, and census data. Children were also categorized into one of two developmental stages, middle childhood (6–11) and adolescence (12–18) (Table 1). As noted in the introduction, these stages are differentiated by distinct physical, social, and hormonal changes. Other considerations for age groupings came from Tsimané girls age of menarche (Gurven, Stieglitz et al., 2017; Walker et al., 2006) and voice change in boys (Hodges-Simeon, Gurven, Cárdenas, & Gaulin, 2013). Our small sample size precluded a finer age breakdown.

2.2. Harm avoidance

We assessed harm avoidance associated with physical harm, spatial anxiety, and social anxiety. For physical harm, we asked the following two questions: (1) Do you get worried you will see or be hurt by animals (e.g., snakes, jaguars, leopards) when you are traveling in the forest? (2) Do you worry about being injured when you are traveling alone? Answers (rarely = 0, sometimes = 0.5, often = 1) were averaged to create a scale of harm avoidance from 0-1. To assess spatial anxiety we asked (3) Are you concerned that if you take a new route, you might get lost? Answers (rarely = 0, sometimes = 0.5, often = 1). Finally, to assess social anxiety we asked (4) When you visit communities that you don't know well, do you feel safer if you go with other people or do you feel comfortable going alone? Responses were coded 1 = comfortable going alone, and 2 = prefer to go with others.

2.3. Daily mobility (average daily distance, farthest distance, and track sinuosity)

Participants were given QStarz BT-Q1000XT GPS data loggers on randomly selected days during the study period. Each GPS unit was placed inside a small, water-resistant travel case, and secured to a lanyard that each child wore around their neck. After three days, participants returned the device and the individual's tracks were recorded using QStarz GIS software on a laptop. Children were then asked to recall places visited, time spent out of the community and purpose of travel (e.g. work, school, or play) during the tracking period. The following variables were calculated from the tracks data: (a) average daily distance traveled; (b) farthest distance traveled each day, and (c) track sinuosity, the mean sinuosity of the individual's daily tracks. Sinuosity is a measure of whether the path is straight or meandering and was used as an indirect measure of the complexity of travel. The main road to the market town has low sinuosity, whereas tracks with high sinuosity are more likely to indicate travel on smaller paths or tributaries, exploratory travel, or travel through densely-wooded jungle terrain.

Each GPS unit required approximately two hours of charging using a solar panel and 12-volt battery. There was variable availability of solar and stored battery power due to cloud cover and tropical storms, and on some days weather conditions also interfered with the ability of the units to maintain contact with satellites. Of the 68 individuals we tested, we discarded 14 individuals with unreliable and incomplete data due to poor battery charging, incomplete tracks, and damaged GPS units.

To confirm that the sub-sample for our remaining GPS data (N = 50) was representative of the entire sample, we checked means, variance, and effect sizes for every variable in our study between the two groups (i.e., has GPS data, has no GPS data). There was no significant difference between the groups by age (d = 0.18), gender (d = 0.19), or between groups binned by developmental phases (i.e., middle childhood and adolescence) (d = 0.12). The samples also showed non-significant differences for mobility measures, spatial measures, and on other cognitive tasks.

2.4. *Annual mobility*

Participants were asked to recall all full day and overnight trips taken during the previous 12 months (its location, purpose of the visit, and who they went with). The measure used in analyses is the number of unique places mentioned. Most young children had little to no travel to other villages, and overnight trips are infrequent.

2.5. *Lifetime mobility*

A list of 30 locations within the region was used to create an ordinal measure of longer-term regional mobility. The measure reflects both number of places and frequency of travel to them. For each location, participants were asked whether they had ever been there, and if so, whether they had been once, a few times, or many times. This formed a 30-item scale with 4 levels (from 0–3) for each item, and the sum formed our measure of lifetime mobility.

2.6. *Pointing accuracy*

As one measure of navigational ability, participants were asked to point to 10 known places in the region using a Brunton compass mounted on a tripod, with the sight extended to act as a pointer. Each participant was trained to point the sight as they would their own finger, and two to three practice rounds were conducted with nearby, visible targets. Error was calculated as the difference between the correct bearing and the pointed bearing. Because gender differences in spatial ability often appear only on more difficult tasks, we also calculated the distance to the location and the sinuosity of the path needed to arrive there, in order to see whether either of these was associated with pointing accuracy. Sinuosity was calculated as the ratio of each location's travel distance (total km from starting pointing to target locations on rivers and roads) divided by bird's flight distance (Fig. 1). In order to distinguish this measure from the sinuosity of an individual's daily travel, we are referring to this as "pointing route sinuosity."

2.7. *Perspective-taking*

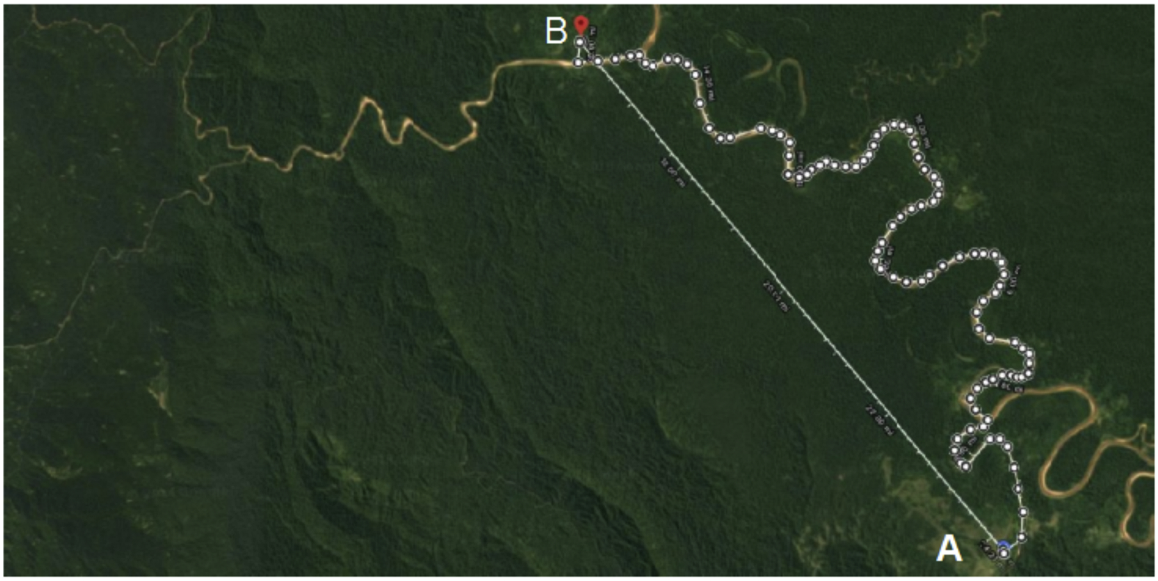
Successful navigation presents two challenges: (1) knowing what landmarks (or environmental features) will look like from another perspective, and (2) knowing how their relative positions will appear from different viewpoints. In order to assess skill at the second of these, we followed the pointing task with a perspective-taking task. The task asked children to imagine that they were not in their current village (A) but in a different location (B), and to point from there to a third location (C). Nearby objects and features, visible to the child, were used for training, and the task itself used four locations, between 5 and 15 km away, that the child had pointed to in the previous pointing task. Error was again measured as the difference between the correct and the pointed bearing. The protocol and training procedure are described in more detail in Supplementary Materials.

2.8. *Mental rotation*

In our previous work with foragers, we found traditional mental rotation tasks to be difficult to explain and implement, and so for this study we used a two-dimensional mental rotation task of our own design, which we have used successfully in previous studies with foraging populations (Vashro & Cashdan, 2015; Fig. 2). The task uses two sets of images presented in separate blocks, one of a figure with an outstretched arm (one block each of front and back bodies), the other of a bent twig. The images are displayed on a touchscreen, with the rotated target image at the top of the screen (images were rotated in increments of 60 degrees and displayed in random order) and two images at the bottom, one of which is the same as the target and the other its mirror image. Participants are asked to touch the one that is the same as the target. As a way to explain ``same" and ``different" non-verbally, training trials show the target image at the top rotating to match the orientation of the correct image. As with traditional mental rotation tasks, both adults and children in foraging societies are less accurate and respond more slowly as the degree of rotation increases, which indicates that the task measures what it was designed to measure. There is a ceiling effect in accuracy when using this task with Western children of this age (although the increasing function with response time remains) but that was not a problem with the Tsimané in this task, nor with our other cognitive measures.

2.9. *Other cognitive tasks*

Years in school was collected from children in the sample. However, in previous research with the Tsimané, formal schooling has been shown to significantly enhance performance on abstract reasoning tasks. Given the variable quality of schools in the region and frequent class cancellations, performance on abstract reasoning tasks act as a more accurate measure of educational exposure.



Imagery ©2018 Landsat / Copernicus, Map data ©2018 Google 5 mi

Fig. 1. GPS map showing (A) subject's location to (B) pointing accuracy target location. The straight line represents bird's flight from (A) to (B) with a total distance of 13.38 km. The dotted line is actual travel distance from (A) to (B) with a total distance of 25.87 km. Pointing route sinuosity (1.93) is the ratio of travel distance divided by bird's flight distance.

Fig. 2. Images from the two mental rotation tasks used in this study. The participant was asked to identify which of the two images on the bottom matched the rotated object above. They made their selection using a touch screen laptop computer.

Relative to schools in industrialized countries, schools among Tsimané groups operate, like many schools in the developing world, at the lower end of a graded educational continuum (e.g., schools operate for fewer hours, difficulties with travel and resources can limit class time, limited teacher resources and training, high student to teacher ratios). Previous work among the Tsimané has demonstrated that 'years in school' does not accurately reflect time spent in school. Both Raven's Colored Progressive Matrices (RCPM) and reading proficiency have been shown to be the most highly correlated with continuous school involvement. In order to examine the influence of formal education on spatial cognition, therefore, we used data on the following tasks that were collected for a previous study of Tsimané education (Davis, 2014; Gurven, Fuerstenberg et al., 2017):

2.10. Raven's Coloured Progressive Matrices (RCPM)

RCPM is a nonverbal test of abstract reasoning without culturally loaded references, which assesses cognitive performance by asking participants to identify and complete a logical pattern among a matrix of geometric shapes. Previous work among the Tsimané has shown that tests of fluid intelligence are positively associated with schooling (Gurven, Fuerstenberg et al., 2017). Unlike years in school, which provides a rough measure of educational investment, RCPM and reading ability have been shown to be better indicators of time spent in school within Tsimané villages (Davis, 2014). Our unpublished findings further demonstrate that RCPM scores can be used as a proxy for access and quality of schooling, but they cannot be used to measure individual cognitive ability.

The test and its objectives were explained by a Tsimané administrator in the native language, whereupon the participant was asked to examine the pattern and point to the piece that fits into the missing space.

2.11. Reading proficiency

Overall, educational quality for the Tsimané is still far below international standards. Bolivian children between 1st and 8th grade have extremely low literacy levels compared to similarly aged peers in the US (Zeng et al., 2012). Despite having a formally written language with native words for numbers, Tsimané children do not become familiar with Arabic numerals or the alphabet until three years later than children in industrialized populations (Piantadosi, Jara-Ettinger, & Gibson, 2014; Reyes-García et al., 2016).

To assess reading ability across all ages, study participants were given a reading test to assess literacy and as a proxy to time invested in schooling for age. Questions for the reading assessment were short but were derived from the Iowa Test of Basic Skills grade 3 (Hoover et al., 2003), with the scoring system adapted to the number of questions and type of questions used in the assessment. Each participant begins with the grade 3 reading assessment, with follow up questions becoming easier or harder depending on performance.

Reading assessments were scored on a Likert scale from 0 to 5 to ascribe a literacy level to each participant, which was cross-validated between two researchers.

0: Cannot identify uppercase/lowercase letters
1: Can identify some uppercase/lowercase letters
2: Can identify letters and potentially sound small words
3: Can comfortably sound small words and potentially short sentences
4: Can read short sentences with few mistakes (2–5 errors)
5: Can read short sentences with no mistakes (0–1 errors)

2.12. Factor score

Because the mental rotation task, RCPM and reading require abstraction without ecological context, it was plausible that basic dimensions of performance on those tasks were related, rather than a function of independent faculties, and we found this to be correct by including these measures in an exploratory factor analysis. Initial data screening showed no out-of-range values. The minimum amount of data for factor analysis was satisfied, with a final sample size of 218 (using listwise deletion), providing a ratio of over 12 cases per variable. Secondly, the Kaiser-Meyer-Olkin measure of sampling adequacy was 0.68, above the commonly recommended value of 0.6, and Bartlett's test of sphericity was significant ($\chi2$ (6) = 69.82, $p < 0.001$). The diagonals of the antiimage correlation matrix were also all over 0.5, and the communalities were all above 0.3. Higher scores indicate more school exposure and greater abstract problem solving abilities.

2.13. Statistical methods

To understand potential individual and ecological differences affecting navigational and spatial ability, we first assessed effects of gender and age on each of the variables of interest. We then used linear regression. logistic regression, and a linear mixed effects model to determine associations between harm avoidance, child development, and gender. Linear regression and a linear mixed effects model was used to determine associations between spatial ability and environmental factors. Second, all data were aggregated into a general linear model to determine how individual mobility affected spatial ability and other cognitive tasks. As described above, factor analysis was engaged to reduce the dimensionality of the abstract cognitive tasks and compute a single composite score. Finally, generalized linear models were produced to assess interaction effects between individual levels of mobility and outcomes on spatial cognitive tasks. All statistical analyses and were performed in R version 3.4.3 (R Foundation for Statistical Computing, Vienna, Austria). Graphical representations are produced in R package ggplot2.

2.14. Outliers

Tracks from two females were removed from the GPS data because they had both traveled extensively in a motorized canoe, and two others were removed because they lived in different communities. Their removal did not significantly affect the results.

3. Results

Table 1 gives summary information about the sample and all variables of interest. The first set of analyses below show how mobility, harm avoidance, and spatial performance change with age in girls and boys, and whether these variables differ by gender. This is followed by evaluations of the hypothesized relationships: whether harm avoidance leads to reduced mobility, and whether greater or more complex travel patterns are associated with better spatial performance.

3.1. Descriptives

Mean ± SD age for all 121 children was 11.00 ± 3.5 (see Table 1), and the mean age was similar for girls (M = 11.16, SD = 3.75) and boys (M = 10.83, SD = 3.43), t(142) = 0.51, p = 0.61, d = 0.09. The sample size for middle childhood (N = 80) is larger than the sample for adolescence (N = 41). However, the number of girls and boys in each developmental stage was also similar, both in middle childhood t(65) = -0.61, p = 0.55, d = 0.15, and in adolescence t(52) = 0.50, p = 0.62, d = 0.14.

3.2. Harm avoidance by age and gender

Boys and girls reported similar levels of harm avoidance regarding physical harm (threat from injury and from dangerous animals), t(119) = 0.44, p = 0.664, d = 0.06. They were also similar in spatial anxiety (concern about getting lost), t(65) = -1.47, p = 0.148, d = 0.36. They differed only in reported social harm avoidance (feeling safer going with others to communities they don't know well), with girls being more concerned (M = 1.61, SD = 0.06) than boys (M = 1.38, SD = 0.06), t(119) = 2.50, p = 0.014, d = 0.47.

We next looked at whether harm avoidance changed with age, by comparing children categorized into one of two developmental stages, middle childhood (boys = 40, mean age = 8.88, SD = 2.20; girls = 40, mean age = 8.92, SD = 2.15) and adolescence (N = 41, boys = 20, mean age = 14.75, SD = 1.55; girls = 21, mean age = 15.43, SD = 1.99). Age and gender were related to physical harm and social harm, but not to spatial anxiety.

Physical harm: A two-way analysis of variance yielded a main effect for increased harm avoidance during adolescence, F(1, 108) = 17.86, $p < 0.001$, such that the average fear of physical harm was significantly higher for adolescents (M = 1.48, SD = 0.51) than for those in middle childhood (M = 1.04, SD = 0.39). The main effect of gender was non-significant, F(1, 68) = 2.24, $p > .05$. However, the interaction effect was significant, F(1, 68) = 0.66, p = 0.008, indicating that the increase with age was greater for boys than girls.

Social harm: Children's developmental stage and gender were subjected to direct logistic regression (Table 2) to assess whether boys or girls reported greater social harm avoidance during adolescence compared to those in middle childhood. The binary dependent variable was coded as positive [coded 1–2]. The full model containing both predictors and the interaction of gender by developmental stage was statistically significant, $\chi2$ (df 3, n = 121: middle childhood = 80, adolescence = 41) 155.95, p = 0.008.

As shown in Table 2, neither gender (OR = 0.74) nor developmental stage (OR = 2.90) significantly related to social anxiety. Though there is no overall effect of either gender or developmental stage, there is a crossover interaction. While the increase in fear of physical harm was greater for boys than for girls, the opposite was the case for social harm: We see a decrease in reported social anxiety among boys during adolescence, while an increase is observed among adolescent girls (OR = 0.14; p = 0.02).

3.3. Mobility and exploration by age and gender

The average daily distance traveled by boys was 5.28 ± 2.58 km and for girls it was 5.23 ± 2.63 km (N = 50). Fig. 3 shows examples of two tracks. Though the variance of daily distances was somewhat greater for boys, t(87.65) = 4.62, p = 0.052, d = 0.53 (Fig. 4), there was not a significant difference for mean daily distance traveled by age, $\beta = 0.11$, p = 0.466, 95% CI [-0.14, 0.30], or gender, $\beta = 0.31$, p = 0.833, 95% CI [-01.40, 1.73], (d = 0.02; Fig. 5).

The other mobility measures also show little or no difference between boys and girls. Across the entire sample, daily sinuosity of routes taken (d = 0.10), reported annual mobility (d = 0.24), and reported lifetime mobility (d = 0.14) produced only small non-significant differences between boys and girls. While the mobility patterns for girls and boys appear to be nearly identical across the mobility variables, our sample size (N = 50) for the daily GPS tracking data, used to calculate daily distance and sinuosity, is smaller than for the other mobility variables, and is unable to detect small effects (we are only able to detect an effect as large as a 1.2 SD difference in means of girls and boys, with 80% power and a p-value of 0.05).

3.4. Spatial ability by age and gender

Age, $\beta = -0.37$, p = 0.001, 95% CI [-3.37, -0.08], but not gender, $\beta = -0.14$, p = 0.14, 95% CI [-14.26, 2.06] predicted overall mean performance on the pointing accuracy task for boys and girls performance (Fig. 6). Mean pointing accuracy error for girls was 31.53 ° and 32.44 ° for boys.

However, pointing accuracy targets varied in distance, pointing route sinuosity, and subject familiarity. Because gender differences in spatial ability may become more apparent with more difficult tasks, we also considered that locations that were less familiar, farther away, and accessed through more meandering paths would be more challenging to point to. We therefore analyzed the gender

Table 2
Logistic regression for gender and developmental stage predicting higher reported social anxiety (harm avoidance).

Predictor	Df	Wald $\chi2$	P	Wald 95% CI limits
Gender	1	0.50	0.53	0.31–1.78
Developmental stage^	1	3.12	0.08	0.89–9.43
Gender × Developmental stage*	1	5.27	0.02	0.03–0.75

* $p < 0.05$.
^ $p < 0.10$.

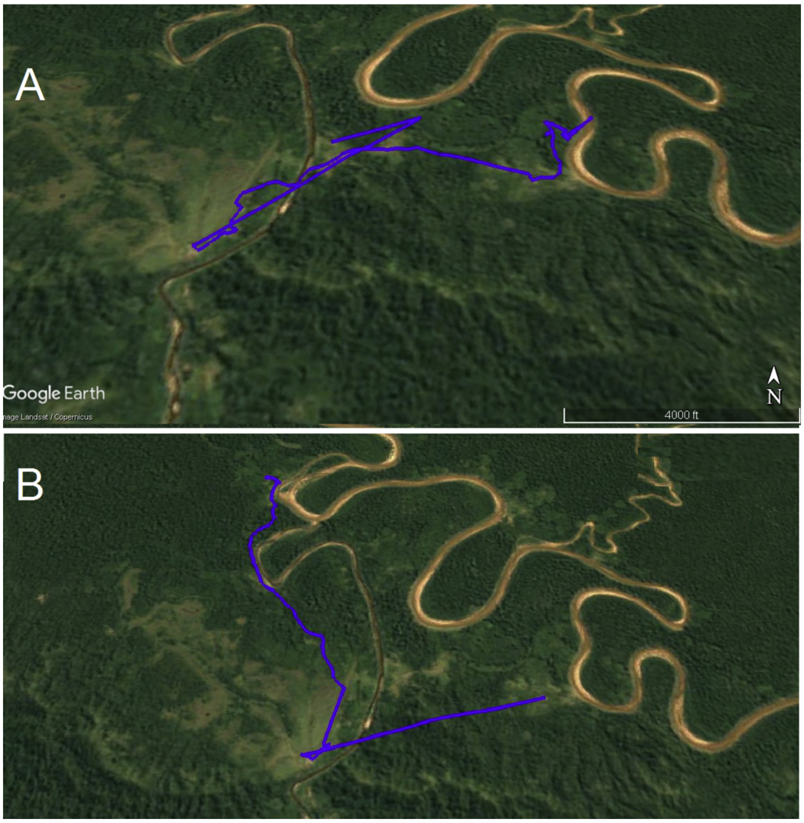


Fig. 3. This shows a travel path for (A) a 7 year old boy (~12 km) and (B) an 11 year old girl (~9 km).

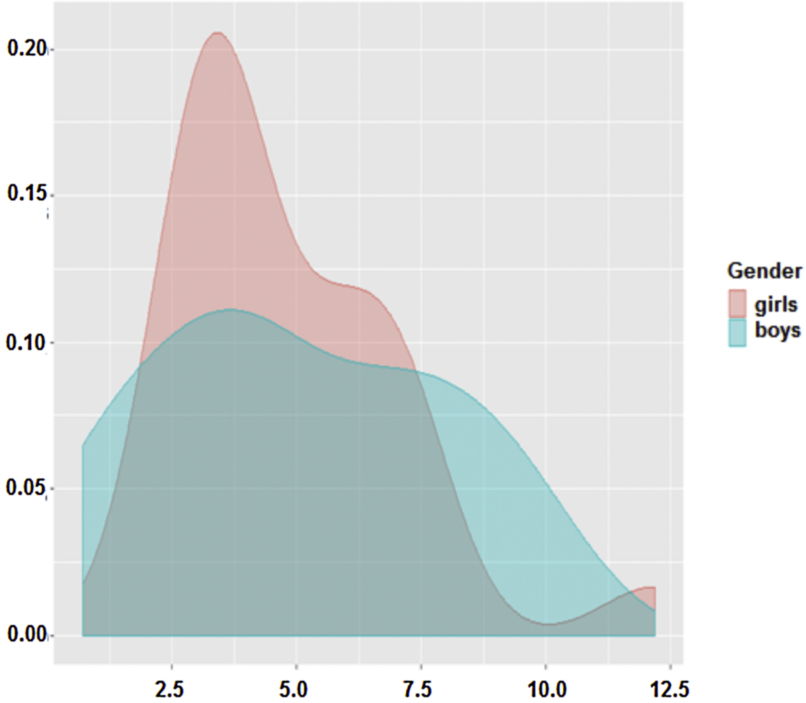


Fig. 4. Density plot of the average daily distance traveled by girls (red) and boys (blue) in two Tsimané villages (N = 50). There is greater variance in average daily distance among boys than girls, but no difference in means.

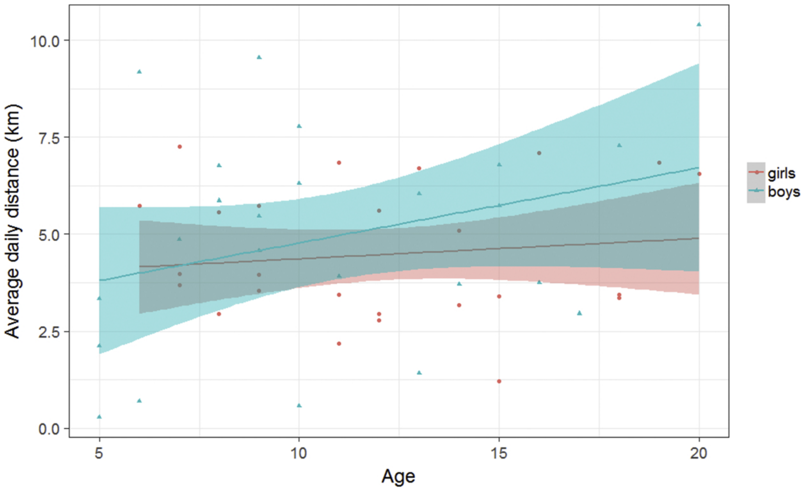


Fig. 5. Age by average daily distance traveled by girls (red) and boys (blue) in two Tsimané villages (N = 50). There is no significant gender difference in daily mobility patterns for children between the ages 6–19 years. Variance in travel distance is greater for boys across the sample.

difference for each target location separately, to see whether the gender difference was larger with greater distance or pointing route sinuosity.

Looking at individual targets within the pointing accuracy task, small to moderate effect sizes were found for four of the ten targets (Fig. 7). To identify predictors of increased error, data were aggregated into a linear mixed-effect model with age, gender, pointing route sinuosity, bird's flight distance, familiarity with the location, and a dummy variable to identify the market towns. Individuals were entered as a random effect due to non-independence of the variable. Pointing route sinuosity and age were the greatest predictors of lower error on the pointing accuracy task (Table 3), with a trend towards improved performance among boys, as well as familiarly with the target.

The perspective-taking task (pointing accuracy from an imagined location) showed a trend towards better performance with age β = -0.18, p = 0.089, 95% CI [-3.01, 0.22] but there was no gender difference, β = -1.62, p = 0.176, 95% CI [-19.55, 3.63] (Fig. 8). Likewise, age also predicted better accuracy in mental rotation, β = 0.32, p < 0.001, 95% CI [0.00, 0.01], but no significant effect of gender was found across children sampled, β = 0.08, p = 0.29, 95% CI [-0.02, 0.05], (Fig. 9).

3.5. School and other cognitive tasks by age and gender

Controlling for age, there was no significant difference between boys and girls for years in school, β = 0.12, p < 0.41; 95% CI [-0.84, 0.41]. Raven's Colored Progressive Matrices (RCPM) scores increased with age, β = 0.28, p < 0.001; 95% CI [0.09, 0.30], and were higher among boys, β = 0.17, p = 0.02; 95% CI [0.15, 2.03], (Table 4). Reading ability is a proxy for schooling and is a

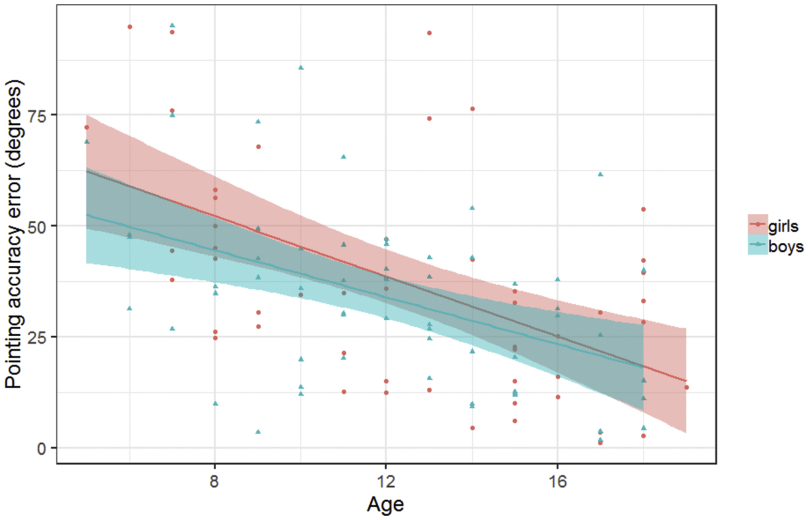


Fig. 6. Age by average pointing accuracy error among for girls (red) and boys (blue) in two Tsimané villages (N = 95).

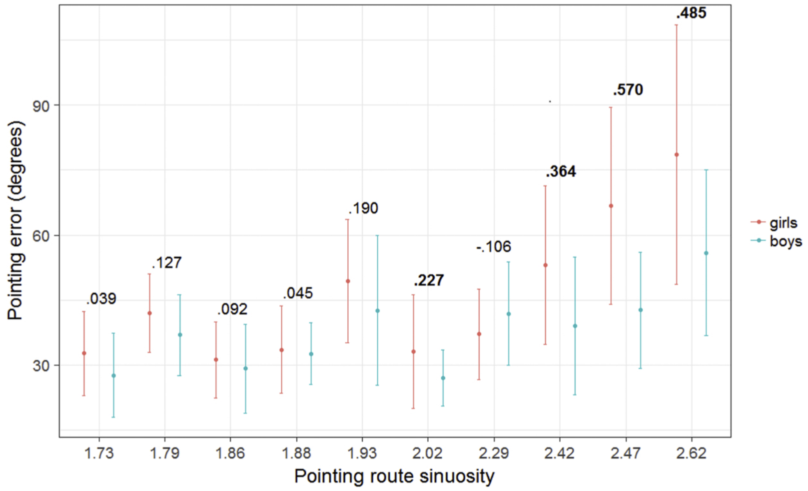


Fig. 7. Results by gender for 10 pointing accuracy targets among Tsimané children (N = 95) organized by sinuosity of travel path. Error bars depict mean 95% CI (t-distribution). Effect size (Cohen's d) for error by gender is reported above each target.

strong predictor of performance on the RCPM in the sample. Age, β = 0.33, p < 0.001; 95% CI [0.22, 0.44], but not gender, β = 0.33, p = 0.24; 95% CI [-0.33, 1.31], predicted better reading scores.

Controlling for age and gender, the mental rotation task was highly correlated with both RCPM, r(54) = 0.38, p = 0.03, and reading r(54) = 0.36, p < 0.001. Mean error during middle childhood may include some children who were still not able to fully comprehend the task, though no one who scored below 40% correct was included (Fig. 9). A single factor loading of the tasks (see Methods for details about the model) explained 68.64% of the variance, producing a composite score of "school-enhanced skills." School-enhanced skills had an expected age effect, β = 0.68, p < 0.001; 95% CI [0.24, 0.10], and no effect by gender, β = 0.18, p = 0.16; 95% CI [-0.14, 0.79].

3.6. Harm avoidance and spatial ability

Pointing error was associated with greater fear of social harm, β = 0.32, p = 0.001; 95% CI [5.55, 21.91], and fear of physical harm, β = 0.25, p = 0.041; 95% CI [0.46, 21.20], when controlling for age and sex. Harm avoidance showed no consistent relationship with the mobility variables. Spatial anxiety was unrelated to either mobility or spatial ability.

Table 3
Results from an aggregate mixed-effects model predicting error on the pointing accuracy task among Tsimané children (N = 96).

	B	*SE B*	*T*	*P*	*95% CIs*
Age	**-1.69**	**0.38**	**-4.44**	**< 0.001**	**-2.44 - -0.94**
Gender	-5.00	2.84	-1.75	0.08	-10.57 - 0.58
Pointing route sinuosity	**21.95**	**6.18**	**3.54**	**< 0.001**	**9.80 - 34.10**
Familiarity (has been to the location)	-1.13	0.65	1.74	0.08	-0.15 - 2.41
Market town (dummy variable)	-1.72	4.31	-0.40	0.80	-10.18 - 6.74

Negative beta for gender indicates greater pointing error for females, positive beta for sinuosity indicates greater pointing error for locations with more sinuosity, negative beta for the variable familiarity indicates lower pointing error.

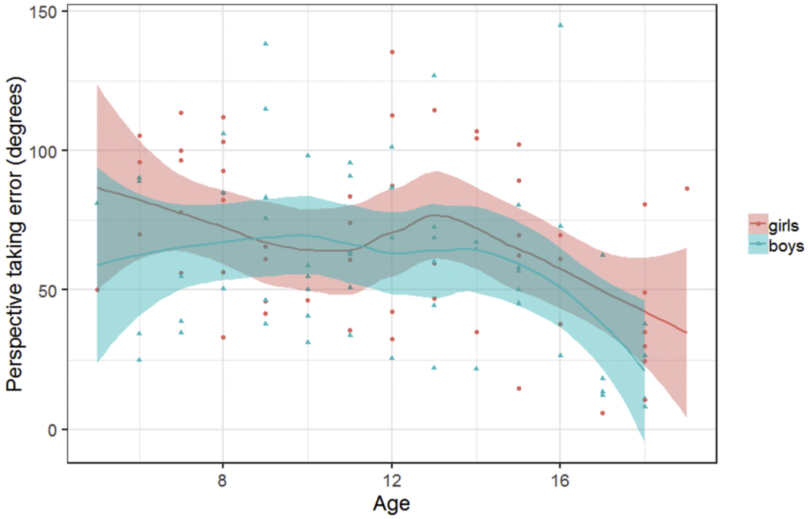


Fig. 8. Loess curve with 95% CI for age by average perspective taking pointing error among girls (red) and boys (blue) in two Tsimané villages (N = 102) trended toward better performance but was not statistically significant.

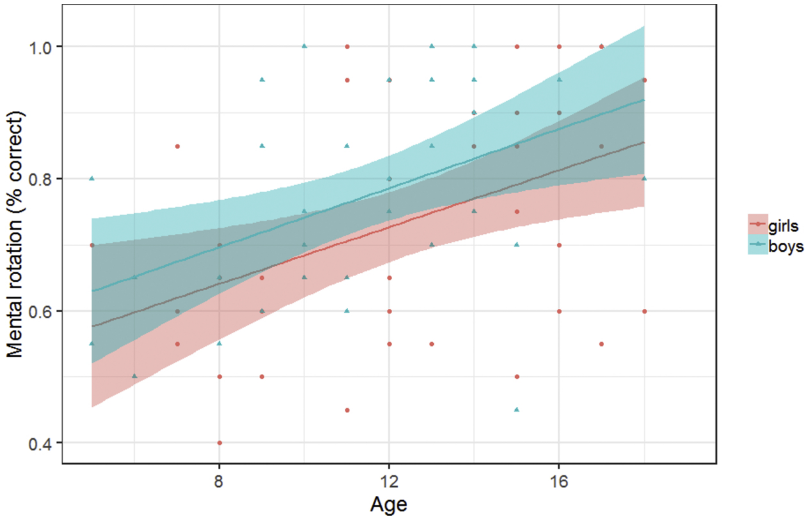


Fig. 9. Percentage of correct answers on mental rotation for girls (red) and boys (blue) in two Tsimané villages (N = 63).

Table 4
Mean, standard deviation and effect sizes for Tsimané children on three cognitive tasks.

	Mean (SD)		Sample size		Cohen's *d*
	Girls	Boys	G	B	
Mental rotation (% correct)	0.76 (0.2)	0.78 (0.2)	50	40	−0.12
RCPM	13.41 (4.5)	15.92 (6.0)	34	25	−0.47
Reading ability (0-4)	1.6 (1.8)	2.1 (2.0)	34	25	−0.26

3.7. Does Greater environmental experience enhance spatial performance?

Mobility and education are both environmental influences that might be expected to affect spatial performance, but we are considering them separately because we anticipate that mobility would have a greater positive influence on the naturalistic navigation measures (pointing and perspective-taking).

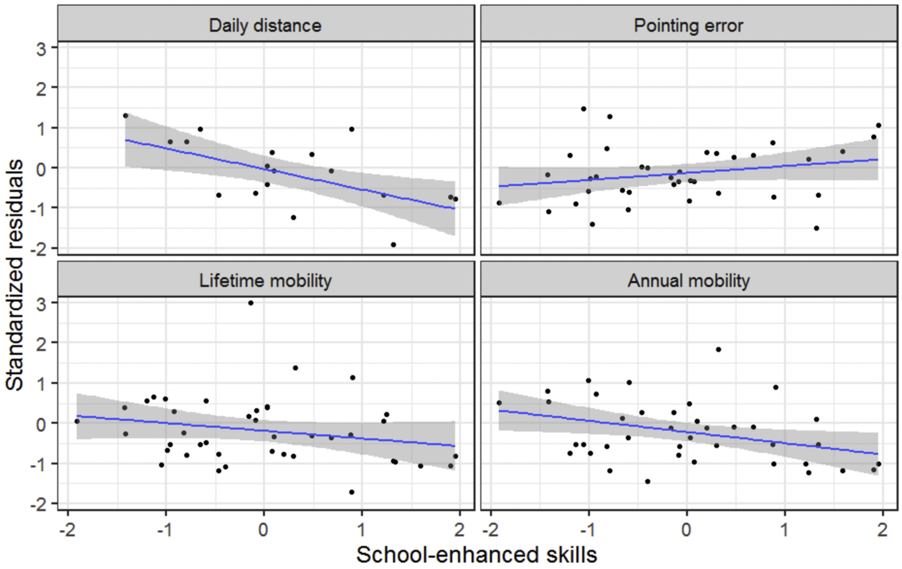


Fig. 10. School-enhanced skills and four measures of mobility and spatial ability partialed for age and gender. Children who score higher on school-enhanced skills had a lower average daily mobility, lower reported annual mobility, and increased pointing error.

3.7.1. Mobility

A general linear model with gender as a fixed effect was employed to assess the effects of mobility on spatial ability. Results indicated trends towards lower pointing error being associated with both greater sinuosity in travel, F(1, 35) = 4.80, p = 0.06, and with greater annual mobility, F(1, 35) = 2.80, p = 0.07. Sinuosity had a similar relationship with lower perspective taking error, when controlling for age and gender, F(1, 39) = 3.91, p = 0.06. No other relationships approached significance.

3.7.2. Schooling

Schooling might also be expected to enhance spatial performance, as it does cognitive performance generally, but when children are in school, they are not running around in outdoor play or doing outdoor tasks. This might therefore act in the opposite direction on spatial ability, particularly navigation. In order to explore this, we used a factor score created from 3 variables: RCPM, reading, and mental rotation, and first looked at school-enhanced skills and six measures of mobility and spatial ability, partialed for age and gender. Results show children who performed better on school-enhanced skills had lower daily mobility, r(16) = -0.59, p = 0.01. Higher performance on school-enhanced skills also correlated with increased error on the pointing accuracy task, r(34) = 0.34, p = 0.04, but not the perspective taking task, r(34) = 0.15, p = 0.39. Annual and lifetime mobility also decreased with improved school-enhanced skills, r(36) = -0.45, p = 0.005 and r(37) = -0.44, p = 0.006, respectively. There was no correlation with sinuosity, r(16) = 0.22, p = 0.49. A general linear model showed significant effects of lower average daily mobility, F(1, 16) = 6.5, p = 0.02, and lower annual mobility, F(1,16) = 14.7,p = 0.002, on improved school-enhanced skills. The relationship of lifetime mobility to school-enhanced skills was in the same direction, but not significant F(1,16) = 3.3, p = 0.09 (Fig. 10).

4. Discussion

Tsimané children have greater freedom to explore than is typical in Western societies, and their tropical forest environment presents different spatial challenges. The environment is navigationally challenging, with visibility often limited by cloud and tree canopy cover, and with most travel on small footpaths and winding rivers and tributaries that can change seasonally. The objective of this paper was to examine the implications of these cultural and environmental differences for age changes and gender differences in mobility, harm avoidance, and spatial abilities during childhood and adolescence. We were specifically interested in how harm avoidance might affect travel patterns, and how spatial experience gained during everyday travel might affect spatial abilities.

4.1. Developmental changes and cultural variation

There was less variation among girls than boys in their daily travel patterns; however, girls and boys did not differ in how far they traveled, either in daily local travel or travel over the region, nor in how direct their travel paths were. Our ability to detect gender differences in the daily travel patterns is limited by the small size of our GPS dataset. However, our interview data on annual and lifetime mobility among a larger sample also finds no significant gender differences. This result differs slightly from that of Miner et al. (2014), who found that Tsimané males traveled farther than females during adolescence. The difference may reflect methodological differences and/or temporal ones, since their data reflect adult recall of childhood and adolescent experiences that took place many years previously, and in those years the Tsimané were less integrated into the broader economy, their reliance on hunting and gathering was probably greater, and mate-seeking and marriage took place at younger ages. Miner et al. interpret the gender difference they see in adolescence as a response to mate-seeking, and our data on young adults (older than 18) suggests something similar. The small increase with age in daily distance traveled by boys (Fig. 4) may also reflect this and might be significant with a larger sample.

Our results are consistent with Miner et al. in finding no gender differences in mobility prior to adolescence, although in Western samples a gender difference in range size first appears in middle childhood. As is the case in many non-industrial societies, the Tsimané begin to participate in gender-specific tasks during middle childhood (Stieglitz et al., 2013). However, Tsimané boys and girls continue to forage and fish together during childhood, and as they age, more skill-specific garden labor is required of both genders. This necessity to be mobile while foraging and traveling through the dense forests to the gardens might be partially responsible for the muted gender differences we see in mobility patterns at this age.

We had anticipated that lower harm avoidance might lead to a willingness to travel in new areas, take short-cuts home, and travel off roads and paths, all of which might improve exploratory navigational strategies, but we did not see consistent relationships between harm avoidance and mobility. We also found no gender differences in harm avoidance during middle childhood in any domain (physical risks, social risk, wayfinding anxiety), and the only gender difference in adolescence was in social harm avoidance, with adolescent girls being more likely than adolescent boys to say they would feel safer going to unfamiliar villages with others. This might reflect a gender difference in the actual risk of assault to females at this age, or due to cultural norms regarding women traveling alone (Miner et al., 2014).

Despite the well-documented increase in risk-taking during adolescence (Steinberg, 2005), particularly among males (Shulman, Harden, Chein, & Steinberg, 2014), harm avoidance about physical threats was greater among Tsimané adolescents than among younger children, and the increased harm avoidance with age was greater among boys. We think this reflects an accurate assessment of the greater risks they face, as they begin taking on potentially dangerous responsibilities outside the household, such as hunting (Stieglitz et al., 2013). The result might appear to run counter to other reports in the literature, which show boys being more risk-prone beginning in middle childhood, both in the West (Slovic, 1966) and in a foraging population (Apicella, Crittenden, & Tobolsky, 2017). However, those studies tested for a preference for risky rewards, not concern about the risk of getting harmed, which was our focus here.

Tsimané boys and girls were similar in the accuracy with which they were able to point to other locations in the region, and with their pointing accuracy on the perspective-taking task. Our (unpublished) data, and that of Trumble et al. (2016), show a similar absence of gender differences in pointing accuracy among Tsimané adults, in contrast to that of other non-Western studies of navigational ability among adults (Cashdan, Kramer, Davis, Padilla, & Greaves, 2016; Vashro et al., 2016). However, pointing target locations varied in route complexity, and separate analyses by location indicated that the four locations with the highest route sinuosity did show better performance by males, with small to moderate effect sizes.

Given that Tsimané males do the vast majority of long distance navigating on the rivers, and that increased trade and market exchange with nearly market towns (~66 km) has increased river travel in recent years, a gender difference would not be surprising. In spite of gender specific roles associated with river navigation, only the reported small to moderate gender differences in error were found among the four targets within the task.

Our conclusion that there are few gender differences in either mobility or spatial ability among Tsimané children must be tentative, due to comparatively small sample sizes, especially when compared with typical studies conducted among school children in industrial societies. This is, unfortunately, a limitation common to research with small-scale anthropological populations, where children live in small, remote communities and must be contacted individually in the villages in which they live. However, the patterning is similar to what we and Trumble et al. (2016) have found with larger samples of Tsimané adults, which lends credence to the conclusion.

4.2. Interactions between environmental exploration and spatial abilities

Children's spatial learning is affected by how they live and navigate within their community, and this may affect spatial performance. Many studies of spatial training in Western societies have shown that spatial abilities of different types are malleable and can be improved, and that these improvements are (in many studies) transferable beyond the task that was the focus of training (Baenninger & Newcombe, 1989; Uttal et al., 2013). Given that most training is of fairly short duration, it is not surprising that participation in spatially challenging activities in daily life is also associated with better performance on spatial tests (Baenninger & Newcombe, 1989; Newcombe, Bandura, & Taylor, 1983); but see Newcombe & Dubas, 1992, who find that the association is due to children with strong spatial skills seeking out spatial activities).

However, the most ubiquitous spatially-challenging task of daily life, navigation, has received comparatively little attention in these studies, and yet it is particularly important in the daily lives of Tsimané children. Among populations like the Tsimané, it is reasonable to expect that children who engage in activities associated with novel or unpredictable routes (for example, hunting and gathering, and fishing) would have stronger survey knowledge of the environment and perform well on navigational spatial tasks. This type of travel is likely to look less direct, and so was measured in this study by the sinuosity of the daily GPS tracks. We found that boys and girls who followed more complex routes by this measure, and children who reported having traveled to more places in the region, showed a trend toward performing better on our large-scale spatial tasks (pointing accuracy and perspective-taking). While tentative, these results support the importance placed by Newcombe and Frick (2010) on spatial training in young children that includes experiencing space in free play and active movement.

Although mental rotation and perspective-taking both involve spatial transformations, they are dissociable abilities, and some evidence indicates that perspective-taking is more directly related to navigational ability than is mental rotation (Allen et al., 1996; Kozhevnikov, Motes, Rasch, & Blajenkova, 2006). We therefore expected that mobility would have a weaker positive relationship with mental rotation than with navigational tasks. What we found, however, was a negative relationship: children who did better on mental rotation and other abstract tasks, which are associated with better education, traveled *less*, both in daily mobility and regional travel in the preceding year. Ironically, therefore, better education, while it improves performance on abstract cognitive tasks (Davis, 2014; Gurven, Fuerstenberg et al., 2017) may interfere with large-scale spatial abilities.

For the Tsimané now, the opportunity costs of education are low—they only attend school four hours a day and are still very active in subsistence and play activities outside of school. But a trend does exist, and it suggests that increased time spent indoors means less exploration and mobility, with consequences for large-scale spatial ability. Though the causal arrows between mobility, reported harm avoidance, and spatial ability likely to go both ways in early life, a profound interaction between spatial cognitive development and environmental conditions cannot be ignored.

Funding

This work was supported by the National Science Foundation grant numberBCS 1628583.

Acknowledgements

We thank Jeanine Stefanucci, Sarah Creem-Regehr, and Anna Shusterman for assistance with instrument design and methodology, Jason S. Leiser for assistance with data collection, the Tsimane people, and Agustina Bani Cayuba for her continued assistance on the project. The University of Utah DIGIT lab assisted with the GIS analysis.

References

Allen, G., Kirasic, K., Dobson, S., Long, R., & Beck, S. (1996). Predicting environmental learning from spatial abilities: An indirect route. *Intelligence, 22*(3), 327–355.

Apicella, C. L., Crittenden, A. N., & Tobolsky, V. A. (2017). Hunter-gatherer males are more risk-seeking than females, even in late childhood. *Evolution and Human Behavior, 38*(5), 592–603.

Baenninger, M., & Newcombe, N. (1989). The role of experience in spatial test performance: A meta-analysis. *Sex Roles, 20*(5), 327–344. https://doi.org/10.1007/BF00287729.

Bock, J. (2002). Evolutionary demography and intrahousehold time allocation: School attendance and child labor among the Okavango Delta peoples of Botswana. *American Journal of Human Biology, 2*, 206–221.

Bock, J. (2005). *What makes a competent adult forager. Hunter-gatherer childhoods*109–128.

Byrnes, J. P., Miller, D. C., & Schafer, W. D. (1999). Gender differences in risk taking: A meta-analysis. *Psychological Bulletin, 125*(3).

Cashdan, E., Kramer, K. L., Davis, H. E., Padilla, L., & Greaves, R. D. (2016). Mobility and navigation among the Yucatec Maya. *Human Nature, 27*(1), 35–50. https://doi.org/10.1007/s12110-015-9250-7.

Cashdan, E., & Gaulin, S. J. C. (2016). Why go there? Evolution of mobility and spatial cognition in women and men. *Human Nature, 27*(1), 1–15.

Choi, J., & Silverman, I. (1996). Sexual dimorphism in spatial behaviors: Applications to route learning. *Evolution and Cognition, 2*, 165–171.

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

Dabbs, J. M., Chang, E.-L., Strong, R. A., & Milun, R. (1998). Spatial ability, navigation strategy, and geographic knowledge among men and women. *Evolution and Human Behavior, 19*(2), 89–98. https://doi.org/10.1016/S1090-5138(97)00107-4.

Davis, H. E. (2014). *Variable education exposure and cognitive task performance among the Tsimané Forager-Horticulturalists.* The University of New Mexico.

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.

Frick, A., Hansen, M. A., & Newcombe, N. S. (2013). Development of mental rotation in 3-to 5-year-old children. *Cognitive Development*(4).

Frick, A., Möhring, W., & Newcombe, N. (2014). Development of mental transformation abilities. *Trends in Cognitive Sciences, 10*, 536–542.

Gagnon, K. T., Cashdan, E. A., Stefanucci, J. K., & Creem-Regehr, S. H. (2016). Sex differences in exploration behavior and the relationship to harm avoidance. *Human Nature, 27*(1), 82–97.

Gagnon, K. T., Thomas, B. J., Munion, A., Creem-Regehr, S. H., Cashdan, E. A., & Stefanucci, J. K. (2018). Not all those who wander are lost: Spatial exploration patterns and their relationship to gender and spatial memory. *Cognition, 180*, 108–117.

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

Gaulin, S. J. C. (1992). Evolution of sex difference in spatial ability. *American Journal of Physical Anthropology, 15*, 125–151.

Geary, D. C. (2010). *Male, female: The evolution of human sex differences* (2nd ed.). Washington, DC, US: American Psychological Associationhttps://doi.org/10.1037/12072-000.

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

Gurven, M., & Kaplan, H. (2006). Determinants of time allocation across the lifespan. *Human Nature, 1*, 1–49.

Gurven, M., Fuerstenberg, E., Trumble, B., Stieglitz, J., Beheim, B., Davis, H., ... Kaplan, H. (2017). Cognitive performance across the life course of Bolivian forager-farmers with limited schooling. *Developmental Psychology, 53*(1), 160–176. https://doi.org/10.1037/dev0000175.

Gurven, M., Stieglitz, J., Trumble, B., Blackwell, A. D., Beheim, B., Davis, H., ... Kaplan, H. (2017). The Tsimane health and life history project: Integrating anthropology and biomedicine. *Evolutionary Anthropology Issues News and Reviews, 26*(2), 54–73. https://doi.org/10.1002/evan.21515.

Halpern, D. F. (2013). *Sex differences in cognitive abilities.* Psychology Press.

Hart, R. (1979). *Children's experience of place.* Irvington.

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.

Hegarty, M., & Waller, D. (2005). *Individual differences in spatial abilities. The cambridge handbook of visuospatial thinking*121–169.

Hewlett, B. S., Fouts, H. N., Boyette, A. H., & Hewlett, B. L. (2011). Social learning among Congo Basin hunter–gatherers. *Philosophical Transactions of the Royal Society B, 1567*, 1168–1178.

Hodges-Simeon, C. R., Gurven, M., Cárdenas, R. A., & Gaulin, S. J. C. (2013). Voice change as a new measure of male pubertal timing: A study among Bolivian adolescents. *Annals of Human Biology, 40*(3), 209–219. https://doi.org/10.3109/03014460.2012.759622.

Hoover, H. D., Dunbar, S. B., Frisbie, D. A., Oberley, K. R., Ordman, V. L., Naylor, R. J., ... Shannon, G. P. (2003). *Iowa Test of Basic Skills guide to research and development.* Itasca, IL: The Riverside Publishing Company.

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

Kozhevnikov, M., Motes, M. A., Rasch, B., & Blajenkova, O. (2006). Perspective-taking vs. mental rotation transformations and how they predict spatial navigation performance. *Applied Cognitive Psychology, 20*(3), 397–417.

Kramer, K. (2005). *Maya children.* Harvard University Press.

Kramer, K. L., & Greaves, R. D. (2011). Juvenile subsistence effort, activity levels, and growth patterns. Middle childhood among Pumé foragers. *Human Nature, 3*, 303–326.

Lancy, D. F. (2016). Playing with knives: The socialization of self-initiated learners. *Child Development, 87*(3), 654–665.

Lancy, D. F., & Grove, M. A. (2011). Getting noticed. *Human Nature, 3*, 281–302.

Lawton, C. A., & Kallai, J. (2002). Gender differences in wayfinding strategies and anxiety about wayfinding: A cross-cultural comparison. *Sex Roles, 9*, 389–401.

Levine, S. C., Huttenlocher, J., Taylor, A., & Langrock, A. (1999). *Developmental Psychology, 4*, 940–949.

Lew-Levy, S., Lavi, N., Reckin, R., Cristóbal-Azkarate, J., & Ellis-Davies, K. (2018). How do hunter-gatherer children learn social and gender norms? A meta-ethnographic review. *Cross-Cultural Research, 2*, 213–255.

Matthews, M. H. (1987). Gender, home range and environmental cognition. *Transactions of the Institute of British Geographers,* 43–56.

Matthews, M. H. (1992). *Making sense of place: Children's understanding of large-scale environments.* Barnes & Noble Books.

Miner, E. J., Gurven, M., Kaplan, H., & Gaulin, S. J. C. (2014). Sex difference in travel is concentrated in adolescence and tracks reproductive interests. *Proceedings of the Royal Society B: Biological Sciences, 281*.

Moffat, S. D., 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, 2*, 73–87.

Moore, D. S., & Johnson, S. P. (2011). Mental rotation of dynamic, three-dimensional stimuli by 3-month-old infants. *Infancy, 4*, 435–445.

Munroe, R. L., & Munroe, R. H. (1971). Effect of environmental experience on spatial ability in an East African society. *The Journal of Social Psychology, 1*, 15–22.

Nerlove, S. B., Munroe, R. H., & Munroe, R. L. (1971). Effect of environmental experience on spatial ability: A replication. *The Journal of Social Psychology, 1*, 3–10.

Neuburger, S., Jansen, P., Heil, M., & Quaiser-Pohl, C. (2011). *Personality and Individual Differences, 8*, 1238–1242.

Newcombe, N., Bandura, M. M., & Taylor, D. G. (1983). Sex differences in spatial ability and spatial activities. *Sex Roles, 9*(3), 377–386. https://doi.org/10.1007/BF00289672.

Newcombe, N., & Dubas, J. S. (1992). A longitudinal study of predictors of spatial ability in adolescent females. *Child Development, 63*(1), 37–46.

Newcombe, N. S., & Frick, A. (2010). Early education for spatial intelligence: Why, what, and how. *Mind Brain and Education, 4*(3), 102–111.

Padilla, L. M., Creem-Regehr, S. H., Stefanucci, J. K., & Cashdan, E. A. (2017). Sex differences in virtual navigation influenced by scale and navigation experience. *Psychonomic Bulletin & Review, 24*(2), 582–590. https://doi.org/10.3758/s13423-016-1118-2.

Piantadosi, S. T., Jara-Ettinger, J., & Gibson, E. (2014). Children's learning of number words in an indigenous farming-foraging group. *Developmental Science, 17*(4), 553–563. https://doi.org/10.1111/desc.12078.

Prezza, M. (2007). Children's independent mobility: A review of recent Italian literature. *Children, Youth and Environments, 4*, 293–318.

Quinn, P. C., & Liben, L. S. (2014). A sex difference in mental rotation in infants: Convergent evidence. *Infancy, 1*, 103–116.

Reyes-García, V., Pyhälä, A., Díaz-Reviriego, I., Duda, R., Fernández-Llamazares, Á., Gallois, S., ... Napitupulu, L. (2016). Schooling, local knowledge and working memory: A study among three contemporary hunter-gatherer societies. *PLoS One, 11*(1), e0145265.

Sandstrom, N. J., Kaufman, J., & Huettel, S. A. (1998). Males and females use different distal cues in a virtual environment navigation task. *Cognitive Brain Research, 4*, 351–360.

Schlegel, A. (1995). A cross-cultural approach to adolescence. *Ethos, 1*, 15–32.

Schmitz, S. (1997). Gender-related strategies in environmental development: Effects of anxiety on wayfinding in and representation of a three-dimensional maze. *Journal of Environmental Psychology, 3*, 215–228.

Shulman, E. P., Harden, K. P., Chein, J. M., & Steinberg, L. (2014). Sex differences in the developmental trajectories of impulse control and sensation-seeking from early adolescence to early adulthood. *Journal of Youth and Adolescence,* 1–17.

Silverman, I., Choi, J., & Peters, M. (2007). The hunter-gatherer theory of sex differences in spatial abilities: Data from 40 countries. *Archives of Sexual Behavior, 2*, 261–268.

Slovic, P. (1966). Risk-taking in children: Age and sex differences. *Child Development,* 169–176.

Stieglitz, J., Gurven, M., Kaplan, H., & Hooper, P. L. (2013). Household task delegation among high-fertility forager-horticulturalists of Lowland Bolivia. *Current Anthropology, 2*, 232–241.

Steinberg, L. (2005). Cognitive and affective development in adolescence. *Trends in Cognitive Sciences, 9*(2), 69–74.

Trumble, B. C., Gaulin, S. J. C., Dunbar, M. D., Kaplan, H., & Gurven, M. (2016). No sex or age difference in dead-reckoning ability among Tsimane forager-horticulturalists. *Human Nature, 27*(1), 51–67.

Uttal, D. H., Meadow, N. G., Tipton, E., Hand, L. L., Alden, A. R., Warren, C., ... Newcombe, N. S. (2013). The malleability of spatial skills: A meta-analysis of training studies. *Psychological Bulletin, 139*(2), 352–402.

Vashro, L., Padilla, L., & Cashdan, E. (2016). Sex differences in mobility and spatial cognition. *Human Nature, 27*(1), 16–34.

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

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, 2*, 250–270.

Walker, R., Gurven, M., Hill, K., Migliano, A., Chagnon, N., De Souza, R., ... Yamauchi, T. (2006). Growth rates and life histories in twenty-two small-scale societies. *American Journal of Human Biology, 18*(3), 295–311. https://doi.org/10.1002/ajhb.20510.

Ward, S. L., Newcombe, N., & Overton, W. F. (1986). Turn left at the church, or three miles north: A study of direction giving and sex differences. *Environment and Behavior, 2*, 192–213.

Whiting, B. B., & Edwards, C. P. (1988). *Children of different worlds: The formation of social behavior.* Harvard University Press.

Zeng, W., Undurraga, E. A., Eisenberg, D. T. A., Rubio-Jovel, K., Reyes-García, V., Godoy, R., ... Team, T. B. S. (2012). Sibling composition and child educational attainment: Evidence from native Amazonians in Bolivia. *Economics of Education Review, 31*(6), 1017–1027.